CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

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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 courtesy of Peggy Edwards.

**Water Strategies**

Water strategies in bryophytes have been approached in a variety of ways, from splashing gemmae (Brodie 1951) to uptake (Proctor 1981; Rice & Schneider 2004; Rice 2012; Jonas & Dolan 2012; Sand-Jensen & Hammer 2012) to transport (Hébant 1977; Mulder *et al.* 2001; Proctor & Tuba 2002; Pressel 2006; Rice 2012) to moving nutrients (Buch 1945, 1947; Proctor 1981) to retention (Kennedy 1993; Mulder *et al.* 2001; Rixen & Mulder 2005).

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 ≤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.
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 (Vitt et al. 2014). Even in bryophytes that seem to lack physiological desiccation tolerance, morphological or life history adaptations permit them to survive periodic drought.

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 (homoiohydry). 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; Norr 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)!

*B. 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.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Revival Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anoectangium compactum</td>
<td>19 years</td>
</tr>
<tr>
<td>Dicranoweisia cirrata</td>
<td>9 years</td>
</tr>
<tr>
<td>Riccia canescens</td>
<td>*7 years</td>
</tr>
<tr>
<td>Grimmia elatior</td>
<td>5 years</td>
</tr>
<tr>
<td>Oxytricha</td>
<td>*4 years</td>
</tr>
<tr>
<td>Anomodon longifolius</td>
<td>2 years</td>
</tr>
<tr>
<td>Bryum argenteum</td>
<td>2 years</td>
</tr>
<tr>
<td>Orthotrichum rupestre</td>
<td>2 years</td>
</tr>
<tr>
<td>Grimmia muehlenbeckii</td>
<td>18 months</td>
</tr>
<tr>
<td>Andreaea rothii</td>
<td>13 months</td>
</tr>
<tr>
<td>Racotritium lanuginosum</td>
<td>11 months</td>
</tr>
<tr>
<td>Syntrichia ruralis</td>
<td>8 months</td>
</tr>
<tr>
<td>Fontinalis flaccida</td>
<td>3 months</td>
</tr>
</tbody>
</table>

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**Figure 3.** *Plagiochasma appendiculatum*, a liverwort with both branching and growth throughout the range of 10-100% moisture. Photo by Michael Lüth, with permission.
Figure 4. *Reboulia hemisphaerica*, a liverwort in which growth and branching occur in the range of 40-90% moisture. Photo by Jan-Peter Frahm, with permission.

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).

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

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, with permission.

Figure 6. *Grimmia laevigata*, a poikilohydric moss, in its wet state. Photo by Michael Lüth, with permission.

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.
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 & Ziober 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 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, with permission.

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

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

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, with permission.

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, with permission.

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.

![Image of Cratoneuron filicinum](image)

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

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. Small features as surface ornamentation of leaves, stems, and rhizoids affect water absorption and retention and influence habitat specificity.

### Structural Adaptations

When I moved to the Upper Peninsula of Michigan, I was struck by the fact that only red oaks were able to live here. A simple difference in one structure made their survival possible in a cold region with long winters – narrow vessels. Large vessels in the other North American species cavitate and the water is unable to reconnect on an appropriate time schedule that permits the oaks to complete their life cycle and gain sufficient energy to continue the establishment of the species.

Many studies have demonstrated the importance of anatomy in determining the mechanical properties of plant tissues, including bryophytes (Hébant 1977; Rossi *et al*., 1998; Niklas *et al.* 2006; Frenzke *et al.* 2011; Atala & Alfaro 2012; Vincent 2012). 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.

### 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 Scafone, 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.
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.

**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. Marchantian 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 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.

**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>, with permission.

**Figure 20.** Scales of *Cyathodium cavernarum*. Photo courtesy of 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.
This high degree of wettability provides a greater possibility for water entry in thalllose 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 44-Figure 45) 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.

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.
Rhizoids

Ventral structures seem to be important in this group. In marchantalian liverworts, two types of rhizoids (Figure 29-Figure 28) provide somewhat different functions. The smooth-walled rhizoids (Figure 28) 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 28) 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).
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).

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).

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 44-Figure 45) 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>, with permission.

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

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

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

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, with permission.

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>, with permission.

