

CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

TABLE OF CONTENTS

Water Strategies	7-3-2
Water Cycle Role in Ecosystem	7-3-7
Structural Adaptations	7-3-7
Thallose Liverworts	7-3-8
Scales	7-3-8
Rhizoids	7-3-9
Fungal Partners	7-3-13
Main Thallus Structure	7-3-13
Spongy Thallus	7-3-14
Cuticle	7-3-14
Pores	7-3-15
Archegoniophores and Antheridiophores	7-3-17
Dormancy	7-3-18
Mosses and Leafy Liverworts	7-3-19
Growth Form	7-3-20
Stems and Branches	7-3-21
Central Strand	7-3-23
Waxes	7-3-24
Rhizoids and Tomentum	7-3-25
Mucilage	7-3-27
Capillary Spaces	7-3-28
Fungal Partners	7-3-30
Leafy Liverwort Gemmae	7-3-31
Sporophyte	7-3-31
Calyptra Protection	7-3-32
Cuticle	7-3-33
Guard Cells and Stomata	7-3-38
Summary	7-3-42
Acknowledgments	7-3-43
Literature Cited	7-3-43

CHAPTER 7-3

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Figure 1. *Tortula muralis* with water drops collected on the leaf awns and setae. Note their collection around the young capsules. Photo by Peggy Edwards.

Water Strategies

Mosses often appear to be completely dead, only to be revived by water. Angela 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 (see 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). As surmised by Oliver *et al.* (2005), **desiccation tolerance** appears to be a primitive trait that permitted plants to invade land. **Desiccation tolerance (DT)** is the ability of an organism or structure to tolerate and survive after equilibrating to a relative humidity (RH) of $\leq 50\%$ (Alpert & Oliver 2002; Koster *et al.* 2010). An understanding of this tolerance in modern bryophytes is fundamental to a general understanding of desiccation tolerance.

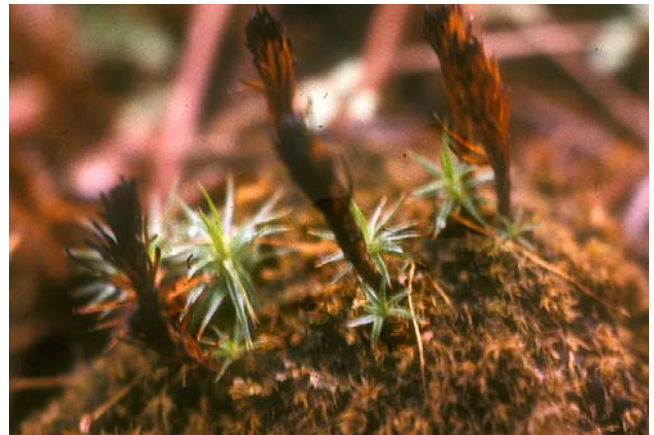


Figure 2. *Polytrichum* showing fresh, green growth one week after a forest fire that scorched adjacent plants in Baraga, Michigan, USA. Photo by Janice Glime.

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

Most people who are not very familiar with bryophyte physiology consider them to be plants that require damp or wet habitats. But compared to **tracheophytes** (non-bryophytes; plants with lignified vascular tissue), bryophytes are the ones adapted to drying conditions. In fact, of the known 18,000 species of bryophytes (Shaw & Goffinet 2000), 210 have been documented as desiccation tolerant (Wood 2007), but most have never been tested. Among seed plants, fewer than 1% of those tested are desiccation tolerant (Proctor & Pence 2002). Even the aquatic moss *Fontinalis* has at least some desiccation-tolerant species (Glime 1971). For example, *Fontinalis flaccida* survived and grew after three months of drying on a herbarium sheet (pers. obs.). If one considers the types of microhabitats bryophytes occupy, and lack in most species of any kind of water storage organ, we should expect that most have at least some degree of desiccation tolerance. This notion is further supported by the high survival rate of bryophytes despite a high surface-to-volume ratio that facilitates rapid drying (Proctor *et al.* 2007).

Proctor and Tuba (2002) considered there to be two contrasting strategies for land plants to deal with the irregular supply of water they faced on land and that these relate closely to the matter of scale. Tracheophytes use internal transport to carry water from the soil to the distant canopy (**homoiohydric**). Bryophytes (and some tracheophytes), on the other hand, depend on desiccation tolerance, becoming dormant when desiccated. Hence, their cells are either **turgid** (swollen) or desiccated. But desiccation tolerance requires a whole series of adaptations to permit the cell to regain its original state. This strategy is particularly beneficial on hard substrates such as rocks and on dry soils in seasonally dry climates. Thus, among tracheophytes, this strategy is most common in warm semiarid climates, whereas in mosses the strategy occurs from polar to tropical regions (Proctor & Tuba 2002; Lakatos 2011). The time scale also differs, with tracheophytes requiring one to several days to resume activity whereas bryophytes (and lichens) typically require an hour or less (Proctor & Tuba 2002).

Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] desiccation tolerance exist among plants (Stark *et al.* 2013) and these will be discussed in Chapter 7-6 of this volume.

Cellular structure remains intact in desiccation, but upon rapid uptake of water it can be disrupted. However, in bryophytes the cellular integrity returns rapidly. Photosynthetic activity recovers quickly, perhaps due to protection of the chlorophyll (Tuba 1984; 1985). During desiccation, there seems to be no gene activity, but gene expression occurs rapidly following rehydration. Among these activities is the production of a number of proteins called **rehydrins**. These seem to be involved in stabilizing and reconstituting membranes that have been damaged by dehydration. Oliver *et al.* (2005) suggest that vegetative desiccation tolerance, at least in bryophytes, has changed little from early land invaders and may be using a mechanism that was first used in spores.

Even though many bryophytes 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** (flattened, nonvascular plant body) size. In *Plagiochasma appendiculatum* (Figure 3), optimum growth occurs at 60% moisture, whereas branching and growth are able to occur from 10-100% moisture (Vishvakarma & Kaul 1988)! *Reboulia hemisphaerica* (Figure 4), 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 3. *Plagiochasma appendiculatum*, a liverwort with both branching and growth throughout the range of 10-100% moisture. Photo by Michael Lüth.



Figure 4. *Reboulia hemisphaerica*, a liverwort in which growth and branching occur in the range of 40-90% moisture. Photo by Jan-Peter Frahm.

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** (dry) microsites. Alpert (1985, 2000) supports the hypothesis that the reason even **xerophytic** mosses (those adapted to dry habitats) 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 5-Figure 6), 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 an "inherent trade-off between desiccation tolerance and growth rate."



Figure 5. *Grimmia laevigata*, a poikilohydric moss, in its dry state. Photo by Michael Lüth.



Figure 6. *Grimmia laevigata*, a poikilohydric moss, in its wet state. 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* (Figure 7), Romose (1940) 10-950% in *Homalothecium sericeum* (Figure 8), Morton (1977) 19-214% in *Pseudoscleropodium purum* (Figure 9), and 58-307% in *Dicranum bonjeanii* (Figure 10). 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.



Figure 7. *Dicranum scoparium*, a moss with measured water content ranging 23.8-258%. Photo by Janice Glime.



Figure 8. *Homalothecium sericeum*, a moss with measured water content ranging 19-214%. Photo by David Holyoak.



Figure 9. *Pseudoscleropodium purum*, a moss with measured water content ranging 19-214%. Photo by Michael Lüth.



Figure 10. *Dicranum bonjeanii*, a moss with measured water content ranging 58-307%. Photo by Michael Lüth.

Richardson (1981) divides mosses into three water strategies by habitat: **aquatic**, **mesophytic** (living in continually moist habitats), and **poikilohydric** (organism dries as its habitat dries and resumes normal metabolic activity after rehydration; Figure 6). 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.

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 & Ziobler 1992). Certainly in those dry places atmospheric humidity must have provided the needed water for these very **hygroscopic** (readily absorbing water from air), **ectohydric** (relying mainly on water transport along external surface of plant by capillarity) 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. A similar phenomenon occurs in geothermal areas (Figure 11).

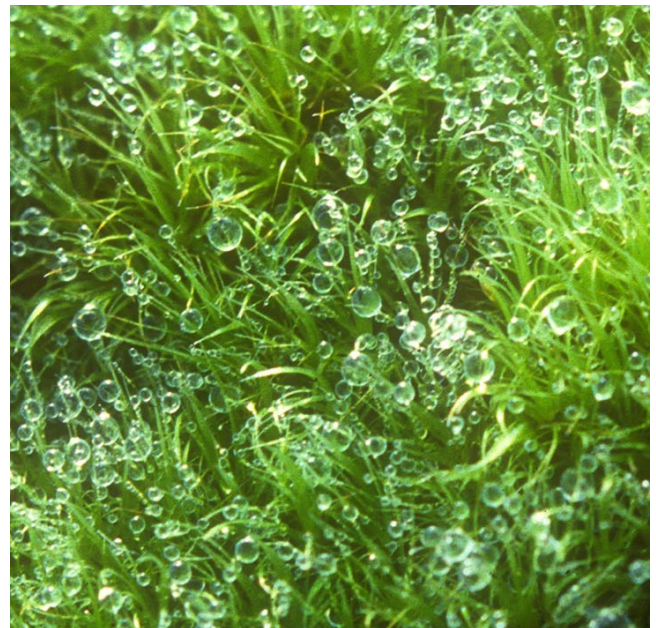


Figure 11. *Campylopus holomitrius* with water droplets captured from the "steam" emitted by geothermal vents in New Zealand. Photo by Janice Glime.

The drought-tolerant *Pseudocrossidium crinitum* (= *Barbula aurea*; Figure 12) 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.



Figure 12. *Pseudocrossidium crinitum*, a xerophyte with low light compensation and saturation levels. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

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 13) are able to survive desiccation for days (Horst Tremp, Bryonet).



Figure 13. *Hookeria lucens*, a drought-intolerant moss. Photo by Michael Lüth.

Glime (1971) found that two aquatic mosses (*Fontinalis* spp.; Figure 14) were able to survive on the stream bank out of water (Figure 15) for up to one year and still grow when rehydrated. However, those dried in the laboratory were apparently dead after only 55 hours, perhaps due to rapid drying. Steere (1976) found that *F. squamosa* (Figure 16) 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 (Figure 14), 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).



Figure 14. *Fontinalis dalecarlica* and *F. novae-angliae* above water, in Fox Run, NH, USA. When these mosses were placed away from the stream bed for up to one year, at least some of them survived from all re-submersion dates (Glime & Carr 1974). Photo by Janice Glime.



Figure 15. *Fontinalis antipyretica* in dry stream. Photo by Janice Glime.



Figure 16. *Fontinalis squamosa* on rock above water near Swallow Falls, Wales. Photo by Janice Glime

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*; Figure 17), 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.



Figure 17. *Cratoneuron filicinum*, a moss that is unable to synthesize protein when rehydrated if it dries too quickly. Photo by Teplov through Arctoa.

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.

Life cycle adaptations, a major means for an immobile organism to cope with changing weather and seasons, have been addressed in Chapter 4-6. Schofield (1981) points out that spore germination patterns, protonemal structure, life span, and methods of propagation are all related to the habitat characteristics. Water availability is important to all of these aspects. Multicellular spores are more common in habitats where the spores are subject to desiccation. Protonematal specialization is common in deeply shaded habitats, whereas in mesic habitats the protonemal cells are elongate, *i.e.*, having typical protonematal structure. In the leafy **gametophore** (upright leafy plant), characters such as leaf shape, leaf arrangement and orientation, leaf anatomy, stem cortical cells, hydroids, leptoids, branch arrangement, presence of rhizoids, and presence of paraphyllia all affect water movement. Such small features as surface ornamentation of leaves, stems, and rhizoids affect water absorption and retention and influence habitat specificity.

Water Cycle Role in Ecosystem

In areas where bryophytes dominate the forest floor, their role in the water cycle can be extraordinary. This is especially true where permafrost prevails (Henry Santeford,

pers. comm.). Bryophytes hold melt water until they become saturated. At that point in time, all new melt water is suddenly released and can cause flooding. It is important in some areas to be able to predict this flooding regime for the safety of both animals and humans. Hence, we need to understand both holding capacity and evaporation rates of water from the bryophytes.

Penman (1948) helps us to understand evaporation as it might apply to bryophytes. Although he compared evaporation from bare soil, grass, and open water, the principles apply. He suggests that we need to combine two theoretical approaches to evaporation, an aerodynamic basin in which evaporation is due to turbulent transport of vapor by eddy diffusion, and an energy basis in which evaporation is a way of degrading incoming radiation. This approach eliminates the problem of measuring surface temperature and overcomes the problem of estimating effects as if one is measuring evaporation from a lake surface. Using this method, supported by empirical data, indicates that evaporation from grass follows a seasonal cycle relative to that evaporating from open water, a phenomenon Penman attributes to the change in photoperiod.

In other circumstances, bryophytes may prevent the underlying roots from getting water (Beth Scafione, unpubl. data). If there is a quick rain shower, bryophytes act as sponges, trapping the water before it reaches the soil. On the other hand, bryophytes can reduce evaporation of water from the soil following heavy rain, thus permitting the roots to grow for longer periods of time.

Structural Adaptations

Getting water and nutrients into and out of a plant is size dependent. Adaptations vary even within a species due to its plasticity in responding to the environment (Sarafis 1971; Buryová & Shaw 2005). As discussed by Raven and Handley (1987), for plankton organisms, any size above ~50 μm diameter restricts the growth rate because of the greater restriction of uptake by the boundary layer. Thus, for macroscopic aquatic photosynthetic organisms, even favorable velocity of water and plant morphology cannot reduce the boundary layer restrictions on nutrient uptake enough to compensate for the decrease in uptake rate. Movement of nutrients within the plant involves **cyclosis** (cytoplasmic streaming) in algae, phloem and xylem in tracheophytes, and in bryophytes it often involves both cyclosis and transport through leptoids and hydroids.

Raven and Handley (1987) consider that the energy cost for transporting nutrients would be higher for those organisms using cyclosis than for those using vascular tissue. They also consider that there is a penalty for height in tracheophytes, causing reduced specific growth rate under both resource-saturated and resource-limited conditions. Coupled with this penalty is reduced resource use efficiency with increased plant height. The reason for these penalties is the need for greater supporting tissue and a greater percentage of the tissue dedicated to vascular tissue. But there is also some compensation. Taller plants can capture more light energy and reach more nutrients and water in the soil. Smaller plants, on the other hand, have a potentially higher specific growth rate under these same resource-limited or resource-saturated conditions. The lack

of need for supporting structures, requiring breadth, permits smaller plants such as bryophytes to have all or nearly all of their tissues as photosynthetic tissues. Raven and Handley left us with the challenge to discover the differences in transport needs and solutions resulting from these different morphologies.

In the desert moss *Syntrichia caninervis* (Figure 18), conservation of moisture is paramount, surpassed only by the need for rapid uptake. It can therefore serve as a model for adaptations against desiccation. Its growth form is tufted and its leaves are folded upward and twisted around the stem when dry (Zheng *et al.* 2010). The leaf cells are endowed on both the upper and lower surfaces with C-shaped papillae that may have a role in deflecting sunlight to protect the DNA and chlorophyll during dry periods or to reduce the temperature. The leaf costa extends beyond the leaf to form an awn that has forked teeth and is able to capture moisture from the atmosphere. The protonemal cells are small and have thick walls; their cytoplasm is highly concentrated with only a small vacuole.

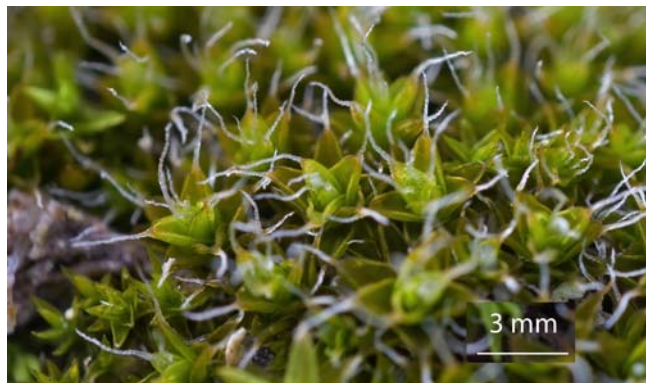


Figure 18. *Syntrichia caninervis*, a desert moss that increases its wax content as it ages. Note the awns that can trap atmospheric moisture from fog. Photo from Proyecto Musgo through Creative Commons.

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* (Figure 19) and *Cyathodium cavernarum* (Figure 20) use ventral appendages (**scales**; Figure 19) 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.

Scales

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.

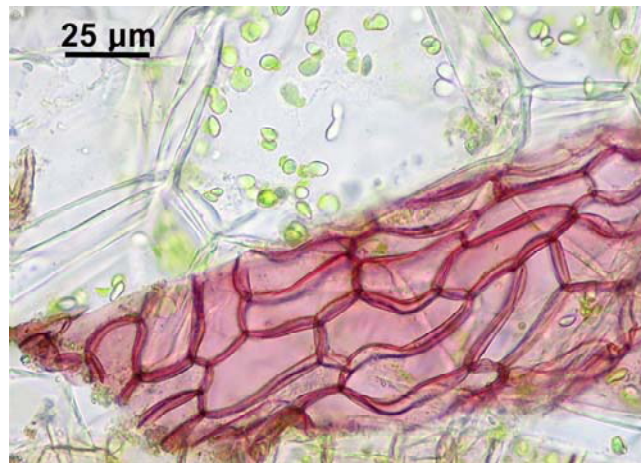


Figure 19. *Conocephalum conicum* showing ventral scale (purple) that provides capillary spaces for external water movement. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>.

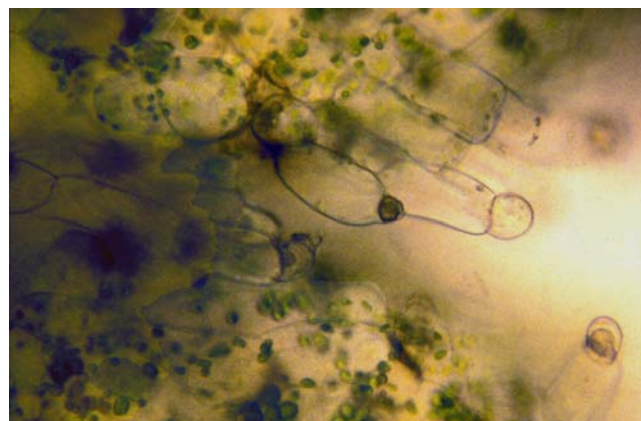


Figure 20. Scales of *Cyathodium cavernarum*. Photo by Noris Salazar Allen.

Kürschner (2004) surmised that the anthocyanin pigments in ventral scales protected the ventral surface from the sun when the thallus was rolled up, as it typically does in many species of *Riccia*. Furthermore, even hyaline scales of *Riccia* and *Oxymitra* (Figure 21) can reduce desiccation. Some species, especially of *Riccia*, sink into the soil surface as the soil dries, reappearing only after precipitation or heavy dew.



Figure 21. *Oxymitra incrassata* showing ventral hyaline scales at the margins. Photo by Michael Lüth.

This high degree of wettability provides a greater possibility for water entry in thallose forms. For example, in *Marchantia* (Figure 22-Figure 23), 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* (Figure 45-Figure 46) and *Reboulia* (Figure 4), 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* (Figure 24) 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.



Figure 22. *Marchantia polymorpha* with gemmae cups located on the midrib. Photo by Walter Obermayer.



Figure 23. *Marchantia polymorpha* ventral surface showing blackish midrib (arrow) and white scales and rhizoids. Photo from Botany website, University of British Columbia, BC, Canada.



Figure 24. *Conocephalum conicum*, where water travels from base to apex in about 20-30 seconds. Photo by Janice Glime.

Ballooning of Epidermis

In some species of *Riccia* the epidermis is balloon-like and may contribute to protection from desiccation (Kürschner 2004). However, I wonder if those cells don't provide a greater role in focussing the light into the thallus to the chlorophyllous cells when the thallus is hydrated. Kürschner suggested that the chimney-like, hyaline air chambers of *Exormotheca* (Figure 25-Figure 27) may also have a function in protecting the underlying tissue during dehydration.

