CHAPTER 11-1

PHOTOSYNTHESIS: THE PROCESS

TABLE OF CONTENTS

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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_2 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_2 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 $^{14}CO_2$ loss in light compared to dark that he attributed to partial reassimilation of the $^{14}CO_2$ 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_3 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_2 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_2.

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_2 concentration has decreased. It would be interesting to see if the number of pores in thalli of the **Marchantiaceae** is affected by CO_2 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_2 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_2 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_2 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^2 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.

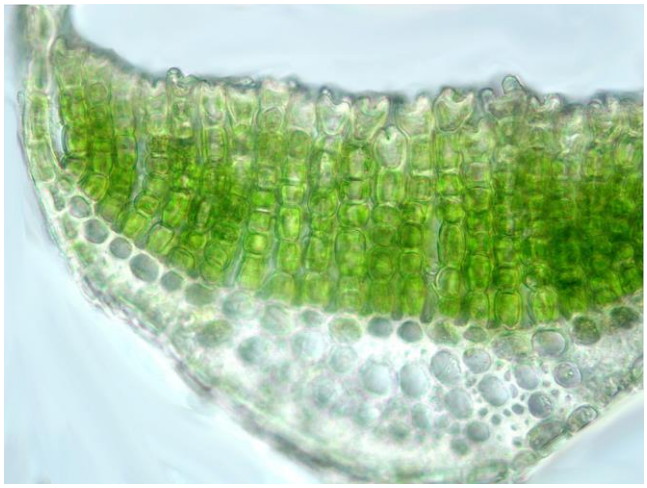

Figure 8. ***Polytrichum commune*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

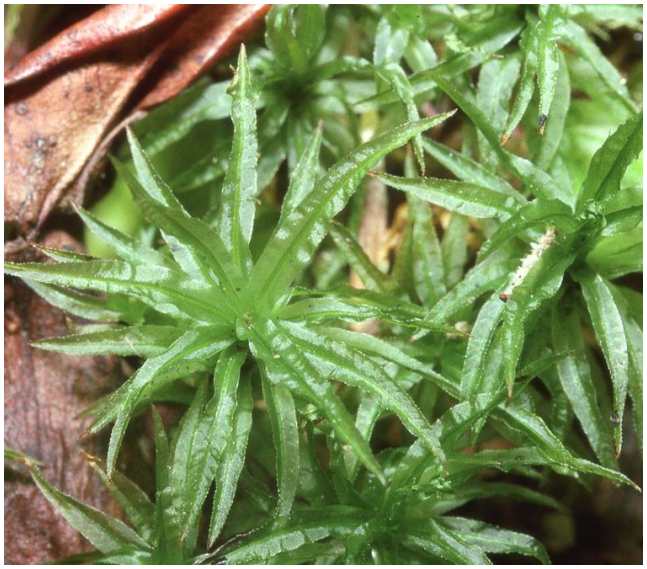

Figure 9. ***Atrichum undulatum***, a species with photosynthetic leaf lamellae. Photo by Janice Glime.

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

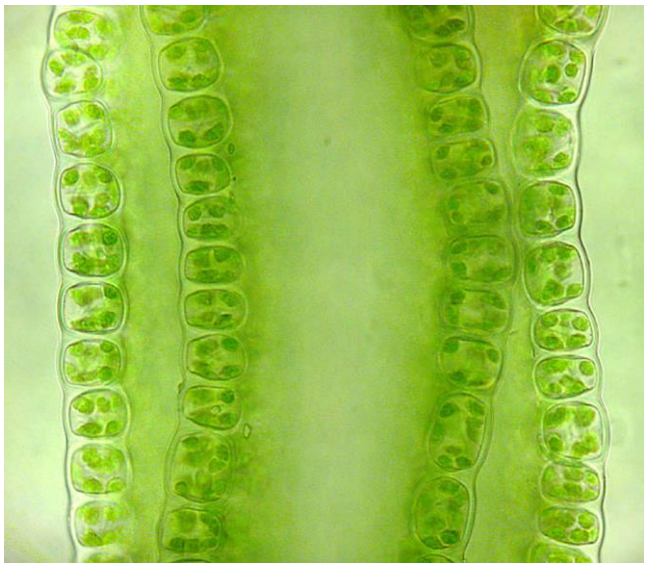

Figure 11. ***Atrichum undulatum*** leaf lamellae showing chloroplasts in the lamellae. Photo by Walter Obermayer, with permission.