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>, with permission.

In *Preissia* (Figure 30), it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that *Riccia* (Figure 43), 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.

**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 43) 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.

The rib of *Lunularia cruciata* (Figure 44-Figure 45) 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 46). 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 43. *Riccia nigrella* showing valleys with midribs that could be used to direct water into the thallus. Photo by Des Callaghan, with permission.

Figure 44. *Lunularia cruciata* indicating rib area (arrows). Photo by Luis Nunes Alberto, through Creative Commons.
**Rolling Thallus:** Midribs may also facilitate rolling of the thallus by creating a crease through the middle of the plant (compare Figure 43 to Figure 47). Rolling conserves water, but at the same time it exposes the ventral surface where scales help to conserve water (Figure 47). Such rolling is common in species of *Riccia* (Figure 69-Figure 70), often supplemented with hairs that cover the thallus.

**Internal Conduction:** The liverwort *Lunularia cruciata* (Figure 44-Figure 45) 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 45) 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 chlorophylllose cells overtopped 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 chlorophylllose 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 48) 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).
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 48) it can be either nodular or sheetlike, and in *Sphagnum fimbriatum* (Figure 49) 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.

The thallose liverwort *Plagiochasma rupestre* (Figure 60) 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.

Figure 49. *Sphagnum fimbriatum*, a species with a cuticle. Photo by Michael Lüth, with permission.

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.

In the Polytrichaceae, waxes may serve a different function. Rather than keeping water in, the leaves of these species must keep water out to permit maximum photosynthesis (Figure 50) (Clayton-Greene et al. 1985). Their lamellae provide extra photosynthetic tissue, but water can become trapped there due to the capillary spaces. This protection from water is further enhanced by the rolled margins (Figure 51) of species like *Polytrichum juniperinum* (Figure 52).

Figure 50. *Polytrichastrum pallidisetum* showing leaf lamellae where photosynthesis occurs. Note thickened end walls that help keep water from entering capillary spaces between lamellae. Photo by Michael Lüth.

Figure 51. *Polytrichum hyperboreum* showing inrolled leaf margins that cover the lamellae and protect them from water logging in the capillary spaces. Photo by Michael Lüth, with permission.

Figure 52. *Polytrichium juniperinum* showing lamellae and leaf edge that is rolled over them to help keep water out of the capillary spaces. Photo by John Hribljan, with permission.

**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 46, Figure 58). Maier-Maercker (1982) found that *Conocephalum conicum* (Figure 24) loses water through transpiration from these dorsal thallus pores (Figure 53), 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 54) and chambers internally (Figure 55). 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.

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 56), 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.

But the photosynthetic cells project into these chambers beneath the pores (Figure 55), 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 56) 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 56-Figure 59) that not only narrows the entrance, but that also repels the water.
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. 

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 60) 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 61-Figure 62, Figure 30), the barrel-shaped pores (Figure 62) 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 55-Figure 57) behave similarly (Raven et al. 2005).

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 63).

Figure 63. *Marchantia polymorpha* antheridial head showing location of rhizoids within the antheridiophore. Photo from Botany website of the University of British Columbia, BC, Canada, with permission.

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 64) 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 65) 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.

Duckett et al. (2013) suggest that the length of the archegoniophore is limited to a maximum of 7-10 cm (in *Conocephalum*; Figure 66) 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).

Antheridiophores provide yet a different mechanism (Duckett & Pressel 2009). Present only in the genus *Marchantia*, they present an antheridial head (Figure 67) 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 68) during rainfall.

Figure 64. *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, through Creative Commons.

Figure 65. *Polytrichum commune*, a moss that wilts in full sun despite its wet substrate and colonial habit. Photo by Michael Lüth, with permission.

Figure 66. *Conocephalum conicum* with tall archegoniophore. Photo by Adolf Ceska, with permission.

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Chapter 7-3: Water Relations: Plant Strategies

**Figure 67.** *Marchantia polymorpha* with antheridial heads where water is absorbed like a sponge. Photo by Rudolf Macek, with permission.

**Figure 68.** *Marchantia polymorpha* young archegoniophores that receive sperm from temporarily taller antheridiophores. Photo by Rudolf Macek, with permission.

