

# CHAPTER 11-1

## PHOTOSYNTHESIS: THE PROCESS

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# CHAPTER 11-1

## PHOTOSYNTHESIS: THE PROCESS



Figure 1. *Antitrichia curtipendula* on a good photosynthetic day in late spring. Photo by Michael Lüth, with permission.

### Photosynthesis: The Productivity Engine

In **primary productivity** of plants, solar energy is transformed to biomass. Using photosynthesis, green plants convert solar energy, carbon dioxide, and water to glucose and other carbon-based compounds and eventually to plant tissue. **Gross primary productivity** is the product of that photosynthetic fixation of carbon, whereas **net primary productivity** is the carbon that is actually converted into biomass, *i.e.*, the fixed carbon that remains once one subtracts that lost to respiration. Consider it like your income. The gross value is your salary, but the net is what is left after taxes, social security, and other "maintenance" deductions. Respiration is the maintenance tax the plant must pay from its gross carbon fixation.

Productivity might be considered the measure of success of a plant. As stated by Anderson *et al.* (1996), photosynthesis provides energy, organic matter, and oxygen for nearly all biotic processes, and it is the only renewable energy source on Earth. If productivity is reduced in the presence of another species, we assume a competitive interaction that deprives the species of some needed resource. Thus, we might think of productivity as being the central issue in ecology around which all other issues revolve.

In order to understand bryophyte productivity, it is necessary to understand the differences in the bryophyte photosynthetic apparatus, especially the structure of the leaf or **phyllid**, compared to that of higher plants. I included the term phyllid here because technically, the bryophyte has no true leaves. This is because bryophytes lack lignified vascular tissue. However, few bryologists use the term phyllid, but rather have chosen to retain the term leaf, recognizing that the structure is different.

The CO<sub>2</sub> concentration in the atmosphere of early land plants was much higher than that found today (Raven & Edwards 2014). This would have supported much higher rates of photosynthesis than the current ones. Since those early times, bryophytes have evolved, adjusting to drastic climatic changes, "surviving and thriving through an incredible range of climatic and environmental variation" (Hanson & Rice 2014). Even some of the early growth forms of bryophytes are still present today, whereas many other groups of early land plants lack any presence today.

### Early Studies

Much of our basic knowledge about the process of photosynthesis was learned through studies including bryophytes. In 1910, Blackman and Smith published their



work on effects of CO<sub>2</sub> concentration on photosynthesis and respiration, including *Fontinalis antipyretica* (Figure 2) in the study. In fact, *F. antipyretica* was included in a number of early landmark studies (Plaetzer 1917; Harder 1921, 1923). One of the most important but overlooked of these early studies on bryophytes is the one by Bode (1940) in which he described a kind of respiration that occurred in the light and that was different from that occurring in the dark. He further described that the greatest respiration occurred in blue light and the greatest photosynthesis in red light. Dilks (1976) further elaborated on this **photorespiration** in bryophytes in a study of many species, demonstrating a lower rate of <sup>14</sup>CO<sub>2</sub> loss in light compared to dark that he attributed to partial reassimilation of the <sup>14</sup>CO<sub>2</sub> produced, a partial inhibition of dark respiration by light, or a low rate of glycolate synthesis and oxidation. We now know that photorespiration typically is greater than dark respiration in **C<sub>3</sub> plants** (see below), and that dark respiration is suppressed in the light, and during the day it occurs mainly in darkened organs of plants, like roots.



Figure 2. *Fontinalis antipyretica*, the subject of many classical studies on photosynthesis. Photo by Michael Lüth, with permission.

In the higher plants, especially seed plants, photosynthesis occurs inside a complex leaf structure that both limits and protects its activity. Only the internal structures of the leaf are involved in photosynthesis, and these are protected by an epidermis on each surface. For photosynthesis to occur in these tracheophyte plants, CO<sub>2</sub> must enter the leaf, which it does through openings called **stomata**. This imposes a limit based on the capacity for holding gases and the speed with which the stomata can open to admit the gases. Furthermore, when the leaf begins to dry, the stomata close, thus ending the entry of new CO<sub>2</sub>.

The tracheophyte method of obtaining water can both limit and enhance tracheophyte photosynthesis. It means that the plant can obtain its water from the soil after the dew has gone and the rain has stopped. On the other hand, replacement of water, and its contained nutrients, is a somewhat slow process that can take minutes to hours following the addition of water by rainfall.

Bryophytes do not have these restrictions. The small size of a bryophyte leaf creates some fundamental differences in the way they achieve photosynthesis. Their

ability to dry to 5-10% of their wet weight (Proctor 1990) and recover is unrivaled by most tracheophytes. Their one-cell-thick leaves have no epidermis, little or no waxy cuticle, and no stomata. Therefore, the photosynthetic cells are directly exposed to light for photosynthesis and have direct access to atmospheric gases. They furthermore have no midrib with lignified vascular conduction, but rather usually absorb their water directly through all their leaf surfaces. This means that they are able to respond to the addition of water from dew or fog and can immediately take advantage of a brief rainfall, but they have limited means of obtaining additional water from the soil to replenish that which is lost to evaporation and use. Nevertheless, many bryophytes do have a **costa**, which is the moss version of a midrib, and which at least in some species can conduct limited amounts of water and most likely other substances as well. The role of the costa and other water-responsive cells has been discussed in the chapter on water.

With these gross morphological structures in mind, we can examine the internal workings of the photosynthetic organ, the leaf. It is here that most of the chlorophyll resides and it is here that most of the photosynthesis occurs.

## Structural Adaptations

Based on the foregoing discussion of tracheophyte leaves, one might assume that a plant like *Marchantia polymorpha* (Figure 3) would be well adapted to photosynthesis. It has a thallus with tissue arranged like the spongy mesophyll of a maple leaf, abundant air chambers, pores surrounded by tiers of cells that function somewhat like guard cells, and a cuticularized epidermis (Figure 4) (Green & Snelgar 1982). But when compared to the functioning of a solid thallus in *Monoclea forsteri* (Figure 5), *Marchantia foliacea* (Figure 6) achieves little photosynthetic advantage over the simple *Monoclea forsteri*. Furthermore, although the chambering of *Marchantia* provides an advantage for water relations, *Monoclea* still seems to have the photosynthetic advantage in very moist habitats. Woodward (1998) asked if plants really need stomata, and answered this question by citing evidence that the number per unit area has increased in geologic time as the CO<sub>2</sub> concentration has decreased. It would be interesting to see if the number of pores in thalli of the **Marchantiaceae** is affected by CO<sub>2</sub> concentration.



Figure 3. *Marchantia polymorpha*, a species with a chambered thallus and pores. Photo by David Holyoak, with permission.



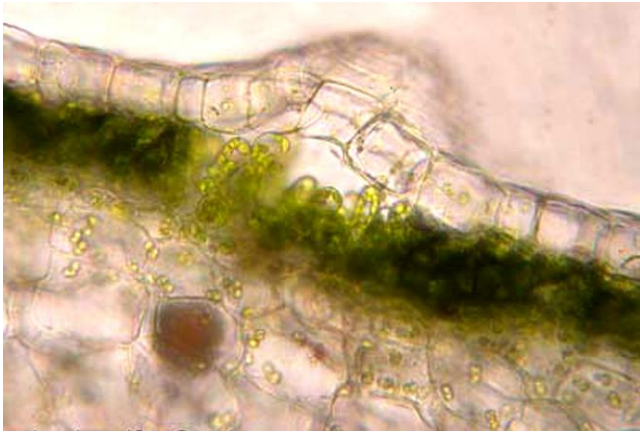


Figure 4. Cross section of the thallus of *Marchantia polymorpha* showing a pore and the chambered photosynthetic tissue beneath it. Photo by Jennifer Steele, Botany Website, UBC, with permission.



Figure 5. *Monoclea forsteri*, a solid thallose liverwort. Photo by Jan-Peter Frahm, with permission.



Figure 6. *Marchantia foliacea*, a thallose species with a solid thallus. Photo by Jan-Peter Frahm, with permission.

But our suggestion that internal spaces and an epidermis should benefit photosynthesis is not all wrong. Some bryophytes do benefit from added internal spaces that contribute to surface area for gas exchange. In

*Polytrichum commune* (Figure 7), leaf lamellae (Figure 8) increase the surface area 2.4-fold (Thomas *et al.* 1996). This seed plant "want-to-be" also has a waxy cuticle to prevent water loss and repels water that could block the movement of CO<sub>2</sub> into the leaf. Proctor (2005) demonstrated that this arrangement of lamellae seemed to protect these mosses from non-photochemical quenching that occurred in other mosses in exposed habitats. He showed that unistratose leaves are limited in their photosynthetic output by their CO<sub>2</sub> diffusion resistance, especially at high light levels. Mosses in the **Polytrichaceae**, on the other hand, enjoy more than a six-fold increase in leaf area, reducing the CO<sub>2</sub> diffusion constraint. The importance of these lamellae can be illustrated by *Atrichum undulatum* (**Polytrichaceae**; Figure 9-Figure 12) compared to non-polytrichaceous mosses (Krupa 1984). Leaves of this species had a higher photosynthetic rate per cm<sup>2</sup> than did leaves of *Rhizomnium punctatum* (Figure 13) or *Funaria hygrometrica* (Figure 14) with single-layered leaves. And the tiny *Aloina rigida* (Figure 15-Figure 16) with succulent, lamellose leaves had a photosynthetic rate nearly 4.5 times that of *Funaria hygrometrica*, a moss of similar size.



Figure 7. *Polytrichum commune*, a plant with leaf lamellae and no rolled over leaf edges. Photo by James K Lindsey, with permission.

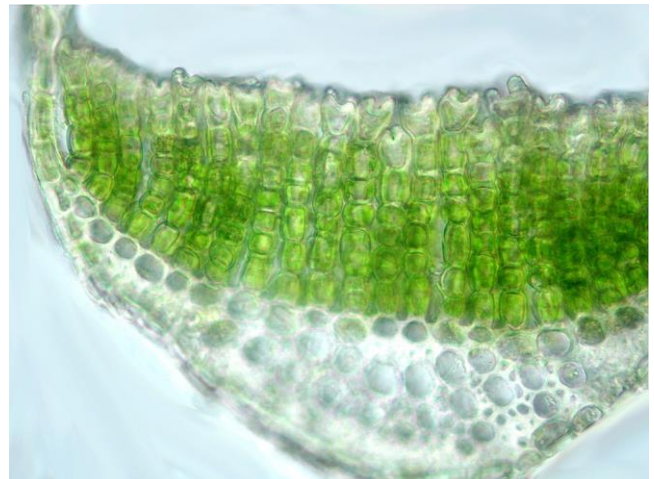


Figure 8. *Polytrichum commune* leaf cross section showing lamellae. Photo by Michael Lüth, with permission.



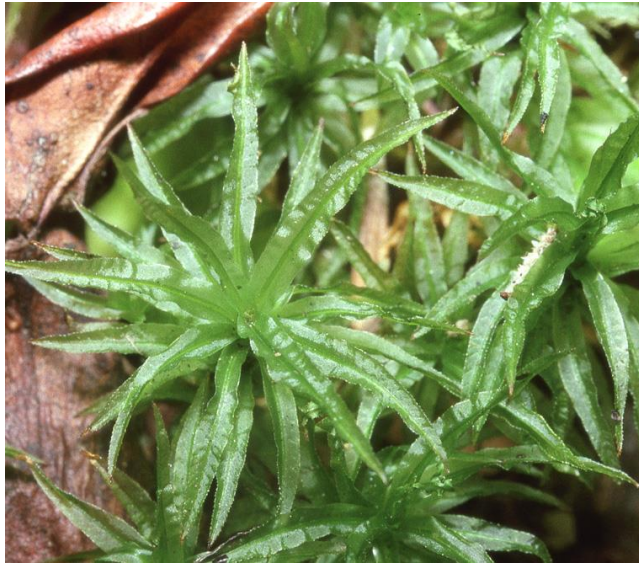


Figure 9. *Atrichum undulatum*, a species with photosynthetic leaf lamellae. Photo by Janice Glime.



Figure 10. *Atrichum undulatum* leaf with lamellae showing their platelike structure. Photo by Walter Obermayer, with permission.

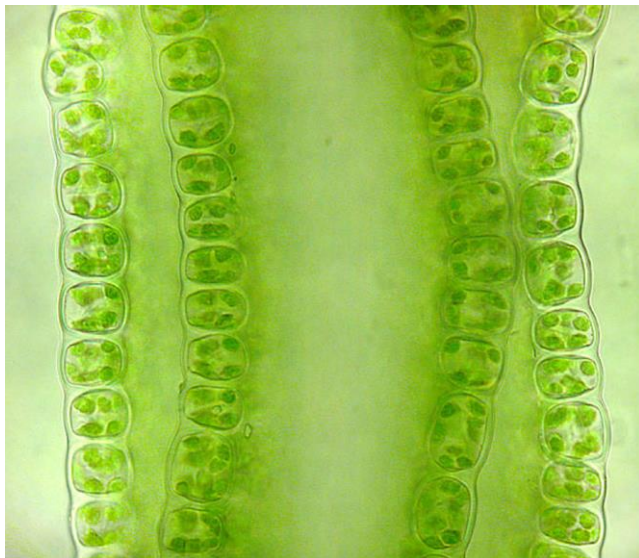


Figure 11. *Atrichum undulatum* leaf lamellae showing chloroplasts in the lamellae. Photo by Walter Obermayer, with permission.

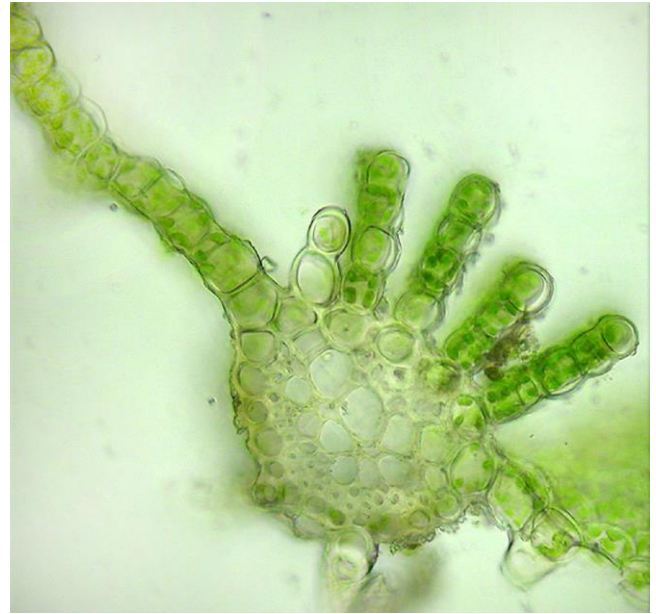


Figure 12. *Atrichum undulatum* leaf cs showing lamellae. Photo by Walter Obermayer, with permission.



Figure 13. *Rhizomnium punctatum*, a species with single-layered leaves and lower photosynthetic rates than species with lamellae. Photo by Bob Klips, with permission.



Figure 14. *Funaria hygrometrica*, a species with single-layered leaves and lower photosynthetic rates than species with lamellae. Photo by Janice Glime.





Figure 15. *Aloiina rigida*, a species with inrolled leaf margins that cover lamellae. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

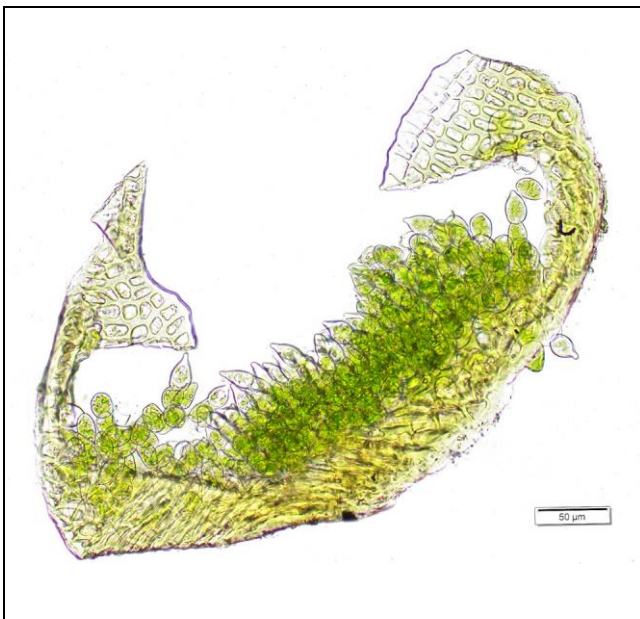


Figure 16. *Aloiina rigida* leaf cs showing lamellae that add to its photosynthetic capability, and inrolled leaf margins that give this species its succulent look. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species of *Polytrichum* have an additional adaptation similar to that of *Aloiina rigida* (Figure 15-Figure 16). They have colorless margins that fold over the leaf lamellae (Figure 20). In alpine populations of *Polytrichum juniperinum* (Figure 17-Figure 20), this margin forms a greater part of the leaf than in the woodland populations. Bazzaz *et al.* (1970) suggested that this is an adaptation to the alpine habitat. This interpretation is consistent with the higher light saturation intensity for the alpine population (10,000 lux) compared to that of the woodland population (5000 lux).



Figure 17. *Polytrichum juniperinum* showing leaves with overlapping edges. Photo by Michael Lüth, with permission.

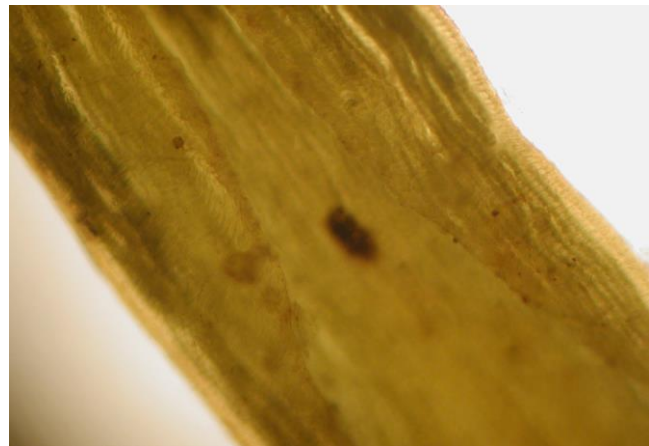


Figure 18. *Polytrichum juniperinum* leaf section showing tops of lamellae. Photo courtesy of John Hribljan.

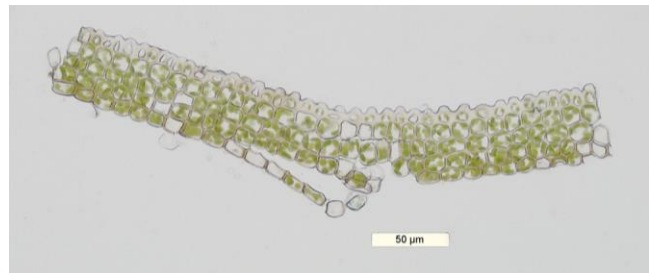


Figure 19. *Polytrichum juniperinum* lamella showing photosynthetic tissue. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 20. Leaf cross section of *Polytrichum juniperinum* showing leaf lamellae and rolled over leaf edge. Photo courtesy of John Hribljan.



Mosses can actually change the structure of their chloroplasts in response to different **wavelengths** of light. In *Funaria hygrometrica* (Figure 14), the chloroplasts responded to red light by an increase in area and a decrease in thickness, shrinking in volume by about 10% (Zurzycki 1974). In low intensity of blue light, the effects were similar, but in high levels of blue light, there was a strong reduction of the surface area and a 35% shrinkage in volume. Both effects were reversible. In *Marchantia polymorpha* (Figure 3-Figure 4), far-red light at the end of the photoperiod caused 20-30% drop after only a 5-minute exposure following 8-hour days for one week (Fredericq & DeGreef 1968). Longer days caused less reduction.

CO<sub>2</sub> concentration can also modify the size and shape of chloroplasts (Bockers *et al.* 1997). In *Marchantia polymorpha* (Figure 3-Figure 4), high CO<sub>2</sub> concentrations caused a modification of the chloroplast shape, and the cell had ~70% more chloroplasts. However, the chlorophyll content differed little, indicating that the greater number of chloroplasts exhibited less chlorophyll per chloroplast. The cells themselves were ~37% smaller in the high (2.0%) CO<sub>2</sub> concentrations compared to the 0.4% concentrations. These changes did not imbue the cells with any greater photosynthetic capacity or efficiency. Furthermore, the CO<sub>2</sub> levels are very high compared to an atmospheric concentration of less than 0.04%, so the responses may be somewhat meaningless. Sonesson *et al.* (1992) reported only 0.04-0.045% CO<sub>2</sub> around *Hylocomium splendens* (Figure 21) plants growing on soil.



Figure 21. *Hylocomium splendens*, a plant that grows in a relatively low CO<sub>2</sub> environment on the forest floor. Photo through Wikimedia Commons.

Despite their small size, bryophytes respond to light much as do tracheophytes. Bryophytes increase their chlorophyll content as the light intensity decreases and increase their mean leaf area as light intensity increases (Sluka 1983).

**Water** is clearly a factor that limits photosynthesis. *Sphagnum* (Figure 22-Figure 26) has a unique way of avoiding a water problem most of the time, making photosynthesis possible long after other bryophytes are too dry (Rice & Giles 1996). It maintains its own reservoir. Each photosynthetic cell is in contact with a large **hyaline** (transparent) cell (Figure 23, Figure 25-Figure 26) that holds water. When Rice (1995) compared three species pairs, the submerged member of the pair always had greater allocation to photosynthetic tissue and greater relative

growth rates than did the non-aquatic member of the pair. This can be accomplished by allocating more tissue to photosynthetic cells rather than to hyaline cells and by increasing the light-harvesting chlorophyll proteins.



Figure 22. *Sphagnum papillosum*, a sun-dwelling hummock species. Photo by David Holyoak, with permission.

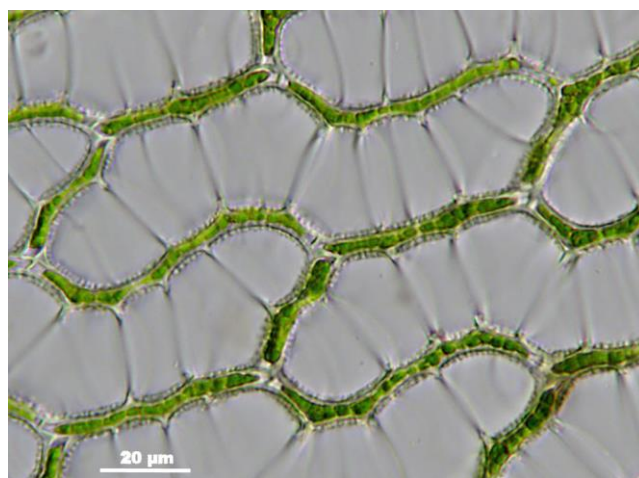


Figure 23. *Sphagnum papillosum*, a hummock species, showing large hyaline leaf cells. Photo by Ralf Wagner <[www.drralf-wagner.de](http://www.drralf-wagner.de)>, with permission.



Figure 24. *Sphagnum palustre*, a species of wet habitats. Photo by Bernd Haynold, through Creative Commons.



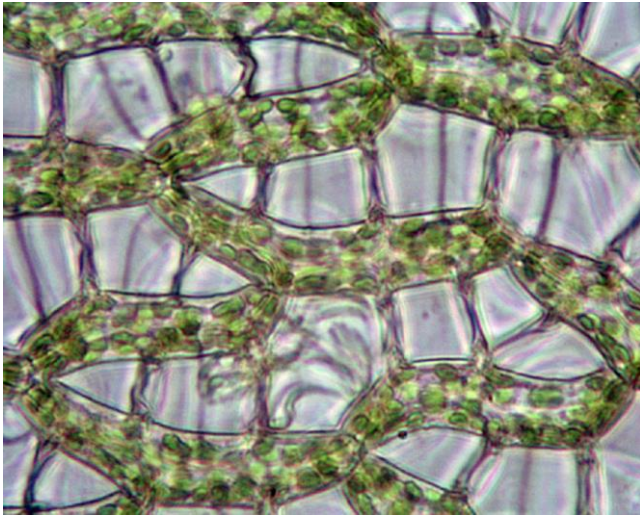


Figure 25. *Sphagnum palustre*, an aquatic species, showing hyaline leaf cells that are reduced in size. Photo by Malcolm Storey through Creative Commons.

But obtaining  $\text{CO}_2$  is especially problematic in the aquatic environment. In *Sphagnum*, reduction in the water-filled hyaline cells (Figure 23-Figure 26) helps. Additional adaptations include larger, thinner branch leaves with fewer per length of branch, reducing the boundary layer resistance to  $\text{CO}_2$  diffusion (Rice & Schuepp 1995). Aquatic photosynthetic cells have more surface exposure than those in leaves of above-water plants. A biochemical adaptation complemented this structural adaptation by a shift that favors light-reaction proteins (Rice 1995). Proctor *et al.* (1992) demonstrated that the  $\Delta^{13}$  for *Sphagnum* photosynthetic cells with hyaline enclosure on both sides (compare Figure 26 to Figure 27) is significantly lower than for other terrestrial species, being consistent with the greater resistance to  $\text{CO}_2$  uptake with increasing submersion.

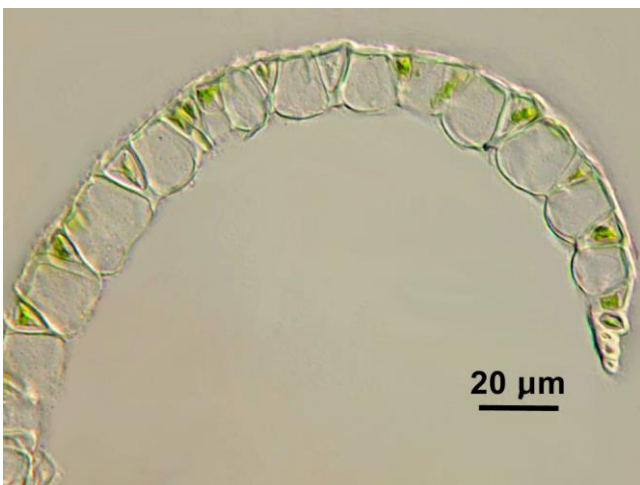


Figure 26. *Sphagnum obtusum* branch leaf cs showing photosynthetic cells that are exposed on the outer side of the leaf. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 27. *Sphagnum centrale* leaf cross section showing photosynthetic cells completely surrounded by hyaline cells. This species lives on the forest floor and on logs. Photo by Jutta Kapfer, with permission.

Bryophytes have a variety of ways to trap air within or among the leaves. Interestingly, some of our evidence comes from fossils in amber (Robinson 1985). Fossil *Octoblepharum* (Figure 28-Figure 29) shows trapped air in the leaves. Live *Sphagnum* (Figure 22-Figure 27), on the other hand, does not have air trapped in the hyaline cells – or does it? *Leucobryum* (Figure 30-Figure 33) has large air bubbles in its hyaline cells, with bubbles that actually extend through many cells. Unlike *Octoblepharum*, *Leucobryum* leaves develop air pockets as they enlarge, but non-functional older leaves lose their air-entrapment ability. Furthermore, older leaves at the base of the plant use the hyaline cells to hold water.



Figure 28. *Octoblepharum albidum*, a moss that is white due to hyaline cells. Photo by Michael Lüth, with permission.



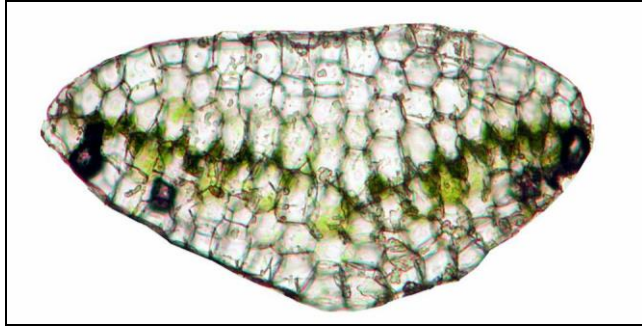


Figure 29. *Octoblepharum albidum* leaf cs showing a single layer of photosynthetic cells surrounded by hyaline cells. Photo by Michael Lüth, with permission.



Figure 30. *Leucobryum glaucum* showing its whitish color due to hyaline cells. Photo by Janice Glime.



Figure 31. *Leucobryum glaucum* showing its thick leaves due to the extra layers of hyaline cells. Photo by Bob Klips, with permission.

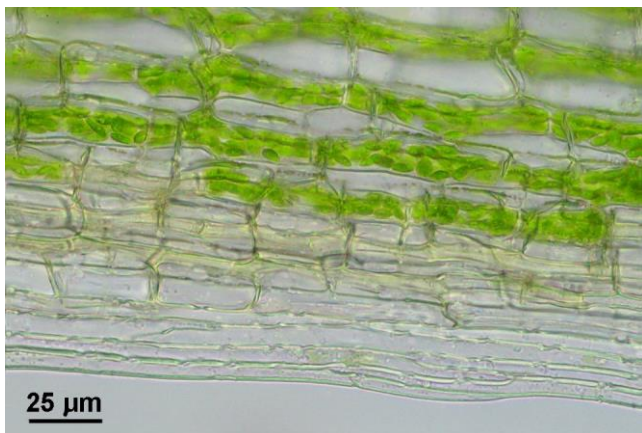


Figure 32. *Leucobryum glaucum* leaf section showing hyaline and photosynthetic cells. Photo by Ralf Wagner <[www.drralf-wagner.de](http://www.drralf-wagner.de)>, with permission.



Figure 33. *Leucobryum glaucum* leaf cs showing layer of photosynthetic cells surrounded by hyaline cells. Photo by Walter Obermayer, with permission.

One possibility to consider is that as air bubbles from photosynthesis form on the surfaces of the plants, CO<sub>2</sub> may enter the bubble by diffusion, much like the diving bell or the plastron used by some aquatic insects. But it would seem this would provide very small amounts indeed.

## Photosynthetic Apparatus – the Chloroplast

### Chloroplast Structure

Bryophytes, like tracheophytes and green algae (among others), have **chlorophylls a** and **b** and these chlorophyll molecules are organized within a complex structure called the **chloroplast**. These two photosynthetic pigments are supplemented by the **chlorophyll antenna system** of **xanthophylls** and **carotenes** that serve to trap light energy and transfer it to the chlorophyll *a* action center, all within the **chloroplast**. In all plants and green algae, **starch** is stored within the chloroplast, but it will disappear after as little as 24 hours in darkness (Raven *et al.* 1992).

Chlorophyll in all plants resides in special double-membrane-bound structures called **chloroplasts** (Figure 34). These chloroplasts have within them stacks of membrane-bound structures called **thylakoids**, and it is within these thylakoid membranes and the surrounding fluid, the **stroma**, that the photosynthetic reactions take place (Figure 35).



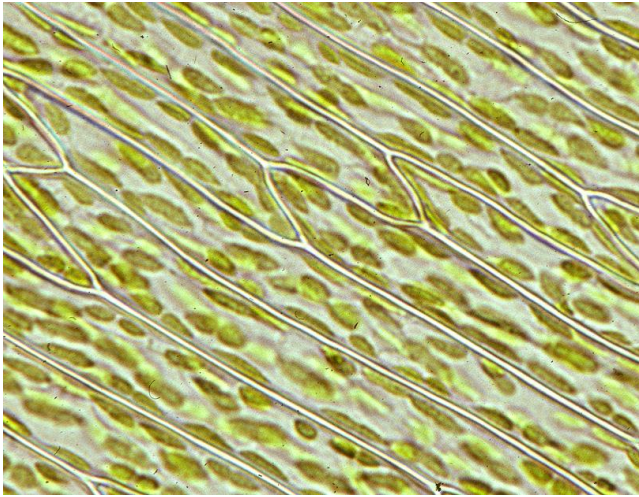


Figure 34. Cells of *Fontinalis antipyretica* showing chloroplasts in cells. Photo by Janice Glime.

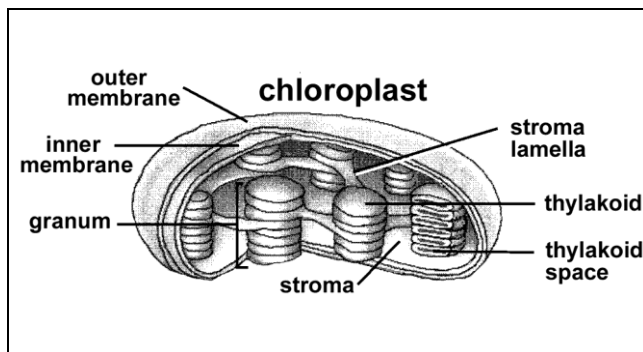


Figure 35. Structure of a single chloroplast. The chlorophyll molecules occur in the thylakoid membranes. Drawn by Janice Glime.

### Associated Proteins

Associated with the chlorophyll molecules are proteins, known as **light-harvesting chlorophyll proteins (LHCP)**. There is some evidence that the protein association with chloroplasts in bryophytes might be unique. Aro (1982a) demonstrated differences in the protein complexes associated with photosystems I and II, using *Ceratodon purpureus* (Figure 36), *Pleurozium schreberi* (Figure 37), and *Marchantia polymorpha* (Figure 3-Figure 4). This is suggested by their ability to survive desiccation and freezing much more easily than plastids of tracheophytes (Tuba 1985). Further evidence came from their limited solubility in acetone when dry, but ability to dissolve much more easily if rehydrated for 15 seconds first (personal observation). Genetic evidence also supports the presence of chlorophyll proteins that are unique to bryophytes. *Marchantia polymorpha* has an *frxC* gene that codes for the sequence for an ATP-binding, Fe-protein that is a bacterial type not present in the tobacco chloroplast (Fujita *et al.* 1989). Furthermore, Neuhaus *et al.* (1990) found only 94% sequence conservation of I polypeptide of Photosystem II between *Marchantia* and mustard (*Sinapis alba*, Figure 38).



Figure 36. *Ceratodon purpureus*, a species with protein complexes associated with PS I and PS II. Photo by Michael Lüth, with permission.



Figure 37. *Pleurozium schreberi* on the forest floor of a northern forest, a species with protein complexes associated with PS I and PS II. Photo by Janice Glime.



Figure 38. *Sinapis alba*, a species with photosystem II polypeptides that differ from those of *Marchantia*. Photo by Ariel Palmon, through Creative Commons.



Aro (1982b) compared bryophyte chlorophyll protein composition to that of the floating aquatic plant duckweed (*Lemna*, Figure 39) and cucumber (*Cucurbita*, Figure 40). Both the moss *Ceratodon purpureus* (Figure 36) and the thallose liverwort *Marchantia polymorpha* (Figure 3- Figure 4) had more chlorophyll associated with the light-harvesting chlorophyll protein (LHCP) complexes and fewer with reaction center complexes than did the two tracheophytes. Harrer (2003) supported that observation with his study on *Marchantia polymorpha*, demonstrating that more than 50% of the PS II particles from *Marchantia polymorpha* carry one or two additional masses in the protein complex. So it is possible that bryophytes may have both differences in their kinds of chlorophyll protein, and have different amounts associated in different ways, giving their chlorophyll unique protection.



Figure 39. *Lemna minor*, member of a genus for which chlorophyll associations differ from those of the tested bryophytes. Photo through Creative Commons.



Figure 40. *Cucurbita*, a species in which chlorophyll associations differ from those of the tested bryophytes. Photo by Maja Dumat, through Creative Commons.

### Fatty Acids

Valanne (1984) and Gellerman *et al.* (1972) have suggested that the C<sub>20</sub> polyunsaturated fatty acids increase the ability of mosses to adapt to extreme conditions. Those taxa living in shaded habitats have larger grana and contain even more polyunsaturated fatty acids than do sun-adapted species (Karunen & Aro 1979). It appears that polyunsaturated lipids play a role in maintaining structure

and thermal stability of chloroplast membranes (Hugly *et al.* 1989), but little has been done to help us understand this relationship in bryophytes. Current studies on the genome and its function in the moss *Physcomitrella patens* (Figure 41) and liverwort *Marchantia polymorpha* (Figure 3- Figure 4) (*e.g.* Ikeuchi & Inoue 1988) are likely to help us understand these roles in the near future.



Figure 41. *Physcomitrella patens*, a species that permits us to test gene function. Photo by Michael Lüth, with permission.

## Need for Light

### Color Retention in the Dark

Light is required to make chlorophyll. In the dark, chlorophyll can degrade, and dry mosses can lose chlorophyll in the light. Hence, when bryophytes first encounter light after a prolonged period of darkness, one might expect them to be pale and have reduced photosynthetic activity. But Valanne (1977) found that protonemata of *Ceratodon purpureus* (Figure 36) that had been in darkness for 1-2 months were able to produce starch within 30 minutes. Maximum photosynthesis, however, was not reached until the second day, providing enough time for the development of light-type chloroplasts. PS I had much higher activity in the dark-adapted protonemata than in that grown in light, whereas the activity of PS II was greater in light-grown protonemata.

### Chloroplast Replication

Chloroplast replication requires light. Hahn and Miller (1966) demonstrated this in *Polytrichum commune* (Figure 7) by showing that in the light chloroplasts replicated, but in the dark, chloroplasts would only replicate when sucrose was present in the medium. Rather, in continuous dark, and when given 15 minutes of far-red light per six hours, chloroplasts became larger. Electron micrographs revealed that the increase in size was due at least in part to the synthesis and degradation of starch.