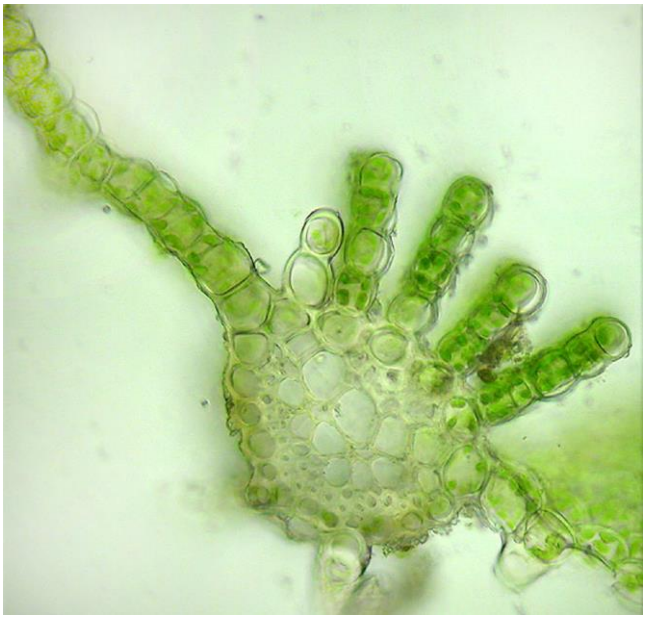

Figure 12. ***Atrichum undulatum*** leaf cs showing lamellae. Photo by Walter Obermayer, with permission.

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

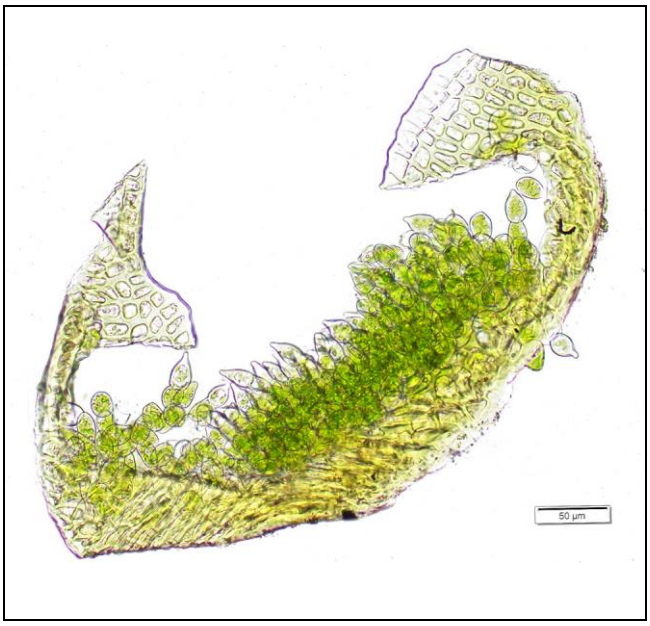

Figure 16. ***Aloina rigida*** leaf cs showing lamellae that add to its photosynthetic capability, and inrolled leaf margins that give this species its succulent look. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species of ***Polytrichum*** have an additional adaptation similar to that of ***Aloina 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.

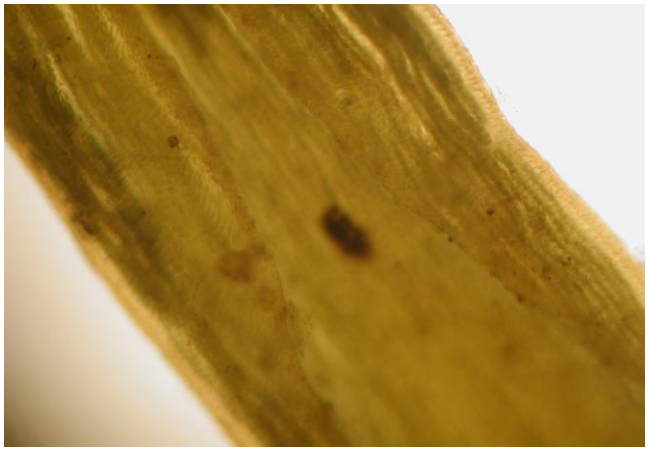

Figure 18. ***Polytrichum juniperinum*** leaf section showing tops of lamellae. Photo courtesy of John Hribljan.

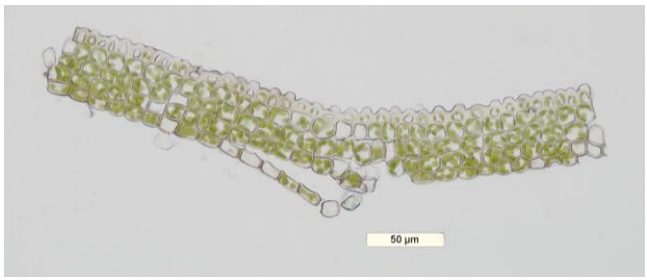

Figure 19. ***Polytrichum juniperinum*** lamella showing photosynthetic tissue. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

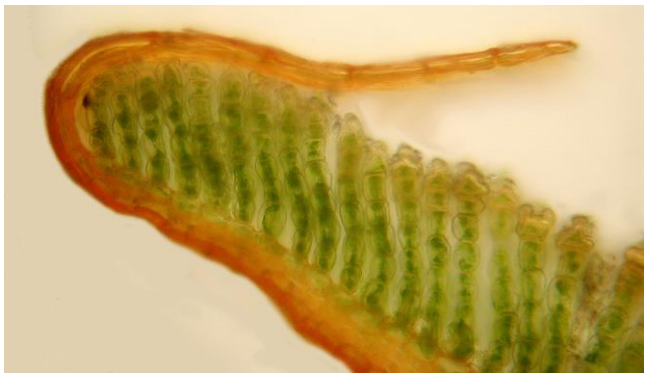

Figure 20. Leaf cross section of ***Polytrichum juniperinum*** showing leaf lamellae and rolled over leaf edge. Photo courtesy of John Hribljan.

