CHAPTER 8-5

NUTRIENT RELATIONS: TRANSLOCATION AND TRANSPORT

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Figure 1. ***Bazzania trilobata*** and other bryophytes growing together. Note the dead tissue in the lower right part of the clump, where nutrient sinks can be mobilized to supply growing apical tissues. Such clumps can play a significant role in the distribution of forest nutrients. Photo by Michael Lüth, with permission.

Translocation and Transport

One of the most poorly understood abilities of bryophytes by "vascular" botanists is the ability of bryophytes to transport nutrients within the plant. Understanding that transport of nutrients occurs through specialized vascular tissue (xylem and phloem), they have sometimes assumed that the "non-vascular" bryophytes are unable to move substances from one part of the plant to another. Hence, the assumption has been that as bryophytes die (Figure 1), decomposition will return the component nutrients. But while bryophytes lack tracheids, vessels, and sieve cells, they do not lack the ability to transport substances from one part of the plant to another, *i.e.* **translocation**. In some cases, such as ***Polytrichum*** (Figure 17), they actually transport substances through their **leptoids** (phloem-like cells; Figure 2) and **hydroids** (xylem-like cells; Figure 2). Those mosses such as ***Polytrichum*** with well-developed leptoids form a **leptome**, similar to the cylinder of phloem in a tree trunk. The collective hydroids in the center of the stem form the **hydrome**, also known as the **hydrom**. But it is clear that lack of even these special conducting cells is no deterrent to transport or to translocation in bryophytes. Hence, we can find nutrient elements in a number of locations within and upon the plant (see subchapter 8-4).

One aid to the transport of substances from cell to cell is the presence of **plasmodesmata** in the cell walls (Mahmoud 1965; Oliver & Bewley 1984). These connecting threads permit substances to move from cell to cell without traversing cell membranes, although the movement is undoubtedly slower than that of the movement of water in the interstitial capillary spaces of cell walls.

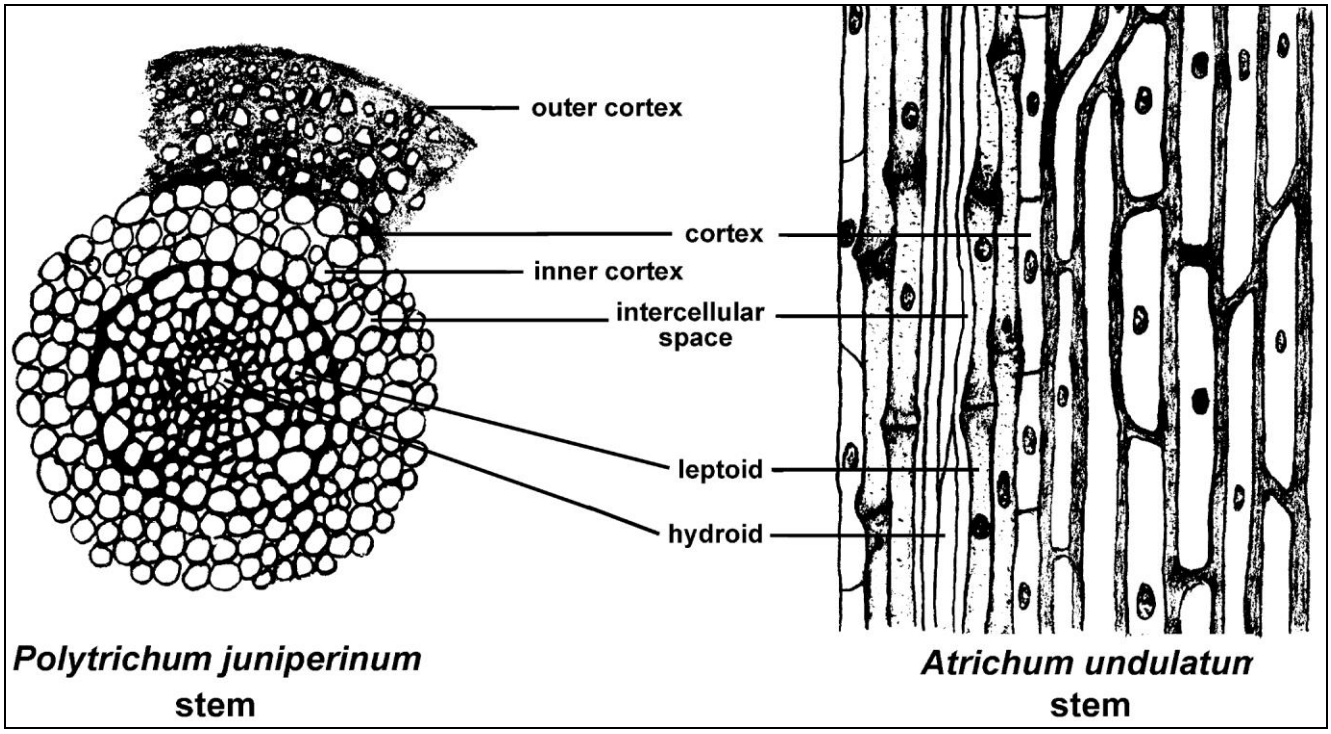

Figure 2. Cross section of ***Polytrichum juniperinum*** and longitudinal section of ***Atrichum undulatum*** stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, based on Hébant (1977).

Duckett and Ligrone (2003) list several specific examples in their note "What we couldn't have done if we'd stayed in Europe: Selection and serendipity in the Southern Hemisphere." They demonstrated the presence of "food-conducting cytology" (*i.e.* food conducting cells) in the widespread groups of **Hookeriaceae** (Figure 3), **Neckeraceae** (Figure 4), **Orthotrichaceae** (Figure 5-Figure 6), and ***Sphagnum*** (Figure 7-Figure 11), as well as in most caulonemata and rhizoids. Furthermore, this food conducting organization is present in the axes of the primitive moss ***Takakia*** (Figure 12-Figure 13) and the moss-like leafy liverwort ***Haplomitrium*** (Figure 14-Figure 15), as well as being widespread in Marchantialian thalli.

Figure 3. ***Hookeria lucens*** (**Hookeriaceae**), a family with food-conducting parenchyma cells. Photo by Jonathan Sleath, with permission.

Figure 4. ***Neckera pennata*** (**Neckeraceae**) , a family with parenchyma food-conducting cells. Photo by Michael Lüth, with permission.

Figure 5. ***Orthotrichum pumilum*** (**Orthotrichaceae**), a family with food-conducting parenchyma cells. Photo by Michael Lüth, with permission.

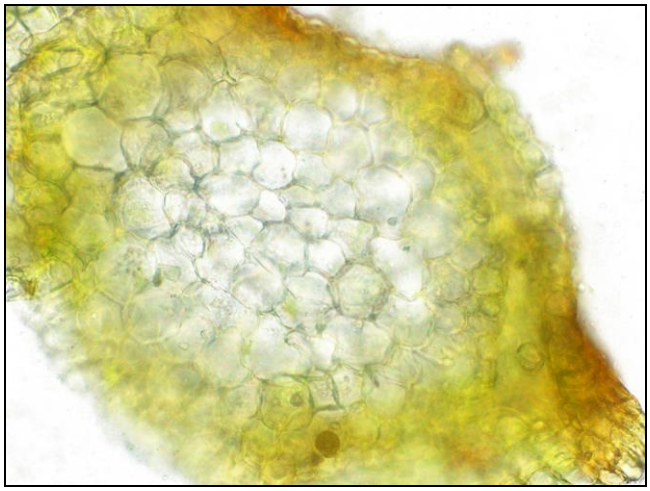

Figure 6. ***Orthotrichum pumilum*** (**Orthotrichaceae**) stem cs showing parenchyma cells in center of stem where nutrients can move from cell to cell. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 7. ***Sphagnum contortum***, a species with non-specialized food conducting cells. Photo by Michael Lüth, with permission.

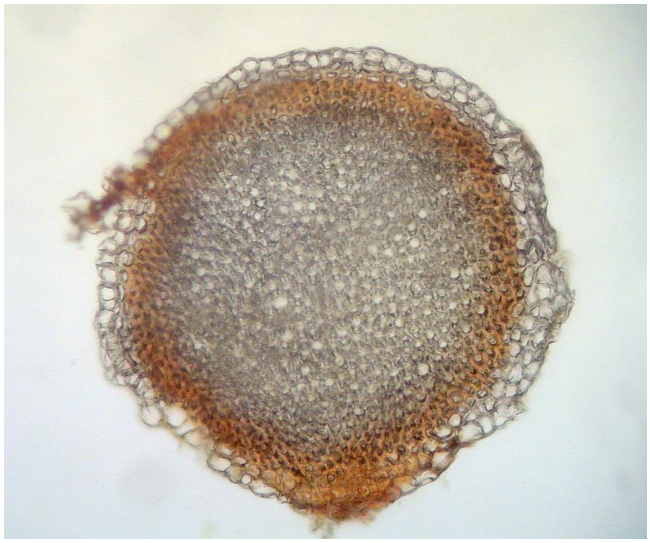

Figure 8. ***Sphagnum contortum*** stem cs showing lack of specialization in central food-conducting cells. Photo by Michael Lüth, with permission.

Figure 9. ***Sphagnum papillosum***, a species with non-specialized food-conducting cells. Photo by David Holyoak, with permission.