## Photosynthetic Capacity

In general, bryophytes are considered to have lower photosynthetic capacity than that of tracheophytes (Martin & Adamson 2001). In support of this, Rao *et al.* (1979) demonstrated that the Hill reaction (light-driven splitting of water in PS II) rates of three marchantialian liverworts are lower than those of seed plants. But Martin and Adamson (2001) have challenged this view. They too found that, when expressed on the basis of dry weight, net CO<sub>2</sub> uptake

was considerably lower in mosses than in the six tracheophytes they studied. But the differences disappear when expressed on the basis of chlorophyll content. It would appear that the photosynthetic capacity of moss chloroplasts at light saturation and normal CO<sub>2</sub> levels is as great as that of tracheophytes.

One factor to be considered in the photosynthetic rate of bryophytes is their photosynthetic enzyme, ribulose biphosphate carboxylase/oxidase (RUBISCO). In a study by Rintamäki and Aro (1985) on a wide range of plant species, it was the moss *Ceratodon purpureus* (Figure 36), along with the grass *Deschampsia flexuosa* (Figure 42), that had the highest ratios of activity of RuBP carboxylase/oxidase to RuBP oxidase, suggesting yet another adaptation for a high photosynthetic capacity. But *Ceratodon purpureus* is a sun moss and is only one example. It is premature to generalize from this single study.



Figure 42. *Deschampsia flexuosa*, a grass that has one of the highest ratios of activity of RuBP carboxylase to RuBP oxidase, as did *Ceratodon purpureus*. Photo by Kelly O'Donnell, through Creative Commons.

### Antenna Pigments

The actual trapping of light energy results in a rapid spin on one of the electrons of a pigment. But this initial pigment need not be chlorophyll. Rather, it can be one of the pigments (chlorophyll *b*, carotene, xanthophyll) in the **chlorophyll antenna system** (Figure 43). These pigments occur in the thylakoid membranes within the chloroplasts and are part of Photosystem I and Photosystem II. This extra spin puts the electron in a higher energy state than before and the electron spins off the pigment molecule and is transferred to another and another of the pigment molecules until it reaches the reaction center, chlorophyll *a*.

The antenna pigments permit the chloroplasts to absorb energy in the regions where chlorophyll *a* has little ability to absorb. The two dimers of chlorophyll *a* absorb best at 680 and 700 nm and very poorly between 450 and 650 nm (Martínez Abaigar & Núñez Olivera 1998). Chlorophyll *b* helps to absorb in this latter range. The carotenoids extend the absorption spectrum farther into the 450–490 nm range. Furthermore, **zeaxanthin**, a xanthophyll pigment, can deactivate singlet chlorophyll, and other carotenoids can deactivate both triplet chlorophylls and singlet oxygen that result from excess light energy. Thus, these serve as protective mechanisms against photo-inhibition and protect the chlorophylls from photooxidation, as discussed below.

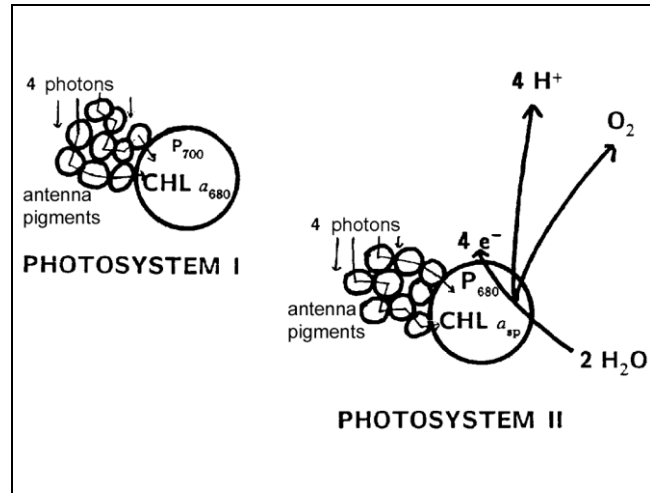


Figure 43. Antenna pigments such as carotene, xanthophyll, and chlorophyll *b* in Photosystem I and Photosystem II transfer light energy to chlorophyll *a* within a single thylakoid membrane. Excitation of electrons in chlorophyll *a* occurs in both photosystems. Modified by Janice Glime from Goodwin & Mercer 1983 and Jensen & Salisbury 1984.

The most frequent of the antenna pigments in bryophytes include  $\alpha$ - and  $\beta$ -carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al.* 1972; Schmidt-Stohn 1977; Czezug 1980, 1985; Czezug *et al.* 1982; Huneck 1983; Farmer *et al.* 1988; Boston *et al.* 1991). Because these antenna pigments include yellow, orange, and sometimes red, as well as the different green of chlorophyll *b*, they are able to trap energy from different wavelengths of light instead of just the red that excites chlorophyll *a*. This is advantageous for the many species that inhabit locations that are low in red light. Among ~60 species tested, pigment types differ little between aquatic and terrestrial habitats (Martínez Abaigar & Núñez Olivera 1998). Among the exceptions is the unusual pigment **aurioxanthin** found in the obligate aquatic *Fontinalis antipyretica* (Figure 2) (Bendz *et al.* 1968).

Heber *et al.* (2005) demonstrated that **zeaxanthin** was necessary for the dissipation of light energy in hydrated mosses. They suggest that only a few molecules of zeaxanthin are needed to suppress the excess energy at the dissipation centers in the antenna system of Photosystem II. Desiccation-dependent quenching, on the other hand, does not require zeaxanthin and apparently is a property of the reaction center complex of Photosystem II.

Many more antenna pigments actually exist among the bryophytes. In a single study on only ten species of liverworts, Czezug (1985) found nineteen carotenoids. In addition to the seven named above, he found lycopene, lycoxanthin,  $\alpha$ -cryptoxanthin,  $\beta$ -cryptoxanthin, lutein epoxide,  $\beta$ -carotene epoxide, antheraxanthin,  $\alpha$ -doradexanthin, adonixanthin, mutatoxanthin, rhodoxanthin, and apo-12'-violaxanthin. All but three of these pigments were already known from mosses. Of the three new ones,  $\alpha$ -cryptoxanthin was known in algae, lichens, and higher plants,  $\alpha$ -doradexanthin is common in Crustacea and fish, and rhodoxanthin is known in club mosses, horsetails, ferns, conifers, and some species of the pondweed, *Potamogeton*, a flowering plant (Figure 44).





Figure 44. *Potamogeton gramineus* showing a red pigment, possibly rhodoxanthin. Photo by Pellaea, through Creative Commons.

## Type of Photosynthetic Pathway

Among the tracheophytes, the **C<sub>3</sub> photosynthetic pathway** is most common, but some have a **C<sub>4</sub> pathway**, and some have a **CAM pathway**, neither of which seems to be available to bryophytes. These pathway names are based of the initial placement of the CO<sub>2</sub> when it is taken into the plant. The **C<sub>3</sub> pathway** is assumed to be the primitive pathway, known from algae and bryophytes, as well as tracheophytes, in which the carbon of CO<sub>2</sub> is fixed into a 3-carbon compound in its initial fixation within the plant. In tracheophytes, photosynthesis occurs in the mesophyll tissue of the leaf. There are no special adaptations for internal storage of the carbon for later use in photosynthesis – it must be used immediately and thus is placed immediately into the photosynthetic pathway to form **PGA** (phosphoglyceric acid; Figure 45), the 3-C compound. This immediate use is apparently characteristic of all bryophytes. This distinction of immediate use versus later use in photosynthesis is best understood by comparison with the other two pathways.

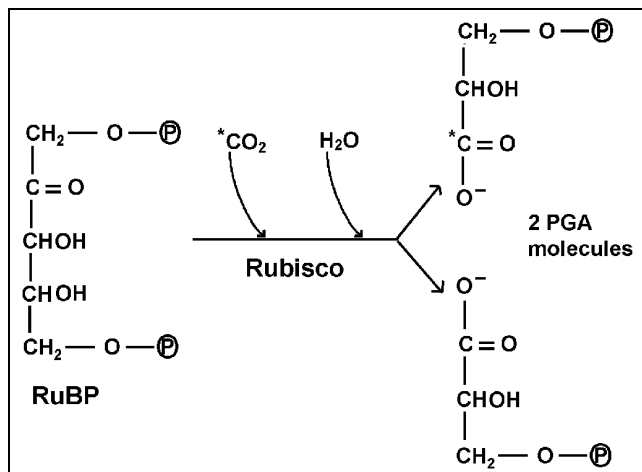


Figure 45. Melvin Calvin and associates found that the carbon from CO<sub>2</sub> is placed into RuBP to make a 6-carbon compound that immediately splits to form two molecules of 3-phosphoglycerate (PGA). This is the first step of the Calvin cycle and is the carbon fixation step for C<sub>3</sub> plants.

The **C<sub>4</sub> pathway** in tracheophytes permits storage of carbon from CO<sub>2</sub> into a 4-carbon compound such as malic or oxalic acid in the mesophyll, to later be transported to the bundle sheath around the vascular tissue, where CO<sub>2</sub> is released and put into the photosynthetic pathway in the bundle sheath. The advantage is that stomata of a C<sub>4</sub> plant can remain open for a short time, CO<sub>2</sub> can be stored rapidly, and photosynthesis can continue for an extended period of time after the stomata are closed. Since the stomata are the major source of water loss from the plant, this is a tremendous savings in water loss and permits the plant to be more productive in dry regions than C<sub>3</sub> plants.

The **CAM pathway** is similar except that stomata open at night instead of daytime as in other plants. Since photosynthesis cannot occur at night, CAM plants survive because carbon from CO<sub>2</sub> is stored in malic acid or other C<sub>4</sub> compound in the mesophyll for use in the daytime. However, in the CAM plant, the CO<sub>2</sub> is released in the mesophyll and photosynthesis takes place in the mesophyll tissue. Table 1 compares many of the structural and physiological attributes of plants with these three pathways.

Each of these has certain ecological advantages and disadvantages (Table 1). The C<sub>3</sub> pathway requires the least energy as ATP and is thus the most energy-efficient. The others, however, impart ecological advantages in hotter and/or drier climates and are more efficient in use of CO<sub>2</sub>.

Table 1. Comparison of tracheophyte plants with different types of CO<sub>2</sub> fixation. From Larcher 1983, compiled from many authors.

Characteristic	C <sub>3</sub>	C <sub>4</sub>	CAM
Leaf structure	Laminar mesophyll, bundle sheaths	Mesophyll radially around chlorenchymatic bundle sheaths (Kranz-type anatomy)	Laminar parenchymatic arranged mesophyll large vacuole
Chlorophyll a/b	~3:1	~4:1	<3:1
CO <sub>2</sub> -compensation concentration at optimal temperature	30-70 $\mu\text{l l}^{-1}$	<10 $\mu\text{l l}^{-1}$	in light: 0-200 $\mu\text{l l}^{-1}$ in dark: <5 $\mu\text{l l}^{-1}$
Primary CO <sub>2</sub> acceptor	RuBP	PEP	In light: RUBP in dark: PEP
First product of photosynthesis	C <sub>3</sub> acids (PGA)	C <sub>4</sub> acids (malate, aspartate)	In light: PGA in dark: malate
Photorespiration	Yes	Not measurable	Yes
Photosynthetic depression by O <sub>2</sub>	Yes	No	Yes
CO <sub>2</sub> release in light (apparent photorespiration)	Yes	No	No
Net photosynthetic capacity	Slight to high	High to very high	In light: slight in dark: medium
Light-saturation of photosynthesis	At intermediate intensities	No saturation at highest intensities	At intermediate to high intensities
Temperature optimum	10-25°C	25-35°C	20-35°C?
Redistribution of assimilation products	Slow	Rapid	Variable
Dry-matter production	Medium	High	Low



In fact, some bryophytes are capable of photosynthesis at temperatures below freezing, and some species of *Fontinalis* (Figure 2) (and probably others) have a temperature optimum near 5°C (Glime 1987a, b). Their light saturation point is less than full sunlight, and they are capable of net photosynthetic gain at very low light intensities (such as caves and deep water). These characteristics are unknown in C<sub>4</sub> plants. These capabilities greatly extend the growing season for mosses and undoubtedly contribute to their success in ecosystems such as the tundra and boreal forest.

In the aquatic system, CAM photosynthesis seems to be an adaptation of some tracheophytes to the low CO<sub>2</sub> concentration, permitting them to gain CO<sub>2</sub> at night when most of the algae and other aquatic plants are respiring CO<sub>2</sub>. The cooler atmosphere may likewise contribute to a reduced loss of the CO<sub>2</sub> from the body of water. It is amazing to me to learn that the C<sub>3</sub> *Fontinalis antipyretica* (Figure 2) has a higher carbon uptake rate than does the CAM plant *Isoetes bolanderi* (Figure 46) (Sandquist & Keeley 1990). Does this relate to its lack of cuticle and epidermis, permitting the immediate availability of CO<sub>2</sub> at any time of the day regardless of the light intensity? Perhaps a storage mechanism is not needed if uptake is always possible.



Figure 46. *Isoetes bolanderi*, a CAM plant that sequesters CO<sub>2</sub>. Photo by Steve Matson, through Creative Commons.

### C<sub>3</sub> Evidence

Several studies have attempted to locate a pathway other than the C<sub>3</sub> pathway among bryophytes, examining the most likely deviants, the aquatic and xerophytic taxa. Thus far, there is no conclusive evidence for any pathway other than C<sub>3</sub>. It appears that bryophytes have all the earmarks of C<sub>3</sub> plants, exhibiting higher CO<sub>2</sub> compensation points than those of tracheophytes (Rudolph 1990). Since C<sub>3</sub> plants are unable to sequester CO<sub>2</sub> and have only RUBISCO to help incorporate it into their photosynthetic pathway, they require higher concentrations of CO<sub>2</sub> than plants with C<sub>4</sub> or CAM pathways.

Raven *et al.* (1998) have reviewed the evidence for the C<sub>3</sub> pathway in bryophytes. Biochemically, bryophytes are C<sub>3</sub> plants, as far as is known. Their first carboxylation reaction accounts for more than 95% of the CO<sub>2</sub>

incorporation. The ratio of *in vitro* RUBISCO carboxylase activity to that of *in vitro* PEP carboxylase activity is far higher than that known for C<sub>4</sub> or CAM plants (Rintamäki & Aro 1985; Farmer *et al.* 1986; Keeley *et al.* 1986). There is insufficient PEP carboxylase activity to support the observed photosynthetic carbon flux (Rintamäki *et al.* 1988; Madsen *et al.* 1993).

The CAM pathway can be excluded because there is no evidence of nighttime activity and there is no increase in acidity or accumulation of malic acid in the dark (Keeley & Morton 1982; Keeley *et al.* 1986; Raven *et al.* 1987).

Raven *et al.* (1987) then evaluated the physiological evidence, which is primarily based on the CO<sub>2</sub> compensation point. These data support the relatively high CO<sub>2</sub> compensation point of a C<sub>3</sub> plant (Fock *et al.* 1969; Ruttner 1947; Allen & Spence 1981; Raven *et al.* 1987).

Further evidence to support that bryophytes use a C<sub>3</sub> pathway comes from the <sup>13</sup>C/<sup>12</sup>C discrimination values. Although there are difficulties with boundary layer resistance, especially in aquatic bryophytes, overall these values are consistent with a C<sub>3</sub> pathway (Raven *et al.* 1987, 1994; Keeley & Sandgren 1992; Rice & Giles 1994, 1996; Smith & Griffiths 1996a, b).

### CO<sub>2</sub>-concentrating Mechanisms – Exceptions to C<sub>3</sub>?

Although bryophytes are considered C<sub>3</sub> plants (Rundel *et al.* 1979, James 1981; Raven *et al.* 1998), certain evidence makes us wonder if there are other variations among them. *Fissidens cf. manateensis* (see Figure 47) and *Fontinalis antipyretica* (Figure 2) seem to have some sort of CO<sub>2</sub>-concentrating mechanism (Salvucci & Bowes 1981; Bowes & Salvucci 1989; Raven *et al.* 1998). CO<sub>2</sub>-concentrating mechanisms permit the plant to obtain CO<sub>2</sub> at a higher concentration than conditions would normally allow for a C<sub>3</sub> plant. This can be especially important for plants living in aquatic habitats with pH values in the range where the equilibrium shifts from CO<sub>2</sub> to bicarbonate or carbonate.

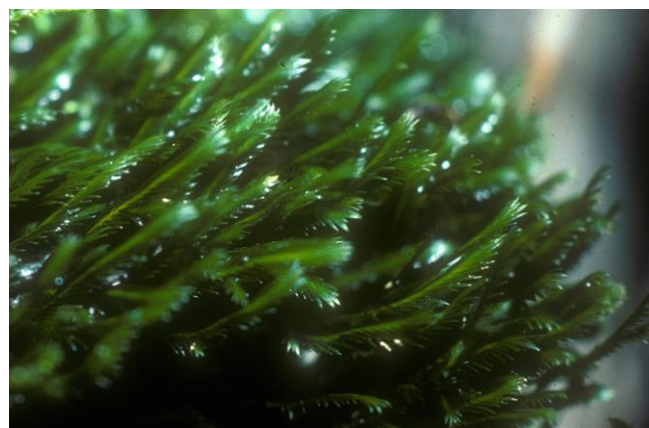


Figure 47. *Fissidens grandifrons*, a species that might have some sort of CO<sub>2</sub>-concentrating mechanism that permits it to live in alkaline water. Photo by Janice Glime.

Raven (1991) summarized the ecological relationships of CO<sub>2</sub>-concentrating mechanisms in plants. He found them to be negatively correlated with areas of CO<sub>2</sub> enrichment caused by respiration of organic carbon that had been produced elsewhere, such as the respiration of



bacteria and other organisms in sediments. Less pronounced relationships seem to exist with low temperatures during the growing season, low  $pH$  external to the plant, and rapid water movement over the plants that could replace the  $CO_2$  as it is used in photosynthesis.

When growing submerged in Florida, USA, winter conditions ( $12^\circ C$ , 10 h day length), *Fissidens cf. manateensis* (see Figure 47) had a typical  $C_3$  compensation point (Salvucci & Bowes 1981). However, when grown in Florida summer conditions ( $30^\circ C$ , 14 h day length), it had the ability to concentrate  $CO_2$ . This concentrating ability can be accomplished either by concentrating  $CO_2$  around the RUBISCO to a greater concentration than that of the medium, using a  $C_4$ -like mechanism, or by using active transport of inorganic carbon across the membrane.

But *Fissidens cf. manateensis* (see Figure 47) is not the only aquatic moss that appears to have some sort of  $CO_2$ -concentrating mechanism. Peñuelas (1985) found two more aquatic mosses [*Fissidens grandifrons* (Figure 47) and *Fontinalis antipyretica* (Figure 2)] that could carry out net photosynthesis in high inorganic carbon concentrations with high  $pH$  values that should have shifted the  $CO_2$  – bicarbonate equilibrium toward the bicarbonate or carbonate end, providing less free  $CO_2$  than that required to reach the compensation point. Several possibilities exist. As suggested earlier, there might be a mechanism for moving this inorganic carbon across the membrane by active transport. Or the moss could use its carbonic anhydrase (Steeman Nielsen & Kristiansen 1949; Arancibia & Graham 2003) externally to convert the  $HCO_3^-$  to free  $CO_2$ . I suggest a third possibility, that  $H^+$  ions available from cation exchange sites might be sufficient to lower the  $pH$  and shift the equilibrium toward  $CO_2$  at the moss surface, despite the  $pH$  being too high elsewhere in the water for that shift to occur. The latter explanation would be consistent with the observations that the  $CO_2$  compensation point and the  $^{13}C/^{12}C$  discrimination values for central and Northern European populations of *Fontinalis antipyretica*, *Fissidens rufulus* (Figure 48), *Riccia fluitans* (Figure 49), and *Ricciocarpos natans* (Figure 50-Figure 51) are consistent with a  $C_3$  pathway (Ruttner 1947; Osmond *et al.* 1981; Allen & Spence 1981; Raven *et al.* 1987, 1994, 1998).



Figure 48. *Fissidens rufulus*, a moss species with a  $CO_2$  compensation point consistent with a  $C_3$  plant. Photo by Hermann Schachner, through Creative Commons.



Figure 49. *Riccia fluitans*, a floating liverwort species with a  $CO_2$  compensation point consistent with a  $C_3$  plant. Photo by Štěpán Koval, with permission.

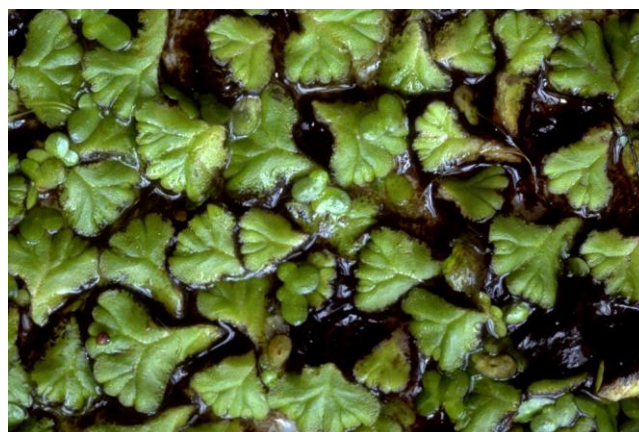


Figure 50. *Ricciocarpos natans*, a floating thallose liverwort species with a  $CO_2$  compensation point consistent with a  $C_3$  plant. Photo by Jan-Frahm, with permission.



Figure 51. *Ricciocarpos natans* section showing internal chambering and photosynthetic cells. Photo by Norbert Stapper, with permission.

This concentrating mechanism, whatever its nature, could explain the presence of bryophytes in calcareous water of streams and lakes where the  $pH$  would suggest there would be insufficient free  $CO_2$  for mosses to reach their  $CO_2$  compensation point. And, in fact, some bryophytes of calcareous streams seem to be limited to



waterfalls where high turbulence permits gaseous atmospheric  $\text{CO}_2$  to come in contact with the moss surface.

One of the most intriguing finds, mentioned above, is that *Fontinalis antipyretica* (Figure 2) has a higher C uptake rate from the water column than does its CAM companion, *Isoetes bolanderi* (Figure 46) (Sandquist & Keeley 1990). It appears that even aquatic bryophytes, contrasting with other aquatic macrophytes, lack or have only poorly developed  $\text{CO}_2$ -concentrating mechanisms (Raven 1991). But what about *Fontinalis*? Steeman Nielsen and Kristiansen (1949) have demonstrated the presence of carbonic anhydrase in that genus. Is it able to concentrate  $\text{CO}_2$ ? Can it convert bicarbonate to  $\text{CO}_2$ , perhaps through a pH-lowering mechanism? And how should we explain the delay in carbon fixation in *Fontinalis antipyretica* (Søndergaard & Sand-Jensen 1979)? Aquatic plants like *Elodea* (Figure 52) have internal air chambers that can delay the emission of respiratory  $\text{CO}_2$  and slow the time from uptake to the time it actually enters photosynthesis. But *F. antipyretica* has no air chambers. However, it has the lowest delay (0.2%) of the three plants tested, with *Elodea* having 8% and *Littorella* (Figure 53) having 14%. Some researchers have treated this delay in *Fontinalis* as evidence of a concentrating mechanism, but the low percent seems insignificant.



Figure 52. *Elodea canadensis*, an aquatic flowering plant species with a delay in carbon fixation. Photo by Kristian Peters, through Creative Commons.

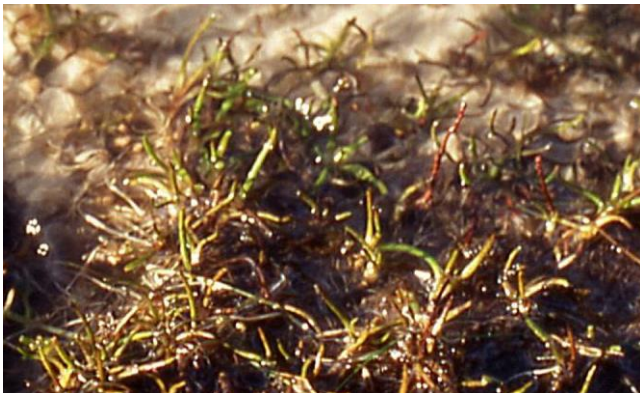


Figure 53. *Littorella uniflora*, an aquatic flowering plant species with a delay in carbon fixation. Photo by Christian Fischer, through Creative Commons.

In a separate comparison between the aquatic moss *Leptodictyum riparium* (Figure 54) and the tracheophyte *Elodea canadensis* (Figure 52), the moss had nearly double the RuBPCase activity ( $11.8$  vs  $6.0 \mu\text{M mg}^{-1} \text{chl h}^{-1}$ ) of the tracheophyte, but also had approximately double the PEPcase activity ( $0.7$  vs  $0.3 \mu\text{M mg}^{-1} \text{chl h}^{-1}$ ) (Keeley *et al.* 1986). Keeley *et al.* concluded that it is very unlikely that *Leptodictyum riparium* can utilize bicarbonate, whereas *Elodea* has been reported to use it freely.



Figure 54. *Leptodictyum riparium*, an aquatic moss. Photo by Michael Lüth, with permission.

### Bicarbonate Uptake

Aquatic tracheophytes typically are able to take in bicarbonate for use in the photosynthetic pathway (Farmer *et al.* 1986). Some aquatic tracheophytes, in particular species of *Isoetes* (Figure 46), have a CAM photosynthetic pathway that permits them to take in  $\text{CO}_2$  at night. But in their study of 15 species of aquatic macrophytes, Farmer *et al.* found that the aquatic moss *Fontinalis antipyretica* (Figure 2) had no PEP carboxylase, took in no  $\text{CO}_2$  at night, and used RUBISCO for its photosynthetic  $\text{CO}_2$  fixation. Steeman Nielsen (1947) stated outright that *Fontinalis antipyretica* "is unable to utilize  $\text{HCO}_3^-$  in the surrounding water for photosynthesis." On the other hand, Harder (1921) showed that as bicarbonate concentration increased from 0.01% to 0.64%, the assimilation plus respiration of *Fontinalis antipyretica* increased from 0.66 to 3.14. Burr (1941) likewise found that *Fontinalis* was more productive in water with bicarbonate than that with  $\text{CO}_2$ . But what does this genus use as a mechanism to get its  $\text{CO}_2$ , especially in water with a high pH where bicarbonates or carbonates predominate? Steeman Nielsen and Kristiansen (1949) suggested that there is evidence that  $\text{CO}_2$  enters the photosynthetic reactions in hydrated form (bicarbonate?). But how is that accomplished?

Perhaps Peñuelas (1985) has discovered the differences behind these contrasting conclusions. He demonstrated that *Fontinalis antipyretica* (Figure 2) from the River Muga in N.E. Spain was able to have a positive net photosynthesis up to a pH of 11.8-12.0 in a  $\text{NaHCO}_3$  solution, a remarkably high pH and indicative of use of a carbon source other than  $\text{CO}_2$ . Further support of this conclusion is that this population of *Fontinalis antipyretica* increased its photosynthetic rate when higher  $\text{HCO}_3^-$  concentrations at constant  $\text{CO}_2$  were used. But in populations from other localities, this same researcher did



not find evidence of its use of bicarbonates, suggesting that physiological races exist. This is consistent with my observations in eastern United States that it is absent in limestone streams and streams with  $pH$  high enough to preclude free  $CO_2$ , but in other parts of the world I have observed it growing on concrete and in alkaline streams.

Bain and Proctor (1980) tested twenty bryophytes from a variety of aquatic habitats to look for evidence of bicarbonate uptake. The ability of some bryophytes, such as *Scorpidium* (Figure 55), to live in water with high  $pH$  suggests that such a mechanism might exist. However, they found that the  $pH$  compensation points were in the range expected for  $C_3$  plants dependent on free  $CO_2$  for their carbon source. Only *Anthoceros husnotii* succeeded in having photosynthetic gain up to  $pH$  9.5 in 2.0 mM  $NaHCO_3$ . For the others, the equilibrium clustered around  $pH$  9.0 for 2.0 mM and 8.0 for 0.2 mM  $NaHCO_3$ . The four species of bicarbonate-using tracheophytes had final  $pH$  values ranging 10.1 – 10.9. As suggested above, there may be physiological races with different capabilities. The other possibility is that the mechanism for using bicarbonates may be inducible and was not sufficiently activated during the short-term lab experiments to make a difference.



Figure 55. *Scorpidium scorpioides* with capsules, a species that is able to live in high  $pH$  water. Photo by Michael Lüth, with permission.

## Pyrenoids

The slightly elevated  $pH$  compensation point for *Anthoceros husnotii* is consistent with other data on *Anthoceros* that suggest the **pyrenoids** (proteinaceous bodies serving as nucleus for starch storage) have a role in concentrating  $CO_2$  in some hornworts. Members of the **Anthocerotophyta** (hornworts; Figure 59) with pyrenoids [*Anthoceros* (Figure 56), *Phaeoceros* (Figure 57)] exhibit a well-developed ability to concentrate  $CO_2$  (Raven 1997; Smith 2000). However, it appears that among land plants, only *Notothylas* (Figure 58), *Phaeoceros*, and *Anthoceros*, all members of the phylum **Anthocerotophyta**, have such a mechanism (Smith & Griffiths 2000; Hanson *et al.* 2002). When a number of bryophytes were subjected to carbonic anhydrase inhibitors, only *Phaeoceros laevis* (Figure 57), a member of **Anthocerotophyta**, exhibited reduced  $CO_2$  affinity and its  $CO_2$  compensation point rose from 2.5 Pa to 20 Pa. No depression occurred in the other liverworts or mosses in the study. These results suggest the role of carbonic anhydrase as a  $CO_2$ -concentrating mechanism.



Figure 56. *Anthoceros crispulus*, member of a genus that uses pyrenoids to concentrate  $CO_2$ . Photo by Manju Nair, through Creative Commons.



Figure 57. *Phaeoceros laevis*, a species that seems to use carbonic anhydrase as a  $CO_2$ -concentrating mechanism. Photo by Robert Klips, with permission.



Figure 58. *Notothylas orbicularis*, member of a genus that uses pyrenoids to concentrate  $CO_2$ . Photo by Michael Lüth, with permission.

Raven *et al.* (1998) have reviewed the evidence supporting a  $CO_2$ -concentrating mechanism in the pyrenoids of some members of the **Anthocerotophyta**. Such a mechanism was already known in algae with pyrenoids (Vaughn *et al.* 1990, 1992). Pyrenoid-containing hornworts exhibited a  $^{13}C/^{12}C$  discrimination of 7.2-11.7% compared to 16.4-35.1% in hornworts lacking pyrenoids



(Smith & Griffiths 1996a, b). The higher values are consistent with a  $C_3$  pathway, whereas the low values of the pyrenoid-containing hornworts are consistent with some sort of  $CO_2$ -concentrating mechanism. The  $CO_2$  compensation point has only been investigated in *Anthoceros crispulus* (Figure 56), with a value of  $26 \mu M CO_2 \text{ mole}^{-1}$ , a value higher than that typical of  $C_4$  plants, but lower than that for  $C_3$  liverworts and mosses in the Smith and Griffiths studies ( $49\text{--}68 \mu M \text{ mole}^{-1}$ ).



Figure 59. *Phaeoceros carolinianus*. Photo by Michael Lüth, with permission.

Plants with a  $CO_2$ -concentrating mechanism have a higher affinity for external  $CO_2$  than do typical  $C_3$  plants. *Notothylas* (Figure 58) and *Phaeoceros* (Figure 57) exhibit  $CO_2$  compensation points of  $11\text{--}13 \text{ ppm } CO_2$  compared to  $31 \text{ ppm}$  for *Megaceros* (Figure 62) and  $64 \text{ ppm}$  for *Marchantia polymorpha* (Figure 3-Figure 4) (Hanson *et al.* 2002), where no concentrating mechanism seems to be present.

Those plants with a  $CO_2$ -concentrating mechanism can maintain a pool of  $CO_2$  that is immediately available after dark-light transition. *Anthoceros crispulus* (Figure 56) exhibited a pool size of  $17.6 \mu mol CO_2 g^{-1} \text{ chlorophyll}$ , whereas four of the five  $C_3$  pathway bryophytes had no pool, and the thallose liverwort (with internal air chambers), *Conocephalum conicum* (Figure 60-Figure 61), had only  $5.5 \mu mol CO_2 g^{-1} \text{ chlorophyll}$  (Raven *et al.* 1998). *Notothylas* (Figure 58) and *Phaeoceros* (Figure 57) have an inorganic carbon pool of  $19\text{--}108 \mu M g^{-1} \text{ chlorophyll}$ ; *Megaceros* (Figure 62) does not maintain any dissolved inorganic carbon pool (Hanson *et al.* 2002).



Figure 60. *Conocephalum conicum*, a thallose liverwort with pores and air chambers. Photo by Michael Lüth, with permission.



Figure 61. Cross section of thallus of *Conocephalum conicum* showing the pore, air chamber, and photosynthetic vs non-photosynthetic cells. Photo from Botany Website, UBC, with permission.



Figure 62. *Megaceros* sp., member of a genus in *Anthocerotophyta* that seems to have no  $CO_2$  concentrating mechanism. Photo by Juan Larrain, with permission.

But what is this  $CO_2$ -concentrating mechanism? The concentrating mechanism of the pyrenoid suppresses the oxygenase activity of RUBISCO, hence reducing the loss of  $CO_2$  and energy through photorespiration. We do not know the immediate  $CO_2$ -fixation products in these pyrenoid-bearing hornworts. Nor do we know the PEP carboxylase to RUBISCO ratios. Is this some primitive  $C_4$  plant struggling between relative amounts of PEP carboxylase and RUBISCO?

### The Bottom Line

Nevertheless, no one has been able to demonstrate any direct evidence of a  $C_4$  pathway, and consideration of a CAM pathway seems illogical since there are no stomata in the leaves. Therefore, we can only infer certain characteristics of bryophyte photosynthetic physiology. Like the tracheophytes, we should expect bryophytes to have low photosynthetic temperature optima, ranging  $10\text{--}20^\circ C$  in most species. This is in part due to the loss of  $CO_2$  beyond that gained in photosynthesis at higher temperatures. This loss is from photorespiration, which occurs only in light and increases with temperature more rapidly than does photosynthesis.  $C_4$  plants either lack photorespiration or immediately grab the lost  $CO_2$  and store it as malate. As  $C_3$  plants, all mosses must have photorespiration and would therefore have more photosynthetic gain at low temperatures relative to  $C_4$



plants. It appears that the first record of photorespiration in any plant was in the aquatic moss *Fontinalis* (Figure 2) (Bode 1940), yet the best evidence we have for the possibility of an alternative pathway of CO<sub>2</sub> uptake in bryophytes is in this genus. The bottom line – we still don't understand how these CO<sub>2</sub>-concentrating mechanisms work, especially in bryophytes lacking pyrenoids.

## Diurnal Patterns in Photosynthesis?

Strong daily patterns exist in some bryophytes. *Pohlia wahlenbergii* (Figure 63), in a sub-alpine habitat in midsummer, had its highest light-saturated photosynthetic uptake early in the morning (8 mg CO<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>) (Coxson & Mackey 1990). By late afternoon, this had declined to ~5 mg CO<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>. The plants showed full recovery during late evening and nighttime. The authors considered that these daily oscillations could be recurring photodestruction and repair of the pigment complexes – an unusual response for plants in high light habitats such as this. They suggested that instead these fluctuations may represent a daily, endogenous photosynthetic rhythm as known in some phytoplankton populations. Although this is an intriguing idea that would permit the moss to gain CO<sub>2</sub> at a time when tracheophytes are slowed by the reduced light intensity and cool temperatures, much more evidence is needed to conclude that any endogenous rhythm exists.



Figure 63. *Pohlia wahlenbergii*, a species of wet habitats that strong daily photosynthetic patterns. Photo by Michael Lüth, with permission.

I would be more inclined to attribute these morning and evening increases to the increased moisture in the atmosphere. In some parts of the world, fog and dew are the only sources of water for bryophytes. Bryophytes taken from a desiccator will rapidly gain weight on a balance as they absorb atmospheric moisture. A similar phenomenon may permit these plants to have low levels of photosynthetic gain in the low light but higher moisture levels of early morning and pre-dusk conditions.

## Products of CO<sub>2</sub>

Generally, textbooks present glucose as the final product of photosynthesis, but in fact, this is misleading. Photosynthesis makes PGA that can then be converted to a variety of products, glucose being one of them. In

bryophytes, other products are likewise possible. Valanne (1984) reported that the principal sugars made by bryophytes are sucrose, glucose, fructose, and mannose. She pointed out that evidence for notable exceptions in carbohydrate metabolism of bryophytes compared to that of tracheophytes is lacking (Allsopp 1951; Eschrich & Steiner 1967; Huneck 1969; Margaris & Kalaitzakis 1974; Valanne 1984). In the leafy liverwort *Plagiochila asplenioides* (Figure 65), volemitol, sucrose, and starch are the principal photosynthetic storage products (Suleiman & Lewis 1980).

Lipids are also an important photosynthetic product (Valanne 1984) in bryophytes. In the Arctic, growing shoots typically contain more lipids than carbohydrates (Rastorfer 1972).

