CHAPTER 9-1

LIGHT: THE SHADE PLANTS

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Figure 1. Bryophytes growing in deep shade, with ***Frullania tamarisci*** hanging in the foreground. Photo by Michael Lüth, with permission.

Bryophytes Are Shade Plants

As in tracheophytes, bryophytes become light limited at low light intensities (Tixier 1979). For example, epiphyllous bryophyte cover increased fourfold in a clearing in Costa Rica compared to that in the dark understory (Monge-Nájera 1989). Nevertheless, bryophytes exist in places with very low light intensities (Figure 1). The atmosphere, canopy, and surrounding ground cover all contribute to diminishing the light reaching the moss surface (Figure 2), and latitude reduces the radiation reaching bryophytes near the poles.

It is their ability to make a net gain from photosynthesis at very low light intensities that permits bryophytes to live in places inhospitable to other plants. For example, herbaceous plants of a rich forest floor can retain 43-72% of the light that manages to penetrate the canopy, thus making the potential bryophyte substrate below very low in light indeed (Bodziarczyk 1992). Such total coverage becomes a competitive inhibitor for young seedlings, and even few bryophytes can tolerate such low light. But forests create an even greater toll on the light available to the soil substrate. They drop leaf litter that totally obscures the soil, making it uninhabitable for any bryophyte, and, most bryophytes seem unable to occupy the surface of this constantly changing leaf substrate. Thus, they are excluded from most of the deciduous forest floor by this inevitable litter-caused light limitation.

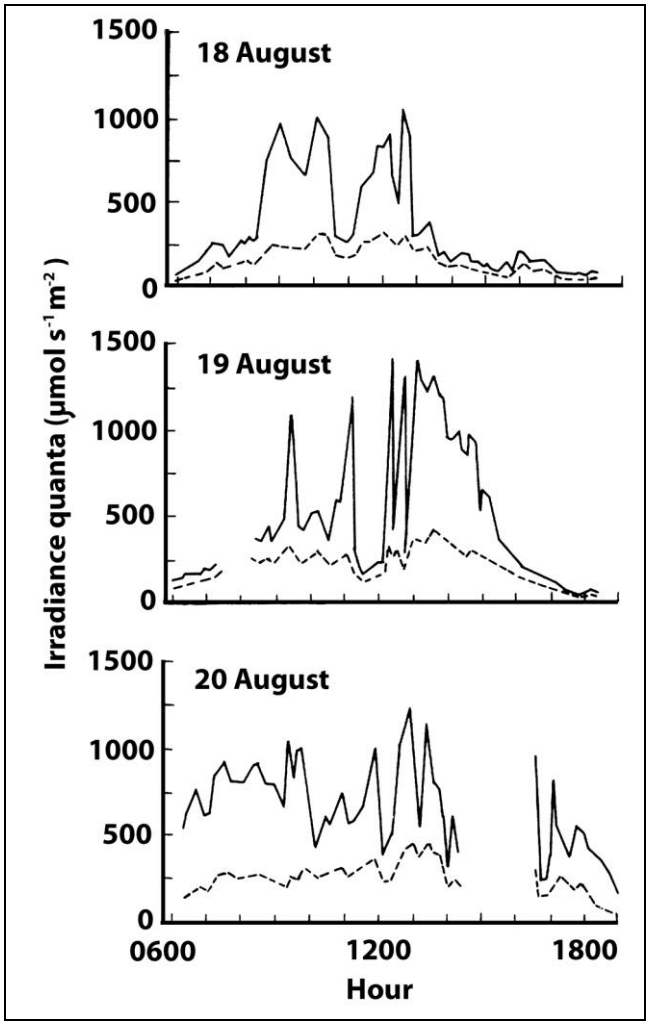

Figure 2. Irradiance at the moss surface - - - and total solar irradiance —— in PAR units for three consecutive days in central Alaska in a black spruce forest. Figure redrawn from Skré *et al*. 1983.

Compensation Point

Net photosynthetic gain is that net carbon which is stored; it reflects net loss of carbon as CO_2 in respiration and photorespiration. Think of it like your paycheck. Your gross income is much greater than that on your paycheck because you have taxes subtracted from it. Think of respiration as the tax and the paycheck as net photosynthesis. The level of light at which CO_2 gain by photosynthesis just equals that lost by respiration is referred to as the **light compensation point**, *i.e.*, the light level at which net photosynthesis is zero. The mean annual light input must be above that level for the plant to maintain positive carbon gain. The highest intensity at which net photosynthesis increases is referred to as the **light saturation point**. And some bryophytes, especially some aquatic taxa, have very low light compensation and light saturation points.

In the bamboo forests (2200-3200 m asl) of Central Africa the bryophytes dry out in the daytime and regain moisture from the vapor-saturated atmosphere at night (Lösch *et al*. 1994). The mountain sites (2200-3200 m asl) had six times higher daily sums of PAR, temperatures 10-25°C, and relative humidities 60-100 %. Nevertheless, photosynthetic optima of lowland (rainforest) species were somewhat higher than that found for bryophytes at the mountain sites. The light compensation points were smaller (3-12 µmol photons m^{-2} s^{-1}) in the lowland than in the highland species (8-20 µmol photons m^{-2} s^{-1}). On the other hand, the slopes of the curves in the low light range of the lowland species were distinctly steeper than in the high light range. Bryophytes in the rainforest (800 m asl) receive extremely high ambient CO_2 due high decomposition. This CO_2 advantage, coupled with their low light requirements and optimal temperature and humidity conditions provide sufficient photosynthetic conditions for them in this dark environment. Those from the higher elevation bamboo forests and tree-heath environments can take advantage of the higher light conditions despite variable temperatures and humidities.

Light Quality

Light quality differs among habitats. In the open, plants experience the full spectrum of sunlight in what we call white light. However, in the forest, the green canopy absorbs much of the red light, reflecting and transmitting green light. These differences in wave lengths and their respective differences in energy are important in a number of plant functions, with photosynthesis being among those affected.

Federer and Tanner (1966) demonstrated these differences in various habitats. The light quality differs even between hardwoods (most deciduous trees) and softwoods (conifers). Furthermore, light quality differs between clear and cloudy days. Light among all species groups tested had an energy maximum at 550 nm, a minimum at 670-680 nm, and a very high maximum in the near infrared. The light within the canopy is both beam solar radiation and diffuse sky radiation and these are both reflected and scattered.

But how do these differences in light quality affect the bryophytes? In ***Physcomitrella patens*** (Figure 3), no inhibition was present under high light illumination (Cerff & Posten 2012). These researchers found that a combination of red and blue light is most effective in reaching high growth rates and chlorophyll formation rates.

Figure 3. ***Physcomitrella patens***, a species that has good photosynthetic output in a combination of red and blue light. Photo by Janice Glime.

Light Measurement

Light has been measured in a variety of units, and unfortunately, most of them are not directly interconvertible because they measure different things. These different aspects of light also play different roles in physiology of bryophytes. Light wavelengths that stimulate photosynthesis are restricted to those that activate chlorophyll, whereas short wavelengths of ultraviolet light can bleach and damage chlorophyll. Other wavelengths stimulate red and yellow accessory pigments. Yellow pigments (**cryptochromes)** help plants measure the duration of light and respond to different wavelengths.

Traditionally, light was measured in **foot candles** – the intensity of light from one candle on a square foot of surface one foot from the candle. This English unit is, fortunately, easily convertible to metric units of **lux** (**lumens per sq meter**) **–** the intensity of light from one candle on one square meter of surface that is one meter from the candle. Thus, one lux is less bright than one foot candle, and to convert from foot candles to lux, one must multiply by 10.764.

PAR (= PhAR) units measure only **photosynthetically active radiation** and are based on measurements in sunlight. In general, about 45% of incoming sunlight lies within the spectral range of 380-710 nm (Larcher 1995), the range used by photosynthesis, thus the range of PAR. Ultraviolet light waves are shorter (UV-A at 315-380 nm; UV-B at 280-315 nm) and have no role in photosynthesis; they do, however, cause chlorophyll and DNA damage. Light available for photosynthesis (PAR) has been reported as photosynthetic photon flux density (**PPFD**), expressed as µmol m^{-2} s^{-1}, or as **watts** per meter square (W m^{-2}). The light reaching the Earth's outer atmospheric limits is 1360 W m^{-2} (the solar constant). By the time it reaches Earth's surface, only 47% remains, thus making full sunlight ~640 W m^{-2}. This varies considerably across the face of the Earth due to reflectance, scattering, cloud cover, and global position.

At sea level, maximum intensity can reach ~1 kW m^{-2}, with PAR intensities of ~400 W m^{-2}. Full sunlight ranges ~70,000-100,000 lux (or 7,000-10,000 foot candles), with the higher number when there is a highly reflective white sand near the equator at midday or a complete snow cover on a sunny day. The generally-accepted value of maximum light is 680 lumens per watt of radiant power (Commission Internationale de l'Eclairage, Paris 1970). Fortunately, it is possible to provide a rough equivalent of PPFD at full sunlight of 1800 µmol photons m^{-2} s^{-1} because we know the spectral quality of sunlight. However, when light is measured in shade, where leaves filter out red light and transmit green, or under water, or other places where the full spectrum of sunlight is not represented in the same proportions, such a conversion is not directly possible.

Table 1 gives approximate conversions under several more predictable conditions.

Having said all this, we have only looked at one end of the spectral effect – the light source (McCree 1973). Once light strikes the leaf, it encounters not only chlorophyll pigments (actually two chlorophylls in the plant kingdom, *a* and *b*), but it also encounters accessory pigments of various mixes of yellow, orange, and red (Figure 4) occurring in cell walls, cytoplasm, and plastids. Furthermore, cell shape can bend and focus or scatter light, depending on cell wall structure.

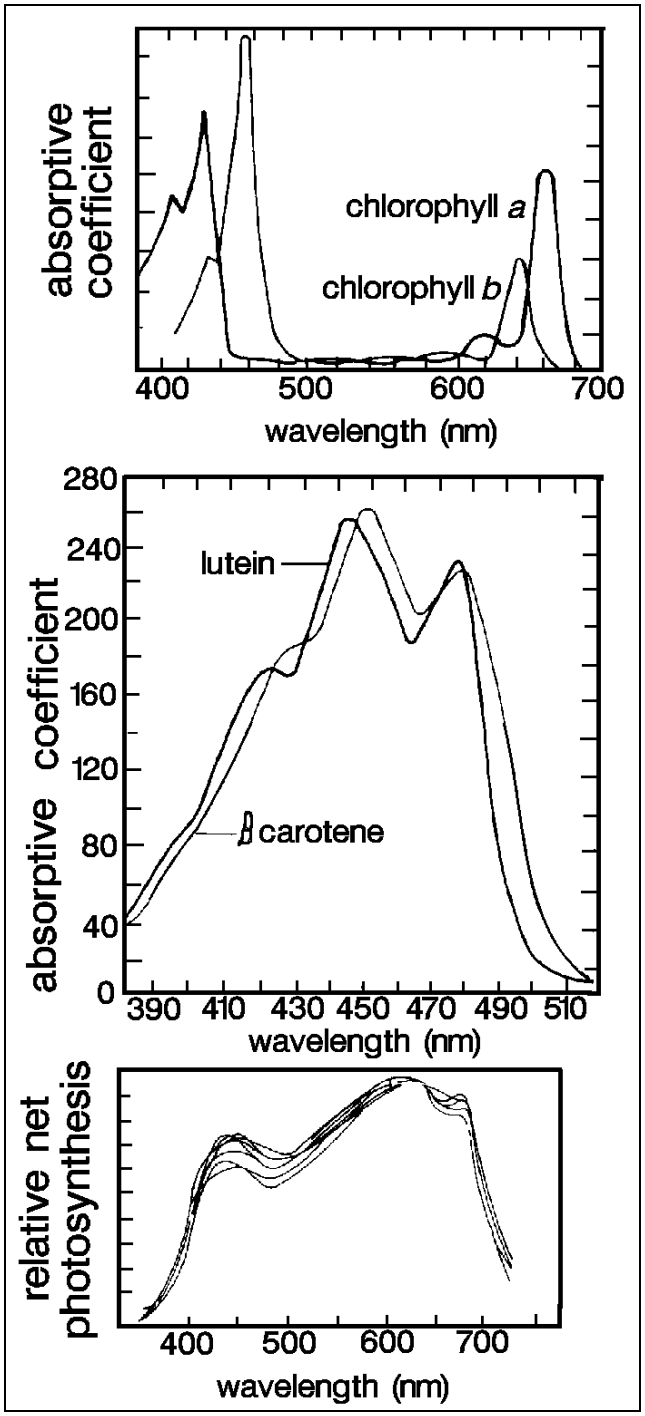

Figure 4. Top: Absorption spectra of chlorophylls *a* and *b*, dissolved in diethyl ether. Middle: Absorbance spectra of lutein and ß carotene in ethanol. Bottom: Action spectra of 22 species of crop plants. From Salisbury & Ross 1978.

Thus, our measurements of light are biased representations of light from the perspective of humans and not that of a plant leaf that must use that energy to activate the photosynthetic pathway. But, alas, it is the best we can do at present. This is not all bad, because the differences in response of various plants to the same measured light output give us indirect indications of differences in adaptations to light capture and cause us to probe further

for causes. Unfortunately, lumens and lux tell us even less because we have no measure of the wavelengths being received by the plant and thus know less about what sorts of adaptations to examine. It is like a human looking at a flower that reflects UV. We don't see what the bee sees.

Table 1. Conversions between PAR (PhAR) units or Klux (400-700 nm) units to µM photons m^{-2} s^{-1} for light under ~predictable spectral conditions. (From McCree 1981; Larcher 1995).

To convert from: Multiply by factor in column to obtain µM m^{-2} s^{-1}	W m^{-2} (PAR)	Klux
daylight (sunny)	4.6	18
daylight (diffuse)	4.2	19
metal halide lamp	4.6	14
fluorescent tube (white)	4.6	12
incandescent lamp	5.0	20

Adaptations to Shade

Just what is it that permits bryophytes to succeed where light levels are so low, particularly when compared to tracheophytes? Certainly simple structure is one factor. Tracheophytes are actually adapted to protect themselves from high light intensity by having a thick, waxy cuticle and an epidermis. And the palisade layer in many taxa protects spongy mesophyll from light by using chlorophyll and other pigments to absorb much of it before it reaches the photosynthetically adapted spongy tissue. Bryophytes, on the other hand, have none of these adaptations and expose their photosynthetic cells directly to the light by having only one leaf cell layer in most cases (Figure 5. Only thallose liverworts like ***Marchantia*** (Figure 6) have an arrangement somewhat similar to spongy mesophyll (Figure 7), and a few mosses like the **Polytrichaceae** have a folded-over leaf margin surrounding leaf lamellae (Figure 8, lower), somewhat resembling palisade tissue of a tracheophyte. In fact, knowing the structure of a bryophyte, we must ask ourselves instead how they survive in the sun.

Figure 5. **Upper:** Leaves of ***Mylia anomala***. **Lower:** Cells showing chloroplasts in one-cell-thick leaf of the leafy liverwort ***Mylia anomala***. Photos by Michael Lüth, with permission.

Figure 6. ***Marchantia polymorpha ruderalis*** showing pores on surface. Photo by David Holyoak, with permission.

