

CHAPTER 8-2

NUTRIENT RELATIONS: CO₂

TABLE OF CONTENTS

CO ₂ Sources and Limitations	8-2-2
Early Carbon Relations	8-2-2
Relationships Today.....	8-2-2
Structural Adaptations	8-2-6
Soil CO ₂	8-2-7
CO ₂ -Concentrating Mechanisms.....	8-2-8
Aquatic CO ₂	8-2-10
Role of pH.....	8-2-13
Bogs	8-2-13
Methane	8-2-15
CO ₂ and Desiccation Tolerance	8-2-15
Translocation.....	8-2-15
Importance of Bryophytes in C Cycling.....	8-2-16
Climate Change – An Antarctic Problem.....	8-2-17
Summary	8-2-18
Acknowledgments.....	8-2-18
Literature Cited	8-2-18

CHAPTER 8-2

NUTRIENT RELATIONS: CO₂



Figure 1. Peat moss, *Sphagnum fimbriatum*, covering the largest area of carbon sink in the world. Photo by Michael Lüth, with permission.

CO₂ Sources and Limitations

Early Carbon Relations

Colonization of life on the land of Earth began billions of years ago (Graham *et al.* 2014). Evidence suggests that bacteria, then **eukaryotic** (having a nucleus) algae, then bryophytes ventured to endure those early conditions. These early forms made possible the development of the first organic soils. To understand this progression and continuation of life, it is prudent to understand carbon cycling. For most terrestrial plants and algae, the source of this carbon is carbon dioxide (CO₂). Both green algae and bryophytes produce a degradation-resistant form of carbon from that CO₂ that is consequently sequestered. This, in turn, reduces the CO₂ in the atmosphere, having an important impact on the Earth's carbon cycle for 40-100 million years.

This early atmosphere was high in CO₂ compared to levels today (Raven & Edwards 2014). Isotope comparisons using liverwort fossils indicate that in the mid-Cretaceous in the Antarctic, CO₂ concentrations ranged 1000-1400 ppm, agreeing generally with

independent proxy data and long-term carbon cycle models (Fletcher *et al.* 2005). Furthermore, the concentration gradient from the atmosphere to the carboxylase in the plant would further drive CO₂ into the plant (Raven & Edwards 2014). This additional CO₂ would permit higher photosynthetic rates per surface area of plant. Later adaptations included increasing the surface area of photosynthetic tissue through development of complex structures and air spaces to permit greater harvesting of light.

Proctor (2010) suggested that in the early atmosphere of plant evolution in the mid-Palaeozoic, the atmosphere had 10X its present concentration of CO₂. It is thus unlikely that these early plants were CO₂ limited. Rather they may have increased their cuticularization, then increased their air spaces to permit them to take up more CO₂ and compensate for the blockage by the cuticle.

Rod Seppelt (Bryonet 27 June 2022) described the interior of the cushions. Due to their tightly packed shoots, they maintain humidity better than do the tracheophytes. This added humidity promotes a high CO₂ concentration

(ca. 2000 ppm compared to 350-400 ppm ambient), largely due to the microbial associates.

Relationships Today

In 1958, the CO₂ in the atmosphere had a concentration of 315 ppm (Scripps CO₂ Program 2016). In December 2016 it had grown to 404 ppm. Elbert *et al.* (2012) estimated that cryptogams (including Cyanobacteria, algae, fungi, lichens, and bryophytes) extract ~3.9 Pg carbon per year, or around 7% of the net production of terrestrial vegetation. Thus, the CO₂ uptake by bryophytes is an important component of global carbon cycling and a necessary contributor to climate modelling.

Normally we don't think of carbon as a limiting resource, although experiments on higher plants have shown that increased carbon dioxide usually increases productivity. Mosses are typically **C₃ plants** with high **CO₂ compensation points** (CO₂ concentration at which net CO₂ fixation is zero) (Raven *et al.* 1998). In other words, they require high levels of CO₂ to balance the CO₂ lost to respiration. **C₃ plants** are those plants that have no special mechanism for storing carbon from CO₂ temporarily in a compound such as **malate** or **oxalate**. Instead, they put all their CO₂ directly into the photosynthetic pathway in a 3-carbon compound, hence the term C₃. This pathway is less efficient because the enzyme **Rubisco** (Ribulose biphosphate carboxylase/oxidase) is much less effective at binding the atmospheric CO₂ into a 3-C compound within the cell than is **PEP carboxylase**, the enzyme used in the C₄ and CAM pathways to put the carbon in temporary storage C₄ compounds for later use in photosynthesis. However, mosses are not limited by guard cell closure in obtaining CO₂ and thus should be able to obtain CO₂ any time of the day.

In examining 32 terrestrial C₃ plants, Bauer and Martha (1981) found an average CO₂ compensation point of 36.2 µl L⁻¹ (=71 mg m⁻³). However, among these, two mosses showed a somewhat higher CO₂ compensation point of ~43 µl L⁻¹. The compensation point for tracheophytes ranged 31-40 µl L⁻¹. Bain and Proctor (1980) found that the CO₂ compensation point of the aquatic bryophytes they studied were over 100 times higher than those of the C₃ aquatic tracheophyte *Elodea* (Figure 2) and the alga *Chara* (Figure 3). They were likewise somewhat higher than those of terrestrial bryophytes reported by Dilks (1976).



Figure 2. *Elodea canadensis*, an aquatic plant with a very low CO₂ compensation point compared to that of mosses. Photo by Sean Blaney, through Creative Commons.



Figure 3. *Chara* in Keweenaw Peninsula, Michigan, USA, an aquatic alga with very low CO₂ compensation point compared to that of mosses. Photo by Jason Oyadomari, with permission.

Among tracheophytes, CAM plants, convert CO₂ to malate at night and store it to be used in the daytime, permitting the plants to conserve water by keeping stomata closed in the daytime. In C₄ plants a bundle sheath permits plants to convert CO₂ to a 4-carbon compound for use later. This likewise permits the plants to conserve water by closing stomata when the air is dry but to continue using CO₂ derived from the stored 4-C compounds for photosynthesis.

Bryophytes must live in a delicate balance between sufficient moisture and sufficient CO₂. When leaves are wet on the outside, that water offers significant resistance to CO₂ diffusion. Surprisingly, a thin cuticle permits greater diffusion than even a thin film of water, so mosses living in very wet habitats often are protected from waterlogging by well-developed waxes or other cuticular material (Proctor 1984). *Polytrichum commune* (Figure 4) and *P. strictum* (Figure 5) are good examples of this, but less obvious examples are *P. wahlenbergii* (Figure 6), *Pohlia cruda* (Figure 7), *Philonotis* (Figure 8), *Schistostega pennata* (Figure 9), *Saelania glaucescens* (Figure 10), and *Bartramia pomiformis* (Figure 11), all with a whitish appearance to the naked eye (Proctor 1984).



Figure 4. *Polytrichum commune* showing its somewhat waxy leaves. Photo by Michael Lüth, with permission.



Figure 5. *Polytrichum strictum* showing waxy leaves. Photo by Janice Glime.



Figure 8. *Philonotis fontana* showing its waxy leaves. Photo by Michael Lüth, with permission.



Figure 6. *Pohlia wahlenbergii* var. *glacialis* showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.



Figure 9. *Schistostega pennata* showing waxy leaf surface. Photo courtesy of Martine Lapointe.



Figure 7. *Pohlia cruda* showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.



Figure 10. Waxy-looking leaves of *Saelania glaucescens*. Photo by Ivanov, with permission.



Figure 11. *Bartramia pomiformis* showing waxy leaves. Photo by Jan-Peter Frahm, with permission.

Sphagnum (Figure 1) partially solves this balance by having water-holding cells (**hyaline cells**) that bathe the photosynthetic cells (Figure 12), while exposing at least one surface (in most) of the photosynthetic cell to the atmosphere. Furthermore, air bubbles become trapped among the leaves and between the leaves and the stem, thus providing an additional source of CO₂. Robinson (1985) considered that no CO₂ was obtained from the **hyaline** (water-holding) cells because all the chloroplasts of the cells were positioned along the wall most exposed to light. On the other hand, members of *Leucobryum* (Figure 13- Figure 16) do indeed trap air bubbles in their colorless cells (Robinson 1985), providing an internal source of CO₂ for the chlorophyllous cells residing there and causing these plants to somewhat mimic the internal structure of a seed plant. This same character seems to be present throughout the **Leucobryaceae** family, permitting their multi-layered leaves to function photosynthetically.

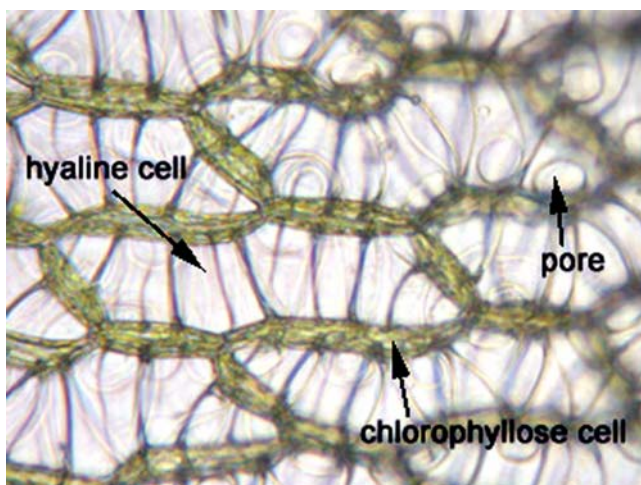


Figure 12. *Sphagnum* cells indicating the hyaline cells with pores, holding water, and chlorophyllose (photosynthetic) cells exposed to atmosphere. Photo with from Botany Website, UBC, with permission.



Figure 13. *Leucobryum glaucum* showing whitish color caused by hyaline cells that surround the photosynthetic cells. Photo by David T. Holyoak.

