

CHAPTER 8-1

NUTRIENT RELATIONS: REQUIREMENTS AND SOURCES

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CHAPTER 8-1

NUTRIENT RELATIONS: REQUIREMENTS



Figure 1. Mosses growing on an old iron stove, demonstrating their rather low nutrient requirements. Photo by Janice Glime.

What Do Bryophytes Require?

Bowen (1933) claimed that bryophytes are necessarily limited in nutrient supply by their **poikilohydric** (state of hydration controlled by environment) method of water regulation. Their method of receipt of water – predominantly from rainfall and, for most bryophytes, almost nothing from ground water – relegates them to receive nutrients that are dissolved in rainwater or that accumulate as dust. After the first few minutes of rainfall, those nutrient concentrations are extremely small compared to soil nutrients and are biased in their relative concentrations in very different ways. Therefore, it is not surprising that culture conditions designed for tracheophytes are often unsuitable for bryophytes. But is this what the bryophytes "prefer"? Or are these conditions they tolerate and that provide them relatively less competition from tracheophytes? And do they gain any nutrients from the soil?

Nutrient Requirements

Even in the slow-growing bryophytes, nutrients can be a major determinant of both species composition and diversity (Raabe *et al.* 2010; Stevens *et al.* 2010; Schrijver *et al.* 2011). For tracheophytes, we know that the **trace**

elements (micronutrients) (Fe, Zn, Mn, Cu, Ni, B, Mo, and Cl) are essential (Welch 1995). These seem to be important for bryophytes as well, but in lower concentrations. Nevertheless, the levels of requirements and tolerance can vary widely not only among species, but also within species (Shaw 1988).

Most knowledge about nutrient requirements of bryophytes comes from culturing them (Voth 1943; Brown 1982), although more recently we have learned much through the effects of atmospheric pollution. We soon learned that concentrations that favored the growth of tracheophytes in the laboratory were too strong for the poikilohydric bryophytes, and dilutions of 10:1 seemed more satisfactory.

Hoffman (1966) performed a complex set of experiments on the moss *Funaria hygrometrica* (Figure 2) in which he determined anion (N:P:S) and cation (K:Ca:Mg) combination effects. In his anion experiments, the absence of any of the three nutrients caused poor protonemal growth and no gametophores. On the other hand, the protonemata responded quite differently from the responses of the gametophores to the various cation combinations. This suggests that our usual descriptions of

conditions based on leafy plants may not provide us with any useful information on requirements needed for establishment. Even spores and gemmae may have different requirements (Brown 1982).



Figure 2. *Funaria hygrometrica*, a species of disturbed habitats that requires N, P, and S among its nutrients. Photo by Michael Lüth, with permission.

Bryophytes seem to require the same nutrients, mostly for the same purposes, as do the tracheophytes. An easy way to remember the **macronutrients** (those needed in large quantities) is with the acronym **CHOPKNS Mg CaFe**, read as See Hopkin's mighty good cafe. These essential metabolic nutrients are maintained **within** the cell in relatively consistent high concentrations. The inconsistencies often found in measurements generally result when the bound portion on the cell surface is included. Table 1 lists the concentrations of macro- and micronutrients typical of various tracheophyte groups.

One factor that plays a major role in bryophyte nutrient needs and toxicity is the osmotic effect. Lacking an epidermis (except some thallose taxa) and having little wax

on their surfaces, most bryophytes are especially susceptible to osmotic shock. Voth (1943) used *Marchantia polymorpha* (Figure 3) to show that a concentrated nutrient solution could kill the tips and wings of a growing thallus while reducing dry biomass and production of gemmae cups. At intermediate concentrations that retained the same nutrient ratio, the liverwort increased in size, produced a darker color, had more ascending tips, and developed more rhizoids, especially at the lower end of that concentration range. At the lowest set of concentrations, the rhizoids, scales, and lower epidermis had a more intense red-purple color, rhizoids were quite numerous, and gemmae cups diminished in number. Cell walls were especially thin in the strongest solutions and many cells collapsed, whereas in the most dilute solutions the cell walls were thickest.



Figure 3. *Marchantia polymorpha*, a species that is sensitive to high nutrient concentrations. Photo by David T. Holyoak, with permission.

Table 1. Average mineral element content among plants of several habits. (All data are in parts per thousand). Based on published compilations included in Larcher 1983 and Epstein 1965 for agricultural plants.

Element	Land Plants (g·kg ⁻¹ dry matter)		Stored in Soil (g·kg ⁻¹ DM) Mean	Marine Organisms (g·kg ⁻¹ DM) Mean	Sea Water (g·L ⁻¹)	Agricultural Plants (g·kg ⁻¹ DM)
	Range	Mean				
N	10-50	20	1	50	0.0003	15
P	1-8	2	0.7	6	0.00003	2
S	0.5-8	1	0.7	10	0.9	1
K	5-50	10	14	10	0.4	10
Ca	5-50	10	14	5	0.4	5
Mg	1-10	2	5	4	1.3	2
Fe	0.05-1	0.1	38	0.4	0.00005	0.1
Mn	0.02-0.3	0.05	0.9	0.02	0.000005	0.05
Zn	0.01-0.1	0.02	0.05	0.2	0.000005	0.02
Cu	0.002-0.02	0.006	0.02	0.05	0.00001	0.006
Mo	0.0001-0.001	0.0002	0.002			0.0001
B	0.005-0.1	0.02	0.01	0.02	0.005	0.02
Cl	0.2-10	0.1	0.1	40	19.3	0.1

Considering these osmotic responses, it is not surprising to find that the same species of bryophytes from different habitats can respond quite differently to various concentrations of nutrients and heavy metals (Brown & Beckett 1985). If a plant has grown from spores at a certain nutrient/ion level, then its osmotic potential is more likely to be adjusted to that of its environment. The same is likely to be true for plants grown from fragments and other propagules. Moving a plant to another location can strongly affect that balance. Hence, monitoring studies that move bryophytes from one location to another need to account for normal ambient ion differences. Taxonomists likewise need to account for ionic differences in the environment because these can alter the morphology of the plants (Brown & Beckett 1985; Glime unpub. data).

The needs of young shoots are typically greater than those of older shoots; thus N, P, and K are found in young shoots in their highest concentrations (Tamm 1953). Nitrogen and phosphorus are essential in making proteins and DNA, and phosphorus is needed in ATP to maintain energy. A relatively high content of potassium is believed to be needed for the normal folding of cytoplasmic enzymes (Bates 2000). Magnesium is needed in chlorophyll and as an activator of several enzymes. Calcium acts as a messenger and is rarely present in the cytoplasm; it is, however, needed to maintain integrity of the plant by being part of the "glue" that cements the cell walls together. Calcium is not easily translocated and accumulates in older segments. However, its increasing concentration in older tissues is partly due to the recalcitrance of the cell wall, where Ca is concentrated, and the loss of dry biomass from older cells, increasing the ratio of Ca to leaf biomass (Bates 1979).

Macronutrients

Some macronutrients often are bound in rocks, unavailable to most plants. Nevertheless, bryophytes and lichens can affect biogeochemical cycles by surface weathering (Porada *et al.* 2014). Porada and coworkers calculated the degree of obtaining N and P from the rock substrate by quantifying the amounts needed by the organisms to account for their biomass increase. Using this indirect method, they estimated that these cryptogams contributed to chemical weathering of 0.058 to 1.1 Km³ yr⁻¹ of rock.

Nitrogen

Nitrogen (N) relationships for bryophytes are complex. For that reason, most of the discussion of this important nutrient are treated in a separate subchapter on nitrogen.

Nitrogen is essential for amino acids, proteins, DNA, and RNA. For bryophytes, slow growth means that requirements are low. Bryophytes are able to use both nitrate and ammonium, with differences among species. Nevertheless, some can use both (Schuler *et al.* 1955; Burkholder 1959). Others may have abnormalities in development in media with ammonium (Killian 1923; Southorn 1977).

On the other hand, the aquatic moss *Fontinalis antipyretica* preferentially assimilates ammonium ions (Schwoerbel & Tillmanns 1974). Others have shown that nitrate reductase only forms in the light (Fries 1945; Schwoerbel & Tillmanns 1974). This might explain why nitrate is the best source of N for *Funaria* and *Weissia*

controversa protonemata in the light (Dietert 1979). Nevertheless, growth on a nitrate medium requires the bryophytes to convert it to ammonium ions before they can assimilate it (Brown 1982). In some habitats, at least some species are able to use amino acids for their N source (Simola 1975). (See Chapter on nitrogen in this volume.)

When bryophytes are co-existing with tracheophytes, the tracheophytes can benefit from added nitrogen, growing faster and out-competing the bryophytes (Berendse *et al.* 2001; Malmer & Wallén 2005). On the other hand, high levels of N in the environment can cause the decrease of both tracheophytes and bryophytes (Dupré *et al.* 2010). In this case, low soil pH seems to contribute to the loss of species, but high N levels seem to be more important in the decline of diversity. These results are similar to those of Ferris *et al.* (2000) in coniferous plantations in Britain. In their study, both bryophyte and tracheophyte diversity decreased as available nitrogen increased, but in this case, the pH, calcium, and nitrate increased, whereas ammonia decreased.

Schrijver *et al.* (2011) stated that "elevated inputs of biologically reactive nitrogen (N) are considered to be one of the most substantial threats to biodiversity in terrestrial ecosystems." We know that high N levels can be detrimental to bryophytes. This has been demonstrated for *Leucobryum juniperoideum* (Figure 4) (Wang *et al.* 2014) and *Sphagnum* spp. (Figure 10, Figure 24-Figure 25) (Bragazza *et al.* 2004). Arróniz-Crespo *et al.* (2008) reported decline in bryophyte biomass production and cover in grasslands. Armitage *et al.* (2010) likewise noted that alpine bryophytes have reduced biomass production and reduced cover under high N concentrations. Using transplants of *Racomitrium lanuginosum* (Figure 5) they determined that at least this moss has the ability to recover when the high loading of N is gone.



Figure 4. *Leucobryum juniperoideum*, a species sensitive to high N levels. Photo by Michael Lüth, with permission.

In the Arctic, Gordon *et al.* (2001) found that added nitrogen caused a decrease in lichen cover but did not affect other functional types of plants. Rather, 10 kg ha⁻¹ yr⁻¹ increased the proportion of active bryophyte shoots while decreasing their nitrate assimilation capacity, suggesting that the critical load is less than 10 kg ha⁻¹ yr⁻¹. It is important to note that not all species responded the same way.



Figure 5. *Racomitrium lanuginosum*, a species that is able to recover from high N loadings. Photo by Michael Lüth, with permission.

To complicate our understanding of suitable levels of N, we find that when N is no longer limiting, P and K can become limiting, as shown for *Sphagnum* (Figure 10, Figure 24-Figure 25) (Bragazza *et al.* 2004). Furthermore, the increased atmospheric N deposition can cause a reduction in the retention of Ca and Mg, a condition that was accompanied by a decrease in stem volumetric density in *Sphagnum* hummocks. Weber and Wiersma (1998) found that in two forested watersheds, the leafy liverwort *Bazzania trilobata* (Figure 6) and moss *Dicranum fulvum* (Figure 7) had elevated N concentrations in the watershed treated with $(\text{NH}_4)_2\text{SO}_4$ while simultaneously expressing a depression of other nutrients (Al, B, Ca, Cu, Fe, K, Mg, Mn, N, P, Zn).



Figure 6. *Bazzania trilobata*, a species that is able to accumulate elevated N. Photo by Robert Klips, with permission.



Figure 7. *Dicranum fulvum*, a rock-dwelling species that is able to accumulate elevated N. Photo by Michael Lüth, with permission.

Phosphorus

Like nitrogen, phosphorus (P) is essential for amino acids, proteins, DNA, and RNA. As in the algae, luxury uptake of P occurs, at least in some mosses, *e.g.* *Pseudoscleropodium purum* (Figure 8) (Bates 1987), but in these experiments there was significant **luxury uptake**, followed by storage, in excess of that is needed) only when plots were fertilized to 50% above the control.

We have seen that P can interact with nitrogen. Ellwood and Whitton (2007) found that the aquatic moss *Warnstorfia fluitans* (Figure 9) uses only organic phosphate, including P from DNA. Cellular P content is important in influencing phosphatase activities.



Figure 8. *Pseudoscleropodium purum* with capsules, a species that is able to take in luxury P when it is increased by at least 50%. Photo by Des Callaghan, with permission.



Figure 9. *Warnstorfia fluitans*, a species that is able to take in luxury P. Photo by Misha Ignatov, with permission.

Gordon *et al.* (2001) found that not only N, but also P changed both the composition and cover of individual species of bryophytes in a high Arctic heath. They pointed out that the species differed in their response to fertilization, warning that the bryophytes should not be

considered as a single functional group, a concept likewise warned by Turetsky (2003) in her review of the role of bryophytes in carbon and nitrogen cycling.

Benner and Vitousek (2007) found that increasing P on the epiphytic community had a strong effect on N-fixing lichens in Hawaii, but mosses and non-N-fixing lichens also increased somewhat in both abundance and diversity. Increased N, however, had no effect on the epiphytic communities.