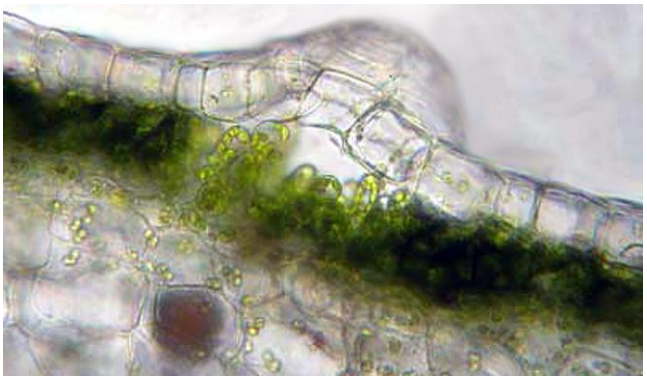

Figure 7. Cross section of thallus, through pore, of ***Marchantia polymorpha***. Note the spongy nature of the photosynthetic layer where it is visible below the pore. Photo by Jennifer Steele, Botany Website, UBC, with permission.

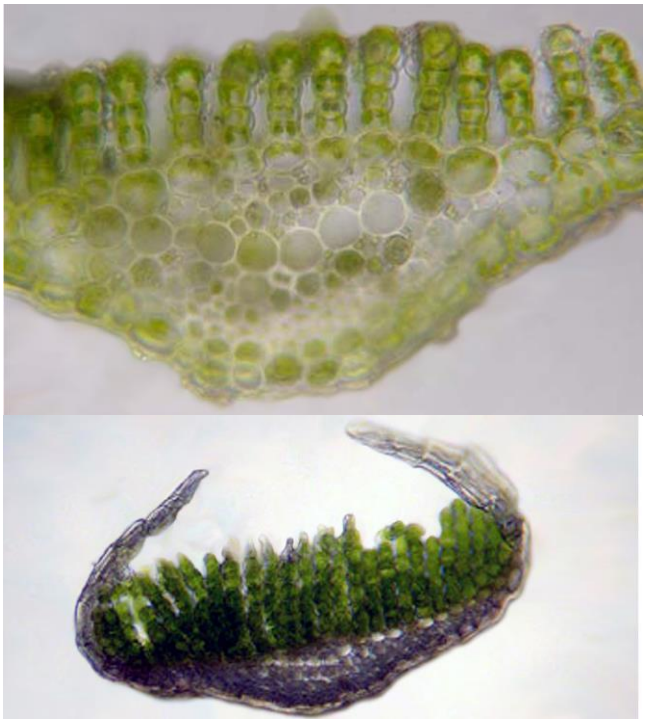

Figure 8. **Upper:** Leaf lamellae of ***Pogonatum contortum***, typical of those found in all members of the Polytrichaceae. **Lower:** Leaf lamellae with leaf lamina rolled over them in ***Polytrichum piliferum***. Photos with permission from Botany Website, UBC, with permission.

Most bryophytes are physiologically adapted to low light intensities and therefore have low chlorophyll *a*:*b* ratios (1.0-2.5:1, Mishler & Oliver 1991) compared to tracheophyte sun plants (C_3 = 3:1, C_4 = 4:1, Larcher 1983). Marschall and Proctor (2004) examined 39 moss and 16 liverwort species and determined that despite considerable variability, chlorophyll values were typical of shade plants. Median values of total chlorophyll were 1.64 mg g^{-1} for mosses and 3.76 mg g^{-1} for liverworts. Mosses had a chlorophyll *a*:*b* ratio of 2.29 and liverworts of 1.99, suggesting that liverworts are more shade-adapted than mosses. The reduced chlorophyll *a*:*b* ratio is due to increased levels of chlorophyll *b*, a typical shade adaptation that permits more trapping of photons that are then transferred to chlorophyll *a*. Even in those bryophytes that are sun species, the ratio tends to be low and the optimum light level likewise low. For example, ***Plagiochasma intermedium*** (Figure 9) has its optimum light intensity at 3500 lux with a day length of 10 hours (Patidar & Jain 1988); ***Riccia discolor*** has the same intensity optimum (Gupta *et al*. 1991). But full sunlight can be 70,000-100,000 lux.

Figure 9. ***Plagiochasma intermedium***, a species with an optimum light intensity of only 3500 lux and 20-hour days. Jan-Peter Frahm, with permission.

Marschall and Proctor (2004) found that the **PPFD** (photosynthetic photon flux density) at 95% saturation had a median of 583 µmol m^{-2} s^{-1} for mosses and 214 µmol m^{-2} s^{-1} for liverworts, again suggesting that liverworts are adapted to a lower light regime. Not surprisingly, two ***Polytrichum*** (Figure 10) species had the highest values. Their system of lamellae (Figure 8) provides them with considerable surface area to exchange gas and enhance their photosynthetic capability. Other bryophytes appear to be limited by their lack of sufficient surface area for CO_2 uptake. Green and Snelgar (1982) report that in the thallose liverwort ***Marchantia foliacea*** (Figure 11) the internal air chambers do little to facilitate photosynthesis compared to ***Monoclea forsteri*** (Figure 12) which has a solid thallus. Rather, the spaces facilitate water retention and the authors suggest that ***Marchantia foliacea*** would fare better photosynthetically if it had a solid thallus in very moist environments. Presumably this would afford it more photosynthetic tissue for light capture.

Figure 10. ***Polytrichum commune***. Two ***Polytrichum*** species have the highest photosynthetic values. Photo by A. J. Silverside, with permission.

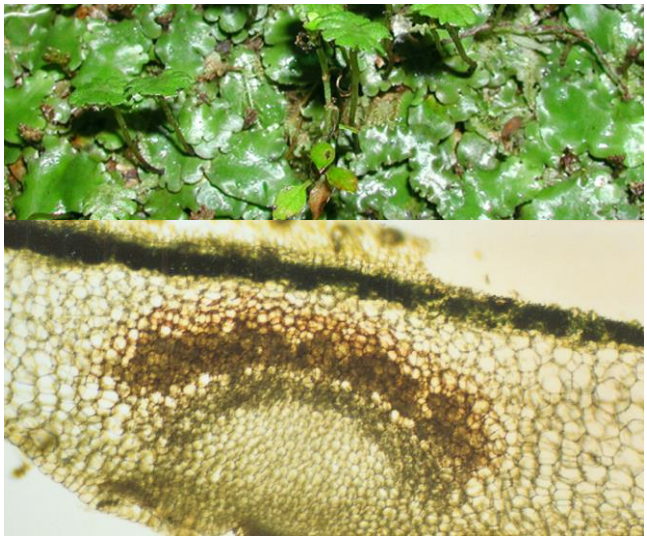

Figure 11. **Upper:** ***Marchantia foliacea*** thallus. **Lower:** Cross section of thallus of ***Marchantia foliacea*** showing the nearly solid nature of the thallus. Air chambers occur within the green layer near the upper surface. The brown layer is a layer of arbuscular mycorrhizal fungi. Photos by Julia Russell, with permission.

Figure 12. Thallus of ***Monoclea forsteri***. Photo by Jan-Peter Frahm, with permission.

Tuba (1987) explains that because poikilohydric plants must depend on atmospheric moisture to regulate their internal water content, they are most likely to photosynthesize during early morning hours when there is dew, and during rainstorms, since those are the only times

their cells are hydrated sufficiently. These plants are most likely to be desiccated during periods of high light levels. Thus, it is logical that their chlorophyll is adjusted to low light levels and that their light compensation (Table 4) and light saturation points are low when compared to those of most flowering plants (Table 2). Nevertheless, the light compensation points seem to be slightly higher than those of shade-adapted flowering plants (Table 2), suggesting that bryophytes may benefit from occasional **sunflecks** (patches of light due to movement or gaps among the canopy leaves), or that we have insufficient data thus far to be making these generalities!

Table 2. Comparison of light compensation and saturation points for photosynthetic organisms from various habitats. From Larcher 1983, compiled from various authors.

Plant group	Compensation light intensity I_k in Klux	Light saturation I_S in Klux
Land plants		
Herbaceous plants		
C_4 plants	1-3	>80
Agricultural C_3 plants	1-2	30-80
Herbaceous sun plants	1-2	50-80
Herbaceous shade plants	0.2-0.5	5-10
Woody plants		
Winter-deciduous foliage trees and shrubs		
Sun leaves	1-1.5	25-50
Shade leaves	0.3-0.6	10-15
Evergreen foliage trees and conifers		
Sun leaves	0.5-1.5	20-50
Shade leaves	0.1-0.3	5-10
Understory ferns	0.1-0.5	2-10
Mosses and lichens	**0.4-2**	**10-20**
Water plants		
Planktonic algae		(7) 15-20
Tidal-zone seaweeds	1-2	10-20
Deep-water algae		1-2
Seed plants	<1-2	(5) 10-30

We do know that bryophytes are able to adjust to low light levels by increasing their number of chloroplasts, as demonstrated for ***Funaria hygrometrica*** in Figure 13.

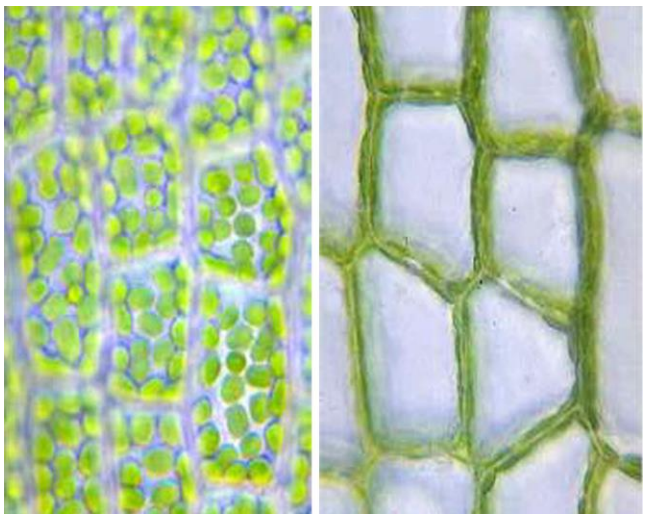

Figure 13. ***Funaria hygrometrica*** cells from dim light (**left**) and strong light (**right**). Photos by Winfried Kasprik.

Compensation Points

Certainly some bryophytes are able to grow over a relatively wide range of light intensities, increasing their growth rate as the intensity increases. For example, in ***Marchantia palacea*** var. ***diptera*** (Figure 9), this growth increase occurs from 5.4 to 60 W m^{-2} (Taya *et al*. 1995). However, above that level, there is a significant and rapid decrease in growth.

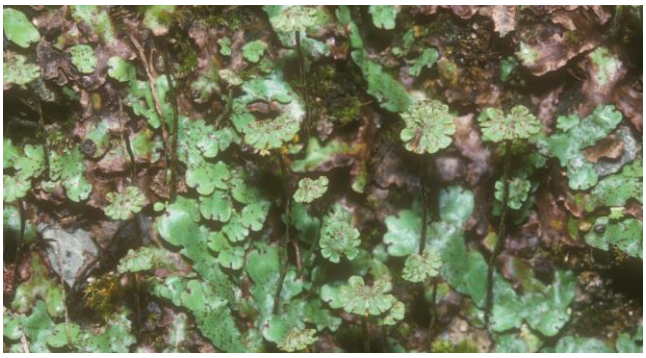

Figure 14. Thalli and archegoniophores of ***Marchantia palacea*** var. ***diptera*** from Japan. Photo by Janice Glime.

Compensation points suggest that there is indeed adaptation within the bryophytes to both low and high light levels (Table 3-Table 4). For example, in Antarctic lakes, ***Drepanocladus*** (*sensu lato*) (Figure 15) has a light compensation point similar to that of algal communities (0.11 W m^{-2}, ~ 0.5 µM m^{-2} s^{-1}), whereas ***Calliergon*** (Figure 16), which occurs in shallower water, has a compensation point of 0.64 W m^{-2}, ~ 2.9 µM m^{-2} s^{-1} (Priddle 1980). ***Fissidens serrulatus*** (Figure 17) could maintain a positive net photosynthesis down to 7 µmol m^{-2} s^{-1} (Gabriel & Bates 2003). This is not surprising for a species that occupies caves and the deep shade of forest ravines. ***Hylocomium splendens*** (Figure 18), typical of conifer forests, required 30 µM m^{-2} s^{-1} to reach its compensation point at natural concentrations of CO_2 of 400-450 ppm (ppm = mg L^{-1}) (Sonesson *et al*. 1992).

Table 3. Published light compensation and saturation points for bryophytes.

	Condition	Comp lux	Sat lux	Reference
Fontinalis	5ºC	15		Burr 1941
	20ºC	40		
Atrichum undulatum	spring	3000	5000	Baló 1987
	summer	1000	10,000	
Polytrichum formosum	spring	4000	10,000	Baló 1987
	summer	1000	25,000	
Plagiomnium affine	spring	4000	15,000	Baló 1987
	summer	1000	25,000	
Chiloscyphus rivularis		1750		Farmer *et al.* 1988

	Condition	Comp µM m^2 s^{-1}	Sat µM m^2 s^{-1}	Reference
Pellia borealis		4.6-	81	Szewczyk 1978
Fissidens serrulatus	21ºC	7	24	Gabriel & Bates 2003
Andoa berthelotiana	21ºC	8	20	Gabriel & Bates 2003
Echinodium prolixum	21ºC	9	27	Gabriel & Bates 2003
Bazzania azorica	21ºC	9	29	Gabriel & Bates 2003

Plagiomnium spp.	25ºC	10	400	Liu *et al*. 1999
Frullania tamarsci	21ºC	10	36	Gabriel & Bates 2003
Lepidozia cupressina	21ºC	12	30	Gabriel & Bates 2003
Myurium hochstetteri	21ºC	31	68	Gabriel & Bates 2003
Pilotrichella ampullacea	tropics		100	Proctor 2002
Floribundaria floribunda	tropics		100	Proctor 2002
Hylocomium splendens	summer	30	100	Sonesson *et al*. 1992
Brachythecium rutabulum	8 May 6 July	65 4	200 30	Kershaw & Webber 1986

Table 4. Published light compensation points, relative to natural (full sun) irradiance, for bryophytes.

Drepanocladus	0.03%		Priddle 1980
Calliergon	0.16%		Priddle 1980
Fissidens serrulatus	~0.4%		Gabriel & Bates 2003
Thuidium cymbifolium	0.57%[+]		Hosokawa & Odani 1957
Hylocomium cavifolium	0.57%[+]		Hosokawa & Odani 1957
Thamnium sandei	0.57%[+]		Hosokawa & Odani 1957
Homaliodendron scalpellifolium	0.57%[+]		Hosokawa & Odani 1957
Calliergonella cuspidata	1%		Kooijman unpubl
Hylocomium splendens	1.7%	summer	Sonesson *et al*. 1992
	~2%	Sept	Skré & Oechel 1981
Racomitrium lanuginosum	~2%	5ºC	Kallio & Heinonen 1975
Pleurozium schreberi	~2.5-5%	Sept	Skré & Oechel 1981
Racomitrium lanuginosum	~7.5%	15ºC	Kallio & Heinonen 1975
Sphagnum angustifolium	2.1%[*]	10ºC	Harley *et al*. 1989
Sphagnum angustifolium	7.1%[*]	20ºC	Harley *et al*. 1989

[*]Converted from μM m^{-2} s^{-1} assuming 1800 μM m^{-2} s^{-1} at full sunlight.
[+]Converted from lux, assuming full sun of 70,000 lux.

