

# CHAPTER 8-4

## NUTRIENT RELATIONS: UPTAKE

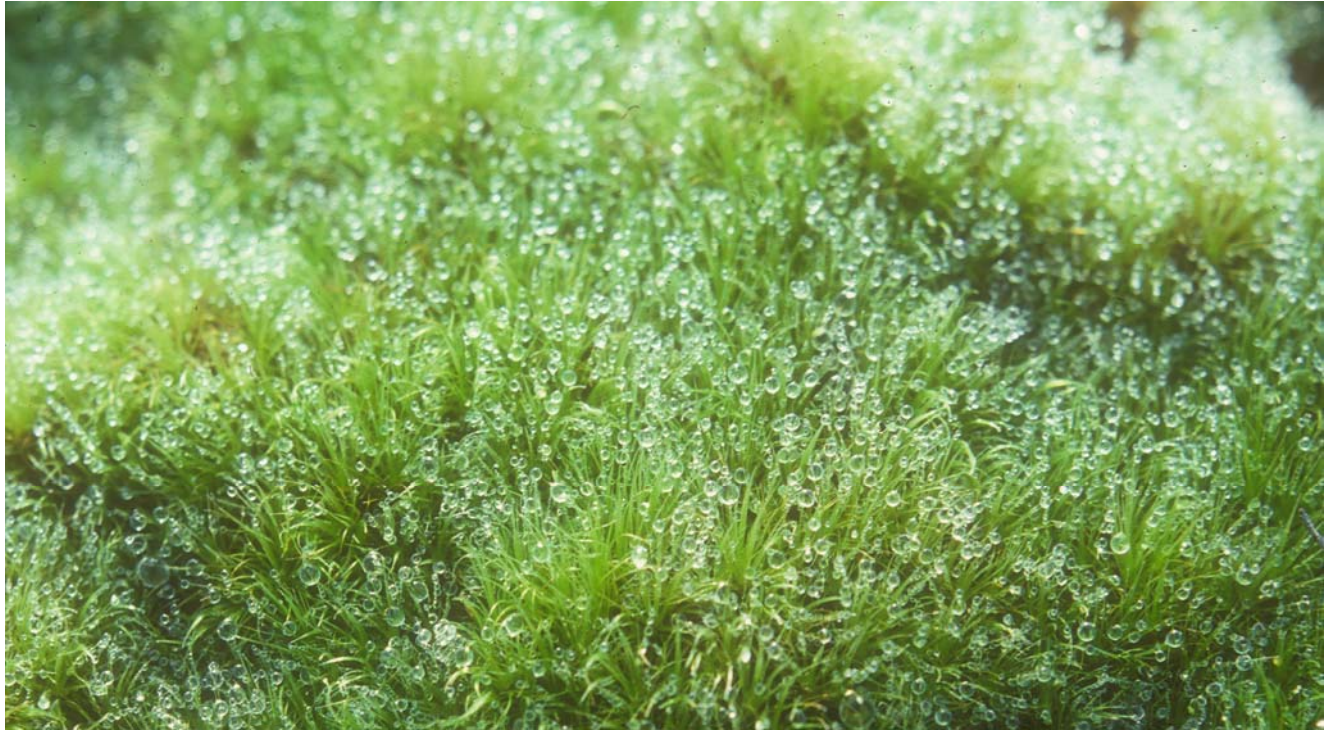


Figure 1. Drops of "steam" from geothermal vents resting on the wire-like leaves of *Campylopus holomitrius* and providing a source of nutrients. Photo by Janice Glime.

### Uptake

The role of bryophytes in nutrient uptake within ecosystems is generally ignored because of their small stature. Weetman and Timmer (1967) showed that the common feather moss *Pleurozium schreberi* in a black spruce (*Picea mariana*) forest took up only 23-53% of the N, P, K, and Mg taken up by trees. Nevertheless, that is a non-trivial figure. On the other hand, their contribution to sequestering nutrients can be substantial. Yet we have little concept of whether their net contribution is beneficial or detrimental in those ecosystems where they abound.

First we need to recall that the sources of nutrients include precipitation, dust, and to a limited extent, substrate (Figure 1). Brown (1982) explains that bryophytes absorb mineral nutrients over their entire surface. This ability is promoted by two characteristics of bryophytes: a large surface area to volume ratio, and a low surface resistance, relative to tracheophytes, due to the limited development of cuticle. This is further enhanced within the bryophyte by typically having leaves of only one cell layer in thickness, hence exposing every leaf cell directly to the nutrient supply immediately. Actual entry into the cell is most likely similar to that of tracheophytes.

Their typical differences in site of uptake would seemingly remove the bryophytes from competition with tracheophytes for soil nutrients. Due to lack of vessels and tracheids, we have assumed that uptake of nutrients by

bryophytes is primarily through their leaves. But even in the endohydric *Polytrichum*, water entry is gained primarily at the tips of the plants by water that has travelled upward through external capillary spaces. Hence, we can expect that most nutrient entry is not through rhizoids, but through leaves, and at least in some mosses may be greater at the tips than in lower parts of the plant.

Even if bryophytes were to use their rhizoids to gather some nutrients, the soil penetration by these structures is generally shallow and well above the zone occupied by fine roots. Instead, we have assumed that bryophytes typically rely largely on dust on their surfaces and on nutrients dissolved in rainfall, largely through leachates acquired in canopy throughfall. This is a quite different strategy from that of tracheophytes, although in *Polytrichum* it appears that some nutrients might enter through the rhizoids (Chapin *et al.* 1987).

Taylor and Witherspoon (1972) found that *Dicranum* (Figure 2), which grows in a relatively tight clump, retains more particles than do open lichens such as *Cladonia*, even though these lichens display considerable surface area. Hence, we should expect such tight cushions to be more effective at trapping than more open bryophytes like *Brachythecium* (Figure 3) or *Mnium*. On the other hand, Shacklette (1965) found that bryophytes were significantly contaminated with soil particles, including insoluble ones

such as Al, Be, Fe, Si, and Zr. But, as already discussed, it would appear that even deeper soil is not immune to moss nutrient scavenging, perhaps through a combination of capillary action and concentration gradient.



Figure 2. *Dicranum* in its dry state, showing growth form that traps dust particles easily. Photo by Herschel Horton.



Figure 3. *Brachythecium rutabulum*, showing open growth form that traps less dust than the more cushiony forms like *Dicranum*. Photo by Janice Glime.

The standing or flowing water habitat of *Sphagnum* fen species contrasts sharply with the rainfall source of many other bryophytes. Although species occupying raised bogs with no ground water input may rely almost entirely on rainfall, those mosses in fen situations undoubtedly get nutrients from the ground water as well. In a study of 21 species of *Sphagnum* in Poland, this genus demonstrated its ability to accumulate N, P, and K in the upper parts of the plant through active uptake, whereas Ca, Mg, and Na accumulated through passive **cation exchange** (Wojtun 1994; see below), suggesting an arrangement of nutrients within the plant similar to that of the tracheophytes.

Bryophyte uptake can relate to age. In studying the Alaskan black spruce forest, Chapin *et al.* (1987) found that in three of the moss taxa studied, the phosphate absorption capacity increases with age of green tissue, but decreases with age of brown tissue.

## Cation Exchange

Once we understand external transport, we must examine how the nutrients actually enter the moss. Are all nutrients equally capable of entry? Most likely not. And

can these bryophyte leaves function as well as roots of tracheophytes in the absorption of nutrients?

The ability of bryophytes to take up nutrients from weak solutions (Babb & Whitfield 1977) permits them to grow in situations that may be limiting to tracheophytes. We know that many (perhaps all) bryophytes sequester nutrients on exchange sites (Clymo 1964; Craigie & Maass 1966; Wells & Brown 1990; Bates 1997), but that the exchange capacity varies among species (Büscher *et al.* 1983). **Cation exchange capacity** (CEC) is due to high concentrations of non-esterified pectates, mostly polyuronic acids, within the cell walls (Clymo, 1963; Craigie & Maass, 1966) and seems to be the first step in uptake of nutrient cations (Koedam & Büscher 1983). Koedam and Büscher (1983) demonstrated that CEC in mosses, typically much higher than in tracheophyte roots (Table 1; Knight *et al.* 1961), was related to soil preference and carbonate content.

Popper and Fry (2003) have demonstrated that bryophytes (including hornworts, thalloid and leafy liverworts, and basal mosses) have higher concentrations of glucuronic acid in their primary cell walls than any of the other land plants. Basal mosses have higher concentrations than more advanced mosses, and the highest occurs in *Sphagnum*.

Table 1. Mean cation exchange capacity of cell walls of tracheophyte roots compared to that of bryophyte gametophores. Tracheophytes from Klein & Horst (2005); bryophytes from Bates (1982b).

