

CHAPTER 7-2

WATER RELATIONS: MOVEMENT

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CHAPTER 7-2

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Figure 1. *Grimmia nutans* supporting drops of water that will eventually be absorbed into the moss through the leaf surface. Photo by Michael Lüth, with permission.

Water Movement

Early experiments with dyes demonstrated that in mosses water is able to move in conducting tissue of the central cylinder, leaf traces, and the costa (Zacherl 1956), depending on capillary spaces, as it does in tracheophytes (Table 1). Bopp and Stehle (1957) confirmed not only these internal pathways, but that movement also occurs from cell to cell (**symplastic**) in the cortex of the lower part of the stem, as well as on the outer surfaces of leaves and stems (Figure 1). But it is more likely that most of the movement across the cortex and internal leaf is through the free space of the cell walls where it does not have to cross cell membranes until it reaches its destination (Proctor 1984). Such **apoplastic** (outside cell membrane or in free space) movement across the cortex is known even in *Polytrichum juniperinum* (Figure 2) (Trachtenberg & Zamski 1979), where a central strand and leaf traces are available to facilitate movement of water.

Table 1. Relationship of bryophyte structures, size of space, and capillary rise. From Proctor (1982), based on Slatyer (1967).

Radius of meniscus	Ht of capillary rise	Bryophyte structures in similar size range
1 mm	1.5 cm	Large, concave leaves; spaces among shoots
100 μm	15 cm	Spaces between leaves, paraphyllia
10 μm	1.5 m	Space within sheathing leaf base, tomentum, hyalocyst of <i>Sphagnum</i> & <i>Leucobryum</i>
1 μm	15 m	Interstices between leaf-surface papillae
100 nm	150 m	Spaces between cell-walls?
10 nm	1.5 km	Spaces between cell-wall microfibrils
1 nm	15 km	Glucose molecule

As in tracheophytes, water movement in both endohydric and ectohydric mosses is facilitated by tension forces (Zamski & Trachtenberg 1976), but unlike the case in tracheophytes, water moves in both directions in a source-sink fashion dependent upon availability (Bowen



1933a). This bi-directional movement applies not only to external movement, but to the hydrome as well. For bryophytes, the first water availability most commonly does not start with the soil, but with the tips of stems and leaves by way of rain, fog, or dew.



Figure 2. *Polytrichum juniperinum*, a moss with good **symplastic** conduction, but that can also use apoplastic movement. Photo by Des Callaghan, with permission.

Early observations showed that in general external conduction is much more rapid than internal conduction (Bowen 1933a, b, c; Clee 1939). This most likely relates to frictional resistance in the small internal routes. On the other hand, we should expect water to rise higher in small internal capillary spaces (Table 1). What seems strange, however, is that the utility of internal conduction in at least some bryophytes can change with age toward greater use of external conduction. Mizushima (1980) found that in older stems of *Entodon rubicundus* no internal conduction could be detected at 75% atmospheric humidity, but in younger stems, a slow internal conduction could be detected in the **central strand**. Both young and old stems exhibited external conduction, travelling up to 1 cm in 12 hours. This loss of internal conduction in older plants may support the contention of Kawai (1991), among others, that mosses may have been derived from vascular plants by reduction.

One item of curiosity is that not all bryophytes have **vacuoles** (Oliver & Bewley 1984). Surely this plays some role in their ability to hold water, and most likely affects nutrient placement and protection from toxic substances as well, but no one seems to have looked at this role in bryophyte physiology (Bates 2000).

## Ectohydric

**Ectohydric** mosses (almost all mosses) rely primarily on external transport of water and can absorb water over the entire plant surface (Figure 3). These taxa generally have no water repellent layers, or these are restricted to such locations as the apices of papillae, and they are easily wetted (Proctor 1982, 1984). Movement is due to capillarity and the relationships are complex. As the moss becomes hydrated, its capillarity changes due to expansion of leaves, untwisting, and other forms of movement and gyration (Deloire *et al.* 1979). They benefit from a large surface area relative to their volume (Proctor 1984) due to numerous leaves and often such structures as **paraphyllia** (reduced leaflike structures on the stem or branches of

some pleurocarpous mosses) and **tomentum** (felt-like covering of abundant rhizoids on stem).



Figure 3. Capillary water (**arrow**) held among the leaves of *Bryum*. Photo courtesy of John Hribljan.