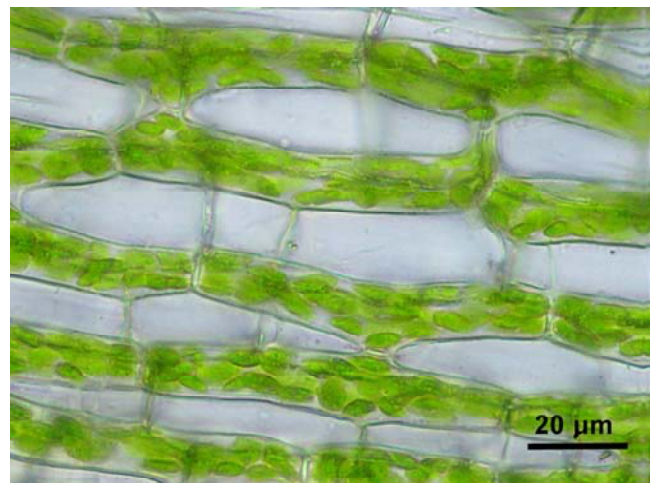


Figure 14. *Leucobryum glaucum* leaf cells in lamina view, showing hyaline cells and photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

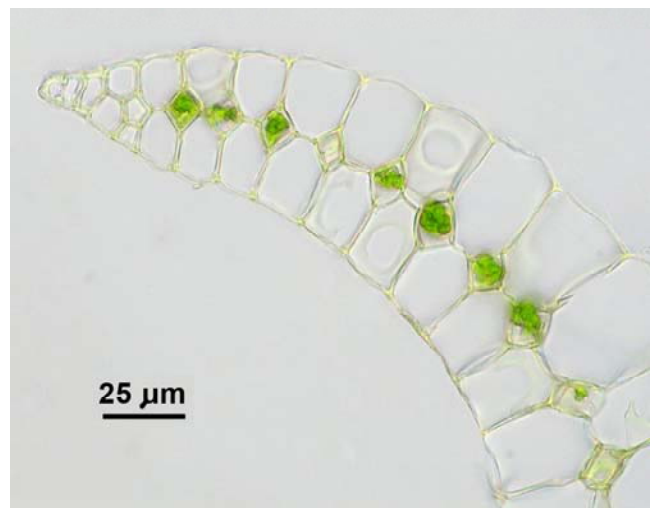


Figure 15. *Leucobryum glaucum* leaf cross section showing the photosynthetic cells surrounded by hyaline cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 16. Whitish leaves due to hyaline cells of *Leucobryum juniperoideum*. Photo by Michael Lüth.

Shinde *et al.* (2015) determined that the moss *Physcomitrella patens* (Figure 17) has 814 genes that are affected by elevated CO₂ (1500 ppmV). These affect transcriptional reprogramming, photosynthetic regulation, carbon metabolism, and stress responses. CO₂ relationships are not simple!



Figure 17. *Physcomitrella patens*, demonstrating its whitish appearance due to a thin cuticle. Photo by Michael Lüth, with permission.

Structural Adaptations

Proctor (2010) explains that the maximum rate of CO₂ diffusion is limited by the difference between the external CO₂ concentration and the CO₂ **compensation point** (level of O₂ at which respiration = photosynthesis), as well as the resistance of the moist external bryophyte cell wall to the liquid-phase diffusion of the CO₂. This is limited by the thickness of the external cell walls. Structural differences can increase the plant uptake. A large, simple thallose liverwort provides a single flat photosynthetic surface. This is improved in an epiphyte such as *Metzgeria* (Figure 18) that exposes both surfaces. *Marchantia* (Figure 19) further increases the uptake surface by its system of internal chambers with photosynthetic cells arranged like tissues of a sponge (Figure 20).



Figure 18. *Metzgeria furcata* showing thalli exposed on both sides, thus doubling its CO₂-absorbing surfaces. Photo by Michael Lüth, with permission.



Figure 19. *Marchantia polymorpha* pores and gemmae cups. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

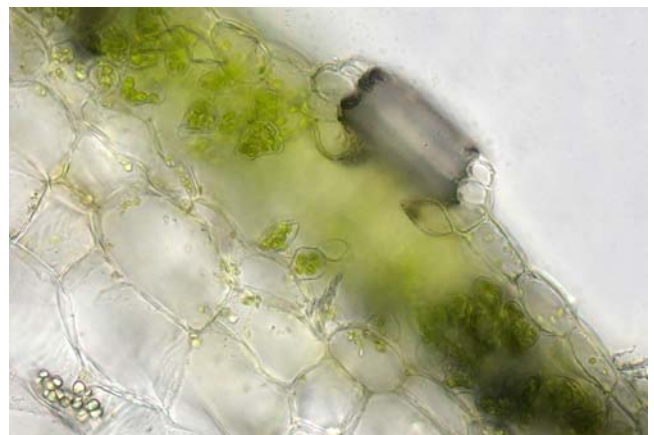


Figure 20. *Marchantia polymorpha* cs showing pore and underlying spongy chlorophyllose cells. Photo by Walter Obermayer, with permission.

Perhaps the most obvious adaptation of plants to intake of CO₂ is having stomata in leaves. This apparatus permits tracheophyte leaves to regulate moisture concentration in the leaves. However, when they are closed to conserve water, they are also closed to atmospheric CO₂ that is vitally needed for photosynthesis. Mosses and leafy liverworts lack stomata in their leaves, but generally have leaves that are only one cell thick, thus exposing two sides of the cell for absorption of CO₂. Some thallose liverworts, on the other hand, have a plant body that consists of multiple layers. These typically have a chambered interior with sponge-like tissues that provide lots of surface area. For these to obtain atmospheric CO₂, the chambers connect to the exterior atmosphere through pores that permit its diffusion into the chamber. Raven (2002) suggested that "stomata evolved from pores in the epidermis of plant organs which were at least three cell layers thick and had intercellular gas spaces and a cuticle."

But does this sponge-like interior make a difference? Meyer *et al.* (2008) demonstrated that both external and internal conductances, as well as water use efficiency, were higher in the ventilated (spongy) liverworts and hornworts. Within these two taxonomic groups, however, the values were similar, suggesting that various factors must serve to optimize the involved species for that life form.

Soil CO₂

Šimůnek and Suarez (1993) modelled the CO₂ transport and production in soil. CO₂ can be transported in the unsaturated zone in both the liquid and gas form. Both root and microbial respiration contribute to soil CO₂. The rate of this respiration is affected by water content, temperature, growth, salinity, and plant and soil characteristics.

In a temperate rainforest of New Zealand, bryophytes form a nearly continuous cover (62%) on the forest floor, with a depth less than 30 mm (DeLucia *et al.* 2003). The CO₂ was elevated relative to the atmosphere, presumably due to bacterial and fungal respiration. The net CO₂ exchange was very dependent on water content. Although the CO₂ uptake was quite variable, the annual net carbon uptake by the forest floor bryophytes was 103 g m⁻², compared to annual loss of carbon from the forest floor (bryophyte and soil respiration) of -1010 g m⁻². This accounted for a reclamation of ~10% of the forest floor CO₂ emitted by respiration.

Tarnawski *et al.* (1994) measured 24-hour changes in atmospheric CO₂ concentrations within and above cryptogam stands in a New Zealand temperate rainforest. They found that CO₂ levels within the forest exceeded those in the open by 30 ppm and had a more variable **diel** (denoting a period of 24 hours) pattern (up to 70 ppm). The mean CO₂ level at a depth of 25 mm in the moss layer was 50% higher than those in the clearing and were higher than in the air of the rainforest.

In the Arctic tundra, there are definite differences in soil respiration rates related to microscale topography, mainly due to differences of soil water table and soil temperatures (Sommerkorn *et al.* 1999). The moss layer serves as a high impact modifier of the CO₂ emission, assimilating 51% to 98% of the daily amount CO₂ released from wet tundra soils.

For most forest floor mosses, the CO₂ should be ample to supply the slow-growing mosses due to production of CO₂ from litter decay. In the tropics, the CO₂ concentrations on the forest floor are greater than those above the canopy (Holtum & Winter 2001), but that enriched supply is still limiting. At 10 cm above the soil the CO₂ level is somewhat higher.

Because CO₂ is often limiting, even in the terrestrial system, increasing levels of CO₂ on the Earth could positively affect the bryophytes. Strain and Cure (1985) reported that the rate of photosynthesis in tracheophytes increases with a rise of atmospheric CO₂. Because bryophytes are C₃ plants, they are able to take advantage of high CO₂ levels. The increased temperatures that accompany the higher CO₂ through the greenhouse effect will cause greater below ground respiratory processes of roots, bacteria, and other organisms (Heal 1979; Silvola 1985). Bryophytes on the soil surface are the first photosynthetic organisms to have an opportunity to use this increased CO₂. Csintalan *et al.* (1997) found a small, but significant increase in CO₂ uptake in the drought-tolerant moss *Syntrichia ruralis* (Figure 21) when grown in a concentration of 700 ppm compared to that at the ambient level at that time of 350 ppm.



Figure 21. *Syntrichia ruralis* hydrated, a species that benefits from higher levels of CO₂. Photo by Misha Ignatov, with permission.

Sonesson *et al.* (1992) were able to show that the boreal forest moss *Hylocomium splendens* (Figure 22-Figure 23) can adapt to higher ambient CO₂ concentrations and utilize higher CO₂. Increasing CO₂ levels to 600 ppm (compared to 350 ppm), resulted in a significant increase in its photosynthesis and growth (Sonesson *et al.* 1996). Botting and Fredeen (2006) similarly showed that CO₂ (430 ppm) was limiting to moss productivity on the sub-boreal forest floor in central British Columbia, Canada.



Figure 22. *Hylocomium splendens* showing its extensive cover in the boreal forest. Photo by Andrew Spink, with permission.