N:P Ratios

One of the interesting aspects of nitrogen deficiency is that it can be offset by phosphorus (Gordon *et al.* 2001). That is, these two nutrients are **colimiting**, so the critical load of nitrogen is lower when available phosphorus is greater. On the other hand, Riis *et al.* (2010) found that the growth rate of *Warnstorfia fluitans* (Figure 9) increased when the moss had increased P content, but did not with increased N content.

Jirousek *et al.* (2011) used a nitrogen deposition gradient in *Sphagnum* (Figure 10, Figure 24-Figure 25) in a highly polluted region of Central-East Europe to assess the N:P ratio. A higher P concentration in the capitula resulted in a lower N:P ratio for these mosses in most of the bogs, despite their N saturation, causing N to still be limiting. Conversely where there was higher atmospheric N deposition, the N:P ratio increased significantly. Species in the *Cuspidata* section (Figure 10) of *Sphagnum* demonstrated significantly lower N:P ratios in locations with low N deposition.



Figure 10. *Sphagnum cuspidatum*, a species with low N:P ratios when N deposition is low. Photo by Michael Lüth, with permission.

Arróniz-Crespo *et al.* (2008) assessed the effects of enhanced N deposition on *Pseudoscleropodium purum* (Figure 8) and *Rhytidiadelphus squarrosus* (Figure 11) in an acidic grassland. The enhanced N deposition caused up to 90% loss of bryophyte cover, with no recovery after 22 months of no further deposition. The N:P ratios increased up to 3X under the enhanced N loading. Activity of the enzyme phosphomonoesterase showed good recovery, especially in *P. purum*. P limitation appears to be the key factor in bryophyte loss in these grasslands.

Calcium and Magnesium

Calcium (Ca) is an essential nutrient for plants and is used in various structural and regulatory roles in cell walls and membranes (White & Broadley 2003). In this role, it is important in maintaining membrane integrity and cellular adhesion (Brown 1982). In *Leucolejeunea* (Figure 12), when Ca was omitted in the growth medium, cells in new growth were not glued together (Fulford *et al.* 1947). There are implications that Ca may be associated with nutrient absorption (Odu 1978), especially at the rhizoid base where it accumulates in *Marchantia* (Figure 3). In *Funaria* (Figure 2), rhizoids developed at the point of maximum Ca entry on the protonema. Iwasa (1965) presented data that implicated its role in promoting bud formation in *Funaria*. This is consistent with its role as a regulator of growth and development in tracheophytes (White & Broadley 2003; Hepler 2005).



Figure 11. *Rhytidiadelphus squarrosus*, a species that is sensitive to excess N deposition. Photo by Michael Lüth, with permission.



Figure 12. *Leucolejeunea*, a leafy liverwort that requires Ca to glue its cells together. Photo by Paul G. Davison, with permission.

Uptake of Ca in plants is passive, requiring no energy. Since Ca is insoluble, once it resides in a cell it will normally stay there and not move to other parts of the plant. In tracheophytes, it is carried to its destination by the xylem. In bryophytes, it is probably carried primarily externally and may accumulate at the tips of stems and branches where it occupies all available exchange sites and makes a visible crunchy, off-white deposit (pers. obs.).

Calcium can be effective in keeping other ions off the exchange sites. In this role, it can cause nutrient deficiencies. This is particularly noticeable in many species of *Sphagnum* (Figure 10, Figure 24-Figure 26).

Magnesium (Mg) is essential as the center of the chlorophyll molecule as well as other plant processes. Sources for this nutrient include bedrock and soil, with alkaline and humus-rich soils containing more than acidic soils. Its dynamics are often intertwined with those of calcium. Because both are cations, they compete for binding sites in cation exchange (CEC). In other cases (Canadian mires), however, they may be taken up in proportion to their concentrations in the environment (Malmer *et al.* 1992). In rich fens, both of these nutrients are supplemented from ions dissolved in surface water. Based on their field data, Malmer and coworkers suggested that Ca could give the brown mosses, typical of rich fens, a competitive advantage over *Sphagnum* (Figure 10, Figure 24-Figure 26).

Iron

Iron (Fe) can be a micronutrient, but in other species it is a macronutrient. It seems premature to make any generalizations about this in bryophytes.

Iron is important in plants in many enzymes and in the production of chlorophyll. Bryophytes can collect iron in dustfall (Gorham & Tilton 1978), but may also obtain it in water that carries it to and around the plant. It is likely that some can also obtain it from rock substrata.

In low oxygen of deep water, iron forms soluble ferric compounds that can be absorbed by bryophytes. In oxygenated streams, this form quickly oxidizes. Instead of being absorbed, it forms plates on the plants, soon covering them sufficiently to block photosynthesis (pers. obs.).

Micronutrients

Tracheophytes require significant quantities of macronutrients and considerably less of those called **micronutrients** (Mn, Cu, Zn, Mo, Ni, Cl, B). Although comprehensive studies of nutrient deficiency for bryophytes are lacking, we have no reason to believe they would have different requirements than these, but nutrients may be required in different proportions, and certainly in different concentrations.

Most micronutrients will not be limiting in most habitats in nature, but must be included for long-term growth in artificial media. For short periods, bryophytes can generally call upon their stored nutrients and those in surface dust until returned to a natural medium.

Rühling and Tyler (1970) found the sorption and retention relationship of the moss *Hylocomium splendens* (Figure 41) to be Cu, Pb>Ni>Co>Zn, Mn. This series has likewise been observed in other bryophyte studies (Brown 1982).

There are many questions about micronutrients for which we have no answers, or have them for very few

species. Can they substitute one micronutrient for another? What processes and structures use these micronutrients? Can the presence, absence, or deficiency of a nutrient change the form of the bryophyte? Can such differences make them look like different species in different habitats? What are their deficiency symptoms?

Boron

Boron (B) is used in plant cell walls and affects nucleic acid and carbohydrate metabolism (Pilbeam & Kirby 1983). Boron is important in maintaining membrane structural integrity. As in monocots, bryophytes do not have a strong requirement for boron. Known symptoms of boron deficiency are usually secondary effects of changes in permeability of the membranes.

Boron is essential in the plant process of making lignin, which is, in turn, essential for tracheophyte vascular tissue (Lewis 1980). Thus, before tracheophytes could evolve, a means for uptake and incorporation of boron was necessary. But we know that uptake of boron is present in bryophytes. Sameka-Cymerman *et al.* (1991) found that boron, among other minerals, was taken up from the water by *Scapania uliginosa* (Figure 13). On the other hand, the amount incorporated into bryophyte cell walls is considerably less than that in tracheophytes (Matsunaga *et al.* 2004). To date, it is not clear that bryophytes actually require boron.

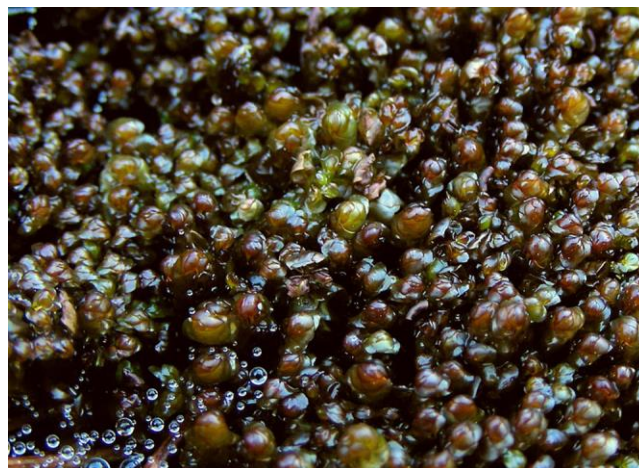


Figure 13. *Scapania uliginosa*, a species that extracts minerals from the water, including boron. Photo by Michael Lüth, with permission.

As for iron, bryophytes can collect boron from dustfall (Sabovljević *et al.* 2005). However, at least some, including *Sphagnum* (Figure 10, Figure 24-Figure 25) species, may not accumulate it to the same degree as do trees (Gorham & Tilton 1978). Obviously, trees have a much greater need for boron because they must make lignin, and they do not generally rely on dust for their nutrients.

Copper

Copper (Cu), like iron, is important in enzymes in plants. As such, it facilitates many plant processes (Yruea 2005). But copper is needed only in small quantities and becomes toxic in larger quantities. This heavy metal is available in soil and can be carried with water that moves up the bryophyte.

Copper can be limiting in some aquatic habitats, and probably some terrestrial ones as well. In their studies on *Fontinalis dalecarlica* (Figure 14), Glime and Keen (1984) found that natural Lake Superior water had less than ideal copper concentrations for maximum chlorophyll concentration, with 0.01 mg per liter providing the best chlorophyll (Figure 15). At higher concentrations, chloroplasts lost their green color and at 10 mg / L the cells became brown (Figure 16). With increasing concentrations, the tips of *F. antipyretica* became yellow (Figure 19).



Figure 14. *Fontinalis dalecarlica*, a species that can, in some environments, be copper deficient. Photo by Janice Glime.

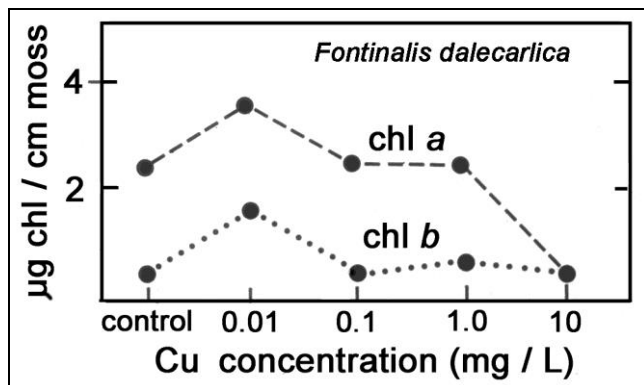


Figure 15. Effect of copper concentration on chlorophyll *a* and *b* concentrations in the aquatic moss *Fontinalis dalecarlica*. Redrawn from Glime & Keen 1984.

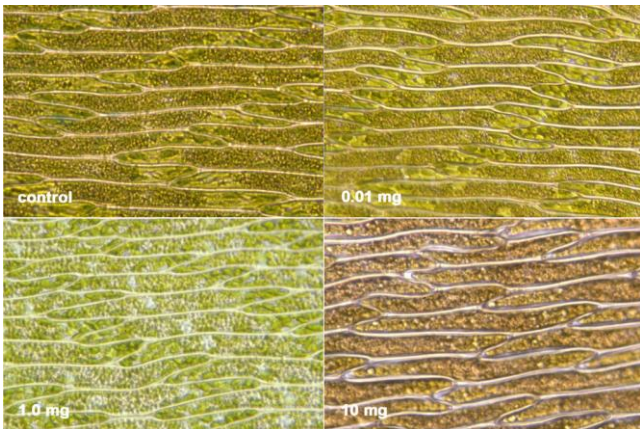


Figure 16. Comparison of cell contents and colors in leaves of *Fontinalis dalecarlica* subjected to concentrations 0.01 mg/L, 1.0 mg/L, 10 mg/L) of copper as copper foil, Lake Superior water as control,. Photos by Janice Glime.

Claveri and Mouvet (1995) found that the aquatic moss *Platyhypnidium riparioides* (Figure 17) suffered from denaturation of chlorophyll pigments after spending 12 days in a copper concentration of 80 µg L⁻¹. They found that uptake of copper was not related to photosynthesis, permitting it to continue uptake even when the chlorophyll was damaged. Furthermore, its uptake does not appear to be influenced by temperature, whereas its damage to chlorophyll increases with temperature. Similar damage to chlorophyll occurs in the aquatic moss *Fontinalis* (Figure 50) (Glime & Keen 1984). But this is not just an aquatic phenomenon. It is known also in *Thuidium* spp. (Figure 18) (Shakya *et al.* 2008) and is likely to be the case in all except perhaps the copper mosses.



Figure 17. *Platyhypnidium riparioides*, a species that loses its chlorophyll in excess copper. Photo by Michael Lüth, with permission.



Figure 18. *Thuidium delicatulum*, member of a genus that is known to be sensitive to copper. Photo by Janice Glime.

