CHAPTER 8-6

NUTRIENT RELATIONS: DEFICIENCY

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Figure 1. *Dicranum spadiceum* in an alpine habitat where nutrients are typically deficient. Photo by Michael Lüth, with permission.

Nutrient-deficient Habitats

Tracheophytes have well-known adaptations to low nutrients. Among the herbaceous seed plants adapted for low nutrient habitats, a small growth form with narrow leaves or basal rosettes seems to predominate (Grime 1977). Evergreenness is common in both dry and wet habitats (bogs and fens), presumably affording the plant the opportunity of using their leaves for several years without having to provide the nutrients to grow a new supply. Like the shade plants, these plants possess an inherently slow growth rate.

Bryophytes in general seem to grow best in low-nutrient habitats (Figure 1). It is interesting that their productivity is no greater in extreme rich fens than in bogs and poor fens (Vitt 1990). Furthermore, the addition of nutrients to bryophytes in intermediate fens does not result in an increase in productivity. If we compare the bryophytes to the low-nutrient-adapted plants described by

Grime (1977), the bryophytes are likewise small, have narrow leaves, and are mostly evergreen (but not leathery). As discussed earlier, they are able to move soluble nutrients from older tissues to growing apices. Furthermore, bryophytes are able to survive in low-nutrient habitats despite their small size and slow growth rate. In nutrient-rich habitats, they have no chance of competing with the fast-growing tracheophytes.

In bogs and fens, *Sphagnum* seems to have its own way of "competing" for the limited supply of nutrients. In experiments where both *Sphagnum fuscum* (Figure 2) and *Drosera rotundifolia* (sundew, Figure 2) were fertilized with N, the *Sphagnum* was able to advance its growth (Svensson 1995), seemingly ready to outcompete the tiny *Drosera* plants for light. However, the *Drosera* tapped into the nutrients at a different depth in the system, elongated its vertical stem that connected two successive years of

growth, and hence kept up with the vertical growth of the *Sphagnum*. Interestingly, the *Drosera* made more but smaller leaves and increased its leaf thickness, thus not increasing its shading effect on the moss. Svensson concluded that the moss relocates the nutrients within itself, thus preventing their potential spread to tracheophytes.

Figure 2. Sundew (*Drosera rotundifolia*) (three round leaves) growing with **Sphagnum fuscum**. Photo by Michael Lüth, with permission.

Bryophytes can be deprived of nutrients in habitats that are rich in nutrients. This paradox results from nutrient competition for the binding sights. Calcium compounds such as $CaCl_2$ can raise both exchangeable and intracellular Ca^{++} concentrations and displace other exchangeable essential nutrients such as K^+ and Mg^{++} (Bates & Farmer 1990), both of which are often in limiting supply. But the interesting response to addition of $CaCl_2$ that Bates and Farmer found is that the low-nutrient mosses *Pleurozium schreberi* (Figure 3) and *Pseudoscleropodium purum* (Figure 4) from acidic clay were unaffected, whereas *Calliergon cuspidatum* (Figure 5) and *Pseudoscleropodium purum* from chalk ($CaCO_3$) soil suffered reduced growth, apparently due to the resulting K^+ and Mg^{++} deficiencies.

Figure 3. **Pleurozium schreberi**, a low-nutrient species that was unaffected by $CaCl_2$. Photo by Janice Glime.

Ion concentrations in the substrate or in water can be misleading relative to nutrient availability. A low-nutrient substrate such as a rock in a forest might actually place the bryophyte in a position to obtain considerable nutrients from throughfall that has collected nutrients from the canopy trees. And bryophytes dwelling in a stream with reasonably fast flow will have a continuous supply of new nutrients that can compensate for low concentrations (Birks & Dransfield 1970).

Figure 4. **Pseudoscleropodium purum**, a low-nutrient species that was unaffected by $CaCl_2$ on acidic soil but suffered on chalk soil. Photo by Michael Lüth, with permission.

Figure 5. **Calliergonella cuspidata**, a species that suffers from addition of $CaCl_2$ on chalk soil. Photo by Michael Lüth, with permission.

Nutrient Deficiency Symptoms

It takes nerve to title a section Nutrient Deficiency Symptoms when you are writing about bryophytes. This has apparently never been systematically studied for bryophytes in general! A search in Cambridge Abstracts brought one reference, a field study following fire: "Germination of **Ceratodon purpureus** (Figure 6) on all the burnt surfaces, and of **Funaria hygrometrica** (Figure 7) on the charred surfaces appeared to be nutrient or pH-limited. Growth of *C. purpureus* and **Dicranella heteromalla** (Figure 8) appeared to be nutrient- or pH-limited on some or all of the burnt surfaces." This 1994 study by Thomas *et al.* appears to be the only field study in recent years even to allude to nutrient deficiency symptoms in any context. And that one is merely a guess.
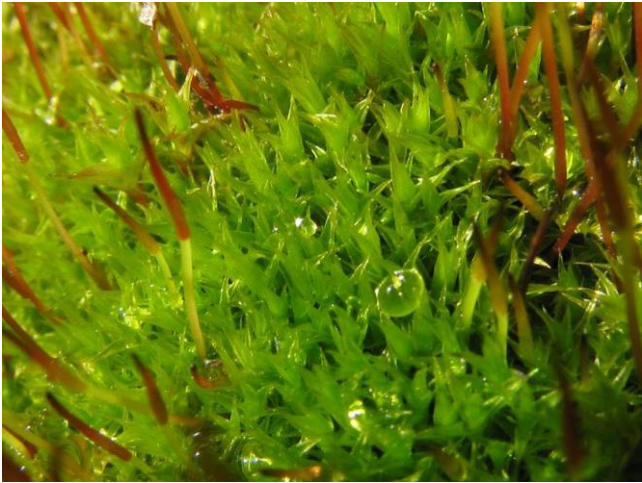
Figure 6.   Healthy *Ceratodon purpureus* with young sporophytes. Photo by Jiří Kameníček, with permission.

Figure 7. *Funaria hygrometrica* growing among charcoal. Photo by Janice Glime.

Figure 8. *Dicranella heteromalla*, a species that appears to be *p*H- or nutrient-limited when growing on burned substrata.

Culture studies for the purpose of keeping bryophytes alive are the most productive avenue for locating possible clues as to the response of bryophytes to limiting nutrients.

But, since bryophytes tend to have much lower nutrient requirements than do tracheophytes (Griggs & Ready 1934; Voth 1943; Burkholder 1959; Southorn 1977; Dietert 1979), most of the trial and error in culture experiments revolves around getting nutrient concentrations low enough that algae, fungi, and bacteria don't predominate.   For whatever reason, the total nutrient content of bryophytes, indicated by what is left in dry matter ash content, is lower than that of any other group of plants, algae, bacteria, or fungi, except for the woody parts of trees and shrubs (Table 1; Larcher 1983, 1995).

Table 1. Comparison of mean dry matter ash content for various groups of organisms. From compilation of Larcher (1983, 1995).