Figure 23. *Hylocomium splendens*, a species that can benefit from a higher CO₂. Photo by Chmee through Creative Commons.

Role of Water in CO₂ Uptake

Both high and low water content are limiting to carbon uptake (Titus *et al.* 1983; Silvola 1991; Zotz *et al.* 1997; Schipperges & Rydin 1998; Jauhiainen & Silvola 1999; Turetsky 2003). This appears to be due to the inability of the bryophytes to use the CO₂ under these conditions. Insufficient water inhibits the enzymes in photosynthesis. When the plants are water saturated, CO₂ diffusion is slowed (Williams & Flanagan 1996; Tuittila 2000). This limitation works differently in *Sphagnum* from its behavior in tracheophytes (Rice 2000). In tracheophytes, water limitation lowers chloroplastic demand and increases the resistance to carbon uptake. By contrast, in *Sphagnum* water limitation actually decreases the resistance to carbon uptake.

CO₂-Concentrating Mechanisms

CO₂-concentrating mechanisms are familiar in tracheophytes. In tracheophytes, allowing CO₂ into the leaf through stomata means allowing water vapor out (Hanson *et al.* 2014). Even chloroplasts leak water as they allow CO₂ in because both require the same pore size.

Bryophytes have neither of these carbon-storing mechanisms and it seems that all bryophytes are C₃ plants. But it appears that at least some do have a means to concentrate CO₂ (Meyer *et al.* 2008). Like members of the green algae, many hornworts (**Anthocerotophyta**; Figure 24-Figure 25) have **pyrenoids** (protein bodies in chloroplasts of some algae and hornworts; Figure 25) associated with the chloroplasts (Hanson *et al.* 2002, 2014). These pyrenoids are able to maintain a pool of dissolved inorganic carbon (DIC) of 19-108 nmol mg⁻¹ chlorophyll (Hanson *et al.* 2002).



Figure 24. *Anthoceros agrestis* (**Anthocerotophyta**), representing a phylum in which many members have pyrenoids. Photo by Michael Lüth, with permission.

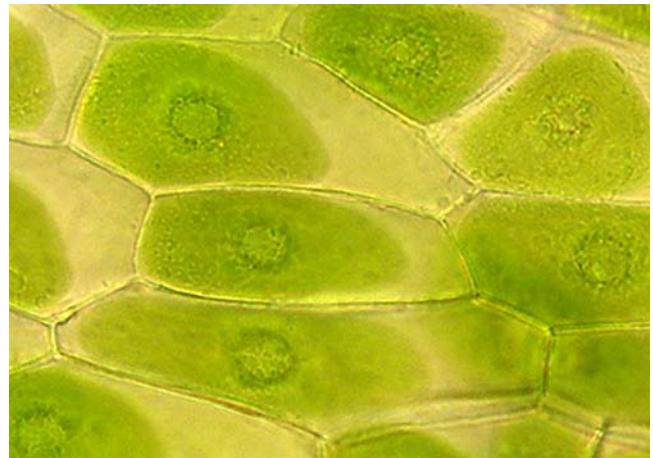


Figure 25. Hornwort (**Anthocerotophyta**) pyrenoids – the dark circles in the cells. Photo by Chris Lobban, with permission.

Villareal and Renner (2012) remind us of the important role of enzyme Rubisco (Ribulose-1,5-Biphosphate-carboxylase-oxygenase) in carbon fixation. But Rubisco is slow compared to PEP carboxylase, which they lack. These researchers noted that many scientists have hypothesized that carbon-concentration mechanisms evolved during periods of low CO₂ to concentrate CO₂ around the enzyme. But the cladistic analyses of Villareal and Renner do not support this hypothesis; pyrenoids have come and gone in the **Anthocerotophyta** (Figure 24-Figure 25) clades multiple times and do not always coincide with low CO₂.

Raven and coworkers (1998) have suggested that some aquatic mosses might have a "CO₂ concentrating mechanism" that differs from a typical C₃ pathway. The

Anthocerotophyta use pyrenoids to accomplish CO₂ concentration, with the exception of *Megaceros* (Figure 26), in which there is no pyrenoid, but the mechanism in aquatic mosses is unknown. In evaluating a number of taxa, Raven's group found no evidence of C₄ or CAM pathways in bryophytes, but Salvucci and Bowes (1981) found that two aquatic taxa, *Fontinalis antipyretica* (Figure 27) and *Fissidens cf. mahatonensis*, seem to be able to concentrate CO₂. What is even more interesting, it appears that it might be facultative. When they measured the CO₂ compensation point of *F. cf. mahatonensis* in the cool Florida winter (12°C, 10 h day length), the compensation point was consistent with that expected for a C₃ pathway. However, when they measured it for the hot Florida summer (30°C, 14 h day length), the CO₂ compensation point was much lower, although not as low as in a C₄ pathway. They found similar summer/winter CO₂ compensation point relationships in all the aquatic bryophytes tested from Florida. This would be a very beneficial adaptive feature since the CO₂ is easily lost from water at high temperatures. The Section below on Aquatic CO₂ will detail what we know about obtaining CO₂ in water.



Figure 26. *Megaceros* (Anthocerotophyta), a genus that lacks pyrenoids. Photo by Juan Larrain, with permission.



Figure 27. *Fontinalis antipyretica*, an aquatic moss that must get its CO₂ from that dissolved in water. Photo by Andrew Spink, with permission.

Bryophytes may be able to use fixed carbon compounds that are different from those used by

tracheophytes. Simola (1969) experimented with *Sphagnum nemoreum* (syn of *S. capillifolium*; Figure 28) in sterile culture and found that whereas **mannose** [hexose monosaccharide (6-carbon sugar) with a structure very similar to glucose] and its 6-carbon derivative, **rhamnose**, are toxic to many flowering plants, mannose promotes the growth of *Sphagnum nemoreum*. On the other hand, other common sugars such as **arabinose**, **galactose**, **ribose**, and **xylose** are toxic to *Sphagnum*. While the literature is not as complete as that on tracheophytes, we know that at least *Funaria hygrometrica* (Figure 29) can use the sugars fructose, glucose, maltose, and sucrose as internal carbon compounds (Simola 1969).



Figure 28. *Sphagnum capillifolium* (*nemoreum*), a species for which **mannose** promotes growth. Photo by Bernd Haynold, through Creative Commons.



Figure 29. *Funaria hygrometrica* with young sporophytes, a species that can use the sugars fructose, glucose, maltose, and sucrose internally. Photo by Andrew Spink, with permission.

Further evidence of differences in carbon usage by *Sphagnum* come from studies on carbon isotope discrimination. In three species that occupy hollows (*S. recurvum* – Figure 30), carpets (*S. palustre* – Figure 31), and hummocks (*S. tenerum* – Figure 32), the delta ¹³C values (indicating their ability to discriminate CO₂ on the basis of the ¹²C or ¹³C isotope) ranged from 19.0 to 27.1, but were unrelated to species (Rice 2000). Rather, they differed significantly ($p < 0.001$) with season. In the spring, discrimination was lower (mean 22.5), with the highest

discrimination in winter (24.7). This difference was mainly due to low photosynthetic rates in winter that reduce the effects of diffusional resistance on carbon isotope discrimination. Microhabitat differences that were present in the field disappeared in the common garden and eliminated any doubt about species differences in ability to discriminate. The observed seasonal differences in carbon isotope discrimination appear to be different from those of tracheophytes, where water limitation lowers chloroplastic demand and increases resistance to C uptake. In *Sphagnum*, water limitation lowers the chloroplastic demand but also decreases the resistance to C uptake, suggesting that the moss continues to incorporate carbon as it dries.



Figure 30. *Sphagnum recurvum*, a species of hollows. Photo by Blanka Aguero, with permission.



Figure 31. *Sphagnum palustre*, a species of carpets. Photo by Bernd Haynold, through Wikimedia Commons.

Carbon isotope ratios have been used for dating all sorts of biological materials, including the age of peatlands. Using carbon isotope technology, MacDonald *et al.* (1987) found that peatland mosses consistently registered carbon ages that were considerably older than those of the macrofossils of the same layer. They found ages that ranged 1400 to 6400 years older than that of their contemporary tracheophytes, and even the live *Drepanocladus longifolius* (Figure 33) had a ¹⁴C content that was only 85% that of other present-day taxa. They

explained this moss phenomenon as an isotope exchange with older sediments, the formation of CO₂ from bicarbonate by chemical processes, and the metabolic production of CO₂, presumably including bacterial decomposition, especially by mycobacteria.



Figure 32. *Sphagnum tenerum*, a hummock species. Photo by Blanka Aguero, with permission.



Figure 33. *Drepanocladus longifolius*, an aquatic moss that apparently derives CO₂ from old sediments. Photo by John Game, through Creative Commons.

Aquatic CO₂

In aquatic systems, CO₂ is not very soluble, is easily lost to the atmosphere at warm temperatures, and availability is pH-dependent, so it can indeed be limiting. The diffusion coefficient for CO₂ in water is only 10⁻⁴ times that found in air. The boundary layer between the moss and the flowing water reduces that availability even more. Aquatic bryophytes have high CO₂ compensation points (> 50 μl L⁻¹), higher than that of typical of C₃ tracheophytes (Bain & Proctor 1980).

Raven *et al.* (1998) indicate that stream mosses such as *Fontinalis antipyretica* (Figure 27) have very little CO₂ limitation because of the constantly flowing water that renews CO₂ and the reduced boundary layer resulting from water flow. On the other hand, in deep, quiet water, this species has much more difficulty getting CO₂, despite

higher concentrations, due to the increased boundary layer surrounding the moss.