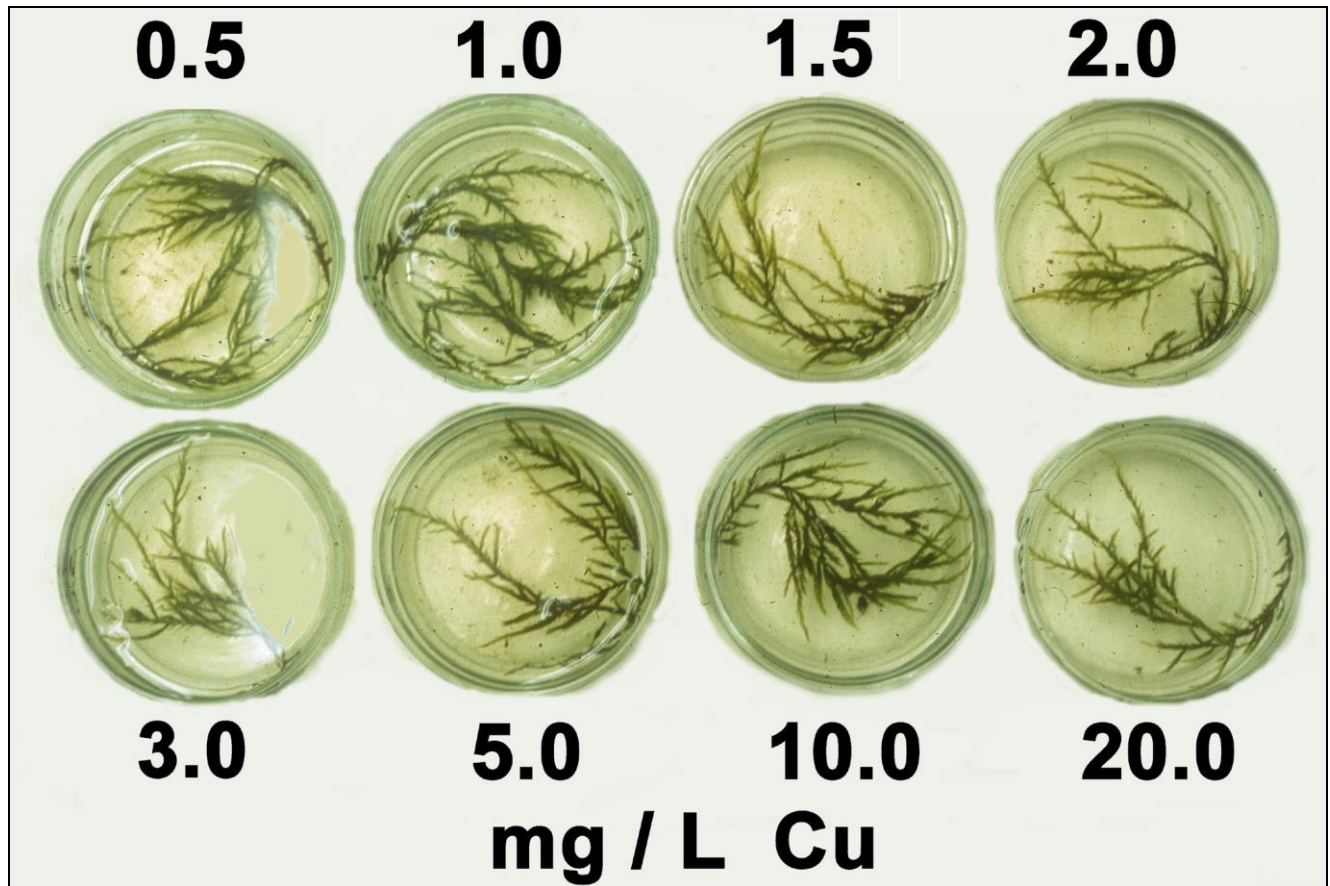


Figure 19. Effects of various concentrations of copper (as copper foil) on the general appearance of *Fontinalis antipyretica* (see also Figure 50). Note the yellowed tips at 1.5 mg/L and above. Photo by Janice Glime.

Heavy Metals

It is perhaps more likely that micronutrients, particularly the heavy metals, will be toxic at greater than trace amounts. Many bryophytes have means of sequestering these in ways that are not toxic. The moss that seems to have the greatest tolerance in many polluted and otherwise heavy metal situations is *Pohlia nutans* (Figure 20-Figure 21), a species with known tolerance to copper, zinc, and nickel (Shaw 1989).

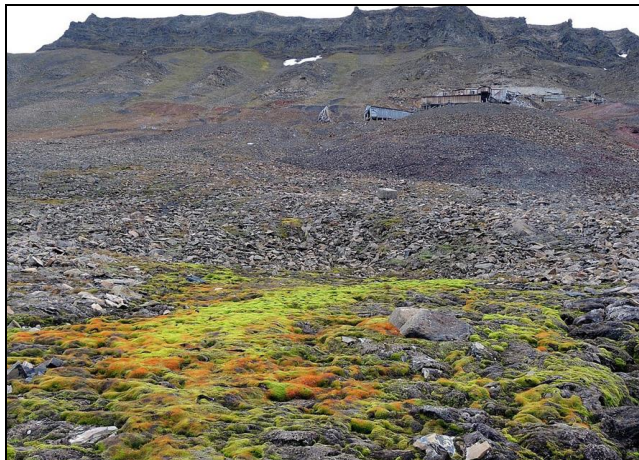


Figure 20. *Pohlia nutans* below old mine. Photo by Michael Lüth, with permission.



Figure 21. *Pohlia nutans*, a heavy metal tolerator. Photo by J. C. Schou, with permission.

Some heavy metals in the environment have no known use by plants, including bryophytes. One such heavy metal is **cadmium**, a toxic by-product of mining and smelting, among other things. In our experiments with *Fontinalis duriaei*, cells became plasmolyzed at 100 μg Cd per liter (Figure 22) (Glime & Keen 1984). At 1000 μg , the cells deplasmolyzed in a way that suggested membranes were damaged.

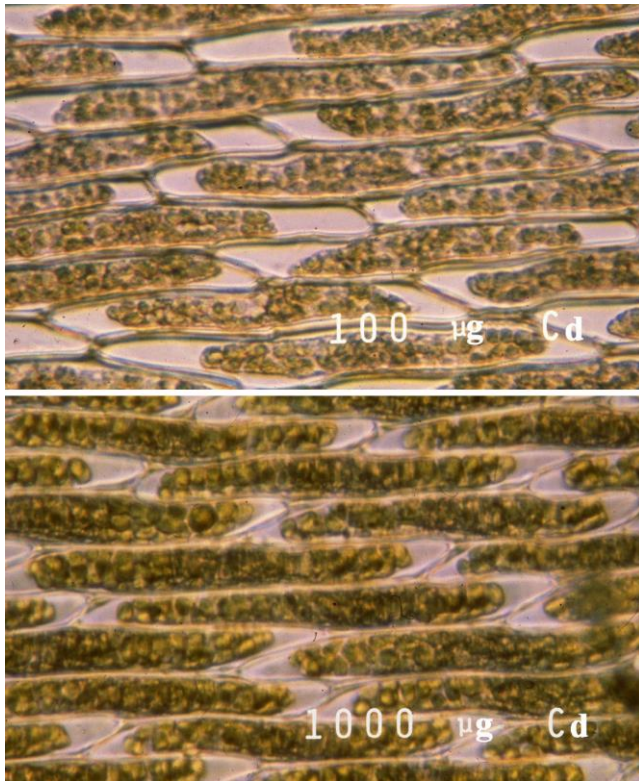


Figure 22. Effects of cadmium on cell contents in *Fontinalis duriae*. At 100 µg per liter, cells become plasmolyzed. At 1000 µg per liter, the cells deplasmolyze, demonstrating membrane damage. Photos by Janice Glime, based on Glime & Keen 1984.

Nutrient Content

What is normal nutrient content for bryophytes? Or is there one? In the scattered literature that addresses nutrients outside the laboratory, we find that content can depend on habitat, season, uptake ability, and source. But our understanding of bryophyte mechanisms for regulating their nutrient content is meager at best.

Habitat Differences

Habitats can range widely in nutrient availability. These differences can serve as limiting factors for bryophytes, but for most species we do not understand these limitations. In his discussion of *Sphagnum* (Figure 10, Figure 24-Figure 25), Malmer (1988) considered that the concentration differences among the species are mainly caused by differences in growth pattern and site conditions. The concentrations in the living moss and those in the underlying dead peat are not related.

Streams

In streams, phosphorus is typically a limiting nutrient, not to mention CO₂ limitations. On the other hand, pollution, including phosphate from such sources as agricultural fertilizers, can often cause bryophytes to disappear or begin to look unhealthy. One problem for stream bryophytes in high nutrient conditions, whether natural or from pollution, is that the high nutrient level may promote the growth of the periphyton living on their surfaces (Glime, unpublished), causing them to suffer from CO₂ and light competition.

Phosphorus often occurs as agricultural pollution or sewage waste. Frequently it arrives in streams, changing the N:P ratio of those streams. Steinman (1994) examined the effect of phosphorus enrichment on the leafy liverwort *Porella pinnata* (Figure 23) in two woodland streams of eastern Tennessee, USA. Not surprisingly, the N:P ratio decreased significantly, and the P:C ratio increased significantly in the liverworts. In this case, the expected epiphyte structure and abundance in the liverworts were not significantly affected, perhaps due to greater grazing by snails.



Figure 23. *Porella pinnata*, a species that can incorporate added phosphate into its cells. Photo by Des Callaghan, with permission.

Christmas and Whitton (1998) compared the phosphorus content of the stream mosses *Fontinalis antipyretica* (Figure 50) and *Platyhypnidium riparioides* (Figure 17) to that in the River Swale-Ouse in NE England. They found that both P and N concentrations increased with downstream distance. The mosses likewise showed their lowest concentrations at the headwater site, with increasing levels of both elements with distance downstream. More interesting was the change in N:P ratio with distance downstream, decreasing from 14.9:1 to 6.8:1 in *F. antipyretica* and from 12.5:1 to 5.5:1 for *P. riparioides*, suggesting luxury uptake of P. The PMEase (phosphomonoesterase) was greatest at the lower pH (5.5) compared to the higher pH values. The enzyme decreased at all three pH values with distance downstream. Nevertheless, mean primary production increased by only 15% following enrichment, a difference that was not statistically significant.

Bogs and Fens

We know that by definition, **bogs** and **poor fens** have low nutrient content, **intermediate fens** are characterized by intermediate nutrient levels, and **rich fens** have the highest nutrient levels among these habitats. The bogs and poor fens have similar nutrient concentrations and similar bryophyte species, but differ in their nutrient sources, whereas the species of bryophytes in the intermediate and rich fens differ from each other and from those of the bogs and poor fens. Wojtuń (1994) found that N, P, K, Ca, Mg, and Na were in significantly higher concentrations in *Sphagnum* (Figure 10, Figure 24-Figure 25) from the **minerotrophic** (nutrient-rich) fens than from the **ombrotrophic** (low-nutrient) bogs and fens, with K and P

having the greatest differences. As already noted, in the aquatic moss *Warnstorfia fluitans* (Figure 9) from an Arctic lake, increased P content caused increased growth, but increased N content did not (Riis *et al.* 2010). Hence we can conclude that at least some nutrients do make a difference to the bryophyte species. This indicates differences in physiology for which we have only minimal understanding.

For *Sphagnum* (Figure 10, Figure 24-Figure 25) species, cation exchange (see Chapter 8-4, Uptake) plays a major role in the ability to take up nutrients in low-nutrient situations, but can make a species intolerant of divalent cations such as Ca^{++} . Cation exchange causes calcium to adhere to cells, replacing H^+ ions along the cell walls. Since the Ca^{++} ion has two positive charges, it occupies two exchange sites. In this way it competes preferentially with other needed nutrients with only one positive charge, especially potassium (Koedam & Büscher 1982).

Hájek and Adamec (2009) found that nutrient content of *Sphagnum* (Figure 10, Figure 24-Figure 25) species varied between contrasting microhabitats. The greatest difference was shown between *S. angustifolium* (Figure 24) and *S. magellanicum* (Figure 25), with the latter having a 40% lower intracellular N content, even when it grew alone. This lower uptake ability by *S. magellanicum* can permit *S. angustifolium* to outcompete *S. magellanicum* when the two are mixed.



Figure 24. *Sphagnum angustifolium*, a species that outcompetes *S. magellanicum* for N. Photo by Jan-Peter Frahm, with permission.



Figure 25. *Sphagnum magellanicum*, a species that is a poor competitor for N. Photo by Michael Lüth, with permission.

In *Sphagnum fallax* (Figure 26) from a fen woodland, its annual accumulation of N, P, and K differed little between a dry and a wet year (Brock & Bregman 1989). How can we account for this ability to maintain the same level of these three essential and often limiting nutrients, despite different opportunities for uptake in different precipitation regimes? On the other hand, Lembrechts and Vanderborcht (1985) examined the mineral content (Na, K, Ca, Mg, Al, Fe, P, Cu, Mn, Pb, Zn) of nine species of *Sphagnum* (Figure 10, Figure 24-Figure 25) in Belgian bogs and found that the concentrations of all elements except Ca, Zn, and Mn were related to the moisture of the habitat. The concentrations of Ca and Cu were lower in one site due to trophic status and air pollution, respectively.



Figure 26. *Sphagnum fallax*, a fen species for which N, P, and K accumulation differences between years seems not to be affected by annual precipitation differences. Photo by Michael Lüth, with permission.

The pH plays an important role in determining how Ca affects bryophytes, best known in bog and fen systems. Clymo (1973) found that most *Sphagnum* (Figure 10, Figure 24-Figure 25) plants grew well in low Ca^{++} at a low pH, at high pH, or at high Ca^{++} , but not when both pH and Ca^{++} concentration were high.

Turetsky *et al.* (2008) found that *Sphagnum* species exhibit resource partitioning, with a tradeoff between metabolic and structural carbohydrates. The way that bryophytes use their nutrients has interesting implications for their decomposition and their roles as ecosystem engineers through sequestration of certain nutrients. And these differences must be examined at the species level, not at the bryophyte level, due to species differences.

Forests

In forests, a primary source of nutrients derives from decomposition of leaf litter. But in industrialized areas, air pollution becomes a major source of N, as well as a number of trace elements. P is often limiting. Species diversity is fostered by habitat diversity that provides nutrient levels differing from those of the forest floor. We can observe considerable species differences on soil, rocks, trees trunks and leaves, and logs, which we usually attribute to differences in moisture, but we lack an understanding of the role that nutrients may play in these species differences.