Koskimies-Soininen and Nyberg (1991) found that the types of lipids were dependent on temperature and light. In *Sphagnum fimbriatum* (Figure 64), the amount of total lipid increased in dim light conditions at both 15 and 25°C. Conversely, in darkness at 25°C the lipids decreased. Under normal light levels, a decrease in temperature in the range of 5-15°C causes a decrease in the amounts of linoleic, α-linolenic, and arachidonic acids. Concomitantly, concentrations of palmitic, stearic, and oleic acids increase. When light intensity is also decreased, there is an increase in palmitic, stearic, linoleic, and arachidonic acids and a decrease in oleic and α-linolenic acids. Both temperature and light decreases elicit similar responses in total fatty acid desaturation and concentration of α-linolenic acid.



Figure 64. *Sphagnum fimbriatum*, a species that stores more lipids in low light. Photo by David T. Holyoak, with permission.

## Dark CO<sub>2</sub> Fixation

These newly incorporated carbohydrates don't necessarily remain in the same products as are initially stored. In as little as two hours, a number of other products are possible. Within two hours in the leafy liverworts *Plagiochila asplenioides* (Figure 65) and *Scapania undulata* (Figure 66), the amino acids asparagine, glutamine, and glutamic acid were dominant products (Gupta 1976). Citric acid and malic acids, along with an unknown acidic compound, were also common in both. In addition, *Plagiochila* contained fumaric, glycolic, and succinic acids, although the fumaric and glycolic acids took longer than two hours to show <sup>14</sup>CO<sub>2</sub>. Soluble carbohydrates included sucrose, glucose, mannitol, fructose, and a series of fructans, differing little from the ones reported by Valanne (1984). But concentrations



differ, with volemitol being the most labelled soluble carbohydrate in *Plagiochila asplenioides* and sucrose in *Scapania undulata*. Interestingly, malic acid, a product associated with CAM photosynthesis, was the most labelled organic acid in both species.



Figure 65. *Plagiochila asplenioides*. Photo by Michael Lüth, with permission.



Figure 66. *Scapania undulata*. Photo by Michael Lüth, with permission.

In the dark, non-photosynthetically fixed carbon is incorporated into amino acids (>60% of total non-photosynthetic carbon fixation), making primarily aspartate, alanine, and glutamate (Dhindsa 1985). Most of the remaining non-photosynthetic fixation incorporates carbon into organic acids (<40%). This dark fixation permits rehydrated mosses in the dark to repair damage due to desiccation.

## Transport of Photosynthate

Little is known about the movement of most substances in mosses and liverworts, but we do have evidence that both nutrients and photosynthate are indeed moved about. Alpert (1989) reported that within 26 hours, at least 10% of the photosynthate was translocated out of the leafy shoot of *Grimmia laevigata* (Figure 67).

Transport of photosynthate in the bryophyte is often similar to that in tracheophytes. In *Polytrichastrum alpinum* (Figure 68), photosynthate is translocated from the above ground shoots to the rhizomes (Hobbs & Pritchard 1987). It does not move in the **hydroids** (water-

conducting cells, but rather moves in the phloem-like **leptoids**, as demonstrated in *Polytrichum commune* (Figure 7) (Eschrich & Steiner 1967). Héban (1975) demonstrated that a cut stem will exude a clear liquid from the leptoids and associated parenchyma. The associated parenchyma cells seem to function much like companion cells of phloem. These cells have high enzyme activity and most likely are responsible for the movement of substances into and out of the leptoids (Richardson 1981).



Figure 67. *Grimmia laevigata*. Photo by Michael Lüth, with permission.



Figure 68. *Polytrichastrum alpinum*. Photo by Michael Lüth, with permission.

While tracheophyte botanists are still trying to understand the mechanisms of xylem and phloem transport in the tracheophytes, bryologists are struggling with much smaller systems in bryophytes. One bryophyte stem is little larger than a single vascular bundle in one of these lignified plants. And the aphids that live on the fluids in the tracheophytes are larger than the diameters of bryophyte stems. So how do bryologists measure something so small when mechanisms of movement in its larger counterpart have been such an enigma for plant physiologists?

For measuring phloem transport, the old adage that if there is a niche, there is an insect to fill it, comes to the rescue of the bryologists. There are indeed tiny aphids (for example *Myzodium*, Figure 69) that live on the fluids in the phloem of *Polytrichum* (Figure 7, Figure 70) species. And Bob Thomas, with his coworkers, has used them to help us understand how mosses transport things from place to place internally.



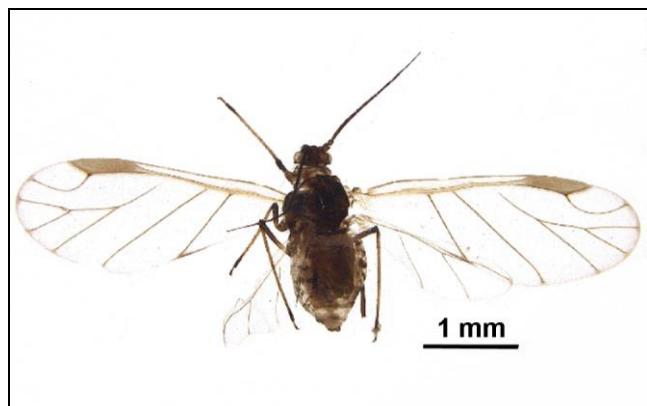


Figure 69. *Myzodium modestum*, an aphid genus with members that feed on substances in leptoids of *Polytrichum* species. Photo by CBG Photography Group, through Creative Commons.

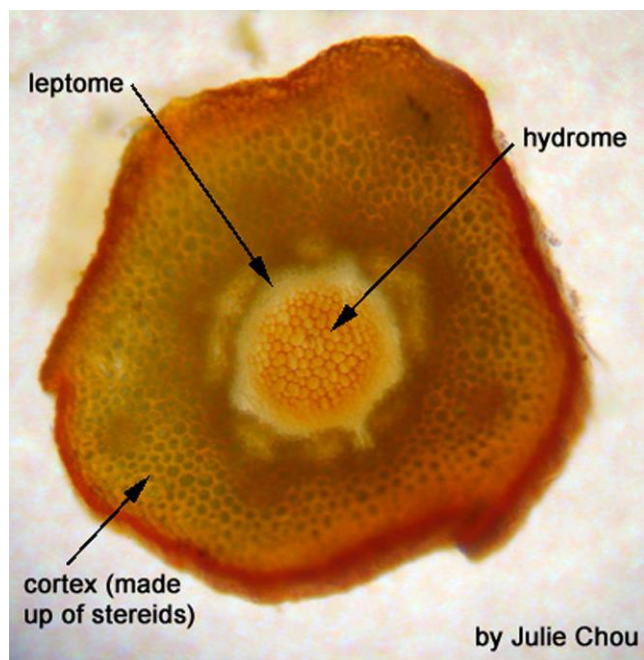


Figure 70. *Polytrichum commune* stem cross section, showing location of the leptoids that carry the sugars. Photo from Botany Website, UBC, with permission.

Thomas and coworkers (1990) found that *Polytrichum commune* (Figure 7, Figure 70) transports things from **source-to-sink**, just as we find in those other plants. Through some of their early experiments, Thomas *et al.* (1988) found glucose, fructose, and sucrose in pulse-labelled stems 30 minutes after treatment in *Polytrichum commune*. The translocated carbon appeared in starch and cell wall polysaccharide pools within 1-6 weeks after treatment and could be used or stored. Perhaps the greater surprise is that 3.3% of the labelled sugar appeared later in neighboring stems, presumably following a source-to-sink gradient. This seems to be attributable to the transport of sugars in the leptome through perennating rhizomes, which often connect multiple stems.

But does it work the same way as in those other plants? Leaf conducting cells of *Polytrichum commune* (Figure 7, Figure 70) have high solute concentrations, as revealed by incipient plasmolysis, and high ATPase activity at membrane surfaces (Thomas *et al.* 1990).

Thomas and coworkers concluded that this permits the moss leaf to use a process analogous to **phloem loading** in minor veins of flowering plants. Furthermore, this sugar loading seems to be coupled with proton transport, suggesting a **proton pump** to get things across cell membranes.

Just how effective is this movement in transporting sugars and other substances from leaves to basal regions? Using petroleum jelly across leaf bases to prevent external capillary movement, Thomas and Lombard (1991) found that 17-38% of the translocated label could be detected in feeding aphids within four hours – not a very rapid rate by tracheophyte standards, where rates are more commonly about 30 cm per hour (Saupe 2005). In fact, the *Myzodium* had to divert nutrients away from the food-conducting tissues of the stem and alter the normal source-to-sink flow in order to get enough. Even then, the aphids had to aggregate in order to compete with the natural source-to-sink travel within the moss. In *Polytrichastrum alpinum* (Figure 68), the photosynthate reached underground rhizomes at a rate of 3 mm h<sup>-1</sup> (Collins & Oechel 1974). On the other hand, this moss can move things upward at 32 cm h<sup>-1</sup> (Eschrich & Steiner 1967).

All this discussion has been on **Polytrichaceae**! We know almost nothing beyond their successful lives to tell us about the other bryophytes in which the conducting system is less well developed. *Hylocomium splendens* (Figure 21), a predominately ectohydric moss, moved its photosynthate so slowly that 98% remained at the fixation site 48 hours later (Callaghan *et al.* 1978).

Skré *et al.* (1983) have helped to demonstrate some of the differences and consistencies between the endohydric **Polytrichaceae** and the more common ectohydric pattern of other mosses. *Polytrichum commune* (Figure 7) behaved much like the C<sub>4</sub> plants and retained most of its labelled <sup>14</sup>C after two hours. However, after 35 days it had sequestered a large portion (second highest of the four species) in its brown tissues. The ectohydric *Sphagnum subsecundum* (Figure 71) retained the least of its labelled <sup>14</sup>C, but moved the highest portion to its brown tissues after 35 days. *Hylocomium splendens* (Figure 21) and *Pleurozium schreberi* (Figure 37) had inconsistent patterns of translocation, but all four species accumulated <sup>14</sup>C in their growing shoot tips and senescent brown tissues and all four experienced high losses of <sup>14</sup>C through respiration during the peak summer growing season.



Figure 71. *Sphagnum subsecundum*, a species that moves large portions of its carbon to its brown tissues. Photo by Michael Lüth, with permission.



## Storage of Photosynthate

Mosses and liverworts differ in their storage of photosynthate. In liverworts, sugar alcohols are important (Suleiman *et al.* 1979). In the mosses, the soluble product is primarily sucrose (Margaris & Kalaitzakis 1974; Suire 1975). Although most of the carbohydrates in aboveground portions of mosses are soluble sugars, the belowground parts are typically richer in starch (Hicklenton & Oechel 1977; Sveinbjörnsson & Oechel 1981). Witt and Teubert (1992) noted the contributions of phosphorylase in starch synthesis in all the sinks for starch in young gemmalings of the thallose liverwort *Riella helicophylla* (Figure 72). This included gemmae, meristems, and regenerating cells.

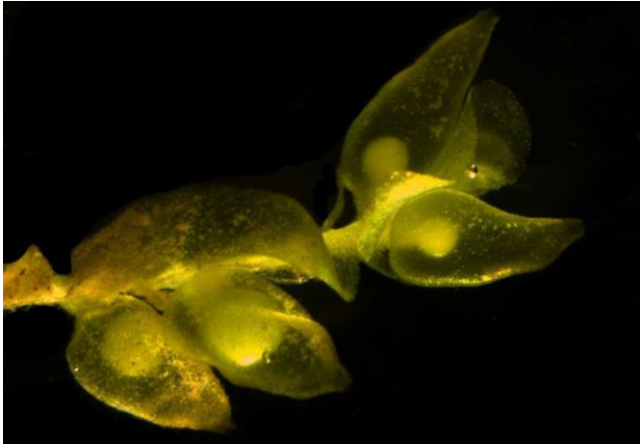


Figure 72. *Riella helicophylla*, a species that uses phosphorylase in starch synthesis in starch sinks of gemmalings. Photo by NACICCA through Creative Commons.

In *Polytrichum* (Figure 7), which may not be typical, the green, photosynthesizing shoot has the largest amount of nonstructural carbohydrate and the stem the least (Sveinbjörnsson & Oechel 1981). Sugars are highest in the green shoots; starches are highest in the belowground parts. The above ground portion can move more than 30% of its daily carbon gain to the below ground rhizome. In a more ectohydric *Dicranum fuscescens* (Figure 73), the green part of the shoot has ~7.0-10.5% ash-free tissue dry mass as carbohydrate (Hicklenton & Oechel 1977), approximating about 0.7-1.3% of its fresh weight (Rastorfer 1972).



Figure 73. *Dicranum fuscescens*, showing lower, light brown, senescent portion near lower portion of picture on right. Photo by Michael Lüth, with permission.

As already seen, even senescent tissue is able to store carbon products (Skré *et al.* 1983). The senescent portion of *Dicranum elongatum* (Figure 74) incorporates labelled carbon into lipids (Hakala & Sewón 1992). Hakala and Sewón concluded that the ability of the moss to transport such substances both upward and downward permitted this senescent portion of the moss to serve as an energy store. However, in *Dicranum fuscescens* (Figure 75) little change is seen in the starch content of brown, senescing parts of the shoot, while the green, leafy part increases its total carbohydrate content during the growing season. Even so, the starch content of the leafy shoots of this species, as well as *Polytrichum commune* (Figure 7) and *Polytrichastrum alpinum* (Figure 68), is less than 2% (Hicklenton & Oechel 1977), with similar values in *Pleurozium schreberi* (Figure 37) and *Ceratodon purpureus* (Figure 36) (Aro & Valanne 1979).



Figure 74. *Dicranum elongatum*, a species in which senescent portions incorporate carbon into lipids. Photo by Michael Lüth, with permission.



Figure 75. *Dicranum fuscescens*, a species that does not seem to store energy in its senescing parts, but rather in the green leafy part. Photo by Michael Lüth, with permission.

*Sphagnum* (Figure 71) increases its lipid content in the spring in growing parts but decreases it in the senescent parts (Rastorfer 1972; Karunen & Salin 1981). *Dicranum elongatum* (Figure 74), on the other hand, stores large quantities of lipids in its senescent parts (Karunen & Mikola 1980; Karunen & Liljenberg 1981). In cold weather, mosses, at least in the Arctic, store high quantities of triglycerides (Karunen & Kallio 1976; Swanson *et al.* 1976; Karunen 1981; Karunen & Salin 1981). Both triglycerides and unsaturated fatty acids diminish in elevated temperatures (Karunen 1981).



Illumination affects the ratio of starch to protein, with *Pleurozium schreberi* (Figure 37) and *Ceratodon purpureus* (Figure 36) in continuous illumination showing an increase in starch content and decrease in protein in the leafy shoots (Aro & Valanne 1979).

During periods of darkness, both the older, senescent portions and active photosynthetic portions of the mosses can lose stored products. In *Racomitrium barbuloide*s (Figure 76), the concentrations of ethanol-soluble sugars and lipids in green portions decreased in the dark, indicating their use as storage substances (Sakai *et al.* 2001). However, sugars and lipids in the brown, senescent portions did not decrease and starches remained constant in both portions. Continuous light caused initial increase of sugars and lipids in the green portion, but later these decreased in these conditions. This regime caused a significant decline in photosynthetic capacity.



Figure 76. *Racomitrium barbuloide*s, a species that uses ethanol-soluble sugars and lipids as storage products. Photo by Digital Museum, Hiroshima University, with permission.

The type of carbohydrate stored determines its rate of turnover from storage. In the leafy liverwort *Plagiochila asplenioides* (Figure 65), breakdown of starch in the dark is rapid, but much carbon still remains as sucrose and volemitol due to their very slow turnover (Suleiman & Lewis 1980).

In limiting habitats where light limits photosynthesis, exogenous sugars may help the plants to maintain a positive carbon balance (Graham *et al.* 2010). In peat mosses, a 1% glucose solution increased photoautotrophic growth by a factor of 1.7. Air-grown mosses exhibited a 28X biomass with a 1% emendment and 39X with a 2% emendment of glucose. Similarly, fructose enhanced growth by 21X at 1% and sucrose at 2% enhanced it by 31X. Graham and coworkers suggest that this **mixotrophy** is a trait that evolved early in evolution of photosynthetic organisms. This ability to use external sugars correlates with the development of protective cell wall polyphenolics, suggesting that the sugars may "subsidize" the cost of producing these protective compounds.

## Sporophyte Photosynthesis

Although mature sporophytes are seldom green, they are typically green during the earlier stages of their development. This is easy to suppose in mosses, and confirmed in such mosses as *Funaria hygrometrica* (Figure 14) (Krupa 1969), but liverworts do not elongate

their setae until the sporophyte is mature, and the developing capsule is confined within the perianth (Figure 77). Nevertheless, Thomas *et al.* (1979) confirmed photosynthesis in liverwort sporophytes of *Fossombronina foveolata* (Figure 78-Figure 79), *Lophocolea heterophylla* (Figure 80), *Pellia epiphylla* (Figure 81), *Ptilidium pulcherrimum* (Figure 82), and *Riella affinis*. In the leafy liverwort *Lophocolea heterophylla*, 40% of this photosynthetic activity was attributable to spores. They confirmed that the gametophyte tissue surrounding the young sporophyte did inhibit the photosynthesis of the sporophyte by up to 50%.

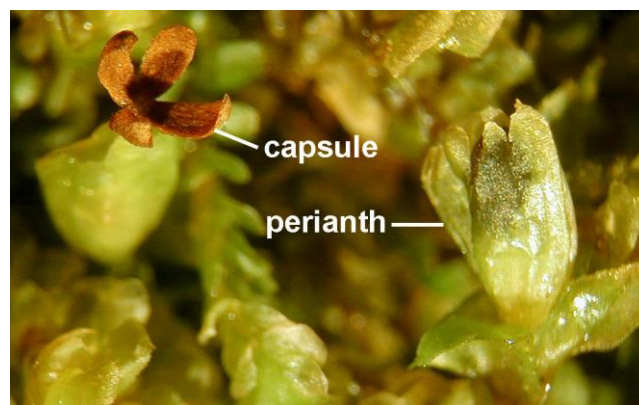


Figure 77. *Scapania gracilis* illustrating the complete covering of the perianth over the immature capsule and loss of green color of the capsule at maturity. Photo by Michael Lüth, with permission.



Figure 78. *Fossombronina foveolata* with young, green capsules. Photo by David T. Holyoak, with permission.



Figure 79. *Fossombronina foveolata* with mature capsules that are no longer green. Photo by Bob Klips, with permission.





Figure 80. *Lophocolea heterophylla* with mature capsules that have lost their green color. Photo by David T. Holyoak, with permission.



Figure 81. *Pellia epiphylla* young capsule emerging from perianth and losing its green color. Photo from Biopix, through Creative Commons.



Figure 82. *Ptilidium pulcherrimum* perianths with some of the young, green sporophytes beginning to emerge. Photo by Michael Lüth, with permission.

Krupa (1969) found that at certain stages in development, the sporophyte of *Funaria hygrometrica* (Figure 14) is photosynthetically self-sufficient. Nurit and Chevallier (1978) confirmed this, finding that the *F. hygrometrica* gametophyte has a constant production of oxygen in the light throughout its development, but that the production of oxygen in the sporophyte decreases as the

capsule matures. Although the weight of the seta (Figure 83) decreases as the weight of the capsule increases (Figure 84-Figure 85) in *Polytrichum* (Figure 7), this is not the case in *Funaria* (Paolillo & Bazzaz 1968), suggesting that in *Funaria* the capsule does its own photosynthesizing. Nevertheless, the gametophyte makes a major contribution to sporophyte biomass in bryophytes.

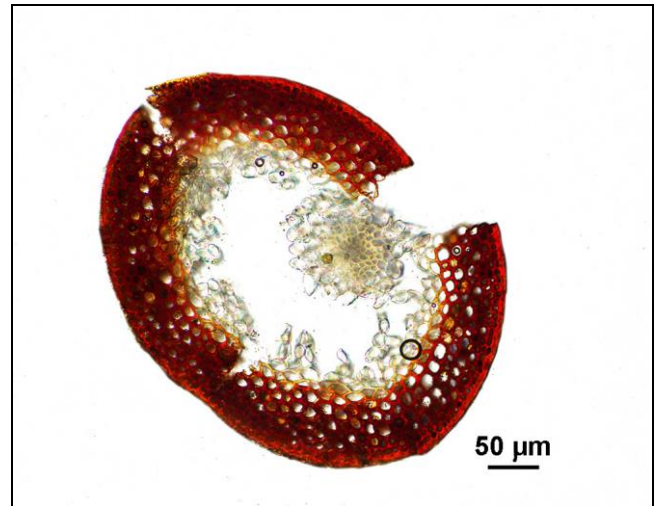


Figure 83. *Polytrichum juniperinum* seta cross section showing conducting tissue in circular cluster of cells just inside the break in the stem. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University.



Figure 84. *Polytrichum juniperinum* with expanding seta, before capsule formation. Photo by Janice Glime.



Figure 85. *Polytrichum juniperinum* capsules with one on left showing mature seta that is thinner than young ones. Photo by Des Callaghan, with permission.



Atanasiu (1975) compared the gametophyte and sporophyte of *Dicranum scoparium* (Figure 86) and *Tortella tortuosa* (Figure 87). The ratios of net photosynthesis to dark respiration were 0.77-0.97 in the sporophyte and 3.50-5.17 in the gametophyte, suggesting little or no net photosynthetic gain by the sporophyte. These differences were supported by the determination that the gametophytes had 3-4 times the chlorophyll content of the sporophytes. Atanasiu concluded that in these two species the sporophyte is not capable of supporting itself photosynthetically.



Figure 86. *Dicranum scoparium* gametophytes and sporophytes showing green capsules. Photo by Michael Lüth, with permission.



Figure 87. *Tortella tortuosa*. Photo by Michael Lüth, with permission.

## Respiration

Bryophytes, like  $C_3$  tracheophytes, have two types of respiration. The productivity of photosynthesis creates an environment in which ATP is produced and dark respiration is suppressed. This respiration, however, occurs in the dark to produce ATP and maintain the biological process of the plant. I am aware of no studies to determine if dark respiration occurs in rhizoids in the daytime, but one might suppose that it does, as it does in roots. But whereas photosynthesis suppresses dark respiration, the presence of the RUBISCO enzyme catalyzes not only photosynthesis, but also catalyzes photorespiration, both in the light. It is this photorespiratory process that causes  $C_3$  plants to have

such a low temperature optimum for net photosynthetic gain. As the temperature rises, the rate of photorespiration increases more rapidly than does the rate of photosynthesis, until ultimately the plant loses more  $CO_2$  and energy than it gains. For example, in the High Arctic Svalbard populations of *Sanionia uncinata* (Figure 88), photosynthesis at near light saturation remained nearly constant in the range of 7 to 23°C, suggesting a  $Q_{10}$  near 1.0, but the respiratory  $Q_{10}$  in that range was 3.0 (Uchida *et al.* 2002). For this reason, most plants, including bryophytes, that have survived the test of time are those that become dormant as the temperature rises, causing both processes to cease. In bryophytes, this is often effected by drying that occurs at higher temperatures.



Figure 88. *Sanionia uncinata*, a species that in the high Arctic does not seem to alter its photosynthetic rate in response to temperature, but that has a respiratory  $Q_{10}$  of 3.0. Photo by Michael Lüth, with permission.

Even dark respiration, which is generally only about 1/2 to 1/3 that of photorespiration, can result in a significant carbon loss. In studying tropical bryophytes, Zotz *et al.* (1997) found that more than half the carbon gained by photosynthesis in the daytime was lost during the night as respiratory loss. This left the bryophytes to gain only about 45% of their initial carbon in new carbon per year. As is common, water was the primary limiting factor for carbon gain.

In early experiments on the effects of light on respiration, Egle and Fock (1965) used, among others, the thallose liverwort *Conocephalum conicum* (Figure 60-Figure 61). They found that the results were similar in the liverwort and tracheophyte leaves, but that the curves for the liverwort were more pronounced. They learned that increasing oxygen concentrations (1, 25, & 75%) severely depressed photosynthesis. Following darkening, the  $CO_2$  output increases steadily for about 5 minutes, at which time the stationary dark respiration rate is reached. Initially, high  $O_2$  concentrations caused a strong burst of  $CO_2$  in the dark, but within 15 minutes the thallus reaches the same equilibrium level of dark respiration. The level of oxygen from 1-99% does not influence the dark respiration. Higher light intensities increase the intensity of the  $CO_2$  outburst at the onset of the next dark period. Using experiments that inhibited photosynthesis in the light, Egle and Fock demonstrated that the liberation of  $CO_2$  in the light is greater than that in the dark. High  $O_2$  concentrations cause this photorespiration to greatly exceed



the uptake of CO<sub>2</sub> by photosynthesis. Furthermore, old leaves exhibit more light respiration than do young leaves, contrasting with the reverse effect in dark respiration (Zelitch & Barber 1960; Fock 1965). Egle and Fock were convinced that this process was not the same respiratory process of decomposing assimilates that occurred in the dark. Rather, they discouraged the terminology "light respiration," considering that the light liberation of CO<sub>2</sub> might be only a side reaction of metabolism.

Peñuelas *et al.* (1988) compared the respiration rates of different parts of aquatic plants with that of the shoots of bryophytes. For the aquatic bryophytes studied, shoots had a respiratory rate of 53-66 μmol O<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>. The green alga *Cladophora glomerata* (Figure 89) had 96 μmol O<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup> respiration. The algae and bryophytes had rates higher than those of flowering macrophyte stems (13-71 μmol O<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>), but lower than that of their leaves (30-142 μmol O<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>).



Figure 89. *Cladophora glomerata* filament, a green alga that, along with bryophytes, has a higher respiratory rate than the flowering aquatic plants. Photo by Noora Hellen, through Creative Commons.

## Summary

Net productivity is the photosynthetic gain, measured as CO<sub>2</sub> uptake or O<sub>2</sub> emission, of a plant, whereas gross photosynthesis is the total CO<sub>2</sub> fixation, frequently obtained by adding respiratory loss to measured CO<sub>2</sub> uptake. However, photorespiration occurs in the light and cannot be measured by the dark respiration method. Photorespiration, apparently first discovered in bryophytes, contributes to CO<sub>2</sub> loss, and its rate is generally higher than that of dark respiration.

Bryophyte photosynthesis can respond quickly to moisture from dew and fog as well as from rain. It likewise responds quickly to light. The structural simplicity of bryophyte leaves, with only a single cell layer and no need to bring CO<sub>2</sub> in through stomata that close in dry atmospheres, permits bryophytes to take advantage of photosynthetic opportunities immediately. In some cases, leaf lamellae increase the surface area and chlorophyll available for photosynthesis. Pores in some liverwort thalli may control CO<sub>2</sub> uptake. In some cases the chloroplast structure changes in response to changes in wavelengths of light.

Bryophyte chloroplasts are typical of plants, but their chlorophyll proteins and fatty acids appear to be somewhat different from those of tracheophytes. Furthermore, the chlorophyll is conserved for long periods in the dark, whereas it is not in tracheophytes.

Bryophyte productivity is generally low, but the photosynthetic capacity, when measured on the basis of chlorophyll concentration, is similar to that of tracheophytes.

The chlorophyll antenna system, as in tracheophytes, permits bryophytes to use and transmit energy in a variety of wavelengths, directing it to chlorophyll *a*. The most common of these antenna pigments are α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin.

Although some bryophytes seem to be able to enhance CO<sub>2</sub> uptake, for example through pyrenoids in many of the Anthocerotophyta, their photosynthetic pathway seems to be entirely C<sub>3</sub>. Some aquatic bryophytes, such as *Fontinalis antipyretica*, seem to be able to take up CO<sub>2</sub> in high pH conditions that should permit only very little free CO<sub>2</sub>, suggesting some sort of concentrating mechanism.

Photosynthate is transported in the phloem, as demonstrated by tiny aphids. It can be stored in a variety of forms, particularly sugar alcohols (liverworts) and sucrose (mosses). Lipids may be stored in senescent portions and used later for spring growth.

Sporophytes of mosses are photosynthetically active in their young stages, but liverworts do not elongate their setae until the capsule matures, causing little light to reach the developing sporophyte.

## Literature Cited

- Allen, E. D. and Spence, D. H. N. 1981. The differential ability of aquatic plants to utilize the inorganic C supply in freshwater. *New Phytol.* 87: 269-283.
- Allsopp, A. 1951. The sugars and non-volatile organic acids of some archegoniates. *J. Exper. Bot.* 1: 121-124.
- Alpert, P. 1989. Translocation in the nonpolytrichaceous moss *Grimmia laevigata*. *Amer. J. Bot.* 76: 1524-1529.
- Anderson, B., Salter, A. H., and Barber, J. 1996. *Molecular Genetics of Photosynthesis*. IRL Press at Oxford University, 252 pp.
- Arancibia, P. and Graham, L. 2003. Carbonic anhydrase in Charophyceae and bryophytes. Abstract. Botany 2003, Aquatic and Wetland Plants: Wet & Wild, Botanical Society of America, Mobile, p. 65.
- Aro, E.-M. 1982a. Polypeptide patterns of the thylakoid membranes of bryophytes. *Plant Sci. Lett.* 24: 335-345.
- Aro, E.-M. 1982b. A comparison of the chlorophyll-protein composition and chloroplast ultrastructure in two bryophytes and two higher plants. *Zeits. Pflanzenphysiol.* 108: 97-105.
- Aro, E.-M. and Valanne, N. 1979. Effect of continuous light on CO<sub>2</sub> fixation and chloroplast structure of the mosses *Pleurozium schreberi* and *Ceratodon purpureus*. *Physiol. Plant.* 45: 460-466.
- Atanasiu, L. 1975. Photosynthesis and respiration in sporophytes and gametophytes of two species of mosses. *Rev. Roum. Biol.* 20: 43-48.



- Bain, J. T. and Proctor, M. C. F. 1980. The requirement of aquatic bryophytes for free CO<sub>2</sub> as an inorganic carbon source: Some experimental evidence. *New Phytol.* 86: 393-400.
- Bazzaz, F. A., Paolillo, D. J. Jr., and Jagels, R. H. 1970. Photosynthesis and respiration of forest and alpine populations of *Polytrichum juniperinum*. *Bryologist* 73: 579-585.
- Bendz, G., Löff, L. G., and Martensson, O. 1968. Moss pigments. 8. The carotenoids of *Fontinalis antipyretica* L. ex Hedw. *Acta Chem. Scand.* 22: 2215-2218.
- Blackman, F. F. and Smith, A. M. 1910-1911. Experimental researches on vegetable assimilation and respiration. IX.- On assimilation in submerged water-plants, and its relation to the concentration of carbon dioxide and other factors. *Proc. Roy. Soc. London Sec. B Biol. Sci.* 83: 389-412.
- Bockers, M., Capkova, V., Tich, I., and Schafer, C. 1997. Growth at high CO<sub>2</sub> affects the chloroplast number but not the photosynthetic efficiency of photoautotrophic *Marchantia polymorpha* culture cells. *Plant Cell Tiss. Organ Cult.* 48(2): 103-110.
- Bode, O. 1940. Assimilation, Atmung und Plastidenfarbstoffe in verschiedenfarbigen Licht aufgezogenen *Fontinalis*-Pflanzen. *Jahrb. Wiss. Bot.* 89: 208-244.
- Boston, H. L., Farmer, A. M., Madsen, J. D., Adams, M. S., and Hurley, J. P. 1991. Light-harvesting carotenoids in two deep-water bryophytes. *Photosynthetica* 25: 61-66.
- Bowes, G. and Salvucci, M. E. 1989. Plasticity in the photosynthetic carbon metabolism of submersed aquatic macrophytes. *Aquat. Bot.* 34: 233-266.
- Burr, G. O. 1941. Photosynthesis of algae and other aquatic plants. In: Needham, J. G. *Symposium on Hydrobiology*. Univ. Wisc. Press, Madison. pp. 163-181.
- Callaghan, T. V., Collins, N. J., and Callaghan, C. H. 1978. Photosynthesis, growth, and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. *Oikos* 31: 73-88.
- Collins, N. J. and Oechel, W. C. 1974. The pattern of growth and translocation of photosynthate in a tundra moss, *Polytrichum alpinum*. *Can. J. Bot.* 52: 355-363.
- Coxson, D. S. and Mackey, R. L. 1990. Diel periodicity of photosynthetic response in the subalpine moss *Pohlia wahlenbergii*. *Bryologist* 93: 417-422.
- Czczuga, B. 1980. Investigation on carotenoids in Embryophyta. I. Bryophyta. *Bryologist* 83: 21-28.
- Czczuga, B. 1985. Investigations on carotenoids in Embryophyta. III. Representatives of the Hepaticae. *Phyton* 25: 113-121.
- Czczuga, B., Gutkowski, R., and Czerpak, R. 1982. Investigations of carotenoids in Embryophyta. II. Musci from the Antarctic. *Nova Hedw.* 36: 695-701.
- Dhindsa, R. S. 1985. Non-autotrophic CO<sub>2</sub> fixation and drought tolerance in mosses. *J. Exper. Bot.* 36: 980-988.
- Dilks, T. J. K. 1976. Measurement of the carbon dioxide compensation point and rate of loss of <sup>14</sup>CO<sub>2</sub> in the light and dark in some bryophytes. *J. Exper. Bot.* 27: 98-104.
- Egle, K. and Fock, H. 1965. Light respiration – Correlations between CO<sub>2</sub> fixation, O<sub>2</sub> pressure and glycolate concentration. *Biochemistry of Chloroplasts*. Academic Press, London, pp. 79-87.
- Eschrich, W. and Steiner, M. 1967. Autoradiographische Untersuchungen zu Stofftransport bei *Polytrichum commune*. *Planta (Berlin)* 74: 330-349.
- Farmer, A. M., Maberly, S. C., and Bowes, G. 1986. Activities of carboxylation enzymes in freshwater macrophytes. *J. Exper. Bot.* 37: 1568-1573.
- Farmer, A. M., Boston, H. L., and Adams, M. S. 1988. Photosynthetic characters of a deepwater bryophyte from a clear, oligotrophic lake in Wisconsin, U.S.A. *Internat. Ver. Theor. Angew. Limnol. Verh.* 23: 1912-1915.
- Fock, H. 1965. Thesis, Science Faculty, University of Frankfurt/M.
- Fock, H., Krotov, G., and Canvin, D. T. 1969. Photorespiration in liverworts and leaves. In: Metzner, H. (ed.). *Progress in Photosynthesis I*. I. U. B. Tübingen, pp. 482-487.
- Fredericq, H. and Greef, J. De. 1968. Photomorphogenic and chlorophyll studies in the bryophyte *Marchantia polymorpha*. 1. Effect of red, far-red irradiations in short and long-term experiments. *Physiol. Plant.* 21: 346-359.
- Fujita, Y., Takahashi, Y., Kohchi, T., and Ozeki, H. 1989. Identification of a novel nifH-like (frxC) protein in chloroplasts of the liverwort *Marchantia polymorpha*. *Plant Molec. Biol.* 13: 551-561.
- Gellerman, J. L., Anderson, W. H., and Schlenk, H. 1972. Highly unsaturated lipids of *Mnium*, *Polytrichum*, *Marchantia* and *Matteuccia*. *Bryologist* 75: 550-557.
- Glime, J. M. 1987a. Growth model for *Fontinalis duriaei* based on temperature and flow conditions. *J. Hattori Bot. Lab.* 62: 101-109.
- Glime, J. M. 1987b. Phytogeographic implications of a *Fontinalis* (Bryopsida) growth model based on temperature and flow conditions for six species. *Mem. N. Y. Bot. Gard.* 45: 154-170.
- Goodwin, T. W. and Mercer, E. I. 1983. Phytohormones and related compounds. In: Goodwin, T. W. and Mercer, E. I. (eds.), *Introduction to Plant Biochemistry*, 2nd Ed., Pergamon Press, New York, pp. 567-626.
- Graham, L. E., Kim, E., Arancibia-Avila, P., Graham, J. M., and Wilcox, L. W. 2010. Evolutionary and ecophysiological significance of sugar utilization by the peat moss *Sphagnum compactum* (Sphagnaceae) and the common charophycean associates *Cylindrocystis brebissonii* and *Mougeotia* sp. (Zygnemataceae). *Amer. J. Bot.* 97: 1485-1491.
- Green, T. G. A. and Snelgar, W. P. 1982. A comparison of photosynthesis in two thalloid liverworts. *Oecologia* 54: 275-280.
- Gupta, R. K. 1976. Soluble constituents and photosynthetic products biosynthesized from <sup>14</sup>CO<sub>2</sub> in leafy liverworts, *Plagiochila asplenoides* (L.) Dum. and *Scapania undulata* (L.) Dum. *Indian J. Exper. Biol.* 14: 595-598.
- Hahn, L. W. and Miller, J. H. 1966. Light dependence of chloroplast replication and starch metabolism in the moss *Polytrichum commune*. *Physiol. Plant.* 19: 134-141.
- Hakala, K. and Sewón, P. 1992. Reserve lipid accumulation and translocation of C<sup>14</sup> in the photosynthetically active and senescent shoot parts of *Dicranum elongatum*. *Physiol. Plant.* 85: 111-119.
- Hanson, D. T. and Rice, S. K. 2014. What can we learn from bryophyte photosynthesis? In: Hanson, D. T. and Rice, S. K. (eds.). *Photosynthesis in Bryophytes and Early Land Plants*. *Advances in Photosynthesis and Respiration* 37: 1-8.
- Hanson, D., Andrews, T. J., and Badger, M. R. 2002. Variability of the pyrenoid-based CO<sub>2</sub> concentrating mechanism in hornworts (Anthocerotophyta). *Funct. Plant Biol.* 29: 407-416.
- Harder, R. 1921. Kritische Versuche zu Blackmans Theorie der begrenzenden Faktoren bei der Kohlensäureassimilation. *Jahrb. Wiss. Bot.* 60: 531-571.



