

# CHAPTER 8-8

## NUTRIENT RELATIONSHIPS: CYCLING

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Figure 1. Nutrients may be tied up in bryophytes for decades, or recycle within months, in forests with abundant bryophytes, as in this forest with *Isoetes myosuroides*. Photo by Michael Lüth, with permission.

### Storage and Release

Bryophytes are of particular importance in cold biomes and tropical forests (Cornelissen *et al.* 2007). In these ecosystems, they offer a number of important contributions:

1. They are substantial members of the above-ground biomass, often along with lichens.
2. They host N-fixing bacteria, thus providing a major soil N input.
3. They control soil chemistry and nutrient availability through their leakage of recalcitrant polyphenols, control of soil hydrology, and temperature modification.
4. They erode rocks but prevent soil erosion.
5. They provide food for animals.
6. They both protect and compete with tracheophytes.

In all of these roles, they influence the nutrient cycling of these ecosystems.

Few quantitative studies have addressed the role of bryophytes in ecosystem nutrient cycling (Brown & Bates 1990). Nevertheless, bryophytes may play a significant role in the retention and release of important limiting nutrients like nitrogen in many types of ecosystems (Figure 1). Nutrients collected from aerial dust and throughfall are returned to the ecosystem from bryophytes through leaching and decomposition. Bowden (1991) found that in primary succession on exposed **New Hampshire sands**, the rate of nitrogen accumulation in *Polytrichum* (Figure 2) was  $10.1 \text{ kg ha}^{-1} \text{ y}^{-1}$ . Even for this endohydric moss, he found that 58% of the annual input of nitrogen is from bulk precipitation. As suggested by this study, the bryological component of the ecosystem often plays a significant role in nutrient cycling (During 1990; Bates 1992; Nakatsubo 1997). When the *Polytrichum* was removed from the soil, nitrogen losses from the ecosystem temporarily exceeded



inputs, underlining the importance of the mosses in sequestering and holding nitrogen at the site. Lamontagne (1998) found that nitrification increased 13-fold under lichen and moss patches. In this case, the lichens did not fix atmospheric nitrogen and thus did not contribute directly to the nitrogen supply. Without the mosses (and lichens), the nitrogen from precipitation and throughfall can be lost to surface water that ultimately ends up in waterways and is carried from the local system. Furthermore, the mosses and lichens can contribute organic acids that leach nitrogen from the underlying bedrock, thus making it available to plants.



Figure 2. *Polytrichum commune*, a species that accumulates carbon in growing shoots and brown portions. Photo by Andrew Spink, with permission.

Only in **peatlands and the polar latitudes** have most ecosystem ecologists traditionally acknowledged the role of the bryophytes in storing or releasing nutrients. Nevertheless, bryophytes play several roles in the nutrient status of their native ecosystems. Whereas tracheophytes obtain nutrients only after mediation by the soil, most bryophytes obtain nutrients before they reach the soil.

The **boreal** feather moss *Hylocomium splendens* (Figure 3) in a subarctic birch woodland has a retention time of 3-10 years for N, transporting the N within the plant to the growing tips (Eckstein 2000). Such a retention can have a strong impact on the nutrient dynamics of a forest with 100% bryophyte cover on the forest floor.



Figure 3. *Hylocomium splendens*, a feather moss. Photo by Michael Lüth, with permission.

In the **Alaskan black spruce forest** (Figure 4), the bryophyte layer intercepts and accumulates more of every nutrient element but  $\text{Ca}^{++}$  than it receives from throughfall and litter (Oechel & van Cleve 1986), again suggesting that soil nutrients are also contributed. In the boreal forest, bryophytes are limited in biomass, but they nevertheless are major contributors to cover and primary productivity (Oechel & van Cleve 1986). They furthermore act much like a sponge in their ability to take up nutrients rapidly. Their further ability to modify the soil temperature and prevent permafrost makes them major ecosystem engineers for the nutrient regime.



Figure 4. Black spruce (*Picea mariana*) forest at Arctic Chalet, Inuvik, NT. Photo through Creative Commons.

Even in **tropical forests**, where trees can create up to five levels of canopy, the "insignificant" bryophytes can be significant in altering the nutrient regime. The bryophytes serve as filters for nutrients in rainfall, throughfall, and stemflow. This role is a complex one, differing among species of bryophytes, seasons, state of hydration, and types of nutrients (Glime 2001).

Working in **chalk grasslands**, During (1990) suggested that even when bryophytes are patchy they have a major impact on nutrients and tracheophytes associated with them, particularly during partial dieback and decomposition in the summer months. In chalk grasslands, bryophytes grow and absorb nutrients during autumn and winter, thus not competing with the inactive tracheophytes. They release nutrients by decomposition in spring and summer, hence serving to sequester nutrients in the ecosystem and provide them to the tracheophytes when nutrients are needed most for growth. It is clear that we cannot afford to ignore their potential role in ecosystem-level nutrient cycling.



## Storage Locations

Many factors determine where nutrients are stored in bryophytes. External storage on exchange sites provides a ready supply as nutrients are used within the cells. Storage in underground stems can provide nutrients for new growth in spring. And many compounds are stored structurally, making them unavailable until the slow process of decomposition once again releases them.

## Methodology Matters

Because of their tremendous surface area, bryophytes are typically "contaminated" with surface dust. This presents serious problems when trying to assess their nutrient content. While it seems obvious that washing would reduce the problem, it brings problems of its own. The success of washing mosses has rarely been quantified. Hence, degree of removal can vary widely between samples and researchers. And some species, with retentive sites such as boat-shaped leaves or clasping bases, will retain more soil particles than others. Furthermore, particulate matter may partially solubilize in the wash and could increase uptake. On the other hand, if the adhering dust contains sulfur or nitrogen oxides, the resulting acids could cause the loss of ions by leaching. The sudden change in ionic balance can have unpredictable influence on the adhering portion (*i.e.* those on exchange sites), causing a shift in the nutrient component of the bryophyte.

Published studies on the nutrient content of bryophytes have used a variety of methods, and one must assess the method to determine if the values given are appropriate for the interpretation needed. Lack of attention to bound ions on the moss surface can give misleading values.

Studies indicating locations of nutrient concentrations of bryophytes often do not provide a true picture of those constituents within the cells. Rather, they include the numerous ions located on exchange sites on the surfaces of the plant. Hence, in reviewing nutrient concentrations we must pay particular attention to the methods in separating the external from the internal components. Nevertheless, both internal and external storage have an impact on the nutrient cycling of the ecosystem.

Determining the positions of ions on and in bryophytes is largely a chemical process. Two different methods have revealed similar locations. Brehm (1968, 1970) found those located on the extracellular exchange sites by displacing the cations with 0.01N mineral acids. He followed this with formaldehyde to rupture the cells, releasing the internal soluble ions. The remaining cations were displaced with normal acid. Brown and coworkers used 1000 mg L<sup>-1</sup> Sr (Bates & Brown 1974) or Ni (Brown & Buck 1978a, b, 1979) to displace the bound extracellular cations, followed by boiling to release soluble ions, and then recovering residual material by a total digestion in concentrated HNO<sub>3</sub>. Both groups found that Na<sup>+</sup> and K<sup>+</sup> occurred in the cytosol, while Ca<sup>++</sup> remained largely as an extracellular exchangeable form on plant external and intercellular surfaces. This makes sense because a major role of Ca<sup>++</sup> is in forming calcium pectate bonds to cement cell walls together. Mg<sup>++</sup> and Zn<sup>++</sup> showed intermediate patterns of location. Nevertheless, a complete understanding of affinities is necessary to interpret the concentrations. Brown and Bates (1972) used Ni to replace Pb, but later Brown (1982) pointed out that they had failed

to release all the Pb from exchange sites and that a concentration greater than 1000 mg L<sup>-1</sup> would be needed to remove elements like Pb that have a very high affinity for exchange sites.

## Mineral Nutrients

Several studies have identified the locations where bryophytes store mineral nutrients. Brown (1982) states that in general the monovalent cations, *e.g.* K<sup>+</sup>, are concentrated near the apex and the divalent elements toward the base. We also know that in tracheophytes N, P, K, Mg, and Cl move easily due to greater solubility, whereas B, Ca, and Fe are relatively insoluble and immobile. One of the factors contributing to high concentrations of ions of such elements as Al, Ca, Fe, and Mn in older segments is that as cells die or other ions move to the apex, new binding sites are exposed, permitting more of these ions to accumulate there.

Brown and Buck (1985) likewise found that K<sup>+</sup> resided in the cytosol of *Grimmia donniana* (Figure 5) and *Calliergonella cuspidata* (Figure 6), whereas Ca<sup>++</sup> and Pb<sup>++</sup> were in extracellular exchangeable forms. Mg<sup>++</sup> and Zn<sup>++</sup> seemed to be intermediate in behavior, with locations depending on the species and total element concentration.



Figure 5. *Grimmia donniana*, a species in which K<sup>+</sup> resides in the cytosol and Ca<sup>++</sup> and Pb<sup>++</sup> in an extracellular locations. Photo by Hermann Schachner, through Creative Commons.



Figure 6. *Calliergonella cuspidata*, a species in which K<sup>+</sup> resides in the cytosol and Ca<sup>++</sup> and Pb<sup>++</sup> in extracellular locations. Photo by Michael Lüth, with permission.



## What We Learned from Heavy Metals

Much of our knowledge of ion storage locations is derived from storage of heavy metal contaminants in the environment. For example, *Rhytidiadelphus squarrosus* (Figure 7) stores Pb in electron-dense regions of the plasma membrane, in vesicles, vacuoles, chloroplasts, and nuclei, and in the cell wall (Gullvåg *et al.* 1974; Ophus & Gullvåg 1974; Skaar *et al.* 1973). But *Hylocomium splendens* (Figure 3) in the same study only contained electron dense regions in the cell wall (Gullvåg *et al.* 1974). The researchers reasoned that the thicker cell wall of *H. splendens* might prevent entry.



Figure 7. *Rhytidiadelphus squarrosus*, a species that stores lead in its plasma membranes. Photo by Michael Lüth, with permission.

In the aquatic moss *Platyhypnidium riparioides* (Figure 8), Cu accumulates in three locations: intercellular in the cell wall free space, exchange sites on the cell wall, and residual within the cell (Mouvet & Claveri 1998). These three locations are those we should expect to hold most of the cations of a bryophyte, suggestion that heavy metals like Cu could compete with nutrients needed in greater quantity.

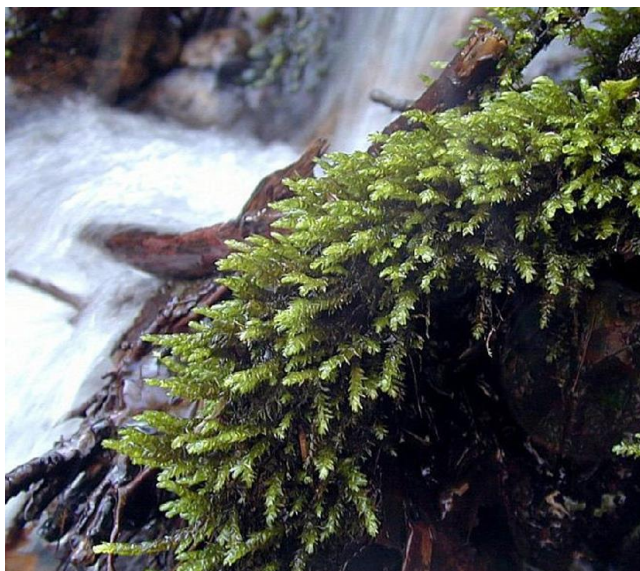


Figure 8. *Platyhypnidium riparioides*, a species that is able to store copper in the cell wall free space, on exchange sites on the cell wall, and residual within the cell. Photo by Michael Lüth, with permission.