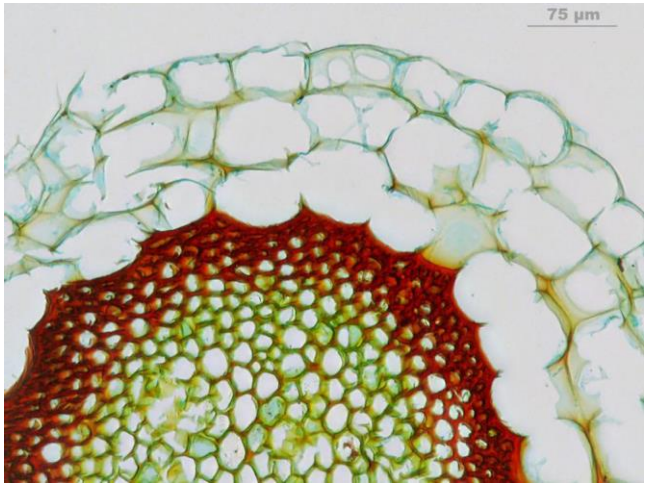

Figure 10. ***Sphagnum papillosum*** stem cs showing differentiation of stem cells with little differentiation in conducting cells in the center. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

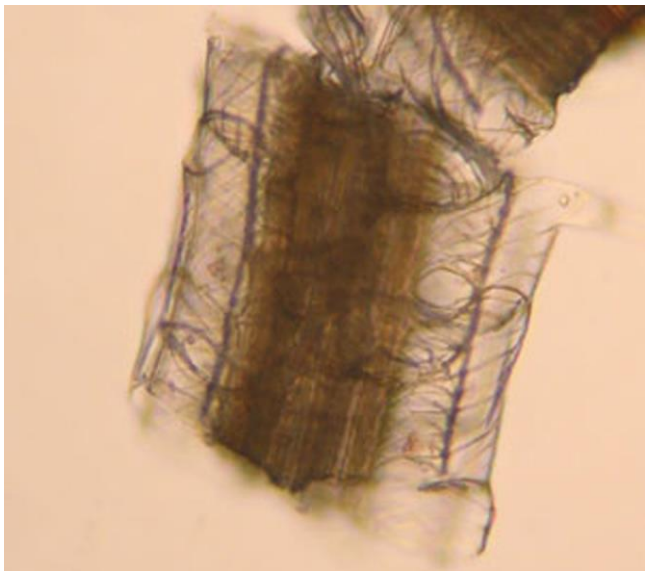

Figure 11. ***Sphagnum papillosum*** stem, vertical view, showing outer thin-walled cells and dense central core. Photo from Botany Website, UBC, with permission.

Figure 12. ***Takakia lepidozioides***, a primitive moss that conducts internally through cells that appear to be unspecialized. Photo by Rafael Medina, through Creative Commons.

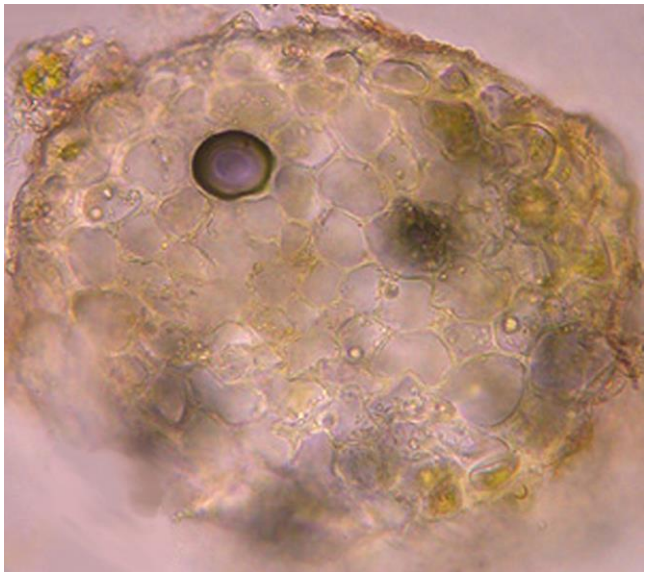

Figure 13. ***Takakia lepidozioides*** stem cs showing unspecialized conducting cells. Photo from Botany Website, UBC, with permission.

Figure 14. ***Haplomitrium hookeri***, a primitive liverwort that has some internal conduction. Photo by Des Callaghan, with permission.

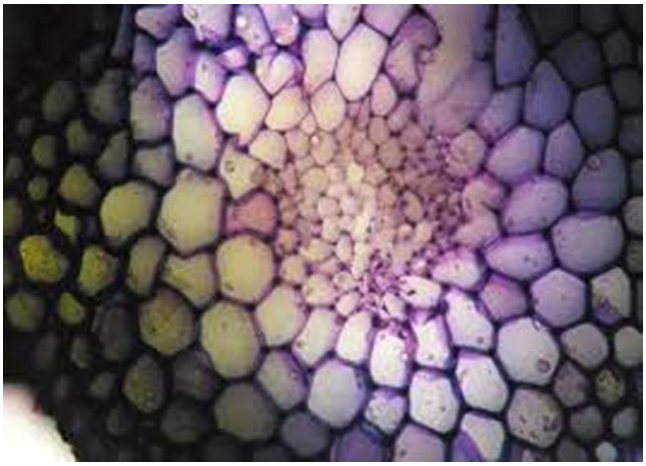

Figure 15. ***Haplomitrium*** stem cs showing differentiated cells in the center of the stem. Photo by Rachel Murray and Barbara Crandall-Stotler, with permission.

We have seen that bryophytes move water about internally as well as externally. There is ample evidence that they likewise move nutrients, hormones, and photosynthate within the plant, and of course, nutrients get moved externally with capillary water as well. Within stems, leptoids may serve to enhance nutrient movement; Hébant (1974) demonstrated that "sieve elements" (**leptome**) of ***Polytrichum commune*** (Figure 16-Figure 17) exude liquid. **Polytrichaceae** have highly specialized leptoids with polarized cytoplasmic organization within the axis. In the endohydric moss ***Polytrichastrum alpinum*** (Figure 18), labeled ^{14}C supplied as CO_2 travelled at the rate of 7.5 cm h^{-1} within the stems of a population in Point Barrow, Alaska, whereas in some tracheophytes, the rate may be little more than 1 cm per hour for water movement. In other mosses, including ***Sphagnum*** (Figure 7-Figure 11), less specialized parenchyma cells of the stem and seta carry out similar functions.

Figure 16. ***Polytrichum commune***, a moss with extensive internal conduction. Photo by Michael Lüth, with permission.

It does not require the sophisticated structures of ***Polytrichum*** (Figure 16-Figure 17) to move substances within mosses. Alpert (1989) demonstrated that photoassimilate moved from the leaves to the stem bases and even underground stems in ***Grimmia laevigata*** (Figure 19), a predominantly ectohydric moss, but he was unable to demonstrate any movement of mineral nutrients in this way (see stem of a related species, Figure 20).

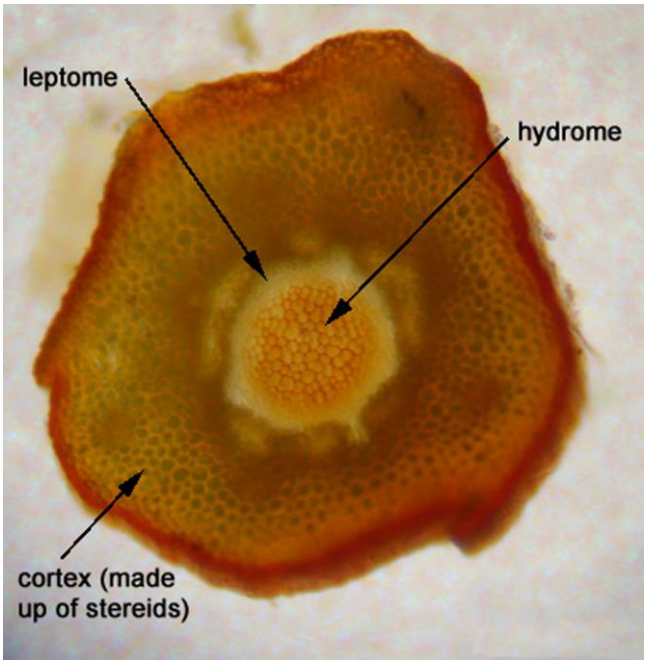

Figure 17. ***Polytrichum commune*** stem cs showing highly specialized conducting system with a leptome and hydrome. Photo from Botany Website, UBC, with permission.

Figure 18. ***Polytrichastrum alpinum*** with capsules, an endohydric moss. Photo by Michael Lüth, with permission.

Figure 19. ***Grimmia laevigata***, an ectohydric moss. Photo by Michael Lüth, with permission.

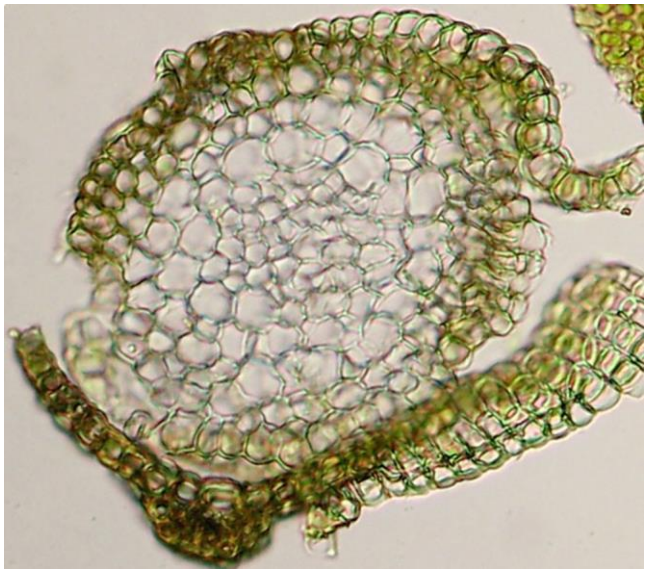

Figure 20. ***Grimmia pulvinata*** stem cs showing smaller cells in the central parenchyma cells of the stem. Photo from Botany Website, UBC, with permission.