Unlike many aquatic tracheophytes, mosses are apparently unable to use bicarbonates as a source of CO₂ (Bain & Proctor 1980; Allen & Spence 1981). Ruttner (1947) first demonstrated this limitation quantitatively in the mosses *Calliergon giganteum* (Figure 34), *Cratoneuron filicinum* (Figure 35), *Eucladium verticillatum* (Figure 36-Figure 37), *Fissidens rufulus* (Figure 38-Figure 39), *Hylocomium splendens* (Figure 22-Figure 23), and *Neckera crispa* (Figure 40) and the thallose liverwort *Marchantia polymorpha* (Figure 19), and Steeman Nielsen (1947) found the same in *Fontinalis antipyretica* (Figure 27), even though *F. antipyretica* has the enzyme carbonic anhydrase needed for the conversion of bicarbonate to CO₂. Bain and Proctor (1980) further examined mosses from alkaline habitats, yet were unable to demonstrate any use at all of bicarbonates; Allen and Spence (1981) independently determined this once more for *Fontinalis antipyretica*.



Figure 34. *Calliergon giganteum*, a species that cannot use bicarbonate as a carbon source. Photo by Misha Ignatov, with permission.



Figure 35. *Cratoneuron filicinum*, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

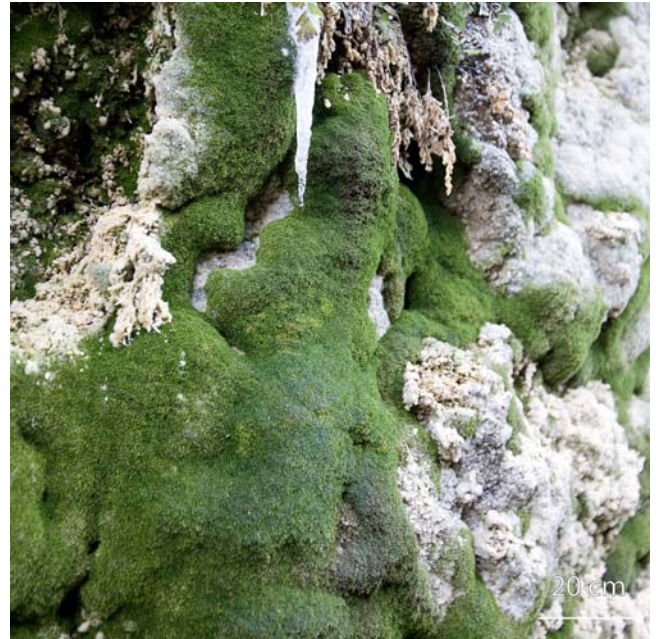


Figure 36. *Eucladium verticillatum* in its wet habitat. Photo by Proyecto Musgo, through Creative Commons.



Figure 37. *Eucladium verticillatum*, a species that is unable to use bicarbonates as a carbon source. Photo by Barry Stewart, with permission.

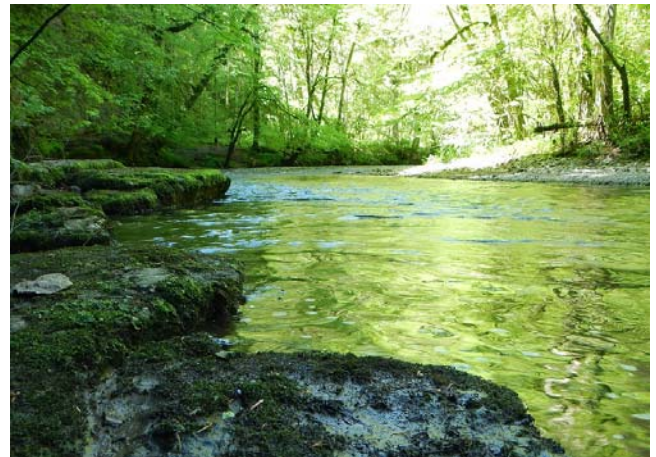


Figure 38. *Fissidens rufulus* habitat. Photo by Michael Lüth, with permission.



Figure 39. *Fissidens rufulus*, a species that is unable to use bicarbonate as a carbon source. Photo by Michael Lüth, with permission.



Figure 40. *Neckera crispa*, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

Therefore, in aquatic systems at higher levels of pH, when the CO₂ equilibrium shifts toward bicarbonate or carbonate, CO₂ becomes unavailable. In these conditions, perhaps the CO₂ is transformed from bicarbonates in some taxa by lower pH values at the moss-water interface, but no experimental evidence has verified this hypothesis. Thus, the number of mosses growing in alkaline waters is limited, and it seems that many of the ones that do occur in alkaline waters are adapted to growing in the highly aerated water of waterfalls and rapids, as, for example, *Fissidens grandifrons* (Figure 41) (pers. obs.). Some grow in very cold glacial meltwater in which more CO₂ is soluble (Vitt *et al.* 1986). Others are restricted to the splash zone at the edge of the water, where CO₂ is trapped as the water moves through the air, as in *Cratoneuron* (Figure 42) species (Vitt *et al.* 1986; Glime & Vitt 1987).

When mosses live at great depths, light and temperature can be low. The ability of mosses to grow slowly reduces their need for CO₂ and light. In great depths of Lake Grane Langos, Denmark, *Sphagnum subsecundum* (Figure 43) and *Drepanocladus exannulatus* (Figure 44) grew faster in deep water than in shallow water! (Riis & Sand-Jensen 1997). Riis and Sand-Jensen concluded that this more rapid growth at greater depths was possible due to lower temperatures that permitted more CO₂ to remain dissolved, CO₂

supersaturation, and nutrient enrichment from the sediments below the thermocline.

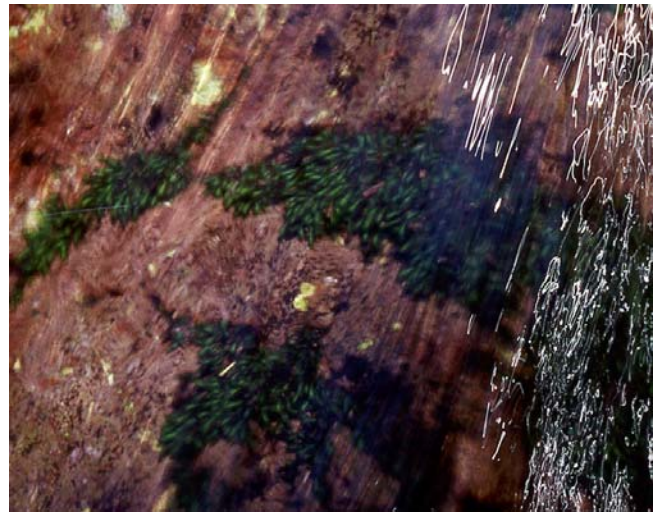


Figure 41. *Fissidens grandifrons*, in fast-flowing water where there is more CO₂ than in quiet water. Photo by Janice Glime.



Figure 42. *Cratoneuron commutatum* var. *fluctuans* at the edge of water. Photo by Michael Lüth, with permission.



Figure 43. *Sphagnum subsecundum*, a species that takes advantage of CO₂ supersaturation in deep water. Photo by Michael Lüth, with permission.



Figure 44. *Drepanocladus exannulatus*, a species that takes advantage of CO₂ supersaturation in deep water. Photo by Michael Lüth, with permission.

Role of pH

In the aquatic system, pH is important in determining the chemical fate of the CO₂. Under acidic conditions, it remains dissolved as CO₂. But if the water is warm, the CO₂ gas is easily lost to the atmosphere.

At circum-neutral pH levels, the CO₂ in water is converted to bicarbonate. At least some tracheophytes are able to use bicarbonates, but studies on use by bryophytes are ambiguous. In basic waters, carbonates are formed and cannot be used by any of the plants.

In situations of higher pH, CO₂ can be present for a short time as it is released from sediments or trapped in turbulent water (Lovalvo *et al.* 2010). Bryophytes could take advantage of these ephemeral concentrations before they are converted to unusable forms.

Within the cell, the enzyme **carbonic anhydrase** converts bicarbonates to CO₂ in both bryophytes and tracheophytes (Steeman Nielsen & Kristiansen 1949; Arancibia & Graham 2003). Some tracheophytes use extracellular carbonic anhydrase to convert bicarbonates to free CO₂ (Allen & Spence 1981). There is no direct evidence that bryophytes can use bicarbonates (James 1928; Ruttner 1947; Steeman Nielsen 1947; Bain & Proctor 1980; Allen & Spence 1981; Osmond *et al.* 1981; Glime & Vitt 1984; Prins & Elzenga 1989; Madsen *et al.* 1993; Ballesteros *et al.* 1998; Raven *et al.* 1998); nevertheless, some bryophytes are able to live in the pH range of bicarbonates. I have an unconfirmed suspicion that bryophytes may convert limited amounts of bicarbonate to CO₂ at the leaf surface, perhaps by the presence of H⁺ released from exchange sites.

To further complicate the story, Farmer *et al.* (1986) found that the aquatic moss *Fontinalis antipyretica* (Figure 27) has no **PEP carboxylase** and uses only Rubisco for its fixation of CO₂ in photosynthesis, supporting the earlier conclusion of Steeman Nielsen (1947) that *F. antipyretica* cannot use bicarbonates from the water for its photosynthesis. Nevertheless, Harder (1921) had already shown that *F. antipyretica* increased its net assimilation from 0.01 to 0.64% when bicarbonate concentration was raised from 0.66 to 3.14 as HCO₃⁻. Later, Burr (1941) likewise demonstrated greater productivity in this species in water with more bicarbonate than in that with CO₂.

Steeman Nielsen and Kristiansen (1949) offered a possible explanation – that CO₂ might enter photosynthetic reactions in its hydrated form, *i.e.* as bicarbonate.