Castaldo Cobianchi and Giordano (1984) concluded that in the ectohydric *Zygodon viridissimus* (var. *rupestris*) (Figure 4-Figure 5), having an apical cell with no surface wax or papillae might provide a "starting-point" for rehydration since the dry leaves are appressed to the stem. When water repellent layers are lacking, plants generally reach full hydration within minutes (During 1992). Thus, virtually all pleurocarpous mosses, many of acrocarpous mosses, and most of leafy liverworts are readily wet by the first few minutes of rain. You will soon know which ones are resistant to uptake by leaves because they will stubbornly refuse to rehydrate for you when you want to make a leaf slide. Only dousing in boiling water seems to coax the water inside the plant to restore its normal hydrated shape.



Figure 4. *Zygodon viridissimus* dry showing leaves appressed to stem. Photo by Michael Lüth, with permission.





Figure 5. *Zygodon viridissimus*, a moss in which the apical cell of the leaf lacks wax, permitting water entry. Photo by David Holyoak, with permission.

The **ectohydric** habit depends on entry of water through the moss surface and permits a moss to respond to dew and fog by absorbing water directly, even though rooted plants may never receive a drop of it. Such bryophytes can live in high elevations and on deserts that receive less than 25 cm rainfall per year, obtaining water that cannot be measured by conventional precipitation methods. Most tuft-forming (acrocarpous) mosses are (partially) endohydric, whereas most mat and carpet formers (pleurocarpous mosses) are ectohydric (Richardson 1981). In addition, some upright mosses such as *Sphagnum* (Figure 6) and *Andreaea* (Figure 7) are ectohydric. Schipperges and Rydin (1998) clearly showed this by clipping the capitula from the stem; these clipped capitula were unable to recover from desiccation, whereas unclipped capitula became rehydrated. But Even *Sphagnum* has highly specialized cells in the stem that have all the traits of a bryophyte type of conducting cell (Ligrone & Duckett 1998).

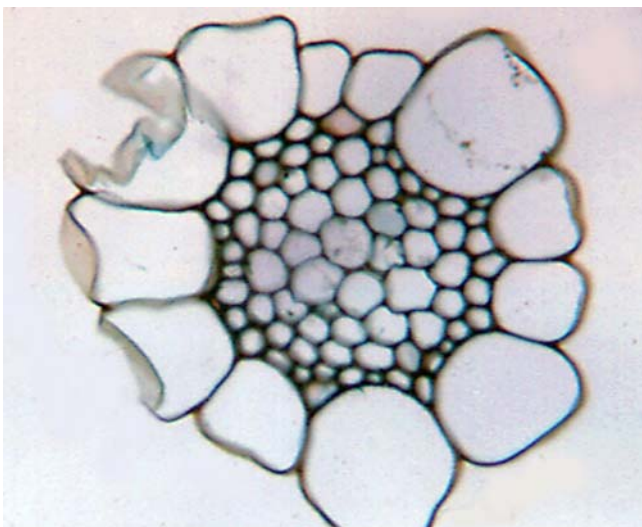


Figure 6. Cross section of *Sphagnum* stem with large, hyaline epidermal cells and small cortex cells. Photo by Janice Glime.

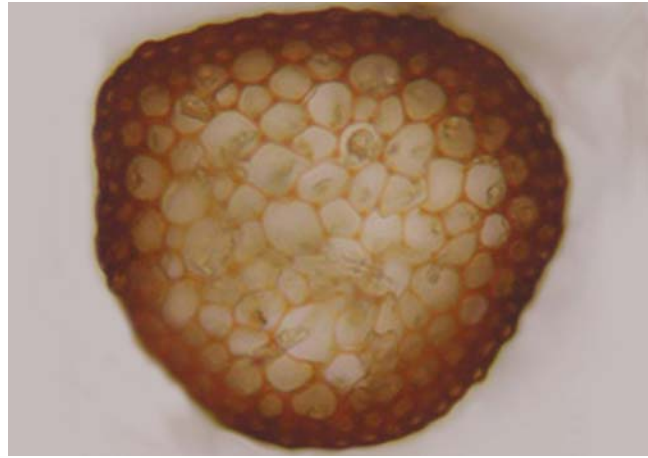


Figure 7. Cross section of *Andreaea* stem with no central strand. Photo from Biology 321 Course Website, University of British Columbia, with permission.

In **ectohydric** bryophytes, the uppermost leaves and shoot apices have the most rapid conduction of water, so that lower leaves are often supplied last (Zacherl 1956). Zacherl believed that no internal conduction was possible in the absence of a central strand. This apical movement may be beneficial in conserving water when water is scarce and only the leaves at the tips of the stems are receiving enough light for photosynthesis. These also are the leaves most exposed to fog and dew.