Movement from Older to Younger Tissues

Consider the impact on our thinking when we discovered that even ***Sphagnum*** (Figure 7-Figure 11) moves nutrients from older, dead portions to younger tissues. Among these, it appears that in ***Sphagnum*** cellular N and P move to shoot segments, but that metallic elements do not (Hájek & Adamec 2009). Such ability permits it to live in extremely low nutrient habitats, yet have sufficient nutrients to sustain life and growth for centuries. Particularly in habitats such as true bogs, where all nutrients arrive through precipitation, the ***Sphagnum*** is able to trap and hold 50-90% of the deposited N (Li & Vitt 1997). This leaves little for tracheophytes, and Aldous (2002) found that the tracheophytes received less than 1% of that N supply.

Rydin and Clymo (1989) had already demonstrated that ***Sphagnum*** (Figure 7-Figure 11) is able to move both P and C upward through 7 cm of stem length. If the ***Sphagnum*** holds and relocates its N within its own tissues, the tracheophytes have little ability to compete for the limited supply of N they so greatly need. For example, Aldous (2002) demonstrated that ***Sphagnum capillifolium*** (Figure 21) translocates its N supply to growing tissues within the capitulum. In a relatively clean site in Maine, it moved 11-32% of its N and in an N-polluted site, it moved 64-83% within the 2-cm segments examined. Gerdol (1990) found that N, P, and K in ***Sphagnum*** of ombrotrophic bogs in the Alps were directly absorbed in the chlorophyllose cells (Figure 22), but also partly recycled from ageing tissues to the growing capitulum.

Figure 21. ***Sphagnum capillifolium*** (***nemoreum***), a species that moves its N to growing tissues in the capitulum. Photo by Aimon Niklasson, with permission.

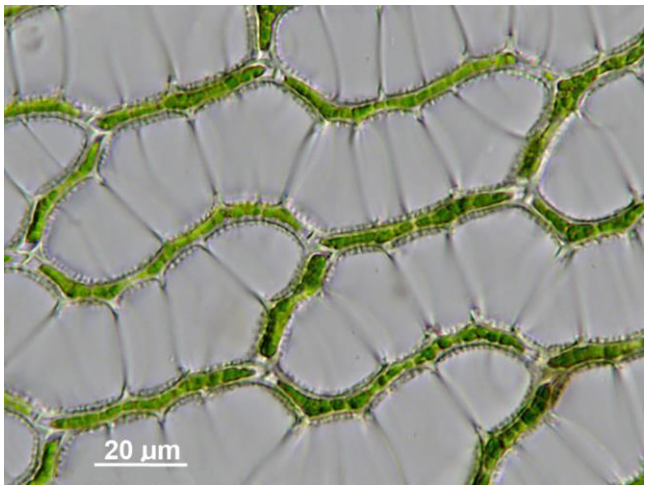

Figure 22. ***Sphagnum papillosum*** leaf cells showing network of green chlorophyllose cells and transparent hyaline cells. Note that the hyaline cells are long with spiral wall thickenings. These cells have pores what expose the inside cation exchange sites. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

Potassium is a highly soluble nutrient. Garciadeblas *et al*. (2007) demonstrated that ***Physcomitrella patens*** (Figure 23) expresses the same potassium and sodium transport systems as that found in flowering plants. Hence, we find that potassium is able to move from older to young tissues.

Bakken (1995) suggested that the reason the acrocarpous moss ***Dicranum majus*** (Figure 24) has a low N demand and persistence of N in young tissues at sites with high N is that it moves N from older to younger tissues. ***Pleurozium schreberi*** (Figure 25), a large, pleurocarpous, feather moss with no central strand or special conducting cells, is even able to move its nutrient supply about. And it is selective about it. It is able to move the soluble K^+ and Mg^{++} from plant base to apex, but, as in tracheophytes, the insoluble Ca^{++} is non-translocatable (Bates 1979). In fact, the concentration of Ca^{++} increases with distance from apex, assumedly reflecting its longer time to accumulate there. As a component of the cell wall, the concentration of Ca^{++} would increase as the cell sap was lost after death. But that is not the full explanation of its increasing concentration there. Ca^{++} supplied below the ***Pleurozium*** mats moves up the stems externally, taking advantage of the exchange sites and capillary movement of water (Bates & Farmer 1990). If it behaves like ***Sphagnum*** (Figure 21-Figure 22), broken cells will expose more exchange sites on the insides of cells, permitting Ca^{++} to be bound there.

Figure 23. ***Physcomitrella patens***, a species that transports K in the same manner as flowering plants. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Dicranum majus*** with sporophytes. Photo by Michael Lüth, with permission.

Figure 25. ***Pleurozium schreberi***. Photo by Michael Lüth, with permission.

Directional Differences

Wells and Brown (1996) demonstrated internal movement in the moss ***Rhytidiadelphus squarrosus*** (Figure 26). By collecting the moss and depriving it of any external nutrient supply, they were able to determine that apical growth continued, facilitated by **acropetal** (base to tip) transfer of cations (K^+, Mg^{++}, and Ca^{++}) from basal segments in proportion to that cation pool. When the mosses were pretreated with these three cations, the status of the shoots did not influence the elements that arrived in the newly grown shoots. Rather, acropetal transfer of externally bound cations occurred.

Figure 26. ***Rhytidiadelphus squarrosus***, a species with internal nutrient transport that seems to depend on living cells. Photo by Michael Lüth, with permission.

Surprisingly, even the heavy metals travel. Rühling and Tyler (1970) found that in ***Hylocomium splendens*** (Figure 27-Figure 28) metals such as Cu, Fe, and Mn are taken in by the young tissues and moved to the older ones. Could this be a means of sequestering them where they are less dangerous to the moss?

Figure 27. ***Hylocomium splendens*** on spruce forest floor. Photo by Janice Glime.

Species Differences

It seems that bryophytes differ among species in their nutrient mobilities, and in which nutrients go where. Eckstein and Karlsson (1999) compared the movement of N in the pleurocarpous moss ***Hylocomium splendens*** (Figure 27-Figure 28) and the acrocarpous ***Polytrichum commune*** (Figure 16-Figure 17), both common in boreal forests. In both species, the current year of growth served as a sink for N. In ***P. commune*** the older segments showed a net loss of N from June to September, a loss the authors interpreted as resorption of N to the subterranean rhizome.

Figure 28. ***Hylocomium splendens*** stem cs, showing central parenchyma cells. Photo by Botany Website, UBC, with permission.

By contrast, in ***Hylocomium splendens*** (Figure 27-Figure 28), the one-year-old segments, like the youngest segments, increased in N, whereas the older segments lost 50% of the N initially measured there (Eckstein & Karlsson 1999). All the N lost from the older segments could be identified in the two youngest segments. Thus, as the three-year-old segments of ***H. splendens*** died and became brown, N moved upward in the plant to younger segments. It is interesting that one species (***P. commune***, Figure 16-Figure 17) behaved as trees do in the fall, moving the N downward, whereas the other (***H. splendens***) behaved as trees or crop plants do in spring, moving it to the new growth.

Even the aquatic mosses behave like tracheophytes in their transfer of nutrients from older to younger segments. The soluble N, P, and K are concentrated in the apical regions of ***Fontinalis squamosa*** (Figure 29) and ***F. antipyretica*** (Figure 30-Figure 31), whereas the less soluble Ca, Mg, and Fe increase toward the base (Mártínez Abaigar *et al*. 2002). However, there are two possible explanations for this: N, P, and K are moved from older to younger tissues, just as they are in tracheophytes, or younger, more active tissues actively uptake these three nutrients. Mártínez Abaigar and coworkers considered both factors to be contributing.

Figure 29. ***Fontinalis squamosa*** in Wales, an aquatic species that concentrates its N, P, and K in apical portions. Photo by Janice Glime.

Figure 30. ***Fontinalis antipyretica***, an aquatic species that concentrates its N, P, and K in apical portions. Photo by Dick Haaksma, with permission.

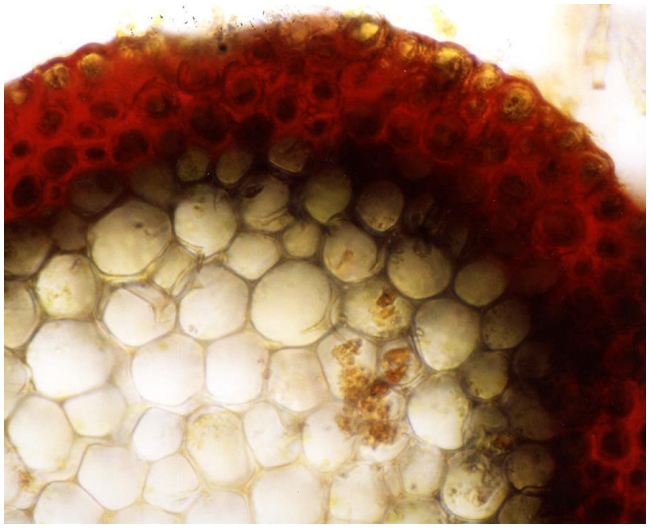

Figure 31. ***Fontinalis antipyretica*** stem cs stained with Aniline blue + eosin, showing differentiation of the cells. Photo courtesy of Isawo Kawai.

Mechanisms of Transport

Source to Sink?

This evidence of movement leads us to the question of how movement occurs. One possible mechanism is the **source to sink** phenomenon. In this case, a substance moves from an area of higher concentration (**source**) to one of lower concentration (eventual **sink**). But for this movement to continue, the final destination (**sink –** site of accumulation) must metabolize or store the substance in an insoluble form so that the recipient tissues become a sink and concentration gradients can continue from the source. For example, carbon moved as sucrose can be converted to starch or cellulose, or other constituent, causing the concentration of sucrose to continue to be higher at the source (see discussion under Sporophyte Conduction below).