Figure 15. ***Drepanocladus aduncus***, a genus that in Antarctic lakes has a light compensation point similar to that of algae. Photo by Michael Lüth, with permission.

Figure 16. ***Calliergon richardsonii***, a genus of shallow water and with a much higher light compensation point than that of the submersed ***Drepanocladus***. Photo by Michael Lüth, with permission.

Figure 17. Gametophyte with sporophyte of ***Fissidens serrulatus***. Photo by Michael Lüth, with permission.

Figure 18. Side view of the feather moss ***Hylocomium splendens***. Photo from Botany Website, UBC, with permission.

A low compensation point and a low light saturation value are typical for C_3 plants, and thus for bryophytes (Table 2). The low light compensation point in tracheophytes is in part due to the ability of C_3 plants to open their stomata quickly to take advantage of CO_2 exchange whenever sufficient light is available. However, lacking stomata, bryophytes are not limited by stomatal opening speed, so response time to take in CO_2 should not impose the same kinds of limits it does in tracheophytes. On the other hand, higher levels of CO_2 permit photosynthetic gain at high light intensities by increasing

the light saturation point. For light energy to be used in photosynthesis, there must be sufficient CO_2 for the fixation of photosynthetic product. Otherwise, excess excitation energy can damage the photosynthetic apparatus. Therefore, we should expect to find a higher light saturation point when the CO_2 concentration is higher, as already seen for ***Hylocomium splendens*** (Figure 18) (100 µmol m^{-2} s^{-1} at a CO_2 concentration of 400-450 mg L^{-1}) (Sonesson *et al*. 1992). This is a relatively high level of CO_2 (but a reasonable level at the soil interface) and likewise a high level of light saturation. We will see shortly that such a high light saturation level in this CO_2-enriched environment will permit the plants to take advantage of bursts of light (**sunflecks**; Figure 19) reaching the forest floor. Again, it would appear that lacking stomata, bryophytes are positioned to be able to make immediate use of these short bursts and have the physiological apparatus to accommodate them.

Figure 20. ***Hypnum cupressiforme*** in an open habitat on rock. Photo by Michael Lüth, with permission.

Figure 19. ***Leucobryum glaucum*** with sunflecks. Photo by Janice Glime.

Figure 21. ***Hypnum cupressiforme*** in a shaded habitat on a lob. Photo by Michael Lüth, with permission.

Sunflecks

Importance of sunflecks (patches of bright light due to movement or gaps among the canopy leaves; Figure 19) for forest floor tracheophytes is well known. However, bryophyte usage of these bursts of light has been largely ignored (Kubásek *et al*. 2014). These researchers suggest that the anatomy of bryophyte gametophytes would allow a more rapid induction of photosynthesis due to the one-cell thickness, lack of stomata that must be opened, and only thin cuticle. They compared 10 moss species from sun and shade sites. By providing light after dark acclimation, they found that the moss photosynthesis did indeed induce much faster than observed in tracheophytes, reaching 50% of maximum gross photosynthesis in only 90 seconds. Maximum photosynthesis occurred in only 220 seconds, compared to 500-2000 s for most tracheophytes. Shade-grown mosses had a photosynthetic capacity comparable to that of sun grown plants. ***Hypnum cupressiforme*** (Figure 20-Figure 21) from shade induced photosynthesis slightly faster than did those from sunnier forest gaps (Figure 22). This high photosynthetic capacity permits these forest mosses to make efficient use of sunflecks.

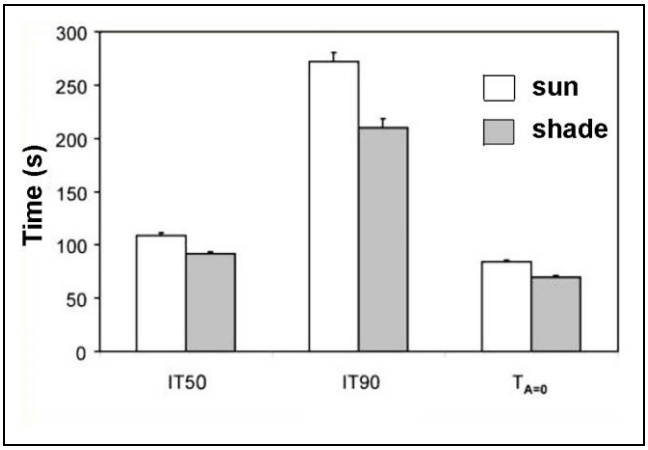

Figure 22. Comparison of induction rates (IT50 and IT90) and time needed to reach net carbon uptake ($T_{A=0}$) of four gap and four shade samples of the forest moss ***Hypnum cupressiforme***. One hour of dark acclimation with ambient CO_2 (400 µmol mol^{-1}) was followed by saturating irradiance of 1200 µmol m^{-2} s^{-1}. Means are ± SEM, n=4. All means comparing gap and shade groups differ at $P<0.025$. Modified from Kubásek *et al*. 2014.

Bryophyte photosynthetic capacity may be higher than is usually understood (Kubásek *et al*. 2014). For example, the sun species ***Bryum argenteum*** (Figure 23) under saturating light had 9 µmol m^{-2} of projected area s^{-1} under ambient CO_2 and 20 µmol m^{-2} of projected s^{-1} under 2000

ppmV of CO_2. This is similar to the photosynthetic capacities of many understory tracheophytes.

Figure 23. ***Bryum argenteum***, a sun-tolerant moss made whitish by hyaline tips of overlapping leaves. Photo by George Shepherd, through Creative Commons.

Some tracheophyte physiologists have expressed surprise that shade-grown mosses do not have significantly lower photosynthetic capacity than gap-grown mosses (Jiri Kubásek, pers. comm. 5 April 2007). But consider the adaptations that cause tracheophytes to have less ability to take advantage of sunflecks. First they must open stomata, the slowest process in the induction of photosynthesis. Then, they have layers of cells to protect them from the high light intensity. And often they have a thick cuticle that reflects the sun, whereas it is thin in bryophytes. Bryophytes have none of these constraints and therefore can respond quickly to the short duration of sunfleck light.

Typically, however, light saturation points for bryophytes are low compared to those of tracheophytes. Gabriel and Bates (2003) found that most of the species they examined from an evergreen laurel forest had a saturation point less than 30 µmol m^{-2} s^{-1}, although the lowest among the seven species they studied was 20 µmol m^{-2} s^{-1}. The highest was for ***Myurium hochstetteri*** (Figure 24-Figure 25), which was saturated at 68 µmol m^{-2} s^{-1}. See also Chapter 9-2 for further discussion of Sunflecks.

Figure 24. ***Myurium hochstetteri*** habitat. Photo by Michael Lüth, with permission.

Figure 25. ***Myurium hochstedteri***, the bryophyte species with the highest light saturation point among those tested in the laurel forest. Photo by Michael Lüth, with permission.

Light Effects on Morphology

Sometimes added light can give unexpected results. Such is the case with ***Calliergonella cuspidata*** (Figure 26). In experiments where tracheophytes were cut, creating more exposure in a calcareous fen in the Swiss mountains, the moss ***Calliergonella cuspidata*** exhibited a number of morphological differences (Bergamini & Peintinger 2002). It had smaller increments in length on the main axis, shorter offshoots, greater branching density, higher number of offshoots, and greater biomass per unit length. On the other hand, there were no observable effects of increased N supply.

Figure 26. ***Calliergonella cuspidata***, a species that has longer leaf intervals when shaded by tracheophytes. Photo by Michael Lüth, with permission.

Summary

In general, bryophytes are adapted to low light, relative to other land plants. They do well in forests as long as they are not buried by leaf litter. Most taxa have a low **light compensation point** and a low **light saturation point**. Light is usually measured as **photosynthetically active radiation** (**PAR**), but this ignores the ability of accessory pigments to trap other wavelengths and transfer the energy to chlorophyll *a*.

Most bryophytes are adapted to capture of low light intensities due to their one-cell-thick leaves and lack of well-developed cuticle. Responses of bryophytes to low light are similar to those of tracheophytes, with increased chlorophylls and antenna pigments, depressed light saturation and compensation points, and deeper green color. However, some bryophytes at least do not have a lower chlorophyll *a*:*b* ratio in low light compared to high light, as would the typical tracheophyte. Rather, bryophytes in general have a lower chlorophyll *a*:*b* ratio in all light conditions than do tracheophytes. This suggests that the bryophyte, with its chlorophyll *a* concentrations maintaining proportionality to chlorophyll *b* concentrations, would be ready for brief opportunities when bright light becomes available. Liverworts seem to be better adapted to shade than mosses, with a lower chlorophyll *a*:*b* ratio, higher concentration of total chlorophyll, and lower **PPFD**.

Such a strategy would adapt these plants well to the forest habitat where so many reside, permitting them to take advantage of changing positions of the sun as it filters through trees and brief bursts of light as **sunflecks** when the wind changes the arrangement of the overarching canopy.

There is a broad range of **light compensation points** among bryophytes, ranging from 0.03% of full sunlight in deep water species to 7.5% in sun species. **Light saturation points** are likewise low, although some bryophytes seem able to use bursts of high light intensity and can increase their saturation points when higher levels of CO_2 are available.

Acknowledgments

I thank Jiri Kubásek for many email discussions about bryophytes and sunflecks.

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CHAPTER 9-2

LIGHT: ADAPTATIONS FOR SHADE

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CHAPTER 9-2

LIGHT: ADAPTATIONS FOR SHADE

Figure 1. Hemlock hardwood forest in West Virginia, showing the absence of bryophytes among the leaf litter on the forest floor but growing on exposed rocks. Photo by Janice Glime.

Structural Adaptations for Light Capture

Among my favorite posters at the meetings of the Ecological Society of America, 1993, were the several posters on light focussing by seed plants (DeLucia *et al*. 1996). These illustrated principles I have considered for bryophytes but been unable to test. They found that epidermal cells (**lens cells**) that are rounded at the surface can focus the light in the leaf. In shade leaves, these lens cells are spherical; in the sun they are elliptical. In bryophytes, some leaves have **mammillose** (swollen) cells that are similar to the lens cells they describe (Figure 5). The ability of these cell surfaces to focus light on the chloroplasts has not been explored, except in the case of the protonemata of ***Schistostega pennata*** (Figure 2-Figure 4), as will be discussed in Chapter 9-5 of this volume.

Figure 2. ***Schistostega pennata*** with mature plants in upper left and luminescent protonemata in lower center. Photo courtesy of Martine Lapointe.

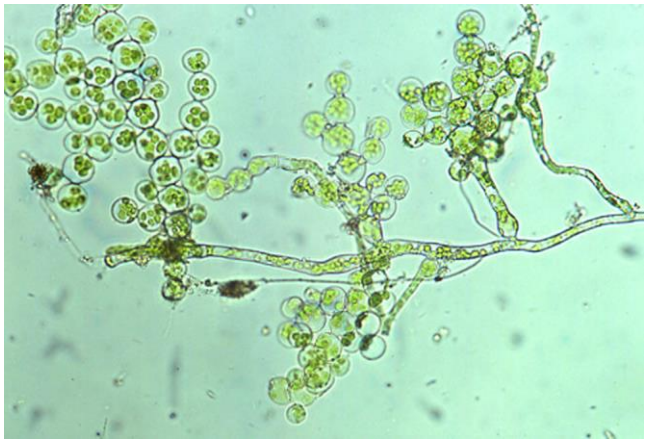

Figure 3. ***Schistostega pennata*** protonema with light-focussing cells. Photo courtesy of Irene Bisang.

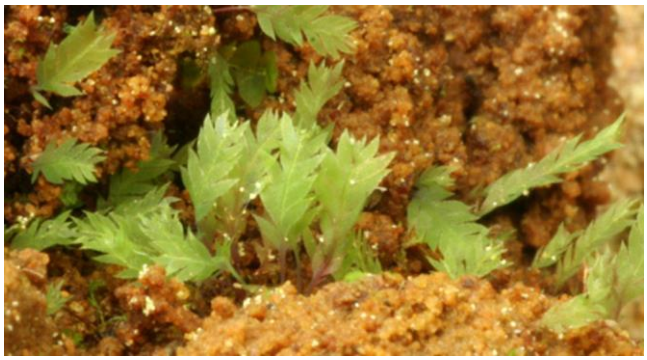

Figure 4. ***Schistostega pennata*** leafy gametophytes. Photo courtesy of Martine Lapointe.

Tracheophytes can move their leaves instead of their chloroplasts. In their study, DeLucia *et al*. (1996) found that further adjustments to the light reaching the chloroplasts of tracheophyte leaves were facilitated by leaf angles. In mesic woods, fewer than 10% of the leaves were angled more than 60º, whereas in xeric sites with high light intensity more than 75% of the leaves were angled. Leaf thickness also related to moisture, with 75% of taxa at the three most open sites having leaves more than 0.4 mm thick, while at more mesic sites less than 12% of the taxa reached such a thickness. High sunlight resulted in palisade tissue on both sides of the leaf.

In a different poster, DeLucia *et al*. (1996) noted attenuation of green light by 2.7 times and red light by 8 times in the air space at the palisade/mesophyll interface. By applying oil to fill the air spaces, they reduced reflectance and caused a decrease in fluorescence by 50%. They interpreted this to mean that reflectance in the air space caused more light to be available for absorbance by the chloroplasts. A thick palisade reduces the reflectance and therefore reduces the light reaching the spongy mesophyll. At light intensities of less than 30 μM m^{-2} s^{-1}, the air space reflectance increased the photosynthetic rate by 30-50%, with lesser increases at higher light intensities.

If we consider the bryophyte branch to act like a leaf, these principles could be tested in bryophytes. Lens-shaped leaf cells (Figure 5) could focus light on cells of overlapped leaves that are more moist because of their internal position. Such a focussing would be facilitated by the tendency for moss chloroplasts to arrange themselves around the periphery of the cell, thus leaving the center of the cell available for focussing without increasing absorption. Can we find any correlation between the leaf or branch position of bryophytes and the light regimes under which they grow?

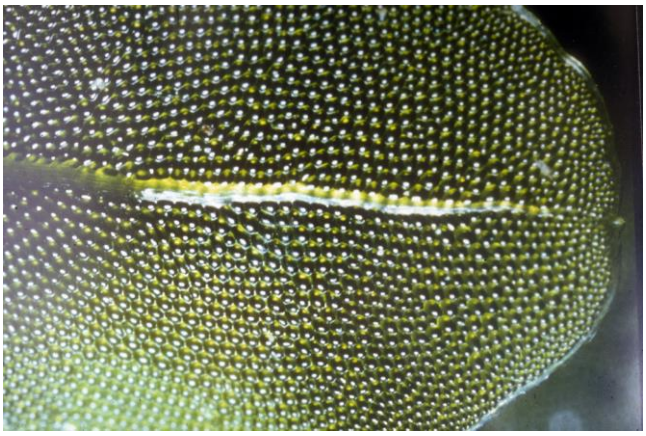

Figure 5. Leaf of ***Plagiomnium tuomikoski*** showing bulging (**mammillose**) cells that could focus light within the cell. Photo by Zen Iwatsuki, with permission.