Using dyes and *Dicranum scoparium* (Figure 8) as a model subject, Bowen (1933c) demonstrated that external conduction was "exceptionally rapid" and internal conduction slow. Mägdefrau (1935), using the same species, determined internal conduction to be only about 1/3 the total conduction – not bad for a bryophyte. Klepper (1963) found that under conditions of desiccation, the protoplasts of this species become dense and evacuate, undoubtedly developing considerable **imbibitional pressure** (due to adsorption of water by colloidal particles, much as seeds do). This would cause them to readily take in water when it becomes available.



Figure 8. *Dicranum scoparium*. Photo by Michael Lüth, with permission.

Once the water enters the plant the distinction between endohydric and ectohydric no longer matters. Although the initial movement of water is clearly ectohydric in most dry mosses, once it has entered the moss it has the opportunity to move apoplastically to reach places where it is needed



for cellular metabolism. It is interesting that endohydric bryophytes can be facultatively ectohydric. Bayfield (1973) found that *Polytrichum commune* (Figure 9) was ectohydric under moderate moisture flux, but under high evaporative flux (*i.e.* dry air) it was predominantly endohydric.



Figure 9. *Polytrichum commune*, a moss that is ectohydric under moderate moisture flux but endohydric under dry air. Photo by George Shepherd, through Creative Commons.

Despite all the laboratory experiments on conduction, we still have little concept of the relative importance of the two pathways over a large time scale in nature. Certainly, as demonstrated in *Polytrichum* (Figure 9), the relationship changes as the moss dries. Is it not likely that internal movement of water from older to younger parts then predominates, keeping the photosynthetic and growing apical tissue wet as long as possible? Surely the same apoplastic routes available to *Polytrichum* are available to all mosses. The natural transpirational stream that carries water from the shoot apices to the atmosphere could be expected to play a similar role to that found in tracheophytes and maintain upward movement (or outward in pleurocarpous mosses) through capillary spaces as long as water was available and internal tension did not exceed that resulting from transpirational loss.

What quantities do the various mosses move from moss mat to atmosphere and how much is moved from the soil to the moss mat? Do the mosses provide an overall net gain to the soil by preventing rapid loss to the atmosphere following rainfall? Do they retain water that would otherwise be lost as runoff, contributing it slowly to the soil and plant roots beneath? Or is their major contribution that of depriving the soil of water during showers of short duration? There is no mass balance equation that includes the role of bryophytes in the overall water budget in any ecosystem.

## Endohydric

**Endohydric** mosses, including *Polytrichum* (Figure 2, Figure 9, Figure 13), *Mnium* *s.l.* (Figure 10, Figure 17), and *Bryum* (Figure 3), generally have surfaces that contain a water-resistant cuticle (Lorch 1931; Buch 1945; Bayfield 1973; Proctor 1979a), thus reducing their ability to take in water through their leaves. In some of these, that cuticle is endowed with a wax similar to that found in tracheophytes (Proctor 1979b; Haas 1982). However, this waxy coating of a moss leaf offers only a low water diffusion resistance

similar to that of tracheophyte mesophyll (Nobel 1977; Proctor 1980) and may be more important in repelling water to permit a higher CO<sub>2</sub> diffusion into the leaf (Proctor 1984). Among ectohydric mosses, waxy cuticles seem to be either generally lacking or very thin. Mosses like *Polytrichum* and many members of the Marchantiales are actually water repellent, thus requiring half an hour or more to take up water (Proctor 1984). These **endohydric** bryophytes utilize, in the case of mosses, the system of non-lignified **hydroids** and **leptoids** to conduct water and sugars, respectively.



Figure 10. *Mnium spinosum* with water droplets on its leaves. This moss is very slow to absorb water due to its water-resistant cuticle. Photo by Michael Lüth, with permission.

But it appears that even these endohydric mosses rely on ectohydric transport. Instead of moving water inside the moss at the first opportunity during its external vertical rise, it is the tips of the plants that exhibit primary water absorption (Brown 1982). Water travels upward through the capillary spaces created by the leaves. Mosses like *Polytrichum* may facilitate this apical absorption by preventing any significant absorption by the cuticularized lower and more mature leaves.

In these predominantly endohydric mosses, rhizoids may serve functions of conduction much as do roots and root hairs. It appears that endohydric mosses such as *Polytrichum* (Figure 2, Figure 9, Figure 13), *Dawsonia* (Figure 11), and *Climacium* (Figure 12) transport water from the substrate beneath to their tips before moving it through an internal conducting system, sometimes called the **central strand**. Although *Polytrichum commune* (Figure 9) has demonstrated the ability to transport water externally along its stems, Mägdefrau (1938) contended that the major conduction is internal through the central strand. However, Trachtenberg and Zamski (1979) determined that despite the ability of rhizoids to absorb and transmit water, the major absorption is still through the aerial gametophyte, due to its greater efficiency. Because of the extensive development of conduction cells in *Polytrichum* (Figure 13), where central **hydroids** are surrounded by a cylinder of **leptoids**, Héban (1970) considers this and other mosses to have similarities to the xylem and phloem of primitive vascular plants.