In ***Rhytidiadelphus squarrosus*** (Figure 26) the rate of movement from old to young tissues is inversely related to the pool size, so that small segments move proportionally more nutrients to the developing tissues (Wells & Brown 1996), following a source-to-sink principle. When side branches were removed from ***Hylocomium splendens*** (Figure 27-Figure 28) to adjust the nutrient pool, loss of those branches led to lower concentrations of K^+, Mg^{++}, Ca^{++}, and Zn^{++} in the young shoots, indicating the importance of movement from older to younger tissues in this boreal forest feather moss (Brümelis & Brown 1997). These young segments did, however, produce more branches when branches on mature segments were removed. It seems that nothing is ever simple.

It appears that ***Pleurozium schreberi*** (Figure 25) could be a nitrogen **sink**. ***Pleurozium schreberi*** absorbs N in quantities apparently beyond its needs (Raeymaekers 1987; Raeymaekers & Glime 1990). And as might be expected, K^+ is easily leached out of the moss under stress of simulated acid rain and desiccation (Raeymaekers & Glime 1990). Thus, it appears that this moss that can provide 100% cover in Jack pine (*Pinus banksiana*; Figure 32) and other northern and boreal forests could have a major impact on nutrient flux. As an accumulator of N, it could become a sink, or it could release its excess load slowly over time. With its propensity for losing K^+ when suffering membrane damage from desiccation, ***P. schreberi*** and other bryophytes could be a means of sequestering K^+ from throughfall and dust, then releasing it later, perhaps hoarding it until rain comes, releasing it to tracheophyte roots at a time when the K^+ is most vulnerable to loss from the roots by leaching and runoff. This seemed to be the case for loss from ***Sphagnum*** when it was released near the end of the growing season, a result of rainfall that ended summer drought in a forested fen (Leary & Glime unpublished data). On the other hand, doe ***P. schreberi*** the very presence of its thick mat could prevent or diminish runoff loss, slowly releasing the K^+ to the soil as the rainfall event progresses. Our understanding of this process of bryophyte storage and later release to roots is as yet too limited to know the net impact.

Figure 32. ***Pinus banksiana*** forest where ***Pleurozium schreberi*** can form 100% ground cover. Photo from Minnesota Department of Natural Resources, through Creative Commons.

Enrichment Effects

When the moss is enriched with a nutrient, the translocated load can likewise be enriched. When input of N as $^{15}NH_4{}^{15}NO_3$ was compared at low and high levels, ***Sphagnum capillifolium*** (Figure 21) increased its annual N translocation from 11% to 80% (Aldous 2002). Aldous (2002) estimated that translocation contributes 0.5-11% of the annual N budget of the moss. This observation is consistent with the observation that N translocation is higher in the high N deposition Adirondack sites than in the low deposition Maine sites in the northeastern USA. However, the Maine sites had a low water table and severe drought during the year of measurement and thus we cannot assume that the greater movement in the Adirondacks was due to the greater concentration of N.

Internal Transport

Internal conducting cells are present in some members of both liverworts and mosses, but are unknown in hornworts (Ligrone *et al*. 2000). In mosses, they can be present in both generations, whereas in liverworts they are present only in the gametophyte. This is predictable in that liverworts form their setae after the capsule matures and is ready for dispersal. Thus, any conducting tissue would be of little value, and furthermore have little time to develop.

Structural Facilitation

Mosses also have the ability to conduct nutrients through **symplastic** transport in rhizoids and caulonemata, and similarly in the thallus parenchyma of liverworts (Ligrone *et al.* 2000). The **symplast** is the living protoplasm of the cells that is interconnected between cells, and substances can move through it following a concentration gradient.

In ***Takakia*** species (mosses), **Calobryales** (liverworts) and **Pallaviciniaceae** (liverworts) the water-conducting cells have perforated walls with pores derived from plasmodesmata. In the bryoid mosses, the water conducting cells (**hydroids**) are imperforate. In the **Polytrichaceae** (Figure 2, Figure 16- Figure 18) the **leptoids** (in this family they are highly specialized food-conducting cells) the cytoplasmic organization is polarized and has a distinct axial system of microtubules. In ***Sphagnum*** (Figure 7-Figure 11) and other mosses there are less specialized parenchyma cells in the leafy stem and seta.

Rydin and Clymo (1989) considered that the dominant understanding of ***Sphagnum*** (Figure 33) was that the lack of any anatomical specialization in the stem (Figure 34-Figure 35) caused those mosses to rely instead on external conduction in the capillary spaces. However, in their experiments they demonstrated that this thinking was wrong. Instead, internal transport is both "rapid and quantitatively important." In fact, when labelled ^{32}P and ^{14}C were supplied below the tips of ***S. recurvum*** (Figure 33), both moved to the top of the plant regardless of the direction of external mass flow. High concentrations of the labelled P and C were in the stem. Furthermore, if the stems were steamed above and below the point of application, the labelled P and C failed to move, suggesting that live cells were needed for the transport. ***Sphagnum recurvum*** has a central mass of parenchyma that is 20-50 cells across. These cells have end walls with perforations of about 100 nm and a density of 7-13 μm^{-2}, providing a single cell wall with ~1500 perforations.

Figure 33. ***Sphagnum recurvum***, a species that transports P and C internally. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.

It is likely that most bryophytes have some sort of conduction specialization within the stem. ***Sphagnum*** (Figure 33-Figure 35) has revealed its internal system within the central portion of the stem (Ligrone & Duckett 1998). This system is manifest by the absence of large central vacuoles, presence of a spindle-shaped nucleus with prominent axial system of endoplasmic microtubules, membrane-bound tubules and vesicles, and a high frequency of plasmodesmata in the crosswalls, all characteristics that are common to food-conducting cells. These same characters are also known in the food-

conducting cells of **Bryopsida** and suggest an organization specialized for symplastic transport. They are also known in rhizoids and caulonemata of mosses and in thallus parenchyma cells of liverworts (Ligrone *et al.* 2000).

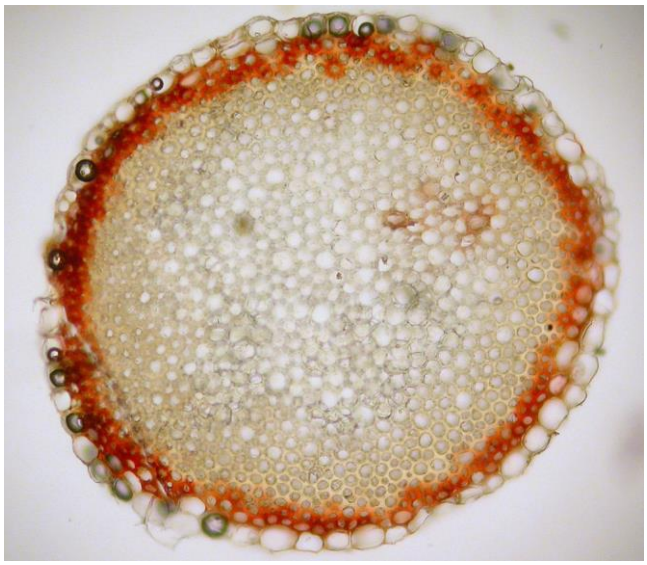

Figure 34. ***Sphagnum*** stem cross section with parenchyma cells in center. Photo by David Tng, with permission.

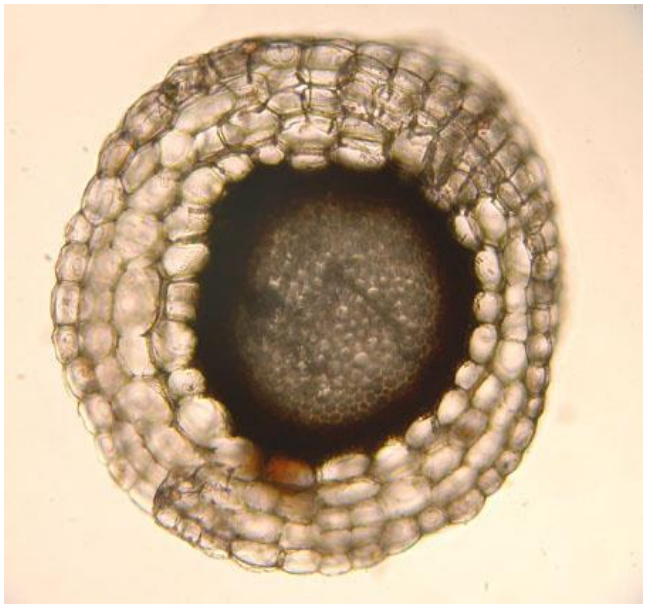

Figure 35. ***Sphagnum*** stem cs showing large outer cortex cells and small cells in central strand. Photo from Botany Website, UBC, with permission.

Leptome Transport

In tracheophytes, we tend to think of the phloem as transporting sugars downward, but other substances are transported there as well, and the direction of flow may at times be reversed. In bryophytes, the same is true.

Trachtenberg and Zamski (1978) determined that in addition to photosynthate, the **leptome** of ***Polytrichum juniperinum*** (Figure 36-Figure 37) moves ionic solutes such as sulfate and lead, whereas the chelated forms of iron and lead move in the **hydroids**. Ions from the moss surface are able to move across the cortex through the free space between the cells (**apoplastically** – see below). The leptome actually acts much like the endodermis of a root in serving as a barrier between the hydrome and the cortex. Thus, it becomes a site where toxic ions accumulate and are not transported to the rest of the plant. In their experiments, Trachtenberg and Zamski found that lead (Pb) moved in this way, accumulating in the leptome, but no Pb was found within the cytoplasm of any cortex cells. The leptoids, on the other hand, had heavy deposits. Hence, it appears that an active **symplastic** mechanism controls the movement of solutes and heavy metals in much the same way as the endodermis of a root. It is interesting that the stem of a moss has developed this same safeguard.