Substrate can make a difference in nutrients available. As already noted, the moss *Leucobryum juniperoides* (Figure 4) is sensitive to high concentrations of nitrogen,

preferring the lower N levels on rocks and logs in some locations with high N in the soil, whereas in others the soil has a low enough concentration to be suitable (Wang *et al.* 2014).

In the highly polluted region of Central-East Europe, Jirousek *et al.* (2011) found that local forestry practice affected the N-limitation experienced in areas with high P and N saturation.

Arctic and Alpine

Bryophytes can be very important in sequestering P in Arctic soils. Chapin *et al.* (1987) found that 75% of the above ground annual P accumulation was in the mosses of an Alaskan black spruce (*Picea mariana*; Figure 27) forest. The mosses *Sphagnum subsecundum* (Figure 28), *Hylocomium splendens* (Figure 41), and *Pleurozium schreberi* (Figure 31) have higher absorption capacity for phosphate than do the fine roots of the spruce. The uptake comparison demonstrated that absorption capacity increases with age in green tissues while decreasing with age in brown tissues in three of the four studied mosses. In the fourth moss species, the endohydric *Polytrichum commune* (Figure 44), phosphate is absorbed most rapidly from stems in mineral soil. When mycorrhizal fungi were killed in the plots, phosphate retention by mosses increased and transfer out of the plots decreased, suggesting that P is transferred from the moss carpet to the tree roots by fungi.



Figure 27. Arctic black spruce (*Picea mariana*) forest. Photo by Michael Lüth, with permission.



Figure 28. *Sphagnum subsecundum*, a black spruce forest moss in the Arctic. Photo by Michael Lüth, with permission.

Species Differences

Nutrient content, as we might expect, can differ widely among species. For example, copper mosses such as *Scopelophila cataractae* (Figure 29) can be expected to have high concentrations of copper, although in some cases it is iron rather than copper that is accumulated (Shaw 1987b).



Figure 29. *Scopelophila cataractae*, a moss with high tolerance of, and possibly dependence on, copper. Photo by David T. Holyoak, with permission.

We have already noted the importance of cation exchange sites in determining the habitat of *Sphagnum* (Figure 10, Figure 24-Figure 25) species. Malmer (1988) found that in three hummock *Sphagnum* species the cation concentrations of Na, Mg, and Ca depended on the exchange capacity of the species. The sum of the divalent ions Ca^{++} and Mg^{++} was the same throughout the plant. Hájek and Adamec (2009) compared locations of various ions in six species of *Sphagnum*, demonstrating differences in locations and concentrations (Figure 30).

To understand the ability of mosses to sequester nutrients differentially, Berg and Steinnes (1997) compared wet deposition data to the concentrations of 48 elements in the feather mosses *Hylocomium splendens* (Figure 41) and *Pleurozium schreberi* (Figure 31). Their results suggest that for some elements, moss content reflects environmental content. This was true for V, Fe, Co, As, Y, Mo, Cd, Sb, Ce, Sm, Er, Tl, and Pb in *Hylocomium splendens*, and for Mg, V, Fe, Co, As, Se, Y, Mo, Cd, Sb, Tl, and Pb in *Pleurozium schreberi*. Among these results, I find the difference in Mg as the most interesting. Mg is the element in the center of a chlorophyll molecule and thus is essential for all photosynthetic plants and algae. *Hylocomium splendens* had the highest concentrations of Cr, Fe, Co, Ni, Cu, Ga, Nb, Mo, Sb, Eu, Gd, Tb, Dy, Er, Tm, Lu, W, Tl, Pb, and Th, whereas V, Mn, Rb and Cd were highest in *Pleurozium schreberi*. These differences are interesting because these two species frequently occur in the same habitats, especially in boreal forests.

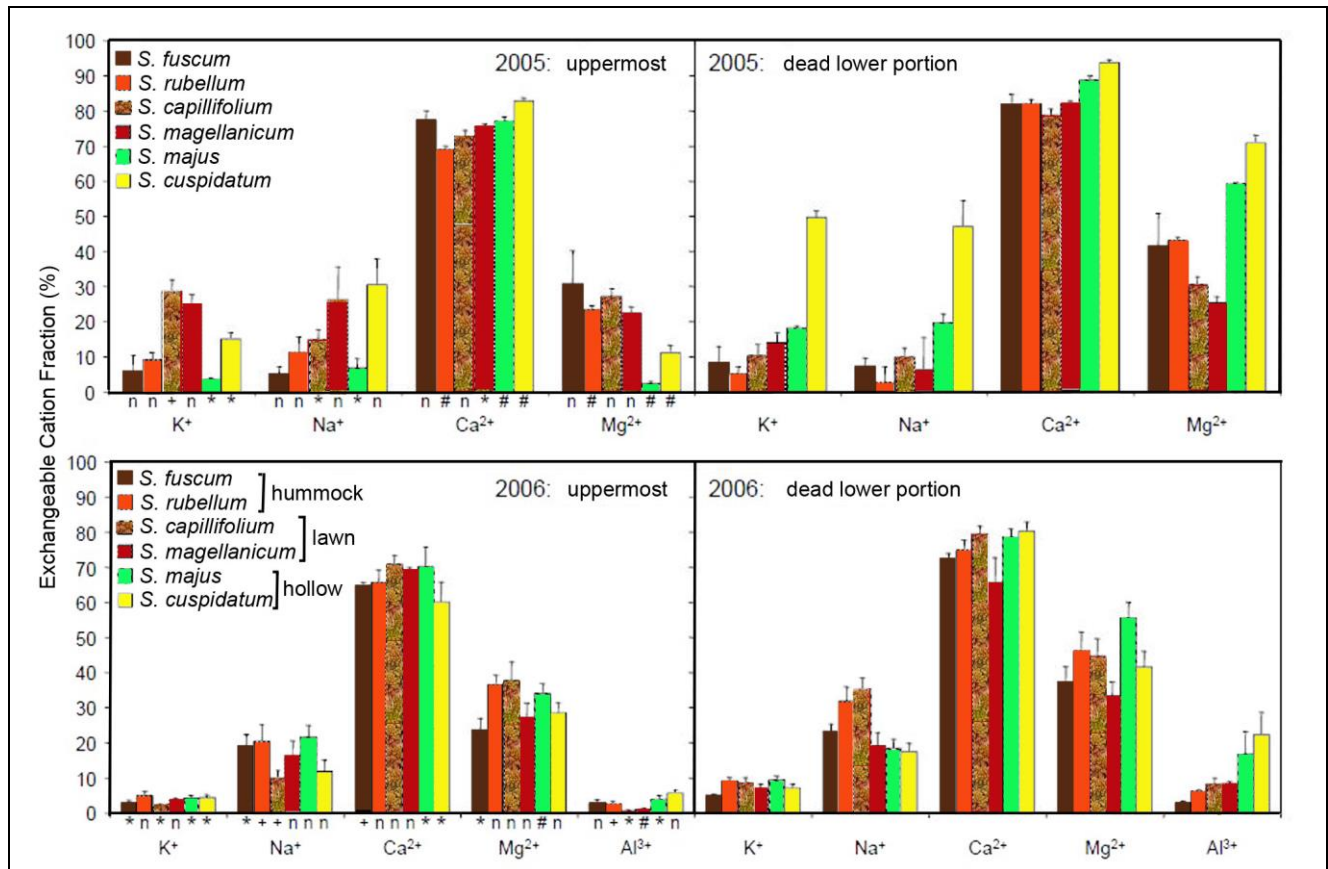


Figure 30. Exchangeable cation fraction from the total cation pool in apical (uppermost) and dead shoot segments of six *Sphagnum* species. Symbols below the columns are *p* values of the t-test for dependent samples testing the differences between shoot segments: # $p < 0.001$; + $0.01 < p < 0.001$; * $0.05 < p < 0.01$; n $p > 0.05$. Redrawn from Hájek & Adamec 2009.



Figure 31. *Pleurozium schreberi*, a species for which cell contents reflect the Mg levels in the environment. Photo by Janice Glime.



Figure 32. *Sphagnum capillifolium*, a hummock species in which N content is proportional to that added. Photo by J. C. Schou, with permission.

Adaptability and Acclimation

Williams *et al.* (1999) found differences in labelled N in waters from two species of *Sphagnum* in a bog in northeast Scotland. In the hummock species *Sphagnum capillifolium* (Figure 32), labelled dissolved organic nitrogen in moss water was proportional to that added as inorganic N, but in the hollow species *S. recurvum* (Figure 33), it was not.

One question that has received little attention is the ability of bryophytes to acclimate or adapt to high concentrations of any given nutrient or pollutant. With the wide range of minerals and other nutrients in the environment, how does an **ectohydric** (moving water on the outside of plant) bryophyte respond to these differences? There is some evidence that they do change

their tolerance. Shaw (1987a) showed that protonemata responded to pretreatment with copper and zinc more than did the stems of *Funaria hygrometrica* (Figure 2). But overall, genetic differences had a greater role than acclimation through pretreatment, with some individuals showing a significant response and others showing little or none.



Figure 33. *Sphagnum recurvum*, a hollow species in which N concentrations do not reflect those of the atmosphere. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.

In culture conditions, Shaw (1988) demonstrated that populations exhibited a wide range of tolerances in the protonemal and stem stages. To confound the story, Shaw found that in experiments with copper and zinc the populations of *Funaria hygrometrica* expressed a greater similarity among environmental correlations than among genotypic correlations, suggesting some sort of acclimation.

A genetic ability to survive and even require some heavy metals such as copper is exhibited by *Scopelophila cataractae* (Figure 29) (Shaw 1987b). Out of six populations in eastern USA, five were associated with high copper concentrations. The sixth was associated with high iron concentrations. When cultivated, these populations grew best on soil contaminated with copper, lead, and zinc. It is interesting that this species lacks sexual reproduction in North America. Could that be related?

Plant Nutrient Locations

Nutrients not only have different purposes, but also are located in different positions within the plant and within the cells they occupy. Some are needed structurally and some are used **constitutively** (always present, such as defense compounds). For example, potassium, a highly soluble and mobile nutrient, is present in *Grimmia donniana* (Figure 34) and *Calliergonella cuspidata* (Figure 35) in a soluble form within the cell, whereas the calcium is primarily in extracellular locations in exchangeable form (Brown & Buck 1985; see also Brehm 1968; Bates 1992; Bates & Brown 1974; Brown & Buck 1979, 1985). Magnesium and zinc, on the other hand, were intermediate, with their locations depending on the species and concentrations. Turetsky *et al.* (2008) demonstrated that a tradeoff between structural and constitutive use of nutrients, especially C and

N, in *Sphagnum* species gave hummock species the ability to maintain their hummocks by putting more nutrients in recalcitrant structural forms that did not decompose easily.



Figure 34. *Grimmia donniana*, a species with soluble K in its cells. Photo by Henk Greven, with permission.



Figure 35. *Calliergonella cuspidata* growing among sedges. Photos by Michael Lüth, with permission.

Wojtuń (1994) determined that N, P, and K accumulate in the upper parts of *Sphagnum* (Figure 10, Figure 24-Figure 25) through active uptake; all three are typically found within the cell, being used in cell metabolism rather than cell wall metabolism (Brown & Wells 1990b). On the other hand, Ca, Mg, and Na are obtained through passive cation exchange. These and other elements acquired through cation exchange tend to accumulate in the lower parts of the plants. The concentration of iron either does not correlate or correlates negatively with the other

elements (Wojtuń 1994). Contents of N, P, K, Ca, Mg, and Na were significantly higher in mosses from **minerotrophic** (high nutrient) habitats than in those from **ombrotrophic** (low nutrient) habitats. The greatest difference among species were for K and P.

Brown and Wells (1990a) showed that heavy metals could alter ion locations, for example by causing potassium leakage due to membrane damage. It is interesting that in the liverwort *Dumortiera hirsuta* (Figure 36), pretreatment with 80 mM KNO₃ actually stimulated cadmium uptake, presumably because the potassium removed potentially competing cations from the exchange sites, thus permitting more Cd to bind and be taken up by the cells (Mautsoe & Beckett 1996). This suggests that potassium ions are able to occupy environmentally exposed exchange sites as well as their interior sites. Such locations could make these ions readily available when needed by the cells.



Figure 36. *Dumortiera hirsuta*, a species in which K⁺ removes competing cations from exchange sites, permitting Cd⁺⁺ to bind and then enter cells. Photo by Michael Lüth, with permission.

Ron *et al.* (1999) used *Hookeria lucens* (Figure 37) to observe the cause of reddish-brown deposits of minerals in the cells. They identified the minerals bohemite, calcite, diaspore, feldspar, ferrihydrite, gibbsite, jarosite, lepidocrocite, opal, pirolusite, and quartz inside the **hydrom** (unit of water-conducting cells), cortex, and leaf cells. Since not all of these minerals were present in the soil substrate, they hypothesized that the additional ones were derived from a biomineralization process inside the moss cells from such elements as Mn and S, and from those in the soil on which the mosses were growing.