Bain and Proctor (1980) found that of the 20 aquatic species tested from a variety of habitats, all but the hornwort *Anthoceros husnotii* (Figure 45) with pyrenoids had pH compensation points in the range expected for CO₂-dependent C₃ plants. Nevertheless, many studies support the concept that all aquatic mosses are C₃ plants (Ruttner 1947; Allen & Spence 1981; Osmond *et al.* 1981; Salvucci & Bowes 1981; Raven 1991; Raven *et al.* 1987, 1994, 1998), despite some living in conditions that have CO₂ concentrations below the expected CO₂ compensation point.



Figure 45. *Anthoceros husnotii*, a species with pyrenoids, giving it a different pH compensation point from that of non-hornworts. Photo from Earth.com, with permission.

Peñuelas (1985) demonstrated what appeared to be use of NaHCO₃ (sodium bicarbonate) by *Fontinalis antipyretica* (Figure 27) as a carbon source. During photosynthesis by this species, the pH increased to 9.6, indicating a CO₂ compensation point of 1.1 mM m⁻³ CO₂. This photosynthetic rate was higher than could be explained by CO₂ alone and when HCO₃⁻ levels were increased, the photosynthetic rate likewise increased, even though CO₂ levels in the water were held constant. In fact, photosynthesis continued until the pH reached 11.8-12.0 for *F. antipyretica* and 10.10 for the alkaline-tolerant *Fissidens grandifrons* (Figure 41). But to further confuse the issue, in a different stream, Peñuelas found that *F. antipyretica* could not use HCO₃⁻ to photosynthesize, suggesting either different physiological races or different acclimation to conditions. We know that there are genetic differences among populations of this highly variable species (Shaw & Allen 2000). Even if these genetic differences are expressed as a physiological mechanism to use bicarbonate, we still do not understand what that mechanism might be!

Bogs

Hummocks present unique habitats, and their CO₂ relations are no exception. Rydin and Clymo (1989)

described their upper parts as obtaining CO₂ from air rather than water between the *Sphagnum* (Figure 28) plants, depending on high CO₂ concentrations in the **acrotelm** (living layer of peat) water. In fact, they found that the CO₂ concentration in that layer was twice that in the outside atmosphere (Rydin & Clymo 1989; Smolders *et al.* 2001).

As the atmospheric levels of CO₂ rise and N deposition provides critical and often limiting nutrients, the composition of plant communities changes. This is particularly true in *Sphagnum* (Figure 46-Figure 51) bogs (Berendse *et al.* 2001). In this case, we expect productivity of tracheophytes to increase as they benefit from greater CO₂, often decreasing the competitiveness of the bryophytes and causing tracheophyte expansion. *Sphagnum* is one of the most important groups of plants to serve as a carbon sink in the Northern Hemisphere, facilitated by its slow decomposition. But when Berendse and coworkers studied the effects of raised CO₂ and N on *Sphagnum* and other plants in four locations in Western Europe, the elevated CO₂ had no effect on *Sphagnum* biomass increase. N, on the other hand, caused a decrease in *Sphagnum* growth due to competition.

In a bog in the Netherlands, *Sphagnum divinum* (previously in *S. magellanicum*; Figure 46) benefitted from elevated CO₂ by exhibiting increased growth in height in the second and third growing seasons (Heijmans *et al.* 2001). Tracheophytes that grew close to the more rapidly growing *S. divinum* were affected negatively by the increased *Sphagnum* height. Mitchell *et al.* (2002) found that on one harvested peatland the initial colonizer was *Polytrichum strictum* (Figure 5). Under a treatment of added CO₂ (560 ppm), the later colonizer *Sphagnum fallax* (Figure 47) was able to successfully compete with the *P. strictum*.



Figure 46. *Sphagnum divinum*, a species that increases in height growth when living in higher CO₂ levels. Photo by David Holyoak, with permission.

Van der Heijden *et al.* (2000a) found that not all *Sphagnum* had the same response to elevated CO₂. *Sphagnum papillosum* (Figure 48), an oligo-mesotrophic species, benefitted in growth from elevated CO₂ (720 ppm). On the other hand, the ombrotrophic *S. balticum* (Figure 49) received no growth benefit, despite elevated sugar in stems and capitula in both species. Unlike many of the studies discussed in subchapter 8-1, in this case additional

N along with elevated CO₂ benefitted *S. papillosum*, but it had no effect on *S. balticum*. Doubling CO₂ without N addition cause lower N levels in both species.



Figure 47. *Sphagnum fallax*, a species that competes better in an atmosphere with higher CO₂. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum papillosum* with sundew. Photo by Michael Lüth.



Figure 49. *Sphagnum balticum*, a species that does not benefit when additional N accompanies elevated CO₂. Photo by Michael Lüth, with permission.

The response of *Sphagnum fallax* (Figure 50) may explain the elevated sugars (van der Heijden *et al.* 2000b).

Initially, elevated CO₂ stimulated photosynthesis, but after 3 days of exposure it was down-regulated to pre-elevation values. However, the elevated CO₂ continued to cause reduced dark respiration. At the same time there was a continuous increase in soluble sugar in the capitula. Doubling the CO₂ caused a decrease of N in the capitula, but not in the stems. This N reduction was coupled with a decrease in amino acids but did not affect soluble protein levels, causing a shift in N partitioning.



Figure 50. *Sphagnum fallax*, a species that stores elevated sugars when the CO₂ is elevated. Photo by Jan-Peter Frahm, with permission.

Not all *Sphagnum* grows in hummocks. *Sphagnum cuspidatum* (Figure 51) grows primarily submerged. When it was subjected to added CO₂ for 12 weeks, only the highest CO₂ concentration in the water caused increased growth in length and biomass (Paffen & Roelefs 1991).



Figure 51. *Sphagnum cuspidatum*, a submerged moss that is indifferent to added CO₂ until the levels are quite high. Photo by Michael Lüth, with permission.

In addition, some bryophytes may be able to tap into a source of carbon we usually don't consider in bryophytes. Rydin and Clymo (1989) have demonstrated that at least in *Sphagnum* the fixed carbon can be transported within the stem. Using ¹⁴C labelling on *Sphagnum papillosum* (Figure 48), they found almost the entire alcohol-soluble fraction moved from older parts to the apex, with little transfer of the insoluble fraction.

Methane

Methane (CH₄) is the product of **anaerobic** (no oxygen) bacterial breakdown. In several bogs of Canada, the highest emissions occurred in raised-bog and patterned-poor-fen pools where the peat is degrading (Bubier 1995). Methane is much more effective as a greenhouse gas compared to CO₂. And wetlands are the largest natural source for methane. Submerged *Sphagnum* (Figure 51) uses methane that is converted through symbiosis with partly endophytic **methanotrophic** (able to gain carbon from methane) bacteria, leading to highly effective *in situ* methane recycling (Raghoebarsing *et al.* 2005). These bacteria live in the hyaline cells and on leaves where they convert the methane to CO₂. This conversion provides 10-15% of the carbon source for these *Sphagnum* species.

CO₂ and Desiccation Tolerance

Syntrichia ruralis (Figure 21) is a common desiccation-tolerant moss. When subjected to elevated CO₂ it showed increased net CO₂ uptake in high CO₂ conditions by more than 30% (Tuba *et al.* 1998). Both desiccation-tolerant and non-tolerant plants, bryophytes included, show initial positive responses of photosynthesis to elevated CO₂, but both groups exhibit reduced or even reversed photosynthetic rates in the longer term (Tuba *et al.* 1999). This slightly later study implies that increased CO₂ levels will have little advantage for either group of bryophytes.

Translocation

Rydin and Clymo (1989) found that carbon is transported within *Sphagnum* (Figure 50) plants. This could provide a physiological mechanism that moves older carbon compounds from deeper parts of the peatlands upward. This could dilute the ¹⁴C pool within the living plant and change both the location and the proportions of ¹²C, ¹³C, and ¹⁴C. If *Sphagnum* is able to take in carbon from deep sediments and move it upward in the water column, this would result in false readings for carbon dating. Might the moss be preferentially moving ¹²C upward from older peat and thus reducing its proportion of ¹⁴C? If so, we need to re-evaluate our methods for dating peat.

By contrast, it appears that mosses like *Grimmia* (Figure 52) that receive their water from above can actually move carbon as photosynthate from the tip of the plant to the base and even to underground parts, much as we would find in a tree (Alpert 1989). Lacking any specialized conducting cells, this moss presents a puzzle as to its mechanism of movement, although as we shall see later in this chapter, it uses the source-sink principle used by tracheophytes.



Figure 52. *Grimmia caespiticia*, a moss that moves photosynthetic carbon from the tip to the base. Photo by Michael Lüth, with permission.

Importance of Bryophytes in C Cycling

Porada *et al.* (2013) estimated that the terrestrial net uptake of carbon by bryophytes and lichens is 0.34 to 3.3 Gt yr⁻¹ (gigatons). This appears to be small until you consider bogs and polar habitats where bryophytes dominate the vegetation. In those locations, the bryophytes are significant carbon sinks.

Turetsky (2003) noted that bryophyte growth and metabolism have a direct influence on the carbon flux into the ecosystem. She found that annual accumulations of C in the bryophytes are a better measure for understanding the carbon cycle. Growth of such species as those of *Sphagnum* (Figure 46-Figure 52) can range from ~19-1,656 g m⁻² yr⁻¹, with carbon comprising about 48% of this biomass. Feather mosses in the boreal forest have a net primary productivity ranging 24-80 g C m⁻² yr⁻¹. In the Antarctic, *Polytrichum juniperinum* (Figure 53) has a net primary productivity of 213-350 g m⁻² yr⁻¹, whereas *Chorisodontium aciphyllum* (Figure 54) living there has 162 g m⁻² yr⁻¹ (Fenton 1980). Nevertheless, Turetsky noted with surprise that the bryophyte net primary productivity (NPP) of polar, boreal, and temperate regions were comparable.



Figure 53. *Polytrichum juniperinum*, a species that has a net primary productivity of 213-350 g m⁻² yr⁻¹ in the Antarctic. Photo by Bob Klips, with permission.