- Harder, R. 1923. Bemerkungen über die variations-breite des Kompensationspunktes beim Gaswechsel der Pflanzen. Ber. Deutsch. Bot. Gesell. 41: 194-198.
- Harrer, R. 2003. Associations between light-harvesting complexes and Photosystem II from *Marchantia polymorpha* L. determined by two- and three-dimensional electron microscopy. Photosyn. Res. 75(3): 249-258.
- Héban, C. 1975. The phloem (leptome) of bryophytes. In: Aronoff, S., Dainty, J., Gorham, P. R., Srivastava, L. M., and Swanson, C. A. (eds.). Phloem Transport. Plenum Press, New York, pp. 211-224.
- Heber, U., Hedrich, R., and Shuvalov, V. A. 2005. Mechanisms of phototolerance in higher plants and poikilohydric organisms. Accessed 12 July 2005 at <<http://www.biozentrum.uni-wuerzburg.de/fileadmin/REPORT/BOT1/bot1004.htm>>.
- Hicklenton, P. R. and Oechel, W. C. 1977. Physiological aspects of the ecology of *Dicranum fuscescens* in the sub-arctic. II. Seasonal patterns of organic nutrient content. Can. J. Bot. 55: 2168-2177.
- Hobbs, V. J. and Pritchard, N. M. 1987. Population dynamics of the moss *Polytrichum piliferum* in north-east Scotland. J. Ecol. 75: 177-192.
- Hugly, S., Kunst, L., Browse, J., and Somerville, C. 1989. Enhanced thermal tolerance of photosynthesis and altered chloroplast ultrastructure in a mutant of *Arabidopsis* deficient in lipid desaturation. Plant Physiol. 90: 1134-1142.
- Huneck, S. 1969. Moosinhaltsstoffe, eine Übersicht. J. Hattori Bot. Lab. 32: 1-16.
- Huneck, S. 1983. Chemistry and biochemistry of bryophytes. In: Schuster, R. M. (ed.). New Manual of Bryology. Hattori Botanical Laboratory, Nichinan, pp. 1-116.
- Ikeuchi, M. and Inoue, H. 1988. A new Photosystem II reaction centre component (4.8-kDa protein) encoded by chloroplast genome. Fed. Eur. Biochem. Soc. Lett. 241: 99-104.
- James, T. A. 1981. Stable carbon isotope analysis of mosses and lichens growing in xeric and moist habitat. Bryologist 84: 79-81.
- Jensen, W. A. and Salisbury, F. B. 1984. Botany, 2nd ed. Wadsworth Publishing Co., Belmont, CA, 699 pp.
- Karunen, P. 1981. Role of neutral lipids in the physiology and ecology of subarctic *Dicranum elongatum*. Can. J. Bot. 59: 1902-1909.
- Karunen, P. and Aro, E. M. 1979. Fatty acid composition of polar lipids in *Ceratodon purpureus* and *Pleurozium schreberi*. Physiol. Plant. 45: 265-269.
- Karunen, P. and Kallio, P. 1976. Seasonal variation in the total lipid content of subarctic *Dicranum elongatum*. Rep. Kevo Subarctic. Res. Stat. 13: 63-70.
- Karunen, P. and Liljenberg, C. 1981. Content and fatty acid composition of steryl and wax esters in germinating spores of *Polytrichum commune*. Physiol. Plant. 53: 48-54.
- Karunen, P. and Mikola, H. 1980. Distribution of triglycerides in *Dicranum elongatum*. Phytochemistry 19: 319-321.
- Karunen, P. and Salin, M. 1981. Seasonal variation of lipids in *Sphagnum fuscum* surface peat. Lindbergia 7: 35-44.
- Keeley, J. E. and Morton, R. A. 1982. Distribution of diurnal acid metabolism in submerged aquatic plants outside the genus *Isoetes*. Photosynthetica 16: 546-553.
- Keeley, J. E. and Sandgren, D. R. 1992. Carbon: freshwater plants. Plant Cell Environ. 15: 1021-1035.
- Keeley, J. E., DeNiro, M. J., and Sternberg, L. O. 1986. The use of stable isotopes in the study of photosynthesis in freshwater plants. Aquat. Bot. 26: 213-223.
- Koskimies-Soininen, K. and Nyberg, H. 1991. Effects of temperature and light on the glycolipids of *Sphagnum fimbriatum*. Phytochemistry 30: 2529-2536.
- Krupa, J. 1969. Photosynthetic activity and productivity of the sporophyte of *Funaria hygrometrica* during ontogenesis. Acta Soc. Bot. Poloniae 38: 207-215.
- Krupa, J. 1984. Anatomical structure of moss leaves and their photosynthetic activity. Acta Soc. Bot. Poloniae 53: 43-51.
- Larcher, W. 1983. Physiological Plant Ecology, corrected printing of the second printing. Springer-Verlag, New York, 303 pp.
- 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.
- Margaris, N. G. and Kalaitzakis, J. 1974. Soluble sugars from some Greek mosses. Bryologist 77: 470-472.
- Martin, C. E. and Adamson, V. J. 2001. Photosynthetic capacity of mosses relative to vascular plants. J. Bryol. 23: 319-323.
- Martínez Abaigar, J. and Núñez Olivera, E. 1998. Ecophysiology of photosynthetic pigments in aquatic bryophytes. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). Bryology for the Twenty-first Century. Maney Publishing and the British Bryological Society, UK, pp. 277-292.
- Neuhaus, H., Pfannschmidt, T., and Link, G. 1990. Nucleotide sequence of the chloroplast psbI and trnS-GCU genes from mustard (*Sinapis alba*). Nucleic Acids Res. 18: 368.
- Nurit, F. and Chevallier, D. 1978. La sporogenese chez *Funaria hygrometrica*: Etude oxygraphique en rapport avec les modifications ultrastructurales. In: Congres International de Bryologie, Bryophytorum Bibliotheca 13: 195-209.
- 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.
- Paolillo, D. J. Jr. and Bazzaz, F. A. 1968. Photosynthesis in sporophytes of *Polytrichum* and *Funaria*. Bryologist 71: 335-343.
- Peñuelas, J. 1985.  $\text{HCO}_3^-$  as an exogenous carbon source for aquatic bryophytes *Fontinalis antipyretica* and *Fissidens grandifrons*. J. Exper. Bot. 36: 441-448.
- Peñuelas, J., Murillo, J., and Azcon-Bieto, J. 1988. Actual and potential dark respiration rates and different electron transport pathways in freshwater aquatic plants. Aquat. Bot. 30: 353-362.
- Plaetzer, H. 1917. Untersuchungen über die Assimilation und Atmung von Wasserpflanzen. Phys. Med. Gesell (Wurzburg) 45: 31-101.
- Proctor, M. C. F. 1990. The physiological basis of bryophyte production. International Symposium on Bryophyte Ecology Edinburgh (UK), 19-22 July 1988. J. Linn. Soc. Bot. 104: 61-77.
- Proctor, M. C. F. 2005. Why do Polytrichaceae have lamellae? J. Bryol. 27: 221-229.
- Proctor, M. C. F., Raven, J. A., and Rice, S. K. 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: Physiological and ecological implications. J. Bryol. 17: 193-202.
- Rao, K. R., Kumar, N. R., and Reddy, A. N. 1979. Studies of photosynthesis in some liverworts. Bryologist 82: 286-288.



- Rastorfer, J. R. 1972. Comparative physiology of four west Antarctic mosses. *Antarct. Res. Ser.* 20: 143-161.
- Raven, J. A. 1991. Implications of inorganic carbon utilization: Ecology, evolution, and geochemistry. *Can. J. Bot.* 69: 908-924.
- Raven, J. A. 1997. Inorganic carbon acquisition by marine autotrophs. *Adv. Bot. Res.* 27: 85-209.
- 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*. Springer, Dordrecht, pp. 29-58.
- 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*. British Ecological Society Special Symposium, Blackwell, Oxford, pp. 129-144.
- Raven, P. H., Evert, R. F., and Eichhorn, S. E. 1992. *Biology of Plants*. Worth Publishers, New York, p. 21.
- 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. 1995. Patterns of allocation and growth in aquatic *Sphagnum* species. *Can. J. Bot.* 73: 349-359.
- Rice, S. K. and Giles, L. 1994. Climate in the Pleistocene. *Nature* 371: 111.
- Rice, S. K. and Giles, L. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. *Plant Cell Environ.* 19: 118-124.
- Rice, S. K. and Schuepp, P. H. 1995. On the ecological and evolutionary significance of branch and leaf morphology in aquatic *Sphagnum* (Sphagnaceae). *Amer. J. Bot.* 82: 833-846.
- Richardson, D. H. S. 1981. *The Biology of Mosses*. John Wiley & Sons, New York, 220 pp.
- Rintamäki, E. and Aro, E.-M. 1985. Photosynthetic and photorespiratory enzymes in widely divergent plant species with special reference to the moss *Ceratodon purpureus*: Properties of ribulose biphosphate/oxygenase, phosphoenolpyruvate carboxylase and glycolate oxidase. *J. Exper. Bot.* 36: 1677-1684.
- Rintamäki, E., Keys, A. J., and Parry, M. A. J. 1988. Comparison of the specific activity of ribulose-1,5 biphosphate carboxylase-oxygenase from some C<sub>3</sub> and C<sub>4</sub> plants. *Physiol. Plant.* 74: 323-331.
- Robinson, H. 1985. The structure and significance of the leucobryaceous leaf. *Monogr. Syst. Bot. Missouri Bot. Gard.* 11: 111-120.
- Rudolph, H. 1990. Biochemical and physiological aspects of bryophytes. In: Zinsmeister, H. D. and Mues, R. (eds.). *Bryophytes, Their Chemistry and Chemical Taxonomy*, Proceedings of the Phytochemical Society of Europe 29, Oxford University Press, Oxford, pp. 227-252.
- Rundel, P. W., Stichler, W., Zander, R. H., and Ziegler, H. 1979. Carbon and hydrogen isotope ratios of bryophytes from arid and humid regions. *Oecologia (Berlin)* 44: 91-94.
- Ruttner, F. 1947. Zur Frage der Karbonatassimilation der Wasserpflanzen, I. *Österr. Bot. Zeits.* 94: 265-294.
- Sakai, N., Nakatsubo, T., Kanda, H., and Masuzawa, T. 2001. Carbon storage and photosynthetic capacity of the moss *Racomitrium barbuloides* Card. under various light conditions. *Hikobia* 13: 327-334.
- Salvucci, M. E. and Bowes, G. 1981. Induction of reduced photorespiration activity in submersed and amphibious aquatic macrophytes. *Plant Physiol.* 67: 335-340.
- Sandquist, D. R. and Keeley, J. E. 1990. Carbon uptake characteristics in two high elevation populations of the aquatic CAM plant *Isoetes bolanderi* (Isoetaceae) [sic]. *Amer. J. Bot.* 77: 682-688.
- Saupe, Stephen G. 2005. *Plant Physiology (Biology 327)*. Accessed on 4 January 2007 at <<http://employees.csbsju.edu/SSAUPE/biol327/Lecture/phloem.htm>>.
- Schmidt-Stohn, G. 1977. Änderungen der plastidenpigmente bei *Sphagnum magellanicum* Brid. in Abhängigkeit von Standort, Verfaerbungsgrad und Alter. *Zeits. Pflanzenphysiol.* 81: 289-303.
- Skré, O., Oechel, W. C., and Miller, P. M. 1983. Patterns of translocation of carbon in four common moss species in a black spruce (*Picea mariana*) dominated forest in interior Alaska. *Can. J. Forest Res.* 13: 869-878.
- Sluka, Z. A. 1983. The dependence of the chlorophyll content and the leaf-area of mosses on the ecological conditions. *Vest. Mosk. Univ. Ser. XVI Biol.* 37(3): 24-29.
- Smith, E. 2000. The role of the photosynthetic carbon concentrating mechanism in bryophytes. *Bull. Brit. Bryol. Soc.* 74: 18-19.
- Smith, E. C. and Griffiths, H. 1996a. The occurrence of the chloroplast pyrenoid is correlated with the activity of a CO<sub>2</sub>-concentrating mechanism and carbon isotope discrimination in lichens and bryophytes. *Planta* 198: 6-16.
- Smith, E. C. and Griffiths, H. 1996b. A pyrenoid-based carbon-concentrating mechanism is present in terrestrial bryophytes of the class Anthocerotae. *Planta* 200: 203-212.
- Smith, E. C. and Griffiths, H. 2000. The role of carbonic anhydrase in photosynthesis and the activity of the carbon-concentrating-mechanism in bryophytes of the class Anthocerotae. *New Phytol.* 145: 29-37.
- Søndergaard, M. and Sand-Jensen, K. 1979. The delay in <sup>14</sup>C fixation rates by three submerged macrophytes, a source of error in the <sup>14</sup>C technique. *Aquat. Bot.* 6: 111-119.
- Sonesson, M., Gehrke, C., and Tjøs, M. 1992. CO<sub>2</sub> environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. *Oecologia* 92: 23-29.
- Steeman Nielsen, E. 1947. Photosynthesis of aquatic plants with special reference to the carbon source. *Dansk. Bot. Ark.* 12(8): 1-71.
- Steeman Nielsen, E. and Kristiansen, J. 1949. Carbonic anhydrase in submersed autotrophic plants. *Physiol. Plant.* 2: 325-331.
- Suire, C. 1975. Les donnees actuelles sur la chimie des bryophytes. *Rev. Bryol. Lichenol.* 41: 105-256.
- Suleiman, A. A. A. and Lewis, D. H. 1980. Carbohydrate metabolism in the leafy liverwort, *Plagiochila asplenoides* (L.) Dum. var. *major* Nees. *New Phytol.* 84: 45-58.
- Suleiman, A. A. A., Bacon, J., Christie, A., and Lewis, D. H. 1979. The carbohydrates of the leafy liverwort *Plagiochila asplenoides* (L.) Dum. *New Phytol.* 82: 439-448.
- Sveinbjörnsson, B. and Oechel, W. C. 1981. Controls on carbon dioxide exchange in two *Polytrichum* moss species, 2. The



- implications of belowground plant parts on the whole plant carbon balance. *Oikos* 36: 348-354.
- Swanson, E. S., Anderson, W. H., Gellerman, J. L., and Schlenk, H. 1976. Ultrastructure and lipid composition of mosses. *Bryologist* 79: 339-349.
- Taylor, A. O., Jesper, N. M., and Christeller, J. T. 1972. Plants under climatic stress. III. Low temperature, high light effects on photosynthetic products. *Plant Physiol.* 47: 798-802.
- Thomas, R. J. and Lombard, C. S. 1991. Aphid infestation and its effects on translocation in *Polytrichum commune*. *Bryologist* 94: 1-4.
- Thomas, R. J., Stanton, D. S., and Grusak, M. A. 1979. Radioactive tracer study of sporophyte nutrition in hepatics. *Amer. J. Bot.* 66: 398-403.
- Thomas, R. J., Schiele, E. M., and Scheirer, D. C. 1988. Translocation in *Polytrichum commune* (Bryophyta) I. Conduction and allocation of photoassimilates. *Amer. J. Bot.* 75: 275-281.
- Thomas, R. J., Schiele, D. M., and Damberg, D. T. 1990. Translocation in *Polytrichum commune* (Bryophyta). II. Clonal integration. *Amer. J. Bot.* 77: 1569-1573.
- Thomas, R. J., Ryder, S. H., Gardner, M. I., Sheetz, J. P., and Nichols, S. D. 1996. Photosynthetic function of leaf lamellae in *Polytrichum commune*. *Bryologist* 99: 6-11.
- Tuba, Z. 1985. Photosynthetic pigment responses in *Tortula ruralis* during daily desiccation. *Abstr. Bot.* 9, Suppl. 2: 231-239.
- Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H. 2002. Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard. *Arct. Antarct. Alp. Res.* 34: 287-292.
- Valanne, N. 1977. The combined effects of light intensity and continuous light on the CO<sub>2</sub> fixation, chlorophyll content and chloroplast structure of the protonema of *Ceratodon purpureus*. *Zeit. Pflanzenphysiol.* 83: 275-283.
- Valanne, N. 1984. Photosynthesis and photosynthetic products in mosses. In: Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, pp. 257-274.
- Vaughn, K. C., Campbell, E. G., Hasegawa, J., Owen, H. A., and Renzaglia, K. S. 1990. The pyrenoid is the site of ribulose 1,5-bisphosphate carboxylase/oxygenase accumulation in the hornwort (Bryophyta: Anthocerotae) chloroplast. *Protoplasma* 156: 117-129.
- Vaughn, K. C., Ligrone, R., Owen, H. A., Hasegawa, J., Campbell, E. O., Renzaglia, K. S., and Monge-Najera, J. 1992. The anthocerate chloroplast: a review. *New Phytol.* 120: 169-190.
- Witt, H.-J. and Teubert, B. 1992. Changes in activities of enzymes involved in starch metabolism during the development of gemmae to 14-day-old plants of *Riella helicophylla*. *J. Plant Physiol.* 140: 375-377.
- Woodward, F. I. 1998. Do plants really need stomata? *J. Exper. Bot.* 49 (spec. iss.): 471-480.
- Zelitch, I. and Barber, G. A. 1960. In: Egle, K. and Fock, H. 1965. Light respiration – Correlations between CO<sub>2</sub> fixation, O<sub>2</sub> pressure and glycolate concentration. *Biochemistry of Chloroplasts*. Academic Press, London, pp. 79-87.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO<sub>2</sub> exchange of tropical bryophytes in a lower montane rain forest in Panama. *Bot. Acta* 110: 9-17.
- Zurzycki, J. 1974. The effect of blue and red radiation on the volume changes of *Funaria* chloroplasts in vivo. *Photosynthetica* 8: 338-343.



# CHAPTER 11-2

## PHOTOSYNTHESIS: PHOTOINHIBITION

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# CHAPTER 11-2

## PHOTOSYNTHESIS: PHOTOINHIBITION



Figure 1. *Conostomum tetragonum* exposed to the high light intensity of an alpine area. Photo by Michael Lüth, with permission.

### Photoinhibition

In high light intensities, chlorophyll can be damaged by the enhanced activity of electrons beyond that which it can process. This results in **photoinhibition** by decreasing the photosynthetic capacity. In tracheophytes, this is particularly pronounced in dehydrated plants, but in bryophytes, it seems the pattern is quite different.

Seel *et al.* (1992) compared the desiccation-tolerant moss *Syntrichia ruralis* var. *arenicola* (= *Tortula ruraliformis*) (Figure 2) with the desiccation-intolerant moss *Dicranella palustris* (Figure 2). It appeared that desiccation in the dark had no effect on total concentrations of chlorophylls or carotenoids in either moss, but in *D. palustris* it resulted in loss of protein and accumulation of TBA, suggesting lipid peroxidation. *Dicranella palustris* was unable to recover its photosynthesis during rehydration, whereas photosynthesis of *Syntrichia ruralis* var. *arenicola* had only marginal depression in photosynthesis upon rehydration, and only at the highest irradiance. In the light, *D. palustris* likewise lost not only protein, but also chlorophyll and carotenoids, while lipid peroxidation increased. Again, *S. ruralis* var. *arenicola* suffered little damage. Greater damage occurred to this species when hydrated and exposed to high irradiance. Thus we can include that desiccation tolerance affords some protection to the chlorophyll in the presence of high light intensities, at least in some bryophyte species.



Figure 2. Upper: *Syntrichia ruralis* var. *arenicola*. Lower: *Dicranella palustris*. Photos by Michael Lüth, with permission.



Temperature plays a major role in photoinhibition and light damage. At low Antarctic temperatures with exposure to high light intensity, *Schistidium antarctici* (Figure 3) experienced reduction in its **photosynthetic capacity** (light-saturated rate), **photosynthetic efficiency** (ratio of energy stored to energy of light absorbed), ratio of **variable to maximum fluorescence**, and rate of **fluorescence quenching** when exposed to moderate light (Adamson *et al.* 1988). Adamson *et al.* suggested that photoinhibition may play a major role in limiting photosynthesis and productivity in the Antarctic region. On the other hand, Alpert (1988) showed that *Grimmia laevigata* (Figure 4-Figure 5) exhibits no chlorophyll damage during 20 months of desiccation if it is shielded from potential photodamage.



Figure 3. *Schistidium antarctici*, a high light species that experiences reduced photosynthetic potential in moderate light. Photo courtesy of Rod Seppelt.



Figure 4. *Grimmia laevigata* in its typical habitat. Photo by Alan Cressler, with permission.



Figure 5. *Grimmia laevigata*, a species that can survive 20 months of desiccation without chlorophyll damage. Photo by David Holyoak, with permission.

### Quenching

Two means, known as **quenching**, seem to be available to plants, or at least to bryophytes, to reduce excessive activation energy and avoid damage from high light activity. In higher plants and bryophytes, this can be done by the reaction center itself. But bryophytes seem to behave somewhat differently from tracheophytes. For example, the leafy liverwort *Bazzania trilobata* (Figure 6) exhibits no decrease in quantum yield in its open reaction centers when oversaturated with light, whereas both peas and barley do (Horton *et al.* 1988), suggesting that the behavior of the reaction center is not essential to prevent photoinhibition in at least some bryophytes. Rather, at least some bryophytes seem to be able to accomplish photoquenching by use of accessory pigments (Paulsen 1998).



Figure 6. *Bazzania trilobata*, a species that does not decrease its quantum yield when oversaturated with light. Photo by Dick Haaksma, with permission.

One might expect such quenching activities to be especially important in alpine bryophytes. Fluorescence in bryophytes in alpine areas with high UV light intensity can result in different effects from those on tracheophytes (Heber *et al.* 2000). When dehydrated, alpine populations of *Grimmia alpestris* (Figure 7) had very low chlorophyll



fluorescence while alpine tracheophytes had high levels. On the other hand, mosses and lichens increase their chlorophyll fluorescence upon rehydration, whereas tracheophytes experience a decrease. Heber *et al.* considered this increase in mosses and lichens to relate to their lack of photodamage in a dry state. Nevertheless, tracheophytes, bryophytes, and lichens all can form chlorophyll fluorescence quenchers as a response to desiccation, but only the bryophytes and lichens exhibit a decrease in fluorescence in response to light energy transfer while dehydrated. Thus, among the alpine taxa they examined, only the bryophyte *Grimmia alpestris* used deactivation to avoid photodamage in both its hydrated and dehydrated states.



Figure 7. *Grimmia alpestris*, a species with low chlorophyll fluorescence. Photo by Henk Greven, with permission.

### Zeaxanthin

One explanation for photo-protective quenching is that in high intensity light, the carotenoid violaxanthin, which itself inhibits quenching, is de-epoxidized to form **zeaxanthin** (Paulsen 1998). The theory is that this transformation to zeaxanthin lowers the energy level sufficiently to permit it to trap energy from the chlorophyll excited state. However, **auroxanthin**, a diepoxy xanthophyll, has an even higher energy level than that of violaxanthin, but it promotes fluorescence quenching and aggregation in isolated major light-harvesting complex II, similar to the effect of zeaxanthin. Ruban *et al.* (1998) have challenged this interpretation of trapping chlorophyll energy because auroxanthin behaves similarly to zeaxanthin as a stimulator of quenching. Rather, Ruban *et al.* contend that it is the flat shape of zeaxanthin and auroxanthin, compared to the perpendicular shape of violaxanthin, that permits them to perform their quenching function.

Sunflecks can initiate rapidly reversible photoprotection within minutes to elicit non-photochemical chlorophyll fluorescence quenching (Matsubara *et al.* 2005). This is vitally important to bryophytes living in forests where low light is supplemented by these ephemeral bursts of bright light. Detectable conversion of the violaxanthin pigment to the protective antheraxanthin or zeaxanthin takes longer, suggesting that there may be more than one mechanism for photoprotection.

In prolonged strong light, photoprotection is usually stabilized within hours of exposure through this reversible violaxanthin cycle, but there is also a slowly reversible conversion of the pigment lutein epoxide to lutein. Matsubara *et al.* suggested that the lutein "locks in" a primary photoprotective mechanism in some species, causing light-harvesting antenna pigments to serve as centers for dissipating excitation energy in high light. Czacuga (1985) found that lutein epoxide accumulated in *Marchantia polymorpha* (Figure 8) thalli in late summer, autumn, and after winter. However, thus far we have no evidence of the specific role of lutein or lutein epoxide in bryophytes.



Figure 8. *Marchantia polymorpha*, a species that accumulates lutein epoxide seasonally. Photo by Jan-Peter Frahm, with permission.

Bukhov *et al.* (2001a) found that light quenching of chlorophyll fluorescence in the moss *Rhytidiadelphus squarrosus* (Figure 9) apparently originated in the pigment antenna system, but in the tracheophytes *Arabidopsis thaliana* (Figure 10) and *Spinacia oleracea* (Figure 11) it appeared to originate in the reaction center. The quenching in *R. squarrosus* was strongly enhanced by the pigment **zeaxanthin** (Bukhov *et al.* 2001b). Short bursts of light were sufficient to cause an increase in levels of zeaxanthin in this moss, albeit in a 20% CO<sub>2</sub> atmosphere. In fact, only one molecule of zeaxanthin was needed to quench the efficiency of charge separation in Photosystem II by 50%.



Figure 9. *Rhytidiadelphus squarrosus*, a moss that quenches high light energy with the pigment **zeaxanthin**. Photo by Michael Lüth, with permission.





Figure 10. *Arabidopsis thaliana* basal rosette, where light quenching originates in the reaction center. Photo through Creative Commons.



Figure 11. *Spinacia oleracea* female plant, a species in which light quenching originates in the reaction center. Photo by Rasbak, through Creative Commons.

Heber *et al.* (2001) concluded that the absence of ATP consumption in reactions associated with the coupled electron transport of PS II permitted the acidification needed in the thylakoids for binding zeaxanthin to the chlorophyll-containing thylakoid protein. These form energy-dissipating traps in the antennae of PS II. Furthermore, the competition for energy capture decreases the activity of PS II. Both mosses and lichens benefit from the protein protonation and zeaxanthin availability in the

dissipation of energy in PS II, whereas this is not the case in tracheophytes. The energy dissipation in mosses and lichens in the dry state is not related to protonation and zeaxanthin availability, as indicated by the absence of chlorophyll fluorescence. For mosses and lichens, the big advantage is that excitation of PS II by sunlight is not destructive when they are dry, whereas dry leaves of tracheophytes rapidly lose their PS II activity under strong illumination.

Rintamäki *et al.* (1994) found that strong light induced the PS II centers to increase their capacity for repair of photochemical damage in the moss *Ceratodon purpureus* (Figure 12). This increased tolerance was associated with a rapid turnover of the D1 protein, apparently mediated by lincomycin. In the absence of lincomycin, strong light resulted in a net loss of this D1 protein, suggesting that the rapid degradation of the protein was independent of the resynthesis of polypeptide. They interpreted this to mean that synthesis was the limiting factor in the turnover of the D1 protein during photoinhibition. Furthermore, the initial level of fluorescence was correlated with the production of inactive PS II reaction centers that were depleted of the D1 protein. The higher the fluorescence level, the greater the depletion of the D1 protein. Addition of lincomycin facilitated the recovery of the D1 protein, and the rate of D1 protein synthesis after photoinhibition exceeded that of control plants during the first hours under recovery conditions.



Figure 12. *Ceratodon purpureus*, a species in which strong light induces PS II centers to increase their capacity for repair of photochemical damage. Photo by Janice Glime.

Deltoro *et al.* (1998) compared a desiccation-tolerant (*Frullania dilatata*, Figure 13) and desiccation-intolerant (*Pellia endiviifolia*, Figure 14) liverwort to examine the effects of desiccation and light on non-photochemical quenching. In *F. dilatata*, there was a rise in the concentration of de-epoxidized xanthophylls that can protect the cells from chlorophyll damage when photosynthesis cannot occur to trap the excited electrons. Dry *Pellia endiviifolia*, on the other hand, experienced less dissipation of electron activity and did not experience a rise in de-epoxidized xanthophylls. The increase in de-epoxidized xanthophylls appears to be induced by desiccation and mediated by zeaxanthin.





Figure 13. The desiccation-tolerant *Frullania dilatata* exhibiting colored protective pigments. Photo by Michael Lüth, with permission.



Figure 14. The desiccation-intolerant *Pellia endiviifolia* lacking any visible protective pigments. Photo by Michael Lüth, with permission.

## Chloroplast Position

The position of the chloroplasts plays a role not only in maximizing the light capture by the cell in low light, as in protonemata of *Schistostega pennata* (Figure 15), but also in minimizing chlorophyll fluorescence during desiccation. Grouping of the plastids during drying may enhance the effect of chlorophyll reabsorption, causing a notable decrease in the F685/F735 ratio in the chlorophyll fluorescence spectrum, as shown in *Rhizomnium punctatum* (Figure 16) leaves (Bartosková *et al.* 1999).



Figure 15. *Schistostega pennata* protonemata, a species that moves its chloroplasts to maximize light absorption. Photo courtesy of Martine Lapointe, with permission.



Figure 16. *Rhizomnium punctatum*, a species that groups its plastids during drying. Photo by Janice Glime.

## Sun and Shade Plants

Photosynthetic organs of plants typically adjust their chlorophyll concentrations as light conditions change (Martin & Churchill 1982). Hence, those organs in high light intensity tend to have lower concentrations of chlorophyll *b* and total chlorophyll than those in the shade (Valanne 1977; Martin & Churchill 1982). The chlorophyll *b* serves as one of the antenna pigments to trap light energy and transfer it to the chlorophyll *a* reaction center.

Within the bryophytes, there are both chlorophyll and plastid structural differences between plants typical of shade and those of sun, but these may not necessarily be accompanied by photosynthetic differences (Aro *et al.* 1981). For example, *Marchantia polymorpha* (Figure 8) has a plastid structure characteristic of shade plants, and *Ceratodon purpureus* (Figure 12) of sun plants, but both have the photosynthetic kinetics of shade plants.

## Chlorophyll Concentration

Bryophytes in general have chlorophyll concentrations typical of shade plants (Tieszen & Johnson 1968; Table 1). Deora and Chaudhary (1991) examined the chlorophyll content in a number of Indian bryophytes and reported the ranges. Chlorophyll *a* ranged  $0.402 \pm 0.052$  to  $2.002 \pm 0.700$  mg g<sup>-1</sup> dry mass. Chlorophyll *b* ranged  $0.265 \pm 0.067$  to  $1.634 \pm 0.070$  mg g<sup>-1</sup> dry mass. The highest level of chlorophyll was in the cave moss *Cyathodium tuberosum* (Figure 17) ( $3.636$  mg g<sup>-1</sup> dw) and the lowest in *Entodon prorepens* (Figure 18) ( $0.667$  mg g<sup>-1</sup> dw). They found that, like the tracheophytes, high solar irradiances corresponded with low chlorophyll content and high *a:b* ratios. Martínez Abaigar and Núñez Olivera (1998) compiled data from a number of studies to show that on either a weight or areas basis, bryophytes have lower chlorophyll concentrations than do tracheophytes (Figure 19). They attributed this higher level in tracheophytes to the more complex structure of these plants.





Figure 17. *Cyathodium* sp.; *C. tuberosum* has the highest chlorophyll concentration of a number of Indian bryophytes. Photo by Li Zhang, with permission.



Figure 18. *Entodon prorepens*, a species with the lowest chlorophyll concentration of a number of Indian bryophytes. Photo by Li Zhang, with permission.

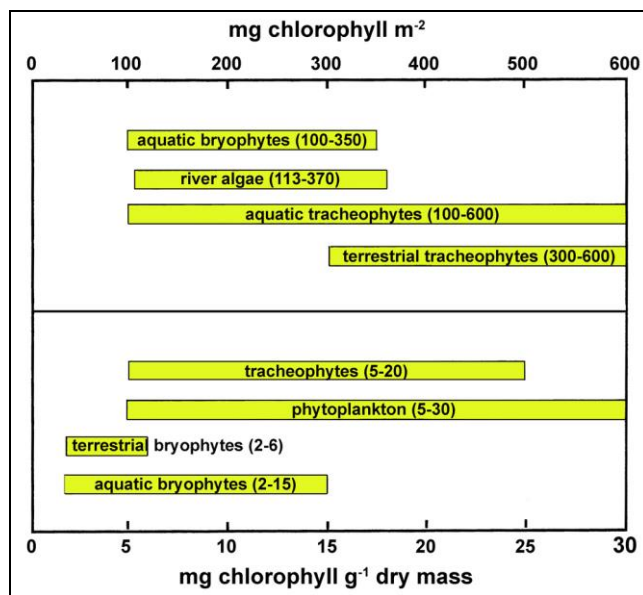


Figure 19. Comparisons of chlorophyll concentrations on an area (upper) and biomass (lower) basis. Redrawn from Martínez Abaigar and Núñez Olivera (1998), based on data from Martínez Abaigar *et al.* 1994.

Marschall and Proctor (2004) examined 39 moss and 16 liverwort species to compare chlorophylls and carotenoids in relation to light intensity and light saturation. They found a median total chlorophyll concentration of 1.64 mg g<sup>-1</sup> for mosses and 3.76 mg g<sup>-1</sup> for liverworts. Mean chlorophyll *a:b* ratios were 2.29 and 1.99, respectively. The chlorophyll:carotenoid ratio mean was 4.74 for mosses and 6.75 for liverworts. Light saturation values were low, with almost all less than 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; the median for mosses was 583 and for liverworts 214  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . These numbers suggest that liverworts, in general, are more shade-adapted than are mosses. Deora and Chaudhary (1991) reached the same conclusion in their study of Indian bryophytes. Pande and Singh (1987) also compared mosses and liverworts during the rainy season in Nainital, Kumaun Himalaya, finding the liverworts to be more prominent in the shade and mosses in the sun, likewise having more chlorophyll and carotenoids in the liverworts. However, they found no chlorophyll:carotenoid differences between liverworts and mosses.

Marschall and Proctor (2004) concluded that bryophytes are **not** "inherently" shade plants and do include sun plants. For example, species of *Polytrichum* have lamellae that provide additional surface area for gas exchange, permitting greater CO<sub>2</sub> uptake; these species had the highest **photosynthetic photon flux density (PPFD)**. Masarovičová and Eliás (1987) supported this conclusion by showing that *Polytrichum commune* (Figure 20-Figure 21), with well-developed lamellae, had a higher saturation photosynthetic rate (3.67-5.62 mg CO<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>) and higher photosynthesis per chlorophyll concentration (0.53 mg CO<sub>2</sub> chl h<sup>-1</sup>) than did *Atrichum undulatum* (Figure 22-Figure 23) (which has less-well-developed lamellae; Figure 23) (3.41 mg CO<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>) or *Hypnum cupressiforme* (Figure 24) (which has no lamellae) (2.56 mg CO<sub>2</sub> g<sup>-1</sup> dry mass h<sup>-1</sup>). Marschall and Proctor found that chlorophyll concentration, chlorophyll *a:b* ratios, and chlorophyll:carotenoid ratios all were significantly correlated with PPFD at 95% saturation in the bryophytes tested. Nevertheless, the light saturation levels of all bryophytes were lower than those for tracheophytes of open sun habitats. Marschall and Proctor attributed the lower saturation levels to the difficulty of obtaining CO<sub>2</sub> into the cells of bryophytes.



Figure 20. *Polytrichum commune*, a species with well-developed leaf lamellae. Photo by Michael Lüth, with permission.





Figure 21. *Polytrichum commune* showing tall lamellae over entire cross section of leaf. Photo from Botany Website, UBC, with permission.



Figure 22. *Atrichum undulatum*, a species with lamellae over the leaf costa. photo by Janice Glime.



Figure 23. *Atrichum undulatum* leaf cross section showing low lamellae over costa of leaf. Photo by Walter Obermayer, with permission.



Figure 24. *Hypnum cupressiforme*, a species with no leaf lamellae. Photo by J. C. Schou, with permission.

Chlorophyll degrades into phaeophytin. Chlorophyll *a* degrades more easily than does chlorophyll *b*; hence,

phaeophytin *a* has been used as an indication of chlorophyll damage that can result from pollution or other stress. Bastardo (1980) suggests that a chlorophyll *a* to phaeophytin ratio of less than 1.0 in the aquatic moss *Fontinalis* (Figure 25) indicates irreversible damage to the chlorophyll component. However, in their study of submerged mosses, Martínez Abaigar *et al.* (1994) found that chlorophyll of aquatic mosses did not degrade into phaeopigments.



Figure 25. *Fontinalis antipyretica* var *gracilis*, a species that exhibits irreversible damage when its chlorophyll *a* to phaeophytin ratio is <1.0. Photo by David Holyoak, with permission.

Deep lakes provide some of the darkest habitats for bryophytes. Fully hydrated, bryophytes are able to take advantage of the CO<sub>2</sub> emitted from the sediments for a slow but steady growth without competition from other macrophytes. These plants are highly shade adapted and have a low light saturation level. The leafy liverwort *Chiloscyphus rivularis* (see Figure 26) in Crystal Lake, Wisconsin, USA, is saturated at ~50 μM photons m<sup>-2</sup> s<sup>-1</sup> (Farmer *et al.* 1988). This leafy liverwort has high concentrations of chlorophylls *a* and *b* as well as carotenoids. The carotenoids produced consist mostly of **lutein**, a yellow-orange pigment that has most of its absorption at 470-500 nm (blue light). The light energy is transferred through the pigment antenna system to chlorophyll *a*. Table 1 compares chlorophyll levels of a number of bryophyte species.