Figure 11. *Dawsonia polytrichoides*, a moss with good internal conduction. Photo by Niels Klazenga, with permission.



Figure 12. *Climacium dendroides*, a moss with external conduction from base to tip. Photo by Jan-Peter Frahm, with permission.

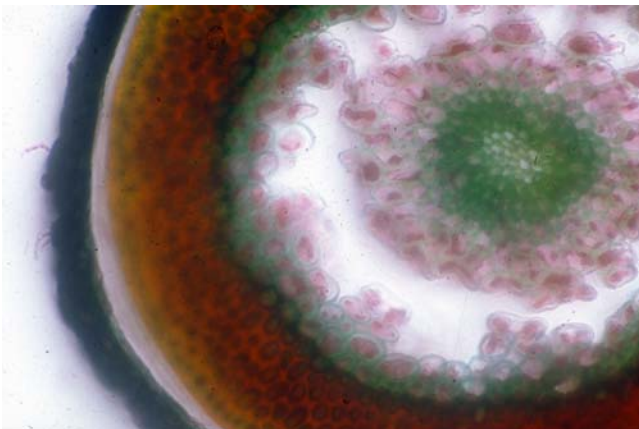


Figure 13. Cross section of a *Polytrichum* stem showing green **hydroids** of the **central strand** in center and larger **leptoids** surrounding them. Photo by Isawo Kawai, with permission.

But how does the water reach the leaves in the **endohydric** mosses? Zacherl (1956) used fluorescent dyes to show that in *Polytrichum* (Figure 2, Figure 9, Figure 13), the **costa** (midrib-like structure) links with the central strand, forming true leaf traces. In many taxa, however,

there is no connection between the central strand and the costa, and in some cases there is no costa at all. Furthermore, Colbert (1979) showed that there is no connection between the central strand of the stem and that of the branches in *Climacium americanum* (Figure 14), *C. dendroides* (Figure 12), *Rhytidiadelphus triquetrus* (Figure 15), and *Rhytidium rugosum* (Figure 16).



Figure 14. *Climacium americanum*, a moss with a central strand with no connection to the leaf. Photo by Bob Klips, with permission.



Figure 15. *Rhytidiadelphus triquetrus*, a moss with a central strand that does not connect to the leaves. Photo by Janice Glime.



Figure 16. *Rhytidium rugosum*, a moss with a central strand that does not connect to the leaves. Photo by Michael Lüth, with permission.



Nevertheless, in the absence of those connections the extension of the costa into the stem cortex still can function to complete internal transport across normal cortical cells (Zacherl 1956). For example, in *Mnium* (Figure 10) the costa does not link directly with the central strand of the stem, but ends blindly in the ground tissue, forming **false leaf traces** (Figure 17). The ends of the costae (Figure 18) act as wicks, transferring liquids across the ground tissue from the central strand and into the leaf costa, most likely using a diffusion gradient across the cortex.

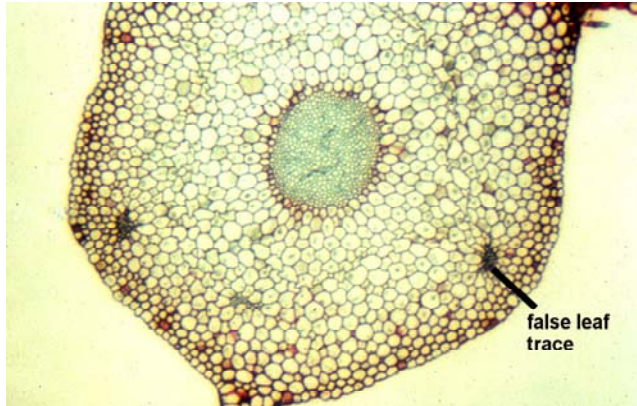


Figure 17. Cross section of *Mnium* stem showing false leaf traces. Photo by Janice Glime.

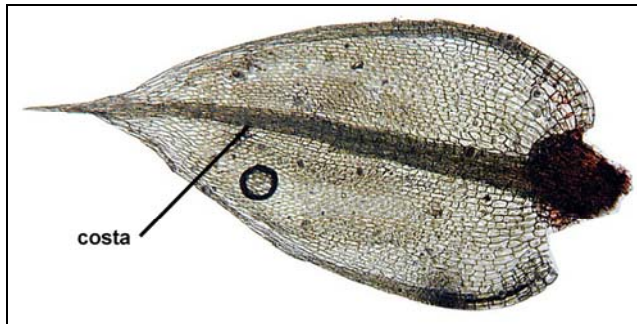


Figure 18. Leaf of *Bryum pallescens*, showing costa of conducting cells. Photo by Michael Lüth, with permission.