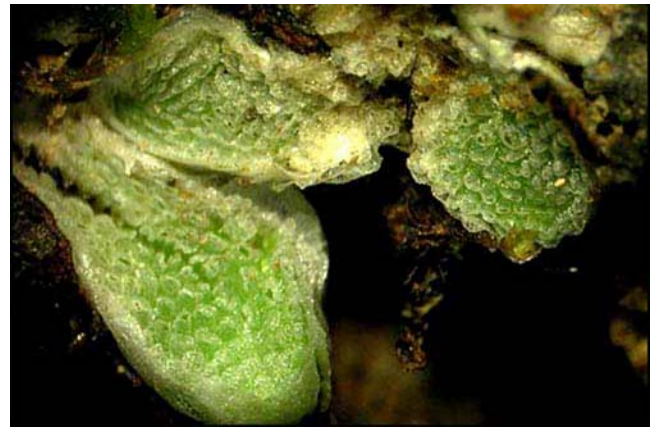


Figure 25. *Exormotheca pustulosa* showing ballooning of epidermal cells. Photo by Jonathan Sleath.



Figure 26. *Exormotheca welwitschii* showing ballooning of epidermal cells. Photo by Michael Luth.



Figure 27. *Exormotheca* thallus section showing columns of photosynthetic tissue and ballooning surface. Photo by William Barthlott.

Rhizoids

Ventral structures seem to be important in this group. In marchantialian liverworts, two types of rhizoids (Figure 28-Figure 29) provide somewhat different functions. The smooth-walled rhizoids (Figure 29) are alive (Duckett & Ligrone 2003) and emerge from beneath the ventral scales (Figure 30), providing contact with the substrate, whereas the **tuberculate** (pegged) rhizoids (Figure 29) are dead (Duckett & Ligrone 2003) and form a capillary system parallel to the thallus beneath each scale (McConaha 1941). The pegged rhizoids begin growth at right angles to the thallus but change their orientation to follow that of the scales. The pegs, extending into the pegged rhizoid cell, prevent the collapse of the cell when dehydrated, thus maintaining its capillary role (Duckett & Ligrone 2003). When the **archegoniophore** (stalk supporting female reproductive organs) forms, the pegged rhizoids are wrapped within the archegoniophore by the folded thallus (Figure 31) 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).



Figure 28. *Riccia* sp. with rhizoids on ventral side. Photo by Berndt through Creative Commons.

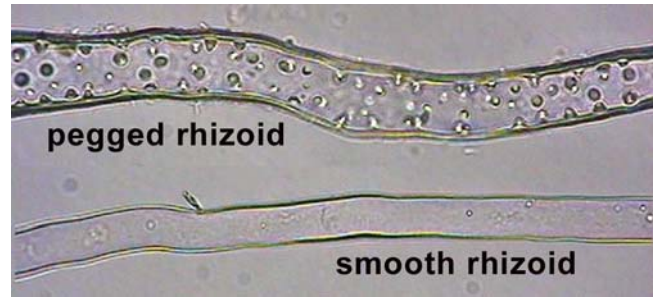


Figure 29. Pegged and smooth rhizoids of *Conocephalum conicum*. Photo by Paul Davison.

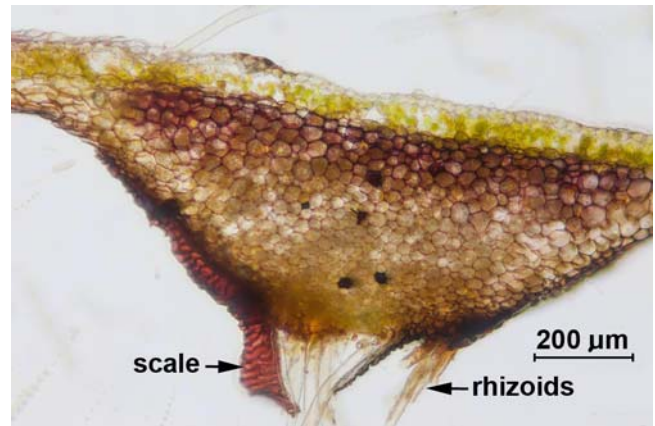


Figure 30. *Preissia quadrata* thallus cross section showing position of scale and rhizoids. Photo by Kristian Peters.



Figure 31. *Marchantia polymorpha* archegoniophore showing white rhizoids that are incompletely enclosed by the stalk of the archegoniophore. Photo by George Shepherd

Previously treated mostly as a taxonomic anomaly, it appears that these two types of rhizoids have distinctly different functions (Duckett *et al.* 2013). The smooth rhizoids are alive, functioning in nutrition, anchorage, and as entry locations and conduits for fungal symbionts. Their role for fungal entry does indeed require that these rhizoids be alive. The pegged rhizoids, on the other hand, are dead at maturity, a condition first noted by Kamerling (1897), and function as water conduits through these empty tubes. Kny (1890) was the first to suggest that pegs prevent the rhizoid walls from collapse with water loss. Duckett *et al.* (2013), however, were the first to test this hypothesis. The

pegs, along with elasticity, seem to provide the ability of the rhizoids to maintain their functional integrity by preventing their collapse when they are dry. This ability is essential to their function in conduction, a role demonstrated by Bowen (1935) and others (McConaha 1939, 1941), who used dyes to show conduction by capillarity and transpiration. The famous German morphologist Goebel (1905) observed that it is the liverworts with high transpiration rates that also have the most highly developed pegged rhizoids. This is in contrast with those of **hygrophilous** (water-loving) taxa such as *Dumortiera* (Figure 32-Figure 33) and *Cyathodium* (Figure 34).



Figure 32. *Dumortiera hirsuta*, a hygrophilous species showing fringe of hairs on thallus and archegonial heads, but lacking the pegged rhizoids and scales of the dry habitat species. Photo by Jan-Peter Frahm.



Figure 33. *Dumortiera hirsuta* thallus showing rhizoids on the ventral surface. Photo by Chris Lobban.

Among the leafy liverworts, thallose liverworts, and ferns, living rhizoids die and collapse upon dehydration, an irreversible response (Pressel 2007). Duckett *et al.* (2013) concluded that smooth rhizoids of liverworts grow at the apex, a character they share with root hairs, fungal hyphae, and moss protonemata. Furthermore, the smooth rhizoids exhibit considerable endoreduplication of Golgi bodies similar to that in moss caulonemata. They reach lengths

that commonly are greater than 20 mm, sometimes reaching 30 mm in *Marchantia polymorpha* (Figure 23), making them the longest cells in liverworts. Duckett and coworkers suggest that this combination of characters may explain their inability to regenerate when damaged (Pressel *et al.* 2008a; Duckett *et al.* 2013).



Figure 34. *Cyathodium tuberosum*, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Jan-Peter Frahm.

On the other hand, rhizoids of mosses (and protonemata) can recover from desiccation except at the apical cell (Pressel 2007; Rowntree *et al.* 2007; Pressel *et al.* 2008b). The pegged rhizoids furthermore are devoid of air bubbles when desiccated, a further indication that they are highly resistant to **cavitation** (formation of a space; collapse of cells), as are the hydroids of mosses (Ligrone *et al.* 2000).

Duckett *et al.* (2013) identified pegged rhizoids in 26 species of thallose liverworts and absence in 5. They compared the diameters of the smooth and pegged rhizoids and measured the time required for dyes to reach the archegonial heads in the taxa compared to time required in several mosses. The rates ranged 30-150 mm h⁻¹ in the thallose liverworts, 28-14 mm h⁻¹ in mosses, and 127-141 mm h⁻¹ in ferns.

Duckett *et al.* (2013) point out that these pegged rhizoids fulfill the three criteria for conduction defined by Raven (1993): dead at maturity, specialized walls, preferential conduction of water. Duckett and coworkers added a fourth criterion, the ability to maintain functional integrity through periods of dehydration, as in moss hydroids (Ligrone *et al.* 2000). This maintenance of functional integrity becomes a problem, because unlike trees and stems, there is no adjacent cell to help in rehydration.

Xerophytic liverworts such as *Riccia* (Figure 35), *Reboulia* (Figure 4), *Targionia* (Figure 36), *Asterella* (Figure 37), and *Lunularia* (Figure 45-Figure 46) have both **tuberculate** (pegged) and smooth rhizoids, scale leaves, and well-defined assimilatory and storage zones, whereas moisture-loving *Dumortiera* (Figure 32), *Cyathodium* (Figure 34), *Pallavicinia* (Figure 38) (Daniels 1998), *Monoclea* (Figure 39), *Neohodgsonia* (Figure 40), and some aquatic *Riccia* species (Figure 41-Figure 42) (Duckett & Ligrone 2003) lack these complex structures. Even in *Marchantia* (Figure 22-Figure 23), 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).



Figure 35. *Riccia sorocarpa* thallus section showing ventral rhizoids, dorsal midribs, and internal photosynthetic layer. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 36. *Targionia hypophylla*, a thallose liverwort with pegged and smooth rhizoids and scales. Photo by Des Callaghan.



Figure 37. *Asterella saccata* showing scales around the thallus margin. Photo by Jan-Peter Frahm.



Figure 38. *Pallavicinia lyellii*, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Des Callaghan.



Figure 39. *Monoclea* cf. *gottschei* with the salamander *Oedipina gracilis*. This liverwort is a simple thallus lacking the complex scales and two types of rhizoids, but clearly having a waxy surface. Photo by William Leonard.



Figure 40. *Neohodgsonia mirabilis* with archegonial heads in New Zealand, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Odontites through Creative Commons.



Figure 41. *Riccia fluitans*, an aquatic species with no rhizoids or scales. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 42. Cross section of thallus of *Riccia fluitans*, an aquatic species with no rhizoids or scales; note the large air spaces for gas exchange and flotation. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

In *Preissia* (Figure 43), it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that *Riccia* (Figure 44), 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** (photosynthetic) cells of the thallus. In others, a crystalloid crust serves a similar function of reflectance.

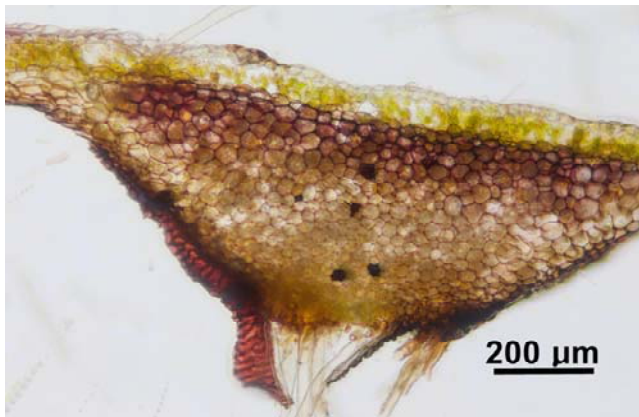


Figure 43. *Preissia quadrata* thallus cross section showing numerous rhizoids in midrib region. Photo by Kristian Peters.

Fungal Partners

Despite their roles in anchorage (smooth rhizoids) and conduction (pegged rhizoids), it seems that smooth rhizoids have a major role in the **endosymbiosis** (internal partnership) of fungi (Pressel *et al.* 2010, 2012; Duckett *et al.* 2013). Our understanding of the value of this partnership is meager. In other plants, fungi serve to increase absorptive surface area and often tap into the roots of a tracheophyte, transferring carbohydrates from plants that reach the canopy to plants that are in the low light beneath them. Such a role remains unknown in the bryophytes, but I am confident that we shall discover that at least some species have this advantage. After all, these partners have been around much longer than the flowering plants, known as **hemiparasites**, that have succeeded in developing this life style. In the leafy liverworts, infections occur exclusively through rhizoids with the Ascomycete *Rhizoscyphus ericae* as partner (Read *et al.* 2000; Pressel

et al. 2008a, c). This is a widespread fungus that lacks host specificity. Fungal partnerships are discussed in more detail below under "Mosses and Leafy Liverworts."

Main Thallus Structure

Midribs: Seeing the midribs in valleys (Figure 35, Figure 44) makes me think that water is directed from the thallus surface to the midrib in some species. I have to wonder if water is absorbed more easily there. Once the water enters the midrib cells, it can be carried to more distant parts of the thallus more quickly than by travelling through other, shorter thallus cells.



Figure 44. *Riccia nigrella* showing valleys with midribs that could be used to direct water into the thallus. Photo by Des Callaghan.

The rib of *Lunularia cruciata* (Figure 45-Figure 46) has parenchymatous cells in which plasmodesmata-derived pores are grouped in small, sparse fields, particularly on transverse oblique walls (Giordano *et al.* 1989). This suggests that the rib cells may be able to transport water and other substances through the ends of cells. These longer cells should, then, move water faster than crossing the many walls of the hyaline parenchyma (Figure 47). Giordano and coworkers suggested that the reticulate cells may serve a water-holding role and facilitate lateral distribution by both **symplastic** (within protoplasm) and **apoplastic** (outside the protoplasm, in intercellular spaces) conduction of substances arriving by way of the rib. They suggest this mechanism may be present in all members of **Marchantiales** with this thallus construction.



Figure 45. *Lunularia cruciata* indicating rib area (arrows). Photo by Luis Nunes Alberto through Creative Commons.

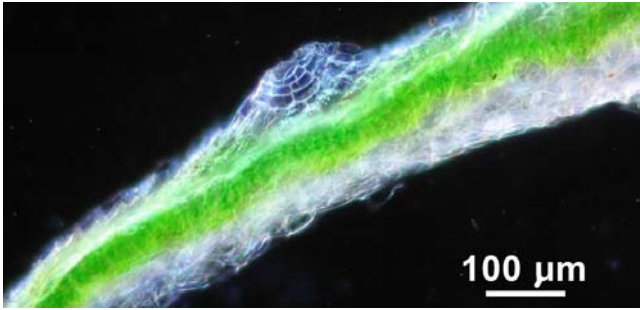


Figure 46. *Lunularia cruciata* thallus showing pore and hyaline parenchyma cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 47. Cross section of *Marchantia* thallus, showing pore. Photo from Department of Botany Teaching Collection, Michigan State University, East Lansing, MI, USA.

Rolling Thallus: Midribs may also facilitate rolling of the thallus by creating a crease through the middle of the plant (compare Figure 44 to Figure 48). Rolling conserves water, but at the same time it exposes the ventral surface where scales help to conserve water (Figure 48). Such rolling is common in species of *Riccia* (Figure 67-Figure 68), often supplemented with hairs that cover the thallus.



Figure 48. *Riccia nigrella* with dry thallus folded at the midrib. Compare this to Figure 44. Photo by Michael Lüth.

Internal Conduction: The liverwort *Lunularia cruciata* (Figure 45-Figure 46) may exemplify a means for water movement between cells in thallose liverworts (Giordano *et al.* 1989). The thallus has **reticulate** (like network) **hyaline** (colorless) **parenchyma** (thin-walled) cells (Figure 46) with between wall thickenings, large **primary pit fields** (thin area in walls of many cells in

which one or more pits usually develop) with numerous pores derived from **plasmodesmata** (narrow threads of cytoplasm that pass through cell walls of adjacent cells and allow communication between cells) on unthickened areas of walls.

Spongy Thallus

The spongy thallus of *Riccia cavernosa* looks like it should have an important adaptive value. The basal layer gives rise to a layer of irregular vertical column of chlorophyllose cells ovetopped by colorless epidermal cells (*Riccia cavernosa* 2012). While these might seem to have functions similar to those of *Exormotheca*, instead some of these epidermal and chlorophyllose cells collapse, creating large air spaces at several levels in the tissue of the thallus. The light that reflects from these cavities has a glistening appearance. But does this sequence of events provide any advantage to the plant? At first glance, it looks very much like a sponge, but at a much smaller scale.

The basal pad of isodiametric cells gives rise to a layer of irregular vertical columns of chloroplast containing cells, topped by colorless oval epidermal cells (*Riccia cavernosa* 2012). But early in development, large air spaces develop at several levels in this tissue due to the collapse of some of the epidermal and chlorenchyma cells. The light reflecting inside these cavities gives the thallus a characteristic glistening appearance.

Cuticle

For many years we considered the cuticle to be absent in bryophytes, with scattered references referring to them, but with no definitive data on their surface chemistry. However, not only are waxy cuticles present, but waxes are present on the leaves and thalli, albeit in less noticeable quantity than in tracheophytes. In fact, Brockington *et al.* (2013) considered the cuticle in the thallose liverwort *Marchantia polymorpha* (Figure 22) to be "an overlooked innovation in land plants."

Knowing that *Marchantia polymorpha* has a cuticle, one should not be surprised that the shiny thallose liverwort *Monoclea gottschei* (Figure 39) and the hornwort *Notothylas orbicularis* (Figure 49) have an **osmiophilic layer** (refers to lipid-containing bodies; a cuticle) with structural resemblance to that of early developmental stage tracheophyte cuticles (Cook & Graham 1998).

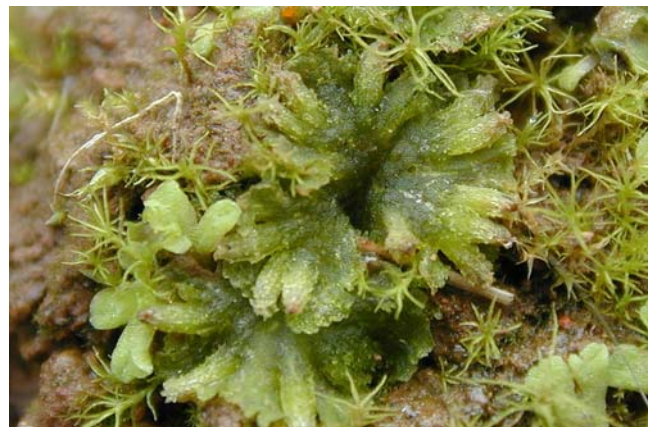


Figure 49. *Notothylas orbicularis*, a species with a demonstrated osmiophilic layer, *i.e.* cuticle. Photo by Michael Lüth.

What emerged as more interesting in this study is that not all of these bryophyte versions are created equal. In the liverwort *Monoclea gottschei* (Figure 39) the layer is nodular, in the hornwort *Notothylas orbicularis* (Figure 49) it can be either nodular or sheetlike, and in *Sphagnum fimbriatum* (Figure 50) it is sheetlike with regular ridges that run parallel to the edges of the "thalli" (Cook & Graham 1998). It appears that cuticle is ancient, and Cook and Graham suggest that it may have arisen before the charophycean algae and bryophytes diverged from their common ancestor.



Figure 50. *Sphagnum fimbriatum*, a species with a cuticle. Photo by Michael Lüth.

The thallose liverwort *Plagiochasma rupestre* (Figure 58) has a non-wettable thallus endowed with hydrophobic wax globules, preventing it from absorbing water through its surface (Kürschner 2004). Instead, it uses the pegged rhizoids for water uptake, a phenomenon that may be common to all members of *Marchantiales*. This dorsal surface wax may have an important role in preventing water logging in the underlying air chambers.

The presence of a cuticle on the upper surface of a thallose liverwort raises the question of water absorption in these species. One might surmise that it occurs through the ventral surface, facilitated by the scales and rhizoids. Presumably there is no cuticle on that surface, but that does not yet seem to have been demonstrated.

Pores

The wonderful ventral efficiency of rhizoids and scales is often challenged 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 47, Figure 56). Maier-Maercker (1982) found that *Conocephalum conicum* (Figure 24) loses water through transpiration from these dorsal thallus pores (Figure 51), accumulating radioactively labelled ions in the cells surrounding the air pores.

The single-layered leaves of mosses and leafy liverworts preclude the presence of stomata there as they would provide only a hole through the leaf, hardly a useful character. Even multicellular layers of moss leaves have no use for stomata because there is no chamber where the gases may gather. But thallose liverworts meet those two requisites – multiple cell layers (Figure 52) and chambers internally (Figure 53). Furthermore, as mentioned above for *Marchantia polymorpha* (Figure 22), the thallus has a

cuticle that can at least to some degree repel water. Hence we might presume that it likewise is somewhat resistant to gas exchange, creating a problem for photosynthesis. Raven (2002) provided evidence that stomata evolved from pores of an epidermis over plant organs at least three cell layers thick, with intercellular gas chambers, and with a cuticle. In this anatomical arrangement, the presence of pores most likely confers an adaptive advantage for photosynthesis.