Figure 36. ***Polytrichum juniperinum***, a species that moves ionic solutes such as sulfate and lead in the **leptome**, but moves the chelated forms of iron and lead in the **hydroids**. Photo by Janice Glime.

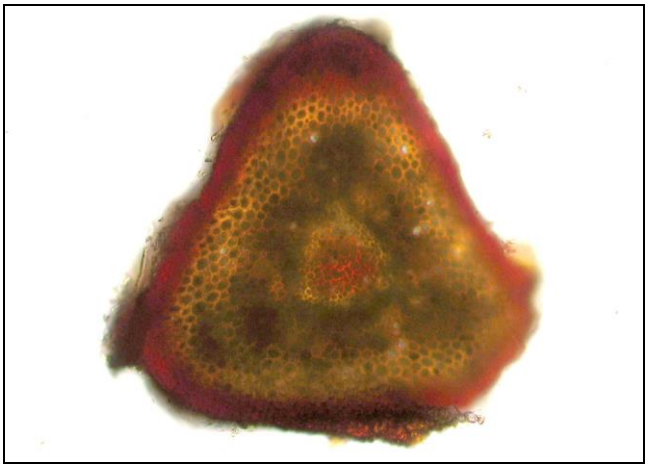

Figure 37. ***Polytrichum juniperinum*** stem cs with central hydroids and surrounding leptoids. Photo from Botany Website, UBC, with permission.

To obtain the same toxicity with the EDTA (chelated) Cu and Zn requires 500X more concentrated solution than with the ionic form. The chelation changes the mode of translocation within the bryophyte, with bound (chelated) ions moving in the free space to the leptome. These observations are consistent with the structure of the leptoid cells, which have large nuclei and an abundance of endoplasmic reticula (Eschrich & Steiner 1967; Hébant 1976), both permitting the cells to exercise high metabolic activity.

A similar phenomenon for copper and zinc has been seen in gemmae of ***Marchantia polymorpha*** (Figure 38) and protonemata of ***Funaria hygrometrica*** (Figure 39-Figure 40) (Coombes & Lepp 1974). Copper was more toxic than zinc to both species at levels above 8 mg L^{-1}. Protonemata did not grow and spores did not germinate in ***Funaria hygrometrica***. Even at 1 mg L^{-1}, few buds formed in ***Funaria***. In zinc, it produced rounded protonemal cells that could be interpreted as brood cells, known to occur as a response to unfavorable conditions (Van Andel 1952). In ***Marchantia***, rhizoid formation on gemmalings was inhibited at 1 ppm copper. Zinc did not cause any noticeable changes. In these bryophytes, there was a delicate line between essential levels and toxic levels of copper, with levels above 0.5 mg L^{-1} being deleterious to development.

Figure 38. ***Marchantia polymorpha*** gemmae cups showing gemmae. Copper and zinc are toxic to these gemmae. Photo by Walter Obermayer, with permission.

Figure 39. ***Funaria hygrometrica***. Photo by Michael Lüth, with permission.

Carbon Transport

We know that the **leptome** (that part of the stem of some mosses composed of **leptoids**, Figure 41) conducts assimilates, and that sucrose applied to the outside of the plant ends up in the leptoids (Trachtenberg & Zamski 1978). In tracheophytes, many other substances can travel in the phloem, the tracheophyte counterpart of the leptome. But, in a bryophyte, how does one examine what is travelling in a tube so small it cannot be seen without a microscope, for which preparation is likely to disrupt the whole process?

Figure 40. ***Funaria hygrometrica*** spore with developing protonema. Zinc and copper are toxic to both the spore and the protonema. Photo by Janice Glime.

One of the most fascinating techniques (to me at least) in all biology is the use of aphids to determine what travels in conducting tissues. Well, even bryophytes can have aphids! And Thomas and Lombard (1991) have taken advantage of this fascinating tool to determine just what travels in the leptoids of ***Polytrichum commune*** (Figure 16-Figure 17). The aphid, ***Myzodium modestum*** (Figure 42), a moss aphid and thus quite small, inserts a needlelike stylet into the moss conducting tissue (leptoids) to get nutrients. Thomas and Lombard found that when ***P. commune*** leaves are treated with ^{14}C-sucrose, 17-34% of the labelled carbon can be detected in 2-15 aphids within four hours. In fact, these aphids are so efficient at removal that the movement of sucrose to other parts of the plant and to shared underground rhizomes is reduced from its normal 4% to 1% or less.

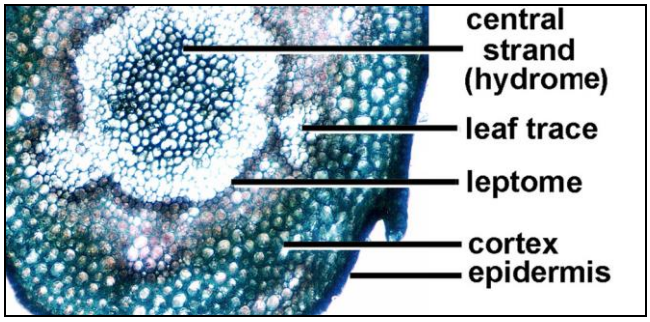

Figure 41. Cross section of ***Polytrichum*** stem. Photo courtesy of Isawa Kawai.

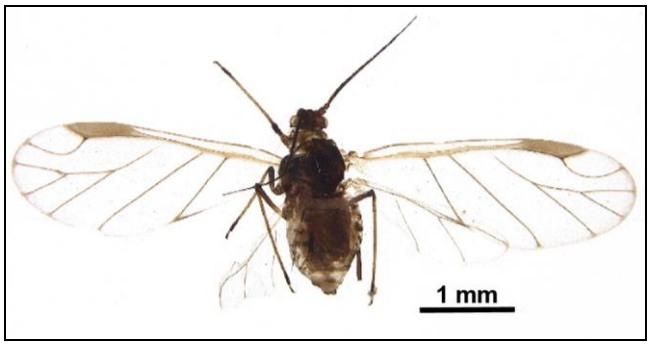

Figure 42. ***Myzodium modestum*** adult, a species that taps into the "sap" in leptoids of ***Polytrichum***. Photo from CBG Photography Group, through Creative Commons.

In ***Polytrichum commune*** (Figure 16-Figure 17), labelled ^{14}C from sucrose applied externally quickly appeared in the growing stem apex, young leaves, bud initials, and underground axes, all sinks for this C source (Reinhart & Thomas 1981). It appears that the C is more likely to move **acropetally** (toward the tip) than **basipetally** (toward the base). Nevertheless, labelled C travels from the leaves both acropetally (Eschrich & Steiner 1967) to the growing shoot apex and basipetally to underground rhizomes (Collins & Oechel 1974). The movement of externally applied sucrose requires ATP as an energy source for uptake, followed by movement from the **apoplastic** free space (see below) into the leptome, similar to **phloem loading** in tracheophytes (Reinhart & Thomas 1981).

The movement of externally applied labelled ^{14}C in ***Polytrichum commune*** (Figure 16-Figure 17), and by implication also the plant's own photosynthate, reaches several other leaves within two hours and reaches the rhizome within 72 hours or less (Reinhart & Thomas 1981). Experiments using radioactively labelled ^{14}C demonstrate that C moves in mosses in a **source-to-sink** fashion, as it does in tracheophytes. Furthermore, movement to the underground axis in this and other mosses allows translocation to neighboring members of a clone (Thomas *et al*. 1988, 1990), either directly through rhizomatal connections or indirectly through carbohydrates that escape into the soil/moss medium and can be absorbed. The carbon is both used and stored, with labelled carbon appearing in starches and cell wall polysaccharides one week and six weeks later, respectively (Thomas *et al*. 1988).

As you might expect, the patterns of translocation will vary between species of bryophytes, even in the same ecosystem. For example, near Fairbanks, Alaska, in a *Picea mariana* forest (Figure 43), ***Polytrichum commune*** (Figure 16-Figure 17) retained the most of labelled ^{14}C after 2 hours, while ***Sphagnum subsecundum*** (Figure 44) retained the least (Skré *et al*. 1983). However, after 35 days, it was ***Sphagnum subsecundum*** that had the highest fraction of radiolabelled ^{14}C in the brown tissues, with ***Polytrichum commune*** coming in second. The two pleurocarpous feather mosses, ***Hylocomium splendens*** (Figure 27-Figure 28) and ***Pleurozium schreberi*** (Figure 25), had no consistent pattern of translocation after 2 hours or 35 days. All four species exhibited high loss of labelled ^{14}C to respiration (presumably photorespiration) during the first 2 hours, which coincided with the peak of the growth season.

Sphagnum papillosum (Figure 9-Figure 11) translocated ^{14}C in the soluble fraction from older parts of the moss to the apex, with very little transfer into the insoluble fraction, to neighbors, or into the gas phase (Rydin & Clymo 1989). In fact, the transfer of ^{14}C to the capitulum from lower portions of the plant was about equal to that lost from the capitulum through respiration. The capitulum also transferred about twice as much ^{14}C to the insoluble fraction and about half as much to its neighbors. After 22 weeks, about 25% of the remaining labelled carbon was incorporated into new tissues.

Figure 43. Black spruce (***Picea mariana***) in Alaska taiga, home of ***Polytrichum commune***, ***Sphagnum subsecundum***, and feather mosses ***Pleurozium schreberi*** and ***Hylocomium splendens***. Photo from NOAA, through public domain.

Figure 44. ***Sphagnum subsecundum***, a species that stores carbon in its lower brown tissues. Photo by Michael Lüth, with permission.

Apoplastic Transport

Cell walls and extracellular spaces form the **apoplast** of a plant, including any bryophyte. Because the apoplast provides capillary spaces, it facilitates the movement of water and solutes across the plant tissues (Figure 45). Even the cell wall is composed of cellulose fibers that provide minute capillary spaces (Figure 46). But little seems to be published about apoplastic transport in bryophytes. (See above under Leptome Transport and under Carbon Transport; below under Sporophyte Conduction).