The cortex behaves as capillary tubes and draws the water across the stem parenchyma to the leaf, much as water traversing the roots of tracheophytes. Trachtenberg and Zamski (1979) demonstrated, using PbS and Pb-EDTA (which accumulates Pb ions in tissues in proportion to the amount of water passing through), that the water actually moves in the capillary spaces of the cell walls – **apoplastic conduction**. Beckett (1997), using pressure volume isotherms, determined that cryptogams, including bryophytes, contain significant amounts of intercellular water when fully hydrated, whereas flowering plants do not. It is this extracellular pathway that permits water to move from leaf surfaces inward and into stems, where it can be conducted in the hydrome as well as apoplastically. It is interesting that the uppermost leaves are the first ones to receive water internally (Zacherl 1956), just as in the ectohydric mosses.

Trachtenberg and Zamski (1979) further learned that the **sterome**, assumed to be supporting tissue, can provide an alternative pathway for water conduction. That its mass was much greater than needed for support had already been

noted by Lorch (1931). Furthermore, xerophytic mosses have a very large sterome (Goebel 1915) that is used for conducting and holding water. In mosses such as Fabroniaceae and Orthotrichaceae that lack a hydrome, the sterome is large (Van der Wijk 1932) and seems to supply this function. In fact, Trachtenberg and Zamski (1979) suggest that the transport from hydrome to leaves in *Mnium* (Figure 17) may take place through stereids. They support their hypothesis by demonstrating that the lead chelate solution applied to the leaves penetrates the sterome. They suggest that the most probable means of translocation of water from leaves into the stem is through the dense mass of stereids in leaves and leaf bases to the central cells of leaves and leaf traces to the hydrome. But only in the Polytrichaceae does there seem to be a connection between the leaf traces and both the leaf and hydrome. Rather, the apoplastic route through cell walls in the stem cortex is a more likely route in most cases.

**Mixohydric** bryophytes are those in which both endohydric and ectohydric methods are important. Many of the species in this group are small, acrocarpous mosses of loams or clays. These soils dry out frequently, but their fine texture permits them to maintain a moist top layer for a period of time after rain. Héban (1977) contends that truly mixohydric mosses are not very abundant, implying that the ectohydric pathway is far more important in most. However, in reality, most (perhaps all) mosses are mixohydric in that they have both internal and external means of conduction to at least some degree.

### Nocturnal

For many mosses, nighttime is the only period of rehydration. This is especially true for desert mosses such as *Syntrichia ruralis* (Figure 19). Csintalan *et al.* (2000) found that this moss obtained sufficient water through nighttime dew to accomplish 1.5 hours of net photosynthetic gain immediately after dawn. They suggested that such early morning periods might permit regular molecular repair due to desiccation damage during prolonged dry periods.



Figure 19. *Syntrichia ruralis*. Photo by Michael Lüth, with permission.

But it appears that desert habitats are not the only places where nighttime moisture benefits the bryophytes. Carleton and Dunham (2003) contended that the uppermost growing tips of mosses could not be hydrated by simple capillary movement of water from the forest floor in the boreal forest. Rather, even in this mossy habitat, they

showed a nocturnal gain in mass due to vapor from the forest floor. As the forest floor cooled at night, distillation occurred with moisture condensing on the moss surface. The cooling temperatures and moisture provided by the forest floor was sufficient to cause the moss tips to reach dew point. This seems to be most evident in late summer when the lower organic layers have warmed the most and the surface temperature is thus relatively lower at night, causing the condensation. When a vapor barrier was used to prevent ground water from rising, no mass gain was in evidence.

### Mechanisms of Water Movement

Bopp and Stehle (1957) found that a mechanism similar to the diffusion pressure deficit seen in higher plants worked in moving water up the moss. By using fluorescent dyes, Bopp and Stehle showed that water moved up the leafy gametophyte both internally and externally, but that dye went quickly to the foot of the sporophyte imbedded in the gametophyte, then moved up the seta through the central strand. In mosses with the calyptra removed, the flow rate increased, suggesting that transpiration loss may perform a function of pulling water, similar to that found in tracheophytes. Maier-Maercker (1982b) found an accumulation of radio-labelled and heavy metal ions in the annulus of the moss *Plagiomnium cuspidatum* (Figure 20), similar to that found in tracheophyte guard cells, suggesting that this area may be one of transpirational water loss.



Figure 20. *Plagiomnium cuspidatum* capsules showing annulus (arrows) where labelled metal ions accumulated, suggesting a site of transpiration loss. Photo by Robert Klips, with permission.