	$\mu\text{g g}^{-1}$ dry mass	
<b>Calcicolous bryophytes</b>		
<i>Ctenidium molluscum</i>	15,510	
<i>Tortella tortuosa</i>	15,160	
<i>Schistidium apocarpum</i>	12,940	
<i>Homalothecium sericeum</i>	12,460	
<i>Orthotrichum cupulatum</i>	12,250	
<i>Syntrichia ruralis</i>	10,160	
<b>Calcifugous bryophytes</b>		
<i>Ptychomitrium polyphyllum</i>	6,690	
<i>Racomitrium fasciculare</i>	3,330	
<i>Dicranoweisia cirrata</i>	3,200	
<i>Andreaea rothii</i>	2,660	
<i>Grimmia donniana</i>	2,610	
<i>Racomitrium lanuginosum</i>	2,330	
<b>Tracheophytes</b>	<b>0-5 mm</b>	<b>5-20 mm</b>
field bean	491.0	543.7
yellow lupine	422.0	527.4
barley	106.8	59.1
rye	63.1	65.5

This nutrient uptake in poor nutrient habitats is further supported by the greater ability of *Sphagnum* to exchange  $\text{Ca}^{++}$  and  $\text{Mg}^{++}$  ions for  $\text{H}^{+}$  ions, providing them with a mechanism to obtain very limited nutrients in their habitats. For example, Temple *et al.* (1981) reported the exchange capacity of *Sphagnum* to range 0.9 to 1.5 meq per gram dry biomass, whereas that of other mosses generally ranges 0.6-1.1. On the other hand, if the  $\text{Ca}^{++}$  content of the habitat is too high, *Sphagnum* will bind so much  $\text{Ca}^{++}$  to its leaf surfaces that it will eventually kill the moss (personal observation). Although this cation exchange process is

beneficial in obtaining nutrients, it can also result in accumulation of high levels of heavy metal pollutants (Brown 1984) such as Cd because the moss lacks sufficient selectivity in either binding or uptake of these non-nutrients (Brown & Bates 1990).

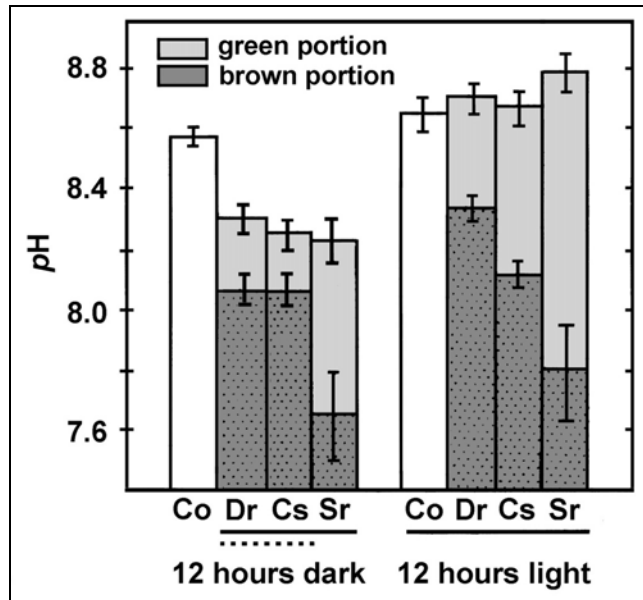
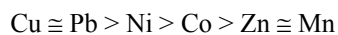


Figure 4. Comparison of pH-lowering ability of three mosses from an alkaline fen, Lawrence Lake, Barry County, Michigan, USA, following 48-hour incubation. Co = control lake water, Dr = *Drepanocladus revolvens*, Cs = *Campylium stellatum*, Sr = *Sphagnum russowii*. 12 hours dark and light indicate last cycle completed. Dark grey shading = brown portions, light grey shading = green portions of moss. Horizontal lines indicate no significant differences among green (active) (—) and brown (senescent) (- - -) moss species (distribution-free multiple comparisons test,  $\alpha = 0.05$ ;  $n = 10$ ). Starting pH = 8.25.

Breuer and Melzer (1990) commented that *Sphagnum* "shows behaviour of a relatively ideal ion exchanger." And, while species differ in their capacity, the coefficients of selectivity are independent of species. These bound cations can readily be displaced if another cation is present at a higher concentration, has a larger hydrated atomic radius, or has a higher valency (Bates 2000). Rühling and Tyler (1970) demonstrated the order of binding affinity of several heavy metal cations using *Hylocomium splendens*:



These heavier cations preferentially bound to the exchange sites even when lighter cations of  $\text{Ca}^{++}$ ,  $\text{K}^+$ ,  $\text{Mg}^{++}$ , and  $\text{Na}^+$  were present in high concentrations.

Bryophytes, like tracheophyte roots, have **polyuronic acids** that provide binding sites for cations on cell walls. *Sphagnum*, in particular, has extensive binding sites through its use of the polyuronic acid known as **galacturonic acid** (Clymo 1963). Through this capability, *Sphagnum* is able to outcompete tracheophytes. By creating an "intense nutrient impoverishment" for other plants, *Sphagnum* gains a competitive edge (Van Breemen 1995). It can impede growth of peatland shrubs such as *Chamaedaphne calyculata* (Bartsch 1994) by sequestering nutrients the shrubs need for growth.

Seemingly all bryophytes have a large number of exposed exchange sites, compared to those even of roots of

tracheophytes (Knight *et al.* 1961). These exchange sites are essential to the uptake of nutrients in non-*Sphagnum* bryophyte taxa as well. For example, *Pseudoscleropodium purum* ceased absorbing  $\text{Mg}^{++}$  and lost intracellular Mg when the exchange sites were saturated with  $\text{CaCl}_2$ , suggesting adherence to exchange sites may be a necessary prerequisite to  $\text{Mg}^{++}$  uptake (Bates 1989b). Addition of both K and Ca greatly increased their concentrations in the exchangeable fraction of the cell but significantly reduced the concentration of Mg. Furthermore, when bryophytes become desiccated, nutrients leave the cells through leaky membranes (Bewley 1979). But Bates (1997) has shown that in *Brachythecium rutabulum* and *Pseudoscleropodium purum*, leaked  $\text{K}^+$  ions are able to remain on the leaf surface (Figure 5), held there on exchange sites, and are re-absorbed upon hydration. Like tracheophyte roots, bryophytes utilize cation exchange sites to hold nutrients at their surfaces until those nutrients are moved into the plant.



Figure 5. *Pseudoscleropodium purum*. Photo by Michael Lüth.

Bryophyte cell walls are endowed with polyuronic acids such as galacturonic acid. These acids have a **carboxyl group** ( $\text{COOH}^+$ ) protruding on the outer surface of the wall. This carboxyl group freely exchanges its  $\text{H}^+$  for other cations in its surroundings (Figure 6). Hence, when cations such as  $\text{K}^+$ ,  $\text{Mg}^{++}$ , and  $\text{Ca}^{++}$  filter through the bryophyte layer, these ions are often bound on the bryophytes.

Since the ability of an exchange site to hold a given positively charged ion depends not only on the valence of the ion, but also on concentration, when there is a flood of  $\text{H}^+$  ions, these will replace the other, more rare and higher mass cations. Hence, basic cations from the bryophyte surface are released into the soil (Foth & Ellis 1997). A striking example of this phenomenon is the case of acid rain making a *Sphagnum* peatland alkaline and causing the *Sphagnum* to die! (Kilham 1982). The acid rain caused the release of alkaline positive ions from the surrounding hillside, which ultimately washed into the peatland. Although *Sphagnum* is equipped to bind such ions and make its surroundings more acid, it was not equipped to handle the large concentration that resulted from the uphill release. Instead, cations such as  $\text{Mg}^{++}$  and  $\text{Ca}^{++}$  accumulated on the surface of the *Sphagnum* and eventually killed it. In forested ecosystems, cations released from soil exchange sites become available to the roots, may be leached from the organic layer into deeper layers, or may be lost through runoff.

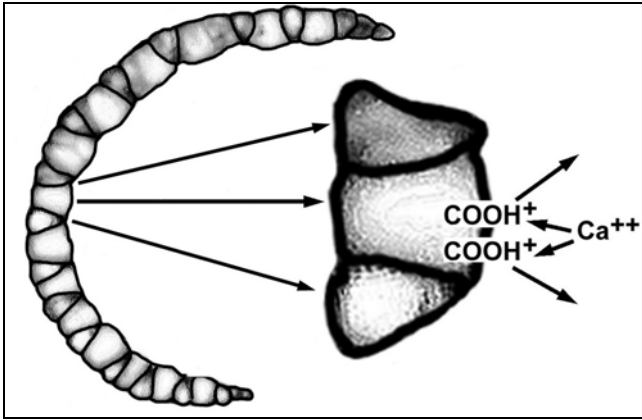


Figure 6. View of leaf cross section of *Sphagnum* (left) with enlarged chlorophyllous cells and hyaline cell on right. Enlargement shows carboxyl groups of the polyuronic acid and one  $\text{Ca}^{++}$  exchanging for two  $\text{H}^+$  ions in cation exchange. Drawing by Janice Glime

Not all parts of mosses necessarily behave equally in their cation exchange. Even in *Sphagnum*, where dead and living parts tend to have similar CEC after the initial exposure of new sites in dead cells, the branches and stems can have very different CEC (Brehm 1968).