**Figure 69.** *Riccia sorocarpa* in a fresh, active state. <www.aphotofauna.com>, with permission.

**Figure 70.** *Riccia sorocarpa* in a dry, dormant state. Photo by Michael Lüth, with permission.

**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 65) 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.

Bayfield (1973) considered that water loss in endohydric *Polytrichum commune* to be controlled by its leaf arrangement changes. This was accompanied by changes in water potential deficit of the shoots, with conduction being primarily internal under high evaporative flux and external under moderate flux. The ectohydric *Racomitrium lanuginosum*, by contrast, has little control over its water loss.

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 71) and *Haplotrichium hookeri* (Figure 72-Figure 73) under high humidity or liquid culture (Hébant 1977). Hair points (colorless, hairlike extensions at leaf tip) of *Schistidium apocarpum* (Figure 75) likewise disappear in humid conditions (Figure 75).
Rhizoids are less well developed or absent in wet conditions (Smith 1988), even in the same species. In Andreaea blyttii (Figure 76), 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 77) compared to those grown out of water (Figure 78), and the reduced light results in greater internode distances (distance between leaf insertions) (Lodge 1959). A similar response is seen in Fontinalis (Figure 79). It is interesting that increases in salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.
Figure 78. *Drepanocladius aduncus* with falcate leaves resulting from growing above water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 79. **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.

Proctor (2010) reminds us that adaptations are subject to phylogenetic constraints and that entire clades may represent adaptations to desiccation. All plants must obtain water and CO\(_2\), but their multiple ways that this can be achieved.

**Growth Form**

Growth form is important both for obtaining and retaining water. For example, *Grimmia pulvinata* (Figure 80) 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 CO\(_2\) exchange rate decreases with increasing size of the cushion, with both net photosynthesis and dark respiration decreasing.

Figure 80. *Grimmia pulvinata* showing cushion form that conserves water. Photo by Michael Lüth, with permission.

Living in clumps affects the ability to gain and to retain moisture. The cushion growth form decreases the surface to volume ratio, thus reducing surface water loss. Clump shape is important in this relationship, particularly in ameliorating wind effects (Proctor 1981; Zotz *et al.* 2000; Rice *et al.* 2001; Rice & Schneider 2004; Rice 2012). But for this system to work, the surface must be as smooth as possible. Greater roughness, resulting from protruding shoots, increases the turbulent air flow, thus increasing evaporation (Proctor 1981; Rice & Schneider 2004). A consequent advantage to the cushion growth form and its retention of water is the slowing the drying rate (Sand-Jensen & Hammer 2012).

Fortunately, this is a self-regulating condition. As a shoot emerges from the surface, the greater exposure and greater evaporation cause its growth to attenuate. Even herbivores might contribute to this evening, choosing the protruding branch because it is easier to munch on. Hence, the surrounding mosses are able to catch up in length, returning the clump to its smooth structure. Thus, moisture limitations create a more matted clump with a smoother surface, limiting turbulent flow and wind penetration into the clump (Longton 1979; Guerra *et al.* 1992; Nakatsubo 1994).

Nakatsubo (1994) examined the importance of the growth form of sub-alpine mosses in controlling their evaporative water loss. The xerophytic species were comprised of large cushions and compact mats. Mesophytic species from the coniferous forest floor were represented by smooth mats, wefts, and tall turfs. The evaporation rate per dry weight was much less in the xerophytic species than in the mesophytic species. However, when compared on a basal area, the evaporation rates were similar. One advantage of the xerophytic species was their ability to increase weight per basal area without increasing roughness.
The density of the clumps seem to be a plastic character that can be modified by the environment (Gimingham & Birse 1957; LaFarge-England 1996; Bates 1998; Rossi et al. 2001). For example, the endohydric *Polytrichum juniperinum* var. *alpestre* (Figure 81), when in humid habitats, forms a looser clump structure and greater roughness than when in drier habitats (Birse 1957).

Elumeeva *et al.* (2011) set out to determine the important characters that maintained moisture in sub-Arctic bryophytes. They found that individual shoot properties seemed to have little effect on colony water retention capacity. That is, leaf cell wall properties, water retention capacity, and desiccation rate of shoots made little difference in the water relations of the colony. Rather, the colony desiccation rate was determined by the density of the water-saturated colony. The desiccation rate of the individual shoot had a marginally significant negative effect on the colony rate.