Figure 26. *Chiloscyphus polyanthos*; *C. rivularis* has high concentrations of chlorophylls *a* and *b* and carotenoids. Photo by Bernd Haynold, through Creative Commons.



In seemingly sharp contrast to this deep-water lutein production, Czeuczuga (1987) grew bryophyte leaves under various light intensities with seemingly conflicting results. As in other studies, in the shade the total carotenoid content and  $\beta$ -carotene increased, along with chlorophyll, but in the

sunlight there was a marked increase in the lutein content of the leaves. Why should these leaves increase their antenna pigments, particularly lutein, in the sunlight? Is it serving as a filter, unconnected to the antenna function?

Table 1. Chlorophyll concentration (mg g<sup>-1</sup> dry mass) in a variety of bryophytes, ordered by *a/b* ratio.

Species	<i>a</i>	<i>b</i>	Total	<i>a/b</i>	Date/ Intensity	Location	Reference
<i>Polytrichum piliferum</i>				3.63			Krupa 1984
<i>Plagiomnium undulatum</i>	7.21	2.62	9.82	2.75	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Atrichum undulatum</i>	6.06	2.27	8.34	2.67	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Ditrichum flexicaule</i>	2.66	1.06	3.72	2.51	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Hypnum cupressiforme</i>	4.87	1.91	6.60	2.44	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Pohlia</i> sp.	8.22	3.46	11.68	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Polytrichum formosum</i>	6.37	2.67	9.04	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Rhizomnium punctatum</i>			14				Krupa 1984
<i>Polytrichum commune</i>	7.74	3.82	11.56	2.14	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Hyophila involuta</i>	1.210	0.713	1.923	1.697	50 klux		Deora & Chaudhary 1991
<i>Riccia billardieri</i>	1.465	0.897	2.362	1.632	12-14 klux		Deora & Chaudhary 1991
<i>Plagiochasma appendiculatum</i>	1.934	1.231	3.165	1.571	12 klux		Deora & Chaudhary 1991
<i>Atrichum angustatum</i>				1.5			Martin 1980
<i>Plagiochasma articulatum</i>	1.651	1.112	2.763	1.485	12 klux		Deora & Chaudhary 1991
<i>Cythodium tuberosum</i>	2.002	1.630	3.636	1.225	10 klux		Deora & Chaudhary 1991
<i>Tortula muralis</i>	1.801	1.388	3.189	1.297	50-70 klux		Deora & Chaudhary 1991
<i>Gymnostomiella vernicosa</i>	1.102	0.687	1.789	1.604	60 klux		Deora & Chaudhary 1991
<i>Fissidens geminiflorus</i>	1.060	0.663	1.723	1.598	55 klux		Deora & Chaudhary 1991
var <i>nagasakinus</i>							
<i>Fissidens curvato-involutus</i>	0.969	0.552	1.521	1.755	45-55 klux		Deora & Chaudhary 1991
<i>Philonotis revoluta</i>	0.964	0.864	1.828	1.115	75 klux		Deora & Chaudhary 1991
<i>Fabronia minuta</i>	0.956	0.891	1.847	1.068	40-50 klux		Deora & Chaudhary 1991
<i>Fissidens diversifolius</i>	0.913	0.645	1.558	1.424	50 klux		Deora & Chaudhary 1991
<i>Bryum cellulare</i>	0.889	0.629	1.518	1.413	50 klux		Deora & Chaudhary 1991
<i>Funaria hygrometrica</i>	0.837	0.587	1.424	1.425	70 klux		Deora & Chaudhary 1991
<i>Bryum capillare</i>	0.544	0.514	1.098	1.058	70 klux		Deora & Chaudhary 1991
<i>Entodon myurus</i>	0.544	0.371	0.915	1.613	80-90 klux		Deora & Chaudhary 1991
<i>Funaria nutans</i>	0.514	0.479	1.020	1.129	70 klux		Deora & Chaudhary 1991
<i>Barbula vinealis</i>	0.406	0.279	0.685	1.455	90 klux		Deora & Chaudhary 1991
<i>Entodon prorepens</i>	0.402	0.265	0.667	1.516	80-90 klux		Deora & Chaudhary 1991
<i>Marchantia polymorpha</i>			0.462*	1.23			Rao et al. 1979
<i>Marchantia polymorpha</i> tips	7.7	2.33	10.03	3.30			Fredericq & De Greef 1968
<i>Marchantia polymorpha</i> bases	6.25	1.88	8.13	3.32			Fredericq & De Greef 1968
<i>Marchantia palmata</i>			0.207*	1.07			Rao et al. 1979
<i>Reboulia hemisphaerica</i>			0.234*	1.11			Rao et al. 1979
<i>Ceratodon purpureus</i>			6.8	2.2	rhythmic lt, 1400 $\mu$ W cm <sup>2</sup>		Valanne 1977
<i>Ceratodon purpureus</i>			3.0	2.0	contin lt, 1400 $\mu$ W cm <sup>2</sup>		Valanne 1977
<i>Ceratodon purpureus</i>			8.5	2.0	rhythmic lt, 200 $\mu$ W cm <sup>2</sup>		Valanne 1977
<i>Ceratodon purpureus</i>			8.1	1.9	contin lt, 200 $\mu$ W cm <sup>2</sup>		Valanne 1977
<i>Dicranum scoparium</i>			1.7				Martin 1980
<i>Brachythecium velutinum</i>			1.8				Martin 1980
<i>Grimmia laevigata</i>			1.6				Martin 1980
<i>Leucobryum glaucum</i>			1.4				Martin 1980
<i>Leucodon julaceus</i>			1.9				Martin 1980
<i>Plagiomnium cuspidatum</i>			1.6				Martin 1980
<i>Polytrichum ohioense</i>			1.8				Martin 1980
<i>Sphagnum lescurii</i>			1.8				Martin 1980
<i>Thelia asprella</i>			1.9				Martin 1980
<i>Thuidium delicatulum</i>			2.1				Martin 1980

\*Fresh weight



## Age Differences

Masarovičová and Eliás (1987) showed that chlorophyll concentrations differ with age. One need only look at bryophytes in the spring to observe that older parts are typically dark and new growth is a light (Figure 27), almost chartreuse, green. However, storage of other substances in senescing parts contributes to their dark color.



Figure 27. *Polytrichum commune* with new, green growth from splash cups and darker, brownish lower parts. Photo by Štěpán Koval, with permission.

## Chlorophyll *a:b* Ratio

Chlorophyll *a:b* ratios can vary considerably, depending on the light available, time of year, and the adaptations of the bryophytes. Martin and Churchill (1982) reported a mean of 2.69 (2.29-2.99) for 20 moss species in an oak-hickory (*Quercus-Carya*, Figure 28) woods in Kansas, USA. But in his study of North Carolina, USA, Martin (1980) reported only 1.14-2.1 for 11 moss species. Masarovičová and Eliás (1987) found a range of 2.14-2.85 for woodland mosses in SW Slovakia in July.

The genus *Riccia* frequents a variety of disturbed habitats as well as living on the water surface of lakes and ponds. Patidar *et al.* (1986) found that within this genus, the highest chlorophyll concentrations occurred in shade-grown *Riccia discolor* (Figure 29). The lowest concentrations occurred in *Riccia fluitans* (Figure 30), a species that floats on the water surface, often in direct sunlight. But surprisingly, the chlorophyll *a:b* ratios did not differ among the species in these different habitats.



Figure 28. Oak-hickory forest. Photo by Brian Stansberry, through Creative Commons.



Figure 29. *Riccia discolor*. When growing in the shade, this species has the highest chlorophyll content among the *Riccia* species tested. Photo by Jan Ševčík, through Creative Commons.



Figure 30. *Riccia fluitans*, the species with the lowest concentration of chlorophyll, in its sunny floating habitat. Photo by Jan-Peter Frahm, with permission.

An increase in irradiance will cause an increase in productivity up to the point where light saturation is reached. In a 36-day laboratory experiment using seven different light levels, Rincón (1993) demonstrated this concept with six bryophyte species [*Brachythecium rutabulum* (Figure 31), *Eurhynchium praelongum* (Figure 32), *Lophocolea bidentata* (Figure 33), *Plagiommium*



*undulatum* (Figure 34), *Pseudoscleropodium purum* (Figure 35), *Thuidium tamariscinum* (Figure 36)]; all responded to the higher light intensities with greater biomass increase. But they also demonstrated (except for *Lophocolea bidentata*) that lower light intensities resulted in greater shoot length increase, a response suggesting that IAA was being inhibited by the greater intensity of light. Like Patidar *et al.* (1986), they found that all species had higher chlorophyll levels at low irradiances, but there were no distinct changes in chlorophyll *a:b* ratios with light intensity.



Figure 31. *Brachythecium rutabulum*, a species with greater productivity in high light, but with greater elongation in low light. Photo through Creative Commons.



Figure 32. *Eurhynchium praelongum*, a species with greater productivity in high light, but with greater elongation in low light. Photo by Michael Lüth, with permission.



Figure 33. *Lophocolea bidentata*, a species with greater productivity in high light, but no greater elongation in low light. Photo by Michael Lüth, with permission.



Figure 34. *Plagiomnium undulatum*, a species with greater productivity in high light, but greater elongation in low light. Photo by Michael Lüth, with permission.



Figure 35. *Pseudoscleropodium purum*, a species with greater productivity in high light, but greater elongation in low light. Photo by Michael Becker, through Creative Commons.



Figure 36. *Thuidium tamariscinum*, a species with greater productivity in high light, but greater elongation in low light. Photo by Janice Glime.

Tieszen and Johnson (1968) pointed out the importance of bryophytes in tundra ecosystems by examining the chlorophyll distribution within several



communities. Those communities with the lowest overall chlorophyll had the greatest amount of it in their moss and ericaceous components. In the Dry Sedge tundra, about one-third of the chlorophyll was in the moss component. However, in the Wet Sedge tundra, only about 2% was in the moss component. Like other studies discussed earlier, they found that the moss layer had the lowest chlorophyll *a:b* ratio, which ranged 1.5-2.5 for all plants. These are relatively low chlorophyll *a:b* ratios overall and correspond with the lower light intensities of Arctic latitudes.

Yang *et al.* (1994) compared bryophyte chlorophyll *a:b* ratios in 17 species from Yuan-Yang Lake. The minimum ratio was 2.17, with a mean of 2.41. This mean was lower than that found for the two aquatic tracheophytes (3.08), but was nevertheless somewhat higher than most bryophyte values reported (Table 1).

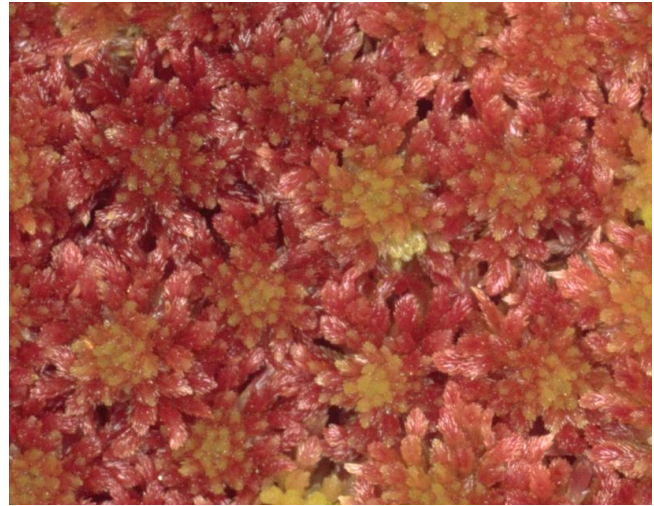


Figure 37. *Sphagnum capillifolium*, exhibiting its colorful pigments. Photo by Jan-Peter Frahm, with permission.

### Seasonal Differences

As light intensity changes, antenna pigments, cytoplasmic water-soluble pigments, and wall pigments change. This results in seasonal changes in the color of the bryophytes.

Martin and Churchill (1982) found that total chlorophyll content of woodland mosses increased from early spring (1.45 mg g<sup>-1</sup> dry mass) before canopy closure to that attained after full canopy closure (4.36 mg g<sup>-1</sup> dry mass), demonstrating the wide range of plasticity in the chlorophyll content in these plants. Kershaw and Webber (1986) found a similar relationship in *Brachythecium rutabulum* (Figure 31), with chlorophyll concentrations increasing from 1.70 mg g<sup>-1</sup> on 8 May to 11.1 mg g<sup>-1</sup> on 11 October. During this time, light saturation declined from 200  $\mu\text{M m}^{-2} \text{s}^{-1}$  to 30  $\mu\text{M m}^{-2} \text{s}^{-1}$  by 6 July, with the light compensation point likewise falling from 65  $\mu\text{M m}^{-2} \text{s}^{-1}$  to 4  $\mu\text{M m}^{-2} \text{s}^{-1}$ . It is clear that at least some bryophytes have a large capacity to adjust to changing light levels.

Epiphytes are subject to almost constant drying in both summer and winter. Their highest chlorophyll production is in the autumn, October to November, in Japan (Miyata & Hosokawa 1961), when autumn rain and temperatures suitable for C<sub>3</sub> plants make photosynthesis possible. Their lowest concentrations are in summer.

Gerdol *et al.* (1994) took a novel approach to determining seasonal differences in pigment concentrations in *Sphagnum capillifolium* (Figure 37). They compared plant segments and found that both chlorophylls were highest in the midsummer segment. Carotenoids were fairly stable except in spring. Chlorophyll degradation products (phaeophytin, pheophorbide, and chloride) accumulated in the autumn capitulum segment. They interpreted this autumn segment to indicate a rapid degradation of chlorophyll coincident with the night chilling of the end of the growing season.

Czeczuga (1985) quantified the carotenoid pigment concentration in *Marchantia polymorpha* (Figure 8) from March until November. Percentage of total pigments were close to or more than double in June, July, and August (17.8-25.0%) compared to the other sampled months (1.8-9.3%). At the same time, the chlorophyll *a:b* ratio dropped steadily from 1.41 on 1 April to 1.00 by 14 October.

In a study of aquatic bryophytes the chlorophyll *a* and *b* values ranged widely from 1.52 to 6.67 mg chl *a* g<sup>-1</sup> dry mass and from 0.61 to 2.70 mg chl *b* (Martínez Abaigar *et al.* 1994; Figure 38). In autumn and winter, chl *a* ranged 2.11-6.27 and chl *b* ranged 0.91 to 2.95. The ranges of *a:b* ratio remained nearly the same in all four seasons (1.95-3.25). But when the bryophytes were separated by habitat, several patterns emerged. Those from habitats subject to summer desiccation had a low summer concentration of chlorophyll and *a:b* ratio with an increase in the carotenoid portion. Those from under a dense tree canopy increased in chlorophyll content from spring to summer, and some continued that increase into autumn, while others dropped down again. Those that were continuously submerged demonstrated the smallest seasonal pigment variations.

### Habitat Differences in Chlorophyll

#### Desert and Dry Areas

In the desiccation-tolerant *Syntrichia ruralis* (Figure 39) from the Organ Mountains of southern New Mexico, Mishler and Oliver (1991) found that the total chlorophyll on a dry weight basis was higher in late summer and winter than in early summer. The chlorophyll *a:b* ratios were relatively low (1.00-2.50), compared to those of tracheophytes, and seemed to have no regular variation pattern.



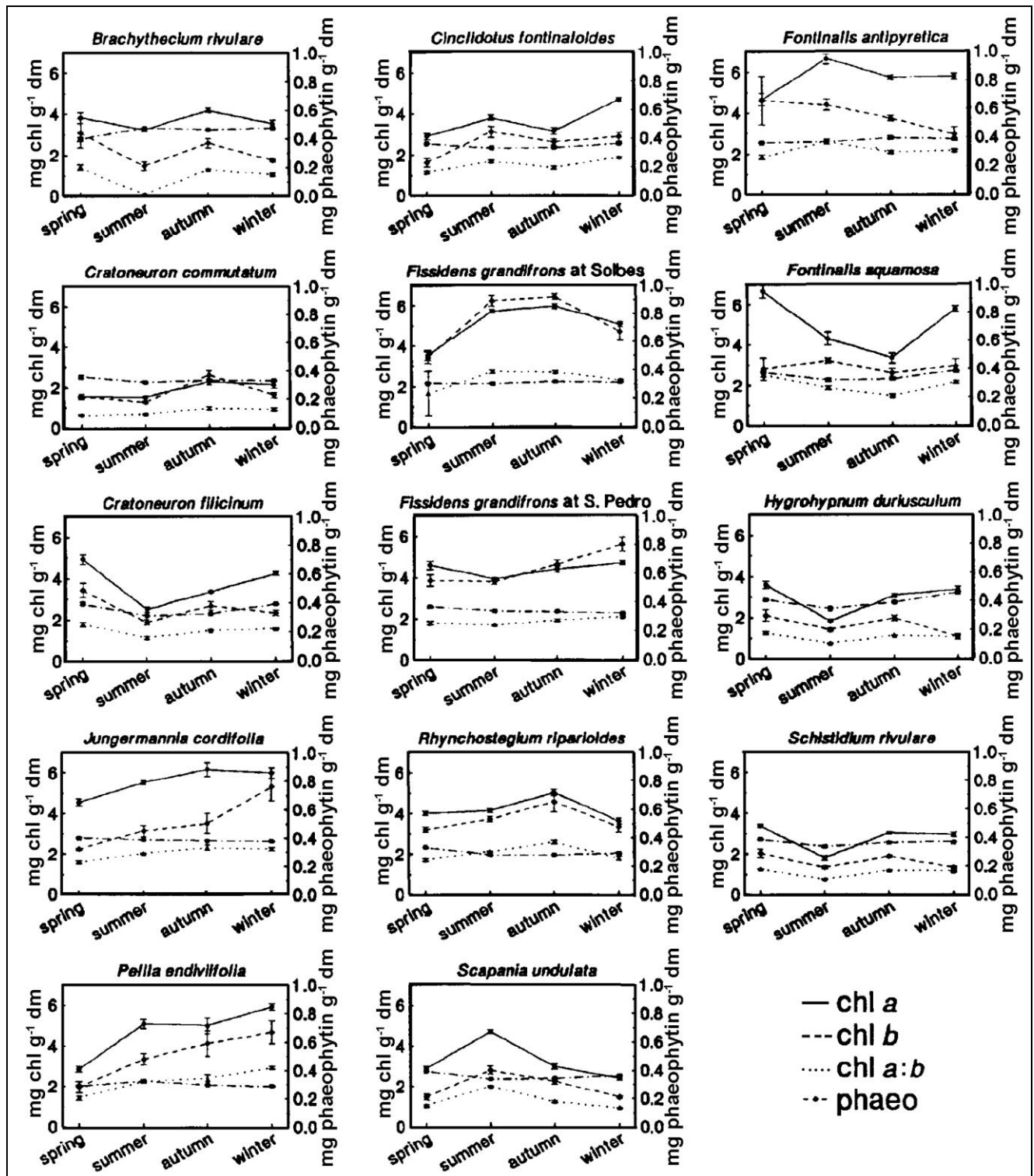
Figure 38. Seasonal changes in chlorophyll in thirteen species of aquatic bryophytes. Based on Martinez Abaigar *et al.* 1994.





Figure 39. *Syntrichia ruralis*, a species in which total chlorophyll on a dry weight basis is higher in late summer and winter than in early summer. Photo by Michael Lüth, with permission.

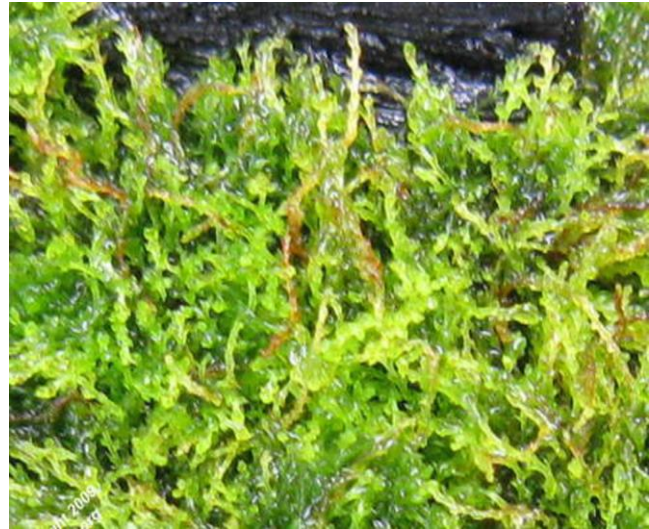


Figure 40. *Cephaloziella exiliflora*, a species that produces a purple anthocyanin-like pigment in response to high light. Photo by Tom Thekathyl, with permission.

### Aquatic

Martínez Abaigar *et al.* (1994) compared stream bryophytes to tracheophytes and found that the chlorophyll concentrations were higher (2.2-92. mg g<sup>-1</sup> dry mass and 97-351 mg m<sup>-2</sup>) than those of terrestrial bryophytes and comparable to those values for epilithic river algae, but lower than for the tracheophytes. The chlorophyll *a:b* ratio of 2.1-2.8 was significantly lower than they found for tracheophytes. Of note is their find that chlorophyll degradation in underwater bryophytes did not produce phaeopigments. This is an important consideration for those persons who would choose a measure of phaeophytin to indicate damage to the bryophytes in pollution studies.

### Antarctic

In a habitat where light is obscured by snow for more than six months of the year, it is not surprising that chlorophyll levels diminish. In the Antarctic, bryophyte chlorophyll levels decrease in winter, as does the chlorophyll *a:b* ratio (Melick & Seppelt 1994). In summer the rise in carotenoid levels corresponds to the period of high light intensity. The only Antarctic liverwort, *Cephaloziella exiliflora* (Figure 40), copes with the high light exposure in the Antarctic summer by producing a purple anthocyanin-like pigment (Post & Vesik 1992). Compared to more protected and shaded plants of the species, these plants had higher carotenoid:chlorophyll ratios, more dispersed thylakoids with fewer grana, fewer appressed thylakoids, more closely spaced leaves, and were larger, growing in a dense turf. Shaded plants had more chlorophyll per unit weight, but their *a:b* ratios did not seem to vary much.

### Summary

Photoinhibition results from over excitation of electrons under conditions when the plant is unable to use all of those electrons in photosynthesis. It is a common occurrence under high light intensities, especially at low temperatures. This temperature relationship may account for the limitations of some species that prevent their surviving in polar regions. Desiccation-tolerant species seem to be able to dissipate this energy better than the desiccation-intolerant species. Unlike tracheophytes, bryophytes can suffer greater damage when hydrated than when dehydrated.

Quenching is the ability of the plant to redirect the energy in a way that it does not damage the chlorophyll. Accessory pigments can do this by filtering the light or stabilizing the energy level. In bryophytes, the pigment **zeaxanthin** has been implicated in this role, along with a number of other pigments that depend on the species, reacting in some cases almost instantaneously and in others taking hours.

In some cases, clumping of chloroplasts and changes in shape permit the plastids to protect each other.

Bryophytes are typical shade plants, although some species do have adaptations to sun. Under low light intensity, bryophytes increase their chlorophyll *b* concentrations, providing more locations for trapping the light energy. Chlorophyll *a:b* ratios generally range between 2 and 3, but can be as low as 1 in some habitats and as high as 3.6 in others.

Lutein is commonly produced in aquatic bryophytes, but also in sunlight, causing its function to be uncertain.

Chlorophyll concentrations change seasonally, with highest concentrations generally being during the rainy growing season.

## Literature Cited

- Adamson, H., Wilson, M., Selkirk, P., and Seppelt, R. 1988. Photoinhibition in Antarctic mosses. *Polarforschung* 58: 103-111.
- Alpert, P. 1988. Survival of a desiccation-tolerant moss, *Grimmia laevigata*, beyond its observed microdistributional limits. *J. Bryol.* 15: 219-227.
- Aro, E.-M., Niemi, H., and Valanne, N. 1981. Photosynthetic studies on two ecologically different bryophytes. In: Akoyunoglou, G. (ed.). *Photosynthesis III. Structure and Molecular Organization of the Photosynthetic Apparatus*. Balaban International Science Services, Philadelphia, pp. 327-335.
- Bartosková, H., Naus, J., and Vykruta, M. 1999. The arrangement of chloroplast in cells influences the reabsorption of chlorophyll fluorescence emission. The effect of desiccation on the chlorophyll fluorescence spectra of *Rhizomnium* leaves. *Photosyn. Res.* 62: 251-260.
- Bastardo, H. 1980. The chlorophyll *a*: phaeopigment ratio as an indicator of the process of decomposition in some freshwater plants. *Acta Biol. Venezuelica* 10: 241-253.
- Bukhov, N. G., Heber, U., Wiese, C., and Shuvalov, V. A. 2001a. Energy dissipation in photosynthesis: does the quenching of chlorophyll fluorescence originate from antenna complexes of photosystem II or from the reaction center? *Planta* 212: 749-758.
- Bukhov, N. G., Kopecky, J., Pfundel, E. E., Klughammer, C., and Heber, U. 2001b. A few molecules of zeaxanthin per reaction centre of photosystem II permit effective thermal dissipation of light energy in photosystem II of a poikilohydric moss. *Planta* 212: 739-748.
- Czczuga, B. 1985. Investigations on carotenoids in Embryophyta. III. Representatives of the Hepaticae. *Phyton* 25: 113-121.
- Czczuga, B. 1987. Carotenoid contents in leaves grown under various light intensities. *Biochem. Syst. Ecol.* 15: 523-527.
- Deltoro, V. I., Calatayud, A., Gimeno, C., and Barreno, E. 1998. Water relations, chlorophyll fluorescence, and membrane permeability during desiccation in bryophytes from xeric, mesic, and hydric environments. *Can. J. Bot.* 76: 1923-1929.
- Deora, G. S. and Chaudhary, B. L. 1991. Chlorophyll content in some bryophytes. *Indian Bot. Contract.* 8: 95-97.
- Farmer, A. M., Boston, H. L., and Adams, M. S. 1988. Photosynthetic characters of a deepwater bryophyte from a clear, oligotrophic lake in Wisconsin, U.S.A. *Internat. Ver. Theor. Angew. Limnol. Verh.* 23: 1912-1915.
- Fredericq, H. and De Greef, J. 1968. Photomorphogenic and chlorophyll studies in the bryophyte *Marchantia polymorpha*. 1. Effect of red, far-red irradiations in short and long-term experiments. *Physiol. Plant.* 21: 346-359.
- Gerdol, R., Bonora, A., and Poli, F. 1994. The vertical pattern of pigment concentrations in chloroplasts in *Sphagnum capillifolium*. *Bryologist* 97: 158-161.
- Heber, U., Bilger, W., Bligny, R., and Lange, O. L. 2000. Phototolerance of lichens, mosses and higher plants in an alpine environment: Analysis of photoreactions. *Planta* 211: 770-780.
- Heber, U., Bukhov, N. G., Shuvalov, V. A., Kobayashi, Y., and Lange, O. L. 2001. Protection of the photosynthetic apparatus against damage by excessive illumination in homoiohydric leaves and poikilohydric mosses and lichens. *J. Exper. Bot.* 52: 1999-2006.
- Horton, P., Oxborough, K., Rees, D., and Scholes, J. D. 1988. Regulation of the photochemical efficiency of Photosystem II. Consequences for the light response of field photosynthesis. *Plant Physiol. Biochem.* 26: 453-460.
- Kershaw, K. A. and Webber, M. R. 1986. Seasonal changes in the chlorophyll content and quantum efficiency of the moss *Brachythecium rutabulum*. *J. Bryol.* 14: 151-158.
- Krupa, J. 1984. Anatomical structure of moss leaves and their photosynthetic activity. *Acta Soc. Bot. Poloniae* 53: 43-51.
- Marschall, M. and Proctor, M. C. V. 2004. Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll *a*, chlorophyll *b* and total carotenoids. *Ann. Bot.* 94: 593-603.
- Martin, C. E. 1980. Chlorophyll *a/b* ratios of eleven North Carolina mosses. *Bryologist* 83: 84-87.
- Martin, C. E. and Churchill, S. P. 1982. Chlorophyll concentrations and *a/b* ratios in mosses collected from exposed and shaded habitats in Kansas. *J. Bryol.* 12: 297-304.
- Martínez Abaigar, J. and Núñez Olivera, E. 1998. Ecophysiology of photosynthetic pigments in aquatic bryophytes. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). *Bryology for the Twenty-first Century*. Maney Publishing and the British Bryological Society, UK, pp. 277-292.
- Martínez Abaigar, J., Núñez Olivera, E., and Sánchez-Díaz, M. 1994. Seasonal changes in photosynthetic pigment composition of aquatic bryophytes. *J. Bryol.* 18: 97-113.
- Masarovičová, E. and Eliás, P. 1987. Some ecophysiological features in woodland mosses in SW Slovakia 2. Chlorophyll content and photosynthesis. *Symp. Biol. Hung.* 35: 113-123.
- Matsubara, S., Naumann, M., Martin, R., Nichol, C., Rascher, U., Morosinotto, T., Bassi, R., and Osmond, B. 2005. Slowly reversible de-epoxidation of lutein-epoxide in deep shade leaves of a tropical tree legume may 'lock-in' lutein-based photoprotection during acclimation to strong light. *J. Exper. Bot.* 56: 461-468.
- Melick, D. R. and Seppelt, R. D. 1994. Seasonal investigations of soluble carbohydrates and pigment levels in Antarctic bryophytes and lichens. *Bryologist* 97: 13-19.
- Mishler, B. D. and Oliver, M. J. 1991. Gametophytic phenology of *Tortula ruralis*, a desiccation-tolerant moss, in the Organ Mountains of southern New Mexico. *Bryologist* 94: 143-153.
- Miyata, I. and Hosokawa, T. 1961. Seasonal variations of the photosynthetic efficiency and chlorophyll content of epiphytic mosses. *Ecology* 42: 766-775.
- Pande, N. and Singh, J. S. 1987. Pigment concentration of ten bryophytes from Nainital, Kumaun Himalayas. *Proc. Indian Acad. Sci.* 97(1): 75-79.
- Patidar, K. C., Solanki, C. M., and Kaul, A. 1986. Chlorophyll concentration and *a/b* ratios in response to habitats in three species of *Riccia*. *Yushania* 3: 1-4.
- Paulsen, H. 1998. Auroxanthin promotes energy dissipation in light-harvesting complexes. *Photochem. Photobiol. Dec.* online abstract <[http://www.findarticles.com/p/articles/mi\\_qa3931/is\\_199812/ai\\_n8818901](http://www.findarticles.com/p/articles/mi_qa3931/is_199812/ai_n8818901)>.
- Post, A. and Veski, M. 1992. Photosynthesis, pigments, and chloroplast ultrastructure of an Antarctic liverwort from sun-exposed and shaded sites. *Can. J. Bot.* 70: 2259-2264.
- Rao, K. R., Kumar, N. R., and Reddy, A. N. 1979. Studies of photosynthesis in some liverworts. *Bryologist* 82: 286-288.



- Rincòn, E. 1993. Growth responses of six bryophyte species to different light intensities. *Can. J. Bot.* 71: 661-665.
- Rintamäki, E., Salo, R., and Aro, E. M. 1994. Rapid turnover of the D1 reaction-center protein of photosystem II as a protection mechanism against photoinhibition in a moss, *Ceratodon purpureus* (Hedw.) Brid. *Planta* 193: 520-529.
- Ruban, A. V., Phillip, D., Young, A. J., and Horton, P. 1998. Excited-state energy level does not determine the differential effect of violaxanthin and zeaxanthin on chlorophyll fluorescence quenching in the isolated light-harvesting complex of Photosystem II. *Photochem. Photobiol.* 68: 829-834.
- Seel, W. E., Hendry, G. A. F., and Lee, J. A. 1992. The combined effects of desiccation and irradiance on mosses from xeric and hydric habitats. *J. Exper. Bot.* 43: 1023-1030.
- Tieszen, L. L. and Johnson, P. L. 1968. Pigment structure of some arctic tundra communities. *Ecology* 49: 370-373.
- Valanne, N. 1977. The combined effects of light intensity and continuous light on the CO<sub>2</sub> fixation, chlorophyll content and chloroplast structure of the protonema of *Ceratodon purpureus*. *Zeit. Pflanzenphysiol.* 83: 275-283.
- Yang, C.-M., Hsu, J.-C., and Shih, C.-F. 1994. Response of chlorophyll *a/b* ratios in Yuan-Yang Lake bryophytes to the alteration of light intensity. *Proc. Natl. Sci. Counc., Rep. China Pt. B Life Sci.* 18(3): 134-137.

# CHAPTER 11-3

## PHOTOSYNTHESIS: LIMITING FACTORS

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# CHAPTER 11-3

## PHOTOSYNTHESIS: LIMITING FACTORS



Figure 1. *Schistidium maritimum* growing on rocks where desiccation and salt spray exceed the limits of most bryophytes. Photo by Michael Lüth, with permission.

### Limiting Factors

"The actual magnitude of assimilation in a leaf at any moment is determined by one or other of the main controlling conditions, light, temperature, or  $\text{CO}_2$ -supply, acting as a limiting factor." That was the conclusion of Blackman and Smith (1910-1911) in the ninth of their series of papers on vegetable assimilation and respiration. We know that water is another important parameter, but we are still trying to understand completely just how these parameters limit bryophyte photosynthesis. Perhaps Blackman and Smith again best sum it up in their statement that studies on photosynthesis "are more harmoniously interpreted from the point of view of interacting limiting factors than by the conception of optima."

Gerdol *et al.* (1998) illustrated this principle of interacting factors in their study of *Sphagnum capillifolium* (Figure 2). They found that low nighttime temperatures could lower growth five-fold, that nutrients limited growth when nighttime temperatures were high, that N and P limited growth at optimum temperatures. Different enzymes are turned on at different temperatures and different pH levels, and Gerdol *et al.* suggested that

enzymatic reactions could be limited at unfavorable temperatures.



Figure 2. *Sphagnum capillifolium*, a species in which productivity is affected by nighttime temperatures, nutrients, and N and P at optimum temperatures. Photo by Li Zhang, with permission.



## Compensation Point

The **compensation point** is that point at which plant assimilation and respiration are compensated, so that gas exchange is null (Harder 1923). The compensation point can be expressed in terms of temperature, CO<sub>2</sub>, or light. When plants are at their compensation point, they have reached a limiting factor for that parameter.

## Water Availability

Water as a limiting factor is probably the best understood. Productivity on a worldwide scale seems to be correlated with water availability, at least in *Polytrichum strictum* (Figure 3) (Longton 1994). *Sanionia uncinata* (Figure 4) in Svalbard, Norway, living on the glacial foreland of the high Arctic, has its highest photosynthetic activities only on rainy days or soon after, indicating that it is not light, but water, that limits the productivity (Uchida *et al.* 2002). Collins (1976) related net productivity to water content in these two species, likewise demonstrating its importance (Figure 5).



Figure 3. *Polytrichum strictum* with capsules, a species in which water limits productivity. Photo by Michael Lüth, with permission.



Figure 4. *Sanionia uncinata*, a species in which water limits productivity. Photo by Janice Glime.

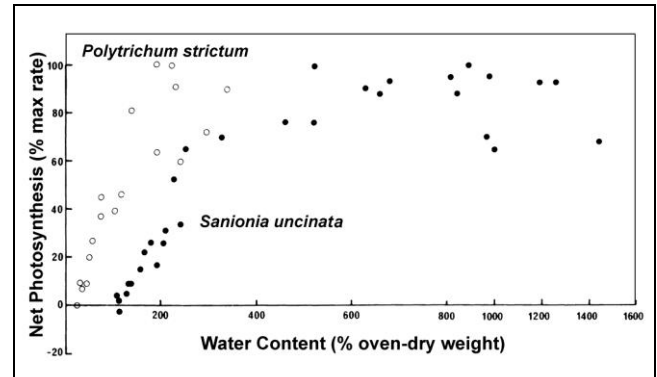


Figure 5. Effect of water content on the net productivity of two mosses from Signy Island. Measurements were at 10°C, 500  $\mu\text{e m}^{-2} \text{s}^{-1}$  (400-700 nm). Redrawn from Collins 1976.

Even in bogs, moisture is limiting. Backéus (1988) found that moisture conditions in August explained about 60% of the variation in *Sphagnum* growth the following year. He concluded that the distribution of moisture within the growing season was more important than the mean values. The importance of water in the growth of various *Sphagnum* species is well documented (Asada *et al.* 2003). Rydin and McDonald (1985b) examined the WC<sub>50</sub> (% water content at which 50% of the plants would recover if dried to their compensation point) in several *Sphagnum* species (Table 1). These ranged from 198% for *S. balticum* (Figure 6) to 283% for *S. tenellum* (Figure 7). *Sphagnum* typically requires more than 100% water content for photosynthesis.

Table 1. WC<sub>50</sub> values for *Sphagnum*. Based on references given in Rydin & McDonald 1985b.

Species	% WC <sub>50</sub>	Reference
<i>S. fuscum</i>	227	Rydin & McDonald 1985b
<i>S. fuscum</i>	400	Silvola & Aaltonen 1984
<i>S. balticum</i>	198	Rydin & McDonald 1985b
<i>S. tenellum</i>	283	Rydin & McDonald 1985b
<i>S. nemoreum</i>	400-620	Titus <i>et al.</i> 1983
<i>S. fallax</i>	250-470	Titus <i>et al.</i> 1983
<i>S. angustifolium</i>	600	Silvola & Aaltonen 1984
<i>S. nemoreum</i>	520	Grace 1970



Figure 6. *Sphagnum balticum*, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.