Bacteria	8-10%
Fungi	7-8%
Planktonic algae without skeletal material	~5%
Diatoms	up to 50%
Seaweed	10-20%
Mosses	**2-4%**
Ferns	6-10%
Grasses	6-10%
Dicotyledonous herbs	6-18%
Geophytes	5-10%
Succulents	10-20%
Halophytes	10-55%
Cacti	10-16%
Tundra herbs	~5%
Swamp plants	5-15%
Ericaceous dwarf shrubs	
Leaves	3-6%
Shoots	1-2%
Broad-leaved trees	
Leaves	3-4%
Wood	~0.5%
Bark	3-8%
Conifers	
Needles	~4%
Wood	~0.4%
Bark	3-4%

In addition to ions that compete for exchange sites, another problem with nutrient solutions is that they may have higher osmotic values than those internal ones of the bryophytes, causing osmotic shock (Brown 1982). Furthermore, the slow growth of bryophytes permits them to call upon nutrient reserves for a considerable time before deficiency symptoms appear. If multiple nutrients are limiting, the result is likely to be simply retarded growth rate, at least in the short term.

In a study on the epiphyllous leafy liverwort *Radula flaccida* (Figure 9), Olarinmoye (1975) found that when grown in distilled water, these liverworts became chlorotic and brittle, but still demonstrated considerable growth extension, indicating they most likely were using nutrient reserves. They did best in a nutrient medium diluted to 10-20% of the normal strength bryophyte medium, a solution already dilute compared to that used for most tracheophytes.

Figure 9. *Radula flaccida*, a species that becomes chlorotic and brittle when grown in distilled water. Photo by Michaela Sonnleitner, with permission.

N and P Deficiency

Nutrient deficiency, especially N and P, can reduce plant growth by hindering physiological and biochemical processes. Deficiency can reduce protein synthesis and photosynthetic rates, while increasing carbohydrate content. But are bryophytes typically nutrient deficient? There are numerous examples that suggest they typically are not. It appears that they require much lower concentrations of nutrients than do other plants, obtaining most of their nutrients from precipitation. For example, when the nutrients of rainwater near Fairbanks, Alaska, were amplified to 2-5 times their normal concentration, bryophytes showed no growth increase, and some responded negatively (Skré & Oechel 1979). Even the large moss *Pseudoscleropodium purum* (Figure 4) showed no response to increased nutrients in a field experiment (Bates 1987). Rather, although *P. purum* may exhibit a temporary increase in internal nutrient concentrations, those relatively quickly return to the concentrations typical under normal rainfall (Bates 1989).

Despite the lack of direct field evidence, Richardson (1981) recognized that inadequate nutrient supply can cause stress and reduce photosynthetic performance of mosses. On the other hand, some bryophytes such as *Ceratodon purpureus* (Figure 12) may alter their growth form under low nutrient conditions. In this moss, greater shoot initiation occurs on media deficient in N (Seppelt & Hancock 1991). Hmmm... Wouldn't that be maladaptive?

Figure 10. *Ceratodon purpureus* showing young capsules and early spring color. Photo by Michael Lüth, with permission

Figure 11. *Ceratodon purpureus* showing color phase that can reflect nutrient differences or hydration differences – or age. Photo by Janice Glime.

Figure 12. *Ceratodon purpureus* with mature capsules, showing dry color phase of leaves. Photo by Michael Lüth, with permission.

Few visible deficiency symptoms seem to have been documented for bryophytes, contrasting with the symptoms that are highly documented for tracheophytes. In tracheophytes, N deficiency causes plants to be light green with lower leaves yellow due to transport of N to growing tissues; stems are short and slender, and the root-to-shoot ratio is high (Salisbury & Ross 1992). Growth is directly related to N availability in feather mosses (Sveinbjörnsson 2002). P deficiency causes plants to become dark green, often with red-purple on the undersides of leaves. As in N deficiency, the stems are short and slender. For those bryophytes that have been studied, similarities in nitrogen and phosphorus deficiency symptoms exist, but bryophyte responses in general for these two deficiencies seem to be more distinct from each other than in tracheophytes. Development of chlorosis is a typical N deficiency symptom in both tracheophytes and bryophytes. *Funaria hygrometrica* (Figure 7, Figure 13) responded to absence of either N or P at the protonemal stage by producing few protonemata on the deficient agar, and those soon became chlorotic in the N-free medium (Hoffman 1966), failing to produce gametophores (Dietert 1979). *Atrichum undulatum* (Figure 14) had a similar response of gametophores becoming yellow (Burkholder 1959). Likewise, no new gametophores were produced in the P-free medium (Hoffman 1966). *Weissia* (Figure 15) also became chlorotic in the absence of N (Dietert 1979), the gametophore tissue soon became tough and fibrous, and the leaves were scalelike. In P-free media, the entire culture became dark brown.
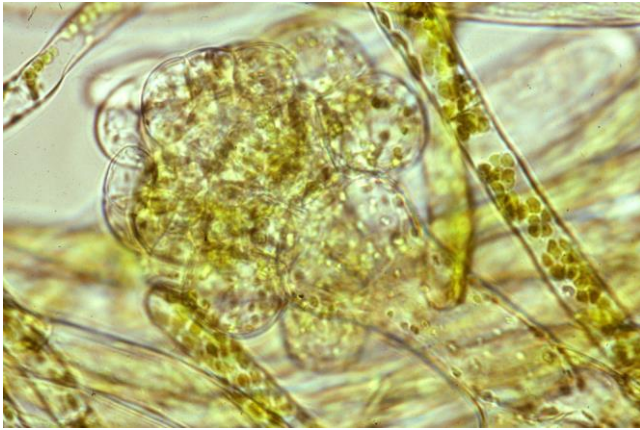
Figure 13. *Funaria hygrometrica* protonema with bud; protonemata development is greatly reduced when P or N is deficient. Photo by Janice Glime.

Figure 14. *Atrichum undulatum*, a species whose leaves turn yellow when N or P is deficient. Photo by Janice Glime.

Figure 15. *Weissia controversa* var. *densifolia* with capsules; some members of the genus become chlorotic in the absence of N. Photo by Barry Stewart, with permission.

When mature *Fontinalis antipyretica* (Figure 16) was cultured in a P-free medium for four weeks, all plants had dark green leaves, as in tracheophytes, although some had scattered chlorotic leaf tips (R. Marr & Glime unpub). In the N-free medium, all had pale green leaves, again being similar to symptoms of tracheophytes. By contrast, in experiments with excess N, *Fontinalis dalecarlica* (Figure 17) and *F. novae-angliae* became deep green (Glime unpub., Figure 18-Figure 19).

Figure 16. *Fontinalis antipyretica*, a species of streams and lakes. Photo from Proyecto Musgo through Creative Commons.
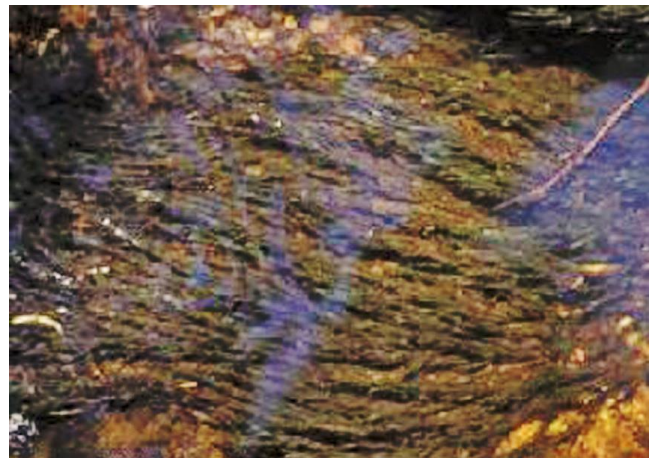

Figure 17. *Fontinalis dalecarlica* in its stream habitat. Photo by Kristoffer Hylander, with permission.