In *Polytrichastrum formosum*, the plants are relatively tall and arranged in loose clumps. Nevertheless, the leaves of adjoining shoots touch, permitting water drops to be trapped by the resulting web. Drop size is an important consideration in conducting experiments using artificial rain. Raindrops usually range 0.5 mm (light rain) to 5 mm (heavy rain) (Best 1950; Brandt 1989; Yakubu *et al.* 2016). Using this size range, Zajączkowska *et al.* (2016) determined that clumps of *P. formosum* were able to retain almost 60% of the applied water. When water was applied to the tips, water ran down the shoots and continued to run down until about 2 minutes after the water application ceased. When a drop lands on a leaf, it is more likely to be trapped by the leaf axil or by a leaf. Thus these clumps are benefitted by the catchment web formed by the overlapping leaves.

With these clump advantages, we might ask why so many mosses use other growth forms that are less compact. But moisture is not the only need for the mosses. A compact nature reduces light penetration, reduces CO₂ diffusion into the clump, and increases shoot-to-shoot competition for nutrients (Bates 1989; Rice 2012).

Mulder *et al.* (2001) explored the role of species richness on biomass, then compared it when these communities were exposed to experimental drought. They found that under drought conditions biomass increased with greater species richness. They determined that the interaction was facilitative rather than niche complementarity or sampling effects. Survivorship increased for almost all species as richness increased, with the least drought-resistant species receiving the most benefit in biomass. Rixen and Mulder (2005) found similar results in the Arctic tundra.

**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 82-Figure 83) 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).
in many biological structures and provide stronger mechanical features (Dunlop et al. 2011; Fratzl et al. 2016). This layering provides the stem with both supportive strength and flexibility that prevents breakage. In Polytrichastrum and other members of the Polytrichaceae, the thicker cell walls surrounding the stem provide a higher bending strength (Niklas 1992), much like a paper straw compared with a paper lollipop stick. We also know that a lollipop stick made with twisted paper threads is stronger than a solid, non-twisted one, and that many trees likewise gain strength this way. This possibility needs to be explored in bryophytes.

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 84). 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.

Sphagnum: Li and coworkers (1992) examined the responses of two closely related Sphagnum hummock species, S. magellanicum (Figure 85) and S. papillosum (Figure 86), 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 87), with thicker hyaline layers (Figure 88-Figure 89), than stems with apical capitula near the water surface (Figure 90), presumably increasing both absorption and water-holding ability.

Sphagnum has pores in its stem (Figure 90), 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 91) on the stems for absorbing water (Figure 91).
Daniels (1989) found that while there is little differentiation between spreading and pendant branches (Figure 92-Figure 93) 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 93). 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.

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 94). However, it will fail to do so if S. papillosum is dominant (Figure 94). This is further supported by lab experiments in which S. magellanicum moved water farther externally in 20 hours than did S. papillosum (Figure 95; Figure 96).
Figure 93. Spreading branches and pendant branches on two hummock \textit{Sphagnum} species. \textbf{Left:} \textit{S. magellanicum}. \textbf{Right:} \textit{S. papillosum}. Photos courtesy of Yenhung Li.

Figure 94. Predominately \textit{Sphagnum papillosum} (olive colored) lower on the hummock (left side of picture) causes both species to be dry, whereas predominately \textit{S. magellanicum} (red) higher on the hummock (right side of picture) causes both species to be wet. Photo by Janice Glime.

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 97) 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 \textit{Dicranum scoparium} (Figure 98) or the lateral walls of hydroids in the gametophyte central strand of the \textit{Polytrichales} (Figure 99). But insufficient data exist to relate these variations to adaptive function.

Figure 95. Comparison of distance travelled by dye in two \textit{Sphagnum} species from lower (\textit{S. papillosum}) and higher (\textit{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 96. Comparison of upward transport in a low (left) and high (right) hummock species of \textit{Sphagnum}. Movement of water is indicated by purple dye. Photo courtesy of Yenhung Li.

Figure 97. Stem cross section of \textit{Rhizogonium} showing narrow cells of central strand. Photo courtesy of Isawo Kawai.