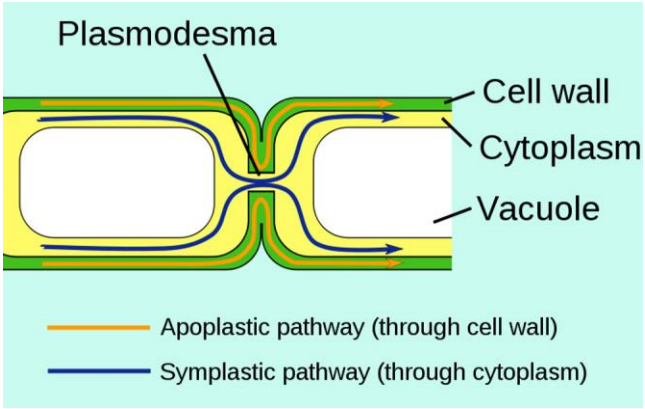

Figure 45. Apoplastic and symplastic pathways through cells. Note that such large vacuoles are not common in healthy bryophytes. Image by Jackacon, through public domain.

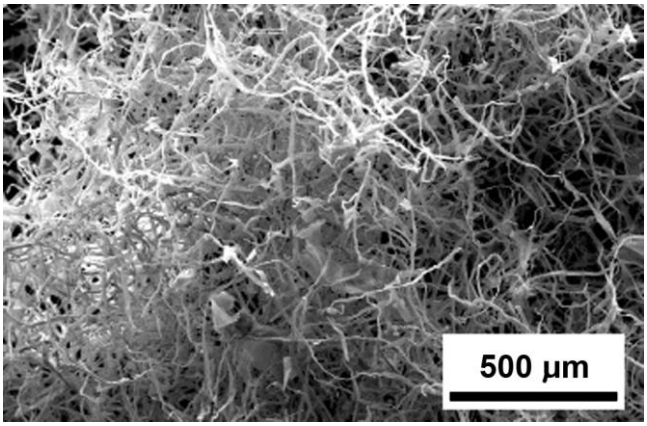

Figure 46. Cellulose SEM showing spaces among the fibers. Photo by Guiotoku *et al.* 2012, through Creative Commons.

David Hanson (Bryonet) has raised the interesting question about apoplastic movement of sugars in bryophytes. Would this sugar excretion that is beneficial to bacteria and fungi be less favorable in flowing water? I might add, would it instead facilitate the proliferation of the microbial community in the water, providing a nearby source of CO_2 for the CO_2-limited aquatic species? There is much to learn about nutrient relationships of bryophytes.

Desiccation Effects

Few studies have addressed the effects of desiccation on internal transport in bryophytes. In particular, the specialized food conduction cells (**leptoids**) of desiccation-tolerant mosses like ***Polytrichastrum formosum*** (Figure 47-Figure 48) undergo numerous changes during dehydration (Pressel *et al*. 2006). The endoplasmic microtubules disappear; the plastids, nucleus, and mitochondria become rounded and lose their longitudinal alignment of organelles. Instead of the typical stacks of endoplasmic reticulum of hydrated tissues, membranous tubules arranged at right angles to the main cellular axis appear. Small vacuoles fill the internal cytoplasm. The plasmalemma forms labyrinthine tubular extensions that outline newly deposited cell wall ingrowths. Leptoids become plugged with electron-opaque material while nearby parenchyma cells are depleted of their starch deposits. However, upon rehydration the leptoids return to their normal cytology within 12-24 hours. When the toxic oryzalin is provided to the plants, it prevents this recovery, indicating the importance of processes of living cells. Pressel and coworkers interpreted this to indicate a key role of the microtubular cytoskeleton in the recovery of the leptoids.

External Translocation

It is well known that water moves externally in mosses (and also internally to varying degrees). Nutrients in the solution move with the water, and nutrients adhering to the leaves can be carried with the water as well. Even soil nutrients can be moved upward this way.

As mosses die, especially those with an upright habit, ions can be moved externally from basal portions to upper portions rather easily (Brehm 1971; Brown 1982). Dead and dying lower tissues release ions that go into solution in the external surface film. Evaporative loss of water (**transpiration**) from the capitulum of ***Sphagnum*** (Figure 7-Figure 11) and from apices of **Bryopsida** causes water to move upward through the external capillary spaces. As it does, it carries with it the ions leaked from dead and dying cells. These can then be absorbed on the exchange sites of the apex. Brown (1982) considered that the higher concentrations of Ca^{++}, K^{+}, and Mg^{++} in ***Mnium hornum*** (Figure 49) in higher light intensities (Thomas 1970, in Brown 1982) could be the result of increased transpiration. But is it moved internally or externally? It has a well-developed internal conduction system (Figure 50).

Figure 47. ***Polytrichastrum formosum*** capsules, a moss with internal conduction. Photo by Michael Lüth, with permission.

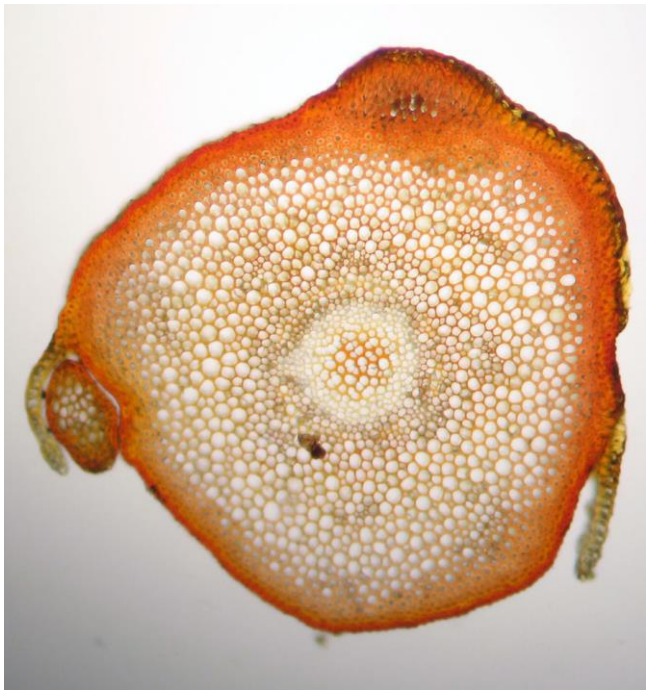

Figure 48. ***Polytrichastrum formosum*** stem cs showing leptoids and hydroids. The leptoids undergo structural changes when dehydrated and regain normal structure when rehydrated. Photo by Botany Website, UBC, with permission.

Figure 49. ***Mnium hornum***, a species that may transport nutrients through a transpiration stream. Photo by Michael Lüth, with permission.

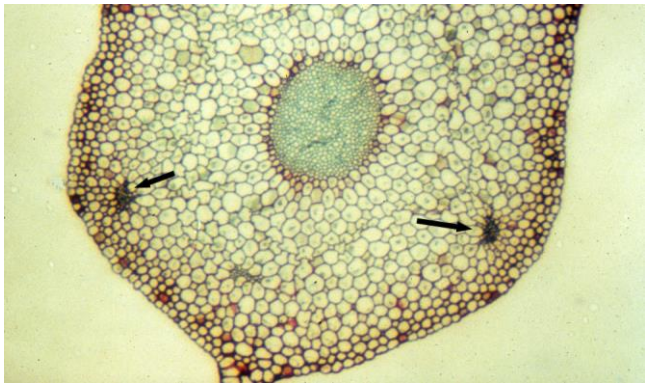

Figure 50. ***Mnium*** stem showing central strand where hydroids occur and leaf traces (arrows) connect to leaf bases. Photo by Janice Glime.

Sporophyte Conduction

As we have already seen for water, the sporophyte gets nutrients, hormones, and an energy supply from the gametophyte through the sporophyte **foot** (Figure 51-Figure 53) (Courtice *et al*. 1978). Some of the evidence for this transfer is indirect. For example, in ***Polytrichastrum formosum*** (Figure 47-Figure 48), a decrease in the amino acid arginine in the gametophyte is coincidental with an increase in the sporophyte (Whel 1975). Whel suggested that this parallels the tracheophyte movement of N from a mature to young organ.

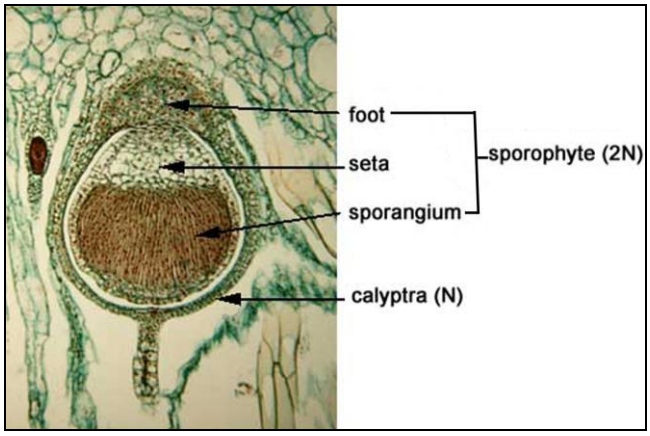

Figure 51. ***Marchantia polymorpha*** (thallose liverwort) capsule ls showing location of the foot next to gametophyte tissues. Photo from Botany Website, UBC, with permission.

