

CHAPTER 8-7

NUTRIENT RELATIONS: FERTILIZATION

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CHAPTER 8-7

NUTRIENT RELATIONS: FERTILIZATION



Figure 1. *Gymnostomum aeruginosum* growing on calcareous rock. Photo by Michael Lüth, with permission.

Fertilization Effects

We often learn about things in science by serendipity. And when it comes to learning about bryophytes in ecosystems, we often learn by what we do to their neighboring tracheophytes. Hence, when we fertilize our gardens or add fertilizers to restore impoverished land, the bryophytes respond, in their own way, along with the intended tracheophytic plants.

In general, fertilizers are detrimental to bryophytes. This is often because added fertilizers benefit tracheophytes that were unable to grow well in their absence and once being fertilized are able to overgrow the slow-growing bryophytes (Virtanen 2000), depriving them of light. One effect of fertilizers is that they frequently change the pH, often making it more alkaline; this is especially true for lime fertilizers. Few bryophytes are favored by high pH levels (Figure 1), and at the very least, the species composition is likely to change (Miles 1968; Miles 1973). Moreover, lime often has a desiccating effect, like that of chalk dust on your hands. However, some specific nutrients may be limiting and certain fertilizers may actually benefit the bryophytes.

Surprisingly, bryophytes in a polar semi-desert at Svalbard Arctic archipelago increased their cover as a benefit from applications of N, P, and K (with little effect by increased temperature), while there was a significant decrease in the cover of the flowering plants *Dryas octopetala* (Figure 2) and *Saxifraga oppositifolia* (Figure 3) (Robinson *et al.* 1998). A strong winter injury seemed to account for the ultimate decrease in *Dryas octopetala*. On

the other hand, *Hylocomium splendens* (Figure 4) and *Rhytidium rugosum* (Figure 5) exhibited significant reductions in growth in a combined temperature and fertilizer enhancement experiment in a subArctic-alpine community in Sweden (Jägerbrand *et al.* 2003).



Figure 2. *Dryas octopetala*, an Arctic species that decreases cover when fertilized with N, P, and K. Photo by Jörg Hempel, through Creative Commons.



Figure 3. *Saxifraga oppositifolia*, an Arctic species that decreases cover when fertilized with N, P, and K. Photo by Smiley.toerist, through Creative Commons.



Figure 4. *Hylocomium splendens*, a species that experienced significant reductions in growth in a combined temperature and fertilizer enhancement experiment in a Swedish sub-alpine zone. Photo by Michael Lüth, with permission.



Figure 5. *Rhytidium rugosum*, a northern species adapted to low nutrients. Photo by Michael Lüth, with permission.

Changes in nutrient concentrations can affect the lipid content of bryophytes, thus affecting their ability to tolerate cold and desiccation. In the Arctic, growing shoots contain more lipids than carbohydrates (Rastorfer 1972). The lipid content of *Sphagnum fuscum* (Figure 6-Figure 7) increases

during spring in the actively growing parts while decreasing in the senescent parts (Karunen & Salin 1981). *Dicranum elongatum* (Figure 8) uses lipids as storage material in its senescent parts (Karunen & Mikola 1980; Karunen & Liljenberg 1981). The conversion to carbohydrates may lower the freezing point, but I have not seen evidence to support this suggestion.



Figure 6. *Sphagnum fuscum* showing its typical hummock growth. Photo by Michael Lüth, with permission.



Figure 7. *Sphagnum fuscum* showing older (lower) parts where lipids decrease in spring, while increasing in the upper, growing parts. Photo by J. C. Schou, with permission.



Figure 8. *Dicranum elongatum*, a moss that stores lipids in its senescent parts (lower). Photos by Michael Lüth, with permission.

Al-Hasan *et al.* (1991) found that the addition of $\text{Ca}(\text{NO}_3)_2$ caused a shift in lipid content in the mosses *Ctenidium molluscum* (Figure 12), *Dichodontium pellucidum* (Figure 10), *Pogonatum urnigerum* (Figure 11), and *Tortella tortuosa* (Figure 12), with total lipids decreasing steadily with increasing concentrations of $\text{Ca}(\text{NO}_3)_2$ in the culture medium. At the same time, the proportion of the predominant polyunsaturated fatty acids also decreased [arachidonic acid (20:4) in *C. molluscum*, eicosatrienic acid (20:3) in *P. urnigerum*, and linoleic (18:2) and linolenic (18:3) acids in *D. pellucidum* and *T. tortuosa*].



Figure 9. *Ctenidium molluscum*, a moss that shifts its lipid content with the addition of $\text{Ca}(\text{NO}_3)_2$. Photo by Michael Lüth, with permission.