## Oil and Lipid Bodies

**Oil bodies** (isoprenoid essential oils; Figure 9-Figure 13) are well known in leafy liverworts, providing distinct diagnostic characters and provide distinctive odors, yet their function seems to remain unknown (He *et al.* 2013). Speculation includes protection from herbivores (Stahl 1888), pathogens, cold temperatures, excessive light (Hieronymus 1892), and UV radiation and desiccation (Gavaudan 1927; Chalaud 1931). These oil bodies are often associated with bryophytes that live in high light, but no physiological studies have demonstrated that they in fact make a difference. Perhaps the best argument for considering them to be food reserves is that most seeds store lipid droplets as a food reserve that is used for germination and subsequent growth (Huang *et al.* 2009).

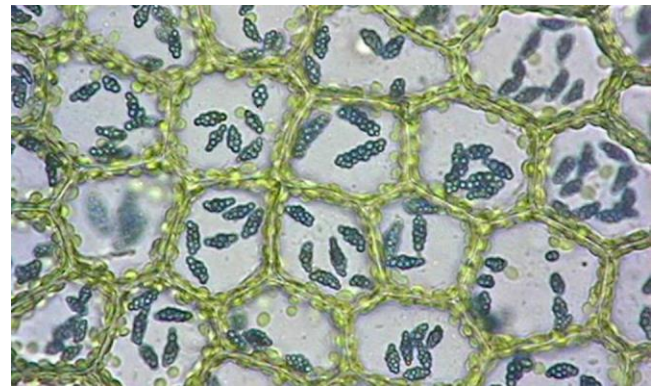


Figure 9. *Calypogeia peruviana* cells with botryoid oil bodies stained blue. Photo by Paul Davison, with permission.

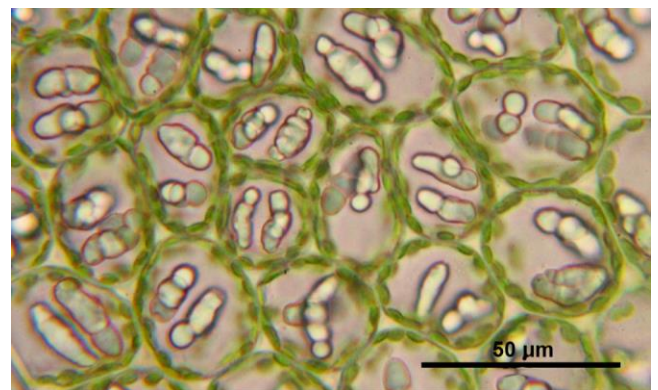


Figure 10. *Nardia scalaris* leaf cells with oil bodies. Photo by Hermann Schachner, through Creative Commons.

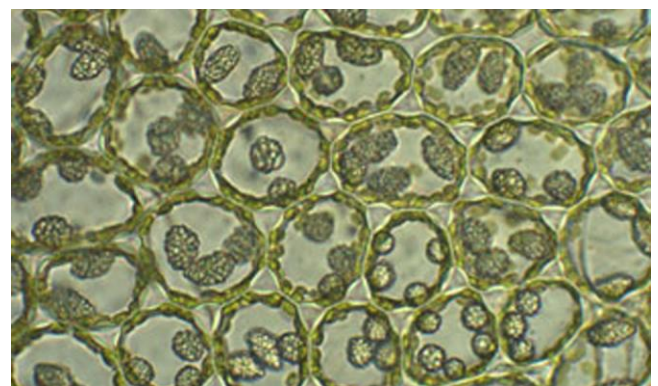


Figure 11. *Nardia lescurii* oil bodies and trigones. Photo by Blanka Shaw, with permission.



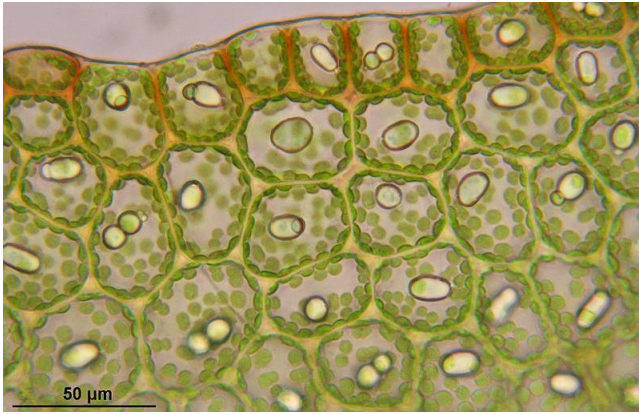


Figure 12. *Nardia compressa* leaf cells. Photo by Hermann Schachner, through Creative Commons

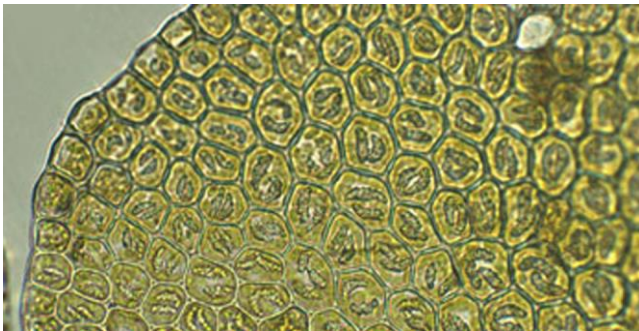


Figure 13. *Rectolejeunea maxonii* oil bodies 1 Blanka Shaw, with permission.

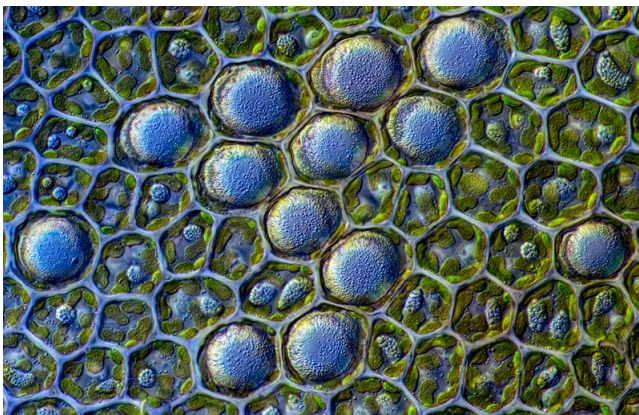


Figure 14. *Frullania fragilifolia* ocelli (blue bulges filling cells) and smaller oil bodies, also stained blue. Photo by Des Callaghan, with permission.

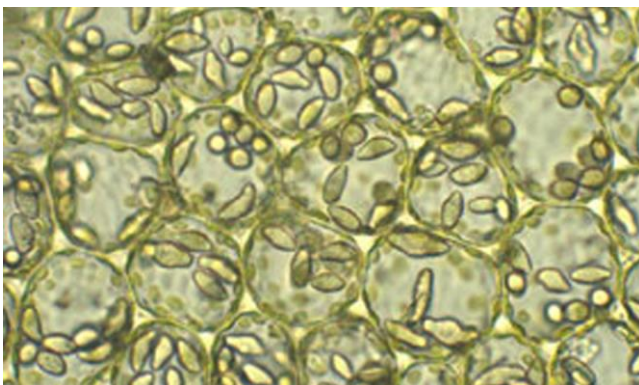


Figure 15. *Jungermannia* sp. oil bodies. Photo by Blanka Shaw, with permission.

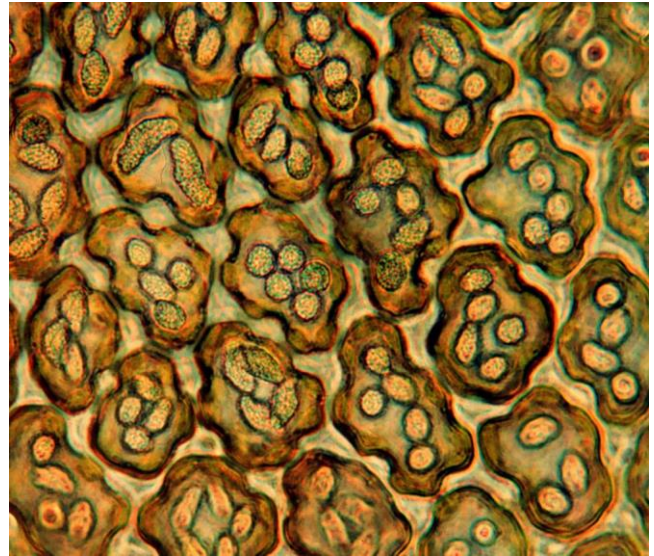


Figure 16. *Frullania pycnantha* oil bodies. Photo by Matt von Konrat, with permission

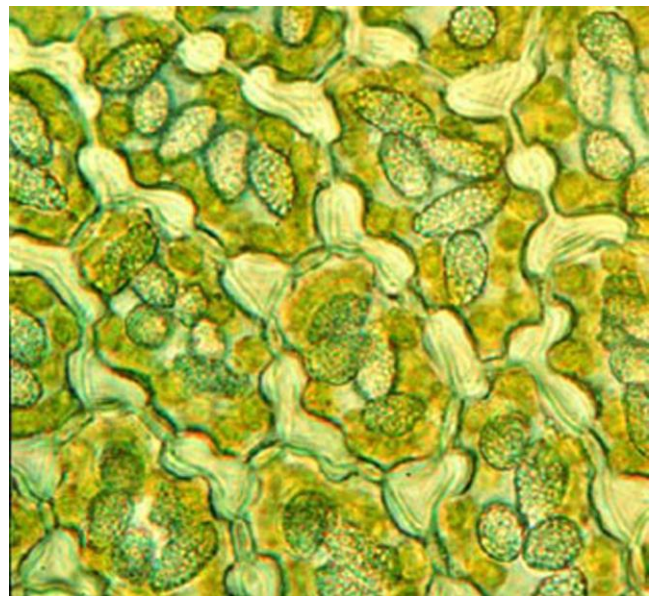


Figure 17. *Frullania squarrosula* oil bodies (granular greenish ovals). Photo by Matt von Konrat, with permission.

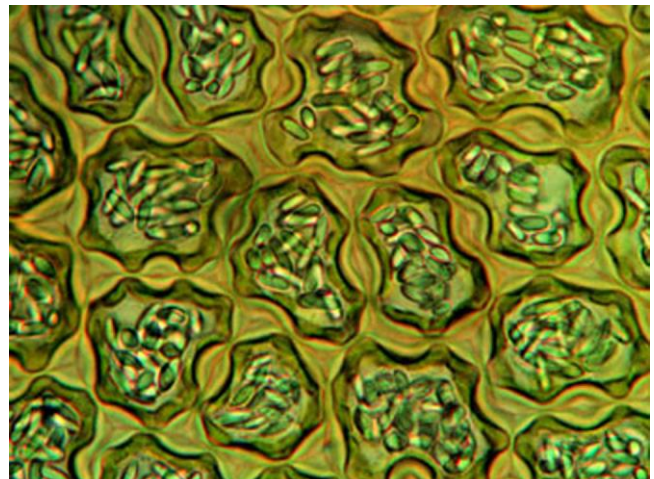


Figure 18. *Jubulopsis novae-zelandiae* oil bodies and cell wall trigones. Photo by Matt von Konrat, with permission.



Nevertheless, the oil bodies of liverworts seem to have an important function in cell metabolism (He *et al.* 2013). Understanding it may help us to understand how these plants tolerate their environment. But is that tolerance to light, desiccation, low temperatures, periods of low nutrients, herbivores, or something else?