Figure 18. *Fontinalis novae-angliae* habitat. Streams typically are N-limited. Photo by Janice Glime.
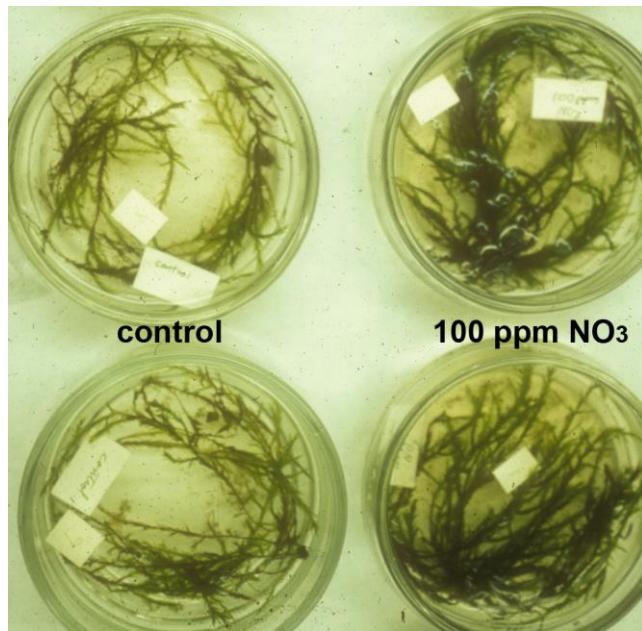
Figure 19. *Fontinalis novae-angliae* in control stream water and 100 ppm NO$_3$, showing much darker green in the high N medium. Photo and research by Janice Glime.

Although roots of tracheophytes are affected by nutrient deficiencies, there seem to be no studies that examine the effects on bryophyte rhizoids.

Phosphorus has been considered a major limiting factor for mire plant growth (Watt 1966; Small 1972; Moore & Bellamy 1974; Li & Glime 1990). On the other hand, mosses may be more competitive against tracheophytes under low P conditions; Richards (1959) reported that mosses can uptake most of the phosphate fertilizer when mosses and grasses are growing together. Apparently the phosphorus can be stored and used later in other locations; Rydin and Clymo (1989) reported the transport of phosphorus in *Sphagnum* (Figure 20-Figure 29), suggesting that it was being stored for use later.

Figure 20. *Sphagnum magellanicum*, a species for which growth is typically limited by inadequate P. Photo by Michael Lüth, with permission.

The greatest number of field studies on nutrient additions have been done on the genus *Sphagnum*, but

deficiency information is again based primarily on lab studies. Sanville (1988) and Aerts and coworkers (1992) found that *Sphagnum* production in the field increases in response to nutrient addition, suggesting that it has been growing under deficiency conditions. In support of this, Li and Glime (1990) used lab studies to demonstrate that low nutrient concentration is a major factor causing low productivity or death of parts of *Sphagnum*. Limiting P can limit the growth of mature *Sphagnum magellanicum* (Figure 20-Figure 21) and *S. papillosum* (Figure 22-Figure 23). Boatman and Lark (1971) found that P was likewise limiting for the protonema growth of *Sphagnum magellanicum* (Figure 21, *S. papillosum* (Figure 23), and *S. cuspidatum* (Figure 24).
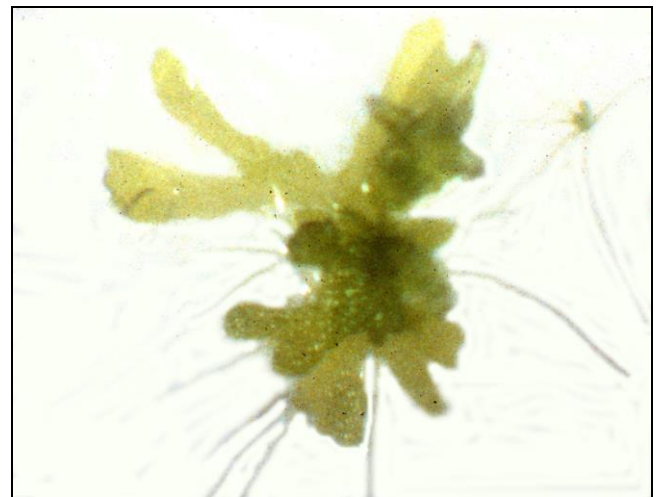

Figure 21. *Sphagnum magellanicum* protonema, a stage harmed by limiting P in the environment. Photo courtesy of Yenhung Li.

Figure 22. *Sphagnum papillosum* supporting the moisture needs of the sundew *Drosera rotundifolia*. *Sphagnum papillosum* is limited in its growth by inadequate P. Photo by Michael Lüth, with permission.
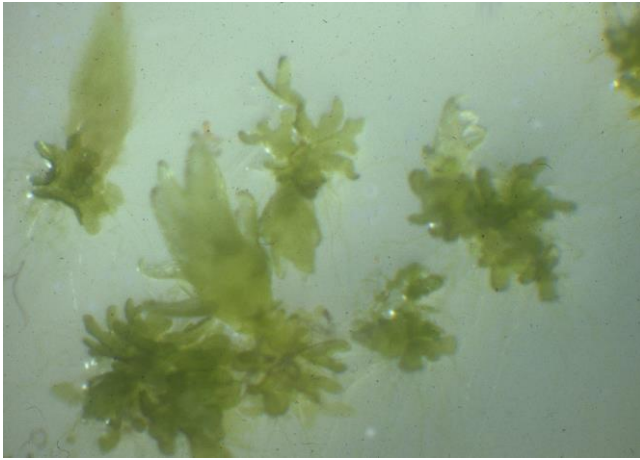
Figure 23. *Sphagnum papillosum* protonema buds, a stage that is limited by low P in its environment. Photo courtesy of Yenhung Li.

Figure 24. *Sphagnum cuspidatum*, a species of peatland valleys and pools that has reduced protonema growth in media with low P. Photo by Michael Lüth, with permission.

Li and coworkers (1993) demonstrated that both high and low concentrations of P can cause *Sphagnum magellanicum* (Figure 25) to produce red pigments, a character common for this moss when it is in strong sunlight in nature (Rudolph 1963, 1964; Rudolph & Vowinkel 1969). What are the implications of this? Does absence of red color mean anything relative to P availability, or only that light is inadequate for pigment development?