Figure 10. *Dichodontium pellucidum*, a moss that shifts its lipid content with the addition of $\text{Ca}(\text{NO}_3)_2$. Photo by Michael Lüth, with permission.



Figure 11. *Pogonatum urnigerum*, a moss that shifts its lipid content with the addition of $\text{Ca}(\text{NO}_3)_2$. Photo by Michael Lüth, with permission.



Figure 12. *Tortella tortuosa*, a moss that shifts its lipid content with the addition of $\text{Ca}(\text{NO}_3)_2$. Photo by Michael Lüth, with permission. Photo by Michael Lüth, with permission.

Temperature also plays an important role in the storage of certain lipids and fatty acids. The content of triglycerides increases in *Dicranum elongatum* (Figure 8) plants photosynthesizing at low temperatures of 1-6°C (Karunen 1981).

N Additions

Because bryophytes receive much of their nutrient input directly from the atmosphere, their responses to added atmospheric inputs of such pollutants as NO_3^- and NH_4^+ can be rapid. If mosses are nutrient deficient, they should respond immediately and positively to these additions.

It appears that at least some bryophytes can use more N than they normally get. As noted in Chapter 8-6, *Fontinalis novae-angliae* (Figure 13) and *F. dalecarlica* (Figure 14) both became considerably darker green in response to higher N concentrations (Glime, unpubl.); *Dicranum majus* (Figure 15) likewise had its highest chlorophyll content from the highest N location (Bakken 1995).



Figure 13. *Fontinalis novae-angliae*, a species that attains a darker color in N concentrations much higher than their native streams. Photo by Janice Glime.



Figure 14. *Fontinalis dalecarlica*, a species that attains a darker color in N concentrations much higher than their native streams. Photo by J. C. Schou, with permission.



Figure 15. *Dicranum majus*, a species that increases its chlorophyll content in higher concentrations of N. Photo by Michael Lüth, with permission.

Muller (1997) compared N content of plants from a plot receiving low doses of NH_4NO_3 diluted in rainwater ($30 \text{ kg N ha}^{-1} \text{ year}^{-1}$) to plants from a control plot that received the same amount of rainwater without added N. The treatment simulated a tripling of the natural N deposition, while the added water represented only 7% of its annual precipitation. Although the N found in tracheophytes (0.7 mg N g^{-1}) in this study provided inconsistent results (Schleppi *et al.* 1999), the moss *Thuidium tamariscinum* (Figure 16) had a dry matter increase in N of 1.3 mg g^{-1} (7%) (Muller 1997). At the same time, treated *Hylocomium splendens* (Figure 4) tended to become brown (Muller 1997), while *Sphagnum nemoreum* (= *S. capillifolium*; Figure 17) seemed to have a reduction in photosynthetic pigments as a result of the added N (Schleppi *et al.* 1999). It appears that the mosses were harmed by the added N in this form, except for the greater storage of N in *Thuidium tamariscinum*. On the other hand, Heeschen and coworkers (1996) contended that N is a "critical nutrient" for bryophytes in raised bogs. But the form matters.



Figure 16. *Thuidium tamariscinum*, a moss that benefits from increased N input. Photo by Michael Lüth, with permission.

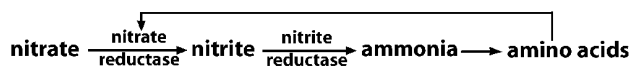


Figure 17. *Sphagnum nemoreum* (= *S. capillifolium*), a species that loses chlorophyll when N is added to its growing medium. Photo by Michael Lüth, with permission.

Li and Vitt (1997) in their experiments on nutrient applications in peatlands in Alberta, Canada, found that the added N increased the productivities of two dominant mosses, *Sphagnum fuscum* (Figure 6-Figure 7) in a bog and *Tomenthypnum nitens* (Figure 18) in a rich fen,

whereas the productivity of two dominant shrubs, *Rhododendron groenlandicum* (= *Ledum palustre* subsp. *groenlandicum*; Figure 19) in the bog and *Betula pumila* (Figure 20) in the rich fen, was unaffected. Furthermore, Nordin and Gunnarsson (2000), working with *Sphagnum fuscum*, *S. magellanicum* (Figure 21), and *S. rubellum* (Figure 22) from two mires in Sweden, found that addition of NH_4NO_3 actually caused decreased growth, but resulted in higher concentrations of amino acids in the tissues. When tissue amino acid concentrations exceeded 2 mg, growth in length decreased, suggesting the amino acids may have reached a toxicity level or that the feedback mechanism caused a toxic buildup of NH_4NO_3 .