Using several references for comparison, Hébant (1977) showed that the number of hydroids within the \textit{Polytrichum commune} central strand (Figure 99) 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.
Although in general, leafy liverworts lack conducting tissues in both leaves and stems (Crandall-Stotler 2014), *Haplotrichium* seems to be an exception. At least it possesses a differentiated central strand (Figure 100). But there seem to be no experiments to demonstrate that this actually serves as conducting tissue.

### Rhizoids and Tomentum

Rhizoids and tomentum (layer of matted woolly down on surface of plant; Figure 101) are adapted for water uptake. Pressel and Duckett (2011) found that rhizoids of all representatives they tested in *Polytrichales*, *Dicranales*, and *Bryales* (Figure 102) 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 103) and the highly hydrophilic tomentum-forming rhizoids (Figure 103) with papillae.

Mosses with dense rhizoids or tomentum (Figure 101-Figure 103) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that *Bryum pseudotriquetrum* (=*Bryum algens*; Figure 102), with a dense rhizoidal tomentum (Figure 102), 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 104), 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.

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**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.
aquatic moss may encounter its substrate in any direction from the stem, the individual rhizoids grow in a spiral (Figure 107) until they encounter the substrate, then form multiple branches (Figure 108) in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).

Figure 102. *Bryum pseudotriquetrum* (Bryales) showing dense rhizoidal tomentum along stem. Photo by Misha Ignatov, with permission.

Figure 103. *Breutelia chrysocoma* (Bartramiaceae) showing rhizoidal tomentum. Photo by Michael Lüth, with permission.

Figure 104. *Schistidium antarctici*, a moss that becomes morphologically modified by moisture conditions. Photo courtesy of 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 105) toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In *Fontinalis* (Figure 106), where rhizoids have a critical function in anchorage, and this

Figure 105. *Hygroamblystegium fluviatile* rhizoids on one side of stem. Photo by Janice Glime.

Figure 106. *Fontinalis novae-angliae* cemented to the rock by its rhizoids. Photo by Janice Glime.

Figure 107. *Fontinalis squamosa* rhizoids growing in a spiral where they are suspended above the substrate. Photo by Janice Glime.

Figure 108. *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 109) 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?

It is noteworthy that both leafy liverworts *Haplomitrium* (Figure 72-Figure 73) and *Treubia* (Figure 110) lack rhizoids (Figure 111) (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 112). But only the thallose liverworts produce two types. Mosses, on the other hand, have multicellular rhizoids that branch (Figure 113).
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 115) there are slime papillae (Figure 114) that may serve a water absorption/retention function as well. The leafy liverwort *Haplomitrium* (Figure 116) produces extensive mucilage on its rhizomes (Figure 116-Figure 117). It is interesting that these slime papillae appear in the green alga *Coleochaete* (Figure 118), 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 113. *Bryum stirtonii* rhizoid showing multiple cells, papillae, and branching. Photo by Michael Lüth, with permission.

Figure 114. Stem of *Takakia lepidozioides* showing slime papillae. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 115. *Takakia lepidozioides*. From the Herbarium of Hiroshima University, Hiroshima, Japan, with permission.

Figure 116. *Haplomitrium gibbsiae* leafy plant with mucous on its rhizomes. Photo courtesy of Jeff Ducket and Silvia Pressel.
Figure 117. *Haplomitrium gibbsiae* rhizome with mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 118. *Coleochaete* thallus, an extant green alga that has the most characters in common with bryophytes. Photo by Yuji Tsukii, with permission.

The thallose liverwort *Conocephalum conicum* (Figure 19, Figure 24, Figure 53) 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 119), 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 120), *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 121) 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 80) and *Syntrichia montana* (=*S. intermedia*; Figure 122). 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 & Dukett 2011).

Figure 119. *Bartramia ithyphylla* illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth, with permission.

Figure 120. *Campylopus introflexus* showing water droplets at tips of plants. Photo by Jan-Peter Frahm, with permission.