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_2 concentration can also modify the size and shape of chloroplasts (Bockers *et al*. 1997). In ***Marchantia polymorpha*** (Figure 3-Figure 4), high CO_2 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_2 concentrations compared to the 0.4% concentrations. These changes did not imbue the cells with any greater photosynthetic capacity or efficiency. Furthermore, the CO_2 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_2 around ***Hylocomium splendens*** (Figure 21) plants growing on soil.

Figure 21. ***Hylocomium splendens***, a plant that grows in a relatively low CO_2 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.

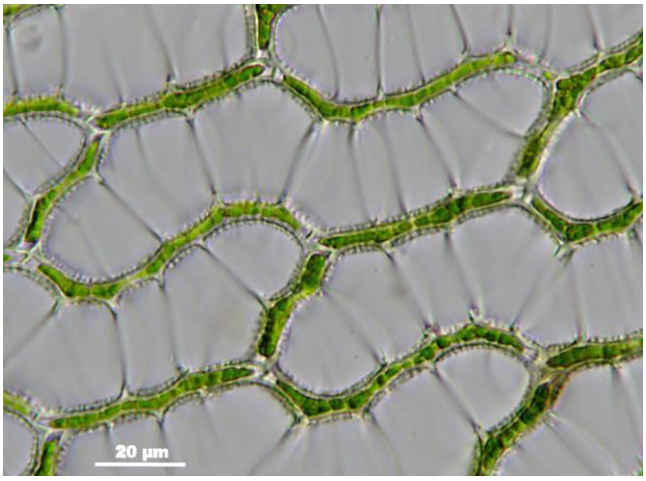

Figure 23. ***Sphagnum papillosum***, a hummock species, showing large hyaline leaf cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

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

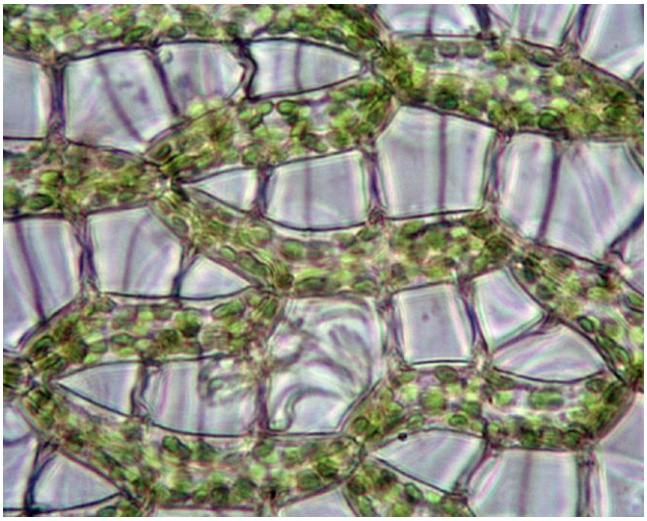

Figure 25. ***Sphagnum palustre***, an aquatic species, showing hyaline leaf cells that are reduced in size. Photo by Malcolm Storey through Creative Commons.

But obtaining **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 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 CO_2 uptake with increasing submersion.

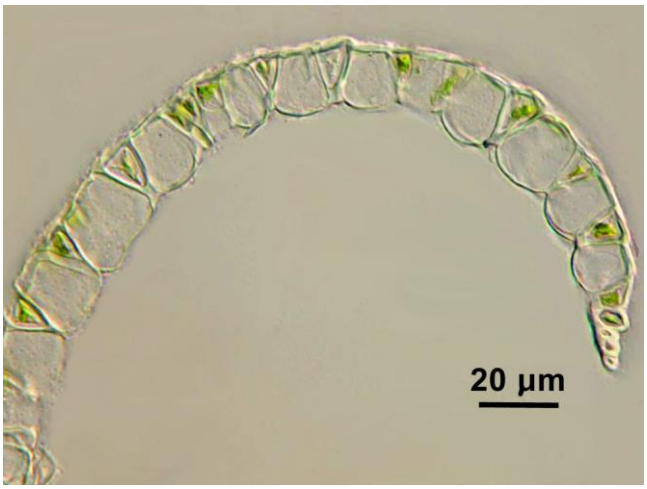

Figure 26. ***Sphagnum obtusum*** branch leaf cs showing photosynthetic cells that are exposed on the outer side of the leaf. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