Woodin *et al.* (1985) found that precipitation high in NO_3^- (as often found in acid rain) induces the nitrate reductase in *Sphagnum fuscum* (Figure 6-Figure 7). Eventually this causes a rise in ammonia, which in turn inhibits the nitrate reductase activity. Nitrate reductase is typically the limiting component in the conversion to amino acids, so it provides a control mechanism that attempts to moderate the concentration of NH_4^+ and amino acids in the plant:



But it is important to keep in mind several intervening factors. Bryophytes in bogs and poor fens typically have **Cyanobacteria** associated with them, and ammonium inhibits nitrate reductase, reducing the symbiotic N fixation by the **Cyanobacteria**. Furthermore, ammonium is more available in acid soils. (See Subchapter 8-3 for further discussion of these intervening factors.)



Figure 18. *Tomentypnum nitens*, a moss with increased productivity when N is added. Photo by Michael Lüth, with permission.



Figure 19. *Rhododendron groenlandicum*, a species that does not seem to respond to added N in a bog. Photo through Creative Commons.



Figure 20. *Betula pumila*, a species that does not seem to respond to added N in a bog. Photo through Creative Commons.



Figure 21. *Sphagnum magellanicum*, a species in which addition of NH_4NO_3 caused decreased growth but increased amino acids. Photo by Michael Lüth, with permission.



Figure 22. *Sphagnum rubellum*, a species in which addition of NH_4NO_3 caused decreased growth but increased amino acids. Photo by Michael Lüth, with permission.

As one might expect, what is good for one bryophyte may destroy another. Dirkse and Martakis (1992) found that in Swedish forests, fertilization with NH_4NO_3 elicited a positive response from *Lophocolea heterophylla* (Figure 24) while causing a "distinctly negative" response from *Ptilidium ciliare* (Figure 24). In another experiment with the aquatic *Sphagnum cuspidatum* (Figure 37), Paffen and Roelofs (1991) were unable to demonstrate any response to added NH_4^+ unless the CO_2 concentration was increased simultaneously. This suggests that it is the usable C source (CO_2) that is limiting in that habitat, not the N source.



Figure 23. *Lophocolea heterophylla*, a liverwort that responds positively to NH_4NO_3 . Photo by Michael Lüth, with permission.

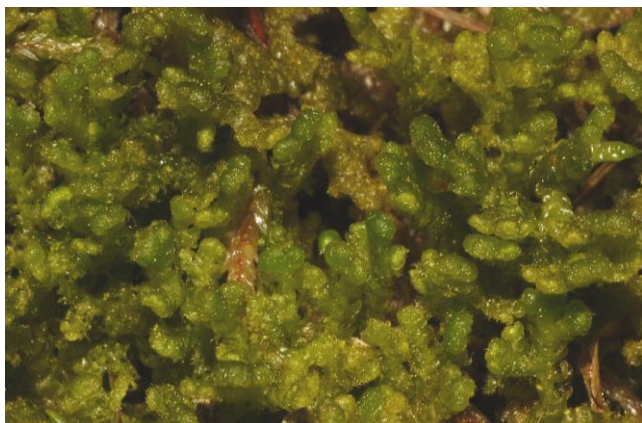


Figure 24. *Ptilidium ciliare*, a liverwort that responds negatively to the addition of NH_4NO_3 . Photo courtesy of Eric Schneider.

Nitrate reductase is formed only in the light in *Fontinalis antipyretica* (Figure 28) (Schwoerbel & Tillmanns 1974). If this is true in other bryophytes, it might explain why Fries (1945) was able to obtain only slight growth of *Leptobryum pyriforme* (Figure 25) and none in *Funaria hygrometrica* (Figure 26) when he cultured them on NO_3^- in the dark. In the light, on the other hand, *Funaria hygrometrica* and *Weissia controversa* (Figure 27) grew best on the NO_3^- source (Dietert 1979), but poorly even on a buffered NH_4^+ medium. And *Fontinalis antipyretica* grew best on NH_4^+ ions because of the suppression of nitrate reductase by NH_4^+ (Schwoerbel & Tillmanns 1974). Many bryophytes can reduce NO_3^- to NO_2^- in the dark, but light is required to stimulate conversion of NO_2^- to NH_4^+ (Brown 1982).



Figure 25. *Leptobryum pyriforme*. Photo by Michael Lüth, with permission.



Figure 26. *Funaria hygrometrica* with its prolific capsules, a species that grows best on nitrate and not on ammonium. Photo by Michael Lüth, with permission.



Figure 27. *Weissia controversa*, a species that grows best on nitrate and not on ammonium. Photo by Michael Lüth, with permission.