Because plants have a finite number of exchange sites, ions must compete with each other for those locations. Thus, if one cation is in excess, it can cause cellular deficiency of other cations that are unable to gain access to these exchange sites. Based on their experiments with *Hylocomium splendens* and *Sphagnum*, using artificial precipitation, Gjengedal and Steinnes (1990) considered that cations such as  $\text{Na}^+$  and  $\text{Mg}^{++}$  in the precipitation may occupy exchange sites and affect the uptake of other ions by this competition. They found that uptake of Zn and Cd were pH dependent and that increasing temperatures increased the uptake for all four of the metals tested (Ca, Cu, Pb, Zn). Complexing reactions with anions such as  $\text{Cl}^-$  may also interfere with uptake. When Bates and Farmer (1990) applied  $\text{CaCl}_2$  to three bryophytes, their responses varied by habitat. *Pseudoscleropodium purum* and *Calliergon cuspidatum* from chalk soil exhibited significantly reduced growth at high Ca concentrations ( $5 \text{ mol CaCl}_2 \text{ m}^{-3}$ ), whereas *P. purum* and *Pleurozium schreberi* from acidic clay were unaffected by the additions. The mosses from the chalk soil had lower initial tissue levels of K and Mg, suggesting that the additional  $\text{CaCl}_2$  caused deficiencies in these nutrients through exchange site competition.

Ions in the external solution will first establish equilibrium with the exchange sites (Brown 1982). This physical process is completed very rapidly in the lab, but may require days in the field (Brown & Bates 1990). Once that is established, the remaining ions are available for uptake to the interior of cells (Pickering & Puia 1969). Hence, high concentrations of minerals will ultimately increase the uptake.

The number of exchange sites seems to be adaptive, at least in *Sphagnum*. *Sphagnum* section *Acutifolia*, which inhabits drier locations, has more exchange sites per unit of biomass than do members of section *Cuspidatum*, which are wet hollow species (Brown 1982). Both Clymo (1963) and Spearing (1972) showed that the number of exchange

sites correlated with height above water of the optimum habitat for *Sphagnum* species.

## Proton Pumps

After ions have reached the surface of the cell, they require energy to enter the cell. In tracheophytes, the **proton pump** is well known in such activities as bringing nutrients into root hairs, opening and closing guard cells, closure of the Venus flytrap, and growth, to name only a few. In bryophytes, the proton pump has likewise been demonstrated, and like that of tracheophytes, it uses ATP to "pump"  $\text{H}^+$  ions out of a cell (Figure 7). This leaves the cell with a negative charge that attracts cations to the cell (Raven *et al.* 1998). The resulting negative charge provides the force needed to bring in  $\text{K}^+$ ,  $\text{NH}_4^+$ ,  $\text{Mg}^{++}$ ,  $\text{Ca}^{++}$ , sugars, and amino acids, and probably other cations that have not yet been confirmed experimentally. As a positively charged ion enters the cell, it typically brings along an associated anion by **cotransport**. The pump, at the same time, regulates the pH within the cell to about 7.3-7.6. In bryophytes, the leaf cell surface and interstitial spaces between the cells provide sites where adhering cations are able to enter the cell through the proton pump mechanism.

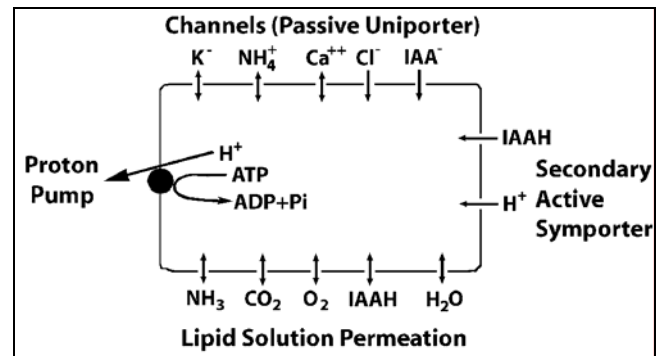


Figure 7. Known transport processes through the plasmalemma of a bryophyte cell. Diagram based on Raven *et al.* (1998).

As a result of ion movement through CEC and the proton pump, the bryophyte most likely has an influence on the **rhizoidosphere** (soil space immediately surrounding rhizoids) similar to that of tracheophytes on the rhizosphere (Raven *et al.* 1998), although in the case of bryophytes, leaves may contribute to the alteration of conditions even more than the rhizoids. The rhizoidosphere is acidified in the process of cation exchange and proton pumping to bring nutrient cations into the cells, creating positive charges within the cells and accumulating organic anions in the cell vacuoles.

In summary, nutrient uptake into the moss is initially dependent on the available exchange sites, but then it depends on the affinity of the particular nutrient for the appropriate transport site of the cell membrane, the presence of competing elements, and the turnover rate of the uptake site (Brown & Bates 1990).

## Specificity

Some nutrients are taken up more easily than others. Leblond (2004) examined the uptake of heavy metals in the moss *Pseudoscleropodium purum*. The nutrient elements manganese and potassium had the highest retention. Non-

nutrient ions of sodium, aluminium, and silica had the least retention. Youngest tissues accumulated the most nutrients, but internal redistribution occurred. Leblond found that soluble materials were taken in more easily than those deposited as particulates.

We know that cation exchange sites selectively bind higher valency cations (Richter & Dainty 1990). But at least in *Sphagnum russowii* there are two classes of exchange sites. The well-known one is associated with polygalacturonic acids and accounts for more than 50% of the cation exchange capacity (Richter & Dainty 1989). In addition to that, **phenolic acids** account for about 25%, whereas **amino acid**, **sulfate ester**, and **silicate deposits** in the cell wall contribute to a lesser degree.

When studying aquatic bryophytes, Burton and Peterson (1979) found that 33% of the cell-wall-bound Zn could be removed by the enzyme **pronase**, suggesting that a considerable portion of its binding might be due to such protein binding. Richter and Dainty (1989) found a small number of binding sites that are more specific to small valency cations such as potassium. If these sites indeed include phenolic compounds, one can presume that such binding sites might be widespread in bryophytes, wherein phenolic compounds are common (Liao 1993). Is this yet another use for these presumed "secondary" compounds? If so, what does it mean for cycling of potassium if it can be bound to the cell walls? Does this help the cell to retain its valuable potassium when cell membranes, damaged by desiccation, permit potassium to leak from the cell? Such a mechanism can contribute to the survival of bryophytes after desiccation and permit them to become a long-term sink for this and other ions.

We know that cation exchange is a somewhat selective process. Higher valency ions are bound preferentially over lower ones because they are able to occupy more than one exchange site. Hence,  $\text{Ca}^{++}$  binds to two exchange sites, whereas  $\text{K}^+$  can only bind to one. Metal ions are classed into three groups (Nieboer & Richardson 1981). **Class A** includes  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and  $\text{S}^{++}$ ; these ions are non-toxic and have a strong binding preference for oxygen-containing binding sites. **Class B** ions include  $\text{Ag}^+$ ,  $\text{Cu}^+$ , and  $\text{H}^{++}$ ; this group is extremely toxic and tends to bind with N- or S-containing molecules. The third group is a borderline class that includes  $\text{Cu}^{++}$ ,  $\text{Ni}^{++}$ ,  $\text{Pb}^{++}$ , and  $\text{Zn}^{++}$ . Nieboer and Richardson (1980) found a divalent metal ion selectivity binding order of  $\text{Pb} > \text{Cu} > \text{Cd} > \text{Co} \cong \text{Fe} > \text{Ni} > \text{Zn} > \text{Mn}$ , although Rühling and Tyler (1970) found a slightly different order for *Hylocomium splendens*:  $\text{Cu} \cong \text{Pb} > \text{Ni} > \text{Co} > \text{Zn} \cong \text{Mn}$ , an order that seems to be widespread in bryophytes (Bates 2000). However, once the sites are nearly fully occupied, this preferential binding is no longer the strongest force, possibly accounting for differences illustrated here. Isolated binding sites are only able to bind one position on the cation, hence eliminating the advantage for higher valency ions. In fact, at this stage, the isolated sites are more likely to bind univalent ions than divalent ones and more likely to bind divalent ones than trivalent ones (Richter & Dainty 1990). It is also likely that in systems with lower pH, more sites are occupied by  $\text{H}^+$  ions, creating more isolated sites. This in turn would favor the binding of lower valency ions such as  $\text{K}^+$  and account for their high selectivity at a low pH.