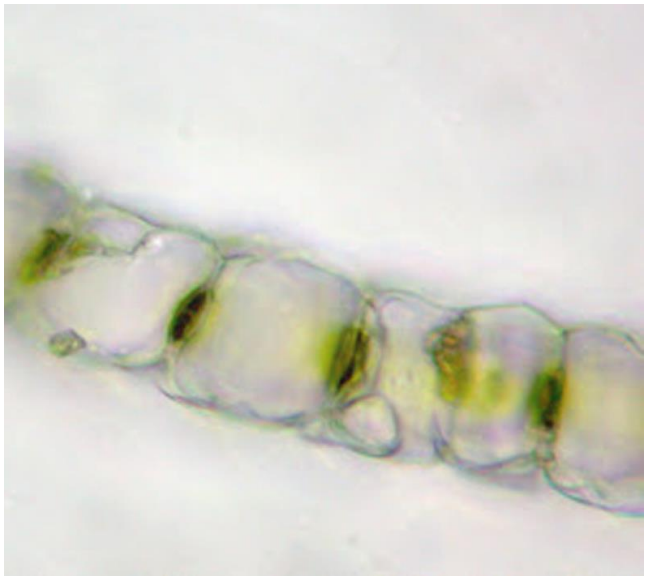

Figure 27. ***Sphagnum centrale*** leaf cross section showing photosynthetic cells completely surrounded by hyaline cells. This species lives on the forest floor and on logs. Photo by Jutta Kapfer, with permission.

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.

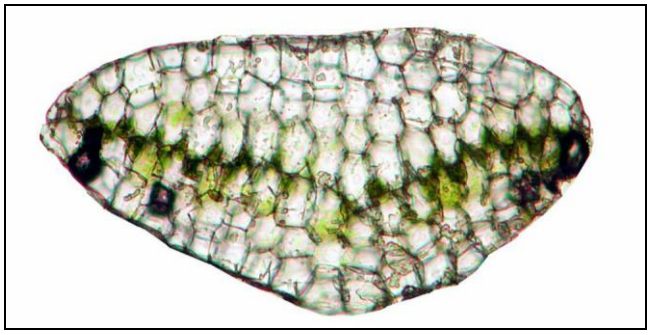

Figure 29. ***Octoblepharum albidum*** leaf cs showing a single layer of photosynthetic cells surrounded by hyaline cells. Photo by Michael Lüth, with permission.

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.

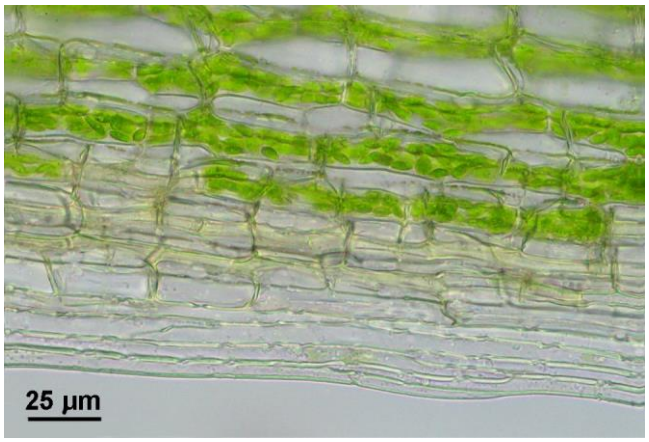

Figure 32. ***Leucobryum glaucum*** leaf section showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

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_2 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).

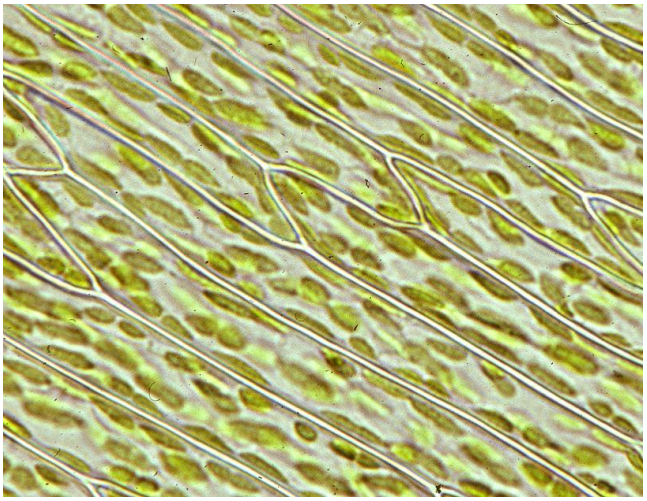

Figure 34. Cells of ***Fontinalis antipyretica*** showing chloroplasts in cells. Photo by Janice Glime.

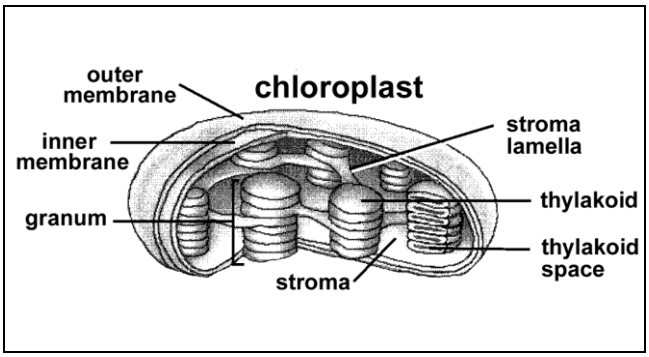

Figure 35. Structure of a single chloroplast. The chlorophyll molecules occur in the thylakoid membranes. Drawn by Janice Glime.