The aquatic moss *Fontinalis antipyretica* (Figure 28) responded to high levels of KNO_3 with a toxicity response that interfered with its physiological gas exchange (Stolz & Weise 1976). Its maximum sensitivity was in late spring, with minimal sensitivity in mid summer. High N levels can cause complete O_2 depletion in *Fontinalis*-colonized waters, interfering with P uptake. Total gas exchange of *F. antipyretica* increased 10-12 fold when air turbulence in the culture system increased from 25 to 45 L h^{-1} ; P uptake increased accordingly.



Figure 28. *Fontinalis antipyretica* in flowing water with lots of oxygen. Photo by Michael Lüth, with permission.

P Additions

Phosphorus typically comes from the mineral substrate, animal dung, and decomposition. The presence of *Funaria hygrometrica* (Figure 26) seems to correlate with the addition of phosphate fertilizer (O'Toole & Synnott 1971). Could this simply be tolerance, or is it a requirement? After all, this moss grows on charcoal, which typically binds ions, providing a low-nutrient habitat. In *Polytrichum formosum* (Figure 29), there seems to be a clear benefit; Vagts and Kinder (1999) reported an "exceptional stimulatory effect of NPK on this moss in a heathland."



Figure 29. *Polytrichum formosum*. Photo by Michael Lüth, with permission.

In an Alaskan study, addition of P in a stream resulted in an increase in cover of the mosses *Hygrohypnum alpestre* (Figure 30) and *H. ochraceum* (Figure 31-Figure 32), suggesting that these mosses had been P limited (Figure 33; Bowden *et al.* 1994). P concentrations are typically low in stream ecosystems and limit algal productivity as well.



Figure 30. *Hygrohypnum alpestre*, a species that increases in cover in the Arctic when P is added to the streams. Photo by Michael Lüth, with permission.



Figure 31. *Hygrohypnum ochraceum* showing its abundance in the splash of a stream. Photo by Michael Lüth, with permission.



Figure 32. *Hygrohypnum ochraceum*, a species that increases in cover in the Arctic when P is added to the streams. Photo by Michael Lüth, with permission.

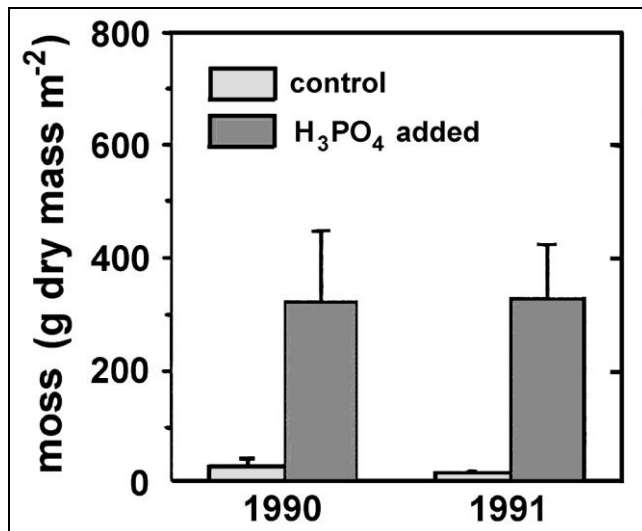


Figure 33. Comparison of moss growth and biomass in unfertilized control reaches (0.05μM) and reaches fertilized by H₃PO₄ to a concentration of 0.3μM in the Kuparuk River, Alaska, USA. From Bowden *et al.* (1994).

In their study on a stream population of *Fontinalis antipyretica* (Figure 28), Stolz and Weise (1976) found that the incorporation of P is an active process and is temperature dependent. The RNA fraction was the cell fraction most sensitive to these concentrations.

N and P seem to act together in strange ways. In *Schistidium* (Figure 34) in Alaska, the addition of either N or P caused the cover to increase, but when both were added together the cover decreased (Gordon *et al.* 2001). In bogs and fens, the nutrient relationship can be quite complex. Thormann and Bayley (1997) found that when N or P was added to the water, net primary productivity of *Sphagnum fuscum* (Figure 6-Figure 7) decreased significantly and that water level was the primary limiting factor.



Figure 34. *Schistidium apocarpum* with capsules; members of *Schistidium* in Alaska respond positively to addition of either N or P, but not when they were added together. Photo by Christophe Quintin, through Creative Commons.

Ca and Mg Additions

Liming (CaCO₃) is a common practice for eliminating bryophytes from lawns and other areas where they are unwanted. ☹ One of the problems created by liming is desiccation. But Ca⁺⁺ from CaCO₃ can also harm bryophytes by competing with other nutrient ions by occupying too many exchange sites. This makes it difficult for other ions to bind to the cell walls and enter the bryophyte. But added Ca⁺⁺ is not always harmful to bryophytes. Helsper *et al.* (1983) found that repeated Ca⁺⁺ applications to a *Calluna*-dominated heathland in the Netherlands resulted in an increase in bryophytes.