Figure 7. *Sphagnum tenellum*, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.

The strange phenomenon in *Sphagnum* is that there seems to be no correlation between habitat (hummock vs hollow) and photosynthetic rate at low water contents. Titus *et al.* (1983) found the expected relationship was reversed in *S. fallax* (Figure 8) and *S. capillifolium* (*S. nemoreum*, Figure 9), with the hollow-dwelling *S. fallax* having the higher photosynthetic rates at low water content. Silvola and Aaltonen (1984), on the other hand, found that the hummock species *S. fuscum* (Figure 10) was less desiccation-sensitive than the hollow species *S. angustifolium* (Figure 11). Rydin and McDonald (1985a) found that the hollow species *S. balticum* (Figure 6) and *S. tenellum* (Figure 7) cannot grow in hummocks, but that the hummock species *S. fuscum* and *S. rubellum* (Figure 12) can tolerate the wet hollows. It appears that some species have wide niches for water availability.



Figure 8. *Sphagnum fallax*, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.



Figure 9. *Sphagnum capillifolium*, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.



Figure 10. *Sphagnum fuscum*, a hummock species that is less desiccation-sensitive than are hollow species. Photo by Michael Lüth, with permission.



Figure 11. *Sphagnum angustifolium*, a desiccation-sensitive hollow species. Photo by Michael Lüth, with permission.





Figure 12. *Sphagnum rubellum*, a hummock species that can tolerate wet hollows. Photo by Michael Lüth, with permission.

Part of this dependency on water relates to the contact the plant is able to make with its substratum, or at least the water level below its capitulum. Schipperges and Rydin (1998) found that contact between capitula and the basal portion of the moss is essential to the survival of the moss, with isolated capitula being unable to recover from complete desiccation. They determined that the limit seems to be 10-20% of the water content of the compensation point. Maintenance of this level is accomplished by avoidance of desiccation through high capillarity and dense growth forms.

Hanslin *et al.* (2001) examined the effects of plant density on growth rate and water relationships. Increasing the density negatively impacted the relative growth rate and production of green biomass in both boreal forest mosses examined [*Dicranum majus* (Figure 13), *Rhytidiadelphus loreus* (Figure 14)]. However, in the mid-density range and low relative humidity, some of the watering treatments resulted in the best relative growth rates and green biomass production. Although there were no consistent patterns for most treatments, the length of the wet-dry cycle positively affected the relative growth rate when the number of wet-dry days remained equal. This is most likely due to the high cost of repair, with the longer cycles providing more time for positive productivity after the repair. The length of the dry cycle is far less important than having the needed time for repair and gain.



Figure 13. *Dicranum majus*, a species in which density impacts growth. Photo by Janice Glime.



Figure 14. *Rhytidiadelphus loreus* with capsules, a species in which density impacts growth. Photo by David Holyoak, with permission.

Alpert and Oechel (1987) studied the responses of bryophytes on granitic boulders in the chaparral of San Diego County, California, USA. Even in this dry habitat, the various bryophyte species had significantly different responses to water content, desiccation, and light. Those species in microsites with low water availability achieved maximum net photosynthesis at lower water contents and had a greater ability to recover from prolonged desiccation. Species from microsites with lower light availability achieved higher net photosynthetic rates at lower light intensities. Such studies illustrate the adaptability of bryophytes to a variety of conditions. In this chapter we will examine those limiting factors and the ways that bryophytes cope with them.

Bryophytes adapted to xeric habitats can regain photosynthesis upon rewetting in incredibly short periods of time. In *Grimmia montana* (Figure 15), this occurs in 6-10 minutes (McKay 1935). Equilibrium is reached in 30-40 minutes.



Figure 15. *Grimmia montana*, a xeric species that can regain photosynthesis in 6-10 minutes of rewetting. Photo by Michael Lüth, with permission.

Loss of water can affect not only photosynthesis, but the actual photosynthetic apparatus. As a result, those bryophytes with the ability to achieve non-photochemical quenching have a better chance of survival. In their study of three mosses, Csintalan *et al.* (1999) found that the two rock-dwelling mosses *Grimmia pulvinata* (Figure 16) and



*Anomodon viticulosus* (Figure 17) had a sharp peak of non-photosynthetic quenching when rewet, whereas quenching seemed to recover slowly in the less desiccation-tolerant *Rhytidiadelphus loreus* (Figure 14). On the other hand, Deltoro *et al.* (1998) suggested that loss of membrane integrity and subsequent loss of potassium might account for the inability to recover its photosynthetic rate.



Figure 16. *Grimmia pulvinata*, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Michael Lüth, with permission.



Figure 17. *Anomodon viticulosus*, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Janice Glime.

The moss *Rhizomnium punctatum* (Figure 18) experiences damage to PS II at 85% relative humidity (Bartosková *et al.* 1999). This is followed by a functional disconnection of the P680 reaction center from the antenna systems that is evident at higher rates of disconnection.



Figure 18. *Rhizomnium punctatum*, a species in which PS II is damaged at a reduction to 85% relative humidity. Photo by Jan-Peter Frahm, with permission.

## Water Excess

Silvola (1991) demonstrated that the water needed for photosynthesis varies widely among species. Even within a single boreal forest and peatland system, the minimum water content before net photosynthesis declines ranges from 170% to 500%. On the other hand, these mosses, except for *Polytrichum commune* (Figure 19), also had an upper limit at which photosynthesis would also decline. This limit was imposed by the difficulty of absorbing CO<sub>2</sub> through a water barrier, a phenomenon also observed in *Sphagnum* (Murray *et al.* 1989). Presumably *P. commune* managed to maintain internal air spaces in its leaves among the photosynthetic lamellae (Figure 20), hence permitting it to continue photosynthesis.



Figure 19. *Polytrichum commune* with capsules, a species that maintains photosynthesis at high moisture contents. Photo by David T. Holyoak, with permission.

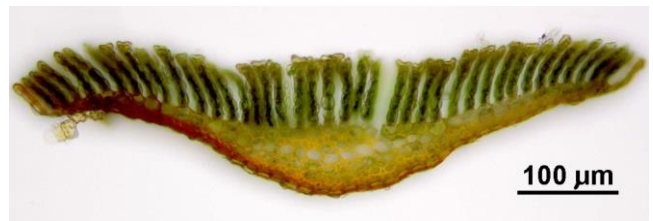


Figure 20. *Polytrichum commune* leaf cross section showing spaces between lamellae. Photo by Amelia Merced, with permission.

Liu *et al.* (2001b) found that in the mosses *Thuidium cymbifolium* (Figure 21) and *Chrysocladium retrorsum* (Figure 22) photosynthesis increased in the range of 20-70% water content. Their optimum water content was 70-80%, but then decreased from 80-95%. *Plagiomnium acutum* (Figure 23) had a somewhat broader range, increasing photosynthesis in the water content range of 20-80%, maintaining its highest photosynthetic level in the 80-95% range.





Figure 21. *Thuidium cymbifolium* with capsules, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Li Zhang, with permission.



Figure 22. *Chrysocladium retrorsum*, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Yao Kuiyu, through Creative Common.



Figure 23. *Plagiomnium acutum*, a species that maintains its highest photosynthetic level in the 80-95% water content. Photo by Show Ryu, through Creative Commons.

In *Sphagnum*, needed water content is much higher. The limiting water level depends on habitat and associated construction of the leaf. For example, in the hummock species *S. fuscum* (Figure 10), optimum conditions for

photosynthesis occurred at 600-1000% water content, with higher water levels causing a decline in photosynthesis (Silvola & Aaltonen 1984). *Sphagnum angustifolium* (Figure 11), which occurred in wetter locations, had its optimum at a wetter 900-1300%. Nevertheless, it often was too wet for optimum CO<sub>2</sub> absorption, whereas in *S. fuscum* it rarely was. But the relationship is never so simple. Using *Sphagnum*, Jauhianen *et al.* (1998) demonstrated that the negative effect of high water content on photosynthesis disappears at higher CO<sub>2</sub> concentrations, with the optimum water concentration increasing as the CO<sub>2</sub> level increases. At 3000 ppm (10X normal atmospheric CO<sub>2</sub> concentrations), there is no decrease in photosynthetic rate with increasing water content in *S. fuscum* (Figure 10) (Silvola 1990), supporting the conclusion that greater water content creates a barrier to the entry of CO<sub>2</sub>.

Similar water content responses occur in *Sphagnum* species from New Zealand (Maseyk *et al.* 1999). Green plants of *S. cristatum* (Figure 24) had an optimum water content of 1200-2000%, whereas brown mosses had a higher optimum content of 1400-3000%. Brown coloration in mosses occurs in response to high light intensity, which usually is accompanied by higher temperatures. This suggests that there is a coordinated suite of responses.



Figure 24. *Sphagnum cristatum*, a species with an optimum water content of 1200-2000%. Photo by Janice Glime.

### Seasonal Water Differences

In the tundra of the foothills north of the Brooks Range, Alaska, USA, up to two-thirds of the annual precipitation occurs during summer thunderstorms. In the boreal spruce (*Picea*) forest (Figure 25) in Manitoba, Canada, evapotranspiration was lowest in spring when the ground was still frozen (Betts *et al.* 1999). It was highest in the summer, dropping again in autumn after frost. Evaporation is, predictably, higher when the surface is wet, but it falls with an increase in light level at all temperatures in the summer because of the transpiration resistance of the forest system (*i.e.* guard cells close). But mosses also play a major role in the water evaporation. A wet moss surface lowers the vegetation resistance to water loss at its midmorning minimum by factor of 4. Mosses keep the soil wet and the atmosphere dry by inhibiting evaporation, particularly when they cover pools of standing water.





Figure 25. *Picea mariana* forest in Northern Alberta, Canada, with *Pleurozium schreberi* and *Hylocomium splendens* on the forest floor. Photo by Richard Caners, with permission.

Photosynthetic rate can be directly related to the length of dehydration period (Davey 1997a, b). However, even some bryophytes from very wet habitats in the Antarctic can exhibit some desiccation tolerance. Hydrophytic mosses were more likely to be harmed by repeated wet-dry cycles than were mesophytic or xerophytic bryophytes. Particularly in hydrophytic bryophyte species, the increase in percentage loss of photosynthetic rate following these wet-dry cycles occurred from spring to summer and from summer to autumn sampling periods. Nevertheless, Davey (1997a) could find only broad scale relationships to water availability and drew the same conclusion as Blackman and Smith (1910-1911), that other factors must be important in explaining the distributions of individual species.

Species differ in their responses to humidity. *Plagiomnium acutum* (Figure 23) has higher photosynthetic rates on cloudy and rainy days than does *Herpetineuron toccoeae* (Figure 26), but lower rates on sunny days (Li *et al.* 1999). *Herpetineuron toccoeae* has a lower rate of transpiration and higher water use efficiency than does *P. acutum*, permitting it to have a higher photosynthetic rate on sunny days. It also has a higher temperature tolerance. Interestingly, both species decrease their dark respiration with increases in temperature and decreases in relative humidity.



Figure 26. *Herpetineuron toccoeae*, a species that has reduced photosynthesis in low light. Photo by Li Zhang, with permission.

## Nighttime Absorption

Nighttime can be an important time for water absorption in bryophytes. Condensation resulting in dew provides moisture on the surfaces of these small plants and can rehydrate them from the desiccation of daytime. Such moistening will reach its maximum just before dawn, preparing the bryophytes to take advantage of the cool temperatures in the early morning light.

Csintalan *et al.* (2000) demonstrated this phenomenon in the desert moss *Syntrichia ruralis* (Figure 27). They found that water was absorbed progressively by this moss throughout much of the night. This provided sufficient water for the moss to have positive net photosynthesis for about 1.5 hours immediately after dawn. Although the cumulative carbon balance between dark and light on the day of measurement was negative, on those days with greater dew the balance would be positive. They suggested that this short time period was sufficient to permit repair following long-term desiccation damage.



Figure 27. *Syntrichia ruralis*, a species that absorbs moisture from the atmosphere at night. Photo by Des Callaghan, with permission.

## CO<sub>2</sub>

With all the talk about the greenhouse effect due to elevated CO<sub>2</sub> in the atmosphere, it is hard to think in terms of CO<sub>2</sub> limits on plant productivity. But indeed it is often what limits productivity. In aquatic systems, CO<sub>2</sub> is usually limiting, except perhaps in deep water where sediment decomposition provides CO<sub>2</sub> but light levels are low (Maberly 1985; Wetzel *et al.* 1985).

Zotz *et al.* (2000) found that gas exchange of CO<sub>2</sub> is negatively correlated with cushion size in *Grimmia pulvinata* (Figure 16). Larger cushions have lower rates of photosynthesis and dark respiration, but alternating dark and light periods cause a complicated response that depends at least in part on the state of hydration.

Despite our increasing CO<sub>2</sub> concentrations in the atmosphere, this gas is often limiting to plants, including bryophytes. For this reason, gas spaces associated with the photosynthetic tissue is important (Raven 1996).

## Compensation Point

The bottom line on the CO<sub>2</sub> limit for a species is its CO<sub>2</sub> compensation point. But this changes with the water content, temperature, and light intensity. A plant cannot use more CO<sub>2</sub> if there is insufficient excitation of electrons



due to low light levels. Dilks and Proctor (1975) reported compensation points from published studies (Table 2).

Table 2. CO<sub>2</sub> compensation points for bryophytes.

	$\mu\text{M/L}$	
<i>Pellia epiphylla</i>	75	Egle & Schenk 1953
<i>Conocephalum conicum</i>	70-105	Egle & Schenk 1953
<i>Bryum argenteum</i>	58	Rastorfer 1970
27 species	25-145	Dilks & Proctor 1975

Hanson *et al.* (2002) compared bryophytes with pyrenoids (hornworts) with *Marchantia polymorpha* (Figure 28), a liverwort with no pyrenoids. Pyrenoids are known for their ability to concentrate CO<sub>2</sub>, permitting them to store inorganic carbon for later use when levels may diminish. The CO<sub>2</sub> compensation points of the two hornworts with pyrenoids was 11-13 ppm CO<sub>2</sub>, whereas in *M. polymorpha* it was 64 ppm, a difference consistent with C<sub>3</sub> photosynthesis in the latter.



Figure 28. *Marchantia polymorpha* with archegoniophores, a species with much higher CO<sub>2</sub> compensation points than hornworts with pyrenoids. Photo by Rudolf Macek, with permission.

## CO<sub>2</sub> Environment

The CO<sub>2</sub> environment around a terrestrial plant may be different from that generally found in the atmosphere. Soil bryophytes benefit from CO<sub>2</sub> emitted from soil decomposition. For example, in a New Zealand temperate rainforest where bryophytes blanket the forest floor, those bryophytes had an annual net uptake of carbon of 103 g m<sup>-2</sup>, whereas the carbon emitted from the forest floor by bryophytes plus soil respiration was 1010 g m<sup>-2</sup> (Delucia *et al.* 2003). This meant that the bryophytes used only about 10% of the CO<sub>2</sub> coming from the forest soil microbes. The bryophyte contribution to carbon fixation would be considerably higher in the boreal forest.

Bryophytes can actually affect the turbulent fluxes of CO<sub>2</sub> in the forest. The combined effects of moss photosynthesis and respiration reduced those fluxes by a mean of 0.6  $\mu\text{M m}^{-2} \text{s}^{-1}$  (Janssens *et al.* 2001).

For the ground-dwelling *Hylocomium splendens* (Figure 25, Figure 29) in a subarctic habitat, the CO<sub>2</sub>

concentration around the plants was 400-450 ppm during the hours when the light intensity was above the compensation point (30  $\mu\text{M m}^{-2} \text{s}^{-1}$ ) (Sonesson *et al.* 1992). Throughout the growing season, it is light, temperature, and water availability that limit the CO<sub>2</sub> uptake.



Figure 29. Ground-dwelling *Hylocomium splendens*. Photo by Michael Lüth, with permission.

Epiphytes compete with tree leaves for limited CO<sub>2</sub> in the canopy. But wherever the bryophytes are growing, no individual limiting factor is able to work alone. The photosynthetic limits of one are dependent on the levels of the others. Examples of this can be seen in a variety of habitats.

The aquatic moss *Fontinalis antipyretica* (Figure 30) has an especially low CO<sub>2</sub> compensation point, but it was consistent with that of C<sub>3</sub> plants (Maberly 1985). The relationship between the photosynthetic rate and the CO<sub>2</sub> concentration showed a photosynthetic increase as the temperature was increased, typical of plants suffering from boundary layer resistance. It is puzzling that this species had a higher assimilation rate in bicarbonate than in pure CO<sub>2</sub> at the same partial pressure (James 1928). This seems to contradict the studies by Bain and Proctor (1980) that indicate its inability to use bicarbonate. Allen and Spence (1981) independently determined this once more for *Fontinalis antipyretica*. Therefore, in aquatic systems at higher levels of pH, when the CO<sub>2</sub> equilibrium shifts toward bicarbonate or carbonate, CO<sub>2</sub> becomes less available to almost non-existent. In these conditions, perhaps the CO<sub>2</sub> 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 grow in the highly aerated water of waterfalls and rapids, as, for example, *Fissidens grandifrons* (Figure 31) (pers. obs.). Others are restricted to the splash zone at the edge of the water, where CO<sub>2</sub> is trapped as the water moves through the air, as in *Cratoneuron* (Figure 32) species (Vitt *et al.* 1986; Glime & Vitt 1987).





Figure 30. *Fontinalis antipyretica*, a species with a low CO<sub>2</sub> compensation point. Photo by Andrew Spink, with permission.

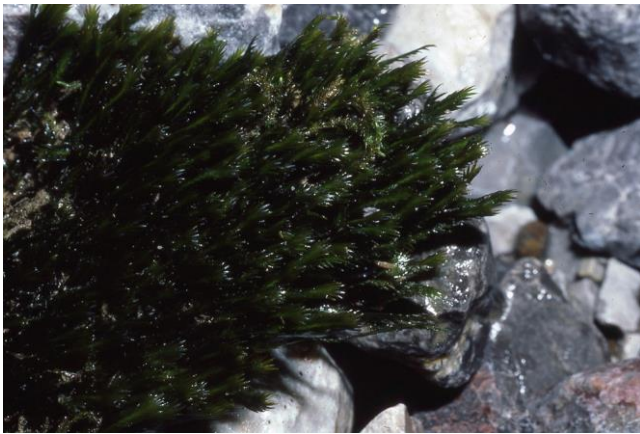


Figure 31. *Fissidens grandifrons*, a species able to live in alkaline waters. Photo by Janice Glime.

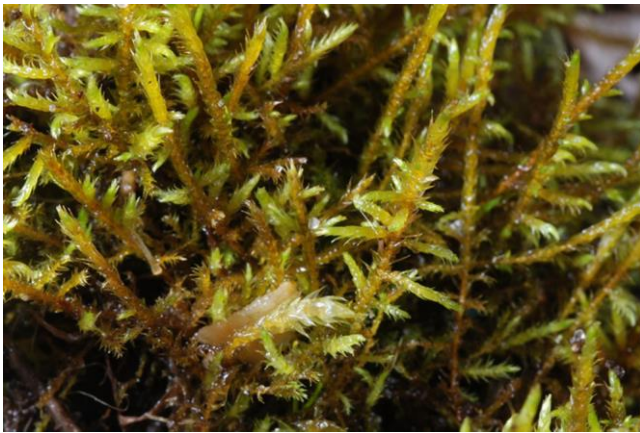


Figure 32. *Cratoneuron filicinum*, in a genus in alkaline areas is restricted to the splash zone. Photo by J. C. Schou, with permission.

Silvola (1990) examined the effects of CO<sub>2</sub> on the hummock moss *Sphagnum fuscum* (Figure 10) productivity and determined that maximum productivity occurred at 600-800% dry mass water content at ambient CO<sub>2</sub> levels of about 380 mg L<sup>-1</sup>, but that at the saturating CO<sub>2</sub> level of 8000 mg L<sup>-1</sup>, a saturated water content was needed (Figure 33). Since a CO<sub>2</sub> level of 8000 mg L<sup>-1</sup> is unrealistic in nature, the curves for 300-1200 mg L<sup>-1</sup> CO<sub>2</sub> are more instructive. One might speculate that the present success of *Sphagnum* in full sun and a temperature of

35°C, where most other bryophytes cannot survive, might be related to the elevated CO<sub>2</sub> emitted from peat.

The conclusion from all these studies is that one cannot look at the limits of CO<sub>2</sub>, or any other factor, in absolute terms. They must be examined as they are affected by the other potential limiting factors (Maberly 1985). So what does that mean for a statement like the title of a paper by Adamson *et al.* (1990), "Photosynthesis in *Grimmia antarctica* (= *Schistidium antarcticum*; Figure 34), an endemic Antarctic bryophyte, is limited by carbon dioxide"? When considering limits, it is appropriate to consider the range of the natural conditions of the plant and to express the limits that affect those plants under those conditions. Thus, a plant that is limited by CO<sub>2</sub> in the Antarctic might be limited by light if it were growing in England.

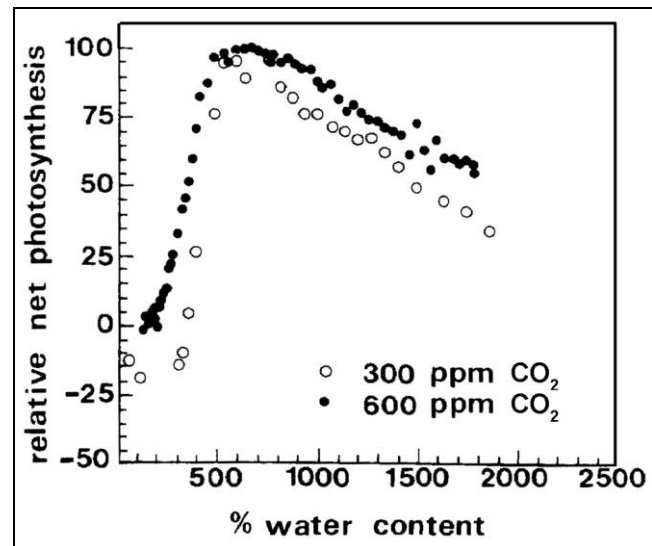


Figure 33. The relationship between net photosynthesis and water content (as percent dry mass) in *Sphagnum fuscum* (Figure 10) at two CO<sub>2</sub> concentrations. Constant conditions were maintained at 20°C, 300 μmol m<sup>-2</sup> s<sup>-1</sup> PAR photon flux density, and drying at 70% relative humidity. Redrawn from Silvola 1990.



Figure 34. Saturated *Schistidium* (formerly *Grimmia*) *antarctica* with *Ceratodon purpureus* between the hummocks. Photo courtesy of Rod Seppelt.

Silvola (1985) showed that bryophytes can be limited by CO<sub>2</sub> in their natural habitat. In the light range of 70-500 μM m<sup>-2</sup> s<sup>-1</sup>, raising the CO<sub>2</sub> concentration from 320 ppm to



640 ppm caused a 1.6-2.6-fold increase in the net daily CO<sub>2</sub> exchange.

But short-term studies in the lab or the field may be misleading. Van der Heijden *et al.* (2000) found that initially photosynthesis of *Sphagnum fallax* (= *Sphagnum recurvum* var. *mucronatum*) (Figure 8) was stimulated by elevated CO<sub>2</sub> (700 µL L<sup>-1</sup>), but that after only three days it had returned to the levels of the controls. Furthermore, at low N deposition levels (6 g m<sup>-2</sup> yr<sup>-1</sup>) and elevated CO<sub>2</sub>, these plants had 17% more biomass after six months, but at high N deposition levels (up to 23 g m<sup>-2</sup> yr<sup>-1</sup>), there was little effect on biomass increase. High levels of CO<sub>2</sub> caused a suppression of dark respiration, resulting in an accumulation of soluble sugars in the capitulum. Doubling the CO<sub>2</sub> also reduced the total nitrogen content of the capitula, but not the stems, possibly as a result of the increased sugar content. This reduction was seen in reduced amino acid content, but not in protein content. Such shifts in the carbohydrate to amino acid content has sobering implications for the food web, necessitating that more of the same food be eaten to gain the same amino acid content, and consequently increasing the sugar content. Can invertebrates get diabetes?

Within the bryophyte layers, the CO<sub>2</sub> environment differs from ambient. The forest floor efflux of CO<sub>2</sub> beneath *Sphagnum* (Figure 53) and feather mosses such as *Hylocomium splendens* (Figure 25, Figure 29) in the boreal black spruce forest (Figure 25) is ~7 M m<sup>-2</sup> s<sup>-1</sup>, a loss from the forest floor of 255.4 g C m<sup>-2</sup> during May-October (Swanson & Flanagan 2001). In *H. splendens*, the upper parts may have 400-450 ppm CO<sub>2</sub> while the light conditions are above the compensation point (*i.e.*, while photosynthesis is occurring), but light levels below saturation during most of the growing season limit CO<sub>2</sub> uptake (Sonesson *et al.* 1992). Nevertheless, the higher than normal atmospheric levels of CO<sub>2</sub> that occur within the mat permit the plants to have photosynthetic levels that are higher than would normally occur at the reduced (below saturating) light levels.

As the CO<sub>2</sub> concentration of the atmosphere increases, productivity of various groups of plants are likely to be affected differently. The rate of net photosynthesis in the hummock peatmoss *Sphagnum fuscum* (Figure 10) increases as the CO<sub>2</sub> concentration increases in the range of 350-2000 ppm CO<sub>2</sub> during half-hour exposures (Jauhiainen & Silvola 1999). The rate at light saturation likewise increases. The effect of radiation fluxes, however, is independent of the level of CO<sub>2</sub>. When the exposure to high CO<sub>2</sub> is maintained for longer times, the rates of net photosynthesis gradually decrease compared to those at 350 ppm. On the other hand, at high CO<sub>2</sub> levels, the depression of net photosynthesis found at high water contents is no longer present.

Tropical forests have huge competition for CO<sub>2</sub> in the canopy, but so little light reaches the forest floor that competition is greatly reduced. In a submontane tropical rainforest in Panama, diel variations in water content of six studied bryophytes were great, with both high and low water content limiting photosynthesis (Zotz *et al.* 1997). Low photon flux density is less important in limiting CO<sub>2</sub> exchange. More than half of the carbon gained in the daytime (2.9 mg C per g plant) is lost at night as respiration. If the productivity of this study is

representative, the bryophytes gain 45% of their initial carbon content in a year in this environment.

## CO<sub>2</sub>-Concentrating Mechanisms

Since CO<sub>2</sub> is frequently a limiting resource, a means of concentrating CO<sub>2</sub> for use later or for grabbing it from water is a useful mechanism. Although bryophytes are known only as C<sub>3</sub> plants (Smith & Griffiths 1996), at least some seem to have such mechanisms. Furthermore, both **Cyanobacteria** and many algae are able to accumulate dissolved inorganic carbon through CO<sub>2</sub>-concentrating mechanisms (Smith & Griffiths 1996). In the green algae (**Chlorophyta**), this is accomplished by a proteinaceous structure associated with chloroplasts, the **pyrenoid**. And indeed, this structure is present in the phylum **Anthocerotophyta** (Figure 35), but not in all genera.

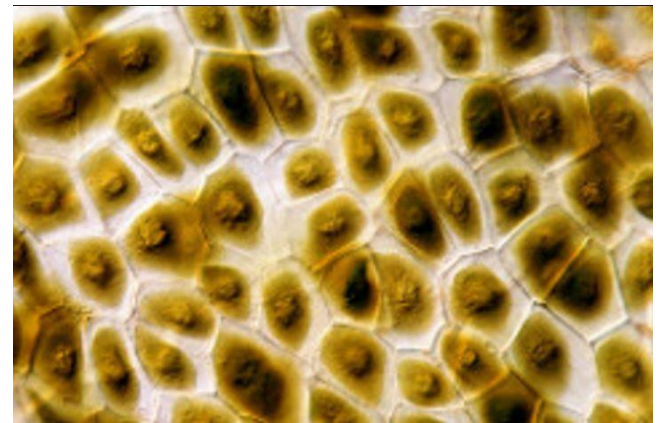
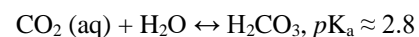
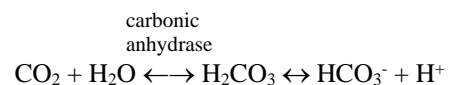


Figure 35. *Phaeoceros* cells with pyrenoids associated with chloroplasts. Photo by George Shepherd, with permission.

I find it interesting that it is a primarily terrestrial group that has this mechanism. Living on the soil permits bryophytes to take advantage of CO<sub>2</sub> emitted through soil respiration. But living in the water, attaining CO<sub>2</sub> can be a severe problem for some bryophytes not receiving CO<sub>2</sub> from the sediments and unable to use the carbonates and bicarbonates in water with non-acid pH. Something is working to permit some bryophytes to live in these conditions, and the mechanism remains unknown.

## pH

On land it is likely that pH has only minimal influence on the uptake of CO<sub>2</sub> from the atmosphere. However, in the aquatic system, pH can be a serious limiting factor. The CO<sub>2</sub> that is dissolved in water seeks equilibrium with the bicarbonate and carbonate. This equilibrium is dependent on pH:



where the pK values are those at 25°C



The  $pK$  is the  $pH$  at which the dissociated and undissociated forms have the same activity, *i.e.*, the two sides of the arrows in the above equations. It is the equilibrium between the two forms. From this we can derive the level at which inorganic carbon exists in the bicarbonate state. At  $pH$  6.35, the solution would be expected to have half  $CO_2$  and half bicarbonate. Above that it becomes predominately bicarbonate. At even higher levels of 10.3, the bicarbonate and carbonate levels are equal. Above  $pH$  10.3, the carbon is predominately in the form of carbonate. Allen and Spence (1981) calculated that at  $pH$  4.4, 99% of the inorganic carbon is present as  $H_2CO_3$  (making free  $CO_2$  available); only 1% is  $HCO_3^-$ , and there is virtually no  $CO_3^{2-}$ . At  $pH$  8.4, this reverses and 99% of the total inorganic carbon is  $HCO_3^-$ ; less than 1% is in  $H_2CO_3$ ; less than 0.03% is in  $CO_3^{2-}$ . At any given moment, some  $CO_2$  will exist as biological and chemical reactions occur to release  $CO_2$  into the water, but as time continues, those small amounts will enter into the equilibrium. Nevertheless, metals and other buffering acids and bases can alter the concentrations.

In aquatic systems,  $CO_2$  is spontaneously hydrated to  $H_2CO_3$ , but this hydration occurs about 2 orders of magnitude slower than the hydration which occurs in the carbonic anhydrase-catalyzed reaction. But remember that the carbonic anhydrase is in the cell where the  $pH$  is generally above 6.5. Or is it? There is evidence that carbonic anhydrase acts extracellularly in some algae (Hobson *et al.* 2001), including *Chlamydomonas* (Figure 36) and some diatoms. Thus it is possible that there is extracellular activity in some aquatic mosses. Furthermore, the  $pH$  of the cell wall is typically lower than that of the cell, ranging 3-6.

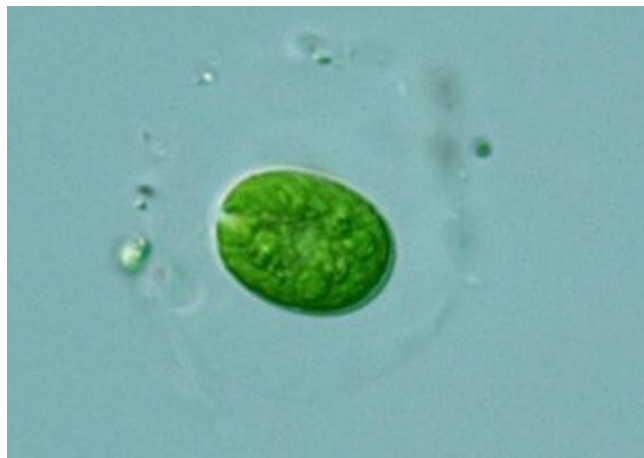


Figure 36. *Chlamydomonas*, a genus that uses carbonic anhydrase extracellularly. Photo by Yuuji Tsukii, with permission.

I am aware of no evidence that this carbonic anhydrase is able to act on water outside the cell in any bryophyte, but then, no one seems to have looked. With such an elevated  $pH$  within the cell, the  $H_2CO_3$  is rapidly converted to bicarbonate and the level of carbonic acid is miniscule. But the enzyme RUBISCO is present in the plant photosynthetic cell, ready to place the  $CO_2$  into the photosynthetic pathway where it is bound into the 3-carbon compound, PGA (Rintamäki 1989). Thus, the problem is getting the miniscule amounts of  $CO_2$  from the water in

systems where the  $pH$  is too high for the equilibrium to shift toward free  $CO_2$  or  $H_2CO_3$ .

**Sphagnum** (Figure 7-Figure 12) and other bryophytes have the ability to lower the  $pH$  through cation exchange, thus keeping more  $CO_2$  in their environment in readily usable form. Consequently, low  $pH$  values in the proximity of bryophytes with polyuronic acid in the cell walls are most likely common, and the cation exchange properties of these acids would provide  $H^+$  ions in the immediate surroundings. This could provide the free  $CO_2$  needed for photosynthesis. In plants living in cool water and low light, such as many aquatic bryophytes, even such low levels of  $CO_2$  are probably adequate. As discussed in the nutrient chapter, this cation exchange and  $pH$ -lowering ability have a number of ecological and physiological implications in the peatland habitat. The  $pH$ -lowering ability and requirements differ with *Sphagnum* species, with hummock species tending to have requirements for the lowest  $pH$  (Haraguchi 1996; Haraguchi *et al.* 2003). After all, it is difficult to have much effect on the  $pH$  of an entire lake, but having an effect on the immediate microenvironment of a hummock is not.

### Limits to Entry

Water limits the entry of  $CO_2$  into cells. For *Sphagnum fuscum* (Figure 10), Silvola (1990) found the optimal water content at ambient  $CO_2$  levels to be 600-800%. However, if the  $CO_2$  level was raised, that optimal water content increased, an observation consistent with the difficulty of getting  $CO_2$  into a wet cell through the water boundary. By increasing the concentration of  $CO_2$ , more of it is able to penetrate the barrier. At 3000 ppm  $CO_2$ , there was no decrease in the photosynthetic rate with increasing water content.

In aquatic habitats, bryophytes may gain  $CO_2$  from that evolved from sediment respiration. Wetzel *et al.* (1985) found that 25-40% of the  $CO_2$  fixed in leaves of tracheophytes comes from the **rhizosphere** (root area). Bryophytes do not have the **lacunae** (minute cavities) to transmit gases in the manner used by many aquatic tracheophytes, but due to their small size, they are able to incorporate the evolving  $CO_2$  as it escapes from the sediments and before it reaches the awaiting phytoplankton.

### Methane

*Sphagnum* (Figure 7-Figure 12) seems to have an alternative source for gaining carbon (Raghoebarsing *et al.* 2005). It is able to obtain carbon through a symbiotic relationship with endophytic methanotrophic bacteria living in the hyaline cells of both stems and leaves. These bacteria oxidize the carbon from the methane to  $CO_2$  that is then used by the *Sphagnum*. This appears to supply about 10-15% of the carbon used by *Sphagnum*. This and other processes in the peatland system recycle the methane in ways that cause little of the methane to reach the atmosphere.

### Light

The majority of bryophytes grow in habitats where the light intensity is less than that of full sunlight. Therefore, it is not surprising that Rincón (1993) found that six forest floor bryophytes all increased their biomass relative to



controls when the light intensity was increased for 36 days. But shoot elongation can have the opposite response. In this study, all species [*Brachythecium rutabulum* (Figure 37), *Eurhynchium praelongum* (Figure 38), *Plagiomnium undulatum* (Figure 39), *Pseudoscleropodium purum* (Figure 40), *Thuidium tamariscinum* (Figure 41)] but *Lophocolea bidentata* (Figure 42) had greater elongation in the lower light intensities. *Dicranum majus* (Figure 13) likewise had its greatest elongation at the lowest light level tested ( $20 \mu\text{M m}^{-2} \text{s}^{-1}$ ) (Bakken 1995).



Figure 37. *Brachythecium rutabulum*, a species with greater elongation in lower light. Photo by J. C. Schou, with permission.



Figure 38. *Eurhynchium praelongum*, a species with greater elongation in lower light. Photo by Blanka Shaw, with permission.



Figure 39. *Plagiomnium undulatum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 40. *Pseudoscleropodium purum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 41. *Thuidium tamariscinum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 42. *Lophocolea bidentata*, a leafy liverwort that exhibits greater elongation in low light. Photo by Michael Lüth, with permission.

Murray *et al.* (1993) found a similar elongation response among Alaskan Arctic tundra *Sphagnum* (Figure 7-Figure 12) species. They experimented by removal of tracheophytes in some plots and by use of shade cloth of others, compared to controls. Moss growth in shaded plots was 2-3 times that of mosses in control plots, whereas significant growth reduction was evident in the canopy removal plots. They suggested that those mosses in the canopy removal plots suffered from photoinhibition. In the



laboratory, such inhibition occurred after only two days of high light treatment and the photosynthetic capacity did not recover during the 14 days of the experiment. They suggested that the low tissue nitrogen levels may have prevented the *Sphagnum* from acclimating to the high light intensity.

