CHAPTER 8-1
NUTRIENT RELATIONS: REQUIREMENTS

What Do Bryophytes Require?

Bowen (1933) reminds us that bryophytes are necessarily limited in nutrient supply by their poikilohydric (state of hydration controlled by environment) method of water regulation. Their 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

Most knowledge about nutrient requirements of bryophytes comes from culturing them. 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 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 to the various cation combinations from the responses of the gametophores. 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.

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 waxy in their cuticles, most bryophytes are especially susceptible to osmotic shock. Voth (1943) used Marchantia polymorpha 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.

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).

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 C'HOPKNS 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.

The needs of young shoots are typically greater than that 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).

### 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.

<table>
<thead>
<tr>
<th>Element</th>
<th>Land Plants (g·kg⁻¹ dry matter)</th>
<th>Stored in Soil (g·kg⁻¹ DM)</th>
<th>Marine Organisms (g·kg⁻¹ DM)</th>
<th>Sea Water (g·L⁻¹)</th>
<th>Agricultural Plants (g·kg⁻¹ DM)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Range Mean</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
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<tr>
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<tr>
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<td>5</td>
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<td>0.005</td>
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<td>0.1</td>
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<td>40</td>
<td>19.3</td>
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### 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, and litter (Babb & Whitefield 1977; Parker 1983; Frego & Carleton 1995). For saxicolous (rock-dwelling) mosses, 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 to obtain radiolabelled ⁸⁹Sr 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.

### Precipitation

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) 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 pleurocarpous Hylocomium splendens. Weetman and Timmer (1967) concluded the same thing for Pleurozium schreberi in the black spruce forest, where N, K, Ca, and Mg 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 (Figure 2) 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 they 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.

Figure 2. 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 grew more under the canopy than in the open, and that its annual dry biomass increments under the canopy increased with distance from the 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 grew more slowly, thus requiring lower concentrations from the environment.

But certainly the water regime was different in the open as well. 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. 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 Picea was only 1%. Niithlård (1970) found that beech retained 19% of the rainfall, permitting only 70% to go through 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 in a Jack pine forest and an open mat, Seafone (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 should be relatively greater than that estimated by concentration levels, because more water reaches them. In the forest, short rain events, which are likely to contain high nutrient levels, may not reach the mosses at all, whereas in the 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 collectors or to block the wind.

Atmospheric Dust

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, sp, snail trails, glands, and other features that trap dust particles. N can be removed from the rainfall by the canopy leaves almost completely, 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 & Csortos 1975). 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, 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 obtained 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. 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.

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.

For the endohydric Polytrichum, 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 (1991) 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. Nevertheless, at least 58% of the N in the plant came from bulk precipitation.

**Micronutrients**

Tracheophytes require significant quantities of macronutrients and considerably less of those called micronutrients (Mn, Cu, Zn, Mo, Ni, Cl, Bo). 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 until returned to a natural medium.

Copper can be limiting in some aquatic habitats, and probably some terrestrial ones as well. In their studies on Fontinalis dalecarlica, 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 3). At higher concentrations, chloroplasts lost their green color and at 10 mg / L the cells became brown (Figure 4).

![Figure 4. Comparison of cell contents and colors in leaves of Fontinalis dalecarlica subjected to different concentrations (Lake Superior water control, 0.01 mg/L, 1.0 mg/L, 10 mg/L) of copper as copper foil. Photos by Janice Glime based on Glime & Keen (1984).](image)

**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 achieved its greatest biomass gain when it was in contact with the stem litter of Urtica dioica, apparently intercepting the nutrients in decay products. Dicranum polysetum, Ptilidium ciliare, and Ptilium crista-castrensis intermixed in a mat of Pleurozium schreberi 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 leaves and supplying to the moss. Nevertheless, litter seems to play an important role in providing a nutrient supply.

![Figure 3. Effect of copper concentration on chlorophyll a and b concentrations in the aquatic moss Fontinalis dalecarlica. Redrawn from Glime & Keen (1984).](image)

<table>
<thead>
<tr>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
<th>Na</th>
</tr>
</thead>
<tbody>
<tr>
<td>mg m⁻² yr⁻¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>throughfall</td>
<td>1900</td>
<td>1000</td>
<td>1390</td>
</tr>
<tr>
<td>litterfall</td>
<td>1920</td>
<td>2100</td>
<td>420</td>
</tr>
<tr>
<td>bryophyte accumulation</td>
<td>1430</td>
<td>410</td>
<td>390</td>
</tr>
</tbody>
</table>

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

Although epiphytic bryophytes (those living on other plants) do not penetrate their substrate to obtain nutrients, it appears that 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 labeled 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. 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 them vulnerable to concentrated pollutants in areas where the tree leaves are able to collect these. 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.