Fortunately, bryophytes seem to have uptake specificity for things they need over things they do not. For example, the thallose liverwort *Dumortiera hirsuta* (Figure 8) preferentially took up Ca, Mg, and Zn over Cd (Mautsoe & Beckett 1996). When  $\text{KNO}_3$  was used to pretreat the plants, Cd uptake occurred, suggesting that the high concentration of  $\text{K}^+$  removed the competing ions from the exchange sites and was subsequently replaced by Cd. Light and increased temperatures also stimulated Cd uptake. Even *Sphagnum*, the champion of cation exchangers, distinguishes among ions in ways that do not seem to depend strictly on valence. It accumulates Al and Mn, but excludes Cu and Zn, accumulating much less of these than the concentrations in the surrounding fen water (Li & Glime 1990).



Figure 8. Thallos of *Dumortiera hirsuta*. Photo by Li Zhang.

Shimwell and Laurie (1972) found that ectohydric and mixohydric mosses differ in their absorption, retention, and excretion of heavy metals. During droughts, ectohydric mosses excrete such heavy metals as Zn and Pb, forming surface crusts containing up to 6% Pb and 1-5% Zn. In mixohydric mosses, on the other hand, the metals generally are located at the base of the moss carpet in the older growth, suggesting their accumulation in older tissues.

## Seasons

Since most bryophytes gain most of their nutrients from precipitation, we might assume that most nutrient uptake therefore occurs when it rains. Yet the relationship is most likely not so simple. Francez and Loiseau (1999) found that *Sphagnum fallax* was more efficient at intercepting applied N (as  $\text{NH}_4\text{NO}_3$ ) in August than in June, even though August had the lowest rainfall. Dust accumulation can benefit bryophytes that are able to absorb nutrients in early morning dew and even on humid nights when there is no benefit for tracheophytes.

Turner and coworkers (2003) found that rates of acid phosphatase activity in moss apices differed markedly among species, but most taxa had the most activity in winter and least in summer. Nevertheless, tissues maintained relatively constant N and P concentrations throughout the year. A negative correlation between phosphatase activity and P concentration in the tissues suggests that the enzyme may become active in response to phosphorus needs and serves to indicate nutrient stress.

Núñez-Olivera *et al.* (2001) found that seasonal differences in several aquatic bryophytes (*Fontinalis*

*antipyretica*, *F. squamosa*, *Jungermannia cordifolia*, and *Pellia endiviifolia*) did not mimic the seasonal differences in their native streams. Rather, the concentrations depended on the interactions of internal and external factors. The elements that had the most persistent annual cycle were mostly essential nutrients: N, P, and Fe, plus the non-essential Na. The lowest concentrations occurred in spring and the highest in autumn. Concentrations were lowest during periods of growth.

## Fungal Connections – Mycorrhizae?

One mode of uptake by bryophytes has largely been ignored by ecologists, potentially causing researchers to be looking in the wrong places for bryophyte effects on ecosystem nutrient budgets. That mode is by means of **mycorrhizae** (fungal associations that function in transfer of nutrients to roots or rhizoids) or similar partnerships with **fungi**.

Ecologists estimate that 95% of all plant species are in genera that form mycorrhizal associations (Sylvia *et al.* 2004). In temperate and boreal forests, up to 95% of the short roots of trees form ectomycorrhizae. Mycorrhizae are critically important to most forest trees, which depend on them to increase surface area and contact nutrients in a much greater volume than the tree is able to reach. Bryophytes, likewise, are able to take advantage of this partnership to reach sources otherwise unavailable to them. Even in the Antarctic, such relationships can be important, as in the leafy liverwort *Cephaloziella exiliflora* (Williams *et al.* 1994; Chambers *et al.* 1999). But we know little of the extent of these relationships.

Although Boros reported a unique parasitic fungus on mosses in 1926, most botanists considered the bryophytes to be almost immune from fungal attack; even less attention was paid to the possibility of any sort of fungal partnership. In 1970, Kamal and Singh reported on the rhizoidosphere fungal flora of bryophytes. In 1975, Pirozynski and Malloch offered the theory that mycorrhizae were an essential part of the invasion of land by the original bryophyte-like plants, helping them to survive in an environment that was poor in nutrients and sustained frequent periods of desiccation. But actual proof of a mycorrhizal partnership, extant or extinct, was not forthcoming.

In 1976, Kottke and coworkers recognized that the ability of mosses to compete was affected by differential growth stimulation of the mosses by fungi. Still, little attention was paid to moss-fungal interactions from an ecosystem perspective, but bryologists began noticing that many mosses seemed to have fungal hyphae associated with their underground parts. Meanwhile, the tree physiologists were recognizing that fungal partners were critical to the nutrient and water uptake of trees. And orchid growers recognized that the native fungi must be kept with the orchids for successful growth. Now, fungi are recognized as essential to the nutrient uptake of tree roots and stories about their partnerships with roots are replacing the traditional teaching emphasis on root hair mechanisms of uptake.

Finally, in the 1980's, reports of bryophyte mycorrhizal (shouldn't it be mycorrhizoidal?) associations began to appear in the literature (Parke & Linderman 1980; Rabatin 1980; Pocock & Duckett 1985a; Iqbal *et al.* 1988a, b;

Ligrone 1988). These have included associations with *Funaria hygrometrica* (Parke & Linderman 1980; Iqbal *et al.* 1988a), *Sphagnum cymbifolium*, *Polytrichum commune* (Iqbal *et al.* 1988a), and in *Marchantia palmata*, both rhizoids and the ventral thallus (Iqbal *et al.* 1988b). Ligrone and Lopes (1989) demonstrated **vesicles** and **arbuscules** ("little trees"; branched structures formed by fungi within plant cells; Figure 9) in both rhizoids and parenchyma cells of the thallose liverwort *Conocephalum conicum* (Figure 10), suggesting a true mycorrhizal association. The arbuscules are thought to be the site of nutrient exchange (Harrison 1999), at least in roots. Even *Phaeoceros laevis*, a member of the Anthocerotophyta and host of a *Nostoc* symbiont, has a fungal associate that appears to be mycorrhizal (Ligrone 1988). When *P. laevis* is infected, the plastid forms a networking structure, the vacuole mass decreases, and the organelle density increases, all modifications suggestive of a partnership.

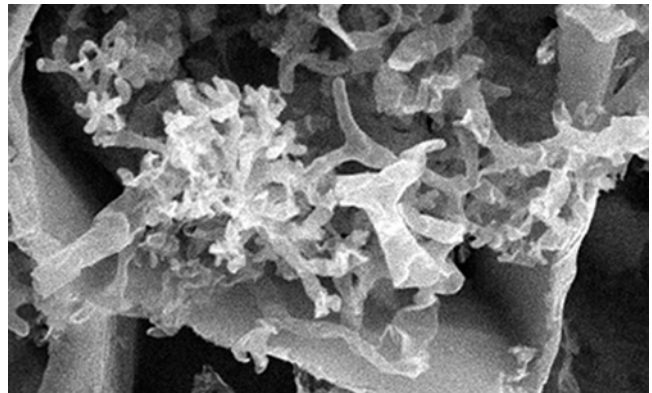


Figure 9. Arbuscules typical of those formed in roots by VAM fungi, but in this case within the thallus of the liverwort *Marchantia foliacea*. Photo by Julia Russell.



Figure 10. Thallus of *Conocephalum conicum*. Photo by Janice Glimme.

Then, in 1985(b), Pocock and Duckett investigated the rhizoids of 206 of the 284 British liverworts. They found that swollen rhizoids occurred in 33 species of the Jungermanniales and were always associated with fungal hyphae. Swollen and branched rhizoids were particularly well developed in the Lepidoziineae and Cephaloziineae and often occurred on flagelliform shoots, but were better developed on the underground axes. Duckett *et al.* (1991) later described the highly specialized associations between ascomycetous fungi, known for their ectomycorrhizal partnerships, and 46 species of British liverworts. They

found the majority of these ascomycetous fungi to occur with the leafy liverwort suborders Lepidoziineae and Cephaloziineae. [Ascomycetous associations are found in a relatively small number of families of leafy liverworts (Read *et al.* 2000)]. Strikingly, 33 of these 46 British liverwort taxa form flagelliform axes (Duckett *et al.* 1991). These axes have elongate parenchyma cells with abundant plasmodesmata in their transverse end walls. Their apices are mucilaginous and the subapical amyloplasts appear to act in detecting gravity, much as they do in protonemata. In addition to serving as perennating structures, these axes appear to be major organs of assimilation. Is this facilitated through a mycorrhizoidal partnership?