Lamellae

Mosses like ***Polytrichum*** (Figure 6-Figure 7) and ***Atrichum*** (Figure 8-Figure 9) have a leaf structure with **lamellae** (Figure 7, Figure 9) similar to the structure of palisade tissue in seed plants, while the internal structure of a branch in most other bryophytes in many ways resembles the air spaces and spongy mesophyll of seed plants.

Figure 6. ***Polytrichum juniperinum*** showing leaf edges rolled over the lamellae. Photo by Janice Glime.

Figure 7. ***Polytrichum juniperinum*** leaf lamellae and rolled over edge of leaf. Photo courtesy of John Hribljan.

Figure 8. ***Atrichum altecristatum*** leaves with lamellae. Photo courtesy of Eric Schneider.

Figure 9. Cross section of leaf showing the **lamellae** of ***Atrichum selwynii***. Photo from Botany Website, UBC, with permission.

Surface Reflectance

Lovelock and Robinson (2002) have found that various mosses differ in their surface reflectance properties and that the differences do not correlate with pigment concentrations, suggesting that surface shape and water content may play a role in surface reflectance. In studying the Antarctic mosses ***Bryum pseudotriquetrum*** (Figure 10), ***Ceratodon purpureus*** (Figure 11), and ***Schistidium antarcticum*** (Figure 11), Lovelock and Robinson (2002) found that the reflectance spectra were similar to those of angiosperm leaves with chlorophyll having the major influence. The mosses likewise did not differ from angiosperms in their UV reflectance, but they did differ significantly at 526, 550, and 850 nm light wavelength and seemed to have a different **cold hard band** – that portion of the absorbance that correlates with the formation of the chlorophyll-protein complex that protects against freezing damage. It is no surprise that ***Ceratodon purpureus*** had higher concentrations of **anthocyanins** (Figure 12), since it is frequently red-tinged, whereas it had lower chlorophyll concentrations than the other two species. ***Bryum pseudotriquetrum*** (Figure 10) had higher levels of UV-absorbing pigments but lower carotenoid levels than the other two taxa, but the other two taxa had higher levels of pigments associated with photoprotection from visible light. The correlation between surface reflectance and plant pigment concentration was low, suggesting that surface structure may have played a major role in reflectance. Rehydration of dry ***Schistidium antarcticum*** resulted in a significant increase in the photosynthetic reflectance (Figure 11), but it is unclear as to the mechanism. The surface reflectance is highly influenced by the environmental conditions under which the mosses are growing and seems to be linked to water content and morphology of the individual plants and their clone.

Figure 10. ***Bryum pseudotriquetrum*** growing in Antarctica. Photo courtesy of Jan Beard.

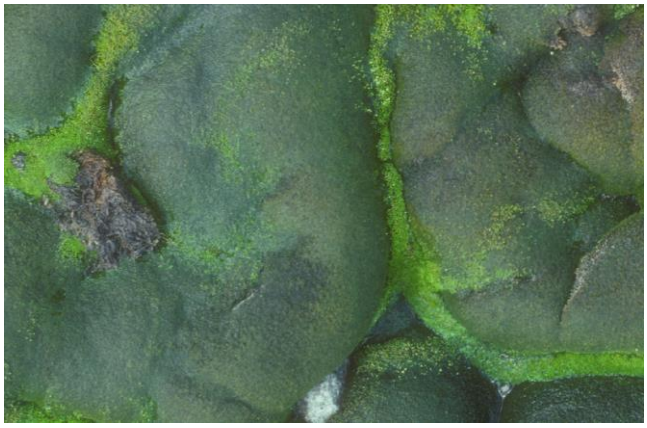

Figure 11. Wet ***Schistidium antarcticum*** hummocks illustrating the high reflectance. ***Ceratodon purpureus*** is in the hollows. Photo courtesy of Rod Seppelt.

Figure 12. ***Ceratodon purpureus*** with anthocyanins protecting it from the high levels of UV light in the Antarctic. Photo courtesy of Rod Seppelt.

Altering Wavelengths

Light is modified as it travels through the atmosphere, losing energy and lengthening the wave lengths, thus

changing the quality of the light. This of course doesn't mean good or bad, but rather means the color composition of the light changes.

The mosses themselves also alter the light quality. They reflect the colors we see, absorb others, and transmit still others. They typically absorb blue and red light, as do tracheophytes, but they differ from tracheophytes in having a green peak that responds to the red, brown, or green coloration of various species (Bubier *et al*. 1997). In their study, Bubier and coworkers examined boreal forest and peatland mosses, including feather mosses (forests; Figure 13), brown mosses (rich fens; Figure 20), and ***Sphagnum*** (bogs and poor fens; Figure 14-Figure 19). They found that the mosses are typically less reflective than are tracheophytes, resulting from strong water absorption features in the range of 1.00-1.20 μm. This absorption results in reflectance peaks at ~0.85, 1.10, and 1.3 μm (NIR 1, 2, & 3). ***Sphagnum*** species have a minor absorption at 0.85 μm that is absent in all brown and feather mosses and in all tracheophytes. Furthermore, the red absorption is narrow in ***Sphagnum***. Bubier and coworkers concluded that the overall moss reflectance in the 1.50-2.50 region is lower than that for tracheophytes because of the higher water content of moss tissue. This is further supported by the high reflectance of lichens, which typically have dry tissues.

Figure 13. ***Pleurozium schreberi***, a feather moss from the forest floor. Photo by Sture Hermansson, with online permission.

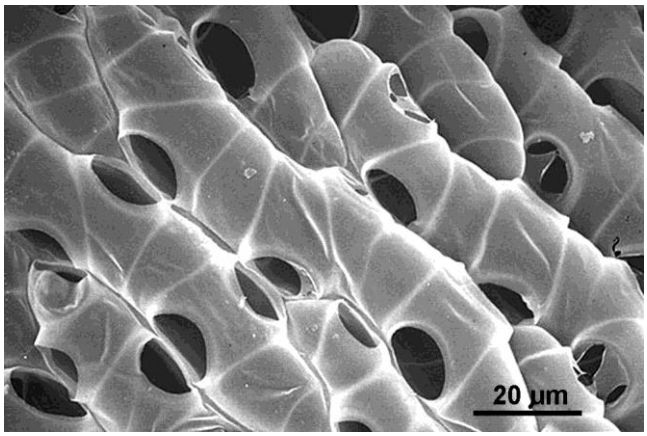

Figure 14. ***Sphagnum*** hyaline cells & pores (SEM), a structure that may alter the light quality that is reflected and that enters the photosynthetic cells. Photo from Botany Website, UBC, with permission.

Figure 15. ***Sphagnum austinii***, exhibiting one of the many colors in the genus ***Sphagnum***. Photo by Des Callaghan, with permission.

Figure 16. ***Sphagnum balticum*** (brownish red) and ***S. cuspidatum*** (light green) showing two contrasting colors in the genus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Sphagnum capillifolium***, one of the red species of ***Sphagnum***. Photo by Blanka Shaw, with permission

Figure 18. ***Sphagnum fuscum***, one of the brown species of ***Sphagnum***. Photo by Andres Baron Lopez, with permission.

Figure 19. ***Sphagnum magellanicum***, one of the species that becomes red in bright light. Photo by Michael Lüth, with permission.

Figure 20. ***Warnstorfia exannulata***, one of the brown mosses. Photo from Biopix, through Creative Commons.

Papillae

I wonder how papillae (Figure 21-Figure 28) might fit the reflectance model. I have long thought that papillae might serve to scatter the light on a dry moss while permitting transmission on a wet one. It would seem like a relatively easy thing to test with a microscope and photometer. And does the shape of the papillae make a difference (Figure 21-Figure 28)?

Figure 21. ***Tortula muralis***, a papillose moss of open habitats. Photo from Botany Website, UBC, with permission.

Figure 22. ***Tortula muralis*** showing leaves that look waxy due to papillae. Photo by Christophe Quintin, through Creative Commons.

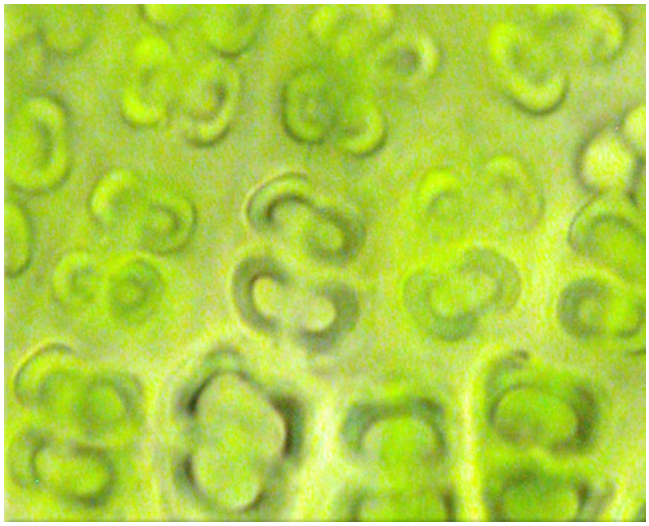

Figure 23. ***Tortula muralis*** leaf cell papillae. Photo by Walter Obermayer, with permission.

Figure 24. ***Tortula muralis*** leaf CS showing papillae on both sides of the leaf. Photo from Botany Website, UBC, with permission.

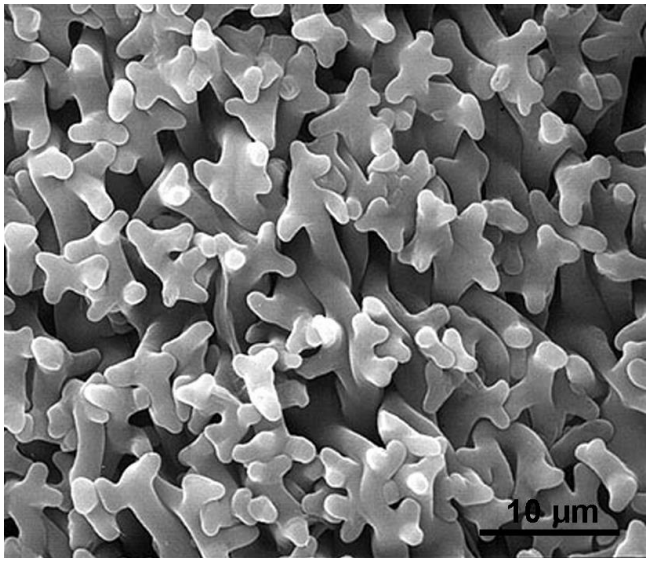

Figure 25. ***Tortula muralis*** papillae (SEM). Photo from Botany Website, UBC, with permission.

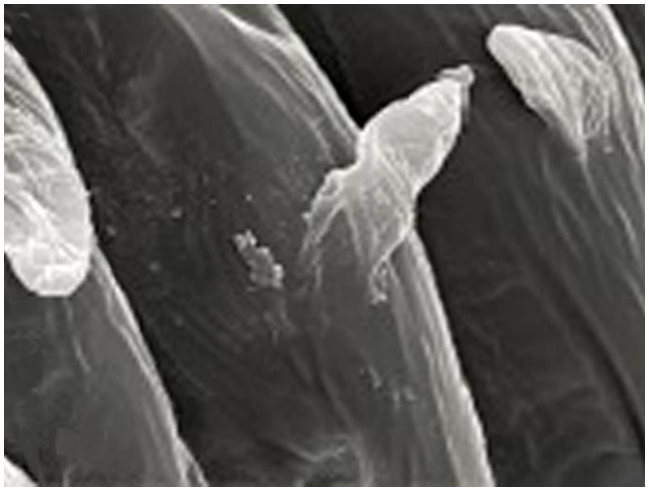

Figure 26. ***Callicostellopsis meridensis*** leaf papillae (SEM). Photo by Duarte-Silva *et al*. 2013, through Creative Commons .

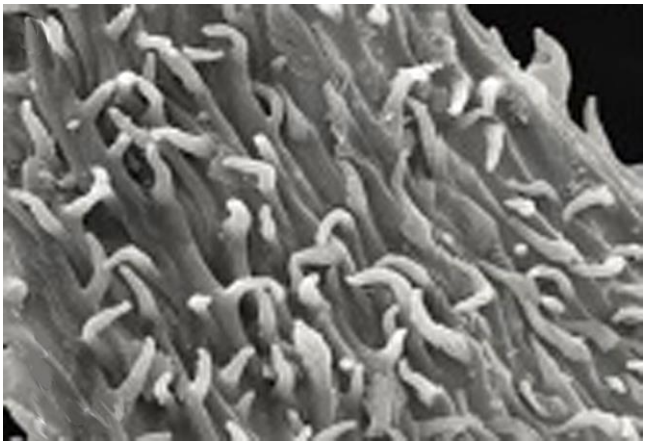

Figure 27. ***Hypnella pilifera*** leaf papillae (SEM). Photo by Duarte-Silva *et al*. 2013, through Creative Commons.

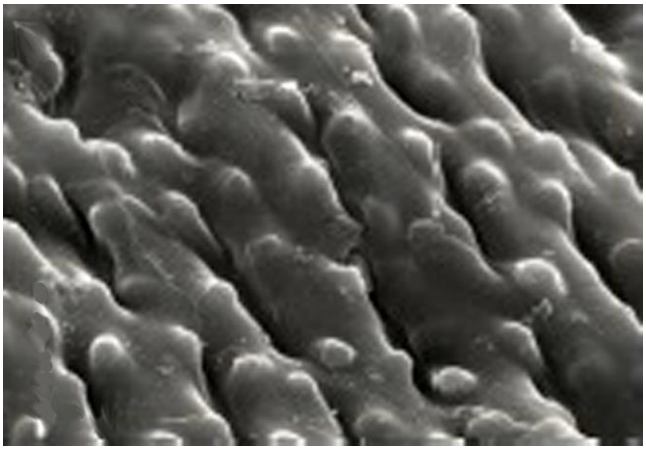

Figure 28. ***Pilotrichidium*** leaf papillae (SEM). Photo from Duarte-Silva *et al*. 2013, through Creative Commons.

The role of papillae has been controversial at best. Crandall-Stotler and Bozzola (1991) have shown that at least ***Andreaeobryum macrosporum*** (Figure 29) leaf papillae have narrow channels through which water can enter upon rehydration. It has occurred to me that these channels might also behave as fiber optics – a notion that remains to be tested.

Figure 29. ***Andreaeobryum macrosporum***, a moss with channelled papillae. Photo from Botany Website, UBC, with permission.

Proctor (1982) explains that in concave leaves, water is held in the concavity while the convex surface remains dry.

It is this convex surface that often is exposed to light. In papillose mosses such as ***Thuidium*** (Figure 30-Figure 31) and ***Hedwigia*** (Figure 32-Figure 35), the tops of papillae tend to remain dry, even when the leaf surface is wet, giving them that waxy or dull appearance. The tiny channels, when present, could function as fiber optics, much as the fur of a polar bear, but on a much smaller scale. Hence, the light could be focussed through the papillae onto the chloroplasts while water is obstructing and altering the light entering other parts of the cell. As can be seen in Table 1, there are lots of potential light adaptations in bryophytes that remain to be tested.