The entry of Ca⁺⁺ and Mg⁺⁺ seem to interfere with each other, most likely through competition for exchange sites. The rich fen moss *Scorpidium revolvens* (Figure 35) responded to applications of MgCO₃ and CaCO₃ in relation to hardness (Tahvanainen 2004). At high Mg:Ca ratios and low hardness or at low Mg:Ca and high hardness, growth was suppressed, causing a bell-shaped response curve. In other words, growth increased, then decreased as Ca⁺⁺ increased (0-18 mg L⁻¹), but increased with the Mg level (0-12 mg L⁻¹).



Figure 35. *Scorpidium revolvens*. Photo by Michael Lüth, with permission.

Fe Additions

Iron can be a micronutrient or a macronutrient in plants and is needed in various enzymes. In oxygenated

water, iron forms iron oxides that are insoluble and precipitate out. However, in an aquatic system, deep water becomes **anaerobic** (lacking oxygen) and the iron then changes to its ferrous state and forms ferrous hydroxide, which is soluble. An interesting consequence of this relationship occurred in our study of a reservoir dam system (Glime & Keen 1984). The dam had the capability of providing outflow from four different depths. When the bottom depth was used, anaerobic water exited the reservoir and joined the shallow river below. The *Fontinalis duriaei* (Figure 36) in that river soon became covered with iron "pebbles." As the ferrous iron reached the photosynthesizing mosses, it changed to its ferric state and formed iron oxides with the photosynthetic oxygen. These ferric oxides adhered to the mosses as chunks or pebbles.



Figure 36. *Fontinalis duriaei*, a species that can become plated with iron when reduced iron meets oxygenated water and plants producing oxygen. Photo by Michael Lüth, with permission.

CO₂ Additions

When plants are submersed, CO₂ can easily be limiting. This seems to be especially true for *Sphagnum* as it enjoys the warmer temperatures of summer when CO₂ is quickly lost from the warm water. Addition of CO₂ to water in which *S. cuspidatum* (wet kitten moss; Figure 37) was growing caused strong increases in both biomass and length (Paffen & Roelofs 1991). Addition of NH₄⁺ without additional CO₂ had no effect on growth.



Figure 37. *Sphagnum cuspidatum* growing in water. Photo by Michael Lüth, with permission.

But once again, relationships are not so simple. When atmospheric CO₂ was increased to 700 ppm in combination with low levels of N deposition (6 g m⁻² yr⁻¹), *Sphagnum recurvum* var. *mucronatum* (Figure 38) responded with increased productivity, exhibiting a 17% increase in dry biomass (Heijden *et al.* 2000). But when N increased with the CO₂, no growth differences occurred. In fact, even at the highest N level coupled with the high CO₂ level there was a reduction of total N in the capitulum but not in the stems. This reduction in the capitulum coincided with reduced amino acids, but the soluble protein levels remained the same.



Figure 38. *Sphagnum recurvum* var. *mucronatum*, a species that benefits from added CO₂, but not when receiving added N at the same time. Photo by Jan-Peter Frahm, with permission.

Excess Nutrients

Some bryophytes require low nutrient conditions, and many simply cannot survive fertilization or high nutrient situations. The effect of high mineral concentrations has been a source of consternation for many bryologists who have attempted terrariums or culture of bryophytes. Standard nutrient concentrations usually need to be diluted to about 10% that used for tracheophytes and algae (Jeff Duckett, pers. comm. 23 February 2017), but as you will see in this chapter, that varies widely.

This problem of excess came to the attention of Bryonetters. Formation of a white crust on the tips of plants has attracted attention in a number of species. The discussion began when Caitlin Maraist (Bryonet 18 July 2016) cultured *Ceratodon purpureus* (Figure 39) on Turface (a clay that has been heated to improve absorption) moistened with DI water. The plants developed a white precipitate on their leaf tips. Timea Deakova (Bryonet 19 July 2016) reported having the same problem when culturing *Dicranum* species (Figure 8, Figure 15).



Figure 39. *Ceratodon purpureus* with capsules, a species that accumulates a white precipitate when grown on Turface. Photo by Michael Lüth, with permission.

Lars Hedenäs (Bryonet 19 July 2016) reported *Syntrichia ruralis* s.l. (Figure 40) as commonly having such a crust when growing in "strongly calcareous and periodically dry habitats... When dry, the upper leaf portions (hair-points and uppermost lamina) become brittle" with what appears to be a precipitated calcium compound.



Figure 40. *Syntrichia ruralis*, a species that precipitates a white crust at the leaf tips when it dries in strongly calcareous habitats. Photo by Michael Lüth, with permission.