Sphagnum (Figure 20-Figure 25) cell structure (Figure 26) and general morphology change in response to nutrient concentrations (Figure 30). Baker and Boatman (1989) found that the stem length between branch fascicles in *Sphagnum cuspidatum* (Figure 24) was positively related to the N content of the capitula, whereas the capitulum dry biomass was negatively related, suggesting that branches continued to develop somewhat normally, but expansion of the stem between these branches was reduced under N deficiency. Yet, there was no correlation between interfascicular length and capitulum dry biomass. Hintikka (1972) found that *Sphagnum fallax* (Figure 27) failed to develop hyaline cells in a medium high in NH_4^+ or organic N, but low in carbohydrates (Figure 28-Figure 29). Furthermore, Baker and Boatman (1992) found that hyaline cell length of branch leaves in *Sphagnum* is directly correlated with the CO_2 concentration, whereas it is inversely correlated with the N and P concentrations (Figure 30). As might be expected, the lengths of the hyaline and chlorophyllose cells were closely correlated with each other, but also correlated with leaf length. On the other hand, short leaves had few and poorly differentiated hyaline cells.
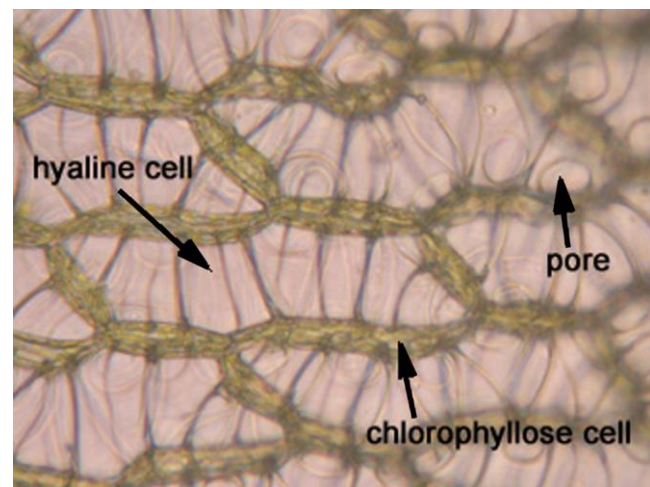

Figure 26. *Sphagnum* cells. Photo from Botany Website, UBC, with permission.

Figure 25. *Sphagnum magellanicum* showing red pigments that are typical of bright light or low P. Photo by Jan-Peter Frahm, with permission.

Figure 27. *Sphagnum fallax*, a species that experiences morphological when it is nutrient deficient. Photo by Michael Lüth, with permission.
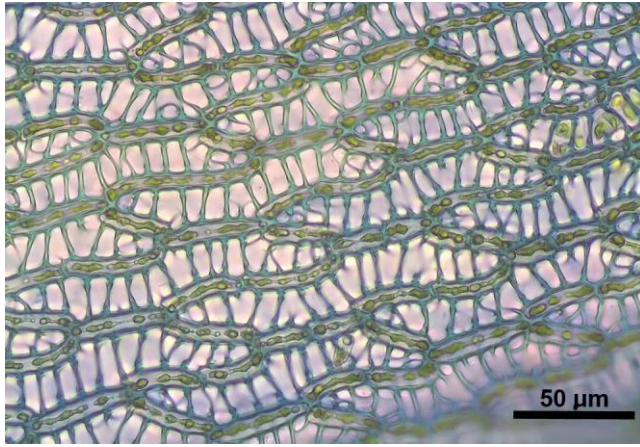
Figure 28. *Sphagnum fallax* leaf cells showing normal hyaline cells with fibrils. Photo by Kristian Peters, with permission.
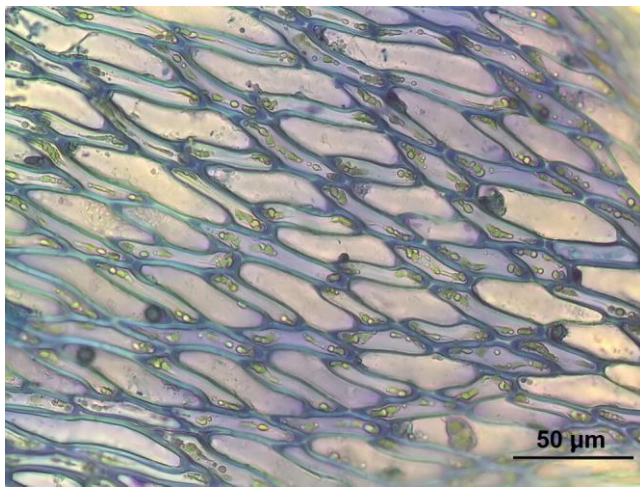

Figure 29. *Sphagnum fallax* with diminished leaf cells, suggesting a nutrient imbalance. Photo by Kristian Peters, with permission.
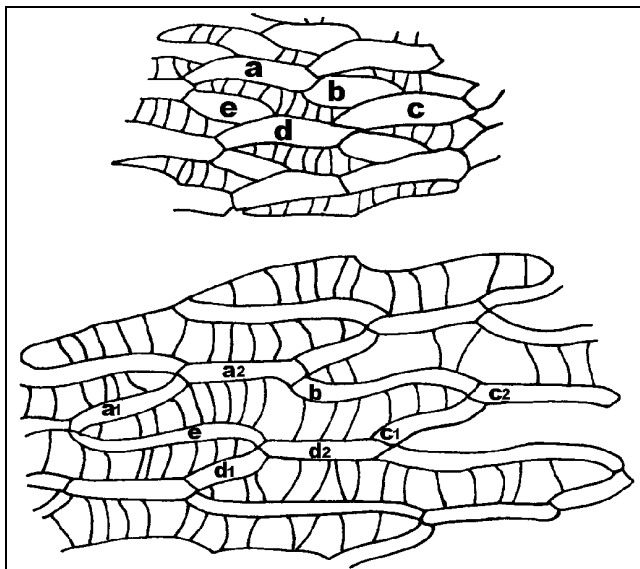

Figure 30. Arrangement of photosynthetic and hyaline cells in *Sphagnum capillifolium* leaves grown in high N & P/low CO_2 (ambient) treatment (**upper**) compared to those in low N & P/high CO_2 (5%) treatment (**lower**). Based on Baker & Boatman (1992).

Baker and Boatman (1992) suggested that the presence of well-differentiated hyaline cells in *Sphagnum* (Figure 26, Figure 28) provided a "scavenging system" for inorganic nutrient ions when they were in low concentration. The additional surface area on the interior of the cells, highly endowed with polyuronic acids, provides a large surface for binding and facilitating uptake. While this suggestion may be true, the notion of cause and effect is questionable. The plant can hardly make a decision that it needs more or longer of these cells in order to get nutrients.

How does this change in hyaline cells affect the desiccation tolerance of the moss? Perhaps one explanation is that bogs and fens are never N limited due to their Cyanobacteria flora, but that if the system is getting dry, little of the N is reaching the new leaves at the top because of the loss of capillary water. This would result in longer leaves and more hyaline cells, providing the hyaline cells needed to hold a water reservoir. But would the timing work? Would these young leaves get the signal soon enough to have the hyaline cells ready when they need them for maintaining hydration?

Liverwort deficiency studies are even more limited than those of mosses. Voth and Hamner (1940) reported that N deficiency caused a reduction in growth of *Marchantia polymorpha* (Figure 31) and the plants were stunted. Symptoms in *Marchantia polymorpha* more closely resembled those of tracheophytes. In cultures lacking N, P, or both, the midrib was darker (Figure 32) and scales, rhizoids, and the lower epidermis became red in about 10 days (Voth 1941). After 2 weeks, the N-free plants ceased growing and produced no gemmae cups; they produced few dichotomies and thalli remained narrow. Eventually the upper surface became chlorotic. Those plants lacking P likewise had a very dark midrib (Figure 32) and red underside, but contrasted sharply with the N-free plants in having frequent dichotomies with broad thalli, giving the thalli a rosette appearance, and producing numerous gemmae cups (Figure 33). As in the mosses, *Leucolejeunea clypeata* (see Figure 34) plants were light yellow to white in the absence of P (Fulford *et al*. 1947).