Figure 121. *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, with permission.
The leafy liverwort *Trichocolea* (Figure 123-Figure 124) is highly adapted to take advantage of capillary spaces. Its leaves are highly dissected and paraphyllia (leaflike appendages between the leaves; Figure 125) 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 126-Figure 127) and *Thuidium tamariscinum* (Figure 128) create capillary spaces much like a tomentum. Other mosses such as *Mniaceae* utilize paraphyses (Figure 129) among the archegonia and antheridia to conserve water, using the same capillary principle.
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 110-Figure 111) and Haplotrichium (Figure 116-Figure 117. In these liverworts they found intracellular fungal lumps, intercellular hyphae, and thick-walled spores. Unlike the well known glomerophytes found as symbionts in thalloid liverworts and lower tracheophytes, these were more ancient fungi (Figure 130-Figure 131).

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 132 shows a member of the Ascomycota inhabiting *Mylia anomala*. In the Basidiomycota, the genus *Sebacina* (Figure 133) 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 130. SEM of Treubia cross section showing the number of cells with resident fungi. Photo courtesy of Jeff Duckett and Silvia Pressel.](image1)

![Figure 131. SEM of Treubia cross section with fungi in cells. Photo courtesy of Jeff Duckett and Silvia Pressel.](image2)

![Figure 132. Swollen rhizoid tip with Ascomycota in leafy liverwort *Mylia anomala*. Photo courtesy of Silvia Pressel and Jeff Duckett.](image3)

![Figure 133. Sebacina incrustans, member of a genus of basidiomycete fungi that is associated with leafy liverworts. Photo by James K. Lindsey, with permission.](image4)

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 134), the wall chemistry changes during maturation, with an increase in electron-opacity.
aborted sporophytes outnumbers that of mature sporophytes. Similarly, in the boreal forest moss *Pleurozium schreberi* (Figure 137) 38% of the sporophytes aborted (Longton & Greene 1969).

### 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 135) and *Tortula inermis* (Figure 136) (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).

### Calyptra Protection

If we imagine the hairy calyptrae of such mosses as *Polytrichum* (Figure 138), 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 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 calyptra development, timing, structure, and its ultimate role.

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 126-Figure 127) (Callaghan *et al.* 1978) and desert moss *Syntrichia caninervis* (Figure 18) (Stark *et al.* 2000), the number of

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**Figure 134.** *Odontoschisma denudatum* with gemmae on apical leaves (yellowish). Photo by Jan-Peter Frahm, with permission.

**Figure 135.** *Microbryum starckeanum*, a species in which the sporophyte is more sensitive to desiccation than the gametophyte. Photo from BBS website, with permission.

**Figure 136.** *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, with permission.

**Figure 137.** *Pleurozium schreberi*, a boreal forest moss with a high percent of abortions. Photo by Michael Lüth, with permission.

**Figure 138.** Hairy calyptra on capsule of *Polytrichum juniperinum*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.
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 139) 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 138) and *Orthotrichum* (Figure 140) 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 139), 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 141), 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 142), *Plagiopus* (Figure 143-Figure 144), and *Mnium* (Figure 145-Figure 147) 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 141. *Buxbaumia viridis* capsule showing shiny, waxy cuticle. Photo by Bernd Haynold, through Wikimedia Commons.

Figure 142. *Bartramia pomiformis* capsule showing waxy surface. Photo by Walter Obermayer, with permission.

Figure 143. *Plagiopus oederiana* with capsules showing waxy surface. Photo by Michael Lüth, with permission.

Figure 144. *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 145. *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 146). 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 140) (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 146. *Orthotrichum pusillum* immersed stoma on calyptra. Photo by Bob Klips, with permission.
But this cuticle story apparently does not begin with the capsule. The young sporophyte is covered by a calyptra. And in *Funaria hygrometrica* (Figure 148-Figure 151) 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 148-Figure 151) as a model organism. These researchers found that the sporophyte cuticle does not mature until the formation of the capsule.
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 154) 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).

As among leaves, the capsule waxes vary in structure. In Tetradontium brownianum (Figure 152), there are fine rods around the stomata, whereas in Pylaisia polyantha (Figure 153) there are both rods and fine whorls (Pressel & Duckett 2011).

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Figure 151. Funaria hygrometrica mature capsule showing waxy surface. Photo by Sarah Gregg, with permission.