When *Syrrhopodon texanus* (Figure 41) grows on mineral-rich sandstones, groups of plants can become white with salts accumulated on leaf tips, but adjoining species do not seem to have these accumulations (David Taylor, Bryonet 18 July 2016). This raises interesting questions about the various abilities of bryophytes to tolerate these salts. Why do some deposit them at their tips and others do not? How does this relate to internal vs external conduction? And what physiological adaptations permit some bryophytes to tolerate these salts without suffering from **exosmosis** (loss of water through the cell membranes due to the higher salt concentration on the outside of the cell)?



Figure 41. *Syrrhopodon texanus*, a species of mineral-rich sandstone where it can accumulate salts on the leaf tips. Photo by Janice Glime.

Fertilization and Community Structure

It is easy to see that, rather than benefit, mosses may suffer from increased fertilization both from acid rain inputs and from airborne farm fertilizers, as shown in many field experiments (Mickiewicz 1976; Brown 1982; Jäppinen & Hotanen 1990; Kellner & Mårshagen 1991). In industrialized areas, heavy metals, needed by the bryophytes in minute quantities, can further result in the decline of bryophytes when the industrial sources greatly increase the quantities of these pollutants. In some cases, this pollution fertilization may be beneficial to the bryophytes, as in the pine-heath system where nutrient levels are especially low. Under such circumstances, mosses including *Pohlia* (Figure 42-Figure 43) and *Pleurozium schreberi* (Figure 44) can replace lichens, including *Cladonia* spp., particularly if irrigation is supplied (Persson 1981). Skré and Oechel (1979) found that *Sphagnum nemoreum* (= *S. capillifolium*; Figure 17) also increased its productivity in fertilizer experiments, as did the litter-inhabiting species *Brachythecium oedipodium* (Figure 45) and *Plagiothecium laetum* (Figure 46) with higher N, P, or Mg (van Dobben *et al.* 1992). Increases in productivity and growth of bryophyte species can lead to changes in community structure.



Figure 42. *Pohlia nutans*, demonstrating its ability to form extensive mats. Photo by Michael Lüth, with permission.



Figure 43. *Pohlia nutans* with capsules, a species that can replace lichens when nutrients are added to nutrient-poor habitats through pollution. Photo by Jan-Peter Frahm, with permission.



Figure 44. *Pleurozium schreberi*, a species that can replace lichens in heathlands when fertilized by pollution. Photo by Sture Hermansson, with online permission.



Figure 45. *Brachythecium oedipodium* increased its productivity in fertilizer experiments with N, P, and Mg. Photo by Michael Lüth, with permission.

By contrast, Skré and Oechel (1979) found that *Hylocomium splendens* (Figure 4) and *Pleurozium schreberi* (Figure 44) in the black spruce (*Picea mariana*; Figure 47) forest near Fairbanks, Alaska, did not increase in cover with fertilizer additions, suggesting that nutrients were already more available than in the pine-heath system studied by Persson (1981) or that these populations were

adapted to lower nutrient levels. Jäppinen and Hotanen (1990) found that these common boreal species, also including *Dicranum* (Figure 48) and *Sphagnum* (Figure 52) species, were killed by fertilizer applications designed to improve timber yield, but that *Polytrichum commune* (Figure 49) seemed unaffected. The overall effect, then, of the addition of nutrients is that species that are typical of poor sites (lichens, Ericaceae, feather mosses) shift toward associations of species typical of rich sites (Poaceae and litter-inhabiting mosses).



Figure 46. *Plagiothecium laetum* increased its productivity in fertilizer experiments with N, P, and Mg. Photo by Kristian Peters, with permission.



Figure 47. Black spruce (*Picea mariana*) forest. Photo by Herbert Pöhl, through Creative Commons.



Figure 48. *Dicranum polysetum*, a boreal forest species that is killed by forest fertilization designed to improve timber productions. Photo by Janice Glime.



Figure 49. *Polytrichum commune*, a boreal forest species that unaffected by forest fertilization designed to improve timber productions. Photo by Michael Lüth, with permission.

On the other hand, disappearance of *Rhytidiadelphus squarrosus* (Figure 50) was not coupled with an increase in tracheophyte cover in either acidic or calcareous grassland (Morecroft *et al.* 1994). Rather, it appears to have responded to additions of NH_4NO_3 or $(\text{NH}_4)_2\text{SO}_4$ (ammonium sulfate) additions through disruption of its N metabolism (Bates 2000).



Figure 50. *Rhytidiadelphus squarrosus* with competing vascular plants. Photo by Michael Lüth, with permission.