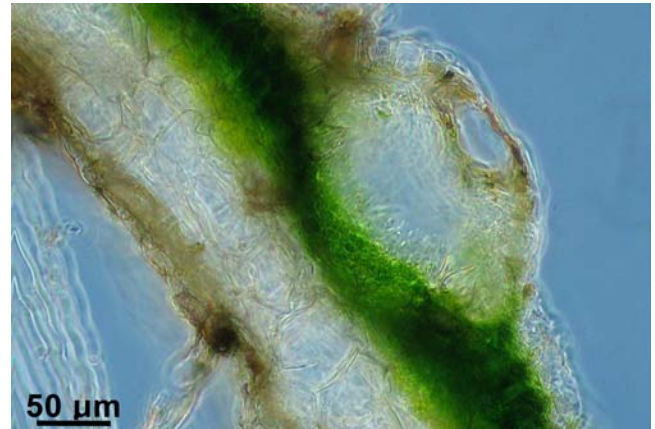


Figure 51. *Conocephalum conicum* pore section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 52. *Conocephalum conicum* photosynthetic cells under epidermis, showing thallus that is more than three cell layers thick. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

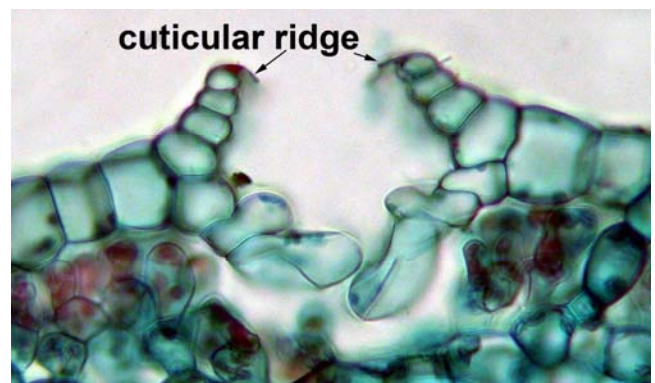


Figure 53. *Marchantia polymorpha* thallus pore in longitudinal section, showing cuticular ridge. Cells stained with purple are photosynthetic cells. Note the chamber beneath the pore. Photo by George Shepherd through Creative Commons.

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 (Figure 54), 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.



Figure 54. *Marchantia chenopoda* pores showing rim of cuticle projecting into the pore opening. The polygons outline the internal chambers that create the areolation. Photo by George Shepherd through Creative Commons.

But the photosynthetic cells project into these chambers beneath the pores (Figure 53), and flooded cells cannot exchange gases freely. It should be no surprise then that the openings themselves prevent the entrance of water into the chamber. Their small size (Figure 54) contributes to this. In the absence of a wetting agent, the cohesive forces of water make the aggregation of water molecules too large to enter the holes. This smallness of the hole is further enhanced by the presence of a **cuticular ridge** (Figure 54-Figure 57) that not only narrows the entrance, but that also repels the water.

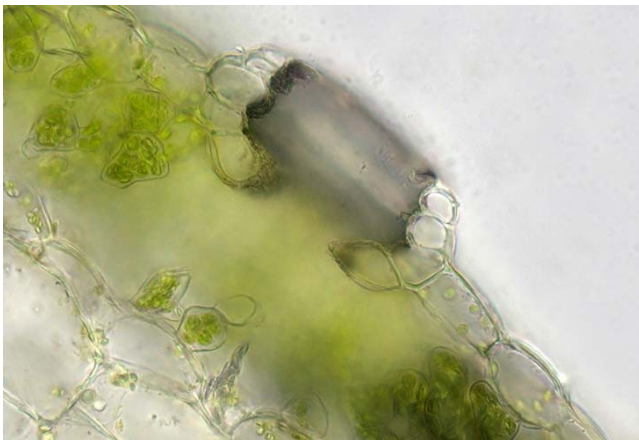


Figure 55. *Marchantia polymorpha* pore in longitudinal section. Photo by Walter Obermayer.

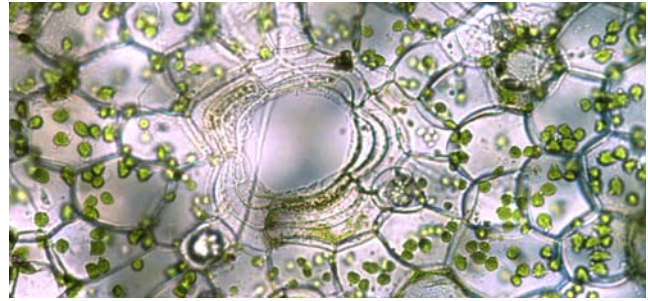


Figure 56. Pore opening in thallus of *Cyathodium cavernarum*. Photo by Noris Salazar Allen.

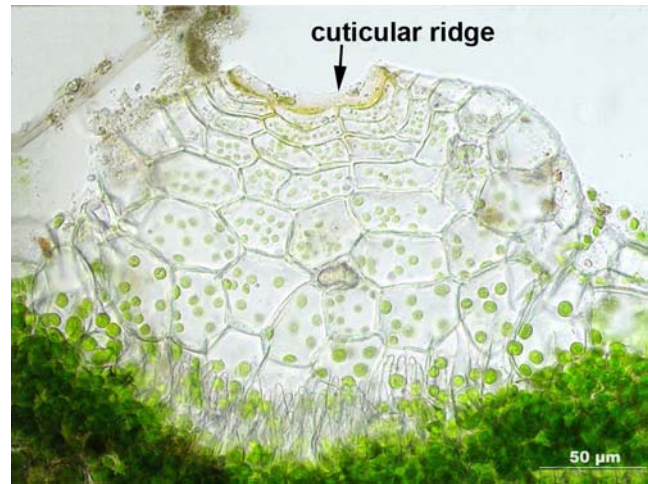


Figure 57. *Conocephalum conicum* pore longitudinal section showing the cuticular ridge. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>.



Figure 58. *Plagiochasma rupestre*, a thallose liverwort with no cuticular ridge on its pores, but with a waxy cuticle on the thallus. Photo by Michael Lüth.

Schönherr and Ziegler (1975) found that of the fourteen thallose liverwort species they studied, twelve of them have such **hydrophobic** (repelling water) ridges, and that **cutin** is present in these ridges. Furthermore, the researchers considered the pores in these species to be "perfect" in keeping water out of the thallus. *Plagiochasma rupestre* (Figure 58) and *P. peruvianum*, on the other hand, lack such ridges and liquids are able to enter the thallus through the pores. While the waxes and

small size of the holes keep water out, the water in vapor form within the thallus is able to escape through the pores, along with oxygen, while CO₂ enters. Therefore, the openings must maximize carbon gain per unit water loss (Raven (2002).

While these pores are an advantage for a hydrated, photosynthesizing thallus, they are a liability for a drying thallus due to the loss of water vapor. But at least some of the liverworts seem to be able to partially control the opening. This is accomplished by curving of the stack of cells surrounding the opening, creating partial closure. In *Preissia* (Figure 59-Figure 60, Figure 30), the barrel-shaped pores (Figure 60) change shape to accomplish control of water loss (Lepp 2008). When turgid with water, the cells at the bottom of the barrel keep the pore open, but when the conditions are dry, the cells lose their turgor and collapse, narrowing the opening at the bottom of this barrel. Those in *Marchantia* (Figure 53-Figure 55) behave similarly (Raven *et al.* 2005).



Figure 59. *Preissia quadrata* thallus showing pores (light-colored dots). Photo by Jan-Peter Frahm.



Figure 60. *Preissia quadrata* thallus showing pores with cuticular ridges. Photo by Kristian Peters.

Archegoniophores and Antheridiophores

In thallose liverworts, the horizontal orientation cannot serve as a model for water movement in the vertical **archegoniophore**. As determined by Duckett *et al.* (2013), the archegoniophore has more efficient water movement than the stems of mosses. They attribute this to the efficiency of movement through the rhizoids and capillary

spaces among them, as well as the hydrophobic nature of the thallus surface surrounding these rhizoids (Figure 61).

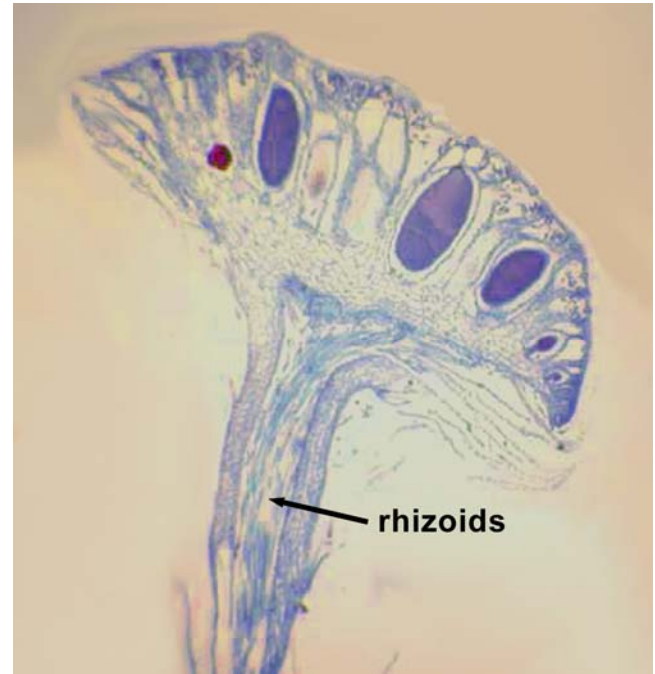


Figure 61. *Marchantia polymorpha* antheridial head showing location of rhizoids within the antheridiophore. Photo from Botany website of the University of British Columbia, BC, Canada.

The importance of this rhizoid-thallus combination for the archegoniophore is suggested by comparing its response to drought with that in mosses. For example, *Marchantia* (Figure 62) archegoniophores and heads can remain fully hydrated for several hours in full sunlight at 20-30°C while the shoots of neighboring *Polytrichum commune* (Figure 63) with their bases in standing water become wilted and must have added rainwater to recover (Duckett *et al.* 2013), suggesting an efficient system of transport in the archegoniophore.



Figure 62. *Marchantia polymorpha* archegoniophore and archegonial head. Note rhizoids along stalk (archegoniophore) where they emerge from the folded thallus that makes the stalk. Photo by George Shepherd Creative Commons.



Figure 63. *Polytrichum commune*, a moss that wilts in full sun despite its wet substrate and colonial habit. Photo by Michael Lüth.

Duckett *et al.* (2013) suggest that the length of the archegoniophore is limited to a maximum of 7-10 cm (in *Conocephalum*; Figure 64) because of the problems of air bubbles in the mucilaginous matrix surrounding the pegged rhizoids in the grooves of the archegoniophore, a condition analogous to an embolism in the vessels of tracheophytes (see Canny 2001 a, b).



Figure 64. *Conocephalum conicum* with tall archegoniophore. Photo by Adolf Ceska.

Antheridiophores provide yet a different mechanism (Duckett & Pressel 2009). Present only in the genus *Marchantia*, they present an antheridial head (Figure 65) on a stalk that is much shorter than that of the mature archegoniophore, rarely exceeding 30 mm. Rather than being hydrophobic, the heads are highly hydrophilic and absorb raindrops much like a sponge. Whereas upward flow occurs in the stalk during dry periods, downward flow carries the motile sperm toward the archegonia on immature (shorter) archegoniophores (Figure 66) during rainfall.



Figure 65. *Marchantia polymorpha* with antheridial heads where water is absorbed like a sponge. Photo by Rudolf Macek.



Figure 66. *Marchantia polymorpha* young archegoniophores that receive sperm from temporarily taller antheridiophores. Photo by Rudolf Macek.

Dormancy

Volk (1984) found that when *Riccia* (Figure 67-Figure 68) has less than 150 mm of rainfall per year, it requires other means to survive, and it seems that dehydration/dormancy is the solution (Figure 67-Figure 68). 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 67. *Riccia sorocarpa* in a fresh, active state. <www.photofauna.com>.



Figure 68. *Riccia sorocarpa* in a dry, dormant state. Photo by Michael Lüth.

Mosses and Leafy Liverworts

We typically think first about structural adaptations for water retention, so we will start there. Sarafis (1971) considered that *Polytrichum commune* (Figure 63) 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 taxonomic 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 (Buryová & Shaw 2005). For example, **conducting strands** disappear in the liverworts *Moerckia flotoviana* (Figure 69) and *Haplomitrium hookeri* (Figure 70-Figure 71) under high humidity or liquid culture (Hébant 1977). **Hair points** (colorless, hairlike extensions at leaf tip) of *Schistidium apocarpum* (Figure 72) likewise disappear in humid conditions (Figure 72).



Figure 69. *Moerckia blyttii*, a thallose liverwort that loses its conducting cells in wet habitats. Photo by Michael Lüth.



Figure 70. *Haplomitrium hookeri*, a liverwort that loses its central strand in wet habitats. Photo by Des Callaghan.

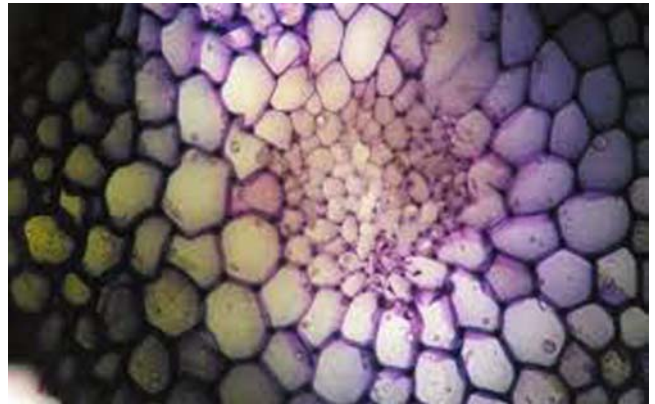


Figure 71. *Haplomitrium* sp. stem cross section with central strand that disappears in wet habitats. Photo by Rachel Murray and Barbara Crandall-Stotler. Permission Pending.



Figure 72. **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* (Figure 73), 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 (Figure 74) compared to those grown out of water (Figure 75), and the reduced light results in greater **internode** distances (distance between leaf insertions) (Lodge 1959). A similar response is seen in *Fontinalis* (Figure 76). It is interesting that increases in salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.



Figure 73. *Andreaea blyttii*, a moss that changes its leaf morphology in response to moisture changes. Photo by Michael Lüth.



Figure 74. *Drepanocladus aduncus* with straight leaves resulting from growing under water. Photo by Michael Lüth.



Figure 75. *Drepanocladus aduncus* with falcate leaves resulting from growing above the water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.



Figure 76. **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.

Growth Form

Growth form is important both for obtaining and retaining water. For example, *Grimmia pulvinata* (Figure 77) forms cushions. In this moss, and most likely others with this growth form, size matters. As the clump grows larger, the surface to volume ratio decreases as the larger cushion is accompanied by greater height in the center. This reduces exposed area for gas exchange, but it also reduces the portion exposed to the atmosphere for water loss. In *Grimmia pulvinata* the larger cushions have lower area-based evapotranspiration rates due to a higher boundary-layer resistance, but the relative water storage capacity per dry weight does not change (Zotz *et al.* 2000). Consequently, the hydrated period is considerably longer in larger cushions. And as predicted, the CO₂ exchange rate decreases with increasing size of the cushion, with both net photosynthesis and dark respiration decreasing.



Figure 77. *Grimmia pulvinata* showing cushion form that conserves water. Photo by Michael Lüth.

Stems and Branches

Most stem and branch arrangements relate to growth form or life form (see Chapter 4-5 of this volume). However, in some cases there is internal or structural modification, exemplifying the plasticity of some bryophytes. For example, *Philonotis fontana* (Figure 78- Figure 79) exhibits variation among populations in leaf dimensions, whereas their cell dimensions show little response to differences in water regime or light level (Buryová & Shaw 2005).



Figure 78. *Philonotis fontana*, a species whose leaf dimensions vary with habitat. Photo by Des Callaghan.

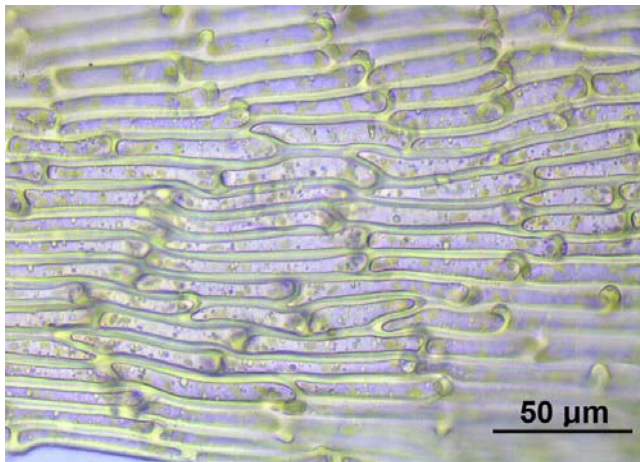


Figure 79. *Philonotis fontana* leaf lamina showing cells. These cells vary little in dimensions in different water or light regimes. Photo by Kristian Peters through Creative Commons.

Schröder (1886) considered the ability of moss stems to resprout from a dormant stem to be one method for withstanding prolonged drought. I had a similar experience with the aquatic moss *Fontinalis dalecarlica* (Figure 80). In this case, the moss was boiled for 14 hours a day for two weeks in the lab, then returned to the stream. One year later, new growth was present on this moss that was still attached to the numbered rock used in the boiling treatment. Such ability of stem tips to recover from environmental stresses have been largely overlooked.

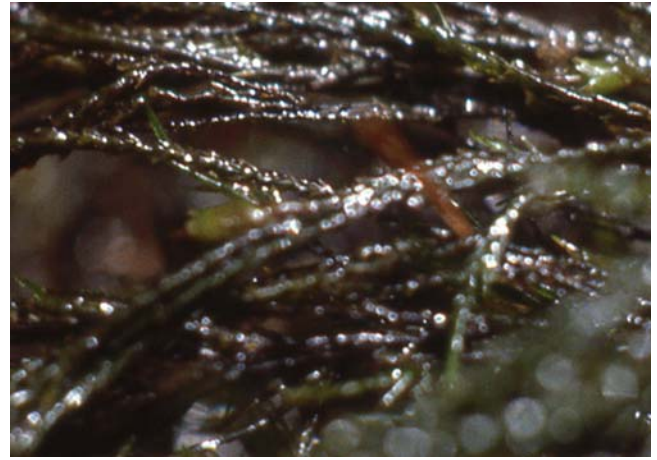


Figure 80. *Fontinalis dalecarlica* with from Fox Run, NH, where a plant similar to this produced a green leaf one year after being boiled for 14 hours a day for two weeks. Photo by Janice Glime.

Sphagnum: Li and coworkers (1992) examined the responses of two closely related *Sphagnum* hummock species, *S. magellanicum* (Figure 81) and *S. papillosum* (Figure 82), to distance from water surface 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 83), with thicker hyaline layers (Figure 84-Figure 85), than stems with apical capitula near the water surface (Figure 86), presumably increasing both absorption and water-holding ability.



Figure 81. *Sphagnum magellanicum*, a hummock species with efficient water movement. Photo by Michael Lüth.

Sphagnum has pores in its stem (Figure 86), 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** (Figure 87) on the stems for absorbing water (Figure 87).



Figure 82. *Sphagnum papillosum*, a species with inefficient water movement. Photo by David Holyoak.

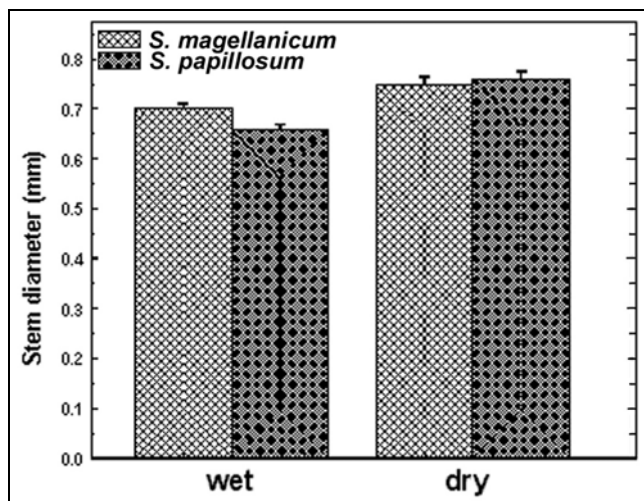


Figure 83. Effect of water level (water availability) on stem diameter in *Sphagnum magellanicum*, a more desiccation-resistant species, and *S. papillosum*, a more desiccation-tolerant species. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard errors; stem diameter in dry treatment is significantly greater (Figure 84) in both species. From Li *et al.* (1992).