More recently, Pressel *et al.* (2009) described the role of liverwort oil bodies in desiccation tolerance. These are well known to "disappear" when the liverworts are dried, thus disappearing in herbarium specimens. However, in their study, Pressel and coworkers found that instead they become unchanged in the dry state, but become flattened upon rewetting. Then, after 48 hours, they regain their normal morphology. Nevertheless, if they are dried too quickly, the oil bodies do indeed vanish upon rewetting and do not reappear. The abilities of these oil bodies to recover as flattened bodies under natural conditions, then regain their shape after 48 hours of recovery suggests that they may shift soluble carbohydrates or other important substances into the cytoplasm, permitting rapid recovery of the cell from drought.

Some mosses may also develop similar structures. Huneck (1984) reported that in mosses these are comprised of lipids, not oil drops. Jönsson and Olin (1898) reported that these lipids occurred only in certain taxonomic groups and exhibited seasonal variation. Among 50 species in Sweden, the contents varied widely, but they generally produced maximum concentrations in spring and autumn during their growth periods. These mosses furthermore lack the distinctive odors exhibited by many liverworts (Lorch 1931).

In mosses, the lipid drops occur in such varied locations as alar cells, basal laminal cells, upper laminal cells, and costa, sometimes occurring in all of these in the same leaf (Frahm 1994). But when present in the **Dicranaceae** (Figure 19), they consistently occur in basal laminal cells, but may also occur elsewhere. Frahm made one interesting discovery in the herbarium specimens he assessed – the lipid bodies tended to be most frequent in specimens collected in the cold season, at high elevations and Arctic regions. If you want to explore these further, they become more visible with a Fuelgen reaction using wet mosses treated with Schiff's reagent; this gives the lipid bodies a deep violet color.



Figure 19. *Dicranum scoparium* leaf base cells showing fat droplets. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Des Callaghan (Bryonet 30 July 2013) reported large oil droplets in the cells of the perichaetial leaf of *Diphyscium foliosum* (Figure 20-Figure 22). Ida Bruggeman (Bryonet 31 July 2013) reported that members of *Fissidens* will often produce several small, shiny droplets, a common occurrence in the *Fissidens* subgenus *Aloma* (Figure 23-Figure 24). Frahm (1994) reported that oil drops in laminal cells of **Dicranaceae** (Figure 19) were taxonomically important and considered these to serve as a means of storage in the species that had them. It is likely that all of these apparent "oil droplets" are in reality fat droplets.



Figure 20. *Diphyscium foliosum* showing perichaetial leaves around capsule. Photo from Botany 321 Website, UBC, with permission.

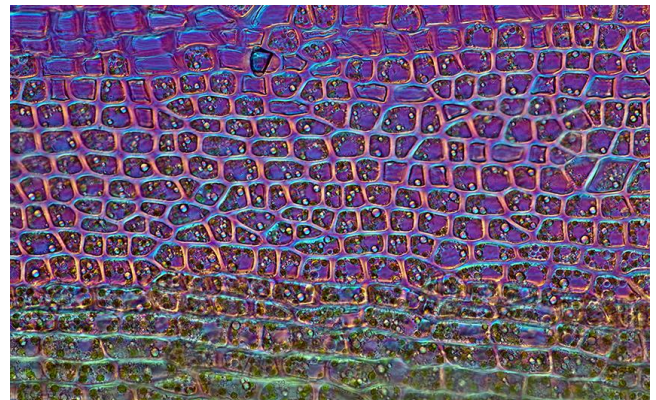


Figure 21. *Diphyscium foliosum* perichaetial leaf with lipid droplets under polarized light. Photo by Des Callaghan, with permission.

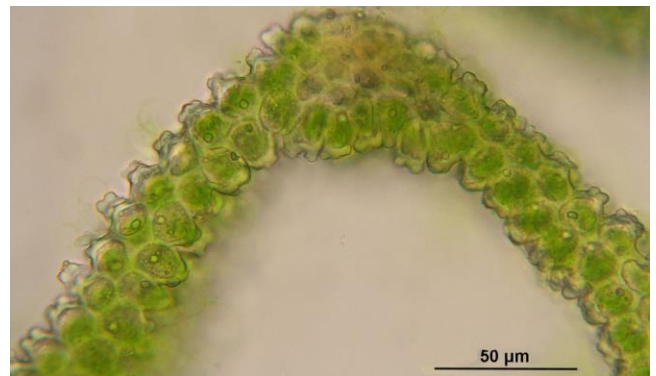


Figure 22. *Diphyscium foliosum* leaf cs showing fat droplets. Photo by Hermann Schachner, through Wikimedia Commons.





Figure 23. *Fissidens exilis* with capsules, a member of the subgenus *Aloma*, that exhibits oil/fat droplets. Photo by Malcolm Storey, through Discover Life, with online permission.



Figure 24. *Fissidens exilis* leaf cells showing fat/oil droplets. Photo by Malcolm Storey, through Discover Life, with online permission.

Silvana B. Vilas Bôas-Bastos (Bryonet 31 July 2013) reported observing oil/fat droplets in the basal cells of the *Dicranella hilariana* (Figure 25). Rut Caparrós (Bryonet 8 August 2013) reported seeing large oil droplets in the vaginula of *Ulota* when the sample is crushed under the cover glass. Alison Downing (Bryonet 1 August 2013) saw what appeared to be oil bodies in *Chrysoblastella chilensis* (Figure 26-Figure 27), but was discouraged by colleagues who said mosses didn't have oil bodies. However, Matteri (1984) reported starch grains and what appeared to be oil drops in *C. chilensis* in the central tissue of tubers and postulated that they might serve as a means of perennation. She noted that these tubers do not readily separate from the stems and thus considered it unlikely that the tubers served in dispersal. Allan Fife (Bryonet 4 August 2013) described these tubers in New Zealand as common in axils of lower stems in this species.

As the bryophytes remain dry for longer periods of time, these oil/fat droplets gradually become smaller (Frahm 1994), disappearing rapidly in liverworts. In the *Dicranaceae* (Figure 19, Figure 35), however, they make take 8 years to completely disappear, slowly becoming smaller. In the leafy liverworts, the species that live in dry habitats manage to keep their oil bodies longer, making it possible to see them even in herbarium specimens.



Figure 25. *Dicranella hilariana*, a species that has oil/fat droplets. Photo by Piers Majestyk, with online permission.



Figure 26. *Chrysoblastella chilensis*, a species that produces oil/fat droplets. Photo by Tom Thekathyl, with permission.

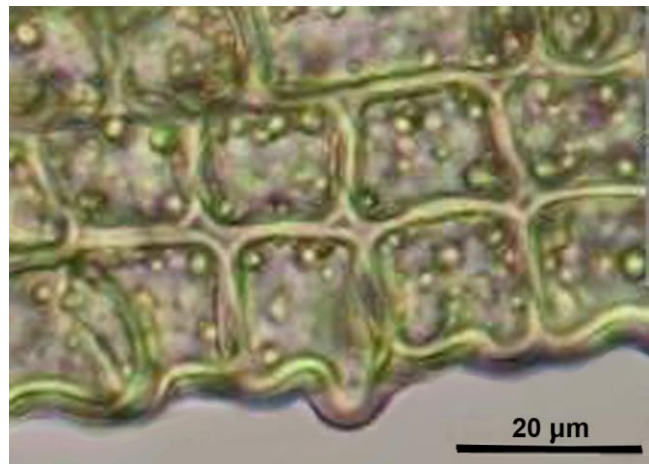


Figure 27. *Chrysoblastella chilensis* leaf margin cells showing oil/fat droplets. Photo by Tom Thekathyl, with permission.

Rod Seppelt (Bryonet 31 August 2013) observed that when cutting stems of some species of *Bryum* (Figure 28), vast quantities of lipids were released – perhaps the same



as those substances being interpreted as oil droplets in moss leaves. It appears that we need help from the biochemists to determine what these substances are. Then we need ecophysiologists to determine their use to the bryophytes and ultimate role in nutrient cycling.



Figure 28. *Bryum* stem cs, a genus in which lipid droplets may be released by the stem when it is cut. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

### External Storage

Bryophytes do not need to store nutrients internally to have an impact on the ecosystem. Their ability to simply trap dust and retain it within the mat can be useful to some taxa while depriving others. Trapped soil and retained nutrients are apparently essential for some epiphytic taxa, especially in the tropics (Pocs 1982). This role has already been reported for orchids in Madagascar, where the moss *Leucoloma* (Figure 29) provides both the substrate and the nutrient source for epiphytic orchids (La Farge 2002).



Figure 29. *Leucoloma triforme* on bark, a moss genus that helps to support epiphytic orchids. Photo by Michael Lüth, with permission.

Rooting in epiphytic mosses is now known for trees! The koa tree (*Acacia koa*) in Hawaii produces nodules containing the N-fixing *Bradyrhizobium* (Figure 30) on adventitious roots (those arising above ground), but much larger and more abundantly, in the mosses growing in lofty places on the same tree (Figure 33-Figure 33; Leary *et al.*

2004)! These mossy habitats trap organic soils largely derived from decomposing heartwood and leaf litter of the host tree and contain significantly higher concentrations of exchangeable cations, total N, and significantly lower Al than the terrestrial soils. Is it the nutrients, the reduced Al, the moisture-holding capacity of the moss, or some moss exudate that stimulates these large nodules? Most likely it is the combination.



Figure 30. *Bradyrhizobium* nodule showing bacteria imbedded in the nodule tissue. Photo by Louisa Howard, through public domain.



Figure 31. Koa tree (*Acacia koa*) showing location of moss and nodules (arrow). Photo courtesy of James Leary.



Figure 32. Koa tree (*Acacia koa*) showing location of nodules with moss. Photo courtesy of James Leary.





Figure 33. Koa tree (*Acacia koa*) nodules among mosses. Photo courtesy of James Leary.

### Bryophytes as Nutrient Sinks

Storage of nutrients in older parts or placing them in structural compounds can result in **nutrient sinks**. These serve as reservoirs that accumulate and store a nutrient; these sinks may result from continually transporting nutrients to new tissues, storing them in older tissues (Figure 34), or binding them in incalcitrant compounds. In any case, the sink makes the nutrient unavailable to other components of the ecosystem.



Figure 34. *Dicranum elongatum* showing brown senescent tissues where insoluble nutrients may remain for many years. Photo by Michael Lüth, with permission.

By trapping nutrients from the throughfall before they ever reach the soil, bryophytes serve as nutrient filters. This leads us to ask their role in parcelling out nutrients to the soil. Do bryophytes serve as nutrient sinks, and if so, do they eventually return their nutrient store to the forest soil? It may be too early to make generalizations, but let us consider some examples.

First of all, we know that bryophytes store their nutrients in structural compounds as well as within localized positions within the leaf cells. For example, Bakken (1995) pointed out that in *Dicranum majus* (Figure 35) N is stored in proteins and in chlorophyll. These organic components may be maintained within the moss for a long time, particularly while it is still alive. We have already seen that bryophytes move nutrients from old to

young tissues, thus depriving the soil of these nutrients through the pathway of decay.



Figure 35. *Dicranum majus*, a species that stores nitrogen in proteins and chlorophyll. Photo by Michael Lüth, with permission.

In an old-growth Douglas fir forest (*Pseudotsuga menziesii*; Figure 36), where bryophytes occupied only 0.13% of the total forest biomass, they contributed 20% to the biomass and 95% to photosynthetic tissue of the forest floor (Binkley & Graham 1981). Their biomass contribution of 1075 kg ha<sup>-1</sup> was composed of 92% *Eurhynchium oregonum* (Figure 37) and 7% *Hylocomium splendens* (Figure 3). The canopy throughfall contributed 3 kg ha<sup>-1</sup> yr<sup>-1</sup> N. By adding the moss component, Binkley and Graham added 10% to the estimates of understory N uptake.



Figure 36. *Pseudotsuga menziesii* forest. photo by Dave Powell, through Creative Commons.