Figure 54. *Chorisodontium aciphyllum*, a species that has a net primary productivity of 162 g m⁻² yr⁻¹ in the Antarctic. Photo by Matt Amesbury, through Creative Commons.

Flushing contributes loss of carbon from plant and litter layers, particularly following desiccation (Turetsky 2003). Soluble organic compounds are lost as membranes become distended and cannot continue to retain the soluble contents. During rewetting, these leaked compounds can become leached to the environment (Proctor 1982; Wilson & Coxson 1999). Mats of the boreal/alpine moss *Hylocomium splendens* (Figure 22-Figure 23) released a pulse of organic carbon equivalent to -15 kg ha⁻¹ following rain events (Wilson & Coxson 1999). The soluble C from living *H. splendens* was 23-75% of that released. Tropical epiphytes can release equivalent to 122 kg ha⁻¹ yr⁻¹ of soluble sugars (Coxson *et al.* 1992).

The carbohydrate leachates from the boreal forest moss *Pleurozium schreberi* (Figure 55) can support the growth of mycorrhizal fungi and can even reach *Pinus contorta* (Figure 56) through this pathway (Carleton & Read 1991). Similarly, soluble carbohydrates can penetrate to deeper layers of peatlands and wetlands where they are taken up by microbes (Charman *et al.* 1999; Chasar *et al.* 2000). They further influence this activity by providing suitable habitat for invertebrates (Gersen 1982; Merrifield & Ingham 1998) that break up the bryophytes into smaller pieces that provide more surface area for the microbes to colonize. Microfungi associated with the bryophytes can decompose organic carbon (Tsuneda *et al.* 2001; Thormann *et al.* 2002). Any of this released carbon can also be exported to streams and lakes (Schindler *et al.* 1997; Carpenter *et al.* 1998; Elder *et al.* 2000).



Figure 55. *Pleurozium schreberi*, a moss species in which carbon leachates support the mycorrhizal fungi of *Pinus contorta*. Photo by Rob Routledge, through Creative Commons.



Figure 56. *Pinus contorta*, a species that can benefit from mycorrhizae that use carbon leachates from mosses. Photo by Walter Siegmund, through Creative Commons.

The bryophytes have physical effects on the return of carbon from other plants. They can reduce soil temperature and increase soil moisture, thus affecting the rate of decay and carbon cycling (Van Cleve *et al.* 1983; Sveinbjornsson & Oechel 1992; Eckstein 2000). Their external capillary action enhances the possibilities for decomposition (Turetsky 2003).

Climate Change – an Antarctic Problem

Bryophytes in the Antarctic must contend with large temperature fluctuations within a single day. Pannewitz *et al.* (2005) note the importance of understanding the effects of climate change on the bryophyte component in order to predict the effects of climate change on vegetation there. Their results from variations in temperature, light, moisture content, and CO₂ suggested that it would be very difficult to predict the effects of climate change on these communities. Increases in temperature are likely to cause increases in CO₂ as long-standing dead portions begin to decay. They found that there was a large response to increases in CO₂ by two of the three bryophytes they tested [*Bryum pseudotriquetrum* (Figure 57), *B. subrotundifolium* (Figure 58)], with increasing temperatures causing a greater response. CO₂ saturation wasn't reached at the 20°C temperature tested. *Bryum pseudotriquetrum* exhibited no saturation up to 2000 ppm CO₂ at 20°C. *Bryum subrotundifolium*, however, became saturated above 1000 ppm. Thus CO₂ was limiting for both species at the ambient CO₂ of 360 ppm.

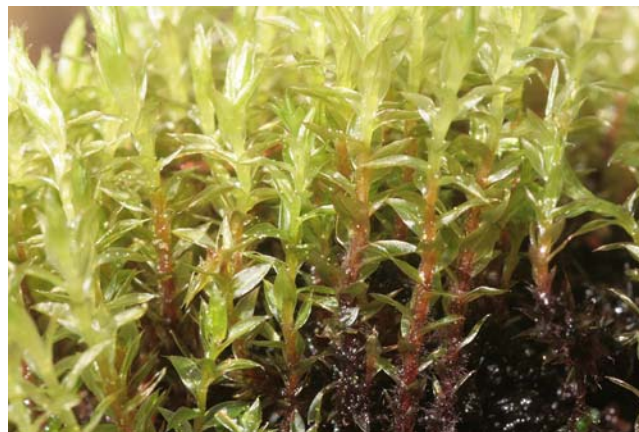


Figure 57. *Bryum pseudotriquetrum*, a species whose CO₂ saturation is above 2000 ppm. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Bryum subrotundifolium*, an Antarctic bryophyte in which CO₂ saturation is reached when CO₂ exceeds 1000 ppm. Photo by Rod Seppelt, with permission.

On the other hand, *Hylocomium splendens* (Figure 22-Figure 23) (Sonesson *et al.* 1996) and Arctic tracheophytes (Oechel *et al.* 1997) demonstrated that such enhancement of photosynthesis could be short-lived. This short-term enhancement could be the result of rapidly reaching nutrient limitation (Oechel & Billings 1992). However, in the Antarctic nutrients are rarely limiting (Kappen & Schroeter 2002), at least in part due to the rich guana deposits (Green *et al.* 2000a, b). Nevertheless, Pannewitz and coworkers (2000) concluded that increased CO₂ in the atmosphere would probably not have long-term effects because the ambient levels might already be high in the Antarctic. On the other hand, I would expect that increased temperatures there would increase the very slow rate of decomposition, thus potentially causing great increases of CO₂ for the bryophytes at the ground level where they live.

Bryophytes and tracheophytes might respond differently to CO₂ and climate change. Green *et al.* (1998) found that the relationships between the electron transfer rate (ETR) and CO₂ in photosynthesis of bryophytes differs from that found in tracheophytes. Dark respiration responds strongly to cause substantial changes in CO₂ exchange rates. In Antarctic populations of *Bryum argenteum*, there is a strong linear relationship between gross photosynthesis and the electron transfer rate, an unusual response exhibited by the C₃ bryophytes compared to that of C₃ tracheophytes. This relationship varied with temperature; Green and coworkers suggested that light suppression of dark respiration might be involved.

Summary

The early atmosphere had considerably more CO₂ than the current one. However, in the last 60 years, CO₂ concentrations have risen from 315 to 404 ppm in the atmosphere.

Soils release CO₂ through respiration by bacteria, fungi, and other soil organisms. Bryophytes are able to trap much of this CO₂ before it reaches the atmosphere.

Thallose liverworts may have a spongy interior with pores to facilitate exposure of internal photosynthetic cells to CO₂. Mosses are C₃ plants that benefit from high CO₂ concentrations and cool to moderate temperatures (up to 25°C). They have difficulty obtaining CO₂ when they are wet and the presence of cuticular waxes in species such as *Polytrichum* spp. and *Saellania glaucescens* facilitates the absorption of CO₂ by repelling water. *Sphagnum* keeps its photosynthetic cells moist on 2-3 sides while permitting 1-2 sides to be exposed to the atmosphere.

Hornworts may have pyrenoids that concentrate CO₂ around the enzyme Rubisco, facilitating photosynthesis. Some aquatic mosses may be able to concentrate CO₂ and this may be facultative, being enhanced on hot days. In acid conditions they use CO₂ dissolved in the water, but some evidence suggests that in the mid-pH range some species may be able to use bicarbonates.

Some bryophytes can use amino acids. At least some *Sphagnum* species use methane as a carbon source. And some species can move C up or down within the plant.

Bryophytes, especially in wet habitats, may be able to move water up from sediments, taking advantage of decompositional carbon. Others may move photosynthate from actively growing apical parts to lower parts for storage.

Bryophytes may serve as carbon sinks, especially in peatlands.

Acknowledgments

I appreciate the contributions of undergraduate Phil Gaudette and M. S. student Jennifer Jermalowicz Jones for their critical reading of the manuscript from the perspectives of students interested in nutrient relationships of bryophytes. Stephen Rice helped to clarify the carbon discussion.