In all these cases, the fungi infect the individual rhizoids independently, but most of these 46 taxa nevertheless have abundant fungi-infected rhizoids that extend 20-30 cm into the peaty substrate (Duckett *et al.* 1991). What an extension for a tiny bryophyte! In the liverworts *Lepidozia*, *Kurzia*, and *Telaranea*, but in no others, the rhizoids swell prior to fungal infection. In *Cladopodiella*, the fungi form a pseudoparenchymatous sheath around the swollen rhizoidal tips.

By 1988, Boullard had presented evidence that the fungal symbiotic relationship with the liverworts was very old. Yet, in 1990, During and van Tooren pointed out that "in only very few cases have these interactions been analysed functionally."

Other associations have been documented in the field. Although not truly mycorrhizoidal because they lack the composite structure definitive of this relationship, bryophytes now are known to enter into partnerships. Even buried wood, inoculated with  $^{32}\text{P}$ , was able to provide P for the living tips of *Hypnum cupressiforme* (Figure 11) through a saprotrophic fungus, *Phanerochaete velutina*, that connected to the older parts of the moss (Wells & Boddy 1995).



Figure 11. Twigs bearing *Hypnum cupressiforme*. Photo by Michael Lüth.

The fungal association may in some small way benefit the neighboring plants, and they in turn the bryophyte (Duckett & Read 1995). Rhizoids of at least some leafy liverworts in the Lepidoziaceae, Calypogeiaceae, Cephaloziaceae, and Cephaloziellaceae can be infected by the same fungus, *Hymenoscyphus ericae*, an ascomycetous fungus that infects members of the Ericaceae such as *Calluna*, *Erica*, *Rhododendron*, and *Vaccinium*. So far, there appears to be no evidence of a transport pathway from moss to fungus to ericaceous plant or vice versa, but

the presence of one of these host plants would enhance the opportunities for the fungus to grow there and thus the opportunities for it to join with the other host.

Chapin *et al.* (1987) have found an association that may indeed benefit the trees. In an Alaskan forest they found that the mycorrhizal fungi of the black spruce (*Picea mariana*) stimulated the moss carpet above to release phosphorus to the tree roots!

### *Cryptothallus mirabilis*

It appears that the fungi may be to some liverworts what the mycorrhizae are to the fern *Botrychium* and to many of the saprophytic forest floor flowering plants – a means of getting sufficient energy when the canopy is blocking an extensive portion of the light. Such a relationship is essential to the thallose liverwort *Cryptothallus mirabilis* (Figure 12). It occurs nestled in mires and lacks chlorophyll. Certainly for it, a partnership is essential. But this liverwort has a Basidiomycota fungus as its ectomycorrhizal partner (Ligrone *et al.* 1993). This liverwort is a **parasite**! It was thought that its fungal partner joined it to a species of *Betula* (birch), from which it ultimately obtained its carbohydrate energy source (Wiehle 1988; Pocock & Duckett 1984; Frey & Kürschner 1991; Read *et al.* 2000), much like the parasitic flowering plant *Monotropa uniflora*, the Indian pipe. However, Ligrone *et al.* (1993) disagree. They found that the fungi in *Betula* roots had a different morphology from those in the associated *C. mirabilis*. It appears that the association of *C. mirabilis* is more like that of the goblin fern *Botrychium mormo*, wherein the fungus derives carbon from decomposing litter and transfers some of it to the fern, permitting it to live in low light.



Figure 12. *Cryptothallus mirabilis*, an achlorophyllous thallose liverwort in the Aneuraceae. This parasitic liverwort depends on a basidiomycete fungus to provide it with nutrients and energy. Photo by Michael Lüth.

When it develops, the *Cryptothallus mirabilis* fungus forms large, intracellular coils in the liverwort (Ligrone *et al.* 1993). Then the liverwort cytoplasm proliferates and the starch content of its plastids decreases. As the hyphae die back and aggregate into large masses, the liverwort cells senesce. In *C. mirabilis*, the fungal hyphae contain abundant glycogen and occasionally amyloid deposits. It is interesting that the fungal partner in *C. mirabilis* is identical to the one in *Aneura pinguis* (closely related but photosynthetic) from alpine sites but different from the

fungus in *A. pinguis* from a chalk pit and sand dunes. In *C. mirabilis*, net carbon transfer is to the liverwort, and it is likely that there is transfer from the fungus to the liverwort in *A. pinguis* as well. In addition to the morphological similarities, further support for this hypothesis in *A. pinguis* is that spores of both liverwort species fail to develop beyond a few cells in **axenic** (sterile) culture.



Figure 13. Thallus of *Aneura pinguis*. Photo by Michael Lüth.

### Other Underground Partnerships

But it appears that *Cryptothallus* is not the only liverwort capable of living below ground with an Ascomycetes fungal partner (Duckett *et al.* 1989). In bog communities, the leafy liverworts (Jungermanniales) *Cephalozia*, *Cladopodiella*, *Kurzia*, *Lepidozia*, *Odontoschisma*, and *Telaranea nematodes* can all develop extensive underground stem systems with numerous rhizoids that have swollen, fungus-containing tips. These liverworts can produce new shoots down to 24-30 cm in peat and to 10 cm in rotten logs (*Lepidozia reptans*, Figure 14). In Malaysia, members of the leafy liverwort family Lepidoziaceae can produce such axes down to 1.5 m in the peaty soil of the upper montane rainforest. When these develop in the dark, they retain their partnership morphology, but when the shoots are exposed to light they regenerate into leafy shoots and lose their gravitropic response. This loss of fungal partnership morphology appears to be related to the disappearance of subapical amyloplasts, known to have a gravimetric response. Duckett and coworkers (1989) suggest that these liverworts may be acting as alternative hosts to ericaceous mycorrhizae, particularly in places like Malaysia. In Great Britain, less than 20% of the Jungermanniales have rhizoidal fungi, whereas in the montane forests of Malaysia, where ericaceous shrubs are extensive, the percentage may be as high as 80-90%.

As the search continues, more and more fungal taxa are being described in bryophyte associations, but not all are mycorrhizal (Khan *et al.* 1997; Doebbler 1997; Brouwer 1999). In fact, a number appear to be parasitic; others are just coexisting. Nevertheless, approximately 300 species of Ascomycota appear to grow obligately on bryophytes (Doebbler 1997). More than 40 species of Ascomycota in six orders occur on the Polytrichaceae alone, primarily on *Polytrichum* and *Dawsonia* (Felix

1988). Some fungi, for example *Lemprospora* and *Octospora*, are known only from bryophytes (Doebbler 1997; Brouwer 1999); in other cases, the bryophyte has never been found without its fungal associate (Doebbler 1997). For example, *Octospora* and other genera infect the subterranean rhizoids of Polytrichaceae, while others occupy the spaces between the vertical leaf lamellae (Felix 1988). In fact, 20 different Ascomycota species are known to occupy that unusual habitat without apparently having any effect on the moss.

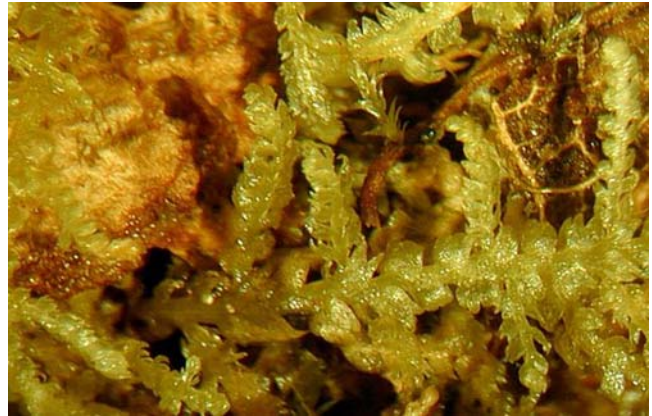


Figure 14. *Lepidozia reptans* growing on rotten wood. Photo by Michael Lüth.

Raspe and DeSloover (1998) suggested that the discomycetous fungus *Mniaecia jungermanniae*, which lives exclusively on leafy liverworts in the Jungermanniales, might have achieved the first step toward mutualism. This destructive parasite grows inside the bryophyte rhizoids but does not seem to afford any direct benefit to the liverwort. It appears it has a long way to go to reach mutualism.

### Arbuscular Mycorrhizae

Harrison (1999) reported that arbuscular mycorrhizae, restricted to the fungal order Glomales (Zygomycota, more recently named Glomeromycota), infected some bryophytes. Schüßler (2000) reported that a member of this order, *Glomus claroideum*, formed a mycorrhiza-like symbiosis with the hornwort *Anthoceros punctatus*. Following inoculation with spores, Schüßler found branched hyphae within the thallus within 20 days. This was the first definite experimental establishment of an arbuscular mycorrhiza-like association between a member of the Glomales and a bryophyte, although Felix (1988) had reported mycorrhiza-like associations in a number of taxa (Table 2). In 2003, Jakucs *et al.* found vesicles of a Glomalean fungus in the moss *Hypopterygium*, suggesting that there might indeed be a mutualistic relationship in which the fungus also benefits, but that hypothesis still awaits verification.