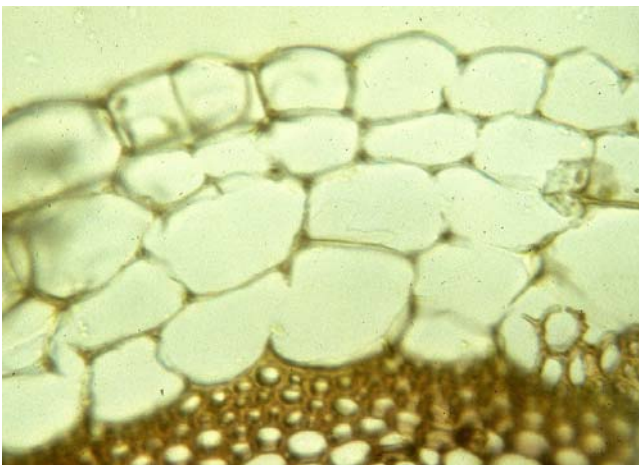


Figure 84. *Sphagnum magellanicum* stem at highest level (5) above water surface. Photo by Yenhung Li.

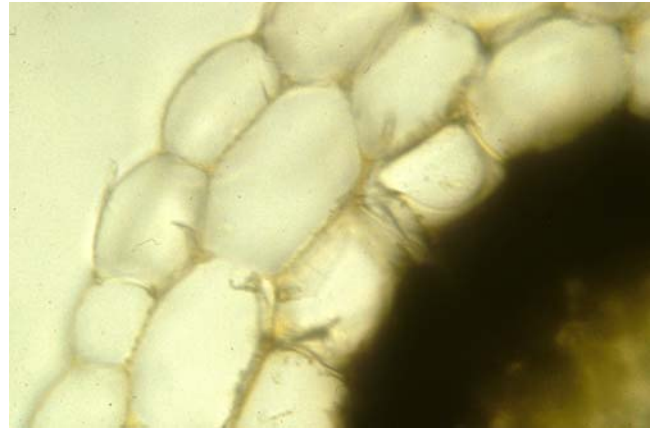


Figure 85. *Sphagnum magellanicum* stem at level 3 above water surface. Photo by Yenhung Li.

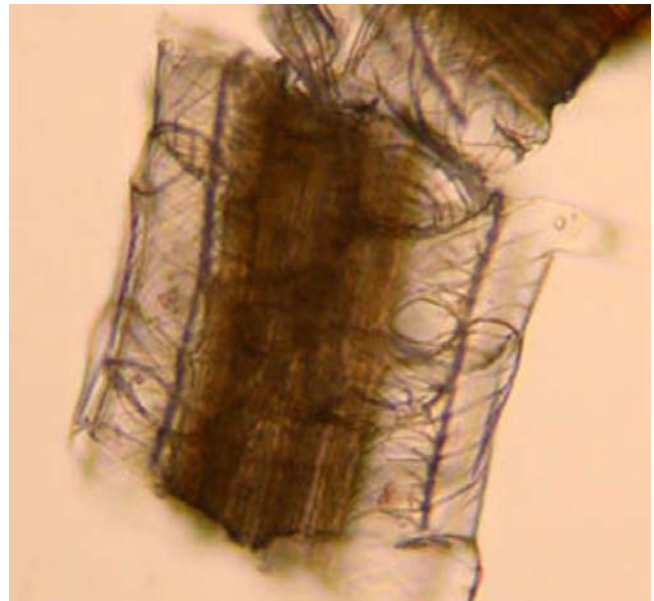


Figure 86. *Sphagnum papillosum* stem showing pores. The spiral thickenings of stem cells are unique in this moss. Photo from Botany website, University of British Columbia, BC, Canada.



Figure 87. Retort cell (arrow) of *Sphagnum*, showing pore. Photo from Botany website, University of British Columbia, BC, Canada.

Daniels (1989) found that while there is little differentiation between **spreading** and **pendant** branches (Figure 88-Figure 89) 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 (Figure 89). 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 (*Sphagnum cuspidatum*) or as wet carpets (*Sphagnum recurvum*) 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 88. *Sphagnum teres* indicating two major branch types, compact capitulum, and joining of branches into fascicles. Photo by Michael Lüth.



Figure 89. Spreading branches and pendant branches on two hummock *Sphagnum* species. Left: *S. magellanicum*. Right: *S. papillosum*. 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 it will keep *S. papillosum* wet (Figure 90). However, it will fail to do so if *S. papillosum* is dominant (Figure 90). This is further supported by lab experiments in which *S. magellanicum* moved water farther externally in 20 hours than did *S. papillosum* (Figure 91; Figure 92).

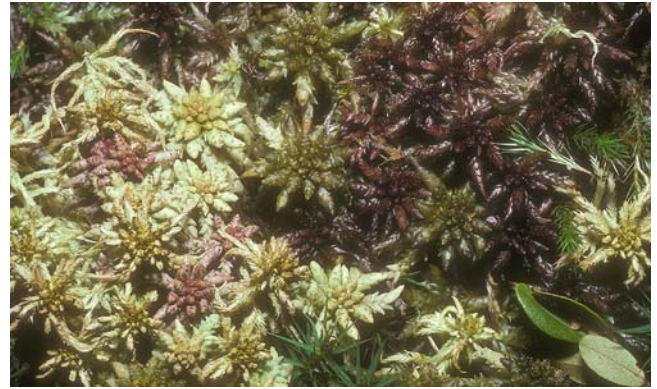


Figure 90. Predominately *Sphagnum papillosum* (olive colored) lower on the hummock (left side of picture) causes both species to be dry, whereas predominately *S. magellanicum* (red) higher on the hummock (right side of picture) causes both species to be wet. Photo by Janice Glime.

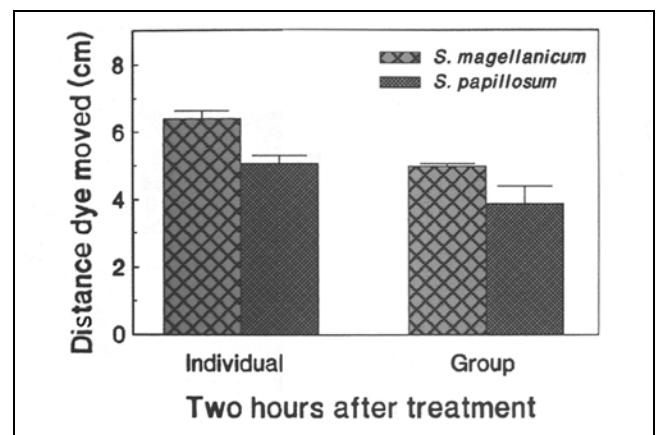


Figure 91. Comparison of distance travelled by dye in two *Sphagnum* species from lower (*S. papillosum*) and higher (*S. magellanicum*) in the hummock after 20 hours. Group refers to those kept together at field density with half of each species. From Li *et al.* (1992).

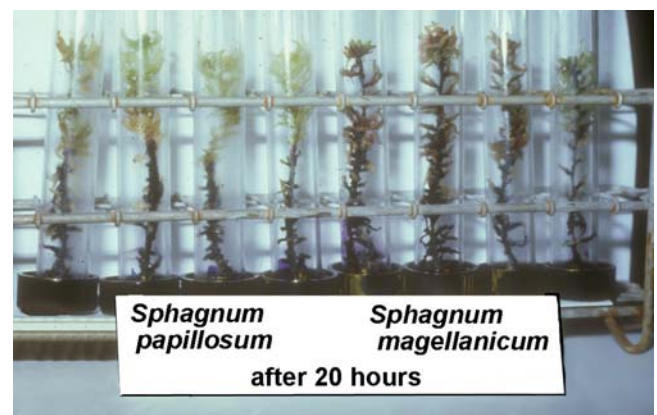


Figure 92. Comparison of upward transport in a low (left) and high (right) hummock species of *Sphagnum*. Movement of water is indicated by purple dye. Photo by Yenhung Li.

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 93) is typically composed of hydroids that are elongated and impose fewer

cell end walls through which water must travel. Hébant (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 swollen walls of hydroids in the setae of *Dicranum scoparium* (Figure 94) or the lateral walls of hydroids in the gametophyte central strand of the **Polytrichales** (Figure 95). But insufficient data exist to relate these variations to adaptive function.

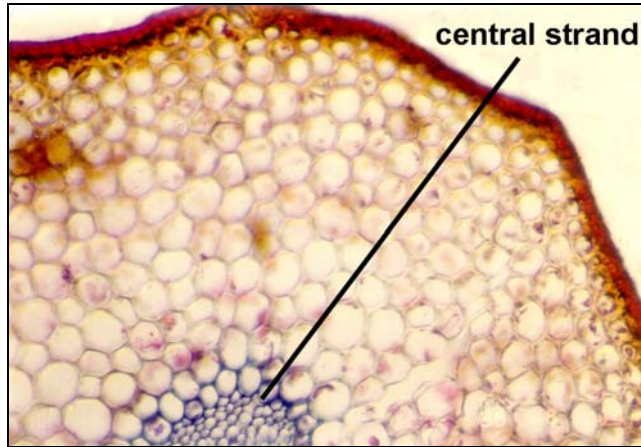


Figure 93. Stem cross section of *Rhizogonium* showing narrow cells of central strand. Photo by Isawa Kawai.

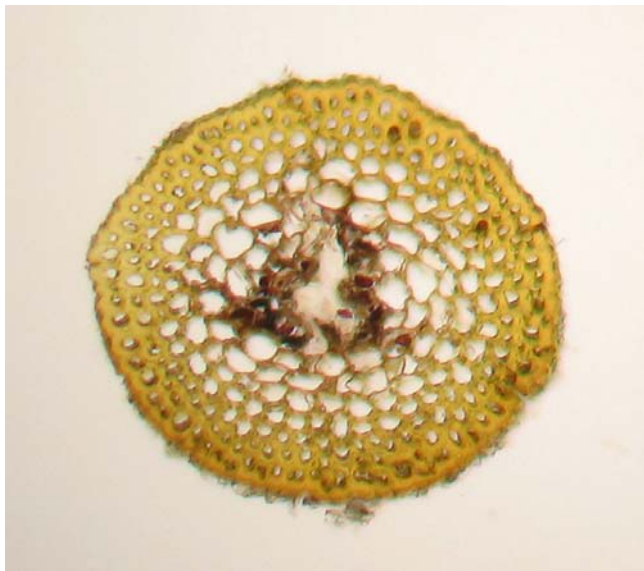


Figure 94. *Dicranum scoparium* seta cross section showing hydroids. Photo from Botany website, University of British Columbia, BC, Canada.

Using several references for comparison, Hébant (1977) showed that the number of hydroids within the *Polytrichum commune* central strand (Figure 95) 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.

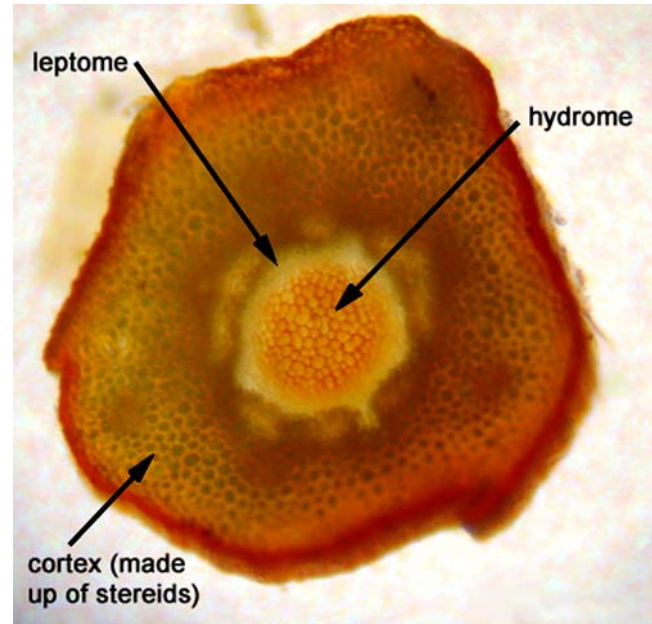


Figure 95. *Polytrichum commune* stem cross section showing central strand. Photo from Botany website, University of British Columbia, BC, Canada.

Although in general, leafy liverworts lack conducting tissues in both leaves and stems (Crandall-Stotler 2014), *Haplomitrium* seems to be an exception. At least it possesses a differentiated central strand (Figure 96). But there seem to be no experiments to demonstrate that this actually serves as conducting tissue.

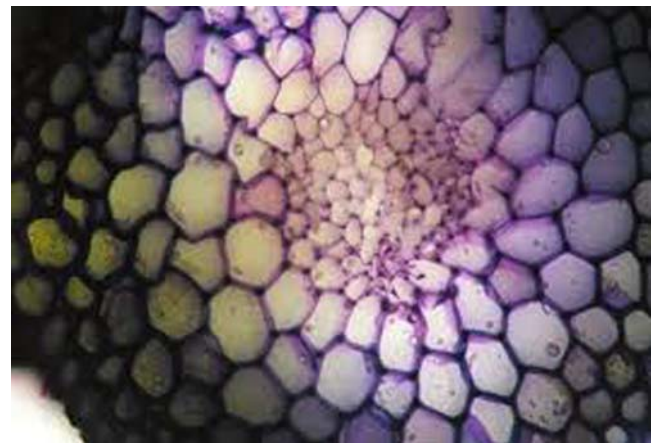


Figure 96. *Haplomitrium* stem cs showing thin-walled central strand. Photo by Rachel Murray & Barbara Crandall-Stotler.

Waxes

Bryophytes leaves have frequently been described as lacking a cuticle. However, this ancient concept has proven to be false. Even leafy liverworts can have a cuticle. The details of the leaf cuticle will be discussed in the next subchapter, but we need to consider how such a cuticle might affect the whole plant water movement. Loss of water from leaves can create a transpiration stream that draws water upward, but in most bryophytes the greater movement of water is external. Hence, it is not surprising that little is known of the effects of a transpiration stream on water movement in bryophytes. It would be interesting

to know if stems have a cuticle, but I am aware of no studies that isolated the stems to look for it. For now, we will concentrate on other aspects of water movement.

Rhizoids and Tomentum

Rhizoids and **tomentum** (layer of matted woolly down on surface of plant; Figure 97) are adapted for water uptake. Pressel and Duckett (2011) found that rhizoids of all representatives they tested in **Polytrichales**, **Dicranales**, and **Bryales** (Figure 98) were **hydrophilic** (tendency to be wetted by water). For example, there is a sharp contrast between the leaves with a waxy cuticle in **Bartramiaceae** (Figure 99) and the highly hydrophilic tomentum-forming rhizoids (Figure 99) with papillae.

Mosses with dense rhizoids or **tomentum** (Figure 97- Figure 99) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that ***Bryum pseudotriquetrum*** (= *Bryum algens*; Figure 98), with a dense rhizoidal tomentum (Figure 98), 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 attributed mostly to loss of water from the tomentum? In ***Schistidium antarctici*** (Figure 100), 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 97. *Rhizomnium magnifolium* showing dense brown rhizoidal tomentum on lower half of stem. Photo by Michael Lüth.



Figure 98. *Bryum pseudotriquetrum* (Bryales) showing dense rhizoidal tomentum along stem. Photo by Misha Ignatov.



Figure 99. *Breutelia chrysocoma* (Bartramiaceae) showing rhizoidal tomentum. Photo by Michael Lüth.



Figure 100. *Schistidium antarctici*, a moss that becomes morphologically modified by moisture conditions. Photo by Rod Seppelt.

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 (Figure 101) toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In ***Fontinalis*** (Figure 102), where rhizoids have a critical function in anchorage, and this aquatic moss may encounter its substrate in any direction from the stem, the individual rhizoids grow in a spiral (Figure 103) until they encounter the substrate, then form multiple branches (Figure 104) in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).



Figure 101. *Hygroamblystegium fluviatile* rhizoids on one side of stem. Photo by Janice Glime.

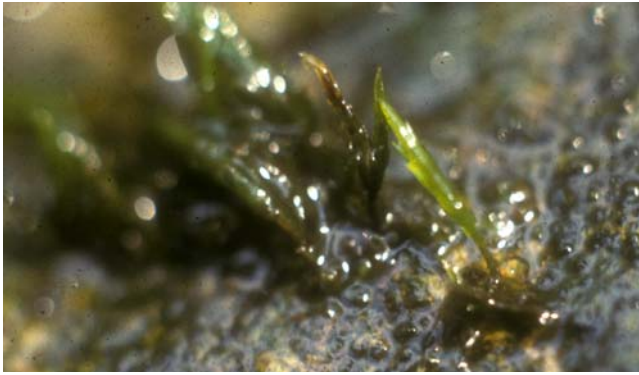


Figure 102. *Fontinalis novae-angliae* cemented to the rock by its rhizoids. Photo by Janice Glime.



Figure 103. *Fontinalis squamosa* rhizoids growing in a spiral where they are suspended above the substrate. Photo by Janice Glime.



Figure 104. *Fontinalis squamosa* rhizoid tips branching. 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 is present in terrestrial cultures is 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 easily. 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*, (Figure 105) 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. Or are these cuticles designed to provide capillary spaces that hold water around the rhizoids and facilitate uptake?



Figure 105. *Polytrichum juniperinum* males, a moss that has a cuticle on its rhizoids. Photo by Jan-Peter Frahm.

It is noteworthy that both leafy liverworts *Haplomitrium* (Figure 70-Figure 71) and *Treubia* (Figure 106) lack rhizoids (Figure 107) (Duckett *et al.* 2013). These unusual liverworts have leaves in three equal ranks and use underground stems (**rhizomes**) for anchorage and for fungal associations. All other liverworts produce **unicellular** (having only one cell) rhizoids (Figure 108). But only the thallose liverworts produce two types. Mosses, on the other hand, have multicellular rhizoids that branch (Figure 109).



Figure 106. *Treubia lacunosa* dorsal view. Photo by Jan-Peter Frahm.



Figure 107. *Treubia lacunosa* with sporophyte, showing absence of rhizoids. Photo by Jeff Duckett & Silvia Pressel.



Figure 108. *Cephalozia* sp. rhizoids showing that they are one-celled. Photo by Jan Fott.



Figure 109. *Bryum stirtonii* rhizoid showing multiple cells, papillae, and branching. Photo by Michael Lüth.

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 of desiccation until they are 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* (Figure 110) there are **slime papillae** (Figure 111) that may serve a water absorption/retention function as well. The leafy liverwort *Haplomitrium* produces extensive mucilage on its rhizomes (Figure 112-Figure 113). It is interesting that these slime papillae appear in the green alga *Coleochaete* (Figure 114), 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 110. *Takakia lepidozioides*. From the Herbarium of Hiroshima University, Hiroshima, Japan.



Figure 111. Stem of *Takakia lepidozioides* showing slime papillae. Photo from Botany website, University of British Columbia, BC, Canada.



Figure 112. *Haplomitrium gibbsiae* leafy plant with mucous on its rhizomes. Photo by Jeff Duckett and Silvia Pressel.



Figure 113. *Haplomitrium gibbsiae* rhizome with mucous. Photo by Jeff Duckett and Silvia Pressel.

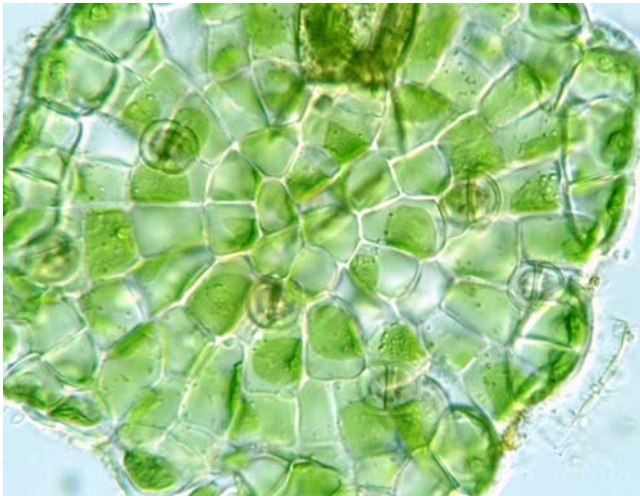


Figure 114. *Coleochaete* thallus, an extant green alga that has the most characters in common with bryophytes. Photo by Yuuji Tsukii.