### Compensation and Saturation Points

Bryophytes in general are shade-adapted plants with low light compensation points and low saturation levels. Gabriel and Bates (2003) showed that bryophytes of the evergreen laurel forest in the Azores were likewise shade-adapted plants that reached their light saturation at  $30 \mu\text{M m}^{-2} \text{s}^{-1}$ . *Andoa berthelotiana* (Figure 43) had the lowest compensation point at  $20 \mu\text{M m}^{-2} \text{s}^{-1}$  and *Myurium hochstetteri* (Figure 44) had the highest at  $68 \mu\text{M m}^{-2} \text{s}^{-1}$ . The deep shade species *Fissidens serrulatus* (Figure 45) had the extremely low compensation point of  $7 \mu\text{M photons m}^{-2} \text{s}^{-1}$ . With leaves remaining on the trees, the low light levels of winter often limit the photosynthetic activity of these bryophytes. Contrasting with these evergreen forest species, the pendulous moss *Pilotrichella ampullacea* (Figure 46) in Uganda has a saturating light intensity of  $400 \mu\text{M m}^{-2} \text{s}^{-1}$  (Proctor 2002).



Figure 43. *Andoa berthelotiana*, a shade-adapted moss in the Azores with the lowest light compensation point there. Photo by Jan-Peter Frahm, with permission.



Figure 44. *Myurium hochstetteri*, a shade-adapted moss in the Azores with the highest light compensation point there. Photo by Michael Lüth, with permission.



Figure 45. *Fissidens serrulatus*, a deep-shade-adapted moss in the Azores with the lowest light compensation point there. Photo by David Holyoak, with permission.



Figure 46. *Pilotrichella ampullacea*, a pendulous moss with a very high light saturation point. Photo by Jan-Peter Frahm, with permission.

It is difficult to compare results from different studies because the units cannot easily be converted to other forms of measure, as discussed in the chapter on light. Older measurements were typically in foot candles or lux, whereas more recent ones are in energy units or PAR (photosynthetically active radiation) units. Conversion is complicated by the composition of the wavelengths of light. For example, Vashistha and Chopra (1989) determined that the optimal growth of the disturbed habitat liverwort *Riccia frostii* (Figure 47) occurred at 3500 lux of continuous light in the lab. But lab light quality differs considerably from that in the field and under fluorescent lights it typically lacks the normal proportion of red light that achieves the highest level of photosynthesis. A light level of 3500 lux is quite low when one considers that full



sunlight is about 70,000 lux. It is likely that at that level of light some other factor became limiting in the lab, perhaps CO<sub>2</sub>.



Figure 47. *Riccia frostii*, a species of disturbed habitats. Photo by Rosemary Taylor, with permission.

The interplay of limiting factors becomes the means of niche partitioning in many of the bryophytes. *Plagiomnium acutum* (Figure 23) and *Herpetineuron toccoeae* (Figure 26) occupy different niches because of this interplay. In *P. acutum*, photosynthesis is lower on sunny days but higher on cloudy and rainy days than that of *H. toccoeae*, indicating its greater ability to absorb and use weak light while having a higher CO<sub>2</sub> assimilation efficiency (Li *et al.* 1999). The greater water use efficiency of *H. toccoeae* and lower rate of transpiration permits that species to tolerate higher temperatures and desiccating conditions. One reason for this is the higher respiratory rate of *P. acutum*.

The mosses *Plagiomnium acutum* (Figure 23) and *P. maximoviczii* (Figure 48) have light compensation points of 20-40  $\mu\text{M m}^{-2} \text{s}^{-1}$  and saturation points of 200-400  $\mu\text{M m}^{-2} \text{s}^{-1}$ , with lower values in winter and higher ones in summer (Liu *et al.* 2001a). Thus it appears that they acclimate to the conditions of light or temperature or both.

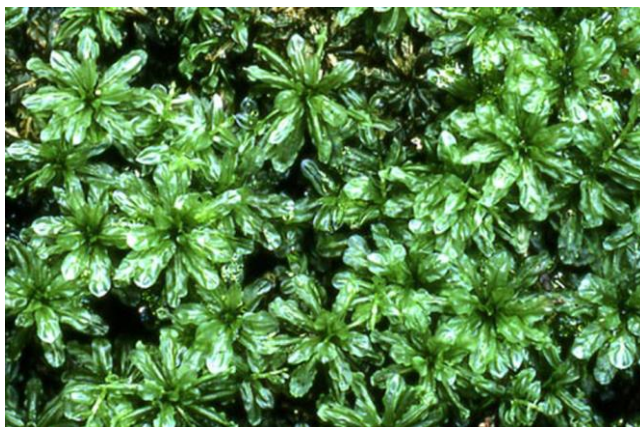


Figure 48. *Plagiomnium maximoviczii*, a species with lower compensation and saturation points in winter. Photo from Hiroshima University Digital Museum of Natural History, with permission.

It is intuitively obvious that light intensity will decrease as one penetrates further into the moss layer. In a

study on Antarctic mosses, Davey and Ellis-Evans (1996) found that not only did the light intensity decrease, but the attenuation maxima were at the wavelengths where chlorophyll has the greatest absorption peaks (675 nm and <450 nm). That again seems intuitive, since it is the green plant that is blocking the light penetration, and that green is the result of the chlorophyll pigments. But it is not quite that simple. Species differ in their absorption spectra, with stem orientation, stem density, leaf size, orientation, and pigment content all affecting absorption. While bryophytes all tend to have similar pigments, the relative proportions differ. Drying causes the wavelength variation to disappear and light to penetrate further into the clump or mat. These light penetration and wavelength changes resulted from both structural changes in the cells and pigment changes. This is adaptive, permitting deeper layers to carry out photosynthesis as the upper parts of the plants dry beyond the point where they can photosynthesize.

Because of its thin ozone layer, the Antarctic has some of the highest UV intensities on Earth. Among fourteen species of mosses, the light saturation level was 30-270  $\mu\text{M m}^{-2} \text{s}^{-1}$  (Davey & Rothery 1997). Nevertheless, these shade-adapted bryophytes exhibited no photoinhibition at any light intensity tested, up to 700  $\mu\text{M m}^{-2} \text{s}^{-1}$ .

The thallose liverwort *Marchantia polymorpha* (Figure 28) is generally a shade plant, but tolerates at least some direct sun. Nevertheless, its light saturation level was only 2000-3000 lux, with inhibition occurring at higher levels (Mache & Loiseaux 1973). This is a very low saturation level when one considers that full sunlight in the temperate zone is typically about 70,000 lux. Isolated chloroplasts had a rate of photosynthesis about one tenth that of those in whole plants, suggesting that the plant may reduce the light level considerably to achieve its optimum low light level. Furthermore, high light stimulates changes in the chloroplast structure, inducing formation of continuous grana instead of the more typical small grana. By contrast, *Hypnum cupressiforme* (Figure 49), an epiphyte, had not reached saturation at any temperature (0-15°C) at light intensities of 12,000 lux (Kallio & Kärenlampi 1975).



Figure 49. *Hypnum cupressiforme* epiphytic habitat, a species with a wide range of temperatures without reaching light saturation. Photo by Dick Haaksma, with permission.

Rastorfer and Higginbotham (1968) measured the light saturation of *Bryum sandbergii* from Idaho, USA, at 20°C in 3% CO<sub>2</sub> and found that photosynthesis attenuated at



about 8 m watts per  $\text{cm}^2$  (Figure 50). However, at  $4^\circ\text{C}$ , the photosynthetic rate declined at 8 m watts per  $\text{cm}^2$ , suggesting photoinhibition at that low temperature (Figure 51).

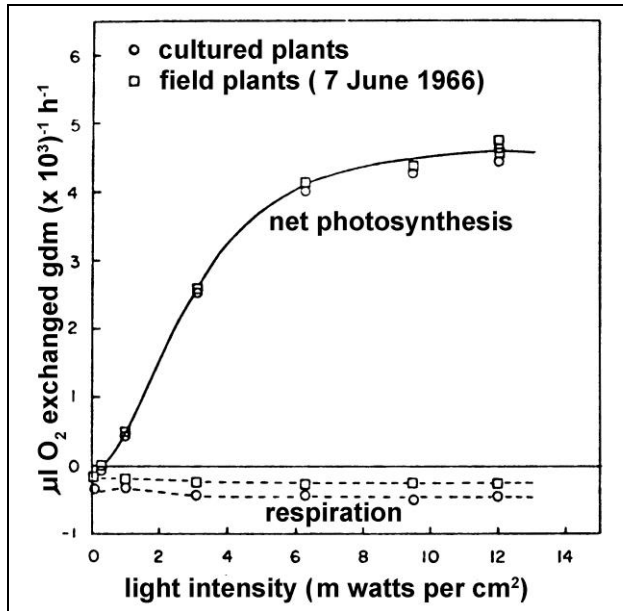


Figure 50. Mean effects of light intensity on net photosynthetic rates of *Bryum sandbergii* in the lab and field at  $20^\circ\text{C}$ , 3%  $\text{CO}_2$ .  $n=5$ . Redrawn from Rastorfer and Higginbotham 1968.

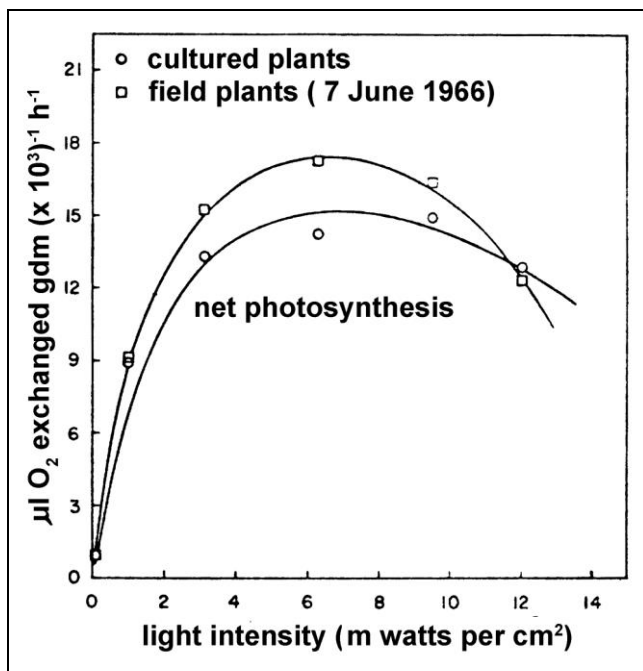


Figure 51. Mean effects of light intensity in the lab and field on net photosynthesis of *Bryum sandbergii* at  $4^\circ\text{C}$ , 3%  $\text{CO}_2$ .  $n=5$ . Redrawn from Rastorfer and Higginbotham 1968.

In *Sphagnum cristatum* (Figure 24) and *S. australe* (Figure 52) from New Zealand, the light saturation point ranges from 111 to  $266 \mu\text{M m}^{-2} \text{s}^{-1}$  (Maseyk *et al.* 1999). Color affected the saturation point of *S. cristatum*, with brown coloration causing an elevated saturation point. This, in turn, resulted in lower photosynthetic rates, lower

quantum efficiencies, and higher light compensation points than those of green plants.



Figure 52. *Sphagnum australe*, a species with a wide range of light saturation points. Photo by Tom Thekathyl, with permission.

In the Alaskan foothills of the Philip Smith Mountains, *Sphagnum angustifolium* (Figure 11) has a light compensation point of  $37 \mu\text{M m}^{-2} \text{s}^{-1}$  and light saturation between 250 and  $500 \mu\text{M m}^{-2} \text{s}^{-1}$  at  $10^\circ\text{C}$  (Harley *et al.* 1989). At  $20^\circ\text{C}$ , this relationship shifted upward, with the compensation point increasing to  $127 \mu\text{M m}^{-2} \text{s}^{-1}$  and the saturation point to  $500 \mu\text{M m}^{-2} \text{s}^{-1}$ . *Sphagnum squarrosum* (Figure 53) experienced decreased photosynthetic capacity and chlorophyll bleaching when the tracheophyte cover was removed.



Figure 53. *Sphagnum squarrosum* 1 J. C. Schou, with permission.

Shade mosses have a light compensation point of 20-400 lux and sun species of 1000-2000 lux (Bazzaz *et al.* 1970). Saturation points generally run 10,000-30,000 lux for sun bryophytes (Proctor 1981). The epiphytic *Ulota crispata* (Figure 54) has a saturation point of 40,000 lux (Miyata & Hosokawa 1961). Thus, sun species of bryophytes have compensation and saturation levels about ten times as high as those of shade mosses. In Kansas, USA, the saturating light level for *Dicranum scoparium* (Figure 55), *Leucobryum glaucum* (Figure 61), and *Thuidium delicatulum* (Figure 62) is  $200 \mu\text{M m}^{-2} \text{s}^{-1}$  (McCall & Martin 1991).





Figure 54. *Ulota crispa*, an epiphyte with a high light saturation point. Photo by Janice Glime.



Figure 55. *Dicranum scoparium*, a forest floor species. Photo by Janice Glime.

Aquatic plants from deep water are likely to have the lowest compensation points due to the low levels of light penetrating to depths. *Fontinalis* (Figure 30) exhibited a compensation point of 150 lux at 20°C, but this declined to 40 lux at 5°C (Burr 1941). Wetzell *et al.* (1985) found extremely low light compensation points for *Sphagnum auriculatum* var. *inundatum* (Figure 56) and *Juncus bulbosus* (a seed plant; Figure 59) from deeper water and higher values for the red alga *Batrachospermum* (Figure 60) from shallower areas.



Figure 56. *Sphagnum auriculatum*, a species with a very low light compensation point. Photo by Jan-Peter Frahm, with permission.

More recent measurements have put light measurements in terms of energy units or photosynthetically active radiation (PAR). Using energy units, Krupa (1978) found a compensation point of 0.6 and saturation point of 15 W m<sup>-2</sup> for the shade plant *Rhizomnium punctatum* (Figure 18). For the sun plants *Polytrichum piliferum* (Figure 57) and *Funaria hygrometrica* (Figure 58), the compensation points were 1.8 and 1.4 W m<sup>-2</sup>, respectively, and the saturation points 55 and 100 W m<sup>-2</sup>, respectively.

Even the bryophytes seem to operate below their light saturation points for most of the growing season. *Hylocomium splendens* (Figure 29) in the subarctic had a compensation point of 30 μM m<sup>-2</sup> s<sup>-1</sup> and a saturation point of 100 μM m<sup>-2</sup> s<sup>-1</sup> during the growing season, but it only experienced its light saturation level 65% of the time in July, 76% in August, and 96% in September (Sonesson *et al.* 1992).



Figure 57. *Polytrichum piliferum*, a sun species showing its hyaline hair points. Photo by Michael Lüth, with permission.



Figure 58. *Funaria hygrometrica*, a sun species. Photos by Michael Lüth, with permission.





Figure 59. *Juncus bulbosus*, a species with low light compensation point in deep water. Photo by Krzysztof Ziarnek, Kenraiz, through Creative Commons.

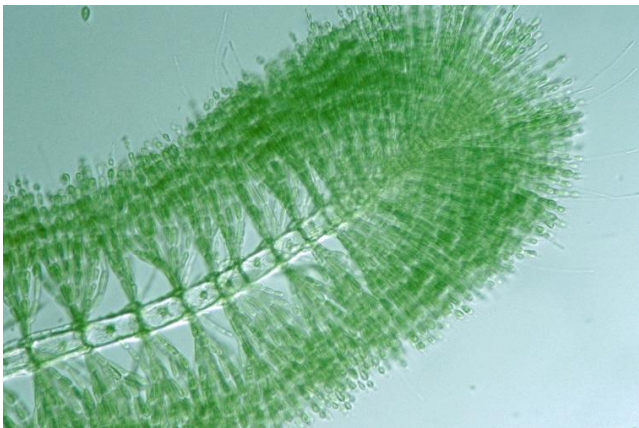


Figure 60. *Batrachospermum*, a shallow-water red alga with a high light compensation point. Photo by Yuuji Tsukii, with permission.

Light intensity, coupled with air humidity, seems to be a limiting factor for distribution of tropical epiphytic bryophytes in the Amazon (Frahm 1987). The low light intensities, coupled with high temperatures in the lowland forests, do not permit the bryophytes to reach their compensation points. Energy lost to respiration at such temperatures is greater than that gained in the low light levels of the lowlands. This relationship accounts for the increasing number of taxa and biomass with increased elevation.



Figure 61. *Leucobryum glaucum*, a forest floor species. Photo by Janice Glime.



Figure 62. *Thuidium delicatulum*, a species of open and forest. Photo by Janice Glime.

### Excess Light

Excess light can limit bryophyte productivity by causing photoinhibition and damage to the chlorophyll. Dehydration usually protects the bryophytes from this damage by making the plants dormant. When dehydrated, *Grimmia alpestris* (Figure 63) from an alpine habitat had little chlorophyll fluorescence when subjected to high UV light intensity, whereas tracheophytes had high levels of fluorescence under the same conditions (Heber *et al.* 2000). When these mosses were rehydrated, their fluorescence increased, but that of the tracheophytes decreased upon rehydration. These mosses typically do not experience photodamage while dry, apparently using the same protective mechanism while dry as they are able to use successfully while hydrated.



Figure 63. *Grimmia alpestris*, a species that loses its chlorophyll fluorescence at high light intensities. Photo by Michael Lüth, with permission.

Experiments in canopy removal consistently indicate that high light intensities are not favorable to moss growth. In the Alaskan Arctic tundra, Murray *et al.* (1993) found that *Sphagnum*-dominated moss growth (Figure 53) increased by 2-3 times in shaded plots, but had a significant growth reduction in plots where the tracheophyte canopy had been removed. They suggested that the reduced growth was due to photoinhibition.



It is not uncommon for bryophytes to become pale in bright sunlight. Others develop red or other energy-absorbing pigments. But some of the effects of greater exposure to light, such as that seen in canopy removal experiments, is that the temperature and moisture conditions change. More of the daylight hours are at temperatures above that which is suitable for  $C_3$  photosynthesis, forcing the plants to become dormant. And the added light and heat cause a greater loss of water by evaporation.

### Continuous Light

As already discussed in Chapter 9-4, we know that continuous light may be deleterious to photosynthesis, causing mosses to lose their chlorophyll (Kallio & Valanne 1975). The stroma thylakoids are destroyed, much like the destruction seen in continuous dark in the cave experiments of Rajczy (1982). However, the continuous light damage observed by Kallio and Valanne occurred in laboratory experiments. Plants living in Polar Regions may acclimate to the seasonal change in continuous photoperiod (Richardson 1981).

It appears that continuous light alters the proportions of sugars and lipids. Sakai *et al.* (2001) found that green portions of the moss *Racomitrium barbuloides* (Figure 64) initially increased their storage of both sugars and lipids, but then they decreased. This decrease was accompanied with a significant decline in photosynthetic capacity. They suggested that the green tissue plays a major role in photoassimilate storage. It appears that accumulation of photoassimilates inhibits photosynthesis, but that such accumulation is unlikely under natural conditions.



Figure 64. *Racomitrium barbuloides*, a species that stores sugars and lipids, depending on environmental conditions. Photo from Digital Museum, Hiroshima University, with permission.

### Bryophyte Canopy Structure

A bryophyte canopy is constructed differently from that of tracheophytes. Yet, while the leaf structure is very different, the mat structure may in many ways resemble the leaf structure of a tree leaf. Rice *et al.* (2008) investigated the trait relationships in ten species of *Sphagnum* (Figure 7-Figure 12). They found no relationship between N content and maximum photosynthesis per mass or area, differing from relationships in tracheophytes. Only capitulum area seemed to be relevant to N storage and maximum photosynthesis. Water content and carotenoid

concentration were the strongest predictors of maximum photosynthesis.

Tobias and Niinemets (2010) noted the large variation of light availability within the moss canopy. Furthermore, the lowest light levels are in the lower portions where the oldest tissues reside. Variation within the temperate-boreal forest moss *Pleurozium schreberi* (Figure 25, Figure 65) canopy can be greater than that between locations. Chl, Chl/N, and Chl/Carotenoid ratios increase with decreasing light availability between locations. Upper layers of the moss within habitat vary similarly, but after the light diminishes to 50-60% of the above-canopy levels, the layers demonstrate characteristics of senescence. At these depths, pigment and N concentration and photosynthetic capacity decrease with light availability. Thus, younger tissues are able to acclimate, but older ones do not.



Figure 65. *Pleurozium schreberi*, a common boreal feather moss. Photo by Janice Glime.

Waite and Sack (2010), in studying ten Hawaiian moss species, found that the moss species had low leaf mass per area and low gas exchange rates. The light-saturated photosynthetic rate per mass did not correlate with light levels in the habitat. Rather, microhabitat irradiance had the greatest influence on other photosynthetic parameters and structural traits, causing correlations of traits of leaf area, cell size, cell wall thickness, and canopy density. Costa size, canopy height, and light-saturated assimilation rate per mass correlated with structural allocation. N concentration correlated negatively with canopy mass per area (replacing leaf mass per area used in tracheophytes). The structures are different from those of tracheophytes, but the leaf size and function have been replaced with canopy mass and function.

### Photoperiod Effects on Physiology

The effects of photoperiod as an event trigger are well known, but their effects on physiology of vegetative plants has been largely ignored (Cvetić *et al.* 2009). In the forest moss *Atrichum undulatum*, day length had no noticeable effect on photosynthetic pigments in the lab. Protein content and malate dehydrogenase activity were both higher in long day (16h light/8h dark) than in short day (8h light/16h dark) growth conditions. Long days produced higher concentrations of total phenolic compounds, greater peroxidase activity, and higher total antioxidative capacity.



## Temperature

Once again we see evidence that limiting factors do not act alone. In *Fontinalis antipyretica* (Figure 30), photosynthesis increases with CO<sub>2</sub> concentration, but the level achieved is further dependent upon temperature (Maberly 1985). As the temperature goes up, boundary layer resistance decreases, permitting more CO<sub>2</sub> to enter the plants.

Aquatic mosses seem to be especially sensitive to high temperature, failing to sustain a healthy state for a prolonged period. Their lethal temperature can be quite low, as illustrated by *Leptodictyum riparium* (Figure 66) with a photosynthetic optimum at 23°C and death at 33°C (Sanford 1979). Several *Fontinalis* (Figure 30) species can do well at 20°C for a period of time; then they lose their green color and stop growing (Fornwall & Glime 1982; Glime 1982, 1987a, 1987b, 1987c, Glime & Acton 1979).



Figure 66. *Leptodictyum riparium*, a species that dies at 33°C. Photo by David Holyoak, with permission.

Interestingly, cold resistance seems to be related to heat resistance, as shown by Balagurova *et al.* (1996) for *Sphagnum* species. For *S. subsecundum* (Figure 67), the lethal temperature of cells was 60.3°C. Lethal cold temperatures ranged -16.1°C to -21.8°C.



Figure 67. *Sphagnum subsecundum*, a species that demonstrates both low and high temperature tolerance. Photo by Michael Lüth, with permission.

But temperature seems to have less detrimental effect on photosynthesis in bryophytes than we might expect from its role in other processes and organisms. While bryophytes have little ability to control temperature physiologically, they do have the ability to respond through

alteration of color that may be induced by day length, light intensity, or temperature itself. Could it be that the red color of the antheridial splash cups of *Polytrichum piliferum* (Figure 68) keeps the sperm warm on cool days in spring?

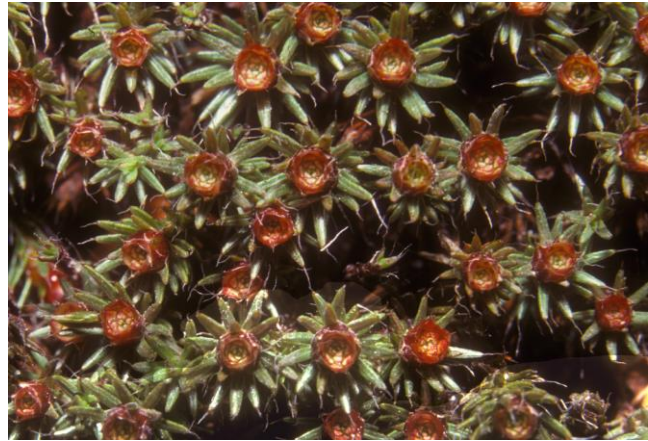


Figure 68. Antheridial splash cups of *Polytrichum piliferum*. Photo by Janice Glime.

Photosynthetic levels in some Arctic mosses seem to be similar over a wide temperature range. Vilde (1988) interpreted the mosses of the Arctic to be well adapted to their temperature regime. He found that photosynthesis has little temperature limitation and even high light intensity has little effect on these Arctic mosses. Uchida *et al.* (2002) found that the net photosynthetic rate in *Sanionia uncinata* in the high Arctic of Svalbard, Norway, was nearly constant at near-saturating light levels across the range of 7 to 23°C, but these same plants exhibited the extraordinarily high Q<sub>10</sub> of 3.0 for respiration in that range. This means that the gross photosynthesis must likewise have experienced a large increase with temperature in that range, with respiration using an increasing differential of that newly fixed carbon.

Temperature can have a threshold effect on bryophyte productivity. Asada *et al.* (2003) found that *Sphagnum* (Figure 7-Figure 12) species in a coastal British Columbia, Canada, peatland had lower temperature thresholds than did *Pleurozium schreberi* (Figure 25, Figure 65) and *Racomitrium lanuginosum* (Figure 69). Winter growth was important in this community, most likely because of greater availability of water; growth was more strongly correlated with precipitation than with temperature.



Figure 69. *Racomitrium lanuginosum*. Photo by Michael Lüth, with permission.



Kallio and Heinonen (1973) found that *Racomitrium lanuginosum* (Figure 69) could photosynthesize at  $-10^{\circ}\text{C}$  (compensation point) and that it returned to 60% of its normal photosynthetic rate within three hours after storage at  $-30^{\circ}\text{C}$ . Its optimum was at  $5^{\circ}\text{C}$ . They interpreted this moss to be pre-adapted to the wide range of temperatures in which it exists, lacking any clear physiological races with respect to temperature response.

Bryophytes acclimate to temperature, altering their optimum temperature for photosynthesis. This is likely to be accompanied by a shift in the light saturation level. However, the respiration rate does not necessarily acclimate at the same time. Both lowland and highland *Dicranum fuscescens* (Figure 70) showed photosynthetic acclimation to higher temperatures of mid summer, with highland plants having maximum rates of  $2.1 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$  and lowland plants having only  $0.74 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$  (Hicklenton & Oechel 1976). The optimum temperature shift can occur in as little as 48 hours in this species. The light saturation levels increased from spring to midsummer, then lowered again toward autumn. Dark respiration, however, did not acclimate.



Figure 70. *Dicranum fuscescens*, a species that acclimates to the higher temperatures of summer. Photo by Michael Lüth, with permission.

But even within the normal range of temperatures, bryophytes perform poorly at higher temperatures that favor most tracheophytes, as shown by the rapid drop in growth rate of the temperate pleurocarpous moss *Brachythecium rutabulum* (Figure 37) at temperatures above  $15^{\circ}\text{C}$  (Furness & Grime 1982). On the other hand, at only  $5^{\circ}\text{C}$  their growth is still 40% of their maximum rate at  $\sim 19^{\circ}\text{C}$ . This moss achieved a growth rate exceeding the maximum reported for seedlings of ten tracheophytes. Furness and Grime show the strong seasonal effects of temperature that help to explain some of the phenology of bryophytes. These results are consistent with its peaks of growth in spring and autumn, allowing it to compete with its tracheophyte neighbors in the British tall herb communities where they grow.

Frahm (1990) determined that high temperatures in tropical lowlands result in high respiration rates. Consequently, at temperatures above  $25^{\circ}\text{C}$ , net assimilation drops sharply. It is that high respiratory loss that limits much of bryophyte distribution in the tropics.

In the New Zealand species *Sphagnum cristatum* (Figure 24) and *S. australe* (Figure 52), the optimum temperatures for photosynthesis are 20 to  $25^{\circ}\text{C}$  (Maseyk *et al.* 1999). Liu *et al.* (2001a) found that *Plagiommium*

*acutum* (Figure 23) and *P. maximoviczii* (Figure 48) could maintain net photosynthetic gain for 10-30 minutes from  $-15^{\circ}\text{C}$  to  $45^{\circ}\text{C}$ . Despite their cold climate, fourteen bryophytes in the Antarctic have a temperature optimum for gross photosynthesis of  $10-20^{\circ}\text{C}$  and of  $0-20^{\circ}\text{C}$  for net photosynthesis (Davey & Rothery 1997). With the relatively high Antarctic light intensity, these bryophytes are usually temperature limited during the growing season.

Like the experiments on *Fontinalis duriaei* (Figure 71) of Glime and Acton (1979), Dilks and Proctor found that prolonged exposure to high temperatures caused a drop in productivity (Figure 72), thus demonstrating that duration of an experiment would influence the determined optimum temperature. While these curves may indicate the general trend of the response, we must exercise caution because the higher than atmospheric level of  $\text{CO}_2$  used would most likely push the temperature optimum to a higher level.



Figure 71. *Fontinalis duriaei*, a species that experiences a drop in productivity after prolonged high temperatures. Photo by Michael Lüth, with permission.

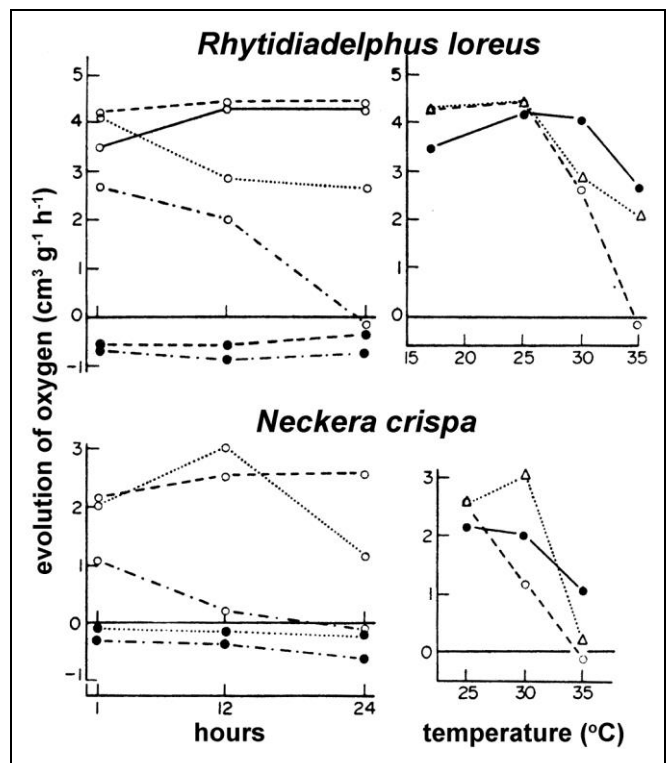


Figure 72. Effect on photosynthesis of prolonged exposure at various temperatures (—  $17^{\circ}\text{C}$ ; - -  $25^{\circ}\text{C}$ ; ....  $30^{\circ}\text{C}$ ; -.-  $35^{\circ}\text{C}$ ) and responses for net assimilation after 1 hour (●), 12 hours (Δ), and 24 hours (○). Redrawn from Dilks & Proctor 1975.



Rastorfer and Higginbotham (1968) demonstrated an increase in net photosynthesis of *Bryum sandbergii* in the range of 4-24°C, with a drop at 34°C. Dilks and Proctor (1975) compared twenty-three mosses and five liverworts at temperatures varying 5-45°C. These bryophytes typically exhibited fourth order polynomial curves that rose to an optimum, then dropped abruptly (Figure 73). However, not all species showed such a sudden drop and some exhibited a broad optimum, as seen in Figure 74. It is interesting that the more Arctic *Racomitrium lanuginosum* (Figure 69) exhibits the opposite curve shape – a sharp rise with temperature to its optimum at 5°C, and a slow decline above the optimum (Kallio & Heinonen 1973; Kallio & Kärenlampi 1975). *Pleurozium schreberi* (Figure 25, Figure 65) seems to exhibit a nearly bell-shaped curve with temperature, exhibiting an optimum at 10-15°C (Kallio & Kärenlampi 1975).

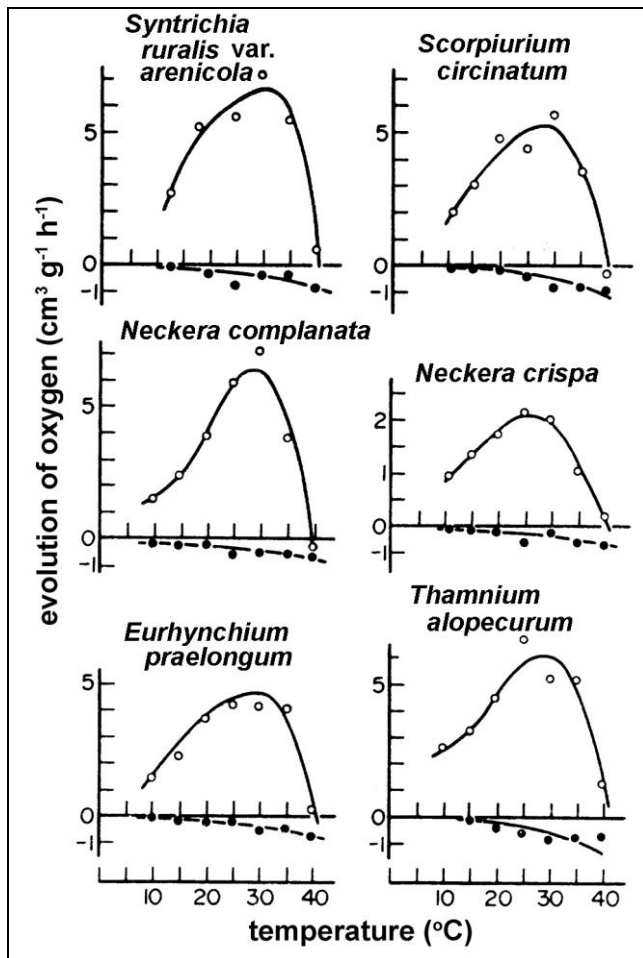


Figure 73. Photosynthesis at various temperatures. O = net assimilation; • = respiration. These responses are modelled with a fourth order curve. Redrawn from Dilks & Proctor 1975.

In the harsh conditions of the Antarctic, we can find some novel responses to temperature and light intensity. The ubiquitous moss *Bryum argenteum* (Figure 75) had a strong dark respiration response to temperature, causing significant changes in CO<sub>2</sub> exchange rates (Green *et al.* 1998). This species had a strong linear correlation between gross photosynthesis and electron-transport rate in PS II. Green and coworkers suggested that this deviation from the curvilinear relationship in tracheophytes might result from

some sort of suppression of dark respiration in the light. In fact, it seems that both bryophytes and C<sub>3</sub> tracheophytes experience photorespiration in the light. Nevertheless, the relationship appears to be different in the bryophytes.

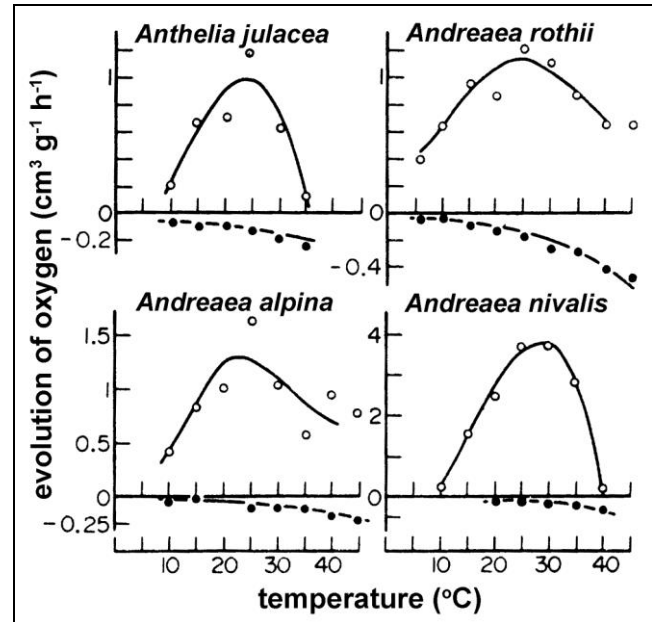


Figure 74. Photosynthesis at various temperatures for several mosses with a northern range. O = net assimilation; • = respiration. These responses are modelled with a fourth order curve but lack the sudden drop seen in Figure 73. Redrawn from Dilks & Proctor 1975.



Figure 75. *Bryum argenteum*, a species with a strong respiratory response to rising temperatures. Photo by Michael Lüth, with permission.

### Compensation Point

In studying 27 temperate bryophytes, Dilks and Proctor (1975) found the high temperature compensation point to be about 35-40°C. However, temperature compensation points are affected by both light intensity and CO<sub>2</sub> concentration and vice versa (Rastorfer 1971).

### Acclimation

**Acclimation** is a physiological change that adjusts to new conditions. It differs from adaptation in that the ability to change is programmed in the genetic code and the changes are temporary and non-heritable. For example, low temperatures can slow down the photosynthetic



apparatus, but in some habitats high light intensities may still cause high excitation of the photosynthetic apparatus. There is evidence [in *Leucodon sciurioides* (Figure 76)] that low temperatures may induce non-radiative dissipation of the absorbed light energy (Deltoro *et al.* 1999). This dissipation is necessary to protect the photosynthetic apparatus from excess excited electrons. This ability to dissipate energy and recover photosynthetically almost immediately upon return to temperatures above freezing permits this bryophyte to survive high light intensity at considerably lower temperature limits. The moss has become acclimated to the new temperature. This moss is one of many examples of preadaptation observed in mosses. This Mediterranean moss is capable of surviving light and temperature conditions that might be encountered in the Antarctic.