Although bryophytes lack leaf stomata, they do lose water through their wax-free leaves. For example, the transpirational loss rates of the moss cover in the lichen tundra (16-20% of total precipitation) is not unlike that from the ericaceous shrubs of the tundra heath (24-26%) or the alpine dwarf shrub heath (16-20%), whereas tracheophytes in a wet meadow can have 135% loss (Larcher 1983 – data from many authors).

Using mosses from five different habitats ranging from wet to dry, Bowen (1933a,b,c) determined that the water ascends the mosses as capillary films between the leaves and stem, being absorbed at the stem and branch apices by

the younger cells with unthickened walls. From there it diffuses through internal tissues laterally, then downward, not upward as in tracheophytes. Conduction from the base through the central strand is slow in cut stems but much slower when the stem base is still intact (Bowen 1933a,b,c). In the latter case, water must penetrate the thick walls of the rhizoids and stem/rhizome. And at least some of the species have cuticles on the rhizoids!

Once water reaches the central strand, it travels there preferentially (Héban 1977). Internal ascending water travels through the narrow, elongated, thin-walled cells (presumably hydroids). In addition to apical absorption, leaves and stem epidermis absorb some of the water, albeit less readily due to cell-wall thickening and cuticles.

The capacity of both internal and external water conduction seems to diminish as the moisture of the habitat increases (Bowen 1933a, b, c). Mägdefrau (1935) contends that at 90% humidity, *Polytrichum* (Figure 2, Figure 9, Figure 13) can maintain its turgor with internal conduction only, but at 70% both internal and external conduction are necessary. For all other families of mosses, with the possible exception of the Mniaceae, a significant amount of external conduction seems necessary.

Vitt (1990) suggests that those mosses that must endure a greater range of fluctuations in water availability may be more plastic in their responses. At least among the boreal mosses, the ectohydric, drought-tolerant *Hylocomium splendens* exhibits highly variable growth over its North American range, but the endohydric, less drought-tolerant *Polytrichum strictum* (Figure 21) exhibits more constant growth throughout its range (Vitt 1990).



Figure 21. *Polytrichum strictum* with sporophytes. Photo by Michael Lüth, with permission.

It is possible that there is some relationship between the absence of conducting cells and the horizontal growth habit of many mosses. However, Blaikley (1932) and Bowen (1933a) disagree as to the mechanisms for external conduction, arguing about the importance of soil water, presumably more available to the pleurocarpous habit. Blaikley feels that water contributed by the soil surfaces is necessary, whereas Bowen found leaf bases had drops of water when the soil surface was dry. The methodology of tracking the water is important here, and one is encouraged to read the arguments presented by Bowen (1933a) against broad interpretations based on the use of dyes. In most cases, she argues, they would be impossible to distinguish from naturally colored tissues, and the faint stain of cortical cells may be overlooked, whereas the presence of dyes in



the central strand may be more concentrated and thus more easily discerned. Rather, Bowen argues that water, and hence dye, accumulate in the central strand, whereas their movement across the cortex is transitory only. Thus, when water appears to have reached a certain height in the stem from internal movement through the hydrome, it may in fact have arrived there from the aerial surfaces across the cortex. Using 12 plants of *Polytrichum commune* (Figure 9) and blocking the entry of water into the hydrome from the cut surface with wax, she was able to demonstrate rapid movement externally, up to 42 cm in one hour, reaching a maximum of 96 cm in 24 hours (Bowen 1931). When basal leaves were removed (and the wounds sealed) and the cut stems were not blocked, she demonstrated considerably less movement internally through the hydrome. Using only three plants, the greatest rise internally was only 12 cm.

It is interesting that the dependence on endohydric gametophytic conduction seems to have diminished in the evolution of bryophytes, with the creeping (pleurocarpous) taxa exhibiting less developed conducting systems. Instead, the ectohydric habit is well-developed. Yet, no pattern exists (Héban 1977). Even the xerophytic *Orthotrichum* (Figure 22) lacks a central strand, although despite its acrocarpous appearance it is technically pleurocarpous and thus related to taxa that have apparently lost the central strand.