Bates (1987) found that in *Pseudoscleropodium purum* (Figure 8) fertilization caused a small net increase in Mg, but shoot N had no significant change in the plant. Ions held on exchange sites did not increase much with fertilizer addition in the field, but in the laboratory, a 30-minute exposure to these caused Ca⁺⁺ and Mg⁺⁺ concentrations to rise notably, whereas exchangeable K⁺ fell. But the disappearance of these exchange site nutrients when the mosses were returned to the field caused Bates to question the utility of the exchange sites. Could they serve to keep a ready supply while at the same time preventing excess within the cells? Weekly watering with fertilizer caused maximum net uptake of P, Mg, and Ca. Pulse watering with more concentrated solutions at greater intervals had the least uptake.



Figure 37. *Hookeria lucens*, a species that can be discolored by minerals in the hydrom, cortex, and leaf cells. Photo by Michael Lüth, with permission.

Determination of the interior location of plant elements has been complicated by damage to the cell membranes during the measurement technique (Brown & Wells 1990b). When this damage happens, ions are released and may become bound to newly exposed cell walls on the insides of the cells.

Cell Wall Sites

The cell walls of tracheophyte roots have exchange sites that permit binding of nutrient ions and facilitate uptake. Similar, and very active, exchange sites are well known on *Sphagnum* (Figure 10, Figure 24-Figure 25) leaves (Clymo 1963; Spearing 1972; Schwarzmaier & Brehm 1975). But other bryophytes can have exchange sites as well (Brown & Buck 1979; Glime *et al.* 1982). Unfortunately, this capacity has scarcely been examined for non-*Sphagnum* bryophytes. Nevertheless, as described above, it appears that such sites exist to varying degrees among the bryophytes in general.

Brown and Buck (1979) reported that in bryophytes Ca⁺⁺ is bound to exchange sites in the cell wall and is insoluble within the cell. The quantity of an element bound to such sites depends on the concentration of that element. The ability of a **cation** (positive ion) to reach a stable equilibrium is relatively rapid, whereas its departure rate when the external supply is removed and replaced with a solution free of the element is often slower, the former taking only about 4.5 minutes to reach half maximum extracellular uptake for 100 µM L⁻¹ Cd in *Rhytidiadelphus squarrosus* (Figure 11) (Brown & Beckett 1985), but taking days at lower concentrations of <0.13 µM L⁻¹ Cd in some aquatic species (Mouvet 1987).

Vázquez Castro *et al.* (1999) examined the location of heavy metals in three aquatic mosses. They found that most of the metal uptake was to the extracellular compartment compared to the intracellular fraction. *Scapania undulata* (Figure 48) in particular has a high exchange site affinity for the heavy metals, whereas *Fissidens polyphyllus* (Figure 38) has a relatively low attraction. On the other hand, *F. polyphyllus* has the highest intracellular contents.



Figure 38. *Fissidens polyphyllus* in limestone cave, a species with low affinity for heavy metals. Photo by Janice Glime.

The mechanism of cation exchange is discussed in the subchapter on Uptake (Chapter 8-4 of this volume). Binding preferences vary with concentrations and can be determined based on availability of the ions, previous filling of the exchange sites, type of ligand in the exchange site, and type of ions (Brown & Wells 1990b). For example, potassium, calcium, and magnesium prefer oxygen-rich **ligands** (ion or molecule that binds to a central metal atom to form a complex) such as carboxylic groups (Nieboer & Richardson 1980). Others such as mercury, lead, and gold prefer sulfur- and nitrogen-rich ligands. Some are borderline and have intermediate preferences with heavier elements tending to prefer the sulfur- and nitrogen-rich ligands.

Intracellular Sites

Brown and Wells (1990b) reminded us of the need to separate the locations of the elements within the cells. They furthermore pointed out that many of the elements became bound into compounds, onto membranes, or onto the interior of the cell walls. Others could be stored in vacuoles. Not only potassium, aluminium, and nitrogen occurred inside cells of *Sphagnum* (Figure 10, Figure 24-Figure 25), but also magnesium and sodium (Hájek & Adamec 2009). Magnesium is stored in the chlorophyll molecule, where it is essential for that molecule to function in photosynthesis (Brown and Wells 1990b). Sodium has no known use in bryophytes.

Brown and Buck (1979) found that potassium is mainly dissolved within the bryophyte cells. Magnesium is found not only in the cells but also adhering to exchange sites and cell membranes. Hájek and Adamec (2009) looked at nutrient locations in *Sphagnum* (Figure 10, Figure 24-Figure 25) and reported that K, Mg, N, Al, and Na occurred within cells, although Mg and Na also could be found on exchange sites. (Note, Al and Na are generally not considered to be plant nutrients.)

Microhabitats and species differences seem to account for nutrient content in *Sphagnum* (Figure 10, Figure 24-Figure 25) (Hájek & Adamec 2009). For example, *Sphagnum magellanicum* (Figure 25), a hummock species, had an intracellular nitrogen content that was about 40% lower than that in associated species. Such unequal

competition for N, even when compared to *S. magellanicum* grown alone, suggests its inability to compete for N in mixed patches.

Vertical Distribution

The base of the plant has different concentrations of most elements compared to the apex (Brown & Wells 1990b; Hájek & Adamec 2009). For example, potassium, a soluble and translocatable nutrient, is most concentrated in the actively growing apex of the plant and is intracellular (Figure 39) (Brown & Wells 1990b). Other cellular metabolic components such as nitrogen and phosphorus are likewise concentrated in the growing apex (Brown & Wells 1990b; Hájek & Adamec 2009 – see Figure 30).

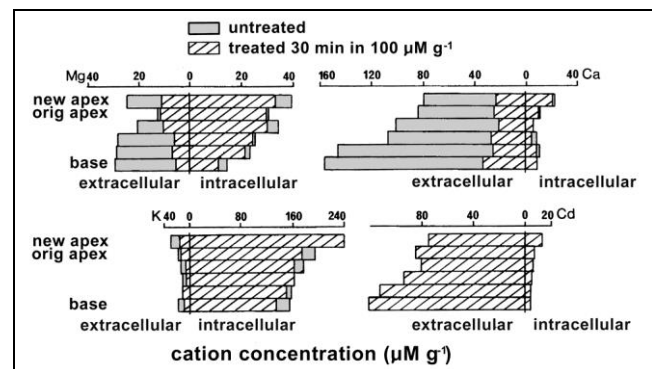


Figure 39. Location of four elements in 2-cm sections from new apical segment to base along the stems of laboratory-grown *Rhytidadelphus squarrosus* (Figure 11). Redrawn from Brown & Wells 1990b.

As in tracheophytes, bryophytes are able to move at least some of their nutrients to actively growing tissue. In *Hylocomium splendens* (Figure 41) less new growth occurred when branches of mature segments were removed (Brümelis & Brown 1997). The metals K, Mg, Ca, and Zn in new growth correlated with the initial contents in the juvenile plus mature segments but not with the levels in the pre-experimental segments, suggesting the importance of moving nutrients to growing tissues.

Those elements that are predominantly bound to extracellular sites tend to accumulate in the basal regions of the plant (Brown & Wells 1990b). These include the heavy metals. Their accumulation at the base may be the result of cell death in that region, exposing exchange sites on the cell interiors. Those elements such as manganese that are poorly bound to exchange sites may move upward through evaporative water movement and accumulate at the apex (Lötschert & Wandtner 1982; Malmer 1988), a phenomenon sometimes referred to as transpiration transport.

Malmer (1988) divided three hummock *Sphagnum* (Figure 24-Figure 25) species into four segments for nutrient and growth analysis. As one might expect, weight increases mostly in the capitulum, but length increases further down. To facilitate this growth, N, P, and K accumulate in the upper parts of the mosses. The trace elements Al, Fe, Zn, Cd, and Pb increase with the age of the plants. Both Ca^{++} and Mg^{++} are at first bound to exchange sites on the outside the plant and the sum of these two minerals is consistent throughout the *Sphagnum* plant.

Nutrient Sources

Mineral nutrients result from weathering and atmospheric deposition (Bates & Farmer 1992). Bryophytes can use five major sources of nutrients: soil, stream water, atmospheric dust, precipitation (including throughfall), and litter (Babb & Whitefield 1977; Parker 1983; Frego & Carleton 1995). For **saxicolous** (rock-dwelling) bryophytes, the only feasible sources are dust and precipitation (Rieley *et al.* 1979), especially for potassium (Bates 1976), although Hébrard *et al.* (1974) demonstrated the ability of *Grimmia orbicularis* (Figure 40) to obtain radiolabelled ^{90}Sr from an artificial rock. For pleurocarpous taxa and taxa living in the forest, the atmosphere (dust and precipitation) is generally considered to be the major nutrient source (Brown 1982), but as we shall see, this may not be the whole story. More to the point, what can we expect in uptake of the macronutrients such as phosphorus, nitrogen, and potassium, and are these values controlled, or are they determined by the concentrations in the ecosystem?



Figure 40. *Grimmia orbicularis*, a species with the ability to take up minerals from its rock substrate. Michael Lüth, with permission.

In a study of bog mosses, Malmer (1988) found that variations in S, Cu, Zn, Cd, and Pb are the results of varying man-made emissions. Na and Mg variations can be traced to oceanic influence. P, Na, Mg, and Ca also seem to vary with moss productivity. Al and Fe are greatest near agricultural and industrialized regions. Unlike the other elements, Mn concentrations are related primarily to the soil and bedrock.

Precipitation

Clearly rainwater has a very different chemical makeup than soil. Some elements are more abundant, whereas others, like Mg, are virtually absent in the open. Hence, mosses that grow in the open and do not get any leachates from canopy trees are likely to be very deficient in some elements. Could the lack of Mg in *Funaria hygrometrica* (Figure 2), a species of open sites, explain why it is so short, or might being short be an adaptation to living there?

Larsen (1980) describes the mosses in the boreal forest as growing vigorously, using nutrients that they receive in throughfall, and Weetman (1968) likewise found that feather mosses in a black spruce (*Picea mariana*; Figure 27) forest relied on dust and precipitation for both nutrients and moisture. Tamm (1953, 1964) found that rainwater was sufficient to account for all the nutrients needed by the

feather moss *Hylocomium splendens* (Figure 41). Weetman and Timmer (1967) concluded the same thing for *Pleurozium schreberi* (Figure 31) in the black spruce forest, where N, K, Ca, and Mg were leached from the canopy. This canopy throughfall source annually supplied 9 kg of N per hectare to the moss. In fact, the spruce trees are known to be N-deficient and root prolifically at the base of the green layer of mosses. Since feather mosses such as *Pleurozium schreberi* and *Hylocomium splendens* are known to mineralize nitrogen, they interpreted this to mean that the moss layer provided the major source of nitrogen for the trees. It is likely that mosses also held a portion of rainfall N in interstitial spaces among leaves in this layer, retaining it where tree roots could absorb it during the time that there was sufficient moisture for them to grow. It is also likely that in late summer when nutrients in the soil are depleted, rehydrating mosses could release nutrients collected as dust, but also from cells with membranes damaged by the drought (Leary & Glime 2005).

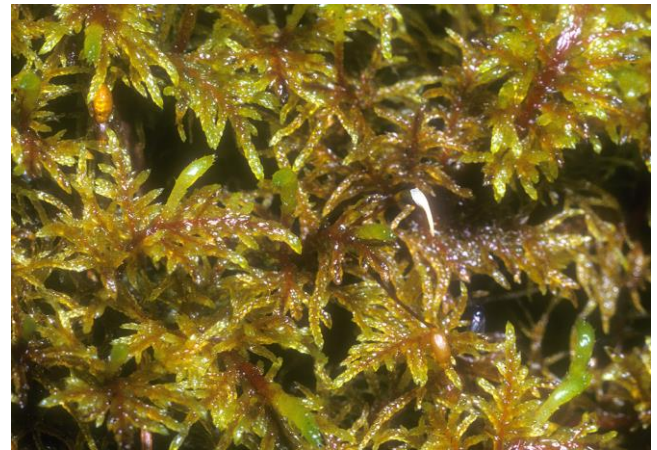


Figure 41. *Hylocomium splendens* gametophytes. Photo by Janice Glime.

Nutrient availability from precipitation can vary widely, depending on the canopy, with the lowest nutrient concentrations occurring in the open. Tamm (1953) showed that *Hylocomium splendens* (Figure 41) grew more under the canopy than in the open, and that its annual dry biomass increments under the canopy increased with distance from the tree trunk. He attributed these differences to light intensity increases outward from the trunk, whereas in the open he considered there to be insufficient nutrients due to lack of canopy trapping and leaching. However, despite the differences in precipitation nutrient concentrations, tissues of those *Hylocomium splendens* plants located in the open had the same nutrient concentrations as did the ones under the canopy, suggesting that they must have obtained their nutrients from something other than rainfall (Brown 1982), but also grew more slowly, thus requiring lower concentrations from the environment.

Forsum *et al.* (2006) not only compared the forms of nitrogen use by *Hylocomium splendens* (Figure 41), but also analyzed the nitrogen components of rain. Typically, amino acids in the rainfall are ignored, but Forsum and coworkers found that rain in their boreal forest study site had 78% of its nitrogen in ammonia (NH_4^+), 17% in amino acids, and 5% in nitrates (NO_3^-). Furthermore, they found

that *H. splendens* absorbed more N from ammonia than from nitrate or the amino acid glycine when they were applied in solutions similar to those of the local rainfall. See the subchapter on Nitrogen in this volume for a further discussion of amino acids as a nitrogen source.

