

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.

CO₂ Sources and Limitations

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** (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 compounds (C-4) 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.

Bryophytes must live in a delicate balance between sufficient moisture and sufficient CO₂. When the 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* and *P. strictum* are good examples of this, but less obvious examples are *Saelania glaucescens* (Figure 2), *Schistostega pennata*, *Pohlia cruda*, *P. wahlenbergii*, *Bartramia pomiformis*, and *Philonotis*, all of which have a whitish appearance to the naked eye (Proctor 1984).

Sphagnum partially solves this balance by having water-holding cells (**hyaline cells**) that bathe the photosynthetic cells (Figure 3), 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, *Leucobryum* does indeed trap air

bubbles in its colorless cells (Robinson 1985), providing an internal source of CO₂ for the chlorophyllous cells residing there and causing this plant to somewhat mimic the internal structure of a seed plant. This same character seems to be present throughout the family, permitting their multi-layered leaves to function photosynthetically.



Figure 2. Waxy-looking leaves of *Saelania glaucescens*. Photo by Michael Lüth.

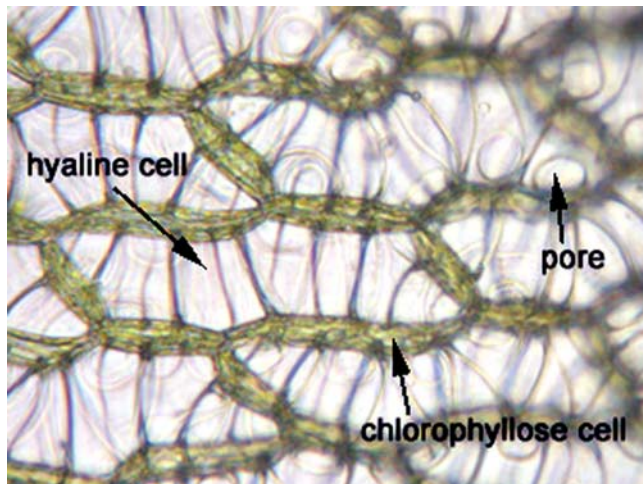


Figure 3. *Sphagnum* cells indicating the hyaline cells with pores, holding water, and chlorophyllose (photosynthetic) cells exposed to atmosphere. Photo with permission from www.botany.ubc.ca/bryophyte/LAB8.htm.

For forest floor mosses, the CO₂ should be ample to supply the slow-growing mosses due to production of CO₂ from litter decay. However, 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 that found in air. The boundary layer between the moss and the flowing water reduces that availability even more. Fortunately, they have low CO₂ compensation points (> 50 μl L⁻¹), typical of C₃ plants Bain & Proctor 1980).

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*, *Cratoneuron filicinum*, *Eucladium verticillatum*, *Fissidens rufulus*, *Hylocomium splendens*, and *Neckera crispa* and the thallose liverwort *Marchantia polymorpha*, and Steeman Nielsen (1947) found the same in *Fontinalis antipyretica*, 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*. 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* (pers. obs.). 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* species (Vitt *et al.* 1986; Glime & Vitt 1987).



Figure 4. Whitish leaves due to hyaline cells of *Leucobryum juniperoideum*. Photo by Michael Lüth.

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*, 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* 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.

Raven *et al.* (1998) indicate that stream mosses such as *Fontinalis antipyretica* 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.

Because CO₂ is often limiting, even in the terrestrial system, increasing levels of CO₂ on the Earth could positively affect the bryophytes. Because bryophytes are C₃ plants, they are able to take advantage of high CO₂ levels. Strain and Cure (1985) reported that the rate of photosynthesis in tracheophytes increases with a rise of atmospheric CO₂. 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. Sonesson *et al.* (1992) were able to show that *Hylocomium splendens* can adapt to higher ambient CO₂ concentrations and utilize higher CO₂.

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 5), they found almost the entire alcohol-soluble fraction moved from older parts to the apex, with little transfer of the insoluble fraction.



Figure 5. *Sphagnum papillosum* with sundew. Photo by Michael Lüth.

Bryophytes may be able to use different fixed carbon compounds from those used by tracheophytes. Simola (1969) experimented with *Sphagnum nemoreum* 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* can use fructose, glucose, maltose, and sucrose as internal carbon compounds (Simola 1969).

Further evidence of differences in carbon usage by *Sphagnum* come from studies on carbon isotope discrimination. In three species that occupy hollows (*S. recurvum*), carpets (*S. palustre*), and hummocks (*S.*

tenerum), 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.

Carbon isotope ratios have been used for dating all sorts of biological materials, including the age of peatlands. But 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 crassicosatus* 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.

Clymo (1989) found that carbon is transported within *Sphagnum* 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* 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.

Summary

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 *Saetania 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.

Some aquatic mosses may be able to concentrate CO₂ and this may be facultative, being enhanced on hot days. Anthocerotophyta use their pyrenoids to concentrate CO₂.

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.

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