Peatlands can respond differently in different geographic regions. Aerts and coworkers (1992) attributed the lower productivity of northern Swedish peatlands compared to those in southern Sweden to the 10X greater input of atmospheric N in the southern location. They supported this hypothesis by adding N and P at both sites. At the northern site, added N increased productivity 4-fold, but added P had no effect. Conversely, at the southern site, added N ($4 \text{ g m}^{-2} \text{ yr}^{-1}$) had no effect on productivity, whereas adding P ($0.4 \text{ g m}^{-2} \text{ yr}^{-1}$) increased productivity 3-fold. This trend is likewise supported by comparing a low and high deposition site in the Netherlands. Atmospheric N deposition there has been increasing, causing peatlands to increase in available N (Limpens *et al.* 2003). This increase in N seems to have coincided with an increase in *Sphagnum fallax* (Figure 52). However, Limpens *et al.* could find no evidence that *S. fallax* outcompeted any of the other five *Sphagnum* species in the area. Nevertheless, when N was added at a low deposition site, this species did expand its coverage. They determined that at the high deposition site *S. fallax* was limited by P. They concluded that when the capitulum N concentration is raised to 7 mg

L^{-1} or higher and the P concentration is 0.7 mg L^{-1} or higher, this species can increase and dominate.

Li and Vitt (1997) found that while moss productivity increased 4-300% with N enrichment ($3 \text{ g m}^{-2} \text{ yr}^{-1}$ as NH_4Cl), the productivity of the peatland shrubs *Betula pumila* (Figure 20) and *Rhododendron (=Ledum) groenlandicum* (Figure 19) did not. In fact, they concluded that the moss layer immediately retained nearly all of the added N. Likewise, Bayley *et al.* (1987) found that when N was added to a boreal peat system in the form of NO_3^- , 90% was taken up by the *Sphagnum* lawn (Figure 51) within 24 hours, resulting in a growth increase by the *Sphagnum*. No growth increase occurred in the tracheophytes, even after five years of experimentation (Vitt 1991). Sanville (1988) likewise found that *Sphagnum* production increased in response to nutrient addition.



Figure 51. *Sphagnum* lawn. Photo through Creative Commons.



Figure 52. *Sphagnum fallax*. Photo by Michael Lüth, with permission.

In the high Arctic heath, bryophytes are a major ecosystem component. When N and P were added to that system for eight years, there was no change in bryophyte cover, but physiological processes shifted in the bryophyte layer (Gordon *et al.* 2001). Only $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of N increased the proportion of physiologically active bryophyte shoots while decreasing their capacity to assimilate NO_3^- . Effects of added P were even greater. When both nutrients were added, the species composition changed, with some bryophytes increasing in abundance

and others decreasing. Since N and P are both limiting in this Arctic system, increasing either will have an effect on the ecosystem. Thus, if mineralization increases as a result of global warming, we can expect shifts in the community structure of the Arctic ecosystems.

Predicting the behavior of tundra and peatland communities is not simple. Chapin and Shaver (1989) found that in Alaska the mosses (and lichens) had the greatest N and P use efficiency, but, unlike deciduous leaves, declined in N use efficiency with the addition of N plus P. Nevertheless, they can be efficient scavengers of available N, competing effectively with tracheophytes. In the Arctic tundra, Marion and coworkers (1987) found that litter recovered 1.3-16.3% and mosses 5.4-16.4% of labelled N, whereas above ground tracheophytes recovered only 2.6-5.0%. Although we tend to think of the tundra as being nutrient limited, it appears that it may not be nutrient limited for the mosses. Oechel and Sveinbjörnsson (1978) found that the addition of a dilute nutrient solution to the mosses there did not increase photosynthetic productivity or growth. One reason for this lack of response, or even decline in productivity, upon the addition of nutrients is that NO_3^- causes the induction of nitrate reductase activity, as shown for *Sphagnum fuscum* (Figure 6-Figure 7) by Woodin and coworkers (1985). Thus it appears that the feedback system controls the N levels in the mosses (see above under N Additions). Skré and Oechel (1979) likewise found that *Hylocomium splendens* (Figure 4) and *Pleurozium schreberi* (Figure 44) did not increase productivity after fertilizer additions, but surprisingly, *Sphagnum capillifolium* (Figure 17) did. Perhaps its position high in the hummock is less suitable than other locations for the N-fixing Cyanobacteria that maintain N levels in bogs and fens.