Figure 30. ***Thuidium delicatulum***, a moss of light shade. Photo by Janice Glime.

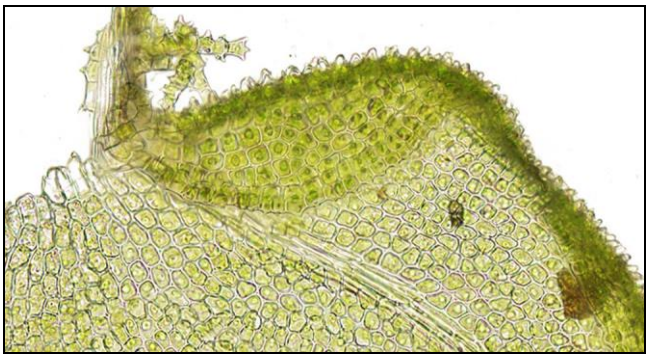

Figure 31. ***Thuidium delicatulum*** leaf showing papillae (see edges). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 32. ***Hedwigia ciliata*** wet on upper left and dry at the edges of the clump on the right. Photo by Janice Glime.

Figure 33. ***Hedwigia ciliata*** showing overlapping leaves with white tips. Photo by Des Callaghan, with permission.

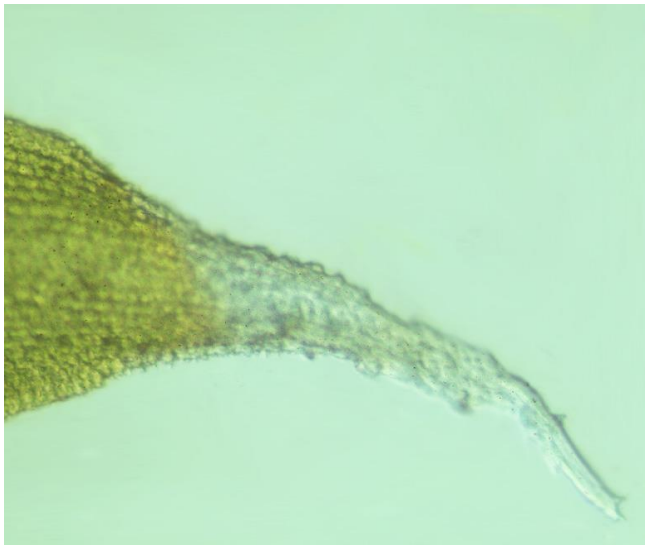

Figure 34. Leaf tip of ***Hedwigia ciliata*** showing papillae on cells. Photo by Janice Glime.

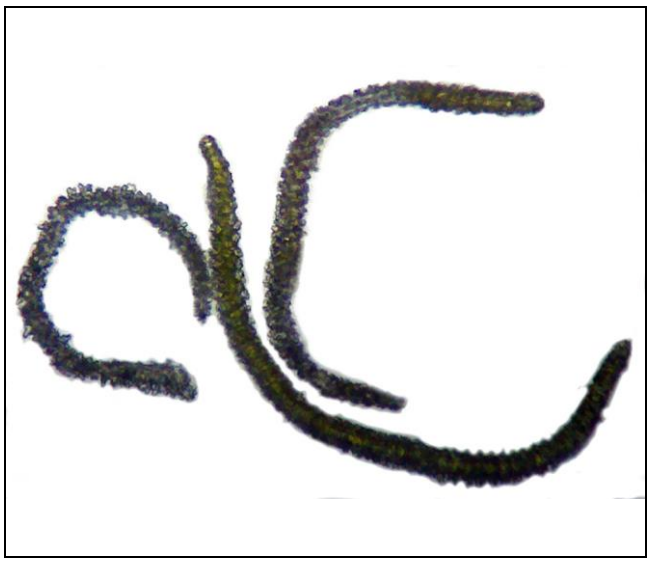

Figure 35. ***Hedwigia ciliata*** leaf cs showing papillae on both surfaces. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Table 1. Comparison of sun and shade leaves of bryophytes and seed plants. + = high rates or large amounts, - = low rates or small amounts, ? = unknown. [Data for seed plants (**tra**) from Larcher 1983, compiled from many authors, with characteristics applying to structures that don't exist in bryophytes omitted; bryophyte (**bry**) data based on literature presented in this volume.]

Characteristic	Sun Leaves		Shade Leaves	
	bry	tra	bry	tra
Structural features				
Area of leaf blade	+	-	+	+
Cell number	?	+	?	-
Chloroplast number per unit area	?	+	?	-
Density of packing of the membrane systems in the chloroplasts	?	-	?	+
Chemical features				
Dry matter	+	+	-	-
Energy content of dry matter	?	+	?	-
Water content of fresh tissue	-	-	+	+
Cell-sap concentration	?	+	?	-
Starch	?	+	?	-
Cellulose	?	-	?	+
Lignin	?	+	?	-
Lipids	?	+	?	-
Acids	?	+	?	-
Anthocyanin, flavonoids	+	+	-	-
Ash	?	+	?	-
Ca/K	?	+	?	-
Chlorophyll *a*/*b*	$\frac{+}{-}$	+	$\frac{+}{-}$	-
Chlorophyll *a* (P-700)	-?	+	+?	-
Photosystem II pigment complex	-	-	+	+
Chlorophyll/xanthophylls	?	-	?	+
Lutein/violaxanthin	+	+	-?	-
Functional features				
Photosynthetic capacity	-	+	+	-
Respiratory intensity	?	+	?	-

Leaf Area Index

The **leaf area index** (**LAI**) has been used to show structural responses of tracheophyte leaves to high vs low light conditions. This value represents the percentage of ground area covered by leaves, hence **(total leaf area) / (area of ground)**. Likewise, bryophytes can exhibit a leaf area index that is directly proportional to the light intensity (Sluka 1983). Unfortunately, few measurements have been taken on bryophytes. Simon (1987) compared two desiccation-tolerant mosses with one more mesic species and found what she considered to be high LAI values. For ***Syntrichia ruralis*** (Figure 36), the LAI was 44, for ***Ceratodon purpureus*** (Figure 37) 129, and for the more mesic ***Hypnum cupressiforme*** (Figure 38) 103. These indeed seem to be enormous. By contrast, forest floor tracheophyte species in a montane forest had an LAI of only 3.8 (Schleppi *et al*. 1999); in a tropical cloud forest the LAI was only 1.6 in a gap less than 8 months old, increasing to the pre-gap level of 5.1 in three years (Lawton & Putz 1988). Larcher (1995) considered 4-6 to be optimal for herbaceous plants with horizontal leaves and 8-10 optimal for grasses. Asner *et al*. (2003) reviewed more than 1000 LAI studies from around the world and found that the maximum for an ecosystem was 18 with a mean of 5.2±4.1. The macroalga *Fucus serratus* (Figure 39) achieved its maximum productivity for an individual at LAI 8-10, while the community did best at 6-8 (Binzer & Sand-Jensen 2002). At the biome level, the LAI seems to range from 0.5 to 16, hardly making a showing against the high values measured by Simon (1987) for bryophytes.

Figure 36. ***Syntrichia ruralis***, a species with a high leaf area index (LAI) compared to most tracheophytes, but not as high as forest bryophytes like ***Hypnum cupressiforme***. Photo by Michael Lüth, with permission.

Figure 37. ***Ceratodon purpureus***, a moss with a very high LAI. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 38. ***Hypnum cupressiforme***, exhibiting a high leaf area index. Photo by Michael Lüth, with permission.

Figure 39. ***Fucus serratus***, a brown alga with a leaf area index (LAI) closer to that of tracheophytes than to bryophytes. Photo by Stemonitis, through Creative Commons.

Just why should bryophytes have such enormous LAI values? As we know from tracheophytes, leaves arranged with minimal overlap vertically will have maximal exposure to sunlight, whereas crowded leaves that overlap (having a high LAI) will cause the plant to exhibit self-shading. Furthermore, leaves that have a strong vertical orientation will have minimal direct exposure to light, thus requiring more leaves. This latter condition would seem to describe some mosses, but not the thallose or two-ranked leafy liverworts. Simon (1987) suggested that the high leaf area found in bryophytes might facilitate uptake of the high levels of CO_2 found near the soil surface. Other advantages might result from the vertical growth and close packing with neighbors, with clustered apical leaves taking maximal advantage of the light. On the other hand, the entire moss branch might behave much like a single leaf of a tracheophyte, with overlapping leaves protecting the chlorophyll from UV damage and maintaining moist internal spaces. New techniques for tracheophytes using models that incorporate both LAI and a foliage clumping index indicate that both measures are needed to separate sun from shade leaves (Chen *et al*. 2003), and it seems that this technique might permit us to explain the high leaf area index of bryophytes, where many leaves are shaded by the upper leaves of the same plant or by overlying branches of prostrate plants.

Self-shading

Because of their three-dimensional nature, plants typically shade themselves. As a result of the high leaf area index, a moss cushion is a source of rapid light extinction due to self-shading. Using Antarctic mosses, Davey and Ellis-Evans (1996) demonstrated that irradiance decreases with increasing depth within the moss – no surprise there. Furthermore, the greatest loss of light was at wavelengths around 675 nm and less than 450 nm, in the neighborhood of those portions of the spectrum causing the greatest chlorophyll activity. Of course species differed in light attenuation, with stem orientation being the most important factor, along with stem density, leaf size, orientation, and pigment content. Light penetration increased upon drying – seemingly a maladaptive trait that would permit light to damage chlorophyll, but an expected result for mosses that curl or fold their leaves upon drying. On the other hand, Davey and Ellis-Evans suggested that this deeper light penetration of dry mosses might permit photosynthesis to occur in the deeper layers (these most likely also being more moist) and thus make up for some of the photosynthetic loss in the drier apical parts.

Bryophyte Canopy

As we have just seen, not only do trees and other tracheophytes provide a canopy over the bryophytes, but the bryophytes themselves provide a canopy that alters the light reaching the lower parts of the plants. This canopy is structured differently and functions differently, relating to issues of scale and external transport of water and nutrients (Rice & Cornelissen 2014). Hence bryophytes demand different methodologies to truly understand their use of light and ultimate photosynthetic product.

Habitats vary in their light quality and intensity and the bryophytes further alter this light in the bryophyte canopy (Figure 40) (Tobias & Niinemets 2010). These authors set out to document bryophyte differences in chlorophyll, carotenoids, nitrogen concentrations, and photosynthetic electron transport capacity as they varied with the light profiles above and within populations of the moss ***Pleurozium schreberi*** (Figure 41). Light differences between habitats resulted in increases in chlorophyll, chlorophyll:N, and chlorophyll:carotenoids as light decreased, thus increasing the light harvesting in low light and increasing light protection in higher light. N levels in the plants were independent of light intensity. In the upper moss canopy (Figure 41) where light was at least 50-60% of the above-canopy light, changes in moss chemistry and photosynthetic output were similar to those observed in the between-habitat light gradient. However, deeper canopy layers mimicked the effects of senescence (Figure 40), with pigment and nitrogen concentrations and photosynthetic capacity decreasing with light availability. They considered the chemical and physiological variation in the moss canopy to be a balance between acclimation and senescence.

Figure 40. ***Pleurozium schreberi*** showing a canopy with an active green layer and a senescent lower layer. Photo by Janice Glime.

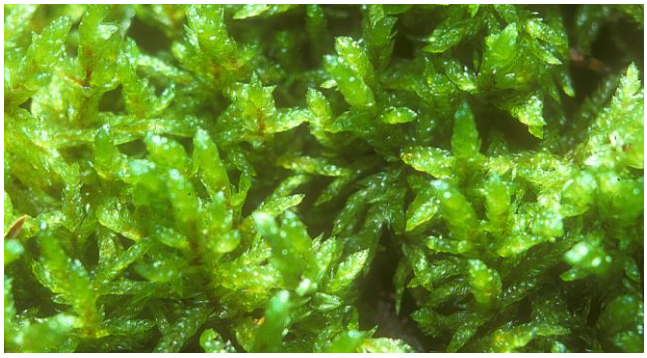

Figure 41. ***Pleurozium schreberi*** as seen at the top of the moss canopy, a typical species in boreal forests. Photo by Janice Glime.

In low light, the foliage is less densely aggregated and plant density is lower, permitting greater light penetration and greater light interception per unit of leaf area (Niinemets & Tobias 2014). In healthy tissues, chlorophyll increases as light levels diminish. But one of the consequences of aging in mosses is that the tissues senesce. This senescent zone is likewise deeper in the moss mat and consequently gets less light. This senescent moss zone has reduced chlorophyll content.

Canopy architecture differs among species. Species, especially of pleurocarpous mosses, that are able to branch and from new leaves from lateral buds are able to extend into areas with greater light as well as providing more opportunities for catching sunflecks (Niinemets & Tobias 2014). One advantage is that plants in high light intensity tend to have cushion growth forms that protect them from the accompanying desiccation. Those in shaded habitats often also experience the greater moisture that permits them to spread horizontally and capture more light.

Rice *et al*. (2014) examined the effects of drying on light relations in ten species of ***Sphagnum*** (Figure 15-Figure 19). They found that spatial variation in the rate of photosynthetic electron transport increased during drying and in high light intensities. There was a positive relationship between that rate and light intensity, but the relationship with drying was negative, and the light and moisture interacted to create the spatial variation. Within the canopy of the moss ***Pleurozium schreberi*** (Figure 41-Figure 41), the mat temperature reached a 9°C span. In the leafy liverwort ***Bazzania trilobata*** (Figure 42), the Lambert-Beer Law predicted the attenuation of light within the liverwort canopy.

Figure 42. ***Bazzania trilobata***, illustrating overlapping branches. Photo by Jan-Peter Frahm, with permission.

Growth and Branching

Low light in plants often results in **etiolation**, elongated growth that often lacks accompanying weight gain, creating thin and often chlorotic plants with long internodes and small, rudimentary leaves. Such growth is seen in grass when a board or rug rests on it for a period of weeks. Bryophytes are no exception to this phenomenon, and increased elongation in incubators should not be mistaken for healthy plants if the plants become long and thin. For example, in one study ***Dicranum majus*** (Figure 43) had its greatest elongation at the lowest irradiance (20 μm m^{-2} s^{-1}) (Bakken 1995).

Figure 43. ***Dicranum majus*** with capsules, a species that has the greatest elongation in low light. Photo by Michael Lüth, with permission.

Bates (1988) examined the effect of shoot spacing on growth and branch development in ***Rhytidiadelphus triquetrus*** (Figure 44). Using intermittent moisture supply and spacings of 5, 10, 20, and 50 mm between shoots, he found that main axis growth was promoted by decreased spacings. Although etiolation occurred when shoots were close together, there was no self-thinning and overall growth seemed to be optimal at or near the closest spacing tested. As a result, productivity was greatest in the most dense colonies (1000 shoots dm^{-2}). Since growth occurs at the tip, there probably is very little effective light loss at these 5 mm spacings between plants, and water is conserved.

Figure 44. ***Rhytidiadelphus triquetrus***. Photo by Janice Glime.