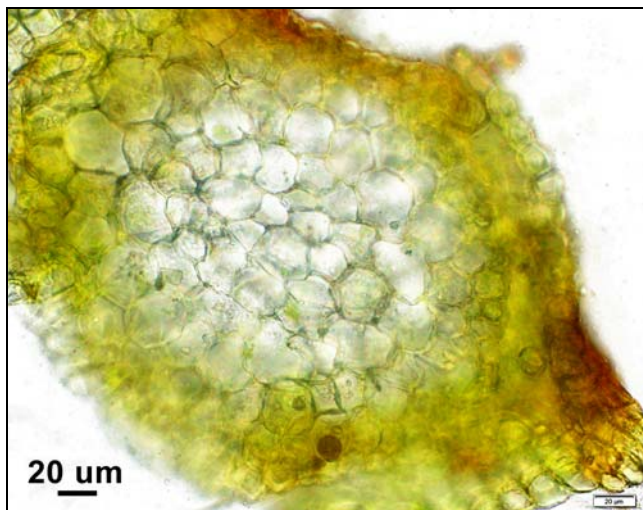


Figure 22. *Orthotrichum pumilum* stem cross section showing absence of central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It seems that for bryophytes, ectohydric conduction may be adaptive. Mägdefrau (1935) contends that the humidity would need to be at least 90% for the plant to succeed with internal conduction only. Gametophyte conduction is slow. Bopp and Stehle (1957) found that it required 40 hours for water to travel 10 cells in the rhizoids of *Funaria hygrometrica* (Figure 28)! The external pathway is much more rapid. The slowness of internal transport relative to external transport (Table 2) can easily account for the success of the external mechanisms. Furthermore, Bowen (1933a) demonstrated that the time required for movement can be more accurately measured by sensitive chemical tests that measure very small amounts of water which advance most rapidly up (or down)

the plant, suggesting that external conduction is even more rapid than supposed.

Mosses such as *Pleurozium schreberi* and *Hylocomium splendens* form important intermediaries between the soil and atmosphere in the boreal forest (Sokołowska *et al.* 2017). Hence, understanding how water movement functions in these keystone species is important. These researchers examined the conduction of both food and water in these species. Both species exhibit symplastic transport for short distances by using food-conducting cells. *Pleurozium schreberi* is furthermore able to transport substances apoplastically over long distances through the central strand of hydroids. *Hylocomium splendens* lacks hydroids (Figure 27). Both species have increased internal transport when air humidity is reduced significantly, but this increase is somewhat greater in *H. splendens*. These differences affect the desiccation tolerance. *Hylocomium splendens* typically dries faster than *P. schreberi* (Hiejmans *et al.* 2004; Elumeeva *et al.* 2011), perhaps explaining why *H. splendens* prefers wetter habitats (Busby *et al.* 1978).



Figure 23. *Pleurozium schreberi*, a species with both apoplastic and symplastic internal conduction. Photo by Bob Klips, with permission.

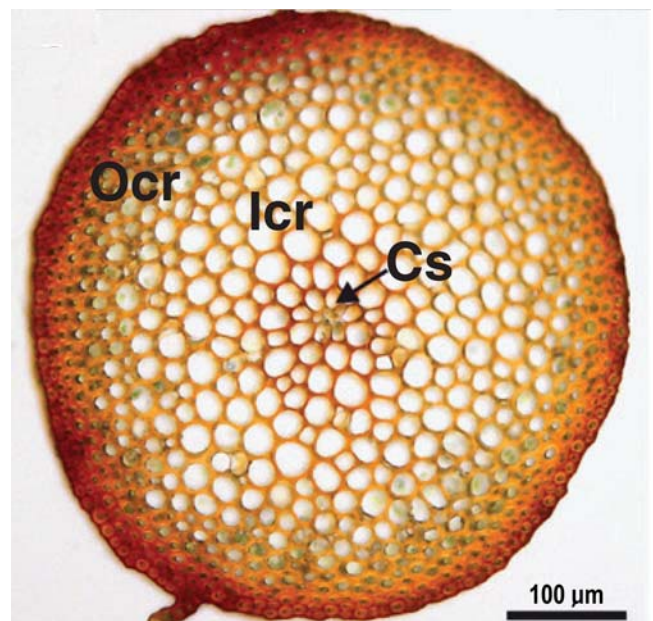


Figure 24. *Pleurozium schreberi* stem cs showing hydroids. Cs = central strand with hydroids; Icr = inner cortex; Ocr = outer cortex. Photo by Katarzyna Sokolowska.





Figure 25. *Pleurozium schreberi* stem cs showing hydroids with yellow walls in center. Photo by Katarzyna Sokolowska.



Figure 26. *Hylocomium splendens*, a species with no central strand and slow internal conduction. Photo by Paul Slichter, with permission.



Figure 27. *Hylocomium splendens* stem cross section showing absence of hydroids. Photo from Botany Website, UBC, with permission.

**To summarize**, water is known to move from one bryophyte part to another by four pathways: hydroids, free spaces in cell walls, cell to cell, and externally.



Figure 28. *Funaria hygrometrica*. Photo by Michael Lüth, with permission.