Figure 37. *Eurhynchium oregonum*. Photo by Matt Goff <[www.sitkanature.org](http://www.sitkanature.org)>, with permission.



In an Alaskan black spruce (*Picea mariana*; Figure 4) forest, *Sphagnum* (Figure 64-Figure 66), *Hylocomium splendens* (Figure 3), and *Pleurozium schreberi* (Figure 38) have a higher capacity to absorb phosphate than do the fine roots of *Picea mariana* beneath them (Chapin *et al.* 1987). In boreal ecosystems, mosses can take up to three times as much N, P, and Mg as can *Picea mariana* (black spruce) (Figure 40; Oechel & van Cleve 1986) and add 5% to  $\text{Ca}^{++}$  and  $\text{K}^{+}$  uptake (Binkley & Graham 1981). Oechel and van Cleve (1986) contend that mosses have a major impact on both nutrient availability and soil temperature, competing with the trees and shrubs for available nutrients. But the question that remains is whether the mosses ultimately return them to the forest soil, thus serving as temporary sinks that release the nutrients when the mosses are dry and dormant. Since many bryophytes are dormant in the summer when the trees are growing, they may serve as reservoirs, providing nutrients at the most crucial time in the fall when the soil is depleted and rains return to leach the nutrients from the bryophytes. On the other hand, it appears that *Polytrichum*, perhaps through use of rhizoids for nutrient uptake, must compete with the fine roots near the surface and thus had the lowest P absorption rate of the four mosses studied in the spruce forest (Chapin *et al.* 1987). *Polytrichum commune* (Figure 39) exhibits translocation of nutrients to younger segments and ramets.



Figure 38. *Pleurozium schreberi*, a feather moss. Photo by Michael Lüth, with permission.



Figure 39. *Polytrichum commune* clone. Photo by Michael Lüth, with permission.

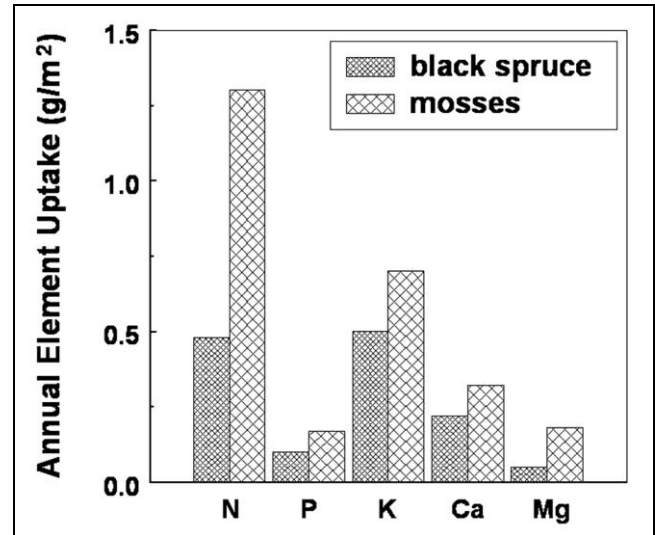


Figure 40. Comparison of annual nutrient uptake by mosses and black spruce trees (*Picea mariana*). Figure based on Oechel & van Cleve 1986, in Glime 2001.

In a different northern black spruce forest in Canada, feather mosses, primarily *Pleurozium schreberi* (Figure 38), sequestered 23-53% of the nutrient uptake estimated for their associated trees (Weetman & Timmer 1967). They prevented nutrient return to the tree roots by retaining those nutrients that reached the mosses as throughfall from canopy leachates. However, despite their sequestering of throughfall nutrients, Weetman and Timmer considered that the mosses were the major source of N for the trees because the mosses were able to accumulate nutrients on the shallow soils of these rocky sites. Weetman (1968) supported this hypothesis by demonstrating that there is a greater concentration of black spruce roots under the moss patches than elsewhere.

Weber and van Cleve (1984) demonstrated that feather mosses, primarily *Hylocomium splendens* (Figure 3) and *Pleurozium schreberi* (Figure 38), in the Alaskan black spruce (*Picea mariana*, Figure 4) forest can retain much of the N that enters the system and release it very slowly to the underlying organic layers, *i.e.* the root zone. But the return is very slow indeed. They found that the deeper layers of soil had incorporated little of the labelled N even three years later. It appears that N storage may work differently from that of other nutrients. In the two most common feather mosses, *Pleurozium schreberi* and *Hylocomium splendens*, 90% of the labelled N could still be recovered in the mosses 28 months after application (Weber & van Cleve 1981). One reason for such a high retention is that these species are able to move their N from older, senescing branches, to young ones (Eckstein & Karlsson 1999); 50% of the labelled N was missing from older branches, all of which could be accounted for in the younger branches.

Behaving in a manner similar to tracheophytes, *Hylocomium splendens* (Figure 3) in a dry pine forest in Latvia was able to move  $\text{Mg}^{++}$ , but not  $\text{Ca}^{++}$ , from brown and decaying segments toward the tips in autumn when it was dry (Brümelis *et al.* 2000). However, both elements were tightly held in green portions with no evidence of return to the environment through leaching. Such sequestering of N, Mg, and Ca would create a sink where



throughfall nutrients might not reach the forest floor for years or even decades, rather than days or weeks. Oechel and van Cleve (1986) suggest that in Alaska bryophytes have such great ability to immobilize nutrients that they can reduce tracheophyte productivity as succession proceeds from deciduous to coniferous woodland.

After 13 years of primary succession in a New Hampshire, USA, **sand pit** that had previously been a mature hemlock-maple-yellow birch forest (*Tsuga canadensis*-*Acer saccharum*-*Betula alleghaniensis*), there was a  $10.1 \pm 1.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$  N accumulation in 50-60 cm of soil beneath *Polytrichum* spp. (Figure 39) (Bowden 1991). The N content in the 50 cm of soil beneath the *Polytrichum* had increased from  $98 \pm 7 \text{ kg ha}^{-1}$  in 1969 to  $229 \pm 26 \text{ kg ha}^{-1}$  in 1982. Bowden reasoned that since the accumulation rate of N was probably much lower during early years in succession, it is likely that the accumulation rate later in succession was even higher than this. Surprisingly, the N content of living biomass of moss below ground was higher than that of above ground portions, with the soil portion accounting for ~55%. Presence of the moss seems to have accounted for a significant trapping and retention of N in the ecosystem, perhaps preparing the environment for success of larger and more N-demanding plants.

In the **chalk grassland**, bryophytes are able to absorb nutrients from the senescing autumn leaves. These nutrients would probably otherwise be leached from the system while the tracheophytes are inactive for the duration of winter (van Tooren *et al.* 1988). These leachates, incorporated into the bryophytes, are then released in the spring and summer from the decomposing bryophytes and used by the high-demand tracheophytes. Furthermore, bryophytes can act as sponges for the N in acid rain during winter when tracheophytes are unable to absorb it. We should expect that bryophytes in many temperate forests likewise are able to act as nutrient reservoirs, storing nutrients and releasing them in the hot, dry summer when availability is low due to tracheophyte demands.

In the **temperate forest**, bryophytes may be rare or abundant. In those forests where they are abundant, they could likewise play the role of a nutrient reservoir. However, the *Pseudoscleropodium purum* (Figure 41) in European **oak forests** demonstrates a different dynamic from that of the bryophytes in the boreal forest. Bates (1989b) found that the levels of cations within the moss component under an oak (*Quercus*; Figure 42) canopy were in dynamic equilibrium with the precipitation and/or throughfall (Bates 1989b; Brown & Bates 1990).



Figure 41. *Pseudoscleropodium purum*. Photo by Michael Lüth, with permission.



Figure 42. European oak (*Quercus*) forest understory habitat. Photo through Creative Commons.

The dominant and invasive moss *Pseudoscleropodium purum* (Figure 41) readily absorbed the natural leachates of  $\text{K}^+$ ,  $\text{Ca}^{++}$ , and  $\text{Mg}^{++}$ , particularly as the tree leaves were senescing in autumn (Bates 1989a, b). When sprayed with dilute solutions containing  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and  $\text{Mg}^{++}$ , this moss absorbed most of the cations, but those that were not absorbed were released back to the ecosystem through the remaining growing season (Bates 1989a). The bulk of these were released during the next 10-15 days. Bates tracked P and K in *P. purum* for 74 days after application and found that only 6.3% of the P and 12.1% of the K were recovered in the moss throughfall, reaching the soil. But only 31% and 23%, respectively, remained in the moss tissues. Bates (1989a) suggested that the missing nutrients may have been incorporated by microorganisms or retained in litter. A likely consequence of this is rapid recycling of nutrients within the ecosystem.

Ecologists have theorized that bryophytes may behave like a slow-release fertilizer. They remove nutrients from the precipitation as it passes through them, then slowly release it during the succeeding weeks. This may be facilitated by the damage caused to membranes during drying. In other cases, cations bound to exchange sites may be released back to the ecosystem instead of being absorbed. This slow release mechanism can be beneficial to the ecosystem by reducing loss through leaching and providing a steady supply of nutrients as they are being removed by the roots. But there seem to be no data thus far to support or refute this hypothesis on a broad scale.

Just as in tracheophytes, we cannot generalize about bryophyte nutrient behavior because bryophytes exhibit differences as vast as those of tracheophytes, perhaps even more so. *Hylocomium splendens* (Figure 3), likewise a large moss, growing on a lime-contaminated site, did not release its excess  $\text{Ca}^{++}$  and  $\text{Mg}^{++}$  when moved to an uncontaminated site (Brümelis *et al.* 2000). Hence, bryophytes can serve as sinks, depriving the soil of nutrients returned by throughfall and stemflow. Since bryophytes tend to grow best, at least in deciduous forests, at the bases of trees where stemflow provides a concentrated pool of nutrients from leaves, branches, and atmosphere, this bryophytic filter could have considerable impact on both the nutrients supplied to the trees and on the herbaceous ground cover in the vicinity. Their presence at tree bases seems to be due to the slight rise in topography that reduces leaf litter accumulation, but could it also be due to the added nutrients?



In a North Wales oak (*Quercus petraea*; Figure 43) woodland, the dominant bryophytes were *Dicranum majus* (Figure 35), *Rhytidiadelphus loreus* (Figure 44), *Plagiothecium undulatum* (Figure 45), *Polytrichastrum formosum* (Figure 46), and *Thuidium tamariscinum* (Figure 47), occupying 90% of the ground vegetation standing crop (Rieley *et al.* 1979). These species were investigated to determine the effects of moss harvesting on the ecosystem. This moss layer readily absorbed the  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and N leached from the canopy (Table 1). It is interesting that *Rhytidiadelphus* removed  $\text{NO}_3^-$  whereas *P. formosum* removed  $\text{NH}_4^+$ . However,  $\text{Mg}^{++}$  suffered a net loss from the bryophyte layer to the soil. *Rhytidiadelphus loreus* actually returned more  $\text{Mg}^{++}$  to the soil than it intercepted, but removed  $\text{Ca}^{++}$  and  $\text{K}^+$ , perhaps exchanging some of these for  $\text{Mg}^{++}$  on exchange sites.



Figure 43. *Quercus petraea* forest. Photo by Rosser, through Creative Commons.



Figure 44. *Rhytidiadelphus loreus*, a species that easily absorbs  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and N leached from the forest canopy leaves. Photo by Michael Lüth, with permission.

*Polytrichastrum formosum* (Figure 46) seemed to have little effect on nutrient concentrations, with leachates from the moss equalling those in the canopy throughfall for  $\text{Ca}^{++}$ ,  $\text{K}^+$ ,  $\text{Mg}^{++}$ , and  $\text{Na}^+$  (Rieley *et al.* 1979). In any case, a large portion of these nutrients were returned to a pathway that would make them available to the root zone. This suggests once more the role of bryophytes as a reservoir for at least some nutrients, providing a slower

release than that of episodic throughfall, a role also supported in the Black Forest (Weetman 1968). Clearly, we need to understand the differences in nutrient retention among species and what causes those differences to be there.