Figure 76. *Leucodon sciurioides*, an epiphyte, showing dry branches to the left and wet ones in the middle. Photo by Michael Lüth, with permission.

Even changes in  $\text{CO}_2$  concentrations can elicit acclimation in bryophytes. *Riccia fluitans* (Figure 77) lives part of its life floating on lakes and ponds. But some of these plants end up stranded on soil out of water. This environment is much higher in both light and  $\text{CO}_2$  than the floating environment from which they came. The relative growth rate under low light and low  $\text{CO}_2$  was  $0.011 \text{ day}^{-1}$ , whereas under high light intensity and high  $\text{CO}_2$  it was  $0.138 \text{ day}^{-1}$  (Andersen & Pedersen 2002). Interestingly, maximum photosynthesis decreased with increasing light intensities, but it increased with increasing  $\text{CO}_2$ . The  $\text{CO}_2$  compensation point was very low at high light and low  $\text{CO}_2$  levels, increasing at low light and high  $\text{CO}_2$  levels. These shifts in compensation point are an advantage for plants that live in dense mats in the water with low  $\text{CO}_2$  availability and high light intensity at the surface and greater  $\text{CO}_2$  and lower light intensity on the lower side of the floating mat.



Figure 77. *Riccia fluitans*, a species in which photosynthetic rate decreases in high light. Photo by Jan-Peter Frahm, with permission.

Glime and Acton (1979) used mosses conditioned for three weeks to a range of temperatures in the lab to demonstrate the effect of temperature on the photosynthesis of *Fontinalis duriaei* (Figure 71). These experiments indicated that the prior history of the moss affected its productivity at a given temperature. Maximum growth occurred in spring and fall and peak assimilation occurred at 5400 lux at  $10^\circ\text{C}$ .

Fornwall and Glime (1982) approached the same seasonal question by using field-acclimated plants and showed that *Fontinalis duriaei* (Figure 71) altered its maximum temperature for photosynthesis seasonally. When mosses were brought from the field and their photosynthesis measured in the range of  $0.5\text{--}40^\circ\text{C}$ , optimal temperatures shifted from  $10^\circ\text{C}$  in January to  $35^\circ\text{C}$  in August. However, these were short-term measurements of photosynthesis with one hour of acclimation to the respirometer flask and two hours of measurement time. Other experiments with growth at these temperatures over a 15-week period showed that the mosses could only sustain this high level of productivity for a short time and that in fact, temperatures above  $20^\circ\text{C}$  caused the mosses to cease growth in the lab (Glime 1982, 1987a, b, c). A more thorough discussion of temperature acclimation is in Chapter 10-1.

The color of these mosses changed with the seasons as well, with the most deep green color in March and April and a brown color in September (Fornwall & Glime 1982). The puzzling result of this study is that not only did mosses from a stream with wide seasonal fluctuations show this acclimation, but those mosses that resided in a stream that maintained a summer temperature of  $8.5^\circ\text{C}$  likewise shifted their summer optimum temperature to  $35^\circ\text{C}$  in the lab photosynthetic experiments. This suggests that the optimum may not result from acclimating to temperature but that it instead may be stimulated by the lengthening photoperiod or other environmental parameter associated with the seasons.

One might expect temperature acclimation in more northern regions. Oechel *et al.* (1975) demonstrated that subarctic populations of *Dicranum fuscescens* (Figure 70) exhibited a high temperature acclimation (Figure 78). Acclimation to warm temperatures caused a higher temperature optimum (similar to mean field temperatures,



ranging 5-15°C), higher maximum net photosynthetic rate, and a lower photosynthetic max at 0°C.

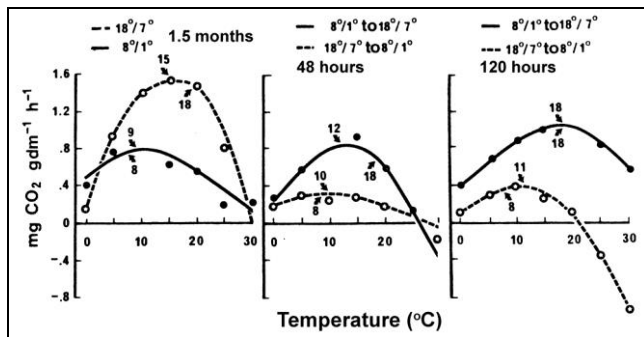


Figure 78. Acclimation responses of net photosynthesis to temperature in *Dicranum fuscescens* (Figure 70) at Schefferville, Quebec (55°N) after cultivation at warm (18°/7°C) and cool (8°/1°C) temperatures for 1.5 months. Modified from Oechel *et al.* 1975.

*Dicranum fuscescens* (Figure 70) in subarctic Canada raised its temperature optimum for photosynthesis from 0-10°C in the beginning of June to 10-20°C by 7 July, with net productivity dropping drastically by 29 July (Figure 79), but its dark respiration rates showed no evidence of acclimation (Hicklenton & Oechel 1976). The tissue temperatures fluctuated between a low of 3°C and a high of 26°C during that period. The remarkable drop in productivity by the end of July suggests that the moss could not sustain the high temperature respiratory cost and eventually lost net gain in productivity. At the other end, net productivity was negative at temperatures above 15°C on 5 June. On the other hand, Arctic populations had an optimum temperature that was generally higher than the mean maximum tissue temperature with optima ranging from 12-19°C (Oechel *et al.* 1975). This high optimum commonly accompanies tolerance for lower temperatures.

Even short-term adjustments to changing light levels are possible. The drought-tolerant *Syntrichia ruralis* (Figure 27) experienced increases in  $F_v/F_m$ , NPQ, and light-adapted PS II yield [ $\phi$  (PS II)] in sun plants transplanted to the shade, and concurrent decreases in shade plants transplanted to the sun (Hamerlynck *et al.* 2002). But these plants also seemed to have a memory of their old habitat; sun plants performed at a consistently lower level in the shade than did non-transplanted shade plants. Nonetheless, the ability to adjust its photosynthetic apparatus to changing light conditions permits this species to take advantage of a habitat in which the canopy above it changes, changing its exposure to sun vs shade.

One of the changes that occurs on a seasonal basis is a change in the light compensation point and light saturation point. In *Plagiommium acutum* (Figure 23) and *P. maximoviczii* (Figure 48) from the temperate zone in China, light compensation points switch from 20  $\mu\text{M m}^{-2} \text{s}^{-1}$  in the winter to 40  $\mu\text{M m}^{-2} \text{s}^{-1}$  in the summer (Liu *et al.* 2001a). Likewise, the light saturation ranges from 200  $\mu\text{M m}^{-2} \text{s}^{-1}$  in winter to 400  $\mu\text{M m}^{-2} \text{s}^{-1}$  in summer. The temperature optimum also ranges from a low of 20°C in winter to a high of 35°C in summer.

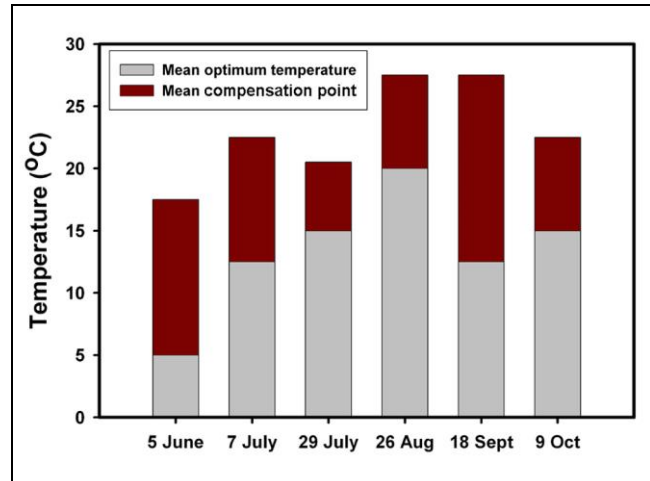


Figure 79. Mean optimum temperatures and upper temperature compensation points for *Dicranum fuscescens* (Figure 70) photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel 1976.

## Aquatic Differences

In streams, the availability of  $\text{CO}_2$  varies widely, dependent on the temperature, pH, and rate of flow. In standing water,  $\text{CO}_2$  can be even more limiting as temperatures rise and the  $\text{CO}_2$  goes out of solution and is lost into the atmosphere. These  $\text{CO}_2$  conditions are typically limiting to plant growth, including bryophytes (Madsen *et al.* 1993; Rice & Schuepp 1995). However, structural modifications of leaf spacing, leaf size, and exposure of photosynthetic cells among hyaline cells in *Sphagnum* (Figure 80-Figure 81) all contribute to making aquatic taxa less resistant to  $\text{CO}_2$  uptake than are non-aquatic taxa (Rice & Schuepp 1995).

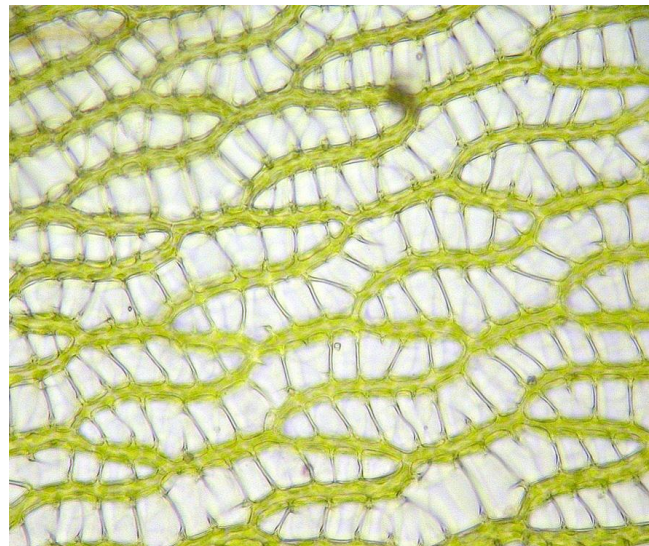


Figure 80. *Sphagnum novo-zelandicum* leaf cells showing hyaline cells and photosynthetic cells. Photo by David Tng, with permission.



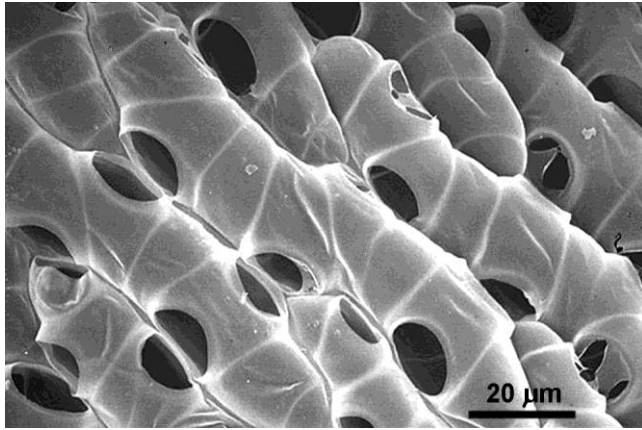


Figure 81. *Sphagnum* hyaline cells and pores. Photo from Botany Website, UBC, with permission.

In the aquatic environment, it is the deep water that has the highest CO<sub>2</sub> concentration (Maberly 1985), a product of microbial activity in the sediments. But deep water has the lowest light intensity. A testimony to the CO<sub>2</sub> limits imposed on aquatic mosses is their ability to grow well at extremely low light levels in the bottoms of lakes. These limits change seasonally, with productivity of *Fontinalis antipyretica* (Figure 30) in the North Bay of Esthwaite Water, England, being limited by light in November and by temperature in March. In August, despite microbial decomposition, intense competition for CO<sub>2</sub> from dense phytoplankton limits the moss productivity.

Another problem for aquatic bryophytes is that not only does the intensity of light decrease, but the spectral quality changes with depth. A reduction in water clarity due to increased load of dissolved organic carbon in Grane Langsoe caused a greater attenuation of blue light, relative to red light (Schwarz & Markager 1999). Photosynthesis is most active in red light, with its second peak in blue. However, red light has long wavelengths with low energy and thus is readily absorbed by water, making it diminish quickly with depth. The additional decrease in blue light, which has a short, high-energy light wave, means that the bryophytes are deprived of both of the most active wavelengths. The most abundant moss (70% of biomass) in these conditions was *Warnstorfia exannulata* (Figure 82), which exhibited its maximum absorption in the young parts that were most highly pigmented.



Figure 82. *Warnstorfia exannulata*, a species with relatively low productivity in deep water. Photo from Biopix, through Creative Commons.

Riis and Sand-Jensen (1997) showed that this species and *Sphagnum subsecundum* (Figure 67) grew faster in deep than in shallow water in a low-nutrient lake in Denmark. Their study supported the hypothesis that supersaturated CO<sub>2</sub> as well as low temperatures and higher nutrient concentrations on the bottom of the lake supported the faster growth, despite the lower light intensity. One advantage of the lower temperature is that gases such as CO<sub>2</sub> stay in solution more easily. *Sphagnum subsecundum* exhibited lower dark respiration (1.3-fold) and higher photosynthesis (3.3-fold) at 9.5 m than at 0.7 m conditions.

In lakes, light attenuates with depth, often creating a photosynthetic desert at the bottom. Bryophytes, already adapted to low light, typically grow to greater depths than their macrophytic tracheophyte counterparts. In the Karelia Republic of northwestern Russia, bryophytes dominate at depths in three acidified lakes (pH of water 5.3-5.9) (Ilyashuk 2002). One lake was dominated by a dense carpet of *Sphagnum denticulatum* (Figure 83) at a depth of 5.0-7.6 m, covering about 50% of the bottom. A second lake had only *Warnstorfia exannulata* s.l. (Figure 82) at 5.0-7.0 m, covering 20% of the bottom. The third had only *Fontinalis hypnoides* (Figure 84) at 4.5-5.5 m, covering 13% of the bottom. In these latter two lakes, the net annual production by the mosses was 32-41 g air-dry mass m<sup>-2</sup> yr<sup>-1</sup>. In the *Sphagnum*-dominated lake, however, the rate was much higher (157 g m<sup>-2</sup>).



Figure 83. *Sphagnum denticulatum*, a species with a high rate of annual production in deep water. Photo by Michael Lüth, with permission.



Figure 84. *Fontinalis hypnoides*, a species with relatively low productivity in deep water. Photo by Ivanov, with permission.



## Summary

Photosynthesis is limited by light intensity, temperature, CO<sub>2</sub> availability, and water availability. The compensation point is the level of any of these variables at which the CO<sub>2</sub> assimilation is equal to the CO<sub>2</sub> respired by the plant. These are influenced not only by the environment and seasons, but also by plant density and the plants themselves.

Limits are at both ends of the scale. There is a minimal level needed for successful net gain, but there are also upper limits beyond which the plants will lose energy. The saturation level is that level at which increase causes no further photosynthetic gain.

During the growing season, water is typically the limiting factor. However, some bryophytes are able to use water from fog and dew. Given enough water, CO<sub>2</sub> is often limiting. However, in some habitats, such as lake sediments, CO<sub>2</sub> emissions from bacteria and various invertebrates may elevate the CO<sub>2</sub> levels above ambient air CO<sub>2</sub>. And some bryophytes, especially *Sphagnum*, may use methane, converted to CO<sub>2</sub> by bacteria, to supply their CO<sub>2</sub>. Aquatic bryophytes may use cation exchange to lower the pH in their immediate vicinity, permitting the use of bicarbonate by shifting the equilibrium toward free CO<sub>2</sub>. Furthermore, it is possible that some may use external carbonic anhydrase to capture bicarbonate, but experiments to support this in bryophytes are lacking. Light may be limiting, but bryophytes seem to have the lowest light compensation point of any plant group. High light intensity can cause photodamage.

Net photosynthetic activity in many, perhaps most, bryophytes exhibits an abrupt drop above its optimum due to the loss of CO<sub>2</sub> through photorespiration.

Bryophytes acclimate to temperature, CO<sub>2</sub> level, and light intensity. This permits changes in the optimum, compensation point, and upper level limit or saturation point.

## Acknowledgments

I appreciate the help of Don Lueking and Heather Youngs, both of Michigan Technological University, in my understanding of *pK* as it might apply to bryophyte CO<sub>2</sub> uptake. Thank you to Weng Zhe for correcting my error.

## Literature Cited

- Adamson, E., Post, A., and Adamson, H. 1990. Photosynthesis in *Grimmia antarctica*, an endemic Antarctic bryophyte, is limited by carbon dioxide. *Curr. Res. Photosyn.* 4: 639-642.
- Allen, E. D. and Spence, D. H. N. 1981. The differential ability of aquatic plants to utilize the inorganic C supply in freshwater. *New Phytol.* 87: 269-283.
- Alpert, P. and Oechel, W. C. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. *Amer. J. Bot.* 74: 1787-1796.
- Andersen, T. and Pedersen, O. 2002. Interactions between light and CO<sub>2</sub> enhance the growth of *Riccia fluitans*. *Hydrobiologia* 477: 163-170.
- Asada, T., Warner, B. G., and Banner, A. 2003. Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. *Bryologist* 106: 516-527.
- Backéus, I. 1988. Weather variables as predictors of *Sphagnum* growth on a bog. *Holarct. Ecol.* 11: 146-150.
- Bain, J. T. and Proctor, M. C. F. 1980. The requirement of aquatic bryophytes for free CO<sub>2</sub> as an inorganic carbon source: Some experimental evidence. *New Phytol.* 86: 393-400.
- Bakken, S. 1995. Effects of nitrogen supply and irradiance on growth and nitrogen status in the moss *Dicranum majus* from differently polluted areas. *J. Bryol.* 18: 707-721.
- Balagurova, N., Drozdov, S., and Grabovik, S. 1996. Cold and heat resistance of five species of *Sphagnum*. *Ann. Bot. Fennici* 33: 33-37.
- Bartosková, H., Komenda, J., and Naus, J. 1999. Functional changes of Photosystem II in the moss *Rhizomnium punctatum* (Hedw.) induced by different rates of dark desiccation. *J. Plant Physiol.* 154: 597-604.
- Bazzaz, F. A., Paolillo, D. J. Jr., and Jagels, R. H. 1970. Photosynthesis and respiration of forest and alpine populations of *Polytrichum juniperinum*. *Bryologist* 73: 579-585.
- Betts, A. K., Goulden, M. L., and Wofsy, S. C. 1999. Controls on evaporation in a boreal spruce forest. *J. Climate* 12: 1601-1618.
- Blackman, F. F. and Smith, A. M. 1910-1911. Experimental researches on vegetable assimilation and respiration. IX. On assimilation in submerged water-plants, and its relation to the concentration of carbon dioxide and other factors. *Proc. Roy. Soc. London Sec. B Biol. Sci.* 83: 389-412.
- Burr, G. O. 1941. Photosynthesis of algae and other aquatic plants. In: Needham, J. G. *Symposium on Hydrobiology*. Univ. Wisc. Press, Madison. pp. 163-181.
- Collins, N. J. 1976. The growth of mosses in two contrasting communities in the maritime Antarctic: Measurement and prediction of net annual production. In: Llano, G. A. (ed.). *Adaptations within Antarctic Ecosystems*. *Proc. 3rd. Symp. on Antarctic Biology*, pp. 921-933.
- Csintalan, Z., Proctor, M. C. F., and Tuba, Z. 1999. Chlorophyll fluorescence during drying and rehydration in the mosses *Rhytidiadelphus loreus* (Hedw.) Warnst., *Anomodon viticulosus* (Hedw.) Hook. & Tayl. and *Grimmia pulvinata* (Hedw.) Sm. *Ann. Bot.* 84: 235-244.
- Csintalan, Z., Takács, Z., Proctor, M. C. F., Nagy, Z., and Tuba, Z. 2000. Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland. *Plant Ecol.* 151: 51-54.
- Cvetić, T., Sabovljević, A., Bogdanović, J., and Sabovljević, M. 2009. Effects of day length on photosynthetic pigments and antioxidative metabolism of in vitro cultured moss *Atrichum undulatum* (Hedw.) P. Beauv. (Bryophyta). *Bot. Serbica* 33(1): 83-88.
- Davey, M. C. 1997a. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. *Oecologia* 110: 25-31.
- Davey, M. C. 1997b. Effects of short-term dehydration and rehydration on photosynthesis and respiration by Antarctic bryophytes. *Environ. Exper. Bot.* 37: 187-198.
- Davey, M. C. and Ellis-Evans, J. C. 1996. The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. *J. Bryol.* 19: 235-242.



- Davey, M. C. and Rothery, P. 1997. Interspecific variation in respiratory and photosynthetic parameters in Antarctic bryophytes. *New Phytol.* 137: 231-240.
- Deltoro, V. I., Calatayud, A., Gimeno, C., and Barreno, E. 1998. Water relations, chlorophyll fluorescence, and membrane permeability during desiccation in bryophytes from xeric, mesic, and hydric environments. *Can. J. Bot.* 76: 1923-1929.
- Deltoro, V. I., Calatayud, A., Morales, F., Abadia, A., and Barreno, E. 1999. Changes in net photosynthesis, chlorophyll fluorescence and xanthophyll cycle interconversions during freeze-thaw cycles in the Mediterranean moss *Leucodon sciurioides*. *Oecologia* 120: 499-505.
- Delucia, E. H., Turnbull, M. H., Walcroft, A. S., Griffin, K. L., Tissue, D. T., Glenny, 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. and Proctor, M. C. F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. *J. Bryol.* 8: 317-336.
- Egle, K. and Schenk, W. 1953. Der Einfluss der Temperatur auf die Lage des CO<sub>2</sub>-Kompensationspunktes. *Planta* 43: 83-97.
- Fornwall, M. D. and Glime, J. M. 1982. Cold and warm-adapted phases in *Fontinalis duriaei* Schimp. as evidenced by net assimilatory and respiratory responses to temperature. *Aquat. Bot.* 13: 165-177.
- Frahm, J.-P. 1987. Which factors control the growth of epiphytic bryophytes in tropical rainforests? *Symp. Biol. Hung.* 35: 639-648.
- Frahm, J.-P. 1990. Bryophyte phytomass in tropical ecosystems. *J. Linn. Soc. Bot.* 104: 23-33.
- Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes. I. An investigation of *Brachythecium rutabulum*. *J. Ecol.* 70: 513-523.
- Gabriel, R. and Bates, J. W. 2003. Responses of photosynthesis to irradiance in bryophytes of the Azores laurel forest. *J. Bryol.* 25: 101-105.
- Gerdol, R., Bonora, A., Marchesini, R., Gualandri, R., and Pancaldi, S. 1998. Growth response of *Sphagnum capillifolium* to nighttime temperature and nutrient level: mechanisms and implications for global change. *Arct. Alp. Res.* 30: 388-395.
- Glime, J. M. 1982. Response of *Fontinalis hypnoides* to seasonal temperature variations. *J. Hattori Bot. Lab.* 53: 181-193.
- Glime, J. M. 1987a. Growth model for *Fontinalis duriaei* based on temperature and flow conditions. *J. Hattori Bot. Lab.* 62: 101-109.
- Glime, J. M. 1987b. Phytogeographic implications of a *Fontinalis* (Bryopsida) growth model based on temperature and flow conditions for six species. *Mem. N. Y. Bot. Gard.* 45: 154-170.
- Glime, J. M. 1987c. Temperature optima of *Fontinalis novae-angliae*: Implications for its distribution. *Symp. Biol. Hung.* 35: 569-576.
- Glime, J. M. and Acton, D. W. 1979. Temperature effects on assimilation and respiration in the *Fontinalis duriaei* – periphyton association. *Bryologist* 82: 382-392.
- 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.
- Grace, J. 1970. The Growth-Physiology of Moorland Plants in Relation to their Aerial Environment. Ph. D. Thesis, University of Sheffield.
- 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 CO<sub>2</sub> gas exchange from field measurements on a moss and lichen. *Planta* 206: 611-618.
- Hamerlynck, E. P., Csintalan, Z., Nagy, Z., Tuba, Z., Goodin, D., and Henebry, G. M. 2002. Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss *Tortula ruralis*. *Oecologia* 131: 498-505.
- Hanslin, H. M., Bakken, S., and Pedersen, B. 2001. The impact of watering regime and ambient relative humidity on the effect of density on growth in two boreal forest mosses, *Dicranum majus* and *Rhytidiadelphus loreus*. *J. Bryol.* 23: 43-54.
- Hanson, D., Andrews, T. J., and Badger, M. R. 2002. Variability of the pyrenoid-based CO<sub>2</sub> concentrating mechanism in hornworts (Anthocerotophyta). *Funct. Plant Biol.* 29: 407-416.
- Haraguchi, A. 1996. Effect of pH on photosynthesis of five *Sphagnum* species in mires in Ochiishi, northern Japan. *Wetlands* 16(1): 10-14.
- Haraguchi, A., Hasegawa, T., Iyobe, T., and Nishijima, H. 2003. The pH dependence of photosynthesis and elongation of *Sphagnum squarrosum* and *S. girgensohnii* in the *Picea glehnii* mire forest in Cape Ochiishi, north-eastern Japan. *Aquat. Ecol.* 37: 101-104.
- Harder, R. 1923. Bemerkungen über die variations-breite des Kompensationspunktes beim Gaswechsel der Pflanzen. *Ber. Deutsch. Bot. Gesell.* 41: 194-198.
- Harley, P. C., Tenhunen, J. D., Murray, K. J., and Beyers, J. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* 79: 251-259.
- Heber, U., Bilger, W., Bligny, R., and Lange, O. L. 2000. Phototolerance of lichens, mosses and higher plants in an alpine environment: Analysis of photoreactions. *Planta* 211: 770-780.
- Heijden, E. van der, Verbeek, S. K., and Kuiper, P. J. C. 2000. Elevated atmospheric CO<sub>2</sub> and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. *Global Change Biol.* 6: 201-212.
- Hicklenton, P. R. and Oechel, W. C. 1976. Physiological aspects of the ecology of *Dicranum fuscescens* in the subarctic. I. Acclimation and acclimation potential of CO<sub>2</sub> exchange in relation to habitat, light, and temperature. *Can. J. Bot.* 54: 1104-1119.
- Hobson, J. A., Hanson, C. E., and Holeton, C. 2001. An ecological basis for extracellular carbonic anhydrase in marine unicellular algae. *J. Phycol.* 37: 717-723.
- Ilyashuk, B. P. 2002. Growth and production of aquatic mosses in acidified lakes of Karelia Republic, Russia. *Water Air Soil Pollut.* 135: 285-290.
- 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. Roy. Soc. London Sec. B Biol. Sci.* 103: 1-42.
- Janssens, I. A., Kowalski, A. S., and Ceulemans, R. 2001. Forest floor CO<sub>2</sub> fluxes estimated by eddy covariance and chamber-based model. *Agric. Forest Meteorol.* 106(1): 61-69.
- Jauhiainen, J. and Silvola, J. 1999. Photosynthesis of *Sphagnum fuscum* at long-term raised CO<sub>2</sub> concentrations. *Ann. Bot. Fenn.* 36: 11-19.



- Jauhiainen, J., Silvola, J., and Vasander, H. 1998. Effects of increased carbon dioxide and nitrogen supply on mosses. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). *Bryology for the Twenty-first Century*. Maney Publishing and the British Bryological Society, UK, pp. 343-360.
- Kallio, P. and Heinonen, S. 1973. Ecology of *Racomitrium lanuginosum* (Hedw.) Brid. Rep. Kevo Subarctic Res. Stat. 10: 43-54.
- Kallio, P. and Kärenlampi, L. 1975. Photosynthesis in mosses and lichens. In: Cooper, J. P. *Photosynthesis and Productivity in Different Environments*, Chapt. 17. IBP, Cambridge University Press, Cambridge, pp. 393-423.
- Kallio, P. and Valanne, N. 1975. On the effect of continuous light on photosynthesis in mosses. *Ecol. Stud.* 16: 149-162.
- Krupa, J. 1978. Photosynthesis rate in moss leaves of various anatomical structure. *Acta Soc. Bot. Polon.* 47: 391-402.
- Li, J., Liu, Y., Cao, T., Wu, Y., and Shi, J. 1999. A comparative study on ecophysiological characteristics of the two overwintering host mosses of gallaphids. *Nova Hedw.* 68: 233-240.
- Liu, Y., Chen, J., Zhang, L., and Cao, T. 2001a. [Photosynthetic characteristics of two *Plagiomnium* mosses in summer and winter.]. Ying Yong Sheng Tai Xue Bao = the Journal of Applied Ecology / Zhongguo Sheng Tai Xue Xue Hui, Zhongguo Ke Xue Yuan Shenyang Ying Yong Sheng Tai Yan Jiu Suo Zhu Ban 12(1): 39-42.
- Liu, Y.-D., Zhu, J.-Y., Chen, J., and Tong, C. 2001b. Relationships of water content to photosynthesis, respiration and water potential in three species of mosses. *J. Wuhan. Bot. Res.* 19(2): 135-142.
- Longton, R. E. 1994. Genetic differentiation within the moss species *Polytrichum alpestre* Hoppe. *J. Hattori Bot. Lab.* 75: 1-13.
- Maberly, S. C. 1985. Photosynthesis by *Fontinalis antipyretica*. 1. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytol.* 100: 127-140.
- Mache, R. and Loiseaux, R. 1973. Light saturation of growth and photosynthesis of the shade plant *Marchantia polymorpha*. *J. Cell Sci.* 12: 391-401.
- 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.
- Maseyk, K. S., Green, T. G. A., and Klinac, D. 1999. Photosynthetic responses of New Zealand *Sphagnum* species. *N. Z. J. Bot.* 37: 155-165.
- McCall, K. K. and Martin, C. E. 1991. Chlorophyll concentrations and photosynthesis in three forest understory mosses in northeastern Kansas. *Bryologist* 94: 25-29.
- McKay, E. 1935. Photosynthesis in *Grimmia montana*. *Plant Physiol.* 10: 803-809.
- Miyata, I. and Hosokawa, T. 1961. Seasonal variations of the photosynthetic efficiency and chlorophyll content of epiphytic mosses. *Ecology* 42: 766-775.
- Murray, K. J., Harley, P. C., Beyers, J., Walz, H., and Tenhunen, J. D. 1989. Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* 79: 244-250.
- Murray, K. J., Tenhunen, J. D., and Nowak, R. S. 1993. Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. *Oecologia* 96: 200-207.
- Oechel, W. C., Hickleton, P., Sveinbjörnsson, B., Miller, P. C., and Stoner, W. 1975. Temperature acclimation of photosynthesis in *D. fuscescens* growing in situ in the Arctic and subarctic. In: *Proceedings of the Circumpolar Conference on Northern Ecology*, National Research Council of Canada in Association with Canadian National Committee/Scientific Committee on Problems of the Environment (CNC/scope), pp. I-131 - I-143.
- Proctor, M. C. F. 1981. Physiological ecology of bryophytes. In: Schultze-Motel, W. (ed.). *Advances in Bryology* 1: 79-166.
- Proctor, M. C. 2002. Ecophysiological measurements on two pendulous forest mosses from Uganda, *Pilotrichella ampullacea* and *Floribundaria floribunda*. *J. Bryol.* 24: 223-232.
- Raghoebarsing, A. A., Smolders, A. J. P., Schmid, M. C., Rijpstra, W. I. C., Wolters-Arts, M., Derksen, J., Jetten, M. S. M., Schouten, S., Damsté, J. S. S., Lamers, L. P. M., Roelofs, J. G. M., Camp, H. J. M. O. den, and Strous, M. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* 436: 1153-1156.
- Rajczy, M. 1982. Effect of the cave environment on some mosses. *Ann. Univ. Sci. Budapest. Rolando Eötvös Nom. Sec. Biol.* 20-21: 125-136.
- Rastorfer, J. R. 1970. Effect of light intensity and temperature on photosynthesis and respiration of two east Antarctic mosses, *Bryum argenteum* and *Bryum antarcticum*. *Bryologist* 73: 544-556.
- Rastorfer, J. R. 1971. Effects of temperature on carbon dioxide compensation points of the moss *Drepanocladus uncinatus*. *Antarct. J. U. S.* 6(5): 162-163.
- Rastorfer, J. R. and Higginbotham, N. 1968. Rates of photosynthesis and respiration of the moss *Bryum sandbergii* as influenced by light intensity and temperature. *Amer. J. Bot.* 55: 1225-1229.
- Raven, J. A. 1996. Into the voids: The distribution, function, development and maintenance of gas spaces in plants. *Ann. Bot.* 78: 137-142.
- Rice, S. K. and Schuepp, P. H. 1995. On the ecological and evolutionary significance of branch and leaf morphology in aquatic *Sphagnum* (Sphagnaceae). *Amer. J. Bot.* 82: 833-846.
- Rice, S. K., Aclander, L., and Hanson, D. T. 2008. Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in *Sphagnum* mosses (Sphagnaceae). *Amer. J. Bot.* 95: 1366-1374.
- Richardson, D. H. S. 1981. Photosynthesis, temperature and nutrients. Chapter 3. In: *The Biology of Mosses*. John Wiley & Sons, Inc., N.Y. & Toronto, pp. 30-47.
- 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.
- Rincón, E. 1993. Growth responses of six bryophyte species to different light intensities. *Can. J. Bot.* 71: 661-665.
- Rintamäki, E. 1989. Ribulose-1,5-bisphosphate carboxylase-oxygenase. Characterization of the enzyme with reference to the CO<sub>2</sub> assimilation capacity in plants. Doctoral dissertation. Reports from the Department of Biology, University of Turku 20: 1-81.
- Rydin, H. and McDonald, A. J. S. 1985a. Tolerance of *Sphagnum* to water level. *J. Bryol.* 13: 571-578.
- Rydin, H. and McDonald, A. J. S. 1985b. Photosynthesis in *Sphagnum* at different water contents. *J. Bryol.* 13: 579-584.
- Sakai, N., Nakatsubo, T., Kanda, H., and Masuzawa, T. 2001. Carbon storage and photosynthetic capacity of the moss *Racomitrium barbuloides* Card. under various light conditions. *Hikobia* 13: 327-334.
- Sanford, G. R. 1979. Temperature related growth patterns in *Amblystegium riparium*. *Bryologist* 82: 525-532.



- Schipperges, 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.
- Schwarz, A.-M. and Markager, S. 1999. Light absorption and photosynthesis of a benthic moss community: Importance of spectral quality of light and implications of changing light attenuation in the water column. *Freshwat. Biol.* 4: 609-623.
- Silvola, J. 1985. CO<sub>2</sub> dependence of photosynthesis in certain forest and peat mosses and simulated photosynthesis at various actual and hypothetical CO<sub>2</sub> concentrations. *Lindbergia* 11: 86-93.
- Silvola, J. 1990. Combined effects of varying water content and CO<sub>2</sub> concentration on photosynthesis in *Sphagnum fuscum*. *Holarct. Ecol.* 13: 224-228.
- Silvola, J. 1991. Moisture dependence of CO<sub>2</sub> exchange and its recovery after drying in certain boreal forest and peat mosses. *Lindbergia* 17: 5-10.
- Silvola, J. and Aaltonen, H. 1984. Water content and photosynthesis in the peat mosses *Sphagnum fuscum* and *S. angustifolium*. *Ann. Bot. Fenn.* 21: 1-6.
- Smith, E. C. and Griffiths, H. 1996. A pyrenoid-based carbon-concentrating mechanism is present in terrestrial bryophytes of the class Anthocerotae. *Planta* 200: 203-212.
- Sonesson, M., Gehrke, C., and Tjus, M. 1992. CO<sub>2</sub> environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. *Oecologia* 92: 23-29.
- Swanson, R. V. and Flanagan, L. B. 2001. Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. *Agric. Forest Meteorol.* 108(3): 165-181.
- Titus, J. E., Wagner, D. J., and Stephens, M. D. 1983. Contrasting water relations of photosynthesis for two *Sphagnum* mosses. *Ecology* 64: 1109-1115.
- Tobias, M. and Niinemets, U. 2010. Acclimation of photosynthetic characteristics of the moss *Pleurozium schreberi* to among-habitat and within-canopy light gradients. *Plant Biol.* 12: 743-754.
- Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H. 2002. Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard. *Arct. Antarct. Alp. Res.* 34: 287-292.
- Vashistha, B. D. and Chopra, R. N. 1989. Effects of some physical factors on vegetative growth and archegonial formation in the female clone of *Riccia frostii* Aust. *Phytomorphology* 39: 141-148.
- Vilde, R. 1988. On the adaption of the photosynthesis of the Arctic mosses to their habitats. *Proc. Acad. Sci. Estonian SSR, Biol.* 37: 44-55.
- 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.
- Waite, M. and Sack, L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytol.* 185: 156-172.
- Wetzel, R. G., Brammer, E. S., Lindström, K., and Forsberg, C. 1985. Photosynthesis of submersed macrophytes in acidified lakes: II. Carbon limitation and utilization of benthic CO<sub>2</sub> sources. *Aquat. Bot.* 22: 107-120.
- Zotz, G., Budel, B., Meyer, A., Zellner H., and Lange, O. L. 1997. Water relations and CO<sub>2</sub> exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.
- Zotz, G., Schweikert, A., Jetz, W., and Westerman, H. 2000. Water relations and carbon gain are closely related to cushion size in the moss *Grimmia pulvinata*. *New Phytol.* 148: 59-67.