Figure 31. *Marchantia polymorpha* showing normal thallus and midrib. Photo from Botany Webpage, UBC, with permission.
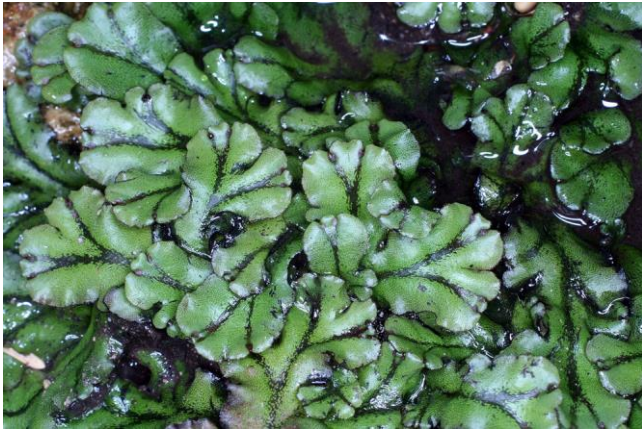
Figure 32. *Marchantia polymorpha* showing darkened midrib typical of severe N or P deficiency. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.
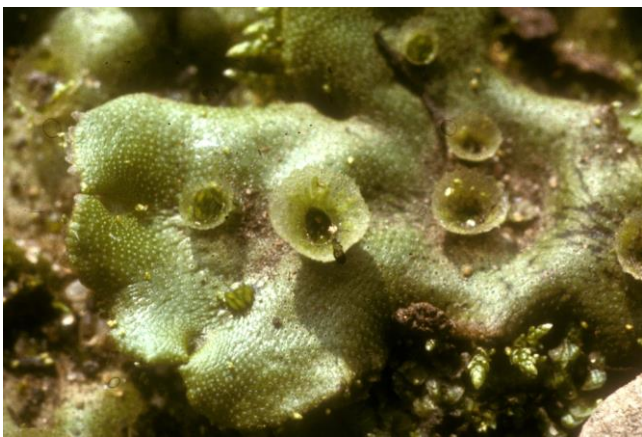

Figure 33. Thallus of *Marchantia polymorpha* with gemmae cups that are more abundant when P is deficient. Photo by Janice Glime.

Figure 34. *Leucolejeunea* sp., a species that becomes white or yellow when it is deprived of P. Photo by Jan-Peter Frahm, with permission.

K Deficiency

Potassium is also a translocatable nutrient, the most easily moved – and lost – of all the nutrients in both tracheophytes and bryophytes due to its high solubility and low ionic mass. When deficient in K^+, tracheophytes exhibit mottled or chlorotic leaves with small spots of dead tissue, usually at the tips and between veins, and especially at the margins; stems are slender. In bryophytes older parts may exhibit leaf margin chlorosis somewhat similar to effects seen on tracheophytes.

When cultured in a liquid medium with no potassium for four weeks, all samples of *Fontinalis antipyretica* (Figure 16) remained bright grass-green in color, although some were slightly pale (R. Marr & Glime unpub). By contrast, *Marchantia polymorpha* (Figure 33) *(*on solid agar) exhibited tan coloration in its older thallus parts, especially along the wing margins near the tip (Voth 1941). In tracheophytes, K^+ is important in the regulation of guard cells. No connection has been made between K^+ and the cells surrounding *Marchantia* pores (Figure 35-Figure 36), but it is possible that K^+ is likewise involved in their tendency to close under dry conditions.

Figure 35. *Marchantia polymorpha* gemmae cup with thallus showing numerous pores. Photo by Bernard de Cuyper, with permission.
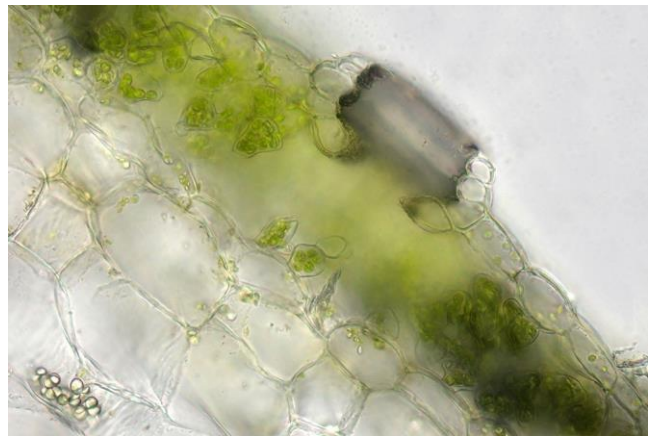
Figure 36. *Marchantia polymorpha* pore cs showing a stack of cells that can bend to decrease the pore diameter. Photo by Walter Obermayer, with permission.

Ca Deficiency

Calcium is important in maintaining membrane integrity (Brown 1982) and in binding cells together. Brown suggests that Ca^{++} may be required in greater concentrations by mosses that grow in Ca^{++}-rich sites. These mosses can have 16-17X as much Ca^{++} as species from Ca^{++}-poor habitats (Bates 1982). Mosses in calcareous habitats have 3-4X as much Ca-exchange

capacity as mosses from Ca^{++}-poor habitats (Bates 1978). Brown (1982) reasons that the Ca^{++} may be used to maintain membrane integrity. He suggests that these **calciphilic** (Ca^{++} loving) bryophytes may have inherently leakier membranes at low Ca^{++} concentrations and that it is also more difficult for them to uptake ions such as K^+. Jefferies (1969) reported that *Cephalozia connivens* (Figure 37) (a **calcifuge** – avoiding Ca) had maximal K^+ uptake at 0.1 mM Ca^{++} and *p*H 4, whereas *Mesoptychia turbinata* (calcicole – of Ca-rich habitats) did best at 3.0 mM Ca^{++} and *p*H 4-8. Nevertheless, K^+ efflux was unaffected by the Ca^{++} concentration in these two liverworts. Patterson (1946) suggested using a K:Ca ratio of 49:1 to maintain membrane integrity when using KCl to test osmotic potential. Osmotic tests that lack Ca^{++} should be suspect because they do not provide the Ca^{++} needed to keep the membrane intact.

pectate. However, these leaves still test positive for pectic substances, but negative for presence of calcium, indicating that some other element such as Mg or K has been used in place of Ca. Geldreich suggests that the rounding is the result of this substitution because magnesium and potassium do not have the hardening property of calcium pectate, thus permitting elasticity to the cell wall. This is an interesting result because some species of *Fissidens* [*F. cristatus* (Figure 39-Figure 40) vs *F. adianthoides* (Figure 41)] are separated based on this rounded cell character difference. Might this simply be an environmental expression of calcium deficiency? On the other hand, Geldreich did not find the cell difference witnessed by Fulford *et al.* (1947) on *L. clypeata* with this same treatment.

Figure 37. *Cephalozia connivens*, a **calcifuge**. Photo by Michael Lüth, with permission.