Figure 45. *Plagiothecium undulatum*, a species that easily absorbs  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and N leached from the forest canopy leaves. Photo by Michael Lüth, with permission.



Figure 46. *Polytrichastrum formosum* with capsules, a species that easily absorbs  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and N leached from the canopy. Photo by Michael Lüth, with permission.



Figure 47. *Thuidium tamariscinum*, a species that easily absorbs  $\text{Ca}^{++}$ ,  $\text{K}^+$ , and N leached from the canopy. Photo by Brian Eversham, with permission.



Table 1. Bryophyte-related behavior of essential nutrients in a Welsh oakwood, in  $\text{mg m}^{-2} \text{yr}^{-1}$ , based on data from Rieley *et al.* 1979 in Longton 1984.

	Ca <sup>++</sup>	Mg <sup>++</sup>	K <sup>+</sup>
Total input to bryophyte layer	3100	1810	2920
Bryophyte accumulation	410	390	1430
Excess input over bryophyte accumulation	2690	1420	1490

Weetman (1968) suggests that mosses may actually supply tree roots more directly. When he found that roots in a **black spruce forest** (Figure 4) were concentrated in decomposing mosses, he considered that mosses might serve as a collecting point for elements, especially N, absorbed by mosses from throughfall. Whether N was obtained from throughfall, soil, or airborne dust for *Hylocomium splendens* (Figure 3), a reservoir that is not easily leached and carried away by rainfall could be an asset to these N-poor forests (Tamm 1953). However, Berg (1984) provides conflicting information that suggests that N may be bound in phenolic compounds in the cell wall and essentially unavailable, even in dead tissue.

Chapin and coworkers (1987) found that mosses account for 75% of the P accumulated annually above ground in an **Alaskan *Picea mariana*** (Figure 4) forest, while they account for only 17% of the P pool in aboveground vegetation. In fact, *Sphagnum subsecundum* (Figure 48-Figure 49), *Hylocomium splendens* (Figure 3), and *Pleurozium schreberi* (Figure 38) have a higher capacity to absorb phosphate than do the fine roots of the black spruce beneath them. Again we beg the question, do they serve as a reservoir for slow release of P, or do they keep recycling it within their own tissues, moving it to growing parts, and depriving the roots?

Even those mosses that release some of their nutrients during senescence may hold them for many years. *Hylocomium splendens* (Figure 3) is an abundant feather moss in the **boreal forests and northern taiga**. In a subarctic birch woods, this species retained N for 3-10 years, depending on which measure was used (Eckstein 2000). Using <sup>15</sup>N labelling, Eckstein found that the mean residence time (MRT) and annual nutrient production (ANP) for N were similar to values found in woody evergreen tracheophytes. These dominant feather mosses may retard the nutrient turnover in these forests first through their **acropetal** (base to apex) movement of nutrients and second by making unfavorable conditions in the forest floor. Eckstein suggested that such dominant taxa of bryophytes could act as ecosystem engineers to retard the nutrient turnover on the forest floor through production of acidic, nutrient-poor litter and depression of summer soil temperatures. These influences help to maintain a system more favorable for the mosses.

Longton (1992) contends that the humus contributed by moss may maintain soil fertility through chemical associations that retain the mineral ions and prevent loss through drainage. Some of these associations are of extraordinary duration. Dowding *et al.* (1981) determined that on Devon Island, Northwest Territories, Canada, 50% of the Ca in the **mesic tundra meadows** was bound in bryophytes with a decomposition time of 22 years.



Figure 48. *Sphagnum subsecundum*, a species that accumulates carbon in growing shoots and brown portions. Photo by Michael Lüth, with permission.



Figure 49. *Sphagnum subsecundum*. Photo by Michael Lüth, with permission.

One mechanism by which bryophytes can create long-term nutrient sinks is through incorporation into less soluble organic compounds. N can be bound to phenolic compounds in the cell wall or retained in proteins bound by tannic acid compounds in the cell (Berg 1984). Furthermore, cation exchange sites can strongly bind divalent positive ions, rendering these ions unavailable to other ecosystem components, thus making the bryophytes effective competitors, much as they are in bogs and fens.

**Soil and rock type** also play a role in nutrient retention by bryophytes. For example, Simon and Szerényi (1985) demonstrated that the level of  $\text{NH}_4^+$  and  $\text{NO}_2^-$ -N in soil under mosses increases from xerophytic to mesophytic species.  $\text{CaCO}_3$  and pH seem to play a role in these differences, but nothing mechanistic can be inferred yet.

Even the **epiphytes** can make perceptible differences in nutrient cycling by intercepting and absorbing throughfall and stemflow nutrients, as demonstrated for Amazonian epiphytes (Herrera *et al.* 1978). But it appears they can also acquire nutrients that are in the vascular tissue of the main trunk! When <sup>137</sup>Cs was introduced into the stems of *Liriodendron*, 60% appeared in those bryophytes and lichens on the tree trunk and only 27% in soil bryophytes, with another 9% in bryophytes at the base of the tree (Hoffman 1972).



### Luxury Nutrients

Most plants have the ability to store nutrients and use them later, at least to some degree. Tracheophytes transport the soluble nutrients from older, lower leaves to upper, growing ones, often leaving the older leaves chlorotic and eventually dying. Algae store luxury nutrients, using them later as supplies in the ecosystem dwindle, perhaps permitting them to accomplish a sexual phase that permits them to become dormant until better nutrient conditions prevail. Brown and Bates (1990), in investigating the moss *Pseudoscleropodium purum* (Figure 41), found luxury consumption and accumulation of some nutrient elements (K, Ca, and P) throughout the year, but other nutrients were retained poorly (Bates 1989b). However, they (Bates 1987; Brown & Bates 1990) found that *P. purum* had poor retention of these luxury nutrients, except for orthophosphate, with rapid transfer of the luxury elements to other parts of the nutrient cycle. Brown and Bates (1990) could find no evidence that these additional nutrient supplies could permanently enhance growth. It would seem that mosses are able to discriminate to a certain extent, maintaining required metabolic levels of N, P, and K, while excluding or excessively storing the ones that normally occur as trace amounts.

Brown (1982) also interpreted the work of Thomas (1970) on light intensity and nutrient concentrations in the moss plant to indicate luxury consumption of N and P. Thomas had found that concentrations of N and P in *Mnium hornum* (Figure 50) were negatively correlated with light intensity, whereas growth was positively correlated with intensity. This suggested to Brown that the faster-growing mosses in the light had sufficient nutrients and that therefore the higher concentrations in the slower-growing plants in lower light were luxury nutrients. Earlier work by Weetman and Timmer (1967) on *Pleurozium schreberi* (Figure 38) tends to support Brown's interpretation. They found that as the light intensity under the forest canopy decreased from 38% to 17% of full sunlight the nutrient concentration increased in the moss without any significant changes in total nutrient uptake. But one could also interpret the decreased concentrations in high light intensity to mean that the moss was using up its nutrient supply and moving nutrients from older tissues to actively dividing cells, consequently lowering the overall concentrations.



Figure 50. *Mnium hornum*, a species in which concentrations of N and P are negatively correlated with light intensity. Photo by Michael Lüth, with permission.

These additional nutrient supplies are not permanently retained within the new growth, but rather stored throughout the plant, as in tracheophytes. Li and Vitt (1997) reported preliminary results using  $^{15}\text{N}$  that indicate mosses may be a major sink for applied N in peatlands, implicating luxury storage.

Martínez Abaigar and coworkers (2002) found that increased levels of  $\text{KH}_2\text{PO}_4$  caused the leafy aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 51) to accumulate significantly more P and K in its tissues. However, as exposure continued, the K concentrations fluctuated whereas P concentrations continued to increase. Concentrations of  $20 \text{ mg L}^{-1} \text{PO}_4^{3-}$  seemed to saturate the liverwort at 0.53% dry biomass (DM). When tissue P concentration exceeded 0.45% DM, the net photosynthesis declined, suggesting toxicity. P enrichment did not affect the chlorophyll concentration, but the chlorophyll *a:b* ratio did decline, as did the ratio of chlorophyll to **phaeopigments** (non-photosynthetic pigments which are degradation products of chlorophyll pigments), likewise suggesting P toxicity.



Figure 51. *Jungermannia exsertifolia* subsp. *cordifolia*, a species that accumulates more P and K when treated with  $\text{KH}_2\text{PO}_4$ . Photo by Des Callaghan, with permission.

Although bryophytes need only minute quantities of heavy metals, the ability to store metals in vesicles or bind them to the cell walls (abilities seemingly missing in tracheophyte leaves) permits bryophytes to store excessive amounts. Under the insult of atmospheric trace metal deposition, *Hylocomium splendens* (Figure 3) accumulated 14-24% more Cu, Fe, Pb, Ni, and V than did *Pleurozium schreberi* (Figure 38), but both mosses maintained similar concentrations of Cd, Mn, Zn, and Cr (Ross 1990), showing an inability to regulate those non-limiting ions. Nevertheless, it appears that bryophytes would accumulate most heavy metals, bound in vesicles or other locations, and release them to the cell if needed. At the very least, they could accumulate a heavy load in the cell walls. Burton (1979) found that *Fontinalis antipyretica* (Figure 52-Figure 53) maintained 80-90% of its accumulated Zn in the cell walls.





Figure 52. *Fontinalis antipyretica* showing its growth habit in a stream. Photo by Janice Glime.

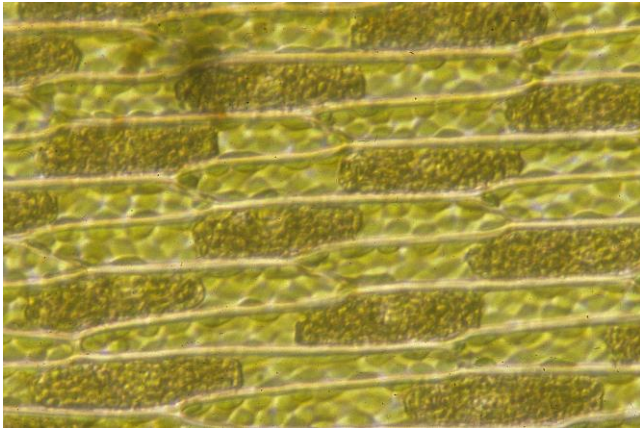


Figure 53. *Fontinalis antipyretica* showing cell walls, where 80-90% of its uptake of zinc is stored. Photo by Janice Glime.

### Carbon Sinks

In addition to the storage of mineral nutrients, bryophytes form carbon sinks. Storage of C as photosynthate, predictably, can be found in leaves, but labelled C soon accumulates in other places as well (Skré *et al.* 1983). In particular, in four boreal forest mosses [*Polytrichum commune* (Figure 2), *Hylocomium splendens* (Figure 3), *Pleurozium schreberi* (Figure 38), and *Sphagnum subsecundum* (Figure 48-Figure 49)] carbon accumulated in the growing shoot tips and in the senescent brown tissues. Large amounts were lost to respiration during the peak summer growing season.