There is a certain degree of specificity among the bryophyte species. Russell and Bulman (2004) found that *Marchantia foliacea* from two locations in New Zealand supported *Glomus* arbuscular fungi internally (Figure 15), but that *M. polymorpha* did not. Every thallus they examined contained this *Glomus* species in the parenchyma tissue around the midrib. The fungus invaded the thallus through the smooth rhizoids and grew upward through the thallus, forming arbuscules only in the upper portion of the

thallus. The hyphae crossed directly through the cell walls of the liverwort. This same fungus forms mycorrhizal associations with the conifer, *Podocarpus*, and it may be that this fungus is shared by both plants. Unfortunately, we still have no evidence if this relationship between the fungus and the liverwort is truly symbiotic.

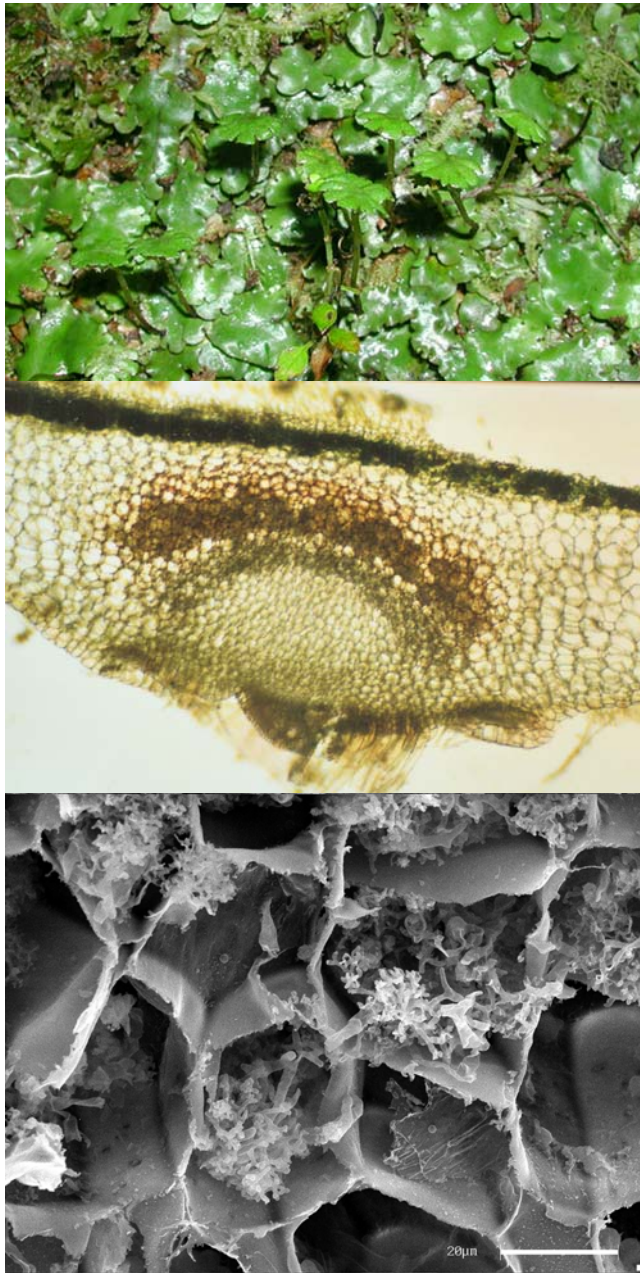


Figure 15. *Marchantia foliacea* thallus (**top**) with arbuscular growth of the mycorrhizal fungus *Glomus* (**bottom**) formed around the midrib (**middle - brown**). Photos by Julia Russell.

The specificity of some of the groups for specific plant phyla is fascinating. For example, Zygomycota colonize members of Anthocerotophyta and Marchantiophyta, but not Bryophyta (Read *et al.* 2000). Members of the Glomales isolated from the flowering plant *Plantago lanceolata* were able to colonize the thallose liverwort *Pellia epiphylla* (Figure 16) and produce arbuscules and vesicles.

Table 2. Mycorrhiza-like fungus-bryophyte associations. From Felix (1988) and Russell & Bulman (2004).

Fungus	Bryophyte	Reference
various spp	<i>Anthoceros</i>	Kamal & Singh 1970, Singh 1974
	<i>Riccia</i>	"
	<i>Funaria</i>	"
	<i>Polytrichum commune</i>	Grasso & Scheirer 1983
	<i>Haplomitrium</i>	Carafa <i>et al.</i> 2003
phycomycetous mycorrhizae	<i>Marchantia berteriana</i>	Baylis 1970
swollen rhizoids	liverworts	Pocock & Duckett 1985b
<i>Endogone</i>	bryophytes	Gerdemann 1968
<i>Glomus tenuis</i>	<i>Pogonatum</i>	Rabatin 1980
<i>Glomus mosseae</i> group	<i>Marchantia foliacea</i>	Russell & Bulman 2004
<i>Glomus claroides</i>	<i>Anthoceros punctatus</i>	Schübler 2000
<i>Mycena cinerella</i>	<i>Atrichum undulatum</i>	Hildebrand <i>et al.</i> 1978
	<i>Brachythecium rutabulum</i>	"
	<i>Funaria hygrometrica</i>	"



Figure 16. *Pellia epiphylla*. Photo by Michael Lüth.

These fungal-bryophyte associations form structural associations similar to those of vesicular-arbuscular mycorrhizae of tracheophytes. Despite the large number of associations recognized between bryophytes and fungi, Read and coworkers (2000) still stressed the "need for analysis of the functional attributes of these symbioses." They presented further evidence that these fungal associations were ancient, being important to the first plants to colonize land. Fossil evidence of Glomalean fungal structures associated with early bryophytes in Ordovician sediments that are 460 and 400 million years old support this contention (Remy *et al.* 1994; Redecker *et al.* 2000).

### Beneficial or Harmful?

The fungal associates are not always beneficial to the bryophytes. Zobel *et al.* (1999) treated a sub-arctic forest community with fungicide and found that the bryophytes and dwarf shrubs increased in biomass relative to the control. Could it be that in some cases the fungi are

stealing from the bryophytes and making nutrients available to trees?

### Summary

Unlike tracheophytes, bryophytes take up nutrients over their entire surface. With leaves only one cell thick in most taxa every leaf cell is thus exposed to environmental sources of nutrients. The three most limiting nutrients (N, P, K) accumulate in the upper parts of the plants through active uptake, whereas Ca, Mg, and Na accumulate through passive **cation exchange**. Bryophytes have high **cation exchange capacity** due to polyuronic acids in their cell walls. Once ions are bound on exchange sites, a **proton pump** removes  $H^+$  ions from the cell, creating a **charge gradient** that brings in positive ions. These bring along negative ions by **cotransport**. It appears that bryophytes have two, perhaps more, types of exchange sites, permitting differential binding of ions. They also seem to have specificity for things they need over things they do not.

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. Increasing temperatures increase the uptake, which is also pH-dependent.

Fungi are often associated with the rhizoids of bryophytes. It may be that a large number of bryophytes are afforded the advantages of fungal partner relationships, providing them with considerably more surface area for acquiring nutrients. The thallose liverwort *Cryptothallus mirabilis* has a fungal partner that provides carbohydrates for this non-chlorophyllous plant.