Literature Cited

- Allen, E. D. and Spence, D. H. N. 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytol.* 87: 269-283.
- Alpert, P. 1989. Translocation in the nonpolytrichaceous moss *Grimmia laevigata*. *Amer. J. Bot.* 76: 1524-1529.
- Arancibia, P. and Graham, L. 2003. Carbonic anhydrase in Charophyceae and bryophytes. Abstract, p. 65. Botany 2003, Aquatic and Wetland Plants: Wet & Wild, Botanical Society of America, Mobile.
- Bain, J. T. and Proctor, M. C. F. 1980. The requirement of aquatic bryophytes for free CO₂ as an inorganic carbon source: Some experimental evidence. *New Phytol.* 86: 393-400.
- Ballesteros, D., García-Sánchez, M. J., Heredia, M. A., Felle, H., and Fernández, J. A. 1998. Inorganic carbon acquisition in *Riccia fluitans* L. *J. Exper. Bot.* 49: 1741-1747.
- Berendse, F., Breemen, N. van, Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., Lee, J. A., Mitchell, E., Saarinen, T., Vasander, H., and Wallen, B. 2001. Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biology* 7: 591-598.
- Botting, R. S. and Fredeen, A. L. 2006. Net ecosystem CO₂ exchange for moss and lichen dominated forest floors of old-growth sub-boreal spruce forests in central British Columbia, Canada. *Forest Ecol. Mgmt.* 235: 240-251.
- Bubier, J. L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J. Ecol.* 83: 403-420.
- Burr, G. O. 1941. Photosynthesis of algae and other aquatic plants. In: Needham, J. G. (ed.). Symposium on Hydrobiology. University of Wisconsin Press, Madison, pp 163-181.
- Carpenter, S. R., Cole, J. J., Kitchell, J. F., and Pace, M. L. 1998. Impact of dissolved organic carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. *Limnol. Oceanogr.* 43: 73-80.
- Charman, D. J., Aravena, R., Bryant, C. L., and Harkness, D. D. 1999. Carbon isotopes in peat, DOC, CO₂, and CH₄ in a Holocene peatland on Dartmoor, southwest England. *Geology* 27: 539-542.
- Chasar, L. S., Chanton, J. P., Glaser, P. H., Siegel, D. I., and Rivers, J. S. 2000. Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH₄ in a northern Minnesota peatland. *Global Biogeochem. Cycles* 14: 1095-1108.
- Cleve, K. van, Dyrness, C. T., Vierack, L. A., Fox, J., Chapin, F. S. III, and Oechel, W. C. 1983. Taiga ecosystems in interior Alaska. *Bioscience* 33: 39-44.
- Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest Guadeloupe French West Indies. *Biotropica* 24: 121-133.
- Csintalan, Z., Takács, A., Tuba, Z., Proctor, M. C. F., Smirnov, N., and Grace, J. 1997. Desiccation tolerant grassland cryptogams, under elevated CO₂, preliminary findings. *Abstr. Biol.* 21: 309-315.
- DeLucia, E. H., Turnbull, M. H., Walcroft, A. S., Griffins, K. L., Tissue, D. T., Glenn, D., McSeveny, T. M., and Whitehead, D. 2003. The contribution of bryophytes to the carbon exchange for a temperate rainforest. *Global Change Biol.* 9: 1158-1170.
- Dilks, T. J. K. 1976. Measurement of the carbon dioxide compensation point and rate of loss of ¹⁴CO₂ in the light and dark in some bryophytes. *J. Exper. Bot.* 27: 98-104.
- Eckstein, R. L. 2000. Nitrogen retention by *Hylocomium splendens* in a subarctic birch woodland. *J. Ecol.* 88: 506-515.
- Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Jüdel, B., Meinrat, O. A., and Pöschl, L. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat. Geosci.* 5: 459-462.
- Elder, J. F., Rybicki, N. B., Carter, V., and Weintraub, V. 2000. Sources and yields of dissolved carbon in northern

- Wisconsin stream catchments with differing amounts of peatland. *Wetlands* 20: 113-125.
- Farmer, A. M., Maberly, S. C., and Bowes, G. 1986. Activities of carboxylation enzymes in freshwater macrophytes. *J. Exper. Bot.* 37: 1568-1573.
- Fenton, J. H. C. 1980. The rate of peat accumulation in Antarctic moss banks. *J. Ecol.* 68: 211-228.
- Fletcher, B. J., Beerling, D. J., and Brentnall, S. J. 2005. Fossil bryophytes as recorders of ancient CO₂ levels: Experimental evidence and a Cretaceous case study. *Global Biogeochem. Cycles* 19: GB2012.
- Gersen, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, NY, pp. 291-332.
- Glime, J. M. and Vitt, D. H. 1984. The physiological adaptations of aquatic Musci. *Lindbergia* 10: 41-52.
- Glime, J. M. and Vitt, D. H. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. *Can. J. Bot.* 65: 1824-1837.
- Graham, L., Lewis, L. A., Taylor, W., Wellman, C., and Cook, M. 2014. Early terrestrialization: Transition from algal to bryophyte grade. In: Hanson, D. T. and Rice, S. K. (eds.). *Photosynthesis in Bryophytes and Early Land Plants*. *Advances in Photosynthesis and Respiration* 37: 9-28.
- Green, T. G. A., Schroeter, B., Kappen, L., Seppelt, R. D., and Maseyk, K. 1998. An assessment of the relationship between chlorophyll a fluorescence and CO₂ gas exchange from field measurements on a moss and lichen. *Planta* 206: 611-618.
- Green, T. G. A., Maseyk, K., Pannewitz, S., and Schroeter, B. 2000a. Extreme elevated *in situ* carbon dioxide levels around the moss *Bryum subrotundifolium* Jaeg., Ber. S. Gall. in Antarctica. *Biblio. Lichenol.* 75: 397-403.
- Green, T. G. A., Schroeter, B., and Seppelt, R. D. 2000b. Effect of temperature, light and ambient UV on the photosynthesis of the moss *Bryum argenteum* Hedw. in continental Antarctica. In: Davidson, W., Howard-Williams, C., and Broady, P. (eds.). *Antarctic ecosystems: Models of wider ecological understanding*. Caxton Press, Christchurch, New Zealand, pp. 165-170.
- Hanson, D., Andrews, T. J., and Badger, M. R. 2002. Variability of the pyrenoid-based CO₂ concentrating mechanism in hornworts (Anthocerotophyta). *Funct. Plant Biol.* 29: 407-416.
- Hanson, D. T., Renzaglia, K., and Villarreal, J. C. 2014. In tracheophytes, Diffusion limitation and CO₂ concentrating mechanisms in bryophytes. In: Hanson, D. T. and Rice, S. K. (eds.). *Photosynthesis in Bryophytes and Early Land Plants*. *Advances in Photosynthesis and Respiration* 37: 95-111.
- Harder, R. 1921. Kritische Versuche zu Blackmans Theorie der begrenzenden Faktoren bei der Kohlensaureassimilation. *Jahrb. Wiss. Bot.* 60: 531-571.
- Heal, O. W. 1979. The decomposition and nutrient release in even-aged plantations. In: Ford, E. D., Malcolm, D. C., and Atterson, J. (eds.). *The Ecology of Even-aged Forest Plantations*. Institute of Terrestrial Ecology, Cambridge, pp. 257-291.
- Heijden, E. van der, Jauhiainen, J., Silvola, J., Vasanden, H., and Kuiper, R. J. P. 2000a. Effects of elevated atmospheric CO₂ concentration and increased nitrogen deposition on growth and chemical composition of ombrotrophic *Sphagnum balticum* and oligo-mesotrophic *Sphagnum papillosum*. *J. Bryol.* 22: 175-182.
- Heijden, E. van der, Verbeek, S. K., and Kuiper, R. J. P. 2000b. Elevated atmospheric CO₂ and increased nitrogen deposition: Effects of C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. *Global Change Biol.* 6: 201-212.
- Heijmans, M. M. P. D., Berendse, F., Arp, W. J., Maaseliuk, A. K., Klees, H., Visser, W. De, and Breeman, N. van. 2001. Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. *J. Ecol.* 89: 269-279.
- Holtum, J. A. M. and Winter, K. 2001. Are plants growing close to the floors of tropical forests exposed to markedly elevated concentrations of carbon dioxide? *Austral. J. Bot.* 49: 629-636.
- James, W. O. 1928. Experimental researches on vegetable assimilation and respiration. XIX. The effect of variations of carbon dioxide supply upon the rate of assimilation of submerged water plants. *Proc. Royal Soc. London Ser B* 103: 1-42.
- Jauhiainen, J. and Silvola, J. 1999. Photosynthesis of *Sphagnum fuscum* at long-term raised CO₂ concentrations. *Ann. Bot. Fenn.* 36: 11-19.
- Kappen, L. and Schroeter, B. 1997. Activity of lichens under the influence of snow and ice. *Proceedings NIPR Symposium on Polar Biology* 10: 163-168.
- Lovalvo, D., Clingenpeel, S. R., McGinnis, S., Macur, R. E., Varley, J. D., Inskeep, W. P., Glime, J., Neelson, K., and McDermott, T. R. 2010. A geothermal-linked biological oasis in Yellowstone Lake, Yellowstone National Park, Wyoming. *Geobiology* 8: 327-336.
- MacDonald, G. M., Beukens, R. P., Kieser, W. E., and Vitt, D. H. 1987. Comparative radiocarbon dating of terrestrial plant macrofossils and aquatic moss from the "ice-free corridor" of western Canada. *Geology* 15: 837-840.
- Madsen, T. V., Enevoldsen, H. O., and Jorgensen, T. B. 1993. Effects of water velocity on photosynthesis and dark respiration in submerged stream macrophytes. *Plant Cell Environ.* 16: 317-322.
- Merrifield, K. and Ingham, R. E. 1998. Nematodes and other aquatic invertebrates in *Eurhynchium oreganum* from Mary's peak, Oregon Coast Range. *Bryologist* 101: 505-511.
- Meyer, M., Seibt, U., and Griffiths, H. 2008. To concentrate or ventilate? Carbon acquisition, isotope discrimination and physiological ecology of early land plant life. *Philosoph. Trans. Royal Soc. B-Biol. Sci.* 363: 2767-2778.
- Mitchell, E. A., Buttler, A., Grosvernier, P., Rydin, H., Siegenthaler, A., and Gobat, J. M. 2002. Contrasted effects of increased N and CO₂ supply on two keystone species in peatland restoration and implications for global change. *J. Ecol.* 90: 529-533.
- Oechel, W. C. and Billings, W. D. 1992. Anticipated effects of global change on carbon balance of Arctic plants and ecosystems. In: Chapin, F. S. I., Jefferies, R. L., Reynolds, J., Shaver, G., and Svoboda, J. (eds.). *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 139-169.
- Oechel, W. C., Cook, A. C., Hastings, S. J., and Vourlitis, G. L. 1997. Effects of CO₂ and climate change on Arctic ecosystems. In: Woodin, S. J. and Marquis, M. (eds.). *Ecology of Arctic Environments*. Cambridge University Press, Cambridge, pp. 255-273.
- Osmond, C. B., Valanne, N., Haslam, S. M., Votila, P., and Roksandic, Z. 1981. Comparisons of $\delta^{13}\text{C}$ values in leaves of aquatic macrophytes from different habitats in Britain and