### The Vernal Dam

The **vernal dam hypothesis** predicts that spring herbs sequester nutrients during the spring when they have maximum growth, thus serving as sinks that retain nutrients that might otherwise be lost during runoff (Tessier & Raynal 2003). In their original hypothesis, Muller and Bormann (1976) considered the forest floor herbs to be sinks that would store nutrients in the spring when the trees were still dormant, then release these in the summer when the herbs were dormant and the trees were active (Rothstein 2000). Although this theory has been widely accepted, its basic assumptions have never been tested: 1. nutrients would otherwise be lost from the system in the spring; 2. forest floor herbs release nutrients to the system in the spring. In their study of a northern hardwood forest in the

Catskill Mountains, New York, USA, Tessier and Raynal (2003) found that evergreen, wintergreen, and deciduous plant species do indeed sequester nutrients during the spring. Soil microbes, on the other hand, seem to remain the same or decrease in their nutrient content during that same period. In forests, a burst of growth occurs in the spring, and nutrient sequestering can occur among spring herbs near the surface while trees are tapping nutrients at lower depths. The high sunlight available while the trees are still barren of leaves permits numerous spring herbs to grow and bloom, slowly resorbing their nutrients to underground organs during the remainder of the year. But do these nutrients ever get released? And would they have been lost otherwise?

Eickmeier and Schussler (1993) have traced the parameters affecting the activity of the spring herb, *Claytonia virginica* (Figure 54), in the forest. They found that shading reduced its biomass, while enhancing its tissue nutrient concentration. This resulted in both reduced specific leaf weight and RUBISCO activity. Fertilization with 192 kg ha<sup>-1</sup> total N, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O caused an increase in above ground vegetative biomass and increased tissue concentrations of N and P, but K concentrations were not affected. In conditions of high irradiance, RUBISCO activity increased, but it was unaffected under shaded conditions. Eickmeier and Schussler have interpreted these results to mean that *Claytonia virginica* is unable to acclimate to low irradiance and therefore depends on the brief period before leaf out to achieve its growth. Thus, it does indeed sequester nutrients that it could not obtain if it did not have this brief period of growth before leaf out. But does this support the vernal dam? It seems that it does. Under low light of summer, *C. virginica* lacks the capacity to store significant quantities of nutrients (Anderson & Eickmeier 1998). However, in brighter light, such as might be found before canopy leaf out, Anderson and Eickmeier (2000) found that *C. virginica* is able to increase the amount of N and P stored in its tissues when fertilized, and it lacks large storage organs such as those found in some spring ephemerals. Rather, it retains many nutrients in its above ground tissues and does indeed release them later in the summer rather than storing them.



Figure 54. *Claytonia virginica*, a species that takes advantage of the brief period before leaf out in spring to bloom, only releasing its nutrients later in summer and therefore creating a **vernal dam**. Photo by Janice Glime.

In sharp contrast, Rothstein (2000) found that the clonal forest herb *Allium tricoccum* (Figure 55) and other forest floor species in one northern hardwood forest did not



take up significant quantities of  $\text{NO}_3^-$  and that removal of the spring ephemerals did not affect the leaching rate of  $\text{NO}_3^-$ . In fact, many spring ephemerals resorb their nutrients and store them in underground parts (Anderson & Eickmeier 2000). Rather, Rothstein found that microorganisms took up eight times as much N as did the spring herbs. Furthermore, there was no decrease in summertime N mineralization when spring ephemerals had been removed, supporting the earlier study by Zak *et al.* (1990). Thus, in his study, Rothstein (2000) found that it was the microbes and forest floor litter that dominated the spring sink and created the vernal dam.



Figure 55. *Allium tricoccum*, a spring ephemeral that does not take up  $\text{NO}_3^-$ . Photo by Hardyplants, through public domain.

But what would occur if this litter were predominantly conifer litter supporting a forest floor that was covered with bryophytes? What is the behavior of bryophytes as the leaves fill the canopy and reduce their light? Certainly in northern ecosystems where the bryophytes are the dominant forest floor vegetation, this question is worthy of consideration. Patterson and Baber (1961) have found that many temperate mosses are dormant in late summer and autumn. Schwabe (1976) found that long days and elevated temperatures often induce dormancy, a phenomenon that can protect them against effects of desiccation during the summer.

Might shade-adapted bryophytes also experience a vernal dam? Light is most available in early spring, and with their  $\text{C}_3$  photosynthesis, the bryophytes are well adapted to the low temperatures following snow melt. The melting snow has provided a continuous supply of moisture, and at least some light penetrates the thin layer of lingering snow. Spring would also seem to be a season of nutrient pulse for the bryophytes with nutrients provided by the melting snow as well as through aerial cleansing by the spring rains. Summer, with few showers, may be a nutrient-poor period, although the rains that occur will surely bring a good nutrient supply from the leachates and dust accumulations of the forest canopy leaves. Summer light availability, coupled with the high temperatures, would logically seem like a period appropriate for dormancy of most bryophytes. But few studies have considered the role of sunflecks in enhancing bryophyte photosynthesis. With no stomata to open and direct contact with the atmosphere, bryophytes would seem to be even better suited than  $\text{C}_3$  tracheophytes at taking advantages of these brief pulses of light and processing the captured

energy while awaiting the next pulse. Such activity has been reported for tracheophytes and is discussed in the chapter on light.

This leaves us with the questions of when do the bryophytes need the most nutrients, when do they retain them best, and when might they release them, making them available to the soil below, and hence to the tracheophytes rooted beneath them. We can hypothesize that they would be most likely to release them when they are first wet after a period of drought, losing them before their membranes are repaired. But how long does that last, and how much is lost? Do their numerous exchange sites retain most ions, awaiting the time when the cell can once again bring them in through active transport? Is potassium preferentially lost because other ions compete for the exchange sites, making this very soluble low valence ion the most easily leached away from the plants? It appears that at least in some ecosystems bryophytes might indeed be vernal dams. The role of bryophytes in nutrient cycling is one of which we know very little.

### Release during Desiccation/Rehydration

Seasonal events are very much the product of the types of seasons of a given area and what differs among them. Temperature, which folks in the temperate zone seem to consider almost exclusively as a seasonal indicator, may not be the factor most important to the bryophyte nutrient regime. Rather, seasonal differences in precipitation and moisture availability may be the primary controlling factors. This seems to be the case with nutrient release in the feather moss *Hylocomium splendens* (Figure 3) in a subalpine spruce-fir forest (Wilson & Coxson 1999), a phenomenon known as **pulse release** because it accumulates (some) nutrients over time, then releases them suddenly. During rehydration, nutrients and C leaked from the desiccated cells is released from the cell surfaces in a pulse release to the throughfall from the mosses. Organic C release to the forest soil can reach up to  $1544 \text{ mg m}^{-2}$  under these conditions. Experiments comparing this release to that of an inert mulch layer indicated that 23-75% of that pulse release originated in the moss mats. Release of both C and K is increased when drying is rapid. Wilson and Coxson compared the mosses to capacitors, storing low concentrations of nutrients from dust and minor rainfall events, then releasing them in higher concentrations during high rainfall events. Such a release would put the nutrients into the soil when it was most usable to the tracheophyte plants through uptake of the abundant water.

Buck and Brown (1979) likewise found that seasonal releases were tied to dehydration-rehydration processes in *Fontinalis antipyretica* (Figure 53) and *Plagiomnium undulatum* (Figure 45). Both  $\text{K}^+$  and  $\text{Mg}^{++}$  were lost from dry cells, but clung to the extracellular exchange sites. Although  $\text{K}^+$  in these plants had much higher concentrations in the intercellular spaces than on the exchange sites, the quantities on the extracellular sites also rose during desiccation, accounting for the losses suffered following desiccation and the pulse release to the soil during rehydration. Scafione (unpubl data) found that a pulse of  $\text{K}^+$  is released from *Sphagnum russowii* (Figure 56) in the autumn at the time it is most beneficial for the tree roots in preparation for winter. In ecosystems where the bryophyte cover is typically significant it could play a



crucial role in the preparation of forest conifers for winter. This relationship might be of considerable importance for management of these forests to survive the occasional extreme winter.



Figure 56. *Sphagnum russowii*, a species that releases a nitrogen pulse in the autumn. Photo by Michael Lüth, with permission.

Bryophytes affect the decomposition rates on the forest floor. Decomposition rates under mosses were more rapid than those under lichens (Sedia & Ehrenfeld 2006), presumably due to higher moisture content.

### Canopy Releases

In the **montane forest of the tropics**, and probably elsewhere, epiphytic bryophytes accumulate considerable N, much of which is fixed from atmospheric N by microbes (Clark *et al.* 2005). The epiphytic bryophytes, along with the full epiphyte assemblage, retained 33-67% of the nitrogen that was deposited by cloud water and precipitation, with the equivalent of a 50% annual accumulation of the nitrogen in the atmosphere. The bryophytes convert the soluble, highly mobile inorganic forms to organic forms that are retained in the canopy community, potentially being released during dehydration/rehydration cycles.

Even the **cloud forest** canopy experiences pulse release of nutrients from the canopy bryophytic epiphytes (Coxson 1991). During episodes of drying and rewetting, nutrients are leached from the newly rehydrated bryophytes. This leaching is greatest for the ions that normally reside in the intracellular pools. Coxson found that effluxes from stem segments of bryophytes from the Guadeloupe tropical montane rainforest could reach 80.1 kg ha<sup>-1</sup> yr<sup>-1</sup> for K, 1.4 kg ha<sup>-1</sup> yr<sup>-1</sup> for P, and 11.8 kg ha<sup>-1</sup> yr<sup>-1</sup> for N, although efflux rates from intact bryophyte mats were considerably smaller: 28.7 kg ha<sup>-1</sup> yr<sup>-1</sup> for K and 0.2 kg ha<sup>-1</sup> yr<sup>-1</sup> for P. Coxson surmised that the lower rate in the field reflected recycling of the leached nutrients within the moss mat. Nevertheless, the through flow loss provides a significant input to the forest floor below and to epiphylls on the leaves below them.

Coxson *et al.* (1992) estimated that more than 30% of the days cause these epiphytes to experience severe desiccation. These wet-dry cycles cause the canopy bryophytes to accumulate 950 kg ha<sup>-1</sup> of sugars and polyols. These sugars are then released in pulse form during rewetting episodes and subsequently translocated by through flow precipitation within the canopy. But the upper canopy leafy liverwort *Frullania atrata* accumulates

sugars and polyols equivalent to 17% of its dry weight, whereas the lower canopy moss *Phyllogonium fulgens* (Figure 57) accumulates less than 6%. Wet-dry cycles cause the release of fructose, mannitol, glucose, erythritol, glycerol, and sucrose into the throughfall. Despite the smaller storage levels of the lower canopy moss, bryophytes at that level released more (0.9 g m<sup>-2</sup>) compared to the upper canopy bryophytes (0.3 g m<sup>-2</sup>). Coxson and coworkers concluded that this release of carbon sources has a significant impact on nutrient cycling by providing suitable carbon for the microbes that carry out decomposition and non-symbiotic nitrogen fixation in these forests.



Figure 57. *Phyllogonium fulgens*, a lower canopy species in the Neotropics that accumulates less sugars and polyols than bryophytes in the upper canopy. Photo by Michael Lüth, with permission.

Hölscher *et al.* (2003) compared nutrient fluxes in three successional stages in an **upper montane rainforest** of Costa Rica. All three sites had *Quercus copeyensis* (Figure 58) as a dominant species, with various other species mixed in. The epiphyte litterfall of bryophytes and lichens differed greatly, with the highest values in the old-growth forest, which likewise had the greatest epiphyte abundance. Nevertheless, total nutrient throughfall and stemflow differed little among the three successional stages. Potassium in stemflow was only 5% in the old-growth forest, whereas it was 17% in the early successional forest and 26% in the secondary forest. Hence, in old-growth canopies the bryophytes retained the most potassium, releasing it almost entirely in throughfall.