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### Literature Cited

- Babb, T. A., and Whitfield, D. W. S. 1977. Mineral nutrient cycling and limitation of plant growth in the Truelove Lowland ecosystem. In: Bliss, L. E. (ed.). Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. University of Alberta Press, Edmonton, pp. 589-606.
- Bartsch, I. 1994. Effects of fertilization on growth and nutrient use by *Chamaedaphne calyculata* in a raised bog. *Can. J. Bot.* 72: 323-329.
- Bates, J. W. 1982b. The role of exchangeable calcium in saxicolous calcicole and calcifuge mosses. *New Phytol.* 90: 239-252.
- Bates, J. W. 1989b. Retention of added K, Ca and P by *Pseudoscleropodium purum* growing under an oak canopy. *J. Bryol.* 15: 589-605.
- Bates, J. W. 1997. Effects of intermittent desiccation on nutrient economy and growth of two ecologically contrasted mosses. *Ann. Bot.* 79: 299-309.
- Bates, J. W. 2000. Mineral nutrition, substratum ecology, and pollution. In: Shaw, A. J. and Goffinet, B. *Bryophyte Biology*. Cambridge University Press, Cambridge, UK, pp. 248-311.
- Baylis, G. T. S. 1970. Root hairs and phycomycetous mycorrhizas in phosphorus-deficient soil. *Plant Soil* 33: 713-716.
- Bewley, J. D. 1979. Physiological aspects of desiccation tolerance. *Ann. Rev. Plant Physiol.* 30: 195-238.
- Boros, A. 1926. A new parasitic fungus on mosses. *Bryologist* 29: 2-3.
- Boullard, B. 1988. Observations on the coevolution of fungi with hepatics. In: Pirozynski, K. A. and Hawksworth, D. L. (eds.). *Coevolution of Fungi with Plants and Animals*. Academic Press, London, pp. 107-124.
- Breemen, N. van. 1995. Nutrient cycling strategies. CEC/IUFRO Symposium on Nutrient Uptake and Cycling in Forest Ecosystems, Halmstad, Sweden, 7-10 Jun 1993. *Plant Soil* 168-169: 321-326.
- Brehm, K. 1968. Die Bedeutung des Kationenaustausches für den Kationengehalt lebender Sphagnen. *Planta (Berlin)* 79: 324-345.
- Breuer, K. and Melzer, A. 1990. Heavy metal accumulation (lead and cadmium) and ion exchange in three species of Sphagnaceae. II. Chemical equilibrium of ion exchange and the selectivity of single ions. *Oecologia* 82: 468-473.
- Brouwer, E. 1999. Mosschijfjes (*Lamprospora* en *Octospora*): Voorkomen en verspreiding in Nederland. *Coolia* 42: 2-20.
- Brown, D. H. 1982. Mineral nutrition. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*, Chapman & Hall, London, pp. 383-444.
- Brown, D. H. 1984. Uptake of mineral elements and their use in pollution monitoring. In: Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, London, pp. 229-256.
- Brown, D. H. and Bates, J. W. 1990. Bryophytes and nutrient cycling. *J. Linn. Soc. Bot.* 104: 129-147.
- Burton, M. A. S. and Peterson, P. J. 1979. Metal accumulation by aquatic bryophytes from polluted mine streams. *Environ. Pollut.* 19(1): 39-46.
- Büscher, P., Koedam, N., and Neirinck, L. 1983. Cation-exchange capacity of mosses in relation to soil preference. In: Cran, W. J., Janáček, K., Rybová, R., and Sigler, K. (eds.). *Membrane Transport in Plants*. Proc. Symp. held in Prague, Czechoslovakia Aug. 15-21, 1983. John Wiley & Sons, New York, pp. 477-478.
- Carafa, A., Duckett, J. G., Ligrone, R. 2003. Subterranean gametophytic axes in the primitive liverwort *Haplomitrium* harbour a unique type of endophytic association with aseptate fungi. *New Phytol.* 160: 185-197.
- Chambers, S. M., Williams, P. G., Seppelt, R. D., and Cairney, J. W. G. 1999. Molecular identification of *Hymenoscyphus* from rhizoids of the leafy liverwort *Cephaloziella exiliflora* in Australia and Antarctica. *Mycol. Res.* 103: 286-288.
- Chapin, F. S. III, Oechel, W. C., Cleve, K. van, and Lawrence, W. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. *Oecologia* 74: 310-315.
- Craigie, J. S. and Maass, W. S. G. 1966. The cation-exchanger in *Sphagnum* spp. *Ann. Bot.* 30: 153-154.
- Clymo, R. S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot. N. S.* 27: 309-324.

- Clymo, R. S. 1964. The origin of acidity in *Sphagnum* bogs. *Bryologist* 67: 427-431.
- Doebbele, P. 1997. Biodiversity of bryophilous Ascomycetes. Symposium on Mycology: Past, Present and Future, at British Mycological Society Symposium Sheffield(UK), Apr 1996. *Biodiv. Conserv.* 6: 721-738.
- Duckett, J. G. and Read, D. J. 1995. Ericoid mycorrhizas and rhizoid-ascomycete associations in liverworts share the same mycobiont: Isolation of the partners and resynthesis of the associations in vitro. *New Phytol.* 129: 439-447.
- Duckett, J. G., Renzaglia, K. S., Pell, K., and Russell, A. 1989. The biology of underground organs of Jungermanniales. *Bull. Brit. Bryol. Soc.* 53: 19-21.
- Duckett, J. G., Renzaglia, K. S., and Pell, K. 1991. A light and electron microscope study of rhizoid-Ascomycete associations and flagelliform axes in British hepatics with observations on the effects of the fungi on host morphology. *New Phytol.* 118: 233-257.
- During, H. J. and Tooren, B. F. van. 1990. Bryophyte interactions with other plants. International Symposium on Bryophyte Ecology Edinburgh (UK), 19-22 Jul 1988. *J. Linn. Soc. Bot.* 104: 79-98.
- Felix, H. 1988. Fungi on bryophytes, a review. *Bot. Helv.* 98: 239-269.
- Foth, H. D. and Ellis, B. G. 1997. *Soil Fertility*, 2nd Ed. CRC Press, Boca Raton, Florida, 290 pp.
- Francez, A. J. and Loiseau, P. 1999. Devenir de l'azote mineral dans une tourbiere a *Sphagnum fallax* Klinggr. et *Carex rostrata* Stokes du Massif central (France). [The fate of mineral nitrogen from peat (*Sphagnum fallax* Klinggr. and *Carex rostrata* Stokes) of the Massif central (France)]. *Can. J. Bot.* 77: 1136-1143.
- Frey, W. and Kürschner, H. 1991. Das *Fossombronio-Gigaspermetum mouretii* in der Judäischen Wüste. 2. [The *Fossombronio-Gigaspermetum mouretii* in the Judean deserts. 2. Ecosociology and life strategy.]. *Ökosozologie und Lebensstrategien. Cryptog. Bot.* 1/3: 73-84.
- Gerdemann, J. W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. *Ann. Rev. Phytopathol.* 6: 397-418.
- Gjengedal, E. and Steinnes, E. 1990. Uptake of metal ions in moss from artificial precipitation. *Environ. Monitor. Assess.* 14: 77-87.
- Grasso, S. M. and Scheirer, D. C. 1981. Scanning electron microscopic observations of a moss-fungus association. *Bryologist* 84: 348-350.
- Harrison, M. J. 1999. Molecular and cellular aspects of the arbuscular mycorrhizal symbiosis. *Ann. Rev. Plant Physiol. Plant Molec. Biol.* 50: 361-389.
- Hildebrand, R., Kottke, I., and Winkler, S. 1978. Untersuchungen über den Einfluß von Pilzen auf die pH-Abhängigkeit von Laubmoosen. *Beitr. Biol. Pflanzen* 54: 1-12.
- Iqbal, S. H., Nasim, G., and Shahjahan. 1988a. Vesicular-arbuscular mycorrhizal fungi associated with three mosses (*Sphagnum cymbifolium*, *Polytrichum commune*, and *Funaria hygrometrica*). *Biologia (Lahore)* 34: 269-273.
- Iqbal, S. H., Nasim, G., and Jahan, S. 1988b. II. Vesicular-arbuscular mycorrhizal fungi associated with a bryophyte: *Marchantia palmata*. *Biologia (Lahore)* 34: 275-278.
- Jakucs, E., Naár, Z., Szedlay, G., and Orbán, S. 2003. Glomalean and septate endophytic fungi in *Hypopterygium* mosses (Bryopsida). *Cryptog. Mycol.* 24(1): 27-37.
- Kamal and Singh, C. S. 1970. Rhizosphere mycoflora of some bryophytes. *Ann. Inst. Pasteur (Paris)* 119: 752-755.
- Khan, M. R., Imamual Huq, S. M., and Hasanuzzaman, M. 1997. Moss rhizosphere and its microflora. *Bangladesh J. Bot.* 26(2): 163-168.
- Kilham, P. 1982. Acid precipitation: Its role in the alkalization of a lake in Michigan. *Limnol. Oceanogr.* 27: 856-867.
- Klein, M. and Horst, W. J. Cation specific exchange capacity of cell wall material isolated from roots of plant species differing in Al resistance. Institute of Plant Nutrition, Department of Horticulture, University of Hannover, Germany. Accessed 6 June 2005 at [http://www.ipe.uni-hannover.de/publication/klein\\_poster1.pdf](http://www.ipe.uni-hannover.de/publication/klein_poster1.pdf)
- Knight, A. H., Crooke, W. M., and Inkson, R. H. E. 1961. Cation-exchange capacities of tissues of higher and lower plants and their related uronic acid contents. *Nature (London)* 192: 142-143.
- Koedam, N. and Büscher, P. 1983. Studies on the possible role of cation exchange capacity in the soil preference of mosses. *Plant Soil* 70: 77-93.
- Kottke, J., Krisch, T., and Winkler, S. 1976. Untersuchungen über den Einfluss von Pilzen auf die Konkurrenzfähigkeit von Moosen. *Beitr. Biol. Pflanzen* 51: 407-415.
- Leblond, S. 2004. Étude pluridisciplinaire du transfert des métaux de l'atmosphère vers les mousses (*Scleropodium purum* (Hedw.) Limpr.): Suivi sur un site rural (Vouzon, France). Thèse de Doctorat, Université Paris 7 – Denis Diderot, Paris, France. [iii] 214 pp.
- Li, Y. and Glime, J. M. 1990. Growth and nutrient ecology of two *Sphagnum* species. *Hikobia* 10: 445-451.
- Liao, C.-L. 1993. Chemical defence in bryophytes with high apparency. *Bryol. Times* 75: 1-4.
- Ligrone, R. 1988. Ultrastructure of a fungal endophyte in *Phaeoceros laevis* (L.) Prosk. (Anthocerotophyta). *Bot. Gaz. (Crawfordsville)* 149: 92-100.
- Ligrone, R. and Lopes, C. 1989. Cytology and development of a mycorrhiza-like infection in the gametophyte of *Conocephalum conicum* (L.) Dum., Marchantiales, Hepatophyta. *New Phytol.* 111: 423-434.
- Ligrone, R., Pocock, K., and Duckett, J. G. 1993. A comparative ultrastructural study of endophytic Basidiomycetes in the parasitic achlorophyllous hepatic *Cryptothallus mirabilis* and the closely allied photosynthetic species *Aneura pinguis* (Metzgeriales). *Can. J. Bot.* 71: 666-679.
- Mautsoe, P. J. and Beckett, R. P. 1996. A preliminary study of the factors affecting the kinetics of cadmium uptake by the liverwort *Dumortiera hirsuta*. *S. Afr. J. Bot.* 62: 332-336.
- Nieboer, E. and Richardson, D. H. S. 1980. The replacement of the nondescript term 'heavy metals' by a biologically and chemically significant classification of metal ions. *Environ. Pollut. (Ser. B)* 1: 3-26.
- Nieboer, E. and Richardson, D. H. S. 1981. Lichens as Monitors of Atmospheric Deposition. *Atmospheric Pollutants in Natural Waters*, Ann Arbor Science Publishers, Inc., Ann Arbor, MI, pp. 339-388.
- Núñez-Olivera, E., García-Álvaro, M., Beaucourt, N., and Martínez-Abaigar, J. 2001. Changes in element concentrations in aquatic bryophytes over an annual cycle. *Arch. Hydrobiol.* 152: 253-277.
- Parke, J. L. and Linderman, R. G. 1980. Association of vesicular-arbuscular mycorrhizal fungi with the moss *Funaria hygrometrica*. *Can. J. Bot.* 58: 1898-1904.
- Pickering, D. C. and Puia, I. L. 1969. Mechanism for the uptake of zinc by *Fontinalis antipyretica*. *Physiol. Plant.* 22: 653-661.
- Pirozynski, K.A. and Malloch, D.W. 1975. The origin of land plants: A matter of mycotrophism. *Biosystems* 6: 153-164.