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_{20} 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_2 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_2 levels is as great as that of tracheophytes.

One factor to be considered in the photosynthetic rate of bryophytes is their photosynthetic enzyme, ribulose bis-phosphate 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.

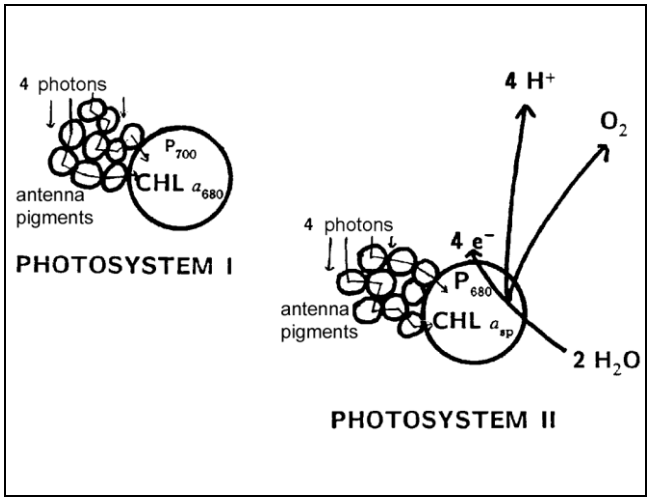

Figure 43. Antenna pigments such as carotene, xanthophyll, and chlorophyll *b* in Photosystem I and Photosystem II transfer light energy to chlorophyll *a* within a single thylakoid membrane. Excitation of electrons in chlorophyll *a* occurs in both photosystems. Modified by Janice Glime from Goodwin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

The most frequent of the antenna pigments in bryophytes include α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al*. 1972; Schmidt-Stohn 1977; Czeczuga 1980, 1985; Czeczuga *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 **auroxanthin** 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, Czeczuga (1985) found nineteen carotenoids. In addition to the seven named above, he found lycopene, lycoxanthin, α-cryptoxanthin, β-cryptoxanthin, lutein epoxide, β-carotene epoxide, antheraxanthin, α-doradexanthin, adonixanthin, mutatoxanthin, rhodoxanthin, and apo-12'-violaxanthal. All but three of these pigments were already known from mosses. Of the three new ones, α-cryptoxanthin was known in algae, lichens, and higher plants, α-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_3 photosynthetic pathway** is most common, but some have a **C_4 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_2 when it is taken into the plant. The **C_3 pathway** is assumed to be the primitive pathway, known from algae and bryophytes, as well as tracheophytes, in which the carbon of CO_2 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.

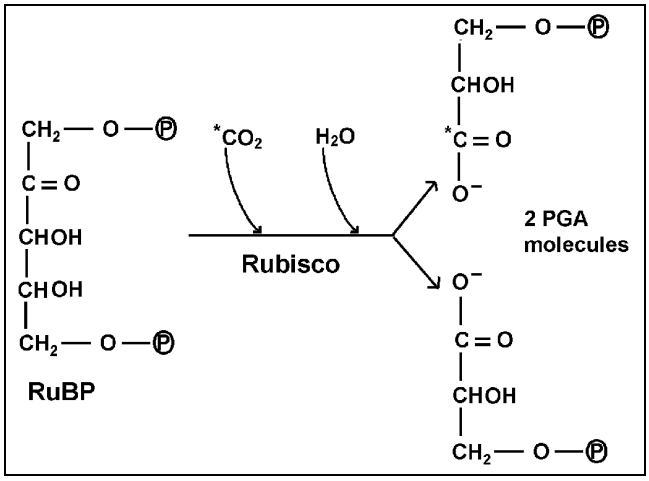

Figure 45. Melvin Calvin and associates found that the carbon from CO_2 is placed into RuBP to make a 6-carbon compound that immediately splits to form two molecules of 3-phosphoglycerate (PGA). This is the first step of the Calvin cycle and is the carbon fixation step for C_3 plants.

The **C_4 pathway** in tracheophytes permits storage of carbon from CO_2 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_2 is released and put into the photosynthetic pathway in the bundle sheath. The advantage is that stomata of a C_4 plant can remain open for a short time, CO_2 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_3 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_2 is stored in malic acid or other C_4 compound in the mesophyll for use in the daytime. However, in the CAM plant, the CO_2 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_3 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_2.

Table 1. Comparison of tracheophyte plants with different types of CO_2 fixation. From Larcher 1983, compiled from many authors.