In fact, van der Hoeven and During (1997) found that when plots of three pleurocarpous mosses (***Calliergonella cuspidata*** (Figure 45), ***Ctenidium molluscum*** (Figure 46), and ***Rhytidiadelphus squarrosus*** (Figure 47) were thinned by 50%, the original density returned rapidly, suggesting that density might be regulated by an intrinsic mechanism. Bates (1988) concluded that this dense packing is an indication of the advantage of reduced water loss in the more densely packed shoots and that this advantage outweighs the reduction in light. However, for ***Ctenidium molluscum***, thinning to 50% caused increased growth, presumably due to increased photosynthesis, while its neighbors, ***Rhytidiadelphus squarrosus*** and ***Calliergonella cuspidata*** gained no advantage from the same thinning (van der Hoeven 1999). The differences in morphology may account for the success of ***C. molluscum*** following thinning, for it has dense, overlapping leaves, compared to the spreading leaves of ***R. squarrosus*** and large, slightly overlapping leaves of ***C. cuspidata***. These mosses, after thinning, returned rather quickly to their original density. Like Bates (1988), Van der Hoeven and During (1997) suggested that they have an intrinsic control over their density.

Figure 45. ***Calliergonella cuspidata***, demonstrating overlapping leaves on exposed, ascending shoots. Photo by Michael Lüth, with permission.

Figure 46. ***Ctenidium molluscum***, demonstrating strongly overlapping leaves and branches. Photo by Michael Lüth, with permission.

Figure 47. ***Rhytidiadelphus squarrosus***, demonstrating spreading leaves on ascending shoots. Photos by Michael Lüth, with permission.

Pedersen and coworkers (2001) tested this moisture/light trade-off using one acrocarpous (***Dicranum majus***, Figure 43) and two pleurocarpous (***Ptilium crista-castrensis*** (Figure 48), ***Rhytidiadelphus loreus***, Figure 49) mosses and a leafy liverwort (***Plagiochila asplenioides***, Figure 50). Using several controlled moisture and light levels, they determined that ***Dicranum majus*** and ***Rhytidiadelphus loreus*** had peak growth rates at intermediate densities where light and moisture were balanced, a relationship noted by Bergamini *et al*. (2001) as well. On the other hand, when the environment was either dark or humid, the effect of increased density was negative. ***Ptilium crista-castrensis*** exhibited decreased growth rates under most experimental combinations and ***Plagiochila asplenioides*** seemed to be unaffected. In all cases, it required light levels that were higher than in their natural spruce forest (Figure 53) habitat before the advantages of greater density were manifest, indicating that it is competition for light that limits optimal density, not low water availability. In a similar experiment, Scandrett and Gimingham (1989) found that ***Pleurozium schreberi*** (Figure 40-Figure 41), ***Hylocomium splendens*** (Figure 51), and ***Hypnum jutlandicum*** (Figure 52) likewise exhibited more intraspecific inhibition from crowding in low light than in high light, but yields were higher among sown fragments in low light.

Figure 48. ***Ptilium crista-castrensis***, a species that seems to exhibit no growth rate change with changes in light and moisture levels. Photo by Janice Glime.

Figure 49. ***Rhytidiadelphus loreus*** with capsules, a species that has peak growth rates at intermediate densities where light and moisture are balanced. Photo by David Holyoak, with permission.

Figure 50. ***Plagiochila asplenioides***, a species for which growth seems unaffected by light and moisture levels. Photo by Michael Lüth, with permission.

Figure 51. ***Hylocomium splendens***, a species in which thinning increases branching. Photo by Michael Lüth, with permission.

One consequence of thinning seems to be increased branching (Rydgren *et al*. 1998; Pedersen *et al*. 2001). And it seems that in ***H. splendens*** (Figure 51), the increased light increases production of gametangia and subsequent sporophytes (Rydgren *et al*. 1998). This species had ten times as many sporophytes two years after half the bryophyte cover had been removed, compared to non-thinned plots.

Figure 52. ***Hypnum jutlandicum***, a common gap species. Photo by Michael Lüth, with permission.

Figure 53. ***Picea mariana*** forest showing reduced light on the forest floor. Photo through Creative Commons.

We know that light is necessary to make new chlorophyll, and thus we might predict that there is a depth within a moss cushion at which the light attenuates beyond that needed for chlorophyll manufacture. Van der Hoeven, *et al*. (1993) found that chlorophyll concentration decreased down the shoot as light intensity decreased, but they considered that where only 50% of the shoot was green, the light intensity was too high to attribute the mortality of leaves to low light values. Skré and coworkers (1983), however, found that self-shading coincided with the transition from green to brown parts in ***Hylocomium splendens*** (Figure 51) and felt that light attenuation helped to explain the death of the green moss tissue.

Skré *et al*. (1983) showed (Figure 54) that in ***Hylocomium splendens***, PAR (photosynthetically active radiation) at a depth of 3 cm in natural moss canopies is reduced to ~17%; to ~8% in ***Pleurozium schreberi*** (Figure 40-Figure 41); to ~12% in a mixed canopy of ***Pleurozium schreberi*** and ***Polytrichum commune*** (Figure 55); and to only 1% in ***Sphagnum subsecundum*** (Figure 56). Visnadi and Vital (1989) found that there were more species entangled among themselves in the indirect sunlight of the riverbank than in the river bed, where direct light was available, indicating that self-shading, and neighbor-shading, might not always be a bad thing.

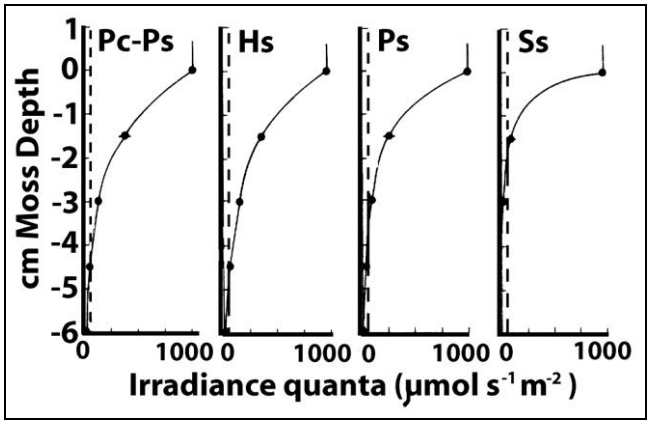

Figure 54. Diminishing PAR in the moss clump. PcPs = ***Polytrichum commune*** and ***Pleurozium schreberi***. Hs = ***Hylocomium splendens***. Ps = ***Pleurozium schreberi***. *Ss* = ***Sphagnum subsecundum***. Figure redrawn from Skré *et al*. 1983.

Figure 55. ***Polytrichum commune***, a species that is able to reduce the light available to ***Pleurozium schreberi***. Photo by Christopher Tracey through Creative Commons, with permission.

Figure 56. ***Sphagnum subsecundum***, a species that can reduce PAR to only 1% in 3 cm. Photo by Michael Lüth, with permission.

Chlorophyll Fluorescence

Chlorophyll fluorescence (light re-emitted by chlorophyll molecules during return from excited to non-excited states; Figure 57) is one measure of stress in leaves. This is expressed as the ratio of variable fluorescence ($\mathbf{F_v}$ = difference between the maximum and minimum fluorescence) to maximum fluorescence ($\mathbf{F_m}$ = fluorescence resulting from flashing a leaf in the dark with bright light), known as $\mathbf{F_v/F_m}$. The ratio is usually about 80% efficiency; lower measures indicate stress.

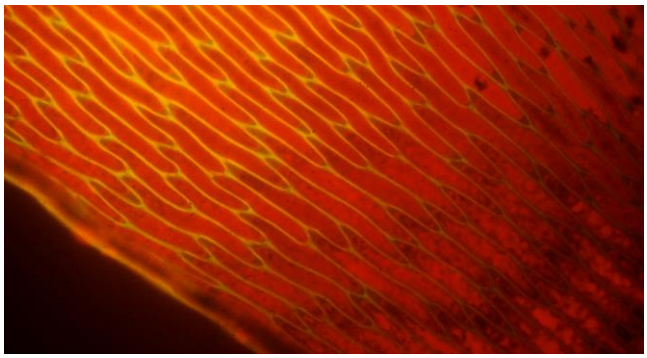

Figure 57. ***Fontinalis antipyretica*** leaf showing red chlorophyll fluorescence. Photo by Janice Glime.

Rice *et al*. (2005) demonstrated that the $\mathbf{F_v/F_m}$ ratio decreased when three bryophytes [***Bazzania trilobata*** (Figure 42), ***Sphagnum girgensohnii*** (Figure 60), ***Pleurozium schreberi*** (Figure 40-Figure 41)] were exposed to high light intensity, indicating stress. But in many bryophytes, while some leaves may be at stress levels, others may be at ideal levels. Using laser technology, Rice *et al*. developed a method to measure surface roughness and depth to first vertical canopy contact, thus permitting a more accurate measurement of light penetration and turbulence and providing a tool that may permit a better understanding of CO_2 exchange.

Morphological Responses

It appears that, like tree leaves, bryophytes might respond structurally to differences in light levels. Dalby (1966b) compared the leaves of the tufa-forming moss ***Eucladium verticillatum*** (Figure 58-Figure 59) from deep shade with those from the open and found that those grown in deep shade had much broader leaves, not unlike the response seen in some tree species (Figure 61).

Figure 58. ***Eucladium verticillatum***, a tufa-forming moss. Photo by Michael Lüth, with permission.

Figure 59. ***Eucladium verticillatum***, a species that when grown in deep shade has much broader leaves. Photo by Michael Lüth, with permission.

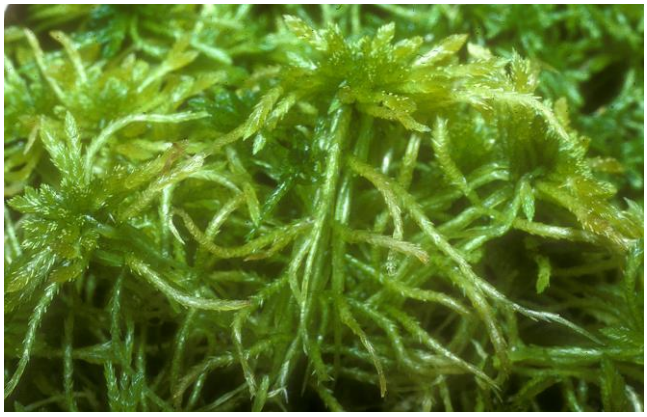

Figure 60. ***Sphagnum girgensohnii***, a species of peatland forests and *Thuja* swamps. Photo by Janice Glime.

At least some species exhibit a seasonal change in their light extinction curves that can be due to a change in leaf weight similar to that seen when tree leaves respond to high light. ***Calliergonella cuspidata*** (Figure 45), ***Ctenidium molluscum*** (Figure 46), and ***Rhytidiadelphus squarrosus*** (Figure 47) all exhibit a higher extinction coefficient in September than in December. In fact, the shoots are 1.5-2.1 times as heavy in September as in December, being so dense that the light intensity at the bottom of the plant approaches zero (van der Hoeven *et al*. 1993; Figure 62).

In culture, the thallose liverwort ***Marchantia paleacea*** var. ***diptera*** (Figure 63) exhibited an increase in growth rate with increasing light intensity over the range of 5.4 to 60 W m^{-2}, whereas a significant decrease occurred at light intensities >60 W m^{-2}. Many ***Sphagnum*** (Figure 15-Figure 19) species are high-light plants. In a growth study, weight increase of the species was greatest in unshaded conditions when the water table was low, but in shaded conditions, there was little difference with water table (Clymo 1973). However, when length was considered, plants of all ***Sphagnum*** species grew less in low water conditions, especially if they were also shaded – hardly an etiolation response.

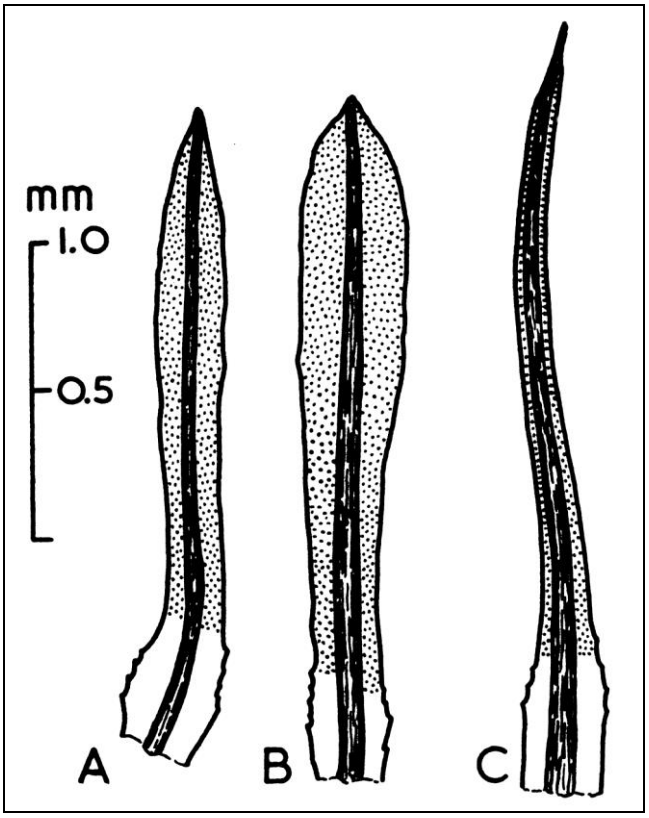

Figure 61. Effect of light intensity on ***Eucladium verticillatum*** leaves. **A** and **B** from deep shade in Kimeridge, Dorset, England; **C** from open at Lyme Regis, Devon. Redrawn from Dalby 1966a.

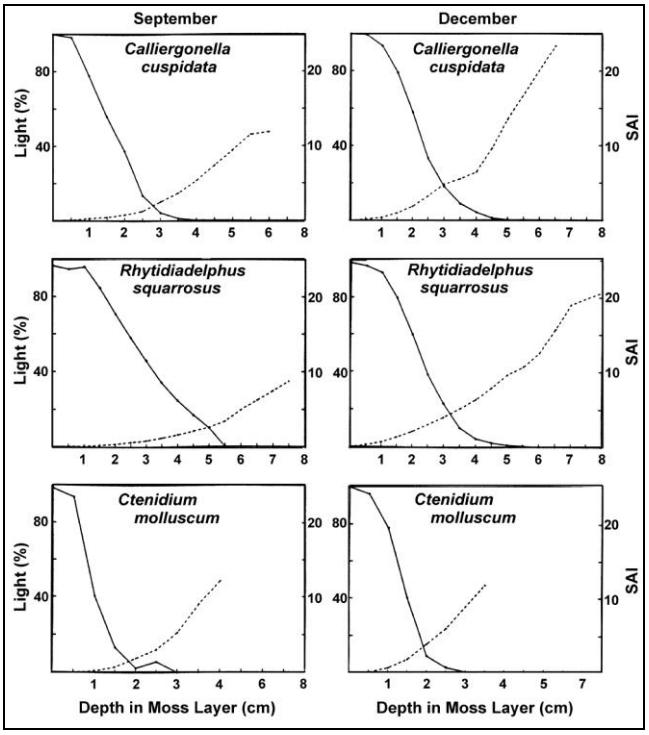

Figure 62. Vertical profiles of light extinction (% of surface; solid line) and shoot area index (SAI, cm^2/cm^2; dashed line) of three mosses in September (n=3) and December (n=5). Redrawn from van der Hoeven *et al*. 1993.