- Pocock, K. and Duckett, J. G. 1984. A comparative ultrastructural analysis of the fungal endophytes in *Cryptothallus mirabilis* Malm. and other British thalloid hepatics. *J. Bryol.* 13: 227-233.
- Pocock, K. and Duckett, J. G. 1985a. The alternative mycorrhizas: Fungi and hepatics. *Bull. Brit. Bryol. Soc.* 45: 10-11.
- Pocock, K. and Duckett, J. G. 1985b. On the occurrence of branched and swollen rhizoids in British hepatics: Their relationships with the substratum and associations with fungi. *New Phytol.* 99: 281-304.
- Popper, Z. A. and Fry, S. C. 2003. Primary cell wall composition of bryophytes and charophytes. *Ann. Bot.* 91: 1-12.
- Rabatin, S. C. 1980. The occurrence of the vesicular-arbuscular-mycorrhizal fungus *Glomus tenuis* with moss. *Mycologia* 72: 191-195.
- Raspe, O. and De Sloover, J. R. 1998. Morphology, ecology and chorology of *Mniaecia jungermanniae* (Ascomycota) in Belgium and the significance of its association to leafy liverworts (Jungermanniales). *Belgian J. Bot.* 131:251-259.
- Raven, J. A., Griffiths, H., Smith, E. C., and Vaughn, K. C. 1998. New perspectives in the biophysics and physiology of bryophytes. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). *Bryology in the Twenty-first Century*. Maney Publishing and the British Bryological Society, UK, pp. 261-275.
- Read, D. J., Duckett, J. G., Francis, R., Ligrone, R., Russell, A., Newton, A. E., and Kenrick, P. 2000. Symbiotic fungal associations in 'lower' land plants. *Philosoph. Trans. Roy. Soc. London B* 355: 815-831.
- Redecker, D., Kodner, R., and Graham, L.E. 2000. Glomalean fungi from the Ordovician. *Science* 289: 1920-1921.
- Remy, W., Taylor, T.N., Hass, H., and Kerp, H. 1994. Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proc. Natl. Acad. Sci. USA* 91: 11841-11843.
- Richter, C. and Dainty, J. 1989. Ion behavior in plant cell walls. I. Characterization of the *Sphagnum russowii* cell wall ion exchanger. *Can. J. Bot.* 67: 451-459.
- Richter, C. and Dainty, J. 1990. Ion behaviour in plant cell walls. IV. Selective cation binding by *Sphagnum russowii* cell walls. *Can. J. Bot.* 68: 773-781.
- Rühling, A. and Tyler, G. 1970. Sorption and retention of heavy metals in the woodland moss *Hylocomium splendens* (Hedw.) Br. et Sch. *Oikos* 21: 92-97.
- Russell, J. and Bulman, S. 2004. The liverwort *Marchantia foliacea* forms a specialized symbiosis with arbuscular mycorrhizal fungi in the genus *Glomus*. *New Phytol.* 2004: 1-13. <[www.newphytologist.org](http://www.newphytologist.org)>.
- Schübler, A. 2000. *Glomus claroideum* forms an arbuscular mycorrhiza-like symbiosis with the hornwort *Anthoceros punctatus*. *Mycorrhiza* 10(1): 15-21.
- Shacklette, H. T. 1965. Element content of bryophytes. *Geol. Surv. Bull.* 1198-D., U. S. Govt. Print. Off., Wash., D. C.
- Shimwell, D. W. and Laurie, A. E. 1972. Lead and zinc contamination of vegetation in the southern Pennines. *Environ. Pollut.* 3: 291-301.
- Singh, H. B. 1974. Rhizosphere fungal flora of bryophytes. *Botanique* 7: 131-136.
- Spearing, A. M. 1972. Cation-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge Bog, central New York state *Bryologist* 75: 154-158.
- Sylvia, D. M., Furhmann, J. J., Hartel, P. G., and Zuberer, D. A. 2004. *Principles and Applications of Soil Microbiology*, 2nd ed. Prentice Hall, Englewood Cliffs, N. J.
- Taylor, F. G. and Witherspoon, J. P. 1972. Retention of simulated fallout particles by lichens and mosses. *Health Phys.* 23: 867-869.
- Temple, P. J., McLaughlin, D. L., Linzon, S. N., and Wills, R. 1981. Moss bags as monitors of atmospheric deposition. *J. Air Pollut. Control Assoc.* 31: 668-670.
- Turner, B. L., Baxter, R., Ellwood, N. T. W., and Whitton, B. A. 2003. Seasonal phosphatase activities of mosses from Upper Teesdale, northern England. *J. Bryol.* 25: 189-200.
- Varma, A. and Hock, B. 1999. *Mycorrhiza*. Springer Verlag, Berlin.
- Weetman, G. F. and Timmer, V. 1967. Feather moss growth and nutrient content under upland black spruce. *Woodlands Research Index, Pulp and Paper Research Institute of Canada, Pointe Claire, P. Q., Canada* 138: 1-38.
- Wells, J. M. and Boddy, L. 1995. Phosphorus translocation by saprotrophic basidiomycete mycelial cord systems on the floor of a mixed deciduous woodland. *Mycol. Res.* 99: 977-980.
- Wells, J. M. and Brown, D. H. 1990. Ionic control of intracellular and extracellular Cd uptake by the moss *Rhytidiadelphus squarrosus* (Hedw.) Warnst. *New Phytol.* 116: 541-553.
- Wiehle, W. 1988. *Cryptothallus mirabilis* – ein mykotrophes Lebermoos. *Boletus* 12: 15-22.
- Williams, P. G., Roser, D. J., and Seppelt, R. D. 1994. Mycorrhizas of hepatics in continental Antarctica. *Mycol. Res.* 98: 34-36.
- Wojtun, B. 1994. Element contents of *Sphagnum* mosses of peat bogs of Lower Silesia (Poland). *Bryologist* 97: 284-295.
- Zobel, M., Pilt, I., Moora, M., Partel, M., and Liira, J. 1999. Small-scale dynamics of plant communities in an experimentally polluted and fungicide-treated subarctic birch-pine forest. *Acta Oecol.* 20(1): 29-37.