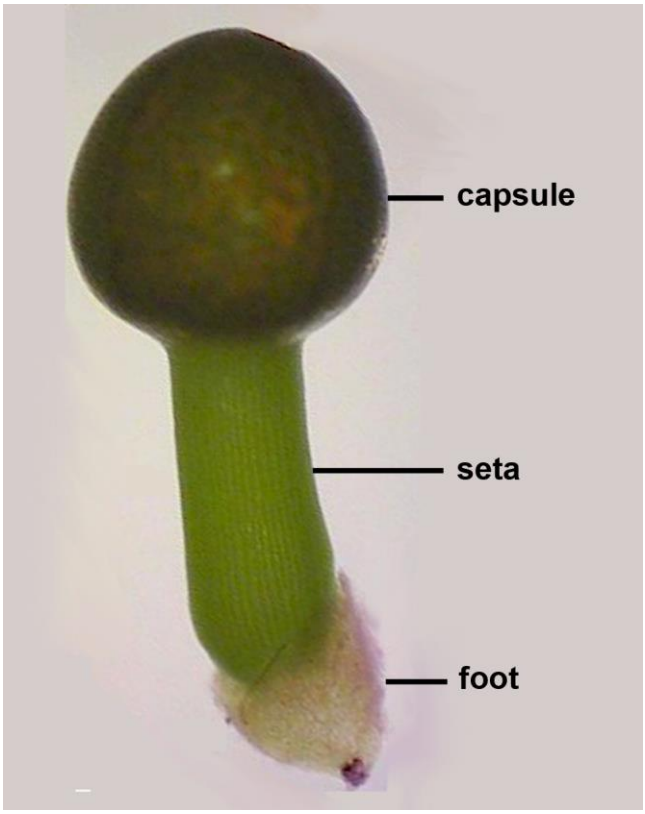

Figure 52. Liverwort (***Pellia***) young sporophyte. Photo by Paul Davison, with permission.

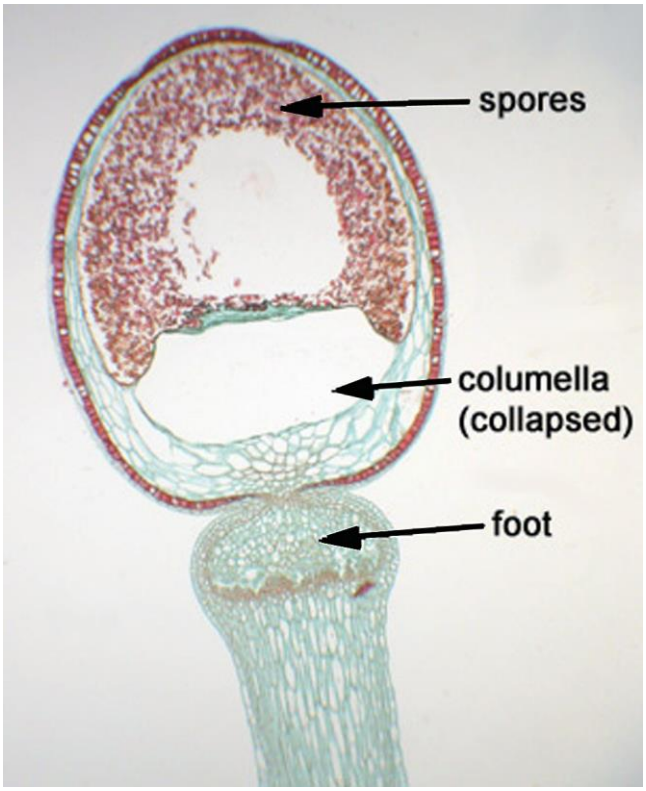

Figure 53. ***Sphagnum*** capsule ls showing foot imbedded in pseudopodium (gametophyte) tissue. Photo from Botany Website, UBC, with permission.

The internal structure reveals **transfer cells** at the gametophyte-sporophyte junction (Figure 54; Lal &

Chauhan 1981). The transfer cells are found in the foot of the sporophyte and in the adjacent gametophyte tissue and are endowed with an extensive and complex wall labyrinth. Ligrone and Renzaglia (1990) demonstrated that the hornwort ***Dendroceros tuberculatis***, as in other hornworts, is endowed with dense protein deposits in the vacuoles of both gametophyte transfer cells and the sporophyte foot. The structure of the transfer cells suggests a function in the movement of metabolites from the gametophyte to the sporophyte by their numerous mitochondria and intense enzyme activity, especially of phosphatases and some respiratory enzymes (Lal & Chauhan 1981).

The junction cells are the first to differentiate in the young sporophyte (Kwok & Rushing 1999). The transfer cells on both sides of the junction have plastids and starch content, with numerous small vacuoles and lipid deposits in the junction cells, further supporting the role of this region in transfer of nutrients to the sporophyte.

Caussin *et al*. (1983) demonstrated that sporophytes of ***Polytrichastrum formosum*** (Figure 47-Figure 48) absorb the amino acids glycine, threonine, and α-aminoisobutyric acid through the **haustorial** (absorptive) foot, using the transfer cells. Removal of the haustorial foot significantly reduced the absorption of these amino acids into the sporophyte.

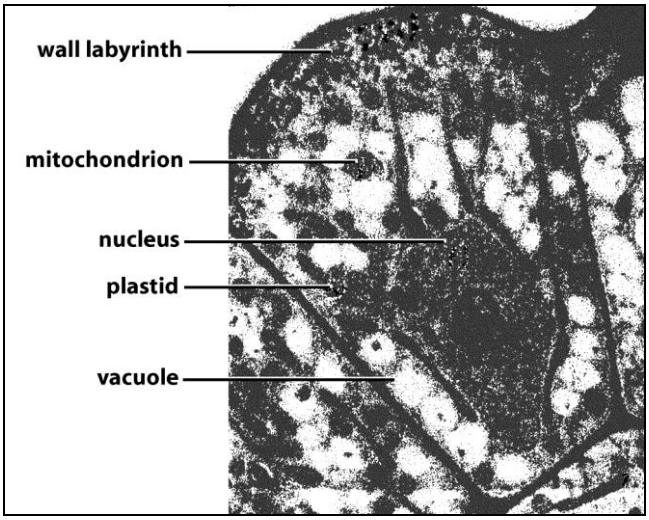

Figure 54. Transfer cell showing wall labyrinth. Computer-drawn from photo in Lal and Chauhan (1981).

Chevallier *et al*. (1977) demonstrated that radioactive orthophosphate moved from the gametophyte to the capsule and eventually to the spores in ***Funaria hygrometrica*** (Figure 55). However, once the capsule turned from green to brown, indicating maturity, the original 18% transfer rate turned to zero. But this is not the only potential means for the sporophyte to get its nutrients. It is, at least in ***Funaria hygrometrica***, able to absorb nutrients directly through its capsule, hence opening the possibility that it gets some sporophyte nutrients from dust and rainwater.

It appears that K^+ moves into the developing sporophyte rapidly, whereas Ca^{++}, which is generally immobile, moves more slowly (Brown 1982). In Brown's study, as the gametophyte senesced, its K^+ diminished and the concentrations of Ca^{++} and Mg^{++} increased, presumably due to movement of K^+ from the senescing gametophyte to the young sporophyte, followed by Ca^{++} and Mg^{++} occupying the vacated exchange sites on the gametophyte.

Figure 55. Capsules of ***Funaria hygrometrica***. Photo by Janice Glime.

Marsh and Doyle (1981) demonstrated that sugars are transported actively by the transfer cells. A more startling discovery is that the sporophyte of ***Anthoceros punctatus*** (Figure 56) transfers sugars from the photosynthetic sporophyte to the thallose gametophyte, where it is used by its ***Nostoc*** (Figure 57) partner (Stewart & Rodgers 1977)!

Figure 56. Thallus of ***Anthoceros punctatus*** with young sporophytes. Photo by Des Callaghan, with permission.

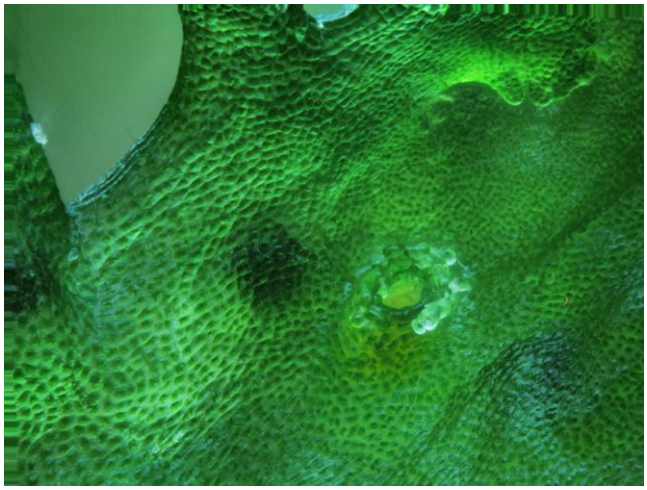

Figure 57. ***Anthoceros punctatus Nostoc*** colonies (dark area). Photo by Des Callaghan, with permission.

As nutrients cross the **placenta** (gametophyte-sporophyte interface) into the sporophyte, there is another opportunity for nutrient discrimination. Basile *et al.* (2001) found that the gametophyte accumulated much greater quantities of Pb and Zn than did the sporophyte in ***Funaria hygrometrica*** (Figure 55). These two elements accumulated in the placental **transfer cells** on both gametophytic and sporophytic sides. When the two metals were applied in the lab, Basile and coworkers found that the two generations had different accumulation quotients.