Characteristic	C_3	C_4	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_2-compensation concentration at optimal temperature	30-70 µl l^{-1}	<10 µl l^{-1}	in light: 0-200 µl l^{-1} in dark: <5 µl l^{-1}
Primary CO_2 acceptor	RuBP	PEP	In light: RUBP in dark: PEP
First product of photosynthesis	C_3 acids (PGA)	C_4 acids (malate, aspartate)	In light: PGA in dark: malate
Photorespiration	Yes	Not measurable	Yes
Photosynthetic depression by O_2	Yes	No	Yes
CO_2 release in light (apparent photo-respiration)	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	20-35ºC?
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 5ºC (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_4 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_2 concentration, permitting them to gain CO_2 at night when most of the algae and other aquatic plants are respiring CO_2. The cooler atmosphere may likewise contribute to a reduced loss of the CO_2 from the body of water. It is amazing to me to learn that the C_3 ***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_2 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_2. Photo by Steve Matson, through Creative Commons.

C_3 Evidence

Several studies have attempted to locate a pathway other than the C_3 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_3. It appears that bryophytes have all the earmarks of C_3 plants, exhibiting higher CO_2 compensation points than those of tracheophytes (Rudolph 1990). Since C_3 plants are unable to sequester CO_2 and have only RUBISCO to help incorporate it into their photosynthetic pathway, they require higher concentrations of CO_2 than plants with C_4 or CAM pathways.

Raven *et al*. (1998) have reviewed the evidence for the C_3 pathway in bryophytes. Biochemically, bryophytes are C_3 plants, as far as is known. Their first carboxylation reaction accounts for more than 95% of the CO_2 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_4 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_2 compensation point. These data support the relatively high CO_2 compensation point of a C_3 plant (Fock *et al*. 1969; Ruttner 1947; Allen & Spence 1981; Raven *et al.* 1987).

Further evidence to support that bryophytes use a C_3 pathway comes from the $^{13}C/^{12}C$ discrimination values. Although there are difficulties with boundary layer resistance, especially in aquatic bryophytes, overall these values are consistent with a C_3 pathway (Raven *et al*. 1987, 1994; Keeley & Sandgren 1992; Rice & Giles 1994, 1996; Smith & Griffiths 1996a, b).

CO_2-concentrating Mechanisms – Exceptions to C_3?

Although bryophytes are considered C_3 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_2-concentrating mechanism (Salvucci & Bowes 1981; Bowes & Salvucci 1989; Raven *et al*. 1998). CO_2-concentrating mechanisms permit the plant to obtain CO_2 at a higher concentration than conditions would normally allow for a C_3 plant. This can be especially important for plants living in aquatic habitats with *p*H values in the range where the equilibrium shifts from CO_2 to bicarbonate or carbonate.

Figure 47. ***Fissidens grandifrons***, a species that might have some sort of CO_2-concentrating mechanism that permits it to live in alkaline water. Photo by Janice Glime.

Raven (1991) summarized the ecological relationships of CO_2-concentrating mechanisms in plants. He found them to be negatively correlated with areas of CO_2 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 *p*H 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 (12ºC, 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 (30ºC, 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 *p*H 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 *p*H and shift the equilibrium toward CO_2 at the moss surface, despite the *p*H 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.

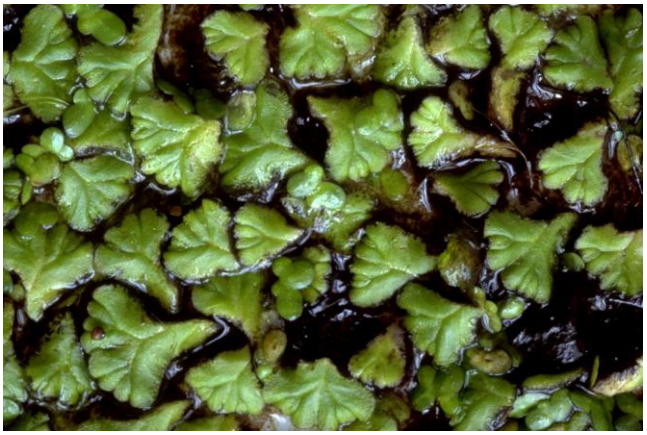

Figure 50. ***Ricciocarpos natans***, a floating thallose liverwort species with a CO_2 compensation point consistent with a C_3 plant. Photo by Jan-Frahm, with permission.

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 *p*H 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 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 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 CO_2? Can it convert bicarbonate to CO_2, perhaps through a *p*H-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 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.

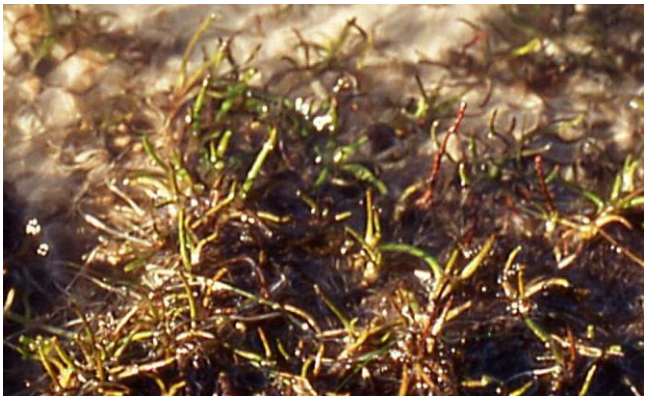

Figure 53. *Littorella uniflora*, an aquatic flowering plant species with a delay in carbon fixation. Photo by Christian Fischer, through Creative Commons.