The thallose liverwort *Conocephalum conicum* (Figure 19, Figure 24, Figure 51) 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 115), 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 (Figure 116), *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 117) 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* (Figure 77) and *Syntrichia montana* (= *S. intermedia*; Figure 118). Thus far, it has been difficult to demonstrate that papillae afford any such advantage (Frey & Kürschner 1991). Nevertheless, in leaves they can act as a rapid capillary water movement system (Proctor 1979; Longton 1988; Pressel & Duckett 2011).



Figure 115. *Bartramia ithyphylla* illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth.

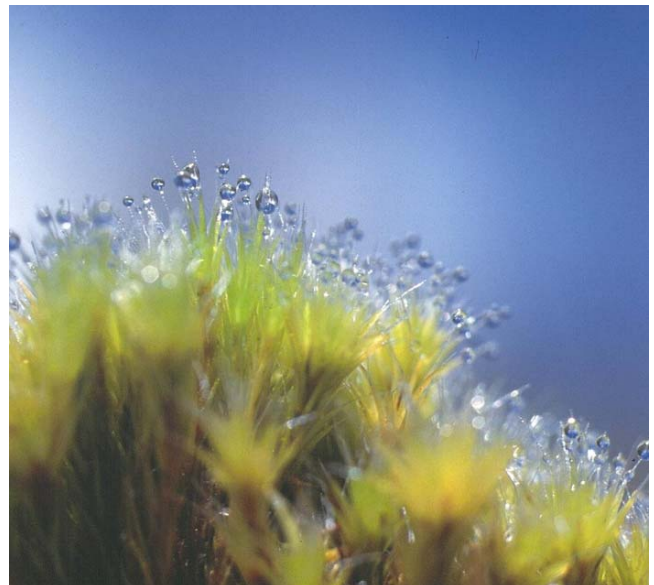


Figure 116. *Campylopus introflexus* showing water droplets at tips of plants. Photo by Jan-Peter Frahm.



Figure 117. *Polytrichum piliferum* illustrating leaf hairs that overlap the next leaf and help shield it from light, at the same time creating capillary spaces. Photo by Michael Lüth.



Figure 118. *Syntrichia montana* showing long hair points that can reduce evapotranspiration by up to 35%. Photo by Michael Lüth.

The leafy liverwort *Trichocolea* (Figure 119-Figure 120) is highly adapted to take advantage of capillary spaces. Its leaves are highly dissected and **paraphyllia** (leaflike appendages between the leaves; Figure 121) 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* (Figure 122-Figure 123) and *Thuidium tamariscinum* (Figure 124) create capillary spaces much like a tomentum. Other mosses such as *Mniaceae* utilize **paraphyses** (Figure 125) among the archegonia and antheridia to conserve water, using the same capillary principle.

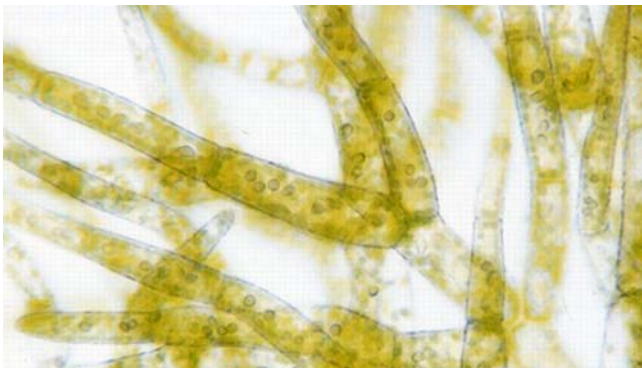


Figure 119. *Trichocolea tomentella* leaf cells. Photo by Malcolm Storey from Discover Life <<http://www.discoverlife.org/mp/20q?search=Trichocoleaceae>>.



Figure 120. *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 divided leaves.

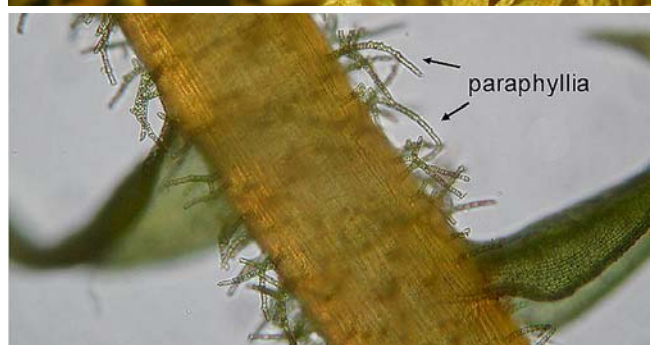


Figure 121. *Thuidium recognitum* showing branched paraphyllia on the stem and branches. Photos by Michael Lüth (**upper**) and Paul Davison (**lower**).

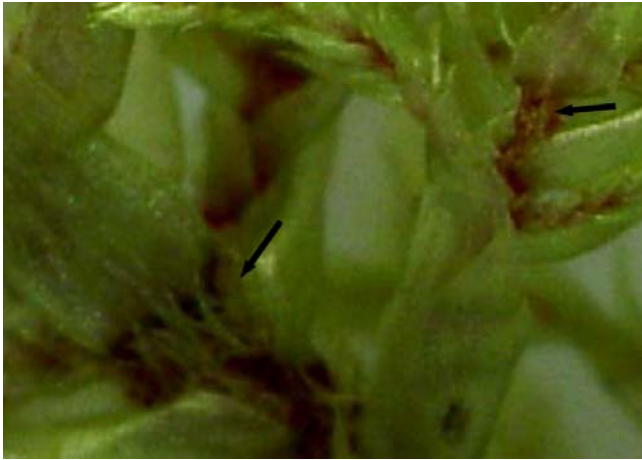


Figure 122. *Hylocomium splendens* showing paraphyllia on stem. Photo by Rosalina Gabriel. Permission Pending.



Figure 123. *Hylocomium splendens* paraphyllia. Photo from Botany website, University of British Columbia, BC, Canada.

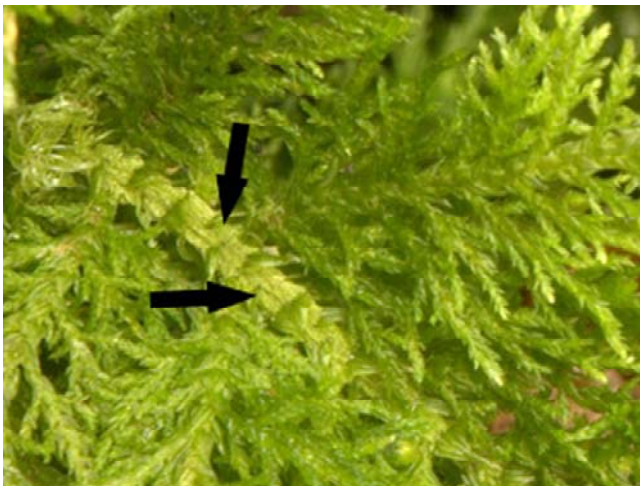


Figure 124. *Thuidium tamariscinum*, showing paraphyllia on stem (arrows). Photo by Brian Eversham.

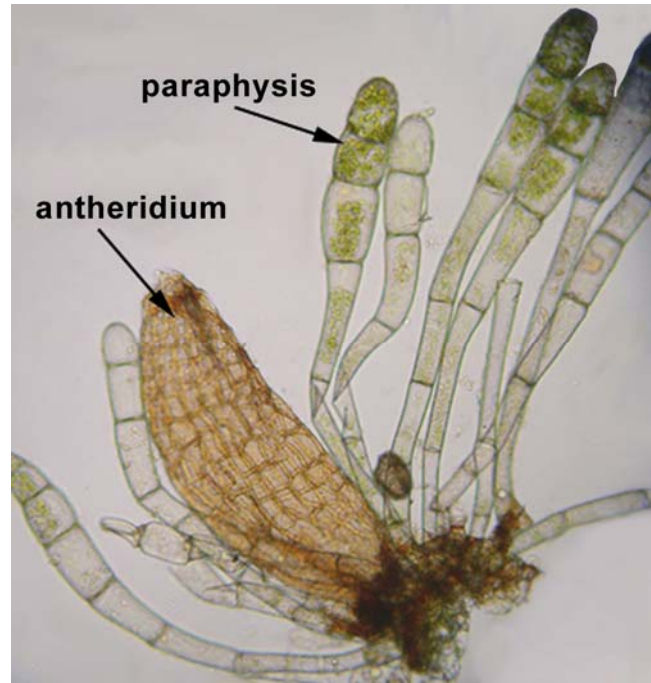


Figure 125. *Plagiomnium insigne* antheridia and paraphyses that create capillary spaces. Photo from Botany website, University of British Columbia, BC, Canada.

Fungal Partners

Fungal partners associated with roots have been termed **mycorrhizae**, and the same term is applied to fungi that serve as fungal partners to bryophytes. The existence of these relationships has been overlooked until recently, although we have recognized for quite some time that many bryophytes had fungi associated with them. Hence, our knowledge of their importance to the bryophyte is meager. It is likely that they serve a similar role to that in tree roots in scavenging a wide area for water, minerals, and perhaps organic nutrients. But I would also consider it likely that at least some of them play a role similar to that in the **hemiparasites** such as Indian pipe (*Monotropa uniflora*). That is, for those bryophytes living in dense shade, they could find a third partner that has more access to light – a leafy tracheophyte – that provides photosynthate that can be transferred from the tracheophyte, by way of the fungus, to the bryophyte. I am afraid I can see no substance that is likely to be produced by the bryophyte that is useful to the tracheophyte, making the bryophyte also a hemiparasite. Nevertheless, such a 3-way linkage remains to be demonstrated.

In an attempt to unravel the evolution of the fungal symbioses of bryophytes, Pressel *et al.* (2010) examined the ancient basal bryophytes *Treubia* (Figure 106-Figure 107) and *Haplomitrium* (Figure 112-Figure 113). In these liverworts they found intracellular fungal lumps, inter cellular hyphae, and thick-walled spores. Unlike the well known glomerophytes found as symbionts in thallose liverworts and lower tracheophytes, these were more ancient fungi (Figure 126-Figure 127).

In leafy liverwort families sister to the **Schistochilaceae**, the ascomycete fungus *Rhizoscyphus ericae* occurs in the rhizoids (Pressel *et al.* 2010). This fungus has a wide range of hosts, including flowering plants in the Ericales (includes blueberries and heath

plants) and an Antarctic species of the leafy liverwort *Cephaloziella*. Figure 128 shows a member of the **Ascomycota** inhabiting *Mylia anomala*. In the **Basidiomycota**, the genus *Sebacina* (Figure 129) is associated with leafy liverworts, but this fungus is host specific. Neither of these liverwort fungi seems to digest its host, whereas the **Basidiomycota** in the thallose liverworts of **Aneuraceae** have regular colonization and digestion cycles. The hornworts also demonstrate mycorrhizal relationships with fungi, but thus far there is no evidence that such a mycorrhizal relationship exists in mosses.

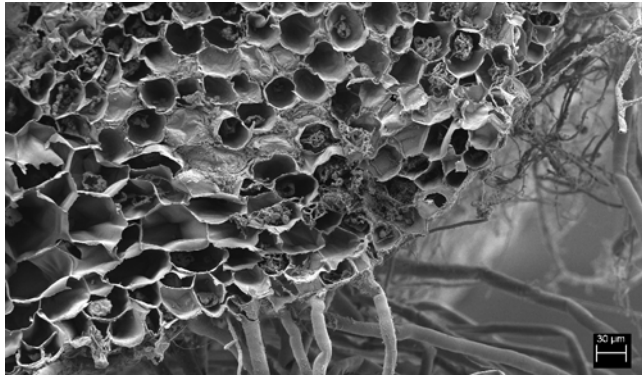


Figure 126. SEM of *Treubia* cross section showing the number of cells with resident fungi. Photo by Jeff Duckett and Silvia Pressel.

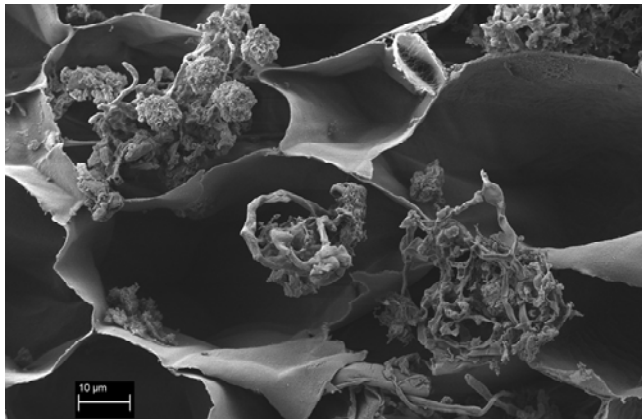


Figure 127. SEM of *Treubia* cross section with fungi in cells. Photo by Jeff Duckett and Silvia Pressel.

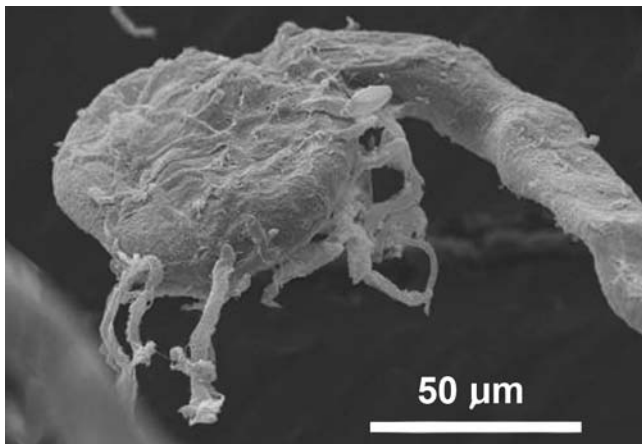


Figure 128. Swollen rhizoid tip with Ascomycota in leafy liverwort *Mylia anomala*. Photo by Pressel and Duckett.



Figure 129. *Sebacina incrustans*, member of a genus of basidiomycete fungi that is associated with leafy liverworts. Photo by James K. Lindsey.

We are at a very early stage in our understanding of mycorrhizae in bryophytes. In tracheophytes these associations permit the host plant to gain water and nutrients from a much wider area by accepting these from a fungus that has grown over a wide area, as much as 15 hectares, weighing 10,000 kg (Smith *et al.* 1992). Their role in bryophytes is less clear, but the ancient origin of this association suggests that by now it could be quite sophisticated and beneficial.

Protonema

The protonema stage of mosses is a delicate threadlike stage in which every cell is surrounded by air with the potential for creating desiccation. But is it really so delicate?

In experiments, Pressel and Duckett (2010) demonstrated that protonemata can survive slow drying but not fast drying. This suggests that during slow drying there is time to manufacture something that protects the cells from the effects of desiccation. Indeed, pre-treatment with abscisic acid permits the protonemata to survive fast drying as well. During slow dehydration the cells undergo profound changes, including vacuolar fragmentation, reorganization of endomembrane domains, changes in cell wall thickness, changes in plastid morphology, changes in mitochondria morphology, and a controlled dismantling of the cytoskeleton. During fast drying, these events do not occur or are incomplete. The abscisic acid permits the rapidly drying cells to partially mimic their behavior during slow drying, permitting them to survive.

Leafy Liverwort Gemmae

Liverworts have leaf gemmae that are usually small structures along the leaf margins. Germination on the leaf is not desirable, so it is no surprise that they have a means of preventing it. This prevention may relate to their hydrophobic surface (Duckett & Ligrone 1995). In *Odontoschisma denudatum* (Figure 130), the wall chemistry changes during maturation, with an increase in electron-opacity.

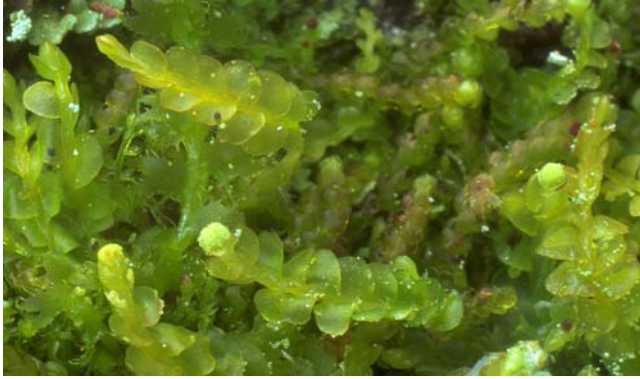


Figure 130. *Odontoschisma denudatum* with gemmae on apical leaves (yellowish). Photo by Jan-Peter Frahm.

Sporophyte

When we examine mature sporophytes with their capsules and spores, we don't give a second thought to the dangers of drying out. But we are misled by this resistant mature sporophyte. Rather, based on studies of field-collected gametophytes of *Microbryum starckeanum* (Figure 131) and *Tortula inermis* (Figure 132) (both species of dry habitats) with immature sporophytes, McLetchie and coworkers found that the sporophyte generation is more sensitive to desiccation and thermal stress than is the leafy gametophyte (McLetchie & Stark 2006; Stark *et al.* 2007). This may of course differ in species with a different phenology in different environmental conditions, but it bears questioning our perception of the importance of desiccation during sporophyte development. This need for desiccation tolerance of the sporophyte may be especially important for species like those of *Polytrichum* that require as much as 20 months for sporophyte development and span an entire year of weather conditions (Arnell 1905; Longton 1972).



Figure 131. *Microbryum starckeanum*, a species in which the sporophyte is more sensitive to desiccation than the gametophyte. Photo from BBS website.

It appears that the embryonic sporophytes are the stage most susceptible to desiccation stress (Stark 2002, 2005). Nevertheless, some desert mosses have embryonic sporophytes that can tolerate desiccation for long periods, most likely benefitting from **desiccation hardening** (development of resistance to desiccation) (Stark *et al.* 2014). Several examples exist from non-desert mosses, although the tie to desiccation is unclear. In the boreal forest moss *Hylocomium splendens* (Figure 122-Figure 123) (Callaghan *et al.* 1978) and desert moss *Syntrichia*

caninervis (Figure 18) (Stark *et al.* 2000), the number of aborted sporophytes outnumbers that of mature sporophytes. Similarly, in the boreal forest moss *Pleurozium schreberi* (Figure 133) 38% of the sporophytes aborted (Longton & Greene 1969).



Figure 132. *Tortula inermis* leaves and immature capsules, a species in which the young capsules are more sensitive to desiccation than the gametophytes. Photo by Michael Lüth.



Figure 133. *Pleurozium schreberi*, a boreal forest moss with a high percent of abortions. Photo by Michael Lüth.

Calyptra Protection

If we imagine the hairy calyptrae of such mosses as *Polytrichum* (Figure 134), we must ask ourselves how the calyptra avoids absorbing water and holding it against the capsule, creating water logging, or contrarily, draws water from the capsule due to the capillary spaces created by the hairs. In other words, why doesn't it behave like a bath towel? To answer this question, we will look at the calyptra development, timing, structure, and its ultimate role.



Figure 134. Hairy calyptra on capsule of *Polytrichum juniperinum*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

The **calyptra** develops from the archegonium, which expands as the embryo develops. In some cases, the calyptra falls early in capsule expansion, but in others, such as *Polytrichum*, it may remain until the spores are shed. One might then question the role of the calyptra in protecting the embryo through to development of spores. Budke *et al.* (2012) demonstrated that the maternal calyptra provides protection of early post-embryonic sporophytes against desiccation, but that later development of the capsule may incur cuticle development that protects as the capsule emerges from the calyptra. This demonstrates that the calyptra cannot be considered a vestigial structure, but rather that it is essential in preventing desiccation. Haig (2013) agrees that the presence of the calyptra delays the onset of transpiration. Hence, it is prudent to examine the calyptra characters that may provide this desiccation protection.

Cuticle: We have already discussed the presence of a 4-layered cuticle for the duration of the calyptra in *Funaria hygrometrica*. Budke *et al.* (2011, 2012, 2013) demonstrated that the cuticle on this calyptra conferred significant protection to the developing sporophyte.