- Finland: Some implications for photosynthetic processes in aquatic plants. *Oecologia* 50: 117-124.
- Paffen, B. G. P. and Roelefs, J. G. M. 1991. Impact of carbon dioxide and ammonium on the growth of submerged *Sphagnum cuspidatum*. *Aquat. Bot.* 40: 61-71.
- Pannowitz, S., Green, T. A., Maysek, K., Schlensog, M., Seppelt, R., Sancho, L. G., Türk, R., and Schroeter, B. 2005. Photosynthetic responses of three common mosses from continental Antarctica. *Antarc. Sci.* 17: 341-352.
- Peñuelas, J. 1985. HCO₃⁻ as an exogenous carbon source for aquatic bryophytes *Fontinalis antipyretica* and *Fissidens grandifrons*. *J. Exper. Bot.* 36: 441-448.
- Porada, P., Weber, B., Elbert, W., Pöschl, U., and Kleidon, A. 2013. Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosciences* 10: 6989-7033.
- Prins, H. B. A. and Elzenga, J.T. M. 1989. Bicarbonate utilization: Function and mechanism. *Aquat. Bot.* 34: 59-83.
- Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. G. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, NY, pp. 333-381.
- Proctor, M. C. F. 1984. Structure and ecological adaptation. In: Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*. Academic Press, London, pp 9-37.
- Proctor, M. C. F. 2010. Trait correlations in bryophytes: Exploring an alternative world. *New Phytol.* 185: 1-3.
- Raghoebarsing, A. A., Smolders, A. J., Schmid, M. C., Rijpstra, W. I. C., Wolters-Arts, M., Derksen, J., Jetten, M. S. M., Schouten, S., Damste, J. S. S., Lamers, L. P. M., Toelofs, J. G. M., Camp, H. J. M. Op den, and Strous, M. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* 436: 1153-1156.
- Raven, J. A. 1991. Implications of inorganic carbon utilization: Ecology, evolution, and geochemistry. *Can. J. Bot.* 69: 908-924.
- Raven, J. A. 2002. Selection pressures on stomatal evolution. *New Phytol.* 153: 371-386.
- Raven, J. A. and Edwards, D. 2014. Photosynthesis in early land plants: Adapting to the terrestrial environment. In: Hanson, D. T. and Rice, S. K. (eds.). *Photosynthesis in Bryophytes and Early Land Plants*. *Advances in Photosynthesis and Respiration* 37: 9-28.
- Raven, J. A., MacFarlane, J. J., and Griffiths, H. 1987. The application of carbon isotope techniques. In: Crawford R. M. M. (ed.). *Plant Life in Aquatic and Amphibious Habitats*, pp 129-144. British Ecological Society Special Symposium, Blackwell, Oxford.
- Raven, J. A., Johnson, A. M., Newman, J. R., and Scrimgeour, C. M. 1994. Inorganic carbon acquisition by aquatic photolithotrophs of the Dighty Burn, Angus, UK: Uses and limitations of natural abundance measurements of carbon isotopes. *New Phytol.* 127: 271-286.
- Raven, J. A., Griffiths, H., Smith, E. C., and Vaughn, K. C. 1998. New perspectives in the biophysics and physiology of bryophytes. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). *Bryology in the Twenty-first Century*. Maney Publishing and the British Bryological Society, UK, pp. 261-275.
- Rice, S. K. 2000. Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. *Oecologia* 123: 1-8.
- Riis, T. and Sand-Jensen, K. 1997. Growth reconstruction and photosynthesis of aquatic mosses: Influence of light, temperature and carbon dioxide at depth. *J. Ecol.* 85: 359-372.
- Robinson, H. 1985. The structure and significance of the leucobryaceous leaf. *Monogr. Syst. Bot. Missouri Bot. Gard.* 11: 111-120.
- Ruttner, F. 1947. Zur Frage der Karbonatassimilation der Wasserpflanzen, I. *Österr. Bot. Zeits.* 94: 265-294.
- Rydin, H. and Clymo, R. S. 1989. Transport of carbon and phosphorus compounds about *Sphagnum*. *Proc. Roy. Soc. London B* 237: 63-84.
- Salvucci, M. E. and Bowes, G. 1981. Induction of reduced photorespiration activity in submersed and amphibious aquatic macrophytes. *Plant Physiol.* 67: 335-340.
- Schindler, D. W., Curtis, P. J., Bayley, S. E., Parker, B. R., Beaty, K. G., and Stainton, M. P. 1997. Climate-induced changes in the dissolved organic budgets of boreal lakes. *Biogeochemistry* 36: 9-28.
- Schippberger, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytol.* 140: 677-684.
- Scripps CO₂ Program 2016. Accessed 19 January 2017 at <http://scrippsco2.ucsd.edu/research/atmospheric_co2>
- Shaw, A. J. and Allen, B. 2000. Phylogenetic relationships, morphological incongruence, and geographic speciation in the Fontinalaceae (Bryophyta). *Molec. Phylog. Evol.* 16: 225-237.
- Shinde, S., Behpouri, A., McElwain, J. C., and Ng, C. K.-Y. 2015. Genome-wide transcriptomic analysis of the effects of sub-ambient oxygen and elevated atmospheric carbon dioxide levels on gametophytes of the moss, *Physcomitrella patens*. *J. Exper. Bot.* 66: 4001-4012.
- Silvola, J. 1985. CO₂ dependence of photosynthesis in certain forest and peat mosses and simulated photosynthesis at various actual and hypothetical CO₂ concentrations. *Lindbergia* 11: 86-93.
- Silvola, J. 1991. Moisture dependence of CO₂ exchange and its recovery after drying in certain boreal forest and peat mosses. *Lindbergia* 17: 5-10.
- Simola, L. K. 1969. The effect of various mono- and disaccharides on the growth of *Sphagnum nemoreum* thalli in sterile cultures. *Physiol. Plant.* 22: 1079-1084.
- Šimůnek, J. and Suarez, D. L. 1993. Carbon dioxide transport and production in soil. 1. Model development. *Water Res. Res.* 29: 487-497.
- Smolders, A. J. P., Tomasson, H. B. H., Pijnappel, H. W., Lamers, L. P. H., and Roelefs, J. G. M. 2001. Substrate derived CO₂ is important in the development of *Sphagnum* spp. *New Phytol.* 152: 325-332.
- Sommerkorn, M., Bölter, M., and Kappen, L. 1999. Carbon dioxide fluxes of soils and mosses in wet tundra of Taimyr Peninsula, Siberia: Controlling factors and contribution of net system fluxes of CO₂ from soil respiration and moss respiration. *Polar Res.* 18: 253-260.
- Sonesson, M., Carola, G., and Martin, T. 1992. CO₂ environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. *Oecologia* 92: 23-29.
- Sonneson, M., Callaghan, T. V., and Carlson, B. Å. 1996. Effect of enhanced ultraviolet radiation and carbon dioxide concentration on the moss *Hylocomium splendens*. *Global Change Biol.* 2: 67-73.
- Steeman Nielsen, E. 1947. Photosynthesis of aquatic plants with special reference to the carbon sources. *Dansk Bot. Ark.* 12: 5-71.

- Steeman Nielsen, E. and Kristiansen, J. 1949. Carbonic anhydrase in submersed autotrophic plants. *Physiol. Plant.* 2: 325-331.
- Strain, B. R., and Cure, J. D. (eds.). 1985. Direct effects on increasing carbon dioxide on vegetation. U. S. Dept. of Energy, Office of Energy Research, Durham, N.C.
- Sveinbjörnsson, B. and Oechel, W. C. 1992. Controls on growth and productivity of bryophytes: environmental limitations under current and anticipated conditions. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 77-102..
- Tarnawski, M. G., Green, T. G. A., Buedel, B., Meyer, A., Zellner, J., and Lange, O. L. 1994. Diel changes of atmospheric CO₂ concentrations within, and above, cryptogam stands in a New Zealand temperate rainforest. *N. Z. J. Bot.* 32: 329-336.
- Thormann, M. N., Currah, R. S., and Bayley, S. E. 2002. The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Can. J. Microbiol.* 48: 204-211.
- Titus, J. E., Wagner, D. J., and Stephens, M. D. 1983. Contrasting water relations of photosynthesis for two *Sphagnum* mosses. *Ecology* 64: 1109-1115.
- Tsuneda, A., Thormann, M. N., and Currah, R. S. 2001. Modes of cell-wall degradation of *Sphagnum fuscum* by *Acremonium cf. curvulum* and *Oidiodendron maius*. *Can. J. Bot.* 79: 93-100.
- Tuba, Z., Csintalen, Z., Szente, K., Nagy, Z., and Grace, J. 1998. Carbon gains by desiccation-tolerant plants at elevated CO₂. *Funct. Ecol.* 12: 39-44.
- Tuba, Z., Proctor, M. C. F., and Takács, Z. 1999. Desiccation-tolerant plants under elevated air CO₂: A review. *Zeit. Natur.* 54c: 788-796.
- Tuittila, E. S. 2000. Restoring vegetation and carbon dynamics in a cut-away peatland. Faculty of Science, Department of Ecology, University of Helsinki.
- Turetsky, M. R. 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* 106: 395-409.
- Villarreal, J. C. and Renner, S. S. 2012. Hornwort pyrenoids, carbon-concentrating structures, evolved and were lost at least five times during the last 100 million years. *Proc. Natl. Acad. Sci.* 109: 18873-18878.
- Vitt, D. H., Glime, J. M., and LaFarge-England, C. 1986. Bryophyte vegetation and habitat gradients of montane streams in western Canada. *Hikobia* 9: 367-385.
- Williams, T. G. and Flanagan, L. B. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against ¹³CO₂ and C₁₈O₁₆O in *Pleurozium* and *Sphagnum*. *Oecologia* 108: 38-46.
- Wilson, J. A. and Coxson, D. S. 1999. Carbon flux in a subalpine spruce fire-forest: Pulse release from *Hylocomium splendens* feather-moss mats. *Can. J. Bot.* 77: 564-569.
- Zotz, G., Budel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.