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 µM mg^{-1} chl h^{-1}) of the tracheophyte, but also had approximately double the PEPcase activity (0.7 vs 0.3 µM mg^{-1} 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 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 CO_2 at night, and used RUBISCO for its photosynthetic CO_2 fixation. Steeman Nielsen (1947) stated outright that ***Fontinalis antipyretica*** "is unable to utilize 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 CO_2. But what does this genus use as a mechanism to get its CO_2, especially in water with a high *p*H where bicarbonates or carbonates predominate? Steeman Nielsen and Kristiansen (1949) suggested that there is evidence that 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 *p*H of 11.8-12.0 in a $NaHCO_3$ solution, a remarkably high *p*H and indicative of use of a carbon source other than CO_2. Further support of this conclusion is that this population of ***Fontinalis antipyretica*** increased its photosynthetic rate when higher HCO_3^- concentrations at constant 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 *p*H 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 *p*H suggests that such a mechanism might exist. However, they found that the *p*H 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 *p*H 9.5 in 2.0 mM $NaHCO_3$. For the others, the equilibrium clustered around *p*H 9.0 for 2.0 mM and 8.0 for 0.2 mM $NaHCO_3$. The four species of bicarbonate-using tracheophytes had final *p*H 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 *p*H water. Photo by Michael Lüth, with permission.

Pyrenoids

The slightly elevated *p*H 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 µM CO_2 $mole^{-1}$, 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 (49-68 µM $mole^{-1}$).

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 11-13 ppm CO_2 compared to 31 ppm for ***Megaceros*** (Figure 62) and 64 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 µmol CO_2 g^{-1} 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 µmol CO_2 g^{-1} chlorophyll (Raven *et al*. 1998). ***Notothylas*** (Figure 58) and ***Phaeoceros*** (Figure 57) have an inorganic carbon pool of 19-108 µM g^{-1} 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 10-20ºC 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_2 uptake in bryophytes is in this genus. The bottom line – we still don't understand how these CO_2-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_2 g^{-1} hr^{-1}) (Coxson & Mackey 1990). By late afternoon, this had declined to ~5 mg CO_2 g^{-1} hr^{-1}. 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_2 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_2

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_2 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 $^{14}CO_2$. 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). Hébant (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.

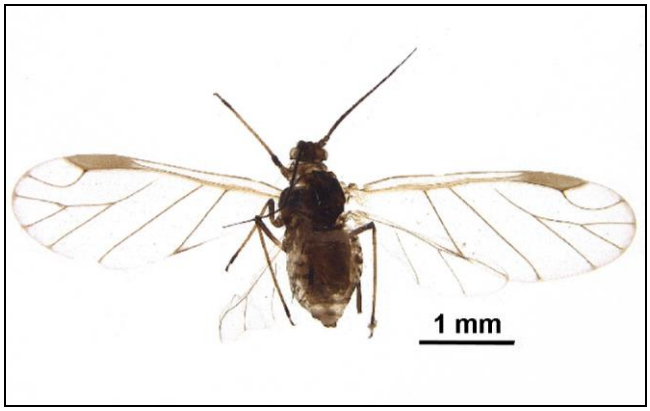

Figure 69. ***Myzodium modestum***, an aphid genus with members that feed on substances in leptoids of ***Polytrichum*** species. Photo by CBG Photography Group, through Creative Commons.

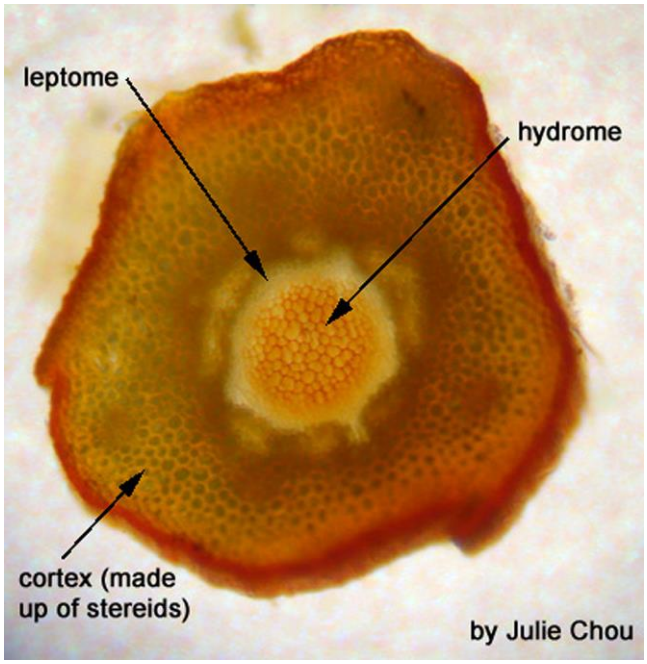

Figure 70. ***Polytrichum commune*** stem cross section, showing location of the leptoids that carry the sugars. Photo from Botany Website, UBC, with permission.