Calcium deficiency is known to interfere with growth because the cell walls cannot cement together properly, lacking the Ca needed for the calcium pectate bonds. In algae, new crosswalls fail to form between newly divided nuclei (Reed 1907). This element has low solubility and is generally not translocatable, so it cannot be taken from older leaves to supply the growing tips. Thus, necrosis of leaf tips and margins and death of the stem apex are common in Ca-deficient tracheophytes, often preceded by chlorosis (Voth 1941). Bryophytes seem to be no exception. In *Marchantia polymorpha* (Figure 31), the Ca^{++}-deficient plants had less growth and biomass increase than controls (Voth 1941). Nehira (1973) also showed that Ca^{++} was required for rhizoid differentiation in *Marchantia*, with Ca^{++} accumulating at the rhizoid base.

In the leafy liverwort *Leucolejeunea clypeata*, the response is somewhat unusual, although perhaps only visible because of the one-cell-thick leaves. Growth in a medium with no calcium causes normally flat cells to become swollen (Figure 38; Geldreich 1948a), although it has no effect on already mature cells, suggesting weak or easily extended cell walls, consistent with insufficient Ca
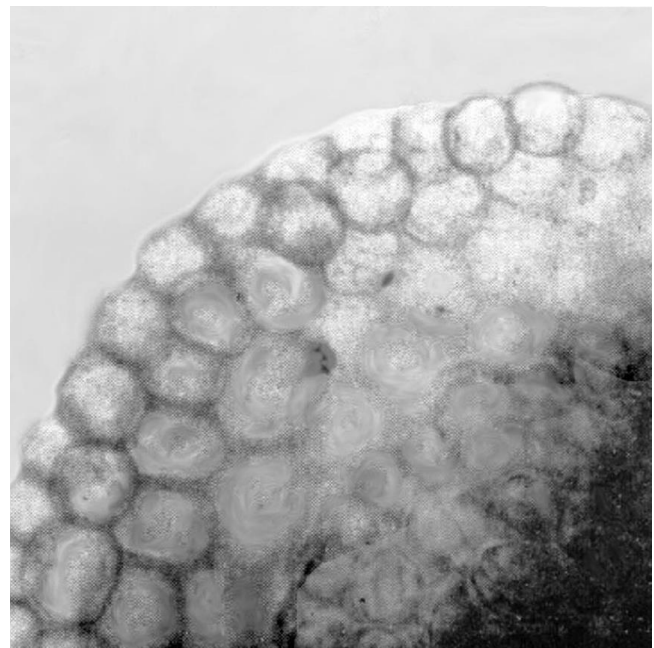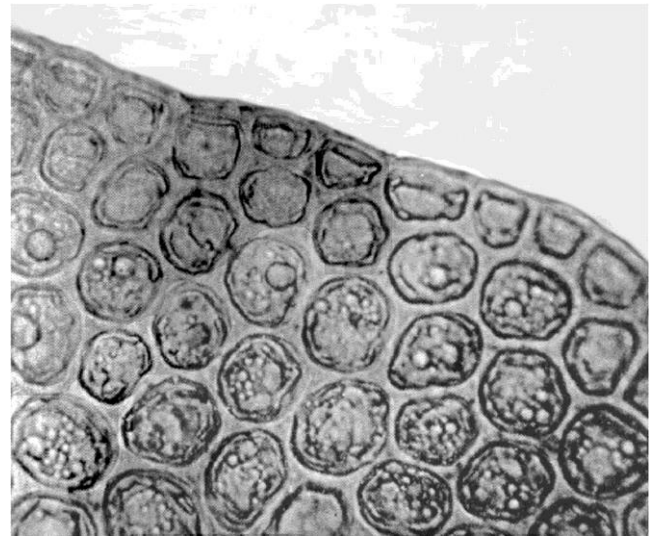

Figure 38. Effects of a Ca-deficient environment on leaf cells of *Leucolejeunea clypeata*. **Upper:** leaf grown on normal nutrient agar, showing distinct cell walls and flat surfaces. **Lower:** leaf grown on Ca-deficient agar, showing bulging cells. Photos retouched from Geldreich 1948a.

Figure 39. *Fissidens cristatus*, a species that has rounded leaf cells.   Photo by Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 40. *Fissidens cristatus* leaf, showing rounded cells. Photo by Malcolm Storey (DiscoverLife), with online permission.

Figure 41. *Fissidens adiantoides* with capsules, a species with hexagonal leaf cells. Photo by Bob Klips, with permission.

A second symptom of Ca^{++} deficiency in *Leucolejeunea clypeata* (Figure 38) is the configuration change in the oil bodies (Geldreich 1948a). In normal cells, the oil bodies are ovoid and typically one per cell. In the Ca^{++}-deficient leaves, the shape varied from globose to ovoid and they numbered up to seven per cell. This is

another trait change that could confound identification in some taxa.

Unlike the response of *Leucolejeunea clypeata* (Figure 38), wherein the protonema failed to develop on a Ca^{++}-free medium (Geldreich 1948b), *Funaria hygrometrica* protonemata (Figure 7, Figure 13) grew rapidly on Ca^{++}-free agar, but these were from already established transplanted cultures (Hoffman 1966). The gametophores that developed were small, a response typical of Ca^{++}-deficient tracheophyte sporophytes, with soft tissues that were easily torn; the entire culture turned black. In the chelated form, Ca^{++} becomes unavailable, at least for *Funaria hygrometrica* (Iwasa 1965), unlike the chelated form of iron, which is the more usable form, suggesting that on organic substrates this moss might suffer from a Ca^{++} deficiency. This should be explored as a possible cause of its preference for inorganic soil and ash and its disappearance when other plants arrive.

Marchantia polymorpha (Figure 31-Figure 33) likewise responded to reduced Ca^{++} supply (12 mg/L) by developing black tips (Voth 1941). The wings of the apical notches became black first, followed by the meristematic region. Then a V-shaped zone developed progressively back from the tip. Many of these blackened tips became watery, but by the end of the 32-day experiment many of the blackened tips were curled upward, dry, and brittle. This is similar to the response of the alga *Spirogyra*, in which the apical cell eventually contains a dark lecithin-like substance (Reed 1907). Voth (1941) showed that in *Marchantia*, early symptoms were internal, with maturing cells having larger vacuoles and fewer chloroplasts. One interesting response is that while dorsal cells are breaking down, the ventral cells surrounding the smooth rhizoids are persistent and become a source of regenerated thalli – tenacity to the end!

Mature *Fontinalis antipyretica* (Figure 16, Figure 43), on the other hand, responded to Ca^{++} deprivation by becoming pale yellow-green with a hint of brown (R. Marr & Glime, unpub).

Mg Deficiency

Deficiency of magnesium in tracheophytes results in lower leaves becoming mottled or chlorotic due to translocation of the Mg^{++} to developing apical tissues; leaves often become reddish; tips and margins turn up, causing the leaves to become cupped. Symptoms such as cupped leaves are more difficult to detect, if they exist, in bryophytes. The absence of veins might even make this trait unlikely. In some cases, lacking definitive studies among the bryophytes, deficiency symptoms can be inferred from the symptoms of excess from a competing nutrient. Most mosses need very little calcium, and calcium from limestone rock is more often detrimental than helpful to mosses. Clymo (1973) demonstrated that Ca^{++} coupled with high pH, at which it is most soluble, actually killed most *Sphagnum* species, with *Sphagnum squarrosum* (Figure 42) being the most tolerant in the study. *Sphagnum* is particularly sensitive to $CaCO_3$, forming crusts on its branch tips and soon losing vigor. Hence, these crusts of $CaCO_3$ are symptomatic that the moss is likely to be deficient in the Mg^{++} and K^+ that must compete for binding sites.