Figure 152. Tetradontium brownianum, a species with fine rods in the cuticle around the stomata of the capsules. Photo by Michael Lüth, with permission.

Figure 153. 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, with permission.

Figure 154. 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, through 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 155), Bryum (Figure 102), Coscinodon (Figure 156), Dicranella (Figure 157), Didymodon (Figure 158), Fissidens (Figure 159), Funaria (Figure 160), Grimmia (Figure 80), Hypnum (Figure 161), Mnium (Figure 145-Figure 147), Rhynchostegium (Figure 162), Schistidium (Figure 75), Syntrichia (Figure 18), Tortula (Figure 1, Figure 136). These water gains and losses permit rapid closure in wet conditions and accelerate opening under dry conditions.
Figure 156. *Coscinodon cribrosus* peristome. Photo by Michael Lüth, with permission.

Figure 157. *Dicranella varia* capsules showing peristome. Photo by Kristian Peters, through Wikimedia Commons.

Figure 158. *Didymodon rigidulus* with capsules. Photo by Michael Lüth, with permission.

Figure 159. *Fissidens adiantoides* peristome. Photo by Kristian Peters, with permission.

Figure 160. 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, through Creative Commons.

Figure 161. *Hypnum cupressiforme* peristome. Photo by Walter Obermayer, with permission.

Figure 162. *Rhynchostegium confertum* with capsules. Photo by Michael Lüth, with permission.
But what happens in capsules with no teeth or only rudimentary peristomes? As an example, in *Weissia* (Figure 163) water is prevented from entering the capsule by a highly water-repellent capsule rim (Figure 163). If water entered the capsule, it could cause premature germination or interfere with ultimate dispersal.

Figure 163. *Weissia fallax* capsule showing rudimentary peristome. Note the waxy appearance of the reddish annulus around the teeth. Photo by Michael Lüth, with permission.

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 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 164-Figure 165) (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 148-Figure 151) and *Buxbaumia aphylla* (Figure 166). 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 164. *Andreaea rothii* with capsules that have no stomata. Photo by Jan-Peter Frahm, with permission.

Figure 165. *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 167-Figure 168), 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.

But wait! While ABA may affect guard cell closure in *Physcomitrella patens* (Figure 168), 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 169-Figure 170) 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 171).
On the other hand, in greenhouse-grown *Funaria hygrometrica* (Figure 172) the stomata (Figure 173) 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.

Indeed it appears that the function changes as the *Funaria hygrometrica* (Figure 172-Figure 173) 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* (Figure 174), *Pogonatum* (Figure 175), *Acaulon* (Figure 176), *Campylopus* (Figure 177), *Leucobryum* (Figure 178), *Cinclidotus* (Figure 179), *Discelium* (Figure 180), *Nanomitrium, Fontinalis* (Figure 183), *Tetraphis* (Figure 182), *Catascopium, Leucodon, Cyclidicyon*) (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 174. *Atrichum crispulum* capsules – in a genus in which at least some species lack stomata. Photo by Robert Klips, with permission.

Figure 175. *Pogonatum urnigerum* capsules, member of a genus in which some species lack stomata. Photo by Kristian Peters, with permission.

Figure 176. *Acaulon muticum* with capsules, a genus in which species lack stomata. Photo by Michael Lüth, with permission.

Figure 177. *Campylopus nivalis* capsules, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 178. *Leucobryum glaucum* with capsules, member of a genus in which capsules often lack stomata. Photo by Janice Glime.
Figure 179. *Cinclidotus fontinaloides*, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 180. *Discelium nudum* capsule, a genus in which at least some members lack stomata. Photo by Des Callaghan, with permission.

Figure 181. *Catoscopium nigritum*, a genus with capsules that lack stomata. Photo by Michael Lüth, with permission.

Figure 182. *Tetraphis pellucida* capsule, a genus that lacks stomata. Photo by Walter Obermayer, with permission.

Figure 183. *Fontinalis squamosa* var *curnowii* with capsules, a species that lacks stomata. Photo by David Holyoak, with permission.

Merced and Renzaglia (2013) demonstrated the remarkable similarity between stomata in the highly developed *Oedipodium* (Figure 184) and the very reduced *Ephemerum* (Figure 185) 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 184) 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.

**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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