In a **montane moist evergreen broad-leaved forest** in Yunnan, China, moss litter (including *Homaliodendron scalpellifolium* (Figure 59), *Symphiodon perrottetii*, *Herberta longifoliosa* (= *Herbertus longifolius* or *H. longifissus*?), and *Bazzania tridens* (Figure 60) had the slowest decay rate (0.22) compared to canopy tree leaf litter and bamboo (Liu *et al.* 2000). Bryophyte decomposition rates were less correlated with nutrient composition and lignin concentration in their initial mass



than were the tracheophyte rates (trees 0.55, bamboo 0.4). Whereas the turnover time for tree leaves was 1.5-2.50 years, it was 4.55 for the bryophytes.



Figure 58. *Quercus copeyensis*, where old-growth forests experience the highest levels of bryophytic epiphyte litterfall. Photo by Heliconius, through Creative Commons.



Figure 59. *Homaliodendron scalpellifolium*, one of the species that have the slowest decay rates (0.22) compared to canopy tree leaf litter and bamboo. Photo from Taiwan Liverworts color illustrations, through Creative Commons.



Figure 60. *Bazzania tridens*, one of the species that have the slowest decay rates (0.22) compared to canopy tree leaf litter and bamboo. Photo by Li Zhang, with permission.

## Bogs and Fens

In **black spruce** (*Picea mariana*; Figure 4) stands, bryophytes are the major source of N for the trees (Weetman & Timmer 1967). But the cation exchange ability of *Sphagnum* (Figure 64-Figure 66) continues even after *Sphagnum* dies, making nutrient release by dead plants slow, at least in forested peatlands (Brock & Bregman 1989), while competition for nutrients continues by means of exchange on the newly exposed walls of dead cells. Exacerbating this problem is the slow rate of organic mass loss during decomposition, as is known for *Sphagnum recurvum* (Figure 61), although the release of N, P, and K was larger than that of organic matter (Brock & Bregman 1989). But even after 12 months of decay, a large proportion of the original N and P remained associated with the peat. This slow decomposition process is supported by the poor colonization by organisms and almost total absence of damage to the dead cells.



Figure 61. *Sphagnum recurvum*, a species with slow decomposition. Photo from Biopix, through Creative Commons

The same cation exchange ability that permits *Sphagnum* (Figure 64-Figure 66) to compete with trees for nutrients can also aid competition by facilitating toxicity to the root zone (Klinger 1988). The peat mosses can trap heavy metals in the root zone, making them more toxic due to the acid conditions; they can create anaerobic conditions in the rooting zone; and their chelation of cations can accelerate iron hardpan formation.

Despite our many studies on nutrients in peatlands, Bedford and coworkers, in a 1999 publication, state that the high variances in plant and soil N:P ratios of wetlands suggest it may be necessary to understand nutrient limitations at both the species and the community level before we can predict the effects of nutrient enrichment. If this need still exists for wetlands, it exists a hundred-fold for non-wetland bryophyte systems.

Bogs and fens are rapidly diminishing on our planet as development fills them in and at best puts a water hole somewhere else for wetland replacement. It is unlikely that any new wetland will become a bog or *Sphagnum* fen, and even if it does, it will be decades to centuries before there is even any evidence it will ever happen. Yet we continue to create conditions unfavorable for these diminishing habitats. Bergamini and Pauli (2001) have shown that fertilization of any sort is likely to destroy these fragile



systems that are not adapted for high nutrient input. In their study, after only 1.5 years, fertilized peatland plots contained 39% less bryophyte biomass on the N-fertilized plots and 53% less on the NPK-fertilized plots than the unfertilized controls. Likewise, bryophyte species diversity diminished. Competition for light by tracheophytes accounted for only part of the decline. Yet, in this ecosystem bryophytes play a crucial role in nutrient cycling and availability, both directly (Rieley *et al.* 1979) and indirectly, through their water-holding capacity (Mägdefrau & Wurtz 1951) and their ability to control water content of the uppermost soil layers (van Tooren *et al.* 1985).

Scheffer *et al.* (2001) compared decomposition rates in a *Sphagnum*-dominated (Figure 62) and a non-*Sphagnum* (Figure 63) fen. In both habitats, the sedge (*Carex*) litter had the highest decomposition rate compared to that of *Sphagnum papillosum* (Figure 64) and *S. squarrosum* (Figure 65-Figure 66). But in the *Sphagnum* site, all litter types exhibited net mineralization, whereas in the sedge-dominated site, there was net immobilization. The researchers postulated that nutrient availability and adaptation of the microbial communities might account for the decompositional differences in the two sites.



Figure 62. Boreal forest fen with *Sphagnum fuscum*. Photo by Richard Caners, with permission.



Figure 63. Intermediate non-*Sphagnum* fen. Photo by Janice Glime.



Figure 64. *Sphagnum papillosum*, a species with a much lower decomposition rate than that of sedges (*Carex*). Photo by Janice Glime.



Figure 65. *Sphagnum squarrosum* habitat. Photo by Janice Glime.



Figure 66. *Sphagnum squarrosum*, a species with a much lower decomposition rate than that of sedges (*Carex*) in a fen. Photo by Janice Glime.

Turetsky *et al.* (2008) found that moss species were more important than micro-environmental conditions in determining the early stages of decomposition in four peatland types in boreal Alberta, Canada. *Sphagnum* (Figure 64-Figure 66) species partitioned resources into metabolic and structural carbohydrates. Hummock species decomposed slowly, but the hummock microhabitat itself corresponded to a rapid decomposition rate. This is at least



partly due to the pore structure created by the mosses. The mosses form tissues that resist decomposition, suggesting that they may stabilize losses of carbon from peatlands as the climate warms.

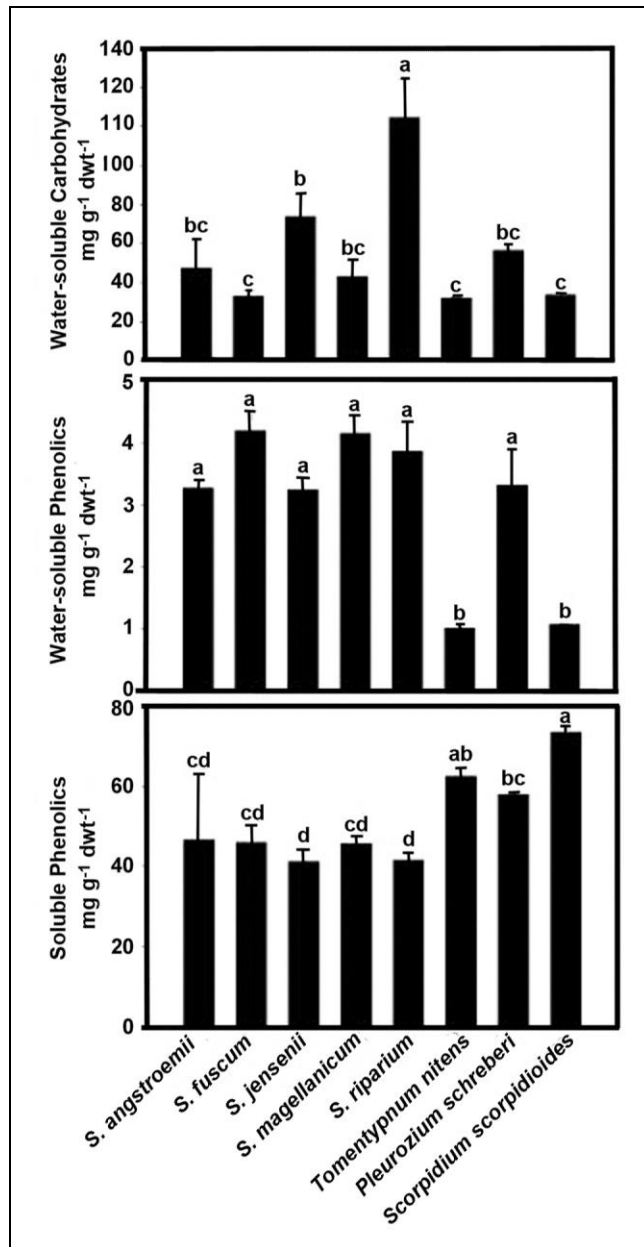


Figure 67. Concentrations of soluble components of moss litter (5 *Sphagnum* and 3 non-*Sphagnum*) collected from Canadian peatlands, including hot water-soluble carbohydrates, hot water-soluble phenolics, and soluble nonpolars (lipids). Data are means  $\pm$  one standard error. Same letter superscripts denote non-significant comparison of means (one-way ANOVA; species  $p < 0.05$ ). Redrawn from Turetsky 2003.

## pH Effects

Nutrient availability is limited by the ability of that nutrient to dissolve in water, reach the plant, then enter the plant. Most nutrients become more soluble at low pH and may be totally unavailable at higher pH levels. At the same time, toxic metals such as Al become more soluble at low pH and can harm the plants.

*Riccia discolor* has better growth in the range of pH 3-5 than at any other pH (Patidar & Kaul 1984). The restriction of various taxa of *Sphagnum* (Figure 64-Figure 66) to specific somewhat narrow pH ranges accounts in part for the successional pattern of bogs and fens. *Sphagnum* taxa that require lower pH ranges tend to occur higher on the hummock where the water level is unable to dilute the effects of cation exchange and its release of  $H^+$  ions.

The species that always surprises me is *Calliergonella cuspidata* (Figure 6). This species grows in the contrasting-moisture habitats of chalk grasslands and fens. There it grows best at a pH of 7.5 and 5 ppm  $Ca^{++}$ , whereas at pH of 6.0 growth stops even with 5 ppm or more of  $Ca^{++}$  (Streeter 1970). These pH differences most likely reflect the differences in uptake ability of  $Ca^{++}$  and other nutrients.

In rivers, taxa seem likewise to be limited by pH. The availability of free  $CO_2$  only at lower pH (Figure 68) levels severely limits productivity for mosses, whereas many, perhaps all, aquatic tracheophytes can utilize bicarbonates. Several attempts to demonstrate use of bicarbonates by aquatic bryophytes have failed, presenting a clear picture of  $CO_2$  limitation (Bain & Proctor 1980, Allen & Spence 1981). Field studies in streams have revealed that the leafy liverworts *Scapania undulata* (Figure 69) and *Nardia compressa* (Figure 70) occur mostly in the pH range of 5.2-5.8, whereas the moss *Fontinalis squamosa* (Figure 71) occurs mostly at 5.6-6.2 (Ormerod *et al.* 1987), suggesting that these bryophytes have somewhat different abilities to acquire  $CO_2$ . *Jungermannia vulcanicola* (Figure 72-Figure 73) survives the low pH of acid streams (1.9-4.7) in Japan (Satake & Miyasaka 1984; Yokouchi *et al.* 1984; Satake *et al.* 1990). *Leptodictyum* (Figure 74) can grow at a pH of 3.4 in organic lakes of Japan (Satake 1980). *Warnstorfia fluitans* (Figure 75) can live in acidic lakes with the low pH range of 3.4-3.8 (Satake 2000). In aquatic habitats, these pH differences affect the uptake of N forms and the ability to obtain  $CO_2$  for photosynthesis, as well as affecting toxicity of pollutants.

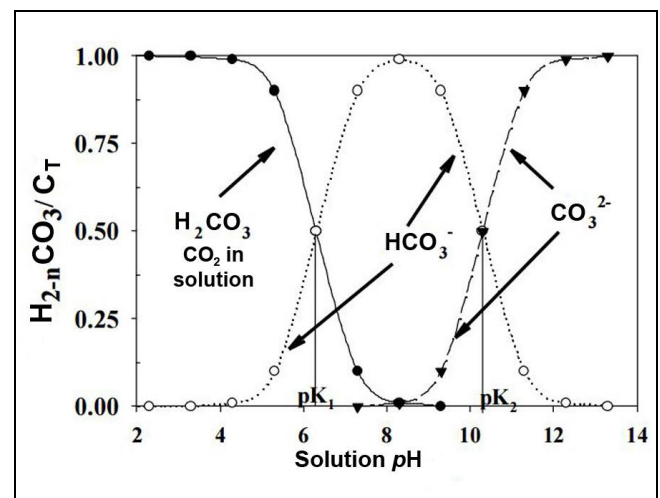


Figure 68. Distribution of carbonate species as a fraction of total dissolved carbonate in relation to solution pH. Note that  $H_2CO_3$  represents  $CO_2$  dissolved in water;  $HCO_3^-$  is bicarbonate, and  $CO_3^{2-}$  is carbonate. Modified from Soil Chemistry 5-1 < <http://lawr.ucdavis.edu/classes/ssc102/Section5.pdf> >.