Table 2. Effectiveness of internal conduction compared to total in mosses after 24 hours in 70% relative humidity. Conduction measurements are grams water/0.2 grams dry mass; % is percent of internal compared to total rate. From Mägdefrau (1938).

	Internal Conduction	Total Conduction	%
<i>Sphagnum recurvum</i>	0.07	6.54	1
<i>Drepanocladus vernicosus</i>	0.79	22.73	3.5
<i>Rhytidiadelphus triquetrus</i>	0.11	1.67	6.5
<i>Thamnobryum alopecurum</i>	0.007	0.019	37
<i>Plagiomnium undulatum</i>	1.13	2.22	51
<i>Polytrichum commune</i>	2.24	3.32	67

### Transport to Sporophyte

The seta, lacking leaves, must necessarily conduct water internally. Conduction from the gametophyte to the **sporophyte** tissue seems to be governed by several factors, as observed in *Funaria hygrometrica* (Figure 28) (Bopp & Stehle 1957). The sporophyte receives its water from the **haustorial foot** that is imbedded deeply into the central strand of the gametophyte.

In *Dicranum undulatum* (Figure 29), it appears that the embryo has a role in development of the conducting strand in the gametophyte stem, as no conducting strands were present below archegonia that had not been fertilized (Roth 1969). Héban and Berthier (1972) made similar observations on *Polytrichastrum alpinum* (Figure 30). This underscores the apparent importance of the transfer of water from the gametophyte central strand to the sporophyte. There are no plasmodesmatal connections between the gametophyte and the foot of the seta (Héban 1977). However, the **transfer cells** have extensive wall ingrowths (**labyrinth**, Figure 31) that greatly increase the surface area of the plasma membrane, thus increasing transport (Héban 1977). In *Funaria hygrometrica* (Figure 28) fluorescent dyes showed that the jacket around this foot was separated by a narrow intercellular space which became colored before the central strand (Bopp & Stehle 1957). This capillary space moved the liquid quickly to the



central strand of the sporophyte. When comparing species that had no transfer cells, Bopp and Weniger (1971) found that uptake by the sporophyte was greatly reduced.



Figure 29. *Dicranum undulatum*, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Jan-Peter Frahm, with permission.



Figure 30. *Polytrichastrum alpinum*, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Michael Lüth, with permission.

Héban (1977) describes detailed studies of a variety of mosses in which the very tip of the sporophyte foot directly penetrates the central strand of the gametophyte. At the end of the foot, an appendage of mostly necrotic cells is the only separation of the conducting cells between the two generations. Conduction in the sporophyte was increased when the calyptra was removed; the apparently non-closing stomata of the capsule may contribute to transpirational water loss.

As can be observed in *Physcomitrium immersum* (= *Physcomitrium cyathicarpum*), both generations have **transfer cells** at the junction, and the foot epidermal cells are rich in organelles (Lal & Chauhan 1981), especially mitochondria (Héban 1977), suggesting there might be considerable active transport between the two generations.

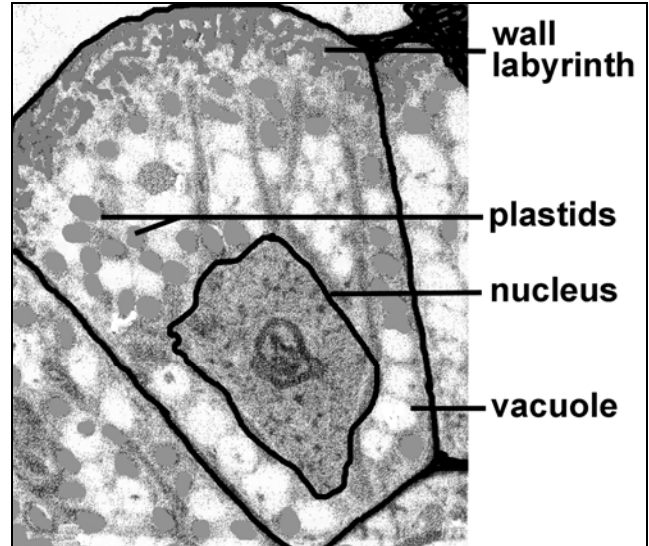


Figure 31. Transfer cell between gametophyte and sporophyte showing wall labyrinth. Computer-drawn from photo in Lal and Chauhan (1981).

## Summary

We have seen that bryophytes have remarkable abilities to gain, retain, and recover from loss of water. They gain it in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Endohydric movement is accomplished either cell-by-cell or through designated elongate cells (**hydroids**). Some mosses survive on moisture in clouds and nighttime dew. Nutrients and water are transferred to the sporophyte through the **foot**, using special **transfer cells** with **labyrinth** walls.

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