The size of the sporophyte seems to play a role in determining the rate of transfer of carbon in the photosynthate from the gametophyte to the sporophyte (Browning & Gunning 1979). In ***Funaria hygrometrica*** (Figure 55), labelled gametophyte photosynthetic products were transported to the sporophyte at a linear rate for up to 12 hours after treatment with $^{14}CO_2$. Movement from the **haustorium** (nutrient exchange area in foot of sporophyte) to the capsule, through the seta, occurs at the slow rate of 1-3 mm h^{-1}. And larger sporophytes received the photosynthate at a faster rate than did smaller ones. Does this mean that there is a source-sink movement, with larger capsules forming a larger sink? Or is there a transpiration stream involved in which larger capsules lose water faster, hence drawing water up from the gametophyte much like a tracheophyte water stream? Both water stress and lack of light inhibited transport, but if only the sporophyte was darkened, it had no effect. This again suggests the possibility of a source-sink movement, with the source (gametophyte) becoming depleted of photosynthate in the dark. But it is also possible that a transpiration stream could be involved, as suggested by the loss of movement under drought stress. Both could contribute.

In members of ***Polytrichum*** *s.l.* (Figure 58-Figure 59), transport of carbon from the gametophyte to the sporophyte is especially important (Renault *et al*. 1992). The calyptra completely covers the capsule and is fortified with dense hairs, limiting photosynthesis by the capsule. In ***Polytrichastrum formosum*** (Figure 47-Figure 48) sucrose serves as the primary soluble sugar for both the sporophyte and gametophyte. However, in the **apoplast** (capillary spaces in cell wall) of the **vaginula** (bottom part of archegonium when calyptra separates; foot of sporophyte is imbedded in vaginula – Figure 60) the sugars are primarily hexoses, with the conversion from sucrose to hexose facilitated by a cell wall **invertase** at *p*H of 4.5. The highest concentration (~230 mM) of soluble invertase occurs in both the haustorium and the vaginula, where a soluble invertase has its highest activity (*p*H 7.0). Glucose uptake is carrier-mediated, with little dependence on external *p*H. Once glucose is absorbed into the haustorium, it is converted to sucrose. Hence, sucrose is converted at the gametophyte-sporophyte interface to fructose and glucose, then converted back to sucrose after the haustorium cells absorb hexose. These changes may permit the sugar accumulation in the haustorium.

A more detailed anatomy of the gametophyte-sporophyte junction in the moss ***Acaulon muticum*** (Figure 61) may clarify some of the nutrient transfer (Rushing & Anderson 1996). This junction has the sporophyte foot imbedded in the gametophyte vaginula, with intervening placental space. The basal cell of the foot develops extensive wall ingrowths. Sporophyte cells that contact that basal cell likewise develop ingrowths on their outer tangential and radial walls that contact the basal cell. These young sporophyte cells have numerous mitochondria, strands of endoplasmic reticulum, and dictyosomes, especially adjacent to areas of extensive wall development. The plastids contain abundant reserves of starch. The wall ingrowths continue to become more extensive on all walls of the sporophyte foot, but never occur on the upper wall of the basal cell where it contacts the remainder of the sporophyte. As the sporophyte develops, the plastids of the foot contain fewer starch reserves. The gametophyte vaginula does not exhibit wall ingrowths until the sporophyte foot is well developed. Rushing and Anderson suggested that the early development of the wall ingrowths in the sporophyte foot and especially the basal cell may facilitate the rapid movement of both water and nutrients from gametophyte to sporophyte.

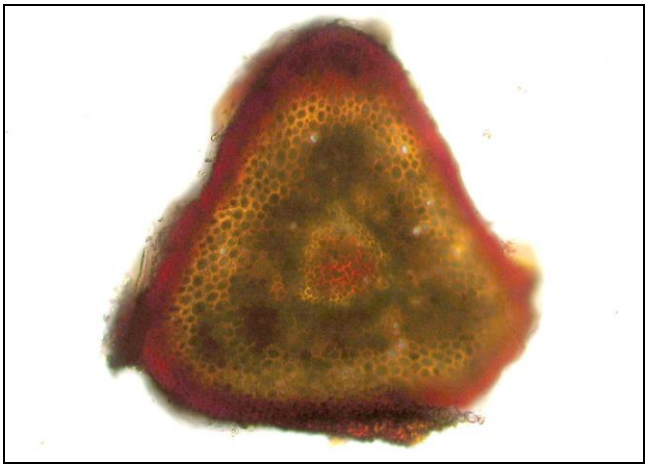

Figure 58. ***Polytrichum juniperinum*** stem CS showing conducting hydrome and leptome that continue into the seta. Photo from Botany Website, UBC, with permission.

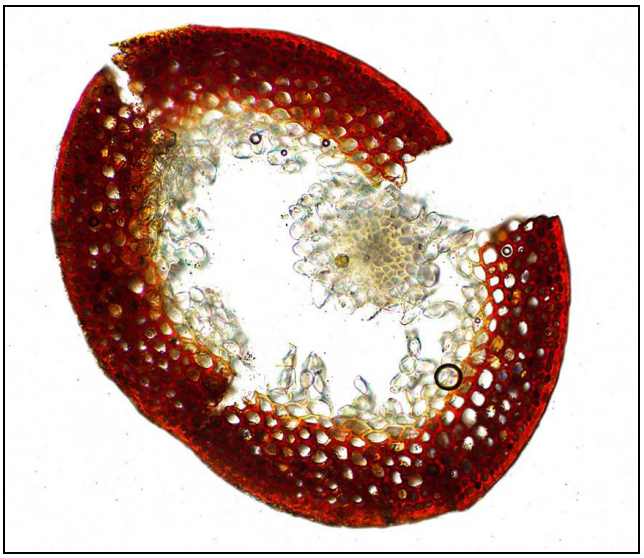

Figure 59. ***Polytrichum juniperinum*** seta cross section showing cells in the center where conduction occurs. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

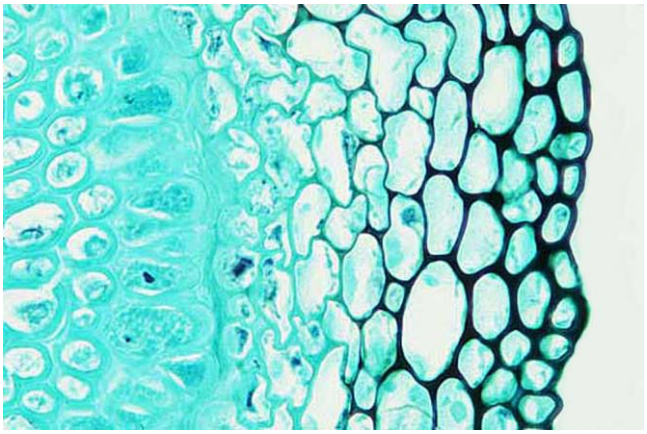

Figure 60. **Vaginula** cross section showing turquoise-stained cells on left that contact the sporophyte foot. Source unknown.

Figure 61. ***Acaulon muticum***, a species with a very short seta that helped us understand the structure of the vaginula and foot. Photo by Michael Lüth, with permission.

There has been much recent speculation into the role of the stomata in the sporophyte of bryophytes. Haig (2013) suggests an important function in conduction. Once the calyptra has been "outgrown" by the capsule, leaving the lower part of the capsule exposed, the stomata may provide a transpiration stream that helps to draw resources from the gametophyte up to the sporophyte, much as the open stomata of tree leaves facilitate the transpiration stream of water and nutrients upward in trees. Haig contends that the seta serves to raise the capsule above the boundary layer, facilitating the movement of moisture from the moss to the air and coincidentally moving the nutrients upward from the gametophyte. Haig further suggests that the calyptra serves to protect the gametophyte from excessive transfer to the developing sporophyte.

Summary

While most bryophytes obtain their nutrients primarily from atmospheric dust and precipitation, acrocarpous mosses may also receive considerable input from the substrate through upward movement externally and subsequent internal movement. Cation exchange sites hold nutrients on leafy surfaces and facilitate uptake and discrimination between ions. Further active processes are able to distinguish ions formed by N, P, and K from more exchangeable cations such as those of Ca^{++} or Mg^{++}, and they are generally able to maintain relatively constant levels of these essential nutrients despite changes in environmental concentrations. Bryophytes use pathways both through cells (**symplastic**) and between cells (**apoplastic**) to move internal substances, just as do the tracheophytes. And they may even have a filter similar to the endodermis, in the form of a **leptome**, at least in the **Polytrichaceae**. Leptome cells may become disfigured during desiccation, but they return rapidly to normal configuration following rehydration.

Many bryophytes also behave like tracheophytes in moving essential ions such as those formed by N, P, and K from older to younger parts, whereas less soluble ions like Ca^{++} remain in older tissues. Their ability to acquire ions from rainwater and hold them in their tissues makes them a sink for forest nutrients, but some, especially K^{+}, may be released in heavy rainfall following a dry period, returning the nutrients to the forest floor as a pulse. Heavy metals may be sequestered in older tissues or on external exchange sites. Movement may additionally occur through **source to sink** mechanisms or a transpiration stream.

Sucrose is transported in the **leptome**, as well as through stem parenchyma cells. Radiolabelled carbon quickly appears in the stem apex, young leaves, bud initials, and underground axes. Most of the movement is toward the apex (**acropetal**), but some also moves to the base (**basipetally**). Some reaches other stems in the clone. The **leptome** also moves ionic solutes, whereas the chelated forms move in the **hydroids**.

Sugars and nutrients move from the gametophyte to the sporophyte through the **transfer cells** in the sporophyte foot. But members of the **Anthocerotophyta** may transfer photosynthate from the green sporophyte to the gametophyte to nourish the ***Nostoc*** colonies. Stomata at the base of the capsule may create a transpiration stream that helps to move resources from the gametophyte to the sporophyte once the capsule is partially free of the calyptra.

Their ability to move nutrients from old to young tissues and to store them both externally and internally raises serious questions about their role in the nutrient cycling in the habitats where they are abundant. On the other hand, they may release potassium when roots need it the most.

Acknowledgments

I appreciate the contributions of undergraduate Phil Gaudette and M. S. student Jennifer Jermalowicz Jones for their critical reading of the manuscript from the perspectives of students interested in nutrient relationships of bryophytes.

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