Soil

Several studies 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 Stokesiella oregana and Hylocomium splendens in an old-growth Douglas fir (Pseudotsuga menziesii) forest and suggested these mosses might obtain some of their N from the underlying soil. Tamm felt that Hylocomium splendens was most likely to obtain its nutrients from accumulations on overlying shoots rather than from the soil, using capillary action. But in the tundra Hylocomium splendens, Aulacomnium palustre (Figure 5), and Sphagnum 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, another pleurocarpous feather moss with a growth form similar to that of Hylocomium splendens, that can obtain calcium from CaCO₃ in soil as well as from dilute solutions on its leaves (Bates & Farmer 1990).

Van Tooren and coworkers (1990) explored the relative importance of soil vs precipitation as a source of nutrients for pleurocarpous Calliergonella cuspidata (Figure 6) 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 demonstrated the ability to absorb ⁵⁴Mn and ⁹⁰Sr from the soil (Hébrard et al. 1972). Even more impressive, however, is the ability of this species to obtain labelled ⁹⁰Sr 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.

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, it 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 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.

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 are brown and appear dead when the snow recedes. Obviously there are still living tissues there because the mosses and M. polymorpha 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?

The Salmon Story

The salmon (Oncorhynchus spp.) is a 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. 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 7), 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. Seven of the eight bryophyte species examined exhibited decreasing N uptake with distance from the spawning region; the exception was Rhizomnium glabrescens, an epiphytic species. Below the falls, the thallose liverworts Conocephalum conicum and Pellia neesiana, both indicators of soil rich in nitrogen and calcium, had the greatest cover. Even species richness was higher in forests near the salmon stream than elsewhere.

Figure 7. Rhytidiadelphus loreus. Photo by Michael Lüth.

Hilderbrand et al. (1999) determined that adult female brown bears 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.

Seasonal Behavior

Bryophytes, like tracheophytes, have different needs for nutrients in different seasons, and their uptake and movement of those nutrients likewise differs with the seasons. In the boreal feather moss Hylocomium splendens, airborne nutrients dominate uptake to the growing tissues during winter; 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. 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.

In their study of the aquatic mosses Fontinalis antipyretica and F. squamosa 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 dependent on winter deicing salts. Ca and Mg seemed to fluctuate randomly throughout the plant.

In *Sphagnum* 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 the cold months, Na, Mg, and Ca were leached from the cell walls.

Markert and Weckert (1989) examined minor elements in *Polytrichum formosum* and 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. Because of their ability to take up large quantities of heavy metals, bryophytes have been used for monitoring heavy metal pollution, as will be discussed in a later volume on pollution. These bryophytes often exhibit symptoms of excess, including chlorosis, brown tips, and plasmolysis (Figure 8). In other cases, the damage is so great that membrane integrity is lost and the cells exhibit deplasmolysis (Figure 9).

Richardson (1981) suggested that there are greater seasonal fluctuations in ectohydric mosses like *Aulacomnium* sp. than in endohydric ones like *Polytrichum* due to the ability of ectohydric mosses to absorb nutrients throughout the plant. In the black spruce forests 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 it to the apex where it is absorbed. The leaves rehydrate slowly, suggesting that they are more water-repellant than absorptive.

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<th>Autumn</th>
<th>Winter</th>
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<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
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<td>Brümelis <em>et al.</em></td>
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<td>2000</td>
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<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>Na</td>
<td>Martínez-Abaigar <em>et al.</em></td>
</tr>
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<td>+K,Fe,P,N</td>
<td>Na</td>
<td>2002</td>
</tr>
<tr>
<td><em>Polytrichum</em></td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>Na</td>
<td>Markert &amp; Weckert</td>
</tr>
<tr>
<td><em>formosum</em></td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>Na</td>
<td>1989</td>
</tr>
<tr>
<td></td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>+K,Fe,P,N</td>
<td>Na</td>
<td></td>
</tr>
</tbody>
</table>

It is hard to generalize from the few studies presented here (see Table 3), but it appears that minor elements may be high in winter when they are not being used and that the three major elements (K, P, N) 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.

![Figure 8. Effects (color loss & plasmolysis) of 1 mg Cu on the leaf cells of *Fontinalis duriaei*. Photo by Janice Glime, based on Glime & Keen (1984).](image)

![Figure 9. Effects of cadmium on cell contents in *Fontinalis duriaei*. 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).](image)
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 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 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. 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. Even salmon, dragged ashore by bears and other predator, contribute to their nutrients.

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