But certainly the water regime is different in the open as well (Tamm 1953). Trees in the forest redirect the rainfall, with much of it flowing down the trunk, or never reaching the forest floor at all. Trees can have either **centripetal water movement** (toward the bole, *i.e.* main trunk), for example *Acer*, *Fagus*, and *Fraxinus*, or **centrifugal** (toward the outer branch tips), for example *Betula*, *Picea*, and *Tilia*, depending on tree morphology. These patterns affect the source of nutrients and degree to which they reach the ground.

Tamm (1953) and Abolin (1974) both found that water volumes increased at the canopy margin. Barkman (1958) found that the percentage of rainfall reaching the tree bole of spruce (*Picea*) was only 1%. Nihlgård (1970) found that beech retained 19% of the rainfall, permitting 70% to go through the canopy as throughfall and 11% as stemflow. For spruce it was 39%, 58%, and 3%, respectively. In the open, all rainfall will reach the mosses. In her study of nutrient cycling through *Sphagnum russowii* (Figure 42) in a Jack pine (*Pinus banksiana*) forest and an open mat, Scafione (unpublished data) often found that moss throughfall collectors in the open had abundant water when those under the canopy were empty. Therefore, since more water reaches the mosses in the open, the total nutrients reaching those mosses could be relatively greater than that estimated by concentration levels, because more water reaches them.

On the other hand, forest trees serve as collectors of minerals in dust, releasing these as they are washed off by rainfall. In the forest, short rainfall events, which are likely to contain high nutrient levels, may not reach the mosses at all, whereas in the open field, they will. Both field and forest mosses will receive nutrients as dustfall, but open field mosses could receive more because there will be no trees to serve as filters or to block the wind.



Figure 42. *Sphagnum russowii*, a species that grows in both the sun and forest where nutrient inputs are very different. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Bates (1992) suggests that growth rate plays a role in the source of nutrients used by the forest bryophytes. The slow-growing moss *Pseudoscleropodium purum* (Figure 8)

obtains its minerals largely from "wet deposition," but phosphate is in low concentration in precipitation. Instead, it typically gets this mineral from the substrate.

Bogs

Bogs are defined by their source of nutrients. These come entirely from precipitation (Malmer *et al.* 1992); ground water does not move through the mat. This may be a bit too exclusive for a definition because dust from the atmosphere will also collect on the mosses, and when rainfall occurs the collected dust can go into solution and subsequently into the mosses. This is in contrast to nutrients in fens, particularly rich fens where Ca and Mg are available in surface water.

Atmospheric Dust

In some habitats, atmospheric dust can provide most or all of the mineral nutrients. In many *Sphagnum* (Figure 10, Figure 24-Figure 25) bog species, the mosses seem to depend exclusively on aerial deposition for their mineral nutrients (Hájek & Adamec 2009).

The composition of rainfall changes during a single rainfall event as it cleanses the atmosphere of its load of dust. Early rainfall in polluted areas is more acidic than later in the storm because it is washing the pollutants such as sulfates and nitrates out of the atmosphere. This lower pH causes more nutrients from the collected dust to go into solution. In the forest, this early rainfall will most likely not reach the mosses on the forest floor, being trapped by the canopy leaves. Meanwhile, the low pH of initial rainfall can leach nutrients from the canopy leaves, making them available in the throughfall that later reaches the mosses on the forest floor and on the tree bole. In the field, this low pH can be an effective way to dissolve the nutrients in the collected dust on the moss surfaces. A heavy rainfall might wash away a considerable portion, but a light rainfall may simply serve as a solvent while being insufficient to drip through the moss to carry the nutrients away.

By these mechanisms, throughfall alters the composition of rainfall considerably. The canopy enriches the rainfall by collecting dust that subsequently releases nutrients into solution in the rainfall. Schlesinger and Reiners (1974) demonstrated, by using artificial, plastic conifer needles, that the particulate matter of throughfall could increase by 4.5X. But living tree leaves can remove nutrients as well, and may hold more than artificial leaves due to hairs, snail trails, glands, and other features that trap dust particles. N can be removed almost completely from the rainfall by the canopy leaves, whereas K and P are typically enriched by the canopy (Brown 1982). Caterpillars in the canopy can contribute substantial amounts of both N and P through their excreta and feces (Szabó & Csontos 1975), presumably recycling that which is stored in leaves and thus including nutrients that originated in the soil. Mn is rich in litter, but apparently not in the soil, and may also possibly be leached from the canopy (Brown 1982).

In a lab study of *Mnium hornum* (Figure 43), Thomas (1970) found that the moss could obtain an adequate supply of Ca and Mg from the substrate below, but that K and P concentrations were less than those found in the soil, suggesting that these nutrients required additional input from precipitation, dustfall, or throughfall. Longton and

Greene (1979) showed similar relationships with *Pleurozium schreberi* (Figure 31). The plants had nutrient deficiency symptoms unless additional nutrients were supplied to the leaves. Precipitation and litterfall in the boreal forest were unable to supply sufficient Ca, Mg, and K for *P. schreberi* (Brown 1982) so we must consider that precipitation, dustfall, and substrate are all needed to meet the nutrient demands of at least some bryophytes.



Figure 43. *Mnium hornum* with capsules, a species that obtains Ca and Mg from the substrate below, but requires additional sources for K and P. Photo by Michael Lüth, with permission.

For the **endohydric** (moving water internally) *Polytrichum* (Figure 44) species, inorganic bulk precipitation of N and dust does not account for the entire N input (Bowden 1991). Even when biological nitrogen fixation by associated organisms is included, 35% of the N that has been accumulated by the plant is unaccounted for. Bowden attributed these missing sources to bulk precipitation of organic nitrogen, dry deposition, and dew. Most likely some soil input was also involved, whether directly through rhizoids or by upward movement through external capillary action. Furthermore, we cannot ignore the possibility of transfer from litter and other sources through **mycorrhizae** ("root"-fungal associations), as we will discuss later in this subchapter. Nevertheless, at least 58% of the N in the plant came from bulk precipitation.



Figure 44. *Polytrichum commune*, an endohydric moss that obtains its N from multiple sources. Photo by Michael Lüth, with permission.

Soil

Several studies cited above have shown that nutrients in rainfall are insufficient to account for the concentrations found in the mosses. Binkley and Graham (1981) found that precipitation could account for only 75% of the nitrogen in *Eurhynchium oregonum* (Figure 45) and *Hylocomium splendens* (Figure 41) in an old-growth Douglas fir (*Pseudotsuga menziesii*; Figure 46) forest, and they suggested these mosses might obtain some of their N from the underlying soil. Tamm (1953, 1964) felt that *Hylocomium splendens* was most likely to obtain its nutrients from accumulations on overlying shoots rather than from the soil by capillary action. But in the tundra *Hylocomium splendens*, *Aulacomnium palustre* (Figure 47), and *Sphagnum* (Figure 10, Figure 24-Figure 25) can obtain nitrogen (as ammonium, nitrate, and the amino acid glycine) from 3-8 cm soil depths (McKane *et al.* 1993). Perhaps the translocation of water upward by capillary action brings the nutrients up from lower soil depths. Or is there a fungal connection? In any event, soil seems to contribute to the moss nutrient supply. This concept of soil contributions is further supported by a study on *Pleurozium schreberi* (Figure 31), another pleurocarpous feather moss with a growth form similar to that of *Hylocomium splendens*, that can obtain calcium from CaCO_3 in soil as well as from dilute solutions on its leaves (Bates & Farmer 1990).



Figure 45. *Eurhynchium oregonum*, a moss that seems to obtain some of its N from the soil, but the rest from precipitation. Photo by Adolf Ceska, with permission.

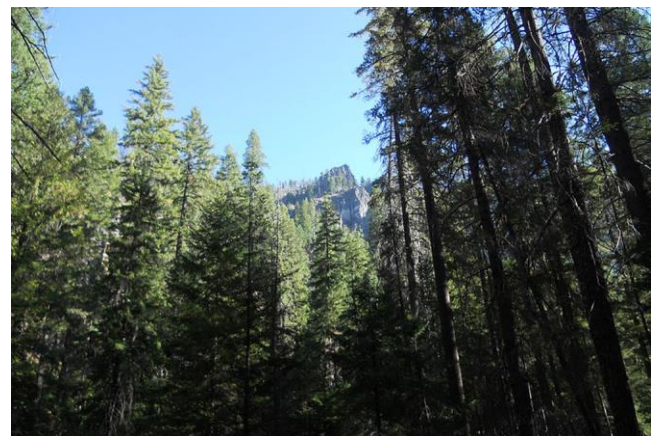


Figure 46. *Pseudotsuga menziesii* and *Pinus ponderosa* forest. Photo by Jsayre64, through Creative Commons.



Figure 47. *Aulacomnium palustre* gametophytes. Photo by Janice Glime.

Van Tooren *et al.* (1990) further supported the concept that *Hylocomium splendens* (Figure 41) as well as *Pleurozium schreberi* (Figure 31) can obtain micronutrients from the soil. They observed that mosses often have bits of soil and detrital matter nestled among the leaf bases. They tested the hypothesis that these could be derived from the soil substrate and found that indeed nutrients did arrive on the plants from the soil. De Caritat *et al.* (2001) found that geological aspects, sea spray, and human activity all influence the nutrients stored in *Hylocomium splendens* and *Pleurozium schreberi* in northern Europe. These two moss species had considerable composition of the elements of the underlying bedrock, including B, Ca, K, Mg, Mn, and P. Part of this substrate input is due to redistribution of the soil as dust from open areas. It is in this arena that human activity is most likely to be a contributor by making open, disturbed areas through mining, construction, agriculture, lumbering, and other surface disturbances.

Bryophytes of many habitats seem to have the ability to obtain nutrients both from the soil and from rainwater. Van Tooren and coworkers (1990) explored the relative importance of soil vs precipitation as a source of nutrients for pleurocarpous *Calliergonella cuspidata* (Figure 35) on sand and chalk grassland soil. They found that the concentrations of N, P, and K in the plants were higher on chalk soil than on sand, and that these were enhanced by fertilization. However, the plants on the chalk soil did not increase growth when fertilized, whereas those on sand did. They concluded that the soil was providing sufficient nutrients on the chalk grasslands and that some other factor must be limiting their growth.

Our first clue that bryophytes are affected by soil nutrients should have come to us with the realization that some prefer acidic soils and some prefer calcareous soils (Nagano 1972; Bates 1978; Büscher & Koedam 1979; Nakanishi & Hiraoka 1981). *Grimmia orbicularis* (Figure 40) demonstrated the ability to absorb ^{54}Mn and ^{90}Sr from the soil (Hébrard *et al.* 1972). Even more impressive, however, is the ability, already noted, of this species to obtain labelled ^{90}Sr from an artificial rock substrate (Hébrard *et al.* 1974). We need to stop thinking of bryophytes as passive collectors and recognize their ability to move substances from one place to another both internally and externally.

Micronutrients

Bryophytes are known for their ability to take up nutrients and accumulate them. This ability has made them useful in geological prospecting and in measuring accumulation of pollutants. Samecka-Cymerman and Kempers (1993) used aquatic bryophytes [*Scapania undulata* (Figure 48), *Pellia epiphylla* (Figure 49), *Fontinalis antipyretica* (Figure 50), *Platyhypnidium riparioides* (Figure 17)] to indicate mineralization in Poland, confirming the presence of geologically documented polymetallic deposits and indicating their presence in areas that had not yet been explored. The interesting story here is that bryophytes are sometimes able to meet these very minor amounts needed by getting them from the rock substrate.



Figure 48. *Scapania undulata*, a species that accumulates minerals from the substrate. Photo by Michael Lüth, with permission.



Figure 49. *Pellia epiphylla*, a species that indicates mineral composition of the substrate. Photo by David Holyoak, with permission.



Figure 50. *Fontinalis antipyretica*, a species that has been used to indicate metal deposits. Photo by Michael Lüth, with permission.

Litter and the Role of Trees

Parker (1983) suggested that atmospheric nutrients include both dry and wet deposition that not only can provide nutrients to the mosses directly but that also can enrich the litter (and leaves on the trees), permitting the leaves to provide nutrients to the mosses secondarily (see Table 2). *Brachythecium rutabulum* (Figure 51) achieved its greatest biomass gain when it was in contact with the stem litter of *Urtica dioica*, apparently intercepting the nutrients in decay products. In a different study, Bates (1992) has related nutrient source to growth rate, concluding that in the rapid-growing species *Brachythecium rutabulum*, mineral inputs from seasonally deposited tracheophyte litter are especially important.



Figure 51. *Brachythecium rutabulum*, a species that obtains nutrients from tracheophyte litter. Photo by Michael Lüth, with permission.

Table 2. Nutrient inputs and moss accumulation in an oakwood in Wales. Based on Rieley *et al.* (1979).

	$\text{mg m}^{-2} \text{yr}^{-1}$			
	K	Ca	Mg	Na
throughfall	1900	1000	1390	10380
litterfall	1920	2100	420	310
bryophyte accumulation	1430	410	390	160

Dicranum polysetum (Figure 52), *Ptilidium ciliare* (Figure 53), and *Ptilium crista-castrensis* (Figure 54) intermixed in a mat of *Pleurozium schreberi* (Figure 31) all experienced enhanced growth from an application of thick needle litter (Frego & Carleton 1995). But we must again question if fungi have a role here, taking from the litter and supplying to the moss. Nevertheless, litter seems to play an important role in providing a nutrient supply.