Hairs: There appear to be two kinds of hairs on calyptrae, "true" hairs and undeveloped archegonia. In *Fontinalis*, the calyptral hairs develop from aborted archegonia whose eggs (Figure 135) were presumably not fertilized (Glime unpubl.). This results in a small number of hairs near the base of the calyptra.

The hairs on the calyptrae in taxa such as *Polytrichum* (Figure 134) and *Orthotrichum* (Figure 136) could function to prevent desiccation during early development or to deter herbivory both early and late in development, but earlier in development they could also serve important functions for the archegonium, helping to conserve moisture to protect the egg or other uses we haven't considered. I haven't followed the development in taxa other than *Fontinalis* (Figure 135), but the hairs seem too large and numerous in most taxa to be just a lingering of the archegonia or associated paraphyses. If they continue to elongate as the calyptra develops, then there may be some advantage that would favor that prolonged use of energy for their development.

Cuticle

It is likely that many bryophyte sporophytes have a **cuticle**. For example, the large, waxy-looking capsule of *Buxbaumia viridis* (Figure 137), and most likely the other members of the genus, has a layered cuticle (Koch *et al.* 2009). And in *B. viridis* this cuticle is waxy with massive wax layers having small embedded and superimposed platelets and granules on top of this complex. Although until recently the only documented sporophyte cuticles had been those of the **Polytrichales**, this complex of cuticle components is common in various groups of tracheophytes.

Pressel and Duckett (2011), suspecting that capsule waxes were more common than those of these two groups, examined a wider array of taxa, particularly those with shiny surfaces. They demonstrated that *Bartramia* (Figure 138), *Plagiopus* (Figure 139-Figure 140), and *Mnium* (Figure 141-Figure 143) invested as much in surface waxes of the capsule as did *Polytrichum*. They interpreted these waxes as having a role in preventing accumulated water

from depressing gas exchange in the capsules, that is, prevention of water logging.

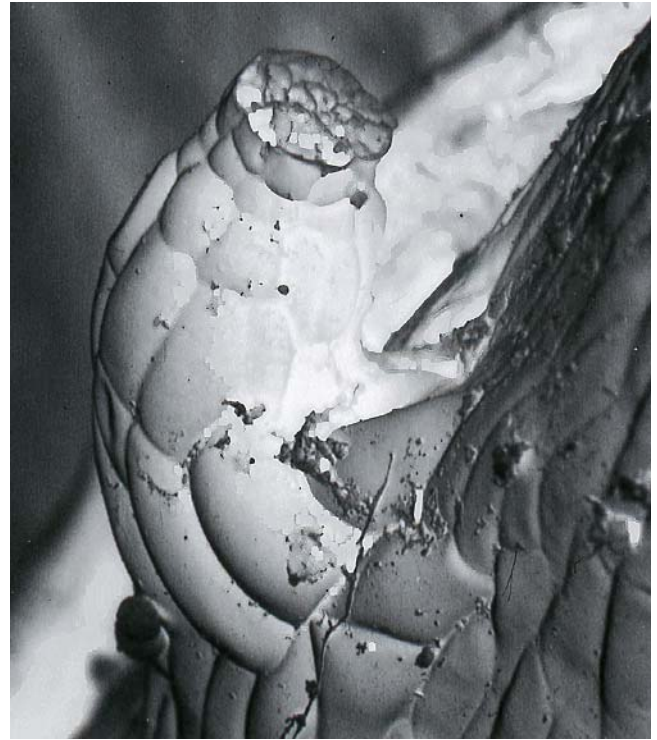


Figure 135. *Fontinalis squamosa* calyptra with young archegonium SEM. Photo by Janice Glime.



Figure 136. *Orthotrichum stramineum* with calyptra showing long hairs. Photo by Des Callaghan.



Figure 137. *Buxbaumia viridis* capsule showing shiny, waxy cuticle. Photo by Berndh through Wikimedia Commons.



Figure 138. *Bartramia pomiformis* capsule showing waxy surface. Photo by Walter Obermayer.



Figure 139. *Plagiopus oederiana* with capsules showing waxy surface. Photo by Michael Lüth.



Figure 140. *Plagiopus oederiana* waxy capsule with calyptra at near maturity. In this case, the calyptra does little to protect the nearly mature capsule, most likely making the cuticle more important. Photo by Janice Glime.



Figure 141. *Mnium* sp. with water on young capsules, illustrating the potential for water logging. Photo by Alan S. Heilman through Creative Commons.

In *Orthotrichum* many species have immersed stomata (Figure 142). These openings are surrounded by protruding cells that maintain an air space between the capsules and the calyptra (which remains attached and covers most of the capsule until the spores are ripe; Figure 136) (Pressel & Duckett 2011). The waxes repel the water on the capsule and prevent it from being drawn under the calyptra by capillary action. That is, a primary role for these surface waxes may be to prevent water logging in this and other species.

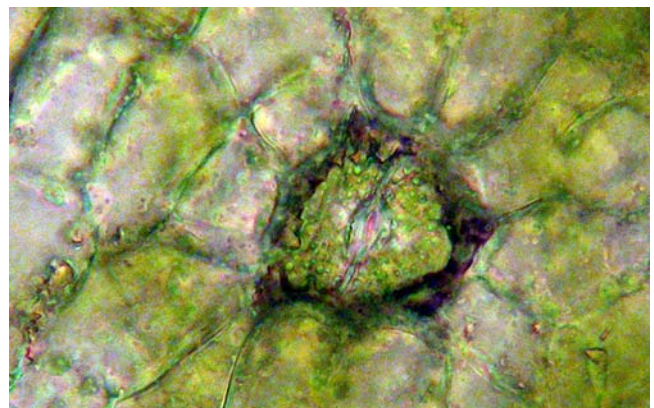


Figure 142. *Orthotrichum pusillum* immersed stoma on calyptra. Photo by Bob Klips.



Figure 143. *Mnium hornum* with capsule showing waxy surface. Photo by J. C. Schou.

But this cuticle story apparently does not begin with the capsule. The young sporophyte is covered by a calyptra. And in *Funaria hygrometrica* (Figure 144-Figure 147) this calyptra is covered by a waxy cuticle four layers thick at all stages, hence providing protection long before the developing sporophyte develops its own cuticle that ultimately arises on the sporangium (Budke *et al.* 2012). When the calyptra cuticle is removed during periods of low moisture, the sporophyte suffers significant damage, including decreased survival, increased tissue damage, incomplete sporophyte development, more peristome malformations, and decreased reproductive output (Budke *et al.* 2013). This is in contrast to the conclusion of Pressel and Duckett (2011) that the cuticles function primarily to prevent water logging. I have for my entire career as an ecologist failed to understand why ecologists get into so many arguments over two or more different explanations for the same thing, in this case the presence of stomata. There seems to me to be no evolutionary argument against multiple functions for the same thing, at the same or at different times. Just consider the many functions of our brains, or the many uses for fingernails.

Budke *et al.* (2012) examined the development of the cuticle on both the calyptra and the capsule, using *Funaria hygrometrica* (Figure 144-Figure 147) as a model organism. These researchers found that the sporophyte cuticle does not mature until the formation of the capsule.



Figure 144. *Funaria hygrometrica* with expanding archegonia (now calyptrae) with young sporophytes still mostly protected within the perichaetial leaves. Photo by Andrew Spink.



Figure 145. *Funaria hygrometrica* young sporophytes and calyptrae emerging from the protection of the perichaetial leaves. Photo by Michael Lüth.



Figure 146. *Funaria hygrometrica* mature capsules that have lost the calyptrae. Photo by Robert Klips.



Figure 147. *Funaria hygrometrica* mature capsule showing waxy surface. Photo by Sarah Gregg.

As among leaves, the capsule waxes vary in structure. In *Tetradontium brownianum* (Figure 148), there are fine rods around the stomata, whereas in *Pylaisia polyantha* (Figure 149) there are both rods and fine whorls (Pressel & Duckett 2011).



Figure 148. *Tetradontium brownianum*, a species with fine rods in the cuticle around the stomata of the capsules. Photo by Michael Lüth.



Figure 149. *Pylaisia polyantha* capsule, a species with both rods and fine whorls in the cuticle around the stomata. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

Peristome: Peristome teeth likewise have cuticles, with differences related to habitat conditions at the time of spore discharge (Pressel & Duckett 2011). In **Polytrichales**, the spores are dispersed when raindrops pounce on the diaphragm (**epiphragm**; Figure 150) that connects the teeth (Watson 1971). For this mechanism to work, the teeth must not only remain dry, but must repel water so that it does not block the small openings between the teeth where spores must exit (Pressel & Duckett 2011).



Figure 150. Top view of *Polytrichum* epiphragm showing the 64 adherent teeth. Water splashing on the membranous epiphragm (like a child on a trampoline) disperses the spores. Photo by George Shepherd Creative Commons.

On the other hand, most mosses disperse their spores when it is dry. Water is taken up and lost rapidly from between the ornamentation on these peristomes (Pressel & Duckett 2011). These include all **Bryopsida** they tested: *Amblystegium* (Figure 151), *Bryum* (Figure 98), *Coscinodon* (Figure 152), *Dicranella* (Figure 153), *Didymodon* (Figure 154), *Fissidens* (Figure 155), *Funaria* (Figure 156), *Grimmia* (Figure 77), *Hypnum* (Figure 157), *Mnium* (Figure 141-Figure 143), *Rhynchostegium* (Figure 158), *Schistidium* (Figure 72), *Syntrichia* (Figure 18), *Tortula* (Figure 1, Figure 132). These water gains and losses permit rapid closure in wet conditions and accelerate opening under dry conditions.



Figure 151. *Amblystegium serpens* capsules. Photo by Michael Lüth.

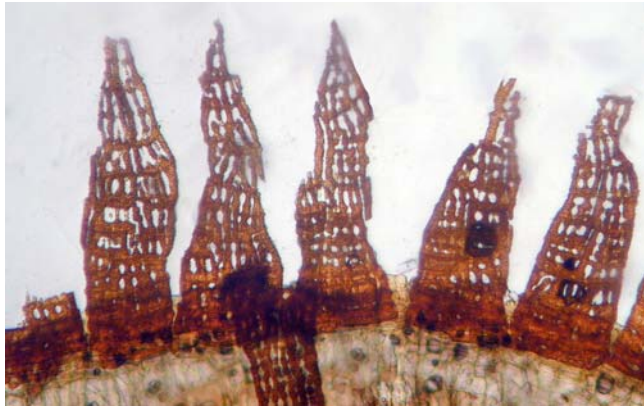


Figure 152. *Coscinodon cribrosus* peristome. Photo by Michael Lüth.



Figure 153. *Dicranella varia* capsules showing peristome. Photo by Kristian Peters through Wikimedia Commons.



Figure 154. *Didymodon rigidulus* with capsules. Photo by Michael Lüth.

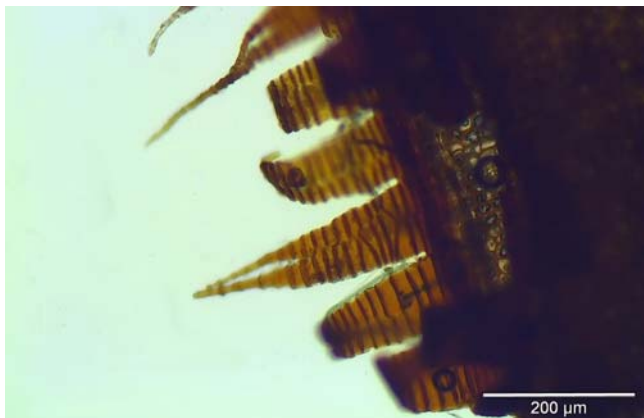


Figure 155. *Fissidens adianthoides* peristome. Photo by Kristian Peters.

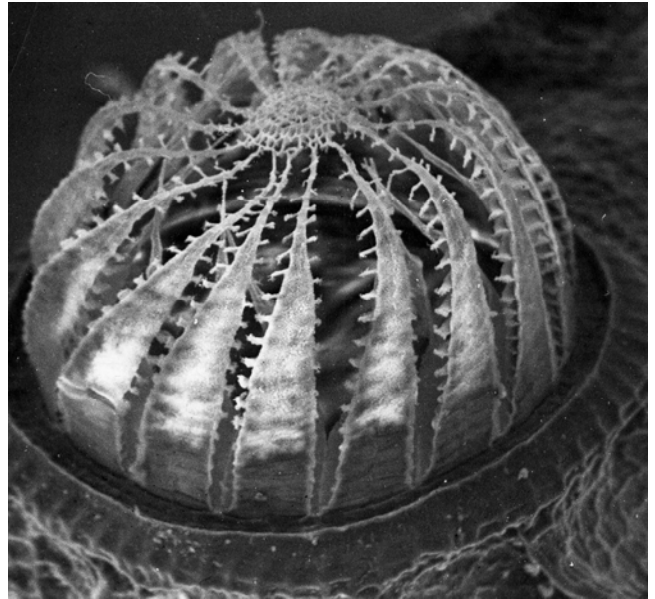


Figure 156. Peristome teeth of *Funaria hygrometrica*, a species in which teeth move in response to drying conditions and spores escape from the spaces between the teeth. Photo by George Shepherd.

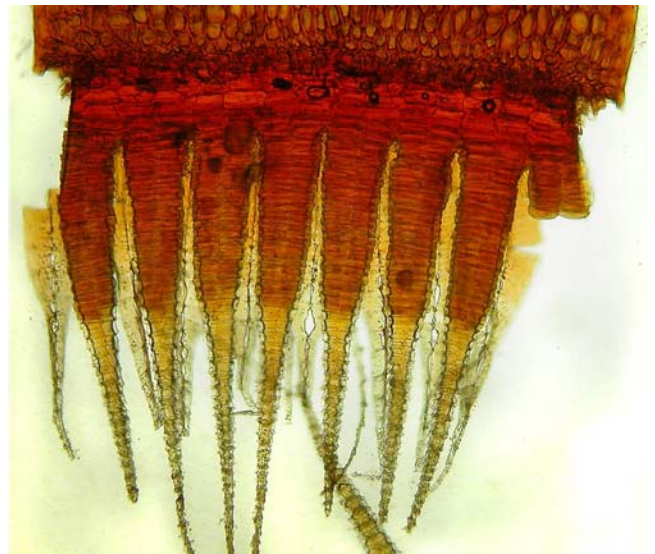


Figure 157. *Hypnum cupressiforme* peristome. Photo by Walter Obermayer.



Figure 158. *Rhynchostegium confertum* with capsules. Photo by Michael Lüth.

But what happens in capsules with no teeth or only rudimentary peristomes? As an example, in *Weissia* (Figure 159) water is prevented from entering the capsule by a highly water-repellent capsule rim (Figure 159). If water entered the capsule, it could cause premature germination or interfere with ultimate dispersal.



Figure 159. *Weissia fallax* capsule showing rudimentary peristome. Note the waxy appearance of the reddish annulus around the teeth. Photo by Michael Lüth.

Guard Cells and Stomata

Capsules of many (most?) mosses have guard cells and stomata. The guard cells usually resemble those of tracheophytes, having a doughnut shape, and surrounding the **stoma** (opening). These are mostly located at the base of the capsule. In addition to the cuticle, we might expect the **guard cells** to play a role in water relations of the capsule. After all, the stomata and guard cells have existed through 400 million years of land plant evolution (Chater *et al.* 2011).

Like the cuticle, the role of the pores and stomata has been overlooked in bryophytes. Although we have known about the stomata in moss capsules for a long time, and used them as taxonomic characters in genera such as *Orthotrichum*, we have largely ignored their function, failing even to ask what it might be.

When thinking about adaptations to drought, we usually think of the survival of the gametophyte. What danger could there be to a dry capsule full of spores, right? But before that capsule is full of spores, it is a photosynthetic body in need of water. Perhaps the young seta with no capsule has little problem, but once the capsule starts to differentiate, water needs most likely increase dramatically. And once meiosis begins, water needs are critical. An interruption during meiosis could lead to a variety of anomalies, many of which could cause spore death.

Paton and Pearce (1957) reviewed the early literature on stomata in bryophytes, pointing out that in *Sphagnum* they do not mature. In fact, the capsule pores of *Sphagnum* are considered **pseudostomata**. Their function seems to be limited, facilitating capsule dehydration, shape change, and dehiscence (Duckett *et al.* 2009; Merced 2015). This is not surprising, because in *Sphagnum*, the seta is only a few cells high. Instead, the capsule is elevated on a **pseudopodium** that is developed from the gametophyte. This pseudopodium does not extend until the

capsule is mature. Hence, the role of the pseudostomata to create a transpiration stream for nutrient transport would seem futile. Rather, Duckett and coworkers (2009) provide evidence that the pseudostomata remain open when the capsule is mature, causing the capsule to dry and shrink, forcing the spores out.

Stomata also are absent in the liverworts (thallus pores excepted), present in at least some hornworts, and absent in the moss order **Andreaeales** (Figure 160-Figure 161) (Paton & Pearce 1957). As in the tracheophytes, the number of guard cells associated with a stoma is usually two. Known exceptions (single circular guard cells) occur in **Funariaceae** (Figure 144-Figure 147) and *Buxbaumia aphylla* (Figure 162). Larger numbers of guard cells (3-4) occur but do not seem to be consistent in any single taxon and are thus considered an anomaly.

The walls of the guard cells are strongly cuticularized (Paton & Pearce 1957). The number of stomata in capsules that have been examined varies from 4 to over 200. Species with a long seta generally have more stomata than species with a short seta or immersed capsules. This supports the hypothesis that they are needed to provide an adequate transpiration stream to transport nutrients from the leafy gametophyte to the sporophyte capsule (Haig 2013).



Figure 160. *Andreaea rothii* with capsules that have no stomata. Photo by Jan-Peter Frahm.

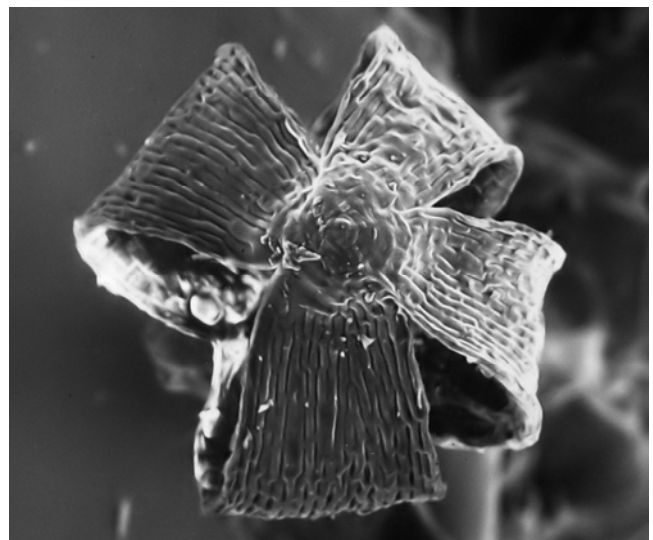


Figure 161. *Andreaea* capsule SEM, a capsule that lacks stomata. Photo by George Shepherd through Creative Commons.

Guard cells are usually located at the base of the capsule. In reality, they tend to be located below the area covered by the calyptra, where gas exchange and water loss are possible. This is consistent with a role to permit water loss, but could they also serve in gas exchange? It appeared that the capsule guard cells did not respond to changes in humidity (Copeland (1902). Rather, they are only able to close when the sporophyte is dehydrated or reopen when it is remoistened. This is consistent with their potential role in bringing nutrients upward.

In the moss *Physcomitrella patens* (Figure 163-Figure 164), the stomata of the sporophytes do indeed respond to environmental signals with the hormone abscisic acid (ABA) serving as a signalling component. In fact, the genes controlling ABA in *P. patens* can be moved to mutant *Arabidopsis thaliana* (flowering plant) that has lost its ABA-regulatory gene and cause stomata in that plant to behave normally. When *P. patens* mutants lack the ABA regulatory gene, the response to ABA is greatly reduced.



Figure 162. *Buxbaumia aphylla* capsules, a species with single circular guard cells. Photo by Štěpán Koval.