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^{-1} (Collins & Oechel 1974). On the other hand, this moss can move things upward at 32 cm h^{-1} (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_4 plants and retained most of its labelled ^{14}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 ^{14}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 ^{14}C in their growing shoot tips and senescent brown tissues and all four experienced high losses of ^{14}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.

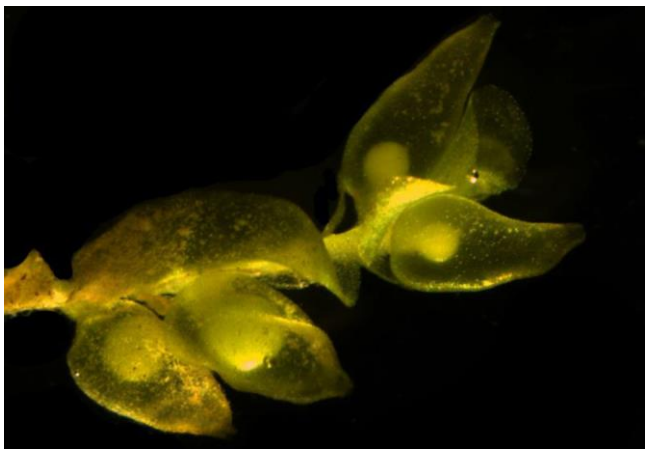

Figure 72. ***Riella helicophylla***, a species that uses phosphorylase in starch synthesis in starch sinks of gemmalings. Photo by NACICCA through Creative Commons.

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 barbuloides*** (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 barbuloides***, 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 ***Fossombronia 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%.

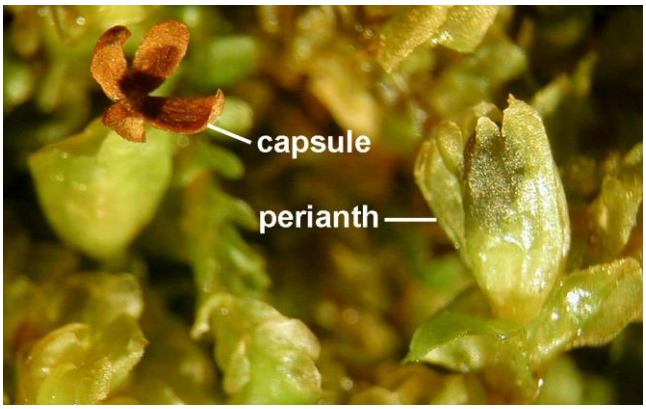

Figure 77. ***Scapania gracilis*** illustrating the complete covering of the perianth over the immature capsule and loss of green color of the capsule at maturity. Photo by Michael Lüth, with permission.

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

Figure 79. ***Fossombronia 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.

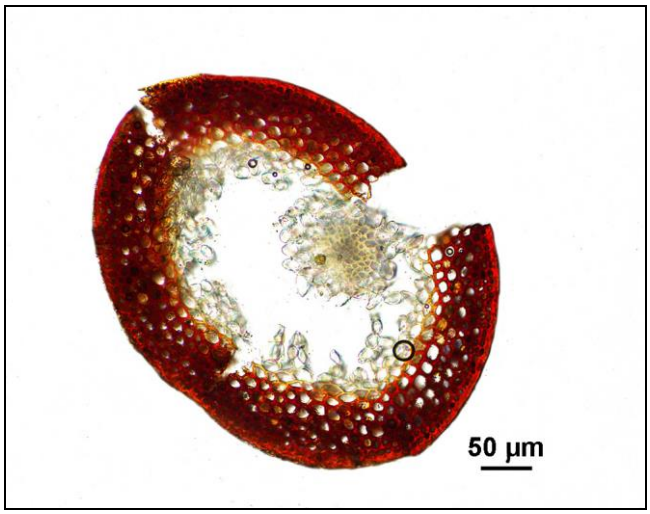

Figure 83. ***Polytrichum juniperinum*** seta cross section showing conducting tissue in circular cluster of cells just inside the break in the stem. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University.

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 23ºC, 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_2 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_2 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_2 g^{-1} dry mass h^{-1}. The green alga *Cladophora glomerata* (Figure 89) had 96 µmol O_2 g^{-1} dry mass h^{-1} respiration. The algae and bryophytes had rates higher than those of flowering macrophyte stems (13-71 µmol O_2 g^{-1} dry mass h^{-1}), but lower than that of their leaves (30-142 µmol O_2 g^{-1} dry mass h^{-1}).

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_2 uptake or O_2 emission, of a plant, whereas gross photosynthesis is the total CO_2 fixation, frequently obtained by adding respiratory loss to measured CO_2 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_2 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_2 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_2 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_2 uptake, for example through pyrenoids in many of the Anthocerotophyta, their photosynthetic pathway seems to be entirely C_3. Some aquatic bryophytes, such as ***Fontinalis antipyretica***, seem to be able to take up CO_2 in high *p*H conditions that should permit only very little free CO_2, 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.

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