Figure 42. *Sphagnum squarrosum*, a species tolerant of high *p*H and Ca levels. Photo by Janice Glime.

The effects of Mg^{++} absence seem to be similar to those of Ca^{++} deficiency for *Funaria hygrometrica* (Figure 7, Figure 13) (Hoffman 1966). Protonemata grew well and new gametophytes formed, but like the Ca^{++}-deficient plants, these were smaller than those receiving the nutrient. In the culture study, the stems turned brown and eventually many entire gametophores turned brown. But other than the color changes, the leafy plants appeared to be quite healthy. When mature *Fontinalis antipyretica* (Figure 43) was cultured in a Mg^{++}-free medium for four weeks, all plants seemed to remain normal in appearance (R. Marr & Glime unpub). *Marchantia polymorpha* (Figure 31-Figure 33) likewise seemed to remain a healthy color, but had less area growth and dry biomass compared to controls (Voth 1941). This differs from tracheophyte symptoms in which the plants become chlorotic. Long-term absence or deficiency of Mg^{++} would undoubtedly cause chlorosis, and eventually death, because Mg^{++} is needed to form the chlorophyll molecule.

S Deficiency

Sulfur is rarely a limiting nutrient, even for tracheophytes, but soils in parts of Australia, Scandinavia, southwestern grain-producing parts of Canada, and northwestern U. S. A. can be sulfur deficient. Sulfur is used in the amino acids cysteine and methionine, thus is needed for building proteins. Sulfur is not readily translocated in plants, so deficiencies are exhibited by young tissues. In tracheophytes, the terminal bud remains alive, but young leaves and veins of older leaves become chlorotic (Salisbury & Ross 1992).

As with Ca^{++} deficiencies, *Funaria hygrometrica* protonemata (Figure 7, Figure 13) grew on S-free agar, developing gametophores (Hoffman 1966). But these gametophores were likewise small and they later became slightly chlorotic. Depriving mature *Fontinalis antipyretica* (Figure 43) of S for four weeks seemed to have no effect on its appearance (R. Marr & Glime unpub). Likewise, *Marchantia polymorpha* (Figure 31-Figure 33) growing on S-free agar showed no visible symptoms (Voth 1941). However, S in the atmosphere during the experiments may be sufficient to provide the needs for these low-nutrient, slow-growing plants.

Fe Deficiency

In the soil, high *p*H contributes to iron deficiency in plants, and in acidic soils Al can interfere with Fe uptake.

Furthermore, Fe needs to be in a chelated form for cells to absorb it across the membrane. Once delivered to the tissues, Fe is also immobile and cannot be moved easily from older to younger tissues. In tracheophytes its deficiency causes interveinal chlorosis similar to that for Mg^{++} deficiency, but in the case of Fe it is the younger leaves that become chlorotic. Although it is not required in chlorophyll, it is apparently needed by the enzymes used to synthesize chlorophyll and it is needed especially in the electron transport system.

In bryophytes, symptoms of Fe deficiency are poorly known and vary with species. When transplanted to agar with no iron, *Funaria hygrometrica* protonemata (Figure 7, Figure 13) grew rapidly, but produced very few new upright gametophores (Hoffman 1966). Those that were produced became chlorotic and the plants eventually turned brown. When mature *Fontinalis antipyretica* (Figure 43) was cultured without Fe for four weeks, the stems became bright red, especially near the base, and some leaves were likewise red at the base (R. Marr & Glime unpub). When unchelated iron was provided as FeCl$_3$, all *F. antipyretica* plants had yellow-brown leaves with bright green stems. Normally the stems of this species are brown. One must ask why the symptoms differed when unchelated iron was supplied. Did something in the medium or in the plant chelate it to a limited extent? What could account for the red coloration with no Fe?

Comparisons of the macronutrient deficiency symptoms in the mosses *Fontinalis antipyretica* (Figure 43) and *Funaria hygrometrica* (Figure 7, Figure 13) and thallose liverwort *Marchantia polymorpha* (Figure 31-Figure 33) are presented in Table 2.

Table 2. Deficiency symptoms in *Fontinalis antipyretica* (Figure 43) based on unpublished data of Robert Marr and Janice Glime, *Funaria hygrometrica* (Figure 7, Figure 13) based on Hoffman (1966), and *Marchantia polymorpha* (Figure 31-Figure 33) based on Voth (1941).

	Fontinalis	*Funaria*	*Marchantia*
N	pale green	few protonemata, chlorotic	midrib dark, scales & rhizoids red
P	dark green	few protonemata, no gametophores	midrib dark, scales & rhizoids red
K	no visible effect		tan coloration of older parts
S	no visible effect	small, chlorotic	no visible effect
Mg	no visible effect	small, stems brown many leaves brown	less growth
Ca	pale yellow-green	small, soft tissues	less growth black tips
Fe	stems bright red	few gametophores, chlorotic, brown	

Micronutrient Deficiency

It is difficult to deprive plants of micronutrients because the minute quantities needed can occur as contaminants. Any bryophytes brought from the field are likely to have sufficient quantities on their surfaces to last them for a long time. Even when grown on nutrient-

deficient agar (missing B, Cl, Cu, Mn, Mo, and Zn), *Funaria hygrometrica* (Figure 7, Figure 13) continued to produce protonemata (Hoffman 1966). Although gametophores developed, they remained stunted and their stems turned dark. The tissues were tough and difficult to tear, much like in the N-deficient cultures. When Marr and Glime (unpub) deprived mature *Fontinalis antipyretica* (Figure 43) of micronutrients for four weeks, most plants exhibited no symptoms, except that 8 apical pieces developed brown tips (in 4/5 replicate containers). On the other hand, when Cu was added to *Fontinalis dalecarlica* (Figure 44) in Lake Superior water, greener cells resulted.

Figure 43. *Fontinalis antipyretica* with brown tips (**arrow**) such as might be seen with a nutrient deficiency.
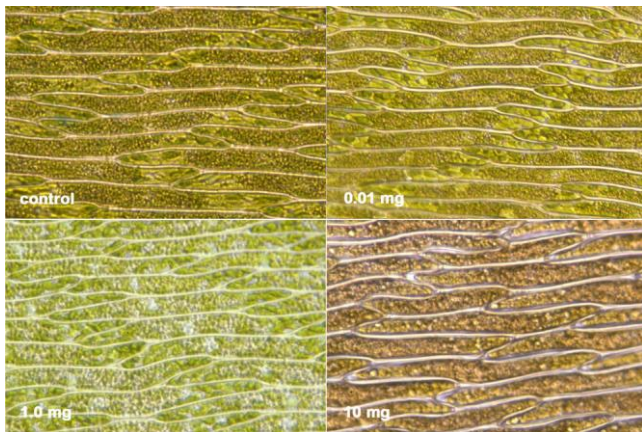

Figure 44. *Fontinalis dalecarlica* showing the greenest leaf cells at 1.0 mg copper per liter. Photo by Janice Glime.