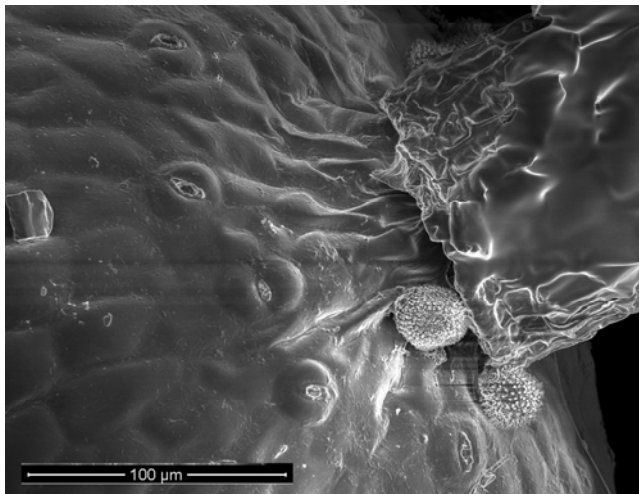


Figure 163. *Physcomitrella patens* capsule stomata SEM. Photo by Jeff Duckett and Silvia Pressel.

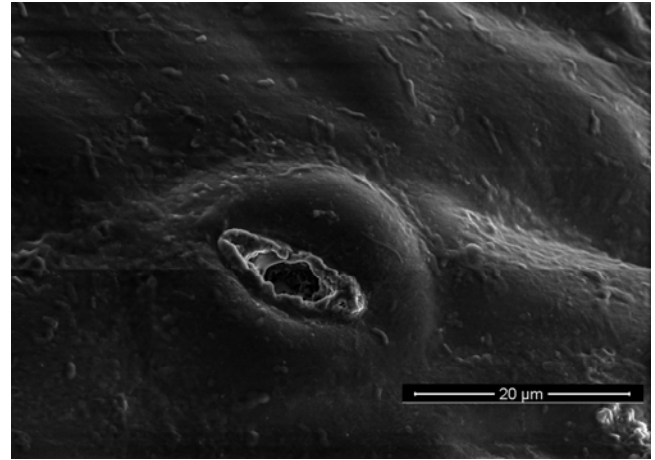


Figure 164. SEM of *Physcomitrella patens* stomata. Photo by Jeff Duckett and Silvia Pressel.

But wait! While ABA may affect guard cell closure in *Physcomitrella patens* (Figure 164), it appears that the guard cells in mosses have a somewhat different function. First of all, there seems to be no potassium-regulating mechanism (Duckett *et al.* 2010a). Instead, their primary role seems to be to permit water to escape when the capsule is mature (Boudier 1988; Beerling & Franks 2009; Duckett *et al.* 2009, 2010b). This loss of water causes the capsule to become distorted enough to force the rather stiff circular cap (**operculum**) to pop off.

It appears that the stomata endow the capsule with multiple advantages. Loss of water during development could be important to create a transpiration stream that moves nutrients upward from the gametophyte to the capsule of the sporophyte (Haig 2013). If this interpretation is correct, the water loss is essential to maintain continuous movement of water and associated nutrients upward. In fact, Haig interprets the elevation of the capsule on an elongated seta to be an adaptation that increases the movement of water by placing the capsule into the zone of turbulent air above the quiet boundary layer. The placement of the stomata at the base of the capsule gives them exposure while the calyptra reduces water loss from the part of the capsule where spores are developing.

Ziegler (1987) pointed out that in some mosses the sporophyte guard cells have thick walls and do not open and close. This type of guard cell occurs in species that have reduced photosynthetic tissue in the capsule and have been considered evolutionarily reduced. Bryophyte guard cells also differ from those of tracheophytes in that they are larger than the surrounding cells, whereas in tracheophytes they are smaller.

Paton and Pearce (1957) found that the stomata become functionless at a relatively early stage in capsule development, suggesting that this loss in function protects the developing spores against desiccation. They were able to demonstrate this early loss of function in the hornwort *Anthoceros* (Figure 165-Figure 166) and in mosses in the **Bryales**. Based on their studies on the hornwort *Phaeoceros*, Duckett and Ligrone (2003) say no to the function of capsule guard cells in gas exchange, at least in hornworts; they could find no response to moisture changes or to ABA in the hornwort *Phaeoceros* stomata (Figure 167).



Figure 165. *Anthoceros agrestis* with capsules. Photo by Michael Lüth.

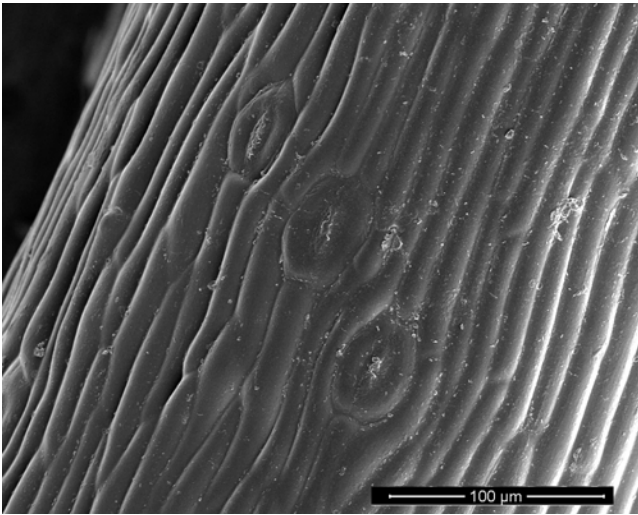


Figure 166. *Anthoceros punctatus* SEM image of sporophyte showing stomata. Photo by Jeff Duckett and Silvia Pressel.

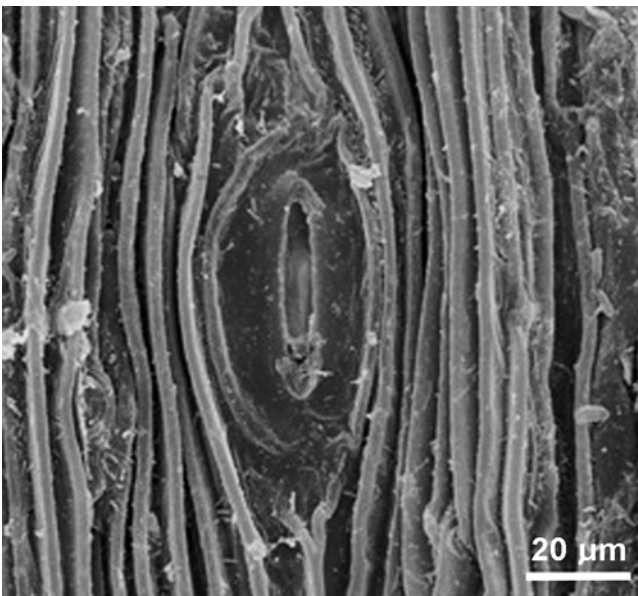


Figure 167. *Phaeoceros laevis*, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo by Jeff Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel.

On the other hand, in greenhouse-grown *Funaria hygrometrica* (Figure 168) the stomata (Figure 169) open on the fourth day of capsule expansion (Garner & Paolillo 1973). By the fifth day, continuing through the tenth day, they close in darkness and reopen in light. They also can be closed by the application of abscisic acid (ABA) (Garner & Paolillo 1973; Chater *et al.* 2011). Thus far we have no evidence to demonstrate the usefulness of this opening and closing. It could enhance gas exchange; it could control water loss during the critical stages of meiosis; and it could serve as a transpiration stream to bring nutrients from the gametophyte. And the function could change or disappear at maturity.



Figure 168. *Funaria hygrometrica* capsules. Photo by Li Zhang.

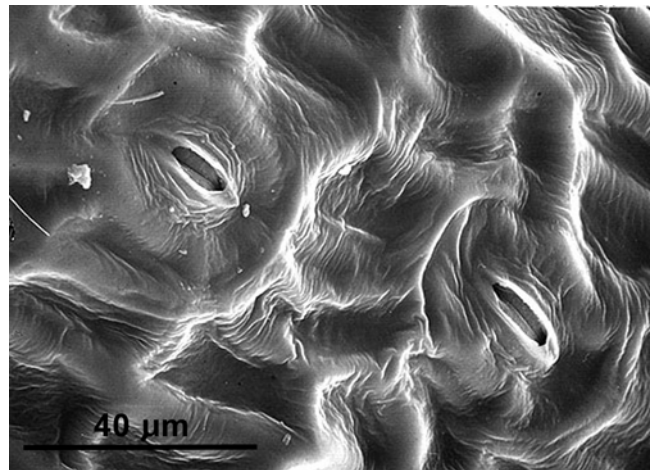


Figure 169. *Funaria hygrometrica* stomata. Photo by Jeff Duckett and Silvia Pressel.

Indeed it appears that the function changes as the *Funaria hygrometrica* (Figure 168) capsule ripens. As maturity approaches, the stomatal responsiveness declines and about half the stomata remain open day and night (Garner & Paolillo 1973)! Furthermore, more stomata become exposed when the calyptra is shed (Duckett *et al.* 2009, 2010a). The stomata no longer provide a mechanism to conserve water.

Further complicating our interpretation of stomatal function during capsule development is the apparent lack of relationship between the presence of stomata and habitat. In the liverworts, stomata are totally absent. But liverworts produce mature capsules before elongation of the stalk occurs, negating the necessity for long distance

translocation of nutrients and being consistent with the observations of Paton and Pearce (1957) that fewer stomata occurred on moss capsules with short or absent setae than on those with emergent, longer setae. The widespread absence of stomata in at least some species among so many moss taxa [e.g. *Atrichum*, *Pogonatum*, *Acaulon* (**Error! Reference source not found.**), *Campylopus* (Figure 170), *Leucobryum*, *Cinclidotus* (Figure 171), *Discelium*, *Nanomitrium*, *Tetraphis*, *Catoscopium*, *Fontinalis* (Figure 172), *Leucodon*, *Cyclodictyon*) (Paton & Pearce 1957)] suggests they are not essential for gas exchange. Furthermore, since most of these genera have long setae, one could argue against their function in creating a transpiration stream for nutrient transport. One might also argue that the well developed vascular tissue in both gametophytes and sporophyte setae of the **Polytrichaceae** makes the presence of stomata to create a transpiration stream unnecessary for nutrient transport, yet some members of the family have stomata and guard cells. And the stomata in tracheophytes are certainly necessary to maintain function of the xylem tissue in these larger plants.



Figure 170. *Campylopus nivalis* capsules, a species that lacks stomata. Photo by Michael Lüth.



Figure 171. *Cinclidotus fontinaloides*, a species that lacks stomata. Photo by Michael Lüth.



Figure 172. *Fontinalis squamosa* var. *curnowii* with capsules, a species that lacks stomata. Photo by David Holyoak.

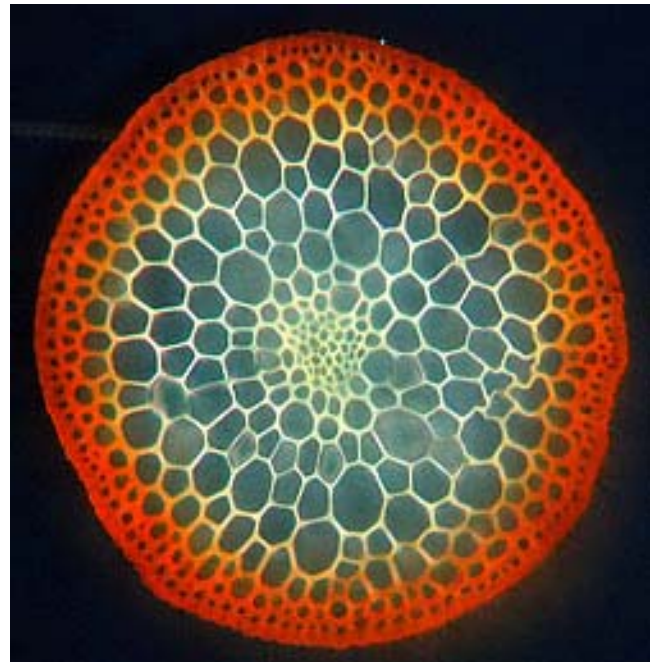


Figure 173. *Plagiomnium undulatum* seta cs showing central conducting strand. Photo by Norbert J. Stapper.

Merced and Renzaglia (2013) demonstrated the remarkable similarity between stomata in the highly developed *Oedipodium* (Figure 174) and the very reduced *Ephemerum* (Figure 175) capsules. The capsule structure differs, with *Oedipodium* having extensive spongy tissue along the capsule apophysis where stomata are concentrated and *Ephemerum* lacks such tissue but has minimal substomatal cavities. Although *Oedipodium* (Figure 174) has numerous long-pored stomata and *Ephemerum* has few round-pored stomata, the stomatal ultrastructure and wall thickenings of these two taxa are quite similar. Both have sporophytes with a cuticle that is thicker on the guard cells and extends on the walls surrounding the stomata. When the capsules are older, epicuticular waxes and pectin clog the pores, closing them much like the stomata of fir trees in winter. Merced and Renzaglia argue that the cuticle, water-conducting cells, and spongy tissues of *Oedipodium* all support the role of stomata in facilitating gas exchange and water transport as

the sporophyte develops. They also contend that the existence of stomata exclusively on capsules may indicate a function in drying and dispersal of spores.

Hence, we have four potential functions for the stomata of capsules. These include a role in creating a transpiration stream to aid in nutrient transport, prevention of water logging that inhibits gas exchange, regulation of gas exchange, and drying that contracts the capsule and aids in spore expulsion.



Figure 174. *Oedipodium griffithianum* with young capsules, a species with a well developed spongy apophysis and many stomata. Photo by Des Callaghan.



Figure 175. *Ephemerum recurvifolium* with capsules, a moss that lacks a spongy apophysis and has few stomata. Photo by Tomas Hallingback.

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, ventral scales, cuticles, and stomata** aid in moving water, facilitating entry, or reducing loss.

Thallose liverworts benefit from ventral transport by rhizoids and scales. The dorsal surface is covered by a cuticle but gas exchange may occur through pores overlying photosynthetic chambers. The pores are ringed by cells with cuticular ridges that prevent water drops from entering but that allow water vapor to escape. Midribs may help to gather and direct water both externally and internally. For many taxa, dormancy is a "last resort" to avoid the effects of desiccation. Fungal partners occur in both thallose and leafy liverworts, but their role is not known. Smooth rhizoids facilitate fungal entry; pegged rhizoids transport water and the pegs prevent collapse upon drying.

In mosses and leafy liverworts, growth form can help in both movement and conservation of water. Clumps reduce transpiration and provide additional capillary spaces. Mixed species can help each other, especially if one is good at moving water and one is good at retaining it. Mosses may have a central strand where water moves, but this is apparently absent in all liverworts except the **Haplomitriopsida**. Leaf cuticles

occur in both mosses and liverworts and may repel water to avoid water logging or reduce loss by transpiration. **Rhizoids** and **tomentum** help in the movement of water upward. **Mucilage** in some liverworts, especially **Haplomitriopsida**, can be of great value in holding water about the plants.

The protonema can usually withstand slow drying. Like the guard cells in some stomata, it is responsive to **ABA**. ABA may be linked to **inducible desiccation tolerance** in the gametophores. **Constitutive desiccation tolerance** is the most common form of desiccation tolerance in bryophytes, but as the plants age they may switch to inducible desiccation tolerance. **Hardening** can occur following slow drying and may last more than a few days.

The sporophyte and calyptra both have **cuticles**, and at least in *Funaria hygrometrica*, the cuticle in the calyptra matures first, helping the calyptra to protect the young embryo. Calyptra hairs, thallus hairs, paraphyllia, and paraphyses all function to help in movement of water and reduce rate of drying. Capillary spaces provided by these can further facilitate absorbing and holding water, bathing the tissues in water and reducing water loss.

The sporophytes of most(?) mosses and hornworts have **guard cells** and **stomata** that cease to function at sporophyte maturity. Their function(s) are ambiguous, but they may contribute to creating a transpiration stream to move nutrients upward, regulating capsule hydration during development, and drying the capsule prior to dehiscence and dispersal.

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Literature Cited

- Alpert, P. 1979. Desiccation of desert mosses following a summer rainstorm. *Bryologist* 82: 65-71.
- Alpert, P. 1982. Poikilohydry and desiccation tolerance in some xerophytic mosses. Ph. D. Dissertation, Harvard University, Cambridge, pp. 19-31.
- Alpert, P. 1985. Distribution quantified by microtopography in an assemblage of saxicolous mosses. *Vegetatio* 64: 131-139.
- Alpert, P. 2000. The discovery, scope, and puzzle of desiccation tolerance in plants. *Plant Ecol.* 151: 5-17.
- Alpert, P. and Oechel, W. A. 1985. Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. *Ecology* 66: 660-669.
- Alpert, P. and Oechel, W. C. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. *Amer. J. Bot.* 74: 1787-1796.
- Alpert, P. and Oliver, M. J. 2002. Drying without dying. In: Black, M. and Pritchard, H. W. (eds.). *Desiccation and survival in plants: Drying without dying*. CABI Publishing, Wallingford, pp. 3-43.
- Arnell, H. W. 1905. Phaenological observations on mosses. *Bryologist* 8: 41-44.
- Beerling, D. J. and Franks, P. J. 2009. Evolution of stomatal function in 'lower' land plants. *New Phytol.* 183: 921-925.
- Berthier, J., Bonnot, E.-J., Fabre, M.-C., and Héban, C. 1974. L'appare sécréteur des Bryales: Données morphologiques, ultrastructurales et cytochimiques. *Bull. Soc. Bot. France* 121(Suppl. Coll. Bryol.): 97-100.
- Bewley, J. D. 1974. Protein synthesis and polyribosome stability upon desiccation of the aquatic moss *Hygrohypnum luridum*. *Can. J. Bot.* 52: 423-427.
- Boudier, P. 1988. Différenciation structurale de l'épiderme du sporogone chez *Sphagnum fimbriatum* Wilson. [Structural differentiation of the epiderm of the sporogone of *Sphagnum fimbriatum* Wilson]. *Ann. Sci. Nat. Bot.* 13(8): 143-156.
- Bowen, E. J. 1935. A note on the conduction of water in *Fimbriaria blumeana*. *Ann. Bot.* 49: 844-848.
- Brockington, S., Glover, B., Duckett, J. G., and Pressel, S. 2013. The cuticle in *Marchantia*: An overlooked innovation in land plants. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.
- Budke, J. M., Goffinet, B., and Jones, C. S. 2011. A hundred-year-old question: Is the moss calyptra covered by a cuticle? A case study of *Funaria hygrometrica*. *Ann. Bot.* 107: 1279-1286.
- Budke, J. M., Goffinet, B. and Jones, C. S. 2012. The cuticle on the gametophyte calyptra matures before the sporophyte cuticle in the moss *Funaria hygrometrica* (Funariaceae). *Amer. J. Bot.* 99: 14-22.
- Budke, J. M., Goffinet, B., and Jones, C. S. 2013. Dehydration protection provided by a maternal cuticle improves offspring fitness in the moss *Funaria hygrometrica*. *Ann. Bot.* 111: 781-789.
- Buryová, B. and Shaw, A. J. 2005. Phenotypic plasticity in *Philonotis fontana* (Bryopsida: Bartramiaceae). *J. Bryol.* 27: 13-22.
- Callaghan, T. V., Collins, N. J., and Callaghan, C. H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. *Oikos* 31: 73-88.
- Canny, M. J. 2001a. Contributions to the debate on water transport. *Amer. J. Bot.* 88: 43-46.
- Canny, M. J. 2001b. Embolisms and refilling in the maize leaf lamina, and the role of the protoxylem lacuna. *Amer. J. Bot.* 88: 47-51.
- Chater, C., Kamisugi, Y., Movahedi, M., Fleming, A., Cumming, A. C., Gray, J. E., and Beerling, D. J. 2011. Regulatory mechanism controlling stomatal behavior conserved across 400 million years of land plant evolution. *Curr. Biol.* 21: 1025-1029.
- Clausen, E. 1952. Hepatics and humidity, a study of the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. *Dansk Bot. Ark.* 15: 5-80.
- Clausen, E. 1964. The tolerance of hepatics to desiccation and temperature. *Bryologist* 67: 411-417.
- Clee, D. A. 1943. The morphology and anatomy of *Fegatella conica* in relation to the mechanism of absorption and conduction of water. *Ann. Bot. N. S.* 7: 185-193.
- Cook, M. E. and Graham, L. E. 1998. Structural similarities between surface layers of selected charophycean algae and bryophytes and the cuticles of vascular plants. *Internat. J. Plant Sci.* 159: 780-787.