Figure 52. *Dicranum polysetum* with capsules and litter that serves as a source of its nutrients. Photo by Janice Glimme.



Figure 53. *Ptilidium ciliare*, a species that benefits from nutrients in needle litter. Photo by Janice Glimme.



Figure 54. *Ptilium crista-castrensis*, a species that benefits from nutrients in conifer needles. Photo by Adolf Ceska, with permission.

Although epiphytic bryophytes (those living on other plants) do not penetrate their substrate to obtain nutrients, they can benefit from nutrients flowing down the bole (main trunk) of a tree, some of which are derived from internal metabolites of that tree. Hoffman (1972) found that bryophytes and lichens at the bases of *Liriodendron tulipifera* (tulip tree) recovered 9% of labelled cesium that had been injected into the tree trunk. This illustrates the cycling of nutrients from the tree, probably through **leachates** (solution that percolates through canopy), to the bryophyte layer. The tree base likewise is the recipient of considerable stemflow that carries with it nutrients washed off the leaves and branches. Hence, the bryophytes at the tree base benefit from both leachates from the leaves and from accumulated dust that may contain important nutrients (Figure 55). Fluctuations in K, Ca, and Mg in nature suggested that appreciable quantities are absorbed by bryophytes during autumn from leaf leachates (Bates 1989). Of course, this also makes epiphytes vulnerable to concentrated pollutants in areas where the tree leaves are able to collect these.



Figure 55. *Dicranum scoparium* growing at tree base where it collects stemflow nutrients and escapes burial by leaf litter. Photo by Janice Glime.

Even in bogs, the critical nutrient potassium, as well as manganese, becomes available to *Sphagnum* (Figure 10, Figure 24-Figure 25) in ombrotrophic bogs through litter decomposition (Malmer 1988).

The more we learn about bryophyte nutrient relationships, the more we realize that they are no simpler than are those of the tracheophytes. Each nutrient and each species must be examined for its own uniqueness, and thus far, we lack sufficient evidence to correlate **functional groupings** (those having similar roles in the ecosystem) with taxonomic or morphological groupings.

Decomposition

The phenomenon that keeps the Earth from running out of nutrients is decomposition. Through a series of breakdowns, organisms return their nutrients to the soil or other substrate. Even bryophytes participate in this process, albeit usually slowly. Rather than losing leaves annually like trees, or dying back and regrowing from underground parts, most bryophytes die from the base while still growing at the tips.

In the taiga, bryophytes form the dominant cover and provide considerable primary productivity in the scheme of things (Oechel & Van Cleve 1986). With this dominance in the ground cover, they play a major role in rapid nutrient absorption, thereby having a large role in controlling ecosystem function. They are able to collect nutrients from dust, incorporate it, and release it slowly. In this way, bryophytes act as **nutrient sinks**.

In a study to understand the effect of climate change on Arctic ecosystems, Lang *et al.* (2009) measured decomposition rates of bryophytes, lichens, and tracheophytes over a 2-year period. Mass loss (decomposition) in tracheophytes was 56%, lichens 44%, and bryophytes a paltry 11%. Nevertheless, percentage loss in **cryptogams** (bryophytes and lichens) varied considerably among species. In particular, *Sphagnum* (Figure 10, Figure 24-Figure 25) loss was much slower than that of other mosses and liverworts. Mass loss of non-*Sphagnum* mosses correlated with the initial N in the plants, a phenomenon that may relate to their nutritive value to the decomposers.

Brock and Bregman (1989) likewise found that organic weight loss during decomposition of the fen moss *Sphagnum fallax* (Figure 26) was low. However, the release of N, P, and K (especially) was in greater proportion than that of organic matter loss. These soluble nutrients could easily leak out from damaged membranes of dead or desiccated cells. But despite this, N and P remained as a large proportion of remaining tissues even 12 months after decay initiated. Instead, they found that after a year of death, the cells demonstrated little damage and were poorly colonized by microorganisms.

The same sequestration seen in the Arctic is also present in the tropics. Tropical epiphytic bryophytes are known to sequester N collected from dust and the atmosphere, putting it into recalcitrant forms that remain in the canopy (Clark *et al.* 1998a, b).

What seems to be a common theme in bryophyte decomposition is that it is slow: Russell 1990 – tundra; Verhoeven & Toth 1995 – *Sphagnum* (Figure 10, Figure 24-Figure 25); Hobbie 1996 – tundra; Sand-Jensen *et al.* 1999 – Arctic lakes; Liu *et al.* 2000 – montane moist evergreen broad-leaved forest; Moore *et al.* 2007 – temperate peatlands; Turetsky *et al.* 2008 – *Sphagnum* in boreal peatlands; Lang *et al.* 2009 – subArctic. This makes the bryophytes a nutrient sink compared to other plant species in most ecosystems. This implies that they get most of their decomposition nutrients from litter decomposition of tracheophytes, not from recycled nutrients from their own tissues.

Snow

We know that snow forms around dust particles in the atmosphere and thus brings nutrients to the soil, efficiently removing them from the atmosphere (Woolgrove & Woodin 1996). As snow partially melts throughout the winter, melt water supplies nutrients to the soil below. When the weather warms in the spring and the snow melts quickly, it typically melts in a flush.

But what role does it have in supplying nutrients to the bryophytes? Are they able to take up nutrients at these near-freezing temperatures? Can they store nutrients to prepare for their spring flush of growth? And what role

does spring melt play in providing a flush of nutrients to be grabbed by mosses before they can reach the soil? Do mosses then serve as sinks, releasing nutrients later as the summer warms and the mosses become desiccated and leak their precious nutrient supply? Or are the mosses damaged and leaking themselves, unable to take advantage of this flush until they have accomplished their own new growth?

If the mosses are able to trap cations on exchange sites, even though they cannot yet absorb and use them, this could later provide a nutrient supply to the roots of tracheophytes at a time when their resources are dwindling, but when they are still actively growing and needing them. Or, bryophytes could deprive them of these atmospheric nutrients by trapping and holding them for an extended period of time – or indefinitely. And how are the important anions held, like NO_3^- and PO_4^{3-} ? Certainly nitrogen compounds arrive in this way, suggesting that mosses may take them in immediately if they are removing them from the system.

Woolgrove and Woodin (1996) examined the effect of snowmelt and nitrate uptake in the moss *Kiaeria starkei* (Figure 56) at a snowbed in the Cairngorm Mountains of Scotland. They found that although the conditions under the snow are unsuitable for photosynthetic activity due to the low light intensity, this moss is capable of photosynthesis as soon as the snow cover is removed. Tissue chlorophyll increases by 250% and carbohydrate concentrations increase 60% within only two weeks. This moss is also capable of nitrate reductase activity at temperatures as low as 2°C and is thus able to assimilate more than 90% of the high levels of pollutant nitrate released during the melting season.



Figure 56. *Kiaeria starkei*, a moss capable of nitrate reductase activity at 2°C. Photo by Michael Lüth, with permission.

On the other hand, in my moss garden in Houghton, Michigan, USA, in an area characterized by northern deciduous forest, the mosses and even the liverwort *Marchantia polymorpha* (Figure 3) are brown and appear dead when the snow recedes. Obviously there are still living tissues there because the mosses and the liverwort both produce new growth within a few weeks, dependent on adequate rainfall and temperature. But under these conditions, it would appear that the mosses should be more

poised to lose nutrients from these brown tissues than to gain them. Certainly more research is needed on the role of individual bryophyte species in sequestering and later releasing nutrients collected during a season of heavy snow. And what effect does a loading of heavy metals, sulfates, and nitrates have on the survival of the bryophyte layer following a sudden snowmelt release?

A further problem occurs once the snow melts in my moss garden. The snow melt water can be gone in a week, and instead of spring rains, this is typically followed by an extended dry period. In some years, it appears that this wet period is insufficient for them to recover before the drought and they can remain largely brown the entire growing season.

The Salmon Story and Other Animals

The salmon (*Oncorhynchus* spp.) are fish, so when I read the title of an article on uptake of salmon-derived nitrogen by mosses and liverworts, I was expecting a story about aquatic mosses (Wilkinson *et al.* 2005). However, instead I was soon reminded of the massive midge outbreaks in Iceland that bring the rich geothermal nutrient source of Icelandic lakes to the terrestrial scene, because these salmon are brought to land by their predators and the remains of the carcasses provide a nitrogen source. In both cases, an aquatic nutrient source is brought to land.

It appears that in at least one forested watershed in coastal British Columbia, Canada, the percent N in moss tissues, especially the common moss *Rhytidiadelphus loreus* (Figure 57), is higher in forest mosses below the falls where the salmon are than above the falls, where they are not. N content was higher in mosses near bony remains from previous years and near wildlife trails (Wilkinson *et al.* 2005). Seven of the eight bryophyte species examined exhibited decreasing N uptake with distance from the spawning region; the exception was *Rhizomnium glabrescens* (Figure 58), an epiphytic species that showed no relationship. Below the falls, the thallose liverworts *Conocephalum conicum* (Figure 59) and *Pellia neesiana* (Figure 60), both indicators of soil rich in nitrogen and calcium, had the greatest cover. Even species richness was higher in forest areas near the salmon stream than elsewhere.



Figure 57. *Rhytidiadelphus loreus*, a species that gets some of its nutrients from salmon dropped on land by predators. Photo by Michael Lüth, with permission.



Figure 58. *Rhizomnium glabrescens*, an epiphytic species that does not benefit from salmon prey dropped on land. Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 61. Brown bear catching salmon that will be carried ashore to be eaten. Photo by Brian W. Schaller, through Creative Commons.



Figure 59. *Conocephalum conicum*, a species that indicates soil rich in N. Photo by Janice Glime.



Figure 60. *Pellia neesiana*, a species that indicates soil rich in N. Photo by Jan-Peter Frahm, with permission.

Hilderbrand *et al.* (1999) determined that adult female brown bears (Figure 61) excrete as urine 97% of the N consumed from salmon. This most likely is distributed primarily along the wildlife trails. Thus, wolves, bears, and river otters contribute to the success of the bryophytes by bringing their dinner into the forest and leaving the scraps, but also as they venture through the forest by distributing the N as urine and possibly feces.

Fungal Partners

A long-neglected aspect of bryophyte nutrient uptake is that of **mycorrhizal** (fungal-"root" symbiosis) associations. This has gotten somewhat recent attention and needs to be considered in understanding bryophyte nutrient relations. Details of studies will be covered in Volume 2 on Interactions – Fungi.

We know that conifers and orchids depend on fungal partners to obtain nutrients, and indeed it may be the case for all forest trees. Now we know that it is a part of some bryophyte relationships, but we lack sufficient data to determine how widespread it is.

In the boreal forest, mycorrhizae are therefore of critical importance. And that forest floor is dominated by feather mosses. Mosses can release significant quantities of N and P from their shoots, especially after drying (Carleton & Read 1991). More of this is released from dead and **senescent** (growing old) parts than from the green parts. Leakage of the sugars glucose, fructose, and sucrose from dry moss shoots is sufficient to support growth of three mycorrhizal fungi in pure culture, so we might hypothesize that the bryophytes at least are capable of enhancing the growth of the tree mycorrhizal fungi. When moss shoots were added to the cultures, the fungi readily colonized them, especially in the senescent regions. Labelled phosphate and carbon previously "fed" to the moss shoots were absorbed by the mycorrhizae and transferred across centimeters to roots infected with these fungi. The extent to which the bryophytes are important in this relationship remains to be investigated.

This raises the question of the value of mycorrhizae to bryophytes. The **achlorophyllous** (lacking chlorophyll) liverwort *Cryptothallus mirabilis* (Figure 62) is unable to fix its own carbon through photosynthesis. Both this species and its photosynthetic sister species *Aneura pinguis* (Figure 63) interact with **endophytic** (living within a plant) **Basidiomycetes** – the group of fungi responsible for producing all the mushrooms (Ligrone *et al.* 1993). In *Cryptothallus*, the young fungal hyphae contain abundant **glycogen** (carbohydrate – polysaccharide that forms glucose on hydrolysis) and sometimes **amyloid** (starch-like protein) deposits within the *Cryptothallus*. The fungi associated with both genera very closely match those of orchids – a group with obligate mycorrhizal associates.



Figure 62. *Cryptothallus mirabilis*, a species that obtains its carbon and most likely other nutrients through a fungal partner. Photo by David Holyoak, with permission.



Figure 63. *Aneura pinguis*, a photosynthetic close relative of *Cryptothallus mirabilis*, that has similar mycorrhizal fungi. Photo by Michael Lüth, with permission.

pH Relationships

It is not unusual to find bryophytes in habitats with low pH. Merunkova and Chytrý (2012) reported that bryophytes in upland grasslands of the southern Czech Republic were mostly on the low-pH soils that were low in Ca and P, as well as on organic soils. Underwater bryophytes are relatively rare in limestone streams where the carbon is present as carbonate and not as free CO₂ (pers. obs.). This is discussed further in the subchapter on CO₂ in this volume.

The pH not only affects the nutrient uptake ability of the bryophytes, but also can affect the toxicity of such minerals as aluminium (Al) (Bates 1992). Low pH makes many minerals, including Al, more soluble. In most cases, this increases the ability of the minerals to enter the bryophyte along with water. Bates found that in woodland soil and on rock substrates, the bryophyte cation exchange capacity (CEC) decreased with decreased Ca and the pH in the substrate.