Figure 63. ***Marchantia palacea*** var. ***diptera***, a species that increases its growth rate with increasing light intensity. Photo by Janice Glime.

Physiological Adaptations to Low Light

Although bryophytes in general seem to be shade adapted, at least in their chlorophyll ratios, there are still differences among the species that adapt them to different habitats or give them a competitive edge. For example, ***Plagiomnium acutum*** (Figure 64) has greater capacity to absorb and use low light, giving it a greater photosynthetic assimilation efficiency than its associate ***Herpetineuron toccoae*** (Figure 65) in shady and wet habitats (Li *et al* 1999).

Figure 64. ***Plagiomnium acutum***. Photo by Yingdi Liu, with permission.

Figure 65. ***Herpetineuron toccoae*** leafy plants with sporophytes. Photo with permission by Li Zhang at <www.hkflora.com>, with permission.

Buryová and Shaw (2005) affirmed that light treatments had a greater effect of growth and other characters of ***Philonotis fontana*** (Figure 66) than did water. Different populations, representing different genetic variants, exhibited different patterns of plasticity of form. Variation of leaf dimensions had a strong genetic component (20-30% of total variation), but cell dimensions (Figure 67) seemed to have little genetic variation.

Figure 66. ***Philonotis fontana***, a species in which growth rate is affected by light intensity more than by water. Photo by Des Callaghan, with permission.

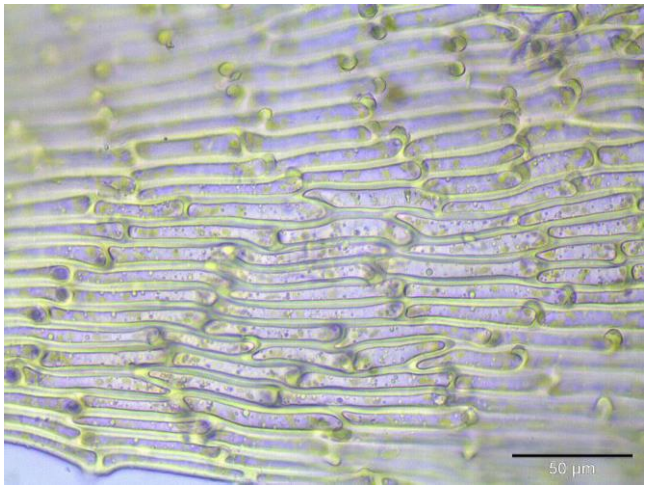

Figure 67. ***Philonotis fontana*** leaf lamina showing prorate cells. These cells have little genetic variation. Photo by Kristian Peters through Creative Commons.

But what are the characteristics that enhance photosynthesis in bryophytes? Waite and Sack (2010) examined ten Hawaiian bryophyte species and quantified 35 physiological and morphological traits. The moss species, typical of shade species, exhibited low leaf mass per area and low gas exchange rate. But their light-saturated photosynthetic rate per mass did not correlate with habitat light intensity. Instead, using canopy mass, not leaf mass, other photosynthetic parameters and morphological traits did correlate with microhabitat light characters. This relationship resulted in an inter-correlation of leaf area, cell size, cell wall thickness, and canopy density. Furthermore, structural allocations such as costa size, canopy height, and mass were linked with these modifications.

Chlorophyll

Bryophytes are C_3 plants. As such, they are adapted to light capture at low light intensities. In tracheophytes, the primary adaptation to low light is to increase the antenna pigment chlorophyll *b*. This provides more opportunities to trap light energy reaching the leaf and to transmit it to the action site of chlorophyll *a*. Sluka (1983) supported the concept of increased chlorophyll concentrations at low light intensities in bryophytes by showing that total chlorophyll content of mosses is inversely proportional to light intensity. As in tracheophytes, it is chlorophyll *b* that increases in response to low light. Szarek (1994), working in the High Tatra Mountains of southern Poland, found that higher light intensities in the middle reaches of the stream did not have any effect on chlorophyll *a* concentrations of mosses compared to areas with less light.

In tracheophytes, this increase in chlorophyll *b* results in a lower *a*:*b* ratio. Thus, it is not surprising that bryophytes, as predominantly shade plants, typically have a low *a*:*b* ratio compared to tracheophytes. Mishler and Oliver (1991) reported *a*:*b* ratios of 1.00-2.5 for the xerophytic moss ***Syntrichia ruralis*** (Figure 36), a desiccation-tolerant moss that likewise has a higher chlorophyll concentration at low light intensities (Hamerlynck *et al*. 2002). Nevertheless, these *a*:*b* ratios, even for sun-grown plants, were typical of shade-adapted tracheophytes, whereas the carotenoid:chlorophyll ratio of sun plants was typical of sun-adapted tracheophytes. These acclimation responses reversed in a reciprocal transplant experiment, indicating that this species is capable of making short-term adjustments. Nevertheless, transplanted sun plants of ***S. ruralis*** did not perform as well in shade as did previously shade-grown plants. Hamerlynck *et al*. (2002) considered this to indicate that the sun-acclimated plants were able to maintain their photoprotective mechanisms, losing them only slowly, whereas the shaded plants were able to maintain activity longer, due to greater moisture, allowing them to adjust to changes rapidly following disturbance that exposed them to greater sunlight. This ability to adjust permits them to persist in their semi-arid grassland home.

Tuba (1987), as already discussed, has a different explanation. He suggests that these low *a*:*b* ratios are important because poikilohydric plants must depend on atmospheric moisture to regulate their internal water content and that such moisture is most typically available during periods of low light – during a storm or early morning. Since these plants are often desiccated during periods of high light levels, Tuba suggests that it is logical that their chlorophyll is adjusted to low light levels, but that having light compensation points slightly higher than those of shade-adapted tracheophytes permits bryophytes to benefit from occasional sunflecks.

It therefore comes as a surprise to find that the chlorophyll *a*:*b* ratio in many bryophytes does not decrease in response to low light, while the total chlorophyll increases. For example, in experiments on three species of the thallose liverwort ***Riccia***, the highest chlorophyll concentrations occurred in the shade-grown ***Riccia discolor***, and the lowest occurred in the floating aquatic species, ***Riccia fluitans*** (Figure 68), as one would expect. But surprisingly, the chlorophyll *a*:*b* ratios did not differ among the species (Patidar *et al*. 1986). In ***Sphagnum fimbriatum*** (Figure 69), both chlorophyll *a* and chlorophyll *b* increased in dim light; in dim light at 25ºC, the *a*:*b* ratio increased only slightly, while at 15ºC, no such increase was observed (Koskimies-Soininen & Nyberg 1991). Similarly, Rincòn (1993) compared six species of bryophytes under seven different light conditions and found, as expected, that the total chlorophyll was highest at the lowest level of light, but that the chlorophyll *a*:*b* ratio did not differ significantly among the treatments.

Figure 68. Terrestrial form of ***Riccia fluitans***. Photo by Michael Lüth, with permission.

Figure 69. ***Sphagnum fimbriatum***, a species that increases both chlorophylls *a* and *b* in low light. Photo by J. K. Lindsey, with permission.

Yang and coworkers (1994) found that seventeen species of bryophytes at Yuan-Yang Lake in China had lower chlorophyll *a*:*b* ratios (mean 2.41) than the two aquatic tracheophytes sampled (mean 3.08), but that these bryophyte ratios were considerably higher than values for bryophytes reported in the literature. They considered this to be a demonstration of the ability of bryophytes to adjust their chlorophyll *a*:*b* ratio within a limited range to a higher light intensity (250 µmol m^{-2} s^{-1}).

As discussed earlier in the study by Marschall and Proctor (2004), chlorophyll content seems to account for liverworts being more common in shade, with more mosses able to survive in bright, open areas. Pande and Singh 1987) found higher concentrations of both carotenoids and chlorophyll in liverworts, with the exception of ***Stephensoniella brevipedunculata***, compared to mosses, but in this study liverworts all came from shade and mosses from open areas. Doera and Chaudhary (1991) examined

chlorophyll content of several bryophytes and found that chlorophyll *a* ranged 0.402 ± 0.052 to 2.002 ± 0.700 mg g^{-1} dry mass, with chlorophyll *b* ranging 0.265 ± 0.067 to 1.634 ± 0.070 mg g^{-1}. Lowest chlorophyll concentrations were found in the moss ***Entodon prorepens*** (Figure 70) (0.667 mg g^{-1} dry mass) and highest in the liverwort ***Cyathodium tuberosum*** (Figure 71) (3.636 mg g^{-1} dry mass), consistent with the observations of Marschall and Proctor (2004). In these bryophytes, low light intensity resulted in increase in total chlorophyll content and lower chlorophyll *a*:*b* ratio. On the other hand, Antarctic populations of ***Ceratodon purpureus*** (Figure 12) can decrease chlorophyll *a*:*b* ratios in high light (Post 1990). Is it any surprise that these responses are not always the same, that they differ with species, temperature, moisture content, and light level?

Figure 70. ***Entodon prorepens***, a species with low chlorophyll concentrations. Photo by Li Zhang, with permission.

Figure 71. ***Cyathodium cavernarum***, a species with a high concentration of chlorophyll. Photo by M. C. Nair, through Creative Commons.

Mártínez Abaigar *et al*. (1993) have compared the chlorophyll concentrations on a per unit area basis. Their results, compared to light and water availability, appear in Table 2. Examination of the table does not reveal any relationship among these species with either light availability or water availability and chlorophyll concentration. However, there seems to be a good correlation between chlorophyll concentration and submersion. Only ***Schistidium rivulare*** (Figure 72-Figure 73) among the emergent taxa has a high chlorophyll concentration. This might be explained by the dark coloration of the cell walls that would filter the high light intensity before it reaches the chlorophyll.

Figure 72. ***Schistidium rivularis*** exposed on rock and illustrating its black coloration. Photo by Janice Glime.

Figure 73. ***Schistidium rivularis*** with sporophyte, showing blackish coloration. Photo courtesy of Betsy St. Pierre.

Table 2. Chlorophyll concentrations as mg m^{-2} for bryophyte species occurring in full sun, sun, shade, and deep shade and five water availabilities (I = immersed, E = emerged, D = dry; LSA = Leaf Specific Area, LSW = Leaf Specific Weight). Species are arranged from highest to lowest chlorophyll concentrations. From Mártínez Abaigar *et al*. 1993.

	chl mg m^{-2}	light availability	water availability	LSA cm^2 g^{-1}	LSW mg cm^{-2}
Schistidium rivulare	351±17	full sun	I-E-D	133±7	7.51±.4
Fontinalis squamosa	341±14	sun	I	271±13	3.7±.18
Fontinalis antipyretica	290±14	full sun	I	226±16	4.42±.31
Fissidens grandifrons	289±13	full sun	I	222±4	4.5±.08
Rhynchostegium riparioides	257±4	deep shade	I-E	224±9	4.47±.18
Cinclidotus fontinaloides	250±13	full sun	I-E-D	164±15	6.11±.56
Cratoneuron filicinum	246±4	full sun	I-E-D	274±15	3.65±.2
Fissidens grandifrons	244±11	deep shade	I	211±8	4.73±.18
Jungermannia cordifolia	173±6	full sun	I	351±15	2.85±.12
Hygrohypnum duriusculum	157±8	full sun	I-E-D	313±25	3.2±.26
Scapania undulata	150±7	shade	I-E-D	262±10	3.81±.15
Cratoneuron commutatum	121±10	full sun	E	187±25	5.36±.72
Brachythecium rivulare	116±5	full sun	I	456±41	2.19±.2
Pellia endiviifolia	97±7	shade	E	446±15	2.24±.08

Figure 74. ***Schistidium rivulare***, exhibiting dark pigmentation. Photo by Michael Lüth, with permission.

Other Pigments

Other pigments also change in response to light intensity, as shown for ***Rhytidiadelphus triquetrus*** (Figure 44), ***R. squarrosus*** (Figure 47), and ***Mnium hornum*** (Figure 75-Figure 76) (Brinkmeier *et al*. 1999). In these mosses biflavonoid concentration was correlated with periods of active growth and varied with light intensity. The shade-adapted liverworts in Nainital, Kumaun Himalaya, exhibited higher carotenoid concentrations than did the mosses growing in the open (Pande & Singh 1987). However, the chlorophyll:carotenoid ratio seemed not to differ, at least during the rainy season, which is the period of maximum growth. It is reasonable that carotenoid content would be adaptive to shade plants because it can serve as an antenna pigment, much like chlorophyll *b*, providing additional light capture capability and transferring that energy to the chlorophyll *a* reaction center. Such an adaptation is known not only in bryophytes, but also in tracheophytes, where total carotenoid content and β-carotene increase simultaneously with chlorophyll in the shade (Czeczuga 1987). On the other hand, **lutein** (deep yellow pigment) increases in the sunlight.

Figure 75. ***Mnium hornum***, a species in which pigments change in response to light. Photo by Bob Klips, with permission.

Figure 76. ***Mnium hornum***, illustrating a lighter color that could be a response to different light conditions. Photo by Michael Lüth, with permission.

It is interesting that many of the pigments seem to vary together in concentration, at least in the Antarctic mosses tested (Lovelock & Robinson 2002). Total chlorophyll was correlated highly with total carotenoids (0.91), which in turn were highly correlated with each other (lutein and xanthophyll cycle pigments). **Anthocyanins** also correlated but somewhat less highly with chlorophyll. However, the photoprotective **zeaxanthin** and **antheraxanthin** were negatively correlated with total chlorophyll, as one would expect if chlorophyll *b* increases in response to low light.

Several researchers have found that hydrated mosses, unlike tracheophytes, require only a few molecules of zeaxanthin per reaction center to dissipate light energy (Bukhov *et al*. 2001; Heber *et al*. 2005). Desiccation-dependent fluorescence quenching, however, is independent of zeaxanthin and appears to be a property of the reaction center complex of photosystem II rather than the antenna system.

Chloroplast Movement

In at least some mosses, the chloroplasts move in response to light direction. This ability of chloroplasts to orient themselves in response to direction of light, thus maximizing absorption of light energy, is known elsewhere in the plant kingdom. The green alga *Mougeotia* (Figure 77) has an axial chloroplast that can rotate on its axis to face the sun. Often the two ends seem to rotate independently so the chloroplast becomes twisted in the middle. The ferns *Adiantum capillus-veneris* (Figure 78), *A. caudatum* (Figure 79), *A. diaphanum* (Figure 80), and *Pteris cretica* (Figure 81) all exhibit chloroplast movement in their leaves, responding to blue light; *A. capillus-veneris* chloroplasts also responded to red light (Augustynowlcz & Gabrys 1999). The prothallus of the fern *Dennstaedtia punctiloba* (Figure 82-Figure 83), growing in lava caves, exhibits a luminescence similar to that seen in the moss ***Schistostega pennata*** (Figure 2-Figure 4) (Glime & Iwatsuki, pers. obs.). In ***Schistostega pennata***, chloroplasts of the protonemata orient themselves to attain maximum light, as discussed in the light subchapter on cave mosses.

Figure 77. ***Mougeotia*** sp, a genus with a flat chloroplast that rotates on its axis to respond to position of incoming light. Photo by Yuuji Tsukii, with permission.