In some habitats, increasing the nutrient content can shift dominance from cryptogams, including mosses, to tracheophytes (van Dobben *et al.* 1992). When N (as NH_4NO_3) was added to a forest ecosystem in Sweden in an 18-year experiment, cryptogams, including the soil mosses *Pleurozium schreberi* (Figure 44) and *Hylocomium splendens* (Figure 4), and the heath family Ericaceae lost dominance to the grass *Deschampsia flexuosa* and **ruderal** (disturbed habitat) species. Both bryophytes were strongly "disfavored" by the addition of N at all levels. The other additions (P, K, Mg, S, and micronutrients) had similar effects but to a much smaller degree. *Pleurozium schreberi* was disfavored by S and micronutrients. Added P and N significantly stimulated the growth of *Pseudoscleropodium purum* (Figure 54), whereas *Brachythecium rutabulum* (Figure 53) did not respond (Bates 1994). The *P. purum* plants showed a greater uptake of P and to a lesser extent N than did the *B. rutabulum* while also conserving them more efficiently. Bates explained this difference in that *P. purum* depends on an unpredictable supply of nutrients from precipitation, whereas *B. rutabulum* probably obtains more of its nutrients from its substrate. Some nutrients are sequestered onto cell wall exchange sites of *P. purum* and taken up later as needed.



Figure 53. *Brachythecium rutabulum*. Photo by Michael Lüth, with permission.



Figure 54. *Pseudoscleropodium purum*, a species for which added P and N significantly stimulated the growth. Photo by Janice Glime.

Natural fertilizers have their effects too. Vanderpuye and coworkers (2002) suggest that fertilization by vertebrates may account for the type of moss tundra seen in Svalbard. Manuring of very cold ecosystems by seabirds (Figure 55) produces moss carpets characterized by a thin active layer over a thick accumulation of peat with no standing water. They suggest that in Sassendalen the role of the seabirds is replaced by reindeer (Figure 56) that create intense manuring in these favorable grazing areas.



Figure 55. Little Auks (*Alle alle*) on Svalbard, a source of manuring that provides nutrients for mosses. Photo by Alastair Rae, through Creative Commons.



Figure 56. Reindeer, large numbers that can contribute to manuring that provides nutrients for bryophytes. Photo by Roger S. Key, with permission.

In the boreal forest, it appears that effects of added nutrients on bryophyte community structure can be long lasting. Even 47 years after N fertilization ceased, the community structure had not returned to pre-fertilization composition (Strengbom *et al.* 2001). *Brachythecium reflexum* (Figure 57) and *Plagiothecium denticulatum* (Figure 58) had increased. On the other hand, the typically abundant *Hylocomium splendens* (Figure 4) had decreased relative to controls. At the same time, there seemed to be no difference in species composition of tracheophytes, but the sporocarp production of the N-sensitive mycorrhizal fungi had decreased.



Figure 57. *Brachythecium reflexum*, a species that increased following N fertilization. Photo by Michael Lüth, with permission.



Figure 58. *Plagiothecium denticulatum*, a species that increased following N fertilization. Photo by Michael Lüth, with permission.

Summary

Fertilizers typically harm bryophytes by benefitting their tracheophyte competitors. They can also raise the pH, creating conditions unfavorable for bryophytes. Only in the Arctic do fertilizers sometimes seem to benefit bryophytes, where nutrients are low and cool temperatures favor bryophyte growth. Fertilizers such as $\text{Ca}(\text{NO}_3)_2$ cause a decrease in the lipids that are needed for tolerance of cold and desiccation, whereas cold temperatures increase them.

Increases in N, especially as nitrate, increases the chlorophyll content in some species, such as *Thuidium tamariscinum*, while causing others, such as *Hylocomium splendens*, to turn brown. Peatland mosses often respond positively to N addition (as NH_4NO_3) while shrubs decrease. Ammonium is toxic, and the amino acid and nitrate balance must be such that it does not inhibit the conversion of NH_4^+ to amino acids. Light is needed for nitrate reductase to work, converting the nitrate to nitrite, which is then converted by nitrite reductase to ammonia and placed into amino acids. CO_2 is often limiting, making the addition of nutrients of little value. High N levels can also deplete the oxygen, preventing P uptake.

Added P seems to benefit aquatic mosses, at least in Alaska, causing an increase in bryophytic cover. Nevertheless, when N and P are added together, they can cause a decrease in productivity, even though each of these benefits when added alone.

Although Ca^{++} is an essential nutrient, it is usually harmful to bryophytes, interfering with uptake of other cations. Ca^{++} and Mg^{++} compete with each other for exchange sites and can reduce the uptake of K^+ .

CO_2 is especially limiting in aquatic environments, especially in warm weather. Under good photosynthetic conditions, iron can form iron oxide on the surface of bryophytes due to the high oxygen concentration resulting from photosynthesis.

Heavy metals, typically added from industrial air pollution, are usually detrimental to bryophytes, often causing loss of chlorophyll and brown tips.

Natural fertilization by seabirds and mammal dung favors the development of some species, especially in the tundra. On the other hand, added fertilizers in the boreal forest can depress bryophyte productivity for many decades.

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