On the margins of forested stream channels, Hylander and Dynesius (2006) found that mosses were more influenced by the pH than were liverworts. They furthermore found that having pockets with higher pH increased the bryophyte richness. Corrales *et al.* (2010)

found that pH was one of three factors in determining bryophyte distribution in secondary and planted montane forests in the Central Cordillera of Colombia. Low pH is a major factor in making nutrients available.

Protective Devices

As already seen, not all minerals are good minerals. At low pH levels, aluminium becomes soluble – and toxic. For some heavy metals the cation exchange sites serve as protection, binding the metals and thus immobilizing them.

The toxic heavy metal lead is accumulated in large quantities in cell walls, but also can occur in the cytoplasm (Basile *et al.* 1994). In bryophytes it accumulates preferentially in gametophyte **hydroids** (water-conducting cells in mosses), sporophyte hydroids at the foot, and transfer cells adjoining the sporophyte. It also occurs in the cytoplasm, chloroplasts, mitochondria, vacuoles, and cytoplasmic reticulum. In *Funaria hygrometrica* (Figure 2), the lead is sequestered in tissues, preventing it from reaching the seta and capsules where it could damage developing spores. The **placenta** that joins the gametophyte and sporophyte blocks the transfer of lead to the sporophyte.

Seasonal Nutrient Behavior

Seasonal differences in available nutrients result from litter fall, snow melt, flooding, runoff, available moisture, and seasonal deposition from some kinds of pollution. Nutrient availability may be further mediated by changes in biological needs during the changing life cycle stages of the bryophytes and the tracheophytes that surround them.

Bryophytes, like tracheophytes, have different needs for nutrients in different seasons, and their uptake and movement of those nutrients likewise differs with the seasons. For example, in the boreal feather moss *Hylocomium splendens* (Figure 41), airborne nutrients dominate uptake to the growing tissues during winter in a pine forest in Latvia; Ca and Mg are held in green tissues (Brümelis *et al.* 2000). During the relatively dry autumn, Mg is transferred from older brown and decaying tissues upward to the young tissues, but Ca is not.

Snow concentrates nutrients and releases them in a spring pulse (Brümelis *et al.* 2000). Yet, despite the fluctuations of availability of nutrients in the surrounding environment, there is no evidence that bryophytes suffer leaching as a means of maintaining chemical equilibrium with their environment. The cell membranes must therefore control the entry and exit of ions.

The forest floor moss *Brachythecium rutabulum* (Figure 51) exploits seasonally deposited vascular plant litter (Bates 1992). *Pseudoscleropodium purum* (Figure 8) seems to depend largely on wet deposition for minerals, making its greatest nutrient availability during the season(s) with the most rainfall. But in their study of *Hylocomium splendens* (Figure 41) and *Pleurozium schreberi* (Figure 31), Berg and Steinnes (1997) found no variations in the element concentrations on different dates in the sampling season. This again raises the question of whether bryophytes are able to regulate their nutrient concentrations, and if so, how?

Markert and Weckert (1989) examined minor elements in *Polytrichastrum formosum* (Figure 64), a weedy species in Europe but somewhat rare in North America. They

found considerable variation between stands as well as between seasons. K had little seasonal variation; Al, Fe, Cr, Mg, Pb, and Ti had roughly 80% variation, with their highest concentrations in winter and lowest in summer.



Figure 64. *Polytrichastrum formosum* with capsules, a species that has considerable variation in nutrient content among locations. Photo by David T. Holyoak, with permission.

Because of their ability to take up large quantities of heavy metals, bryophytes have been used for monitoring heavy metal pollution, as has been discussed already in several books. These bryophytes often exhibit symptoms of excess, including **chlorosis** (loss of chlorophyll), brown tips (Figure 19), and **plasmolysis** (shrinkage of protoplast of plant cell resulting from loss of water from cell; results in space between cell membrane and cell wall) (Figure 22). In other cases, the damage is so great that membrane integrity is lost and the cells exhibit **deplasmolysis** (swelling of the cytoplasm of a previously plasmolyzed cell; reversal of plasmolysis) (Figure 22).

Richardson (1981) suggested that there are greater seasonal fluctuations in ectohydric mosses like *Aulacomnium* sp. (Figure 47) than in endohydric ones like *Polytrichum* (Figure 44) due to the ability of ectohydric mosses to absorb nutrients throughout the plant. In the black spruce forests (Figure 27) of Alaska, *Polytrichum* (*Polytrichastrum*?) had its highest phosphate uptake rates in below-ground portions. But we must also consider that this moss has ectohydric movement of water that carries water and nutrients to the apex where they are absorbed. The leaves rehydrate slowly, suggesting that they are more water repellant than absorptive.

Williams *et al.* (1999) compared the seasonal nitrogen dynamics in two *Sphagnum* species: *S. capillifolium* (Figure 32) occupying hummocks and *S. recurvum* (Figure 33) in hollows. Rather than rely on natural sources, the researchers added labelled NH_4NO_3 at the levels in the ecosystem where the mosses lived. The proportion of labelled N in the mosses ranged from 11 to 100% during the 14-month study. The lowest measurements occurred in October when the water table reached the surface of the mosses. This was particularly true for *S. recurvum*. A very small amount of the labelled N was detected as dissolved organic nitrogen in the moss water. There were also times when they could not account for a large proportion of the added N.

In *Sphagnum* (Figure 10, Figure 24-Figure 25) in the southern Alps, Na, Mg, and to a lesser extent Ca, became progressively more concentrated in the tissues as the growing season progressed; N, and to a lesser extent, P, were enriched in the photosynthetic cells during this period of intense growth, but were leaked from the cells when the growth rate slowed (Gerdol 1990). Likewise, during cold months, Na, Mg, and Ca were leached from the cell walls.

Bryophyte growth periodicity can differ between years, being influenced by precipitation (Brock & Bregman 1989). And surprisingly, capsules of *Sphagnum fallax* (Figure 26) in a fen woodland were formed only during the dry year, somewhat reminiscent of flowering plants that bloom in response to drying conditions or algae that reproduce sexually when nutrients begin to diminish in the water.

Streams have seasonal pulses in nutrients, with the largest usually corresponding to snowmelt and spring runoff. In an acidic stream in Northeast England, Ellwood and Whitton (2007) found that organic phosphate, the form used by those bryophytes, reaches a high peak in late spring. In the moss *Warnstorfia fluitans* (Figure 9) this peak coincided with higher concentrations of organic P.

On the other hand, in their study of the aquatic mosses *Fontinalis antipyretica* (Figure 50) and *F. squamosa* (Figure 65) in a mountain stream in Spain, Martínez Abaigar and coworkers (2002) found that concentrations of K, Fe, P, and N increased in every portion of the plant through summer and autumn and decreased through winter and spring. Since these concentrations did not track the concentrations of the stream water, they presumed that the concentrations of the mobile elements depended on the growth cycle. Na increased in the plants in winter, presumably as a result of winter deicing salts. Ca and Mg seemed to fluctuate randomly throughout the plant.

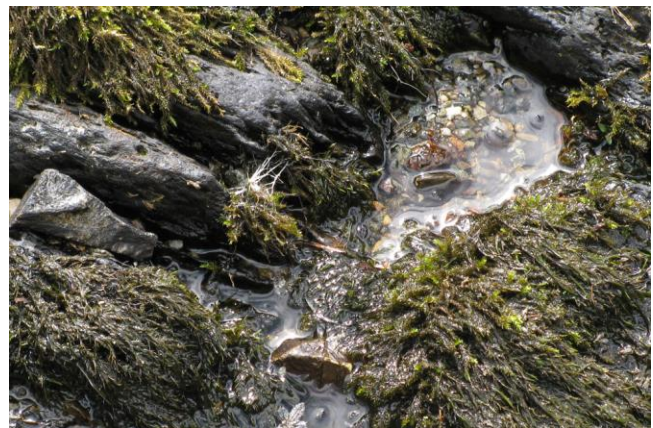


Figure 65. *Fontinalis squamosa*, a species that increases its concentrations of K, Fe, P, and N throughout the plant in summer and autumn. Photo by Janice Glime.

It is hard to generalize from the few studies presented here (see Table 3), but it appears that minor elements may be high in the plants in winter when they are not being used and that the three major elements (N, P, K) are relatively conserved throughout the year. Translocation can provide mobile nutrients from older parts to younger parts prior to and during early stages of growth, thus maintaining sufficient nutrient supply to support the relatively slow growth rate of a bryophyte.

Table 3. Seasons of uptake and loss of nutrients in bryophytes from different habitats. + indicates uptake for that group; - indicates loss for group; no symbol indicates season of highest concentration. These positions should not be interpreted as representative as so few bryophytes have been evaluated seasonally.

Species	Spring	Summer	Autumn	Winter	Reference
<i>Hylocomium splendens</i>				+Ca,Mg	Brümelis <i>et al.</i> 2000
<i>Fontinalis antipyretica</i>	+K,Fe,P,N	+K,Fe,P,N	+K,Fe,P,N	Na	Mártínez Abaigar <i>et al.</i> 2002
<i>Sphagnum</i>		+N,Na,Mg,Ca	+P,Na,Mg,Ca	-N,P,Ca,Mg,Na	Gerdol 1990
<i>Polytrichastrum formosum</i>		K		Ba,Ca,Cd,Cu,Sr,Mg,Zn Al,Fe,Cr,Mg,Pb,Ti,	Markert & Weckert 1989

Effects on Species Composition

When nutrients increase, it is not unusual for bryophyte cover to decline and even disappear (Arróniz-Crespo *et al.* 2008). In an acidic grassland, Arróniz-Crespo and coworkers found that up to 90% of the bryophyte cover was lost due to enhanced nitrogen deposition. The tissue N:P ratio increased up to three times the original levels. They concluded that it was the limitation by phosphorus that caused damage to photosystem II and consequently caused loss of bryophyte biomass. Pigment concentrations and chlorophyll fluorescence were also affected.

We have seen that bryophytes often do not benefit from added N. Armitage *et al.* (2010) found that high N concentrations in alpine mosses can lead to a decline in production of biomass, reducing the cover of bryophytes. In *Sphagnum* (Figure 10, Figure 24-Figure 25) bogs, higher N can increase productivity of tracheophytes and consequently reduce the competitiveness of the bryophytes (Berendse *et al.* 2001). On the other hand, *Sphagnum* is a major sink for the sequestration of carbon in the Northern Hemisphere. Elevated CO₂ has little effect on *Sphagnum* biomass and N depresses it due to increased competitive growth of tracheophytes and the moss *Polytrichum strictum* (Figure 66). Loss of *Sphagnum* can reduce the sequestration of carbon.



Figure 66. *Polytrichum strictum*, a species that can outcompete *Sphagnum* when given an enhanced N source. Photo by Michael Lüth, with permission.

When Armitage *et al.* (2010) did transplant experiments with alpine *Racomitrium lanuginosum*

(Figure 5), they found that after 2 years, tissue N in transplants from high N sites to a lower site only partially equilibrated to its new N availability. On the other hand, reciprocal transplants to the higher N regions almost matched the N concentrations of the native plants. The surprise was that mosses experienced greater shoot growth when stimulated by higher N deposition. In the lower N site, moss depth and biomass increased in transplants, apparently due to a lower C:N ratio that slowed decomposition.

Summary

Although there seems to be little in the way of a comprehensive summary of bryophyte nutrient processes in nature, there are many pieces from which a somewhat clear picture emerges. First off, bryophytes can receive their nutrients from the substrate as well as from precipitation and dust. Those forming thick but horizontal mats are more likely to depend predominantly on precipitation, whereas acrocarpous mosses may receive considerable input from the substrate through upward movement externally and subsequent internal movement.

Bryophytes can suffer osmotic shock when transferred to substrates with high nutrients and most lack sufficient wax in the cuticle to help slow the process. They require the same nutrients as tracheophytes (CHOPKNS Mg CaFe), but in lower concentrations. Needs of young shoots are greater than those of older shoots and nutrients may be moved from old to young tissues. Bryophytes trap nutrients leached from the canopy and may provide it to roots of trees, especially spruce trees, possibly through *mycorrhizae*. Ca and Mg can be obtained from the soil, but K and P require additional sources. Litter of herbaceous and woody plants may supply some of the needed nutrients, provided they don't bury the plants or damage them with tannic acid. Snow collects dust particles and these go into solution as the snow melts, dripping down on the bryophytes. Fungal partners may transfer nutrients into the bryophytes or from the bryophyte mat to tree roots. Even salmon, dragged ashore by bears and other predators, contribute to bryophyte nutrients.

Nutrients tend to increase in bryophyte tissues in late summer and fall, then decrease in winter and spring

when the plants are growing, but this varies with the species, the nutrient, and of course with geographic region. The three major elements (N, P, K) are relatively constant throughout the year. pH affects solubility and toxicity of nutrients and heavy metals.

Protective devices include sequestration of heavy metals on cation exchange sites and blocking transport from gametophyte to sporophyte in the placenta.

Elevated nutrients, especially N, can favor tracheophytes, at the expense of bryophytes, through competition. They can also alter the bryophyte species composition.

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