- Copeland, E. B. 1902. Mechanism of stomata. *Ann. Bot.* London 16: 327.
- Crandall-Stotler, B. 2014. Bryophytes. Accessed 14 March 2015 at <<http://bryophytes.plant.siu.edu/bryojustified.html>>.
- Daniels, A. E. D. 1998. Ecological adaptations of some bryophytes of the Western Ghats. *J. Ecobiol.* 10(4): 261-270.
- Daniels, R. E. 1989. Adaptation and variation in bog mosses. *Plants Today* 2(4): 139-144.
- Davy, V. A. de. 1927. L'action du Milieu sur les Mousses. *Rev. Gen. de Bot.* 39: 711-726.
- Dhindsa, R. S. and Bewley, J. D. 1976. Plant desiccation: Polysome loss not due to ribonuclease. *Science* 191: 181-182.
- Dilks, T. J. K. and Proctor, M. C. F. 1974. The pattern of recovery of bryophytes after desiccation. *J. Bryol.* 8: 97-115.
- Dilks, T. J. K. and Proctor, M. C. F. 1979. Photosynthesis, respiration and water content in bryophytes. *New Phytol.* 82: 97-114.
- Duckett, J. G. and Ligrone, R. 1995. The formation of catenate foliar gemmae and the origin of oil bodies in the liverwort *Odontoschisma denudatum* (Mart.) Dum. (Jungermanniales): A light and electron microscope study. *Ann. Bot.* 76: 405-419.
- Duckett, J. G. and Ligrone, R. 2003. What we couldn't have done if we'd stayed in Europe: Selection and serendipity in the Southern Hemisphere! *Bull. Brit. Bryol. Soc.* 80: 19-21.
- Duckett, J. G. and Pressel, S. 2009. Extraordinary features of the reproductive biology of *Marchantia* at Thursley NNR. *Field Bryol.* 97: 2-11.
- Duckett, J. G., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. S. 2009. Exploding a myth: The capsule dehiscence mechanism and the function of pseudostomata in *Sphagnum*. *New Phytol.* 183: 1053-1063.
- Duckett, J., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. 2010a. The function and evolution of stomata in bryophytes. *Field Bryol.* 101: 38-40.
- Duckett, J., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. 2010b. The *Sphagnum* air-gun mechanism resurrected? Not with a closer look. *New Phytol.* 185: 889-891.
- Duckett, J. G., Ligrone, R., Renzaglia, K. S., and Pressel, S. 2013. Pegged and smooth rhizoids in complex thalloid liverworts (Marchantiopsida): Structure, function and evolution. *Bot. J. Linn. Soc. London* (In press).
- Frey, W. and Kürschner, H. 1991. Morphologische und anatomische Anpassungen der Arten in terrestrischen Bryophytengesellschaften entlang eines ökologischen Gradienten in der Judäischen Wüste. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 112: 529-552.
- Garner, D. L. B. and Paolillo, D. J. Jr. 1973. On the functioning of stomates in *Funaria*. *Bryologist* 76: 423-427.
- Giordano, S., Castaldo Cobianchi, R., Basile, A., and Spagnuolo, V. 1989. The structure and role of hyaline parenchyma in the liverwort *Lunularia cruciata* (L.) Dum. *Giornale Botanico Italiano* 123: 169-176.
- Glime, J. M. 1971. Response of two species of *Fontinalis* to isolation from stream water. *Bryologist* 74: 383-386.
- Glime, J. M. 1987. Temperature optima of *Fontinalis novae-angliae*: Implications for its distribution. *Symp. Biol. Hung.* 35: 569-576.
- Glime, J. M. and Carr, R. E. 1974. Temperature survival of *Fontinalis novae-angliae* Sull. *Bryologist* 77: 17-22.
- Goebel, K. 1905. Organography of Plants. Part II. Special Organography. Translation by I. B. Balfour. Clarendon Press, Oxford.
- Haig, D. 2013. Filial mistletoes: The functional morphology of moss sporophytes. *Ann. Bot.* 111: 337-345.
- Hébant, C. 1973. Diversity of structure of the water-conducting elements in liverworts and mosses. *J. Hattori Bot. Lab.* 37: 229-234.
- Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Lehre, Germany, 157 pp. + 80 Plates.
- Hedenäs, L. 2001. Environmental factors potentially affecting character states in pleurocarpous mosses. *Bryologist* 104: 72-91.
- Heegaard, E. 1997. Morphological variation within *Andreaea blyttii* in relation to the environment on Hardangervidda, western Norway: A quantitative analysis. *Bryologist* 100: 308-323.
- Higuchi, M. and Imura, S. 1987. The effect of submersion on moss rhizoid characters. *Hikobia* 10: 59-63.
- Jedrejko, K. and Ziober, A. 1992. The bryophytes of chosen caves on the Krakow-Wielun upland and its relation to microclimate conditions and ecological differentiation of habitats. *Ziemia Czeszochowska* 18: 107-151.
- Johnson, A. and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. *Bryologist* 73: 682-686.
- Kamerling, Z. 1897. Zur Biologie und Physiologie der Marchantiaceen. *Flora* 84: 1-68.
- Kappen, L., Lange, O. L., Schulze, E. D., Evenari, M., and Buschbom, U. 1979. Ecophysiological investigations on lichens of the Negev desert. 6. Annual course of photosynthetic production of *Ramalina maciformis* (Del.) Bory. *Flora Jena* 168: 85-108.
- Klepper, B. 1963. Water relations of *Dicranum scoparium*. *Bryologist* 66: 41-54.
- Kny, L. 1890. Bau und Entwicklung von *Marchantia polymorpha*. Parey, Berlin.
- Koch, K., Frahm, J.-P., and Pollawatn, R. 2009. The cuticle of the *Buxbaumia viridis* sporophyte. *Flora* 204: 34-39.
- Koster, K. L., Balsamo, R. A., Espinoza, C., and Oliver, M. J. 2010. Desiccation sensitivity and tolerance in the moss *Physcomitrella patens*: Assessing limits and damage. *Plant Growth Reg.* 62: 293-302.
- Kürschner, H. K. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. *Turk. J. Bot.* 28: 73-84.
- Lakatos, M. 2011. Lichens and bryophytes: Habitats and species. *Ecol. Stud.* 215: 65-87.
- Lange, O. L. 1969. CO₂-Gaswechsel von Moosen nach Wasserdampfaufnahme aus dem Luftraum. *Planta (Berlin)* 89: 90-94.
- Lepp, Heino. 2008. Thallose liverworts. Australian National Museum. Accessed 4 March 2015 at <<https://www.anbg.gov.au/bryophyte/liverwort-thalose.html>>.
- Li, Y., Glime, J. M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. *J. Bryol.* 17: 59-70.
- Ligrone, R., Duckett, J. G., and Renzaglia, K. S. 2000. Conducting tissues and phyletic relationships of bryophytes. *Philosoph. Trans. Royal Soc. B* 355: 795-814.
- Lodge, E. 1959. Effects of certain cultivation treatments on the morphology of some British species of *Drepanocladus*. *J. Linn. Soc. Bot.* 56: 218-224.

- Longton, R. E. 1972. Reproduction of Antarctic mosses in the genera *Polytrichum* and *Psilopilum* with particular reference to temperature. *Brit. Antarct. Surv. Bull.* 27: 51-96.
- Longton, R. E. 1988. Adaptations and strategies of polar bryophytes. *J. Linn. Soc. Bot.* 98: 253-268.
- Longton, R. E. and Greene, S. W. 1969. Relationship between sex distribution and sporophyte production in *Pleurozium schreberi* (Brid.) Mitt. *Ann. Bot.* 33: 107-126.
- Mägdefrau, K. 1973. *Hydropogon fontinaloides* (Hook.) Brid., ein periodisch hydro-aerophytisches Laubmoos des Orinocos und Amazonas. *Herzogia* 3: 141-149.
- Maier-Maercker, U. 1982. Accumulation of 86Rb and 43K ions in the cells surrounding the air pores of *Conocephalum conicum*. *Zeits. Pflanzenphysiol.* 105: 92-102.
- Malta, N. 1921. Versuch über die Widerstandsfähigkeit der Moose gegen Austrocknung. *Latv. Univ. Raksti* 1: 125-129.
- McConaha, M. 1939. Ventral surface specializations of *Conocephalum conicum*. *Amer. J. Bot.* 26: 353-355.
- McConaha, M. 1941. Ventral structures effecting capillarity in the Marchantiales. *Amer. J. Bot.* 28: 301-306.
- McLetchie, D. N. and Stark, L. R. 2006. Sporophyte and gametophyte generations differ in their thermotolerance response in the moss *Microbryum*. *Ann. Bot.* 97: 505-511.
- Merced, A. 2015. Novel insights on the structure and composition of pseudostomata of *Sphagnum*. *Amer. J. Bot.* 102: 329-335.
- Merced, A. and Renzaglia, K. S. 2013. Moss stomata in highly elaborated *Oedipodium* (Oedipodiaceae) and highly reduced *Ephemerum* (Pottiaceae) sporophytes are remarkably similar. *Amer. J. Bot.* 100: 2318-2327.
- Morton, M. R. 1977. Ecological studies of grassland bryophytes. Ph. D. Thesis, University of London.
- Nörr, M. 1974. Trockenresistenz bei Moosen. *Flora Jena* 163: 371-378.
- Odu, E. A. 1978. The adaptive importance of moss rhizoids for attachment to the substratum. *J. Bryol.* 10: 163-181.
- Oliver, M. J. and Bewley, J. D. 1984. Desiccation and ultrastructure in bryophytes. *Advances in Bryology* 2: 91-131.
- Oliver, M. J., Wood, A. J., and O'Mahony, P. 1998. "To dryness and beyond" – preparation for the dried state and rehydration in vegetative desiccation-tolerant plants. *Plant Growth Reg.* 24: 193-201.
- Oliver, M. J., Velten, J., and Mishler, B. D. 2005. Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats. *Integr. Compar. Biol.* 45: 788-799.
- Patidar, K. C. 1988. Morphological variation of two isolated geographical field populations of *Asterella angusta* (Steph.) Kachroo. *Yushania* 5(1): 7-18.
- Paton, J. A. and Pearce, J. V. 1957. The occurrence, structure and functions of the stomata in British bryophytes. *Trans. Brit. Bryol. Soc.* 3: 228-259.
- Penman, H. L. 1948. Natural evaporation from open water, bare soil and grass. *Proc. Roy. Soc. London A* 194: 120-145.
- Pressel, S. 2007. Experimental Studies of Bryophyte Cell Biology, Conservation, Physiology and Systematics. Ph.D. Dissertation. University of London, London.
- Pressel, S. and Duckett, J. G. 2010. Cytological insights into the desiccation biology of a model system: Moss protonemata. *New Phytol.* 185: 944-963.
- Pressel, S. and Duckett, J. 2011. Bryophyte surfaces; New functional perspectives from Cryo-Scanning Electron Microscopy. *Field Bryol.* 104: 50-53.
- Pressel, S., Davis, E. C., Ligrone, R., and Duckett, J. G. 2008a. An ascomycetous endophyte induces branching and septation of the rhizoids in the leafy liverwort family the Schistochilaceae (Jungermannniidae, Hepaticopsida). *Amer. J. Bot.* 95: 531-541.
- Pressel, S., Ligrone, R., and Duckett, J. G. 2008b. Cellular differentiation in moss protonemata: A morphological and experimental study. *Ann. Bot.* 102: 227-245.
- Pressel, S., Ligrone, R., and Duckett, J. G. 2008c. Chapter Six: The ascomycete *Rhizoscyphus ericae* elicits a range of host responses in the rhizoids of leafy liverworts: An experimental and cytological analysis. *Field. Bot.* 47: 59-72.
- Pressel, S., Bidartondo, M. I., Ligrone, R., and Duckett, J. G. 2010. Fungal symbioses in bryophytes: New insights in the twenty-first century. *Phytotaxa* 9: 238-253.
- Pressel, S., Duckett, J. G., and Bidartondo, M. I. 2012. Liverwort fungal interactions; the dawn of mycotrophism. *Field Bryol.* 107: 38-39.
- Proctor, M. C. F. 1979. Structure and eco-physiological adaptations in bryophytes. In: Clarke, G. C. S. and Duckett, J. G. (eds.). *Bryophyte Systematics, Systematic Association special volume 14*, Academic Press, London, pp. 479-509.
- Proctor, M. C. F. 1980. Diffusion resistances in bryophytes. In: Ford, E. D., and Grace, J. (eds.). *Plants and their Atmospheric Environment. Symp. Brit. Ecol. Soc.*, pp. 219-229.
- Proctor, M. C. F. 1982. Physiological ecology, water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, London, pp. 333-382.
- Proctor, M. C. F. 2000. The bryophyte paradox: Tolerance of desiccation, evasion of drought. *Plant Ecol.* 151: 41-49.
- Proctor, M. C. F. and Pence, V. C. 2002. Vegetative tissues: Bryophytes, vascular resurrection plants and vegetative propagules. In: Pritchard, H. and Black, M. (eds.). *Desiccation and Plant Survival*. CABI Publishing, Wallingford, UK, pp. 207-237.
- Proctor, M. C. F. and Tuba, Z. 2002. Poikilohydry and homoiohydry: Antithesis or spectrum of possibilities? *New Phytol.* 156: 327-349.
- Proctor, M. C. F., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., and Mishler, B. D. 2007. Desiccation-tolerance in bryophytes: A review. *Bryologist* 110: 595-621.
- Raven, J. A. 1993. The evolution of vascular plants in relation to quantitative functioning of dead water-conducting cells and stomata. *Biol. Rev.* 68: 337-363.
- Raven, J. A. 2002. Selection pressures on stomatal evolution. *New Phytol.* 153: 371-386.
- Raven, J. A. and Handley, L. L. 1987. Transport processes and water relations. *New Phytol.* 106: 217-233.
- Raven, P. H., Evert, R. F., and Eichhorn, S. E. 2005. *Biology of Plants*. W. H. Freeman Co., N. Y., p. 348.
- Read, D. J., Duckett, J. G., Francis, R., Ligrone, R., and Russell, A. 2000. Symbiotic fungal associations in 'lower' land plants. *Philosoph. Trans. Royal Soc. B* 355: 815-832.
- Riccia cavernosa* Hoffm. 2012. Botanical Society of the British Isles. Accessed 14 March 2015 at <<http://www.s231645534.websitehome.co.uk/Riccia%20cavernosa.htm>>.
- Richardson, D. H. S. 1981. *The Biology of Mosses*. John Wiley & Sons, Inc., N. Y., 220 pp.

- Romose, V. 1940. Ökologische Untersuchungen über *Homalothecium sericeum*, seine Wachstumsperioden und seine Stoffproduktion. Dansk Bot. Ark. 10: 1-134.
- Rowntree, J. K., Duckett, J. G., Mortimer, C. L., Ramsay, M., and Pressel, S. 2007. Formation of specialized propagules resistant to desiccation and cryopreservation in the threatened moss *Ditrichum plumbicola* Crundw. (Ditrichales, Bryopsida). Ann. Bot. 100: 483-496.
- Rundel, P. W. and Lange, O. L. 1980. Water relations and photosynthetic response of a desert moss. Flora 169: 329-335.
- Sarafis, V. 1971. A biological account of *Polytrichum commune*. N. Zeal. J. Bot. 9: 711-724.
- Schofield, W. B. 1981. Ecological significance of morphological characters in the moss gametophyte. Bryologist 84: 149-165.
- Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. Planta 124: 51-60.
- Schröder, G. 1886. Über die Austrocknungsfähigkeit der Pflanzen. Untersuchungen aus dem Botanischen Institut zu Tübingen, II: 1-53.
- Seki, T. and Yamaguchi, T. 1985. The effect of climatic factors on the floristic diversity of bryophytes in the Yaeyama Islands, the Ryuku Archipelago, southern Japan. In: Hara, H. (ed.). Origin and evolution of diversity in plants and plant communities, Academic Scientific Book Co. Inc., Tokyo, pp. 60-76.
- Shaw, A. J. and Goffinet, B. 2000. Bryophyte Biology. Cambridge University Press, Cambridge.
- Skre, O., Oechel, W. C., and Miller, P. M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can. J. Forest. Res. 13: 860-868.
- Smith, M., Bruhn, J., and Anderson, J. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. Nature 356: 428-431.
- Smith, R. I. L. 1988. Aspects of cryptogam water relations at a continental Antarctic site. Polarforschung 58: 139-153.
- Stark, L. R. 2002. New frontiers in bryology: Phenology and its repercussions on the reproductive ecology of mosses. Bryologist 105: 204-218.
- Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.
- Stark, L. R., Mishler, B. D., and McLetchie, D. N. 2000. The cost of realized sexual reproduction: assessing patterns of reproductive allocation and sporophyte abortion in a desert moss. Amer. J. Bot. 87: 1599-1608.
- Stark, L. R., Oliver, M. J., Mishler, B. D., and McLetchie, D. N. 2007. Generational differences in response to desiccation stress in the desert moss *Tortula inermis*. Ann. Bot. 99: 53-60.
- Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2013. The desert moss *Pterygoneurum lamellatum* exhibits inducible desiccation tolerance: Effects of rate of drying on shoot damage and regeneration. Amer. J. Bot. 100: 1522-1531.
- Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2014. Physiological history may mask the inherent inducible desiccation tolerance strategy of the desert moss *Crossidium crassinerve*. Plant Biol. 16: 935-946.
- Steere, W. C. 1976. Ecology, phytoecography and floristics of Arctic Alaskan bryophytes. J. Hattori Bot. Lab. 41: 47-72.
- Trachtenberg, S. and Zamski, E. 1979. The apoplastic conduction of water in *Polytrichum juniperinum* Willd. gametophytes. New Phytol. 83: 49-52.
- Tuba, Z. 1984. Changes in the photosynthetic pigment system of the drought tolerant *Tortula ruralis* during a daily desiccation. Proc. Third Meeting Bryologists from Centr. and East Eur. Univ. Karlova, Praha, pp. 343-352.
- Tuba, Z. 1985. Photosynthetic pigment responses in *Tortula ruralis* during daily desiccation. Abstr. Bot. 9, Suppl. 2: 231-239.
- Vishvakarma, K. S. and Kaul, A. 1988. Influence of moisture levels on growth of *Plagiochasma appendiculatum* Lehm. et Lindb. and *Reboulia hemisphaerica* (L.) Raddi on a comparative basis. Cryptog. Bryol. Lichénol. 9: 337-341.
- Volk, O. H. 1984. Beiträge zur Kenntnis der Marchantiales in Suedwest-Afrika/Namibia. IV. Zur Biologie einiger Hepaticae mit besonderer Berücksichtigung der Gattung *Riccia*. [Contribution to the knowledge of the Marchantiales in Southwest Africa/Namibia. IV. The biology of some Hepaticae with particular consideration of the genus *Riccia*.]. Nova Hedw. 39: 117-144.
- Watson, E. V. 1971. Structure and Life of Bryophytes. 3rd edn. Hutchinson & Co. Ltd., London.
- Wood, A. J. 2007. The nature and distribution of vegetative desiccation tolerance in hornworts, liverworts and mosses. Bryologist 110: 163-177.
- Zehr, D. R. 1979. Phenology of selected bryophytes in southern Illinois. Bryologist 82: 29-36.
- Zheng, Y., Xu, M., Zhao, J., Zhang, B., Bei, S., and Hao, L. 2010. Morphological adaptations to drought and reproductive strategy of the moss *Syntrichia caninervis* in the Gurbantunggut Desert, China. Arid Land Research and Management 25: 116-127.
- Ziegler, H. 1987. The evolution of stomata. In: Zeiger, E., Farquhar, G. D., Cowan, I. R. Stomatal Function. Stanford University Press, Stanford, CA, pp. 29-57.
- Zotz, G., Schweikert, A., Jetz, W., and Westerman, H. 2000. Water relations and carbon gain in relation to cushion size in the moss *Grimmia pulvinata* (Hedw.) Sm. New Phytol. 148: 59-67.