Biochemical changes that affect the ability of the plant to tolerate stress may also occur. For example, in *Marchantia palacea* var. *diptera* (Figure 45) grown in copper-deficient media, the enzyme Cu/Zn-superoxide dismutase was inactivated (Tanaka *et al*. 1995). This enzyme group is important in maintaining membrane integrity (Dhindsa & Matowe 1981; Dhindsa *et al*. 1981; Gong *et al*. 1997). Therefore, its destruction or inactivation may result in greater membrane damage during desiccation, resulting in a loss of nutrients from the cell. Such losses can result in a multiplicity of symptoms because other nutrients have become deficient as well.

Figure 45. *Marchantia palacea* var. *diptera*, a species that disables the enzyme Cu/Zn-superoxide dismutase when grown in a copper-free medium. Photo by Janice Glime.

Oxygen Deficiency

One rarely considers plants in the context of oxygen deficiency, but apparently even some members of this oxygen-producing group can suffer from insufficient oxygen. When the aquatic leafy liverwort *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 46) was cultured in a non-aerated solution, it accumulated considerably less phosphorus in the first three days, probably due to blockage of mitochondrial respiration, followed by a net loss of P, indicating probable membrane damage (Mártínez Abaigar 2002).

Figure 46. *Jungermannia exsertifolia* subsp. *cordifolia*, a species that seems to require oxygen to take in P. Photo by Michael Lüth, with permission.

Community Effects of Deficiencies

Although nutrient concentration often may not cause evident deficiency or excess symptoms in bryophytes, it can have a strong effect on community composition. Bryophyte-dominated peatlands provide a good example. Following an extensive literature survey, Bedford *et al*. (1999) suggest several generalizations regarding peatlands: "(1) plant community type changes across broad nutrient gradients; (2) species richness declines as various indicators of nutrient availability increase beyond some

threshold; and (3) rare and uncommon species are almost always associated with species-rich communities." Perhaps it is safer to agree with Bedford *et al.* (1999) in their conclusions that our "generalizations do not always hold within community types; for many community types, the threshold beyond which richness declines has not been established, and high or low diversity may occur below that threshold; and (4) the failure of many studies to include bryophytes precludes drawing strong conclusions about nutrient availability and diversity in peatlands."

Brunkman (1936) found that moss cover in other habitats seemed to have little to do with nutrients. Cover on clays and clay loams in Alberta, Canada, ranged from 7 to 92%, on sandy loams from 59 to 92%, and on Jack pine (*Pinus banksiana*) sand to sandy loams, from 3 to 71%. Brunkman found these data to be "confounding," and interpreted them to mean that the moss does not correlate with soil type, and by inference, probably does not correlate well with nutrients. He had to conclude that mosses were of little or no value as indicators of possible timber values and volumes because "the moss cover wanders all over the site values without any sequence . . ."

On the other hand, Epstein and Yeatman (2003) found that bryophytes increase when tracheophytes such as *Betula nana* resorb higher percentages of N, depriving other shrubs of the nutrient and thus favoring bryophytes. Thus, even if the bryophytes do not directly respond to the nutrients, they may respond because of the resulting change in competition from tracheophytes for space and light.

Nevertheless, Marczonek (1984) showed that *Conocephalum conicum* (Figure 47) population density is dependent on the soil levels of Ca^{++} and Mg^{++}. *Pellia epiphylla* (Figure 48) likewise has increased densities with increases of these two elements as well as N and K. *Meesia triquetra* (Figure 49) occurs where there is both a high *p*H and high concentration of Ca^{++} (Montagnes 1990). These are but few examples of the many *p*H and nutrient relationships that exist among the bryophytes. Many more will be discussed as we examine individual habitats later in this book. This surely is evidence that mosses and liverworts can and do get nutrients from the soil and that bryophytes do have minimal nutrient requirements, which they satisfy with either precipitation or substrate or both. The availability of these nutrients determines their growth and distribution, but not in isolation from other factors such as water availability and competition.

Figure 47. *Conocephalum conicum*, a species in which population density is dependent on soil levels of Ca^{++} and Mg^{++}. Photo by Michael Lüth, with permission.

Figure 48. *Pellia epiphylla*, a species that has increased densities with increases of Ca^{++}, Mg^{++}, N, and K. Photo by Robert Klips, with permission.

Figure 49. *Meesia triquetra*, a species that prefers high *p*H and a high concentration of Ca^{++}. Photo by Michael Lüth, with permission.

Summary

Bryophytes have low nutrient demands compared to tracheophytes, and this may permit them to thrive in habitats such as rock surfaces where they collect dust and throughfall, or in streams where a new supply of nutrients constantly flows by.

N and P deficiency can reduce protein synthesis and photosynthetic rates, while increasing carbohydrate content. N deficiency in bryophytes causes chlorosis and may result in tough, fibrous gametophores with scalelike leaves. In liverworts, at least, it causes a reduction in growth and gemmae cups. Liverworts also may develop red pigments in the absence of N, P, or both. In phosphorus-free media, mosses may become dark brown or may be dark green with only the tips exhibiting chlorosis. Low P limits growth. However, in the liverwort *Marchantia*, absence of P resulted in frequent dichotomies and broad thalli with numerous gemmae cups.

Carbohydrate deficiency, coupled with a high concentration of NH_4^+ or organic N can cause *Sphagnum* to fail to develop hyaline cells. These hyaline cells may provide a "scavenging system" for inorganic nutrient ions when they are in low concentration.

With **potassium** deficiency, older parts may exhibit leaf margin chlorosis somewhat similar to effects seen on tracheophytes. *Marchantia* likewise develops pale thallus margins.

Mosses growing in Ca^{++}-rich habitats may develop 3-4X as much Ca-exchange capacity as those from Ca^{++}-poor habitats. The Ca^{++} may be necessary to maintain membrane integrity and therefore would be important in retaining K^+. Ca^{++} deficiency can result in reduced growth, lack of rhizoid differentiation, failure of protonemata to develop, black thallus tips, change in shape and increase in number of oil bodies in liverwort leaf cells, small gametophores, and soft tissues. If Ca^{++} is absent during cell development, the cell walls can become more elastic and appear rounded. Internal changes may include larger vacuoles and fewer chloroplasts.

Deficiency of Mg^{++} can result in smaller gametophytes with stems and leaves turning brown. Otherwise, Mg^{++}-deficient bryophytes seem to be healthy.

Sulfur deficiency symptoms are similar to those of Ca^{++} and Mg^{++}, with reduced gametophore growth and chlorosis, but few other symptoms. However, there is often sufficient S in the atmosphere to sustain the bryophytes.

Iron deficiency symptoms seem to vary among species. They include reduction in number of upright gametophores, chlorosis, red stems, red leaf bases, and bright green stems (with unchelated iron).

Micronutrient deficiency can result in stunted growth and dark-colored stems with tough tissues. Enzymes needed to maintain membrane integrity may fail, perhaps due to absence of the metal part of the enzyme.

In aquatic habitats, even oxygen can become limiting, resulting in inability to accumulate P.

Nutrient balance affects competition, and bryophytes often gain an advantage when tracheophytes are nutrient-deficient.

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