Figure 69. *Scapania undulata*, a species with a preferred pH range of 5.2-5.8. Photo by Michael Lüth, with permission.



Figure 70. *Nardia compressa*, a species with a preferred pH range of 5.2-5.8. Photo by Michael Lüth, with permission.



Figure 71. *Fontinalis squamosa*, a species with a preferred pH range of 5.6-6.2. Photo by Michael Lüth, with permission.



Figure 72. *Jungermannia vulcanicola* acid stream habitat. Photo courtesy of Angela Ares.



Figure 73. *Jungermannia vulcanicola*, an acidophile that prefers a pH range of 1.9-4.7. Photo courtesy of Angela Ares.



Figure 74. *Leptodictyum riparium*, a species that can grow at a pH of 3.4 in organic lakes. Photo by Michael Lüth, with permission.





Figure 75. *Warnstorfia fluitans*, a species of acidic lakes with the low pH range of 3.4-3.8. Photo by Michael Lüth, with permission.

In an 18-year study of a **pine forest** stand in central Sweden, van Dobben and coworkers (1992) found that *Pohlia nutans* (Figure 76) experienced a 10-fold increase when acidified, whereas *Pleurozium schreberi* (Figure 38) almost disappeared.

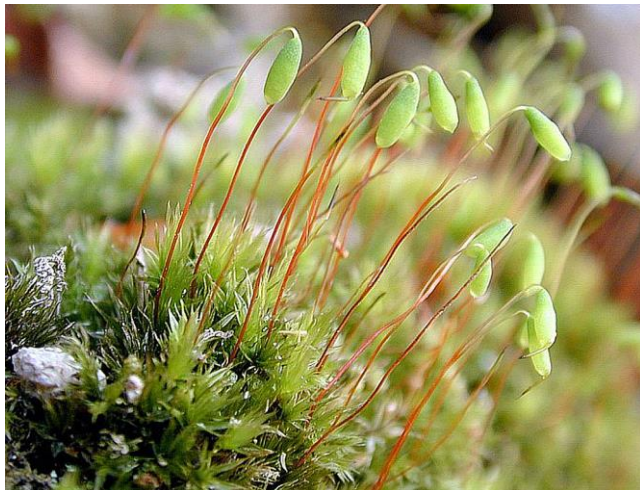


Figure 76. *Pohlia nutans*. Photo by Michael Lüth, with permission.

In **geothermal** areas, as we will discuss later, distribution by pH is pronounced, whether by competition leading to more narrow realized niches, or by real limitations imposed by the acidity, and perhaps the accompanying sulfur. The low pH, and in some cases high pH, can affect nutrient solubility and may make certain ions toxic or, in high pH, make them unavailable.

Although many mosses seem to survive at low pH levels, competition from tracheophytes and limited nutrients can severely limit their abundance. In a **grassland** experiment, Virtanen *et al.* (2000) found that virtually no mosses were present on plots with a soil pH of 3.3-4.5. Rather, bryophyte biomass and diversity increased with soil pH.

### Indicator Species

Despite the limited ability of bryophytes to use soil nutrients, soil characters can still limit their distribution,

making some of them suitable indicators. Some of this may be that they have greater ability to take up soil nutrients than we have imagined, perhaps through mycorrhizae, and some may result from airborne dust derived from the soil. For example, *Ceratodon purpureus* (Figure 77) is able to tolerate high N content (Dierssen 1973), although this widespread moss seems to be able to tolerate roadside gravel and rock ledges where one would expect N content to be low. On the other hand, *Aulacomnium palustre* (Figure 78), *Pleurozium schreberi* (Figure 38), *Pogonatum urnigerum* (Figure 79), and *Polytrichastrum alpinum* (Figure 80) indicate low N. Such mosses as *Funaria hygrometrica* (Figure 81), *Pohlia cruda* (Figure 82), and *Leptobryum pyriforme* (Figure 83) indicate good base saturation, whereas poor base saturation is indicated by good growths of *Psilopilum laevigatum* (Figure 84).



Figure 77. *Ceratodon purpureus* with capsules, a species with wide habitat tolerance that can tolerate high N levels. Photo by J. C. Schou, with permission.



Figure 78. *Aulacomnium palustre* with gemmae, a species that indicates low N. Photo by Janice Glime.





Figure 79. *Pogonatum urnigerum*, a species that indicates low N levels. Photo by Janice Glime.



Figure 80. *Polytrichastrum alpinum*, a species that indicates low N levels. Photo by Michael Lüth, with permission.



Figure 81. *Funaria hygrometrica*, a species that indicates good base saturation. Photo by Michael Lüth, with permission.



Figure 82. *Pohlia cruda* with capsules, a species that indicates good base saturation. Photo by Michael Lüth, with permission.



Figure 83. *Leptobryum pyriforme* with capsules, a species that indicates good base saturation. Photo by Michael Lüth, with permission.



Figure 84. *Psilopilum laevigatum* with capsules, an indicator of poor base saturation. Photo by Michael Lüth, with permission.

Use of mosses for prospecting was popular for a time during mining exploration, but their short penetration into the soil made them of limited value. Copper mosses – *Mielichhoferia* (Figure 85-Figure 86), *Dryptodon* (see Figure 87), *Scopelophila* (Figure 88-Figure 89) to be discussed in the Habitats volume – seem to be reliable indicators of the presence of copper (Persson 1948; Shacklette 1967), although it may actually be the sulfur



associated with the copper that encourages their growth (Hartman 1969). They are unknown in the copper-rich area of the Keweenaw Peninsula of Michigan, where the copper occurs as pure copper with no associated sulfur (pers. obs.). Nevertheless, their tolerance for the ore is higher than that of other mosses.



Figure 85. Habitat of *Mielichhoferia mielichhoferiana*, a copper moss. Photo by Michael Lüth, with permission.



Figure 86. *Mielichhoferia mielichhoferi*, a copper moss with calcium deposits on it. Photo by Michael Lüth, with permission.



Figure 87. *Dryptodon patens*; *Dryptodon atrata* is a copper moss. Photo by Michael Lüth, with permission.



Figure 88. *Scopelophila ligulata*, a copper moss in its habitat. Photo by Michael Lüth, with permission.



Figure 89. *Scopelophila ligulata*, a copper moss. Photo by Michael Lüth, with permission.

## Needed Research

In 1992, Bates summarized our needs for understanding the physiology of nutrient uptake, translocation, and loss in bryophytes. We have made considerable progress since that time, but we still are unable to make sweeping generalizations. To understand clearly the ecosystems in which bryophytes form a significant ground cover or a significant epiphytic element, we must understand the role of the bryophytes in nutrient uptake and sequestering. We still have little understanding of what makes the various species differ in their ability to subsist on low nutrients. We likewise lack understanding of the effects nutrient deficiencies or excess may have on the morphology of the species. And we are only beginning to understand how long nutrients might remain within the bryophyte before being returned to the ecosystem. We have learned that, contrary to the perception of tracheophyte ecologists, the bryophytes move essential nutrients from older tissues to younger ones, often being recalcitrant toward returning anything to the soil unless the whole plant dies. But we don't know how widespread this phenomenon is in the many ecosystems where bryophytes form a significant ecosystem component. We have barely realized that bryophytes obtain their nutrients from the soil as well as the rain, but we can add little to the hypothesis



put forth by Bates (1992) that rapidly growing species may depend on the substrate and slower growing species mostly on precipitation. The nutrient role of bryophytes in ecosystems has come of age – we know that it is significant, and now it demands our attention.

## Summary

Bryophytes can play a significant role in nutrient cycling in many kinds of ecosystems. Their ability to bind nutrients on their cell walls permits them to take these in when they become hydrated. They intercept atmospheric input and often hold it, preventing it from reaching the forest floor. In some locations, under conditions of wetting and drying, they can release nutrients during the first few minutes of rehydration when adhering inorganic and organic molecules dissolve in the throughfall. However, once their membranes are repaired, they tend to hold the nutrients on their surface exchange sites or within cells, or even between cells.

Nutrient concentration studies must be interpreted with caution due to the ability of bryophytes to hold dust readily on their surfaces. But even so, this is a role in the ecosystem that prevents this dust from reaching other plants or that releases it at some later point in time.

Mosses may have a limited capacity to retain **luxury nutrients** such as K, Ca, and P, but most of the essential macronutrients seem to be regulated to a relatively constant level. Heavy metals, on the other hand, tend to accumulate to high levels.

In boreal forests, feather mosses retain nutrients and move the soluble ones to young, growing tissues. Hence, nutrients may be bound within the mosses for decades. Nevertheless, spruce roots seem to flourish under the mosses, suggesting that mosses may accumulate nutrients that become available to the roots. *Polytrichum* seems to compete with the fine roots and therefore has a low absorption rate for P. For some reason, perhaps because the N is moved to underground portions, N is able to accumulate under *Polytrichum*.

In chalk grasslands, bryophytes trap and retain leachates from the autumn leaves, then release them in the summer when demand is highest for tracheophytes. Other nutrients, such as N, are retained in bryophytes as organic compounds that are bound in cell walls or retained in proteins. And the level of  $\text{NH}_4^+\text{-N}$  and of  $\text{NO}_2^-\text{-N}$  in soil under mosses increases from xerophytic to mesophytic species, but we don't know why.

At least some epiphytic mosses even seem to obtain nutrients from the vascular tissue of tree trunks. Epiphytic mosses in the tropics can provide a suitable habitat for legume nodule formation, for example *Bradyrhizobium* in the *Acacia koa* tree in Hawaii, providing a significant contribution to the overall N budget.

Seasonal behavior can, as in the case of *Sphagnum russowii*, release nutrients such as  $\text{K}^+$  in the autumn when the trees need it in preparation for winter. But some bryophytes hold to their nutrients tenaciously at exchange sites, again depriving the soil. *Sphagnum* in bogs and fens can be destroyed by nutrient enrichment,

but even dead plants can retain the nutrients already stored. These mosses can also trap heavy metals and retain them in the soils, making the root zone toxic for trees. Because of their movement of nutrients to young tissues and incorporation into incalcitrant compounds, bryophytes can serve as nutrient **sinks**.

Low pH makes nutrients more soluble, but some bryophytes cannot survive, in some cases due to competition from tracheophytes, but in others most likely because the pH change disrupts the normal balance of nutrient uptake. High pH levels, especially accompanied by high concentrations of  $\text{Ca}^{++}$ , can result in competition for exchange sites that are needed for nutrient uptake. In aquatic systems, high pH reduces the available  $\text{CO}_2$ , thus limiting photosynthesis. Some bryophytes serve as indicator species because of their ability to tolerate or not tolerate such conditions as high  $\text{Ca}^{++}$  or low pH.

Having learned how mosses gain, use, and lose nutrients, we must ask ourselves how these plants are able to subsist on such low concentrations of nutrients. In addition to their efficient absorption of nutrients in low concentrations, they benefit from their generally slow growth habit, thus greatly reducing their requirements per units of time and space.

Their ability to move nutrients from old to young tissues and to store them both externally and internally raises serious questions about their role in the nutrient cycling in the habitats where they are abundant.

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