Figure 78. ***Adiantum capillus-veneris***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Tigerente, through Creative Commons.

Figure 79. ***Adiantum caudatum***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Guz Hengman, through Creative Commons.

Figure 80. ***Adiantum diaphanum***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Phil Bendle, with permission.

Figure 81. ***Pteris cretica***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Forest and Kim Starr, through Creative Commons.

Figure 82. ***Dennstaedtia punctilobula***, a species in which the gametophyte prothallus chloroplasts move in response to the direction and intensity of light, giving them a luminescence similar to that of ***Schistostega pennata***. Photo by John Knouse, through Creative Commons.

Figure 83. ***Dennstaedtia punctilobula*** luminescent prothalli from a lava cave in Iceland. Photo by Janice Glime.

In protonemata of the moss ***Physcomitrella patens*** (Figure 84), the direction of light, intensity, and wavelength are all important to chloroplast arrangement. When the light is perpendicular to the protonema axis the chloroplasts accumulate next to the crosswalls, but when it is parallel to the protonema axis, *i.e.* perpendicular to the crosswalls, there is no accumulation of chloroplasts there (Kadota *et al*. 2000). The response depends on the intensity, with lower intensities (red light 0.118 W m^{-2} or blue light 0.01-85.5 W m^{-2}) inducing accumulation, whereas higher ones (red light $\geq$ 60 W m^{-2} or blue light 285 W m^{-2}) do not. These responses are mediated by phytochrome. But the protonemata of ***Physcomitrella patens*** respond not only to the direction of light (Kadota *et al*. 2000), but also to mechanical stimuli (Sato *et al*. 2003). This causes the chloroplasts to accumulate on the side of the cell where contact is made – in as little as 30 minutes! Could this be an adaptation to high light by placing the chloroplasts on the side next to the substrate and therefore on the side farthest from the light source? Such a position would provide more cytoplasm to serve as a filter from UV light and high light intensity. On the other hand, it would also permit the side toward the sun to act as a focussing lens. There is so much we don't know!

Figure 84. ***Physcomitrella patens*** plants with their protonemata on the left. Photo by Michael Lüth, with permission.

Movement of chloroplasts is a response to blue light intensity (Königer 2014). In low light, they spread out, maximizing light interception. In high light, they move to the sides of the cells in an avoidance reaction, minimizing light interception. But most mosses may be slower to react or not react at all. ***Physcomitrella patens*** (Figure 84) had no net change in light transmission under increasing blue light intensities up to one hour at 100 µmol photons m^{-2} s^{-1}. The fern *Adiantum capillus-veneris* (Figure 78) likewise showed no accumulation response and only a slow avoidance response. The tracheophyte *Arabidopsis thaliana* (Figure 85), on the other hand, exhibited both strong accumulation and avoidance responses.

Figure 85. ***Arabidopsis thaliana***, a species that exhibits both strong accumulation and avoidance responses to increasing levels of blue light. Photo by Nicole Hanley, through Creative Commons.

Light and Storage

The ultimate consequence of changing chlorophyll concentrations and chloroplast position is an altered ability to store photosynthate. Kobe and Silander (1993) have shown that in four trees adapted to low light intensities, survivorship of juveniles in low light conditions is positively related to carbohydrate reserves and inversely related to high-light growth. This demonstrates the importance of storing carbohydrates as opposed to using all of them for growth during periods of high light. Such correlations have not been tested for bryophytes, but may relate to storage of carbohydrates in the spring before the canopy foliage appears for use of the developing sporophyte during the summer and autumn. Kobe and Silander contend that the trade-off between storage and growth relates to survivorship in low-light habitats. Rincòn and Grime (1989) have shown that production of biomass is not correlated with shoot extension in five grassland bryophytes, and that it in fact can be an inverse relationship, with shoot extension occurring later, again indicating the importance of storage. Could this be related to the ability to store carbohydrates for use later in low light when IAA may facilitate more elongation? (IAA is inhibited by light in tracheophytes.)

In ***Sphagnum fimbriatum*** (Figure 87) low light caused increased storage of total lipids (Koskimies-Soininen & Nyberg 1991). However, in darkness, as one might expect, lipid content decreased. When low light was accompanied by a decrease in temperature, the moss stored more palmitic, stearic, linoleic, and arachidonic acids in the galactolipids monogalactosyl diglyceride (MGDG), *i.e.* the chloroplast lipids. At the same time, oleic and α-linolenic acids decreased. The MGDG lipids are important in cold hardening and adjustment of plant metabolism to low temperatures. For example, arachidonic acid has a freezing point of -49.5^{o}C (Gellerman *et al.* 1972), thus maintaining membrane fluidity at any temperature these mosses are likely to experience in nature. Karunen (1982) suggested that the presence both of high quantities of angiospermous type galactolipid fatty acids and the lowest quantities of algal type in the aquatic moss ***Fontinalis*** (Figure 86) had evolutionary significance in placing this as an advanced genus, at least biochemically.

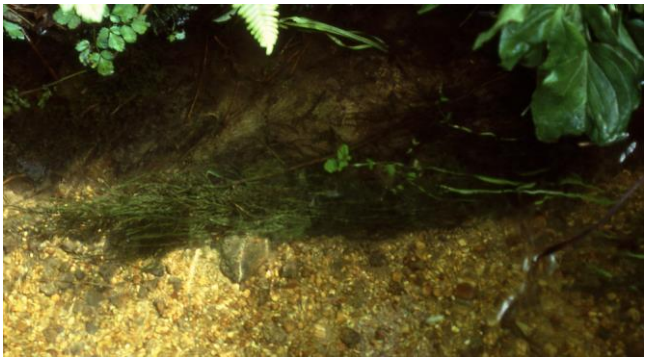

Figure 86. ***Fontinalis duriaei***, a species with high quantities of flowering plant type galactolipid fatty acids and very low quantities of the algal type. Photo by Janice Glime.

Figure 87. ***Sphagnum fimbriatum***. Photo by Michael Lüth, with permission.

One cannot generalize from these results, however. When Koskimies-Soininen and Nyberg (1991) compared their results for the shade plant ***Sphagnum fimbriatum*** (Figure 87) with similar experiments on the high light species ***Sphagnum magellanicum*** (Figure 19), the responses to light and temperature were different. At low temperatures, ***S. fimbriatum*** does not increase its unsaturated glycolipids, reaching its lowest level at 10ºC, whereas ***S. magellanicum*** reaches its lowest level at 0ºC. In fact, we should expect differences among species, as these are the very things that make many species become species. For example, Li and coworkers (1999) compared photosynthesis of ***Plagiomnium acutum*** (Figure 64) and of ***Herpetineuron toccoae*** (Figure 65) under different weather conditions. Photosynthesis of ***P. acutum*** was lower on sunny days than that of ***H. toccoae***, but on cloudy and rainy days it was higher. They determined that ***P. acutum*** has a higher CO_2 assimilation efficiency in shady and wet habitats. Working with mosses on semi-arid granitic boulders, Alpert and Oechel (1987) also found that species occurring in microhabitats with lower light availability had a higher rate of net photosynthesis at low photon flux densities than did other mosses from that site, suggesting a higher chlorophyll concentration.

Based on the literature, it appears that photosynthetic rates of mosses are considerably less than those of tracheophytes. This is consistent with their slow growth rates. For example, in comparing the shade liverwort ***Marchantia polymorpha*** (Figure 88) with the sun moss ***Ceratodon purpureus*** (Figure 37), Aro and coworkers (1981) found that the plastid ultrastructures of these two bryophytes were characteristic of shade and sun plants respectively, but both exhibited the photosynthetic rates typical of shade plants. But Martin and Adamson (2001) disagree with the method of representing these determinations of photosynthetic rates in bryophytes. They found that indeed the CO_2 uptake rate (*i.e.* photosynthetic rate) is much lower than that of tracheophytes when expressed per unit of biomass, but when they used the rate per chlorophyll concentration to compare maximum photosynthetic rates of bryophytes vs tracheophytes under the same conditions of light saturation and ambient CO_2, the photosynthetic rates between bryophytes and tracheophytes did not differ (Shouldn't we expect that?)

The chlorophyll seems to behave the same way in both; it is the concentrations of chlorophyll that differ.

Figure 88. ***Marchantia polymorpha*** with archegoniophores, a shade plant with plastids characteristic of shade plants. Photo by Rudolf Macek, with permission.

Forest Gaps

Forest gaps are well known to foresters as sites where trees experience release growth, expressed in larger tree rings and greater annual production. Wayne and Bazzaz (1993) explored the relative effects of forest gaps compared to shadehouses on two species of birch [*Betula populifolia* (Figure 89) and *B. alleghaniensis* (Figure 90)] and found that leaf structure (specific leaf mass, leaf mass ratio) in shadehouses more closely resembled that of sun plants than did that of the gap-grown plants, but that gap-grown plants behaved more like sun plants in chlorophyll *a*:*b* ratios and maximum net photosynthesis.

Figure 90. ***Betula alleghaniensis***, a forest gap species that exhibits chlorophyll *a*:*b* ratios and max net photosynthesis of sun plants when living in gaps. Photo by Keith Kanoti, through Creative Commons.

Despite their adaptations to low light, many bryophytes also benefit from the brighter spots in the forest. Even in the relatively open forest types like spruce (Figure 53), light attenuation between canopy and forest floor can be considerable (Figure 93) (Tuba & Nyilas 1980). In stands of *Pseudotsuga menziesii* (Figure 91) and *Tsuga heterophylla* (Figure 92) in Oregon, USA, bryophyte abundance increases in canopy gaps and other places with a higher irradiance within the forest (Rambo & Muir 1998).

Figure 89. ***Betula populifolia*** leaves, a forest gap species that exhibits chlorophyll *a*:*b* ratios and max net photosynthesis of sun plants when living in gaps. Photo by Richtid, through Creative Commons.

Figure 91. ***Pseudotsuga menziesii*** & Pinus ponderosa forest showing difference in light at the top of the canopy and in lower parts of the canopy. Photo by Jsayre64, through Creative Commons.

Figure 92. ***Tsuga heterophylla*** forest in Alaska showing the reduced light reaching the forest floor. Photo by Willow and Monk, through Creative Commons.

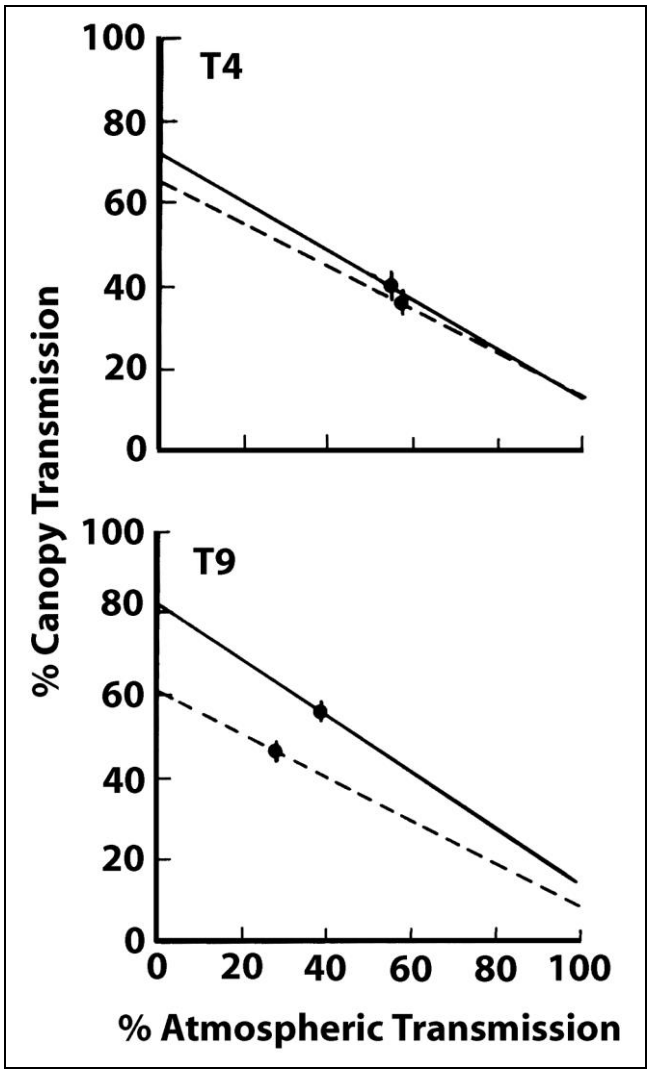

Figure 93. Linear regression of transmission of canopy light to forest floor as a % of atmospheric radiation, expressed as a % of radiation incident on the atmosphere. T4 and T9 are two sites in a mature black spruce forest in central Alaska. In transect 4 ── represents 68% canopy closure; - - - represents 36% canopy closure. In transect 9 ── represents 49% canopy closure; - - - represents 33% canopy closure. Figure redrawn from Skré *et al*. 1983.

For bryophytes, forest gaps provide periods of high intensity light that for some species can enhance growth, while for others the additional desiccation and high temperatures can mean cessation of growth. However, in the margins of the gaps, where sunlight is intermittent during the day, bursts of sun, or sunflecks, can be significant contributors to the productivity. Studies on vascular plants suggest that responses to light gaps having intermittent light can be significantly different from continuous low or high light (Wayne & Bazzaz 1993). There are few studies on bryophytes to explore the importance of sunflecks within the forest or the effect of intermittent light in gaps. Yet, in many temperate forests, such intermittent light may be more the rule than the exception. Wayne and Bazzaz (1993) suggest that the plasticity of response by some species to intermittent light may have potential for niche differences and coexistence. Such studies should not be difficult to do on bryophytes using either laboratory conditions or strobe lighting in the field, and with modern electronic recording equipment, even natural sunflecks can be recorded and productivity monitored..

But not all gaps are beneficial to bryophytes. Brunkman (1936) puzzled over the presence of ***Hylocomium splendens*** (Figure 51) in some of the *Myrtillus* associations but not others. After careful quadrat study, he learned that the ***Hylocomium splendens*** all but disappeared within four years of cutting the forest. He attributed this disappearance to light, since the soil was "decidedly wet," allowing for the indirect effect of sunlight on the available moisture. Since he found the uncut forest to be just as wet as the cut forest, he concluded that light was the factor resulting in the loss of ***H. splendens*** in the open. He likewise cited differences in moss cover between north and south slopes (71% and 3%, respectively) as evidence that light was the critical factor. He reasoned that the south slope would have a much longer light day and light season than the north slope. On the other hand, ***Hylocomium splendens***, ***Pleurozium schreberi*** (Figure 41), and ***Hypnum jutlandicum*** (Figure 52) commonly occur in the gaps formed by degenerate *Calluna vulgaris* (Figure 94) bushes in the dry heathland (Scandrett & Gimingham 1989), so it appears that they can benefit from more light under the right conditions.

Figure 94. ***Calluna vulgaris*** showing reduced cover in areas with shorter or dying plants. Photo by Willow, through Creative Commons.

In one North American forest, where a storm had uprooted nearly half the trees, moss cover disappeared rapidly, whereas in the part where trees remained upright, the moss cover was nearly normal (Brunkman 1936). Brunkman (1936) further cited evidence from two adjacent plots, one of spruce (Figure 53) with 85% mean cover of moss on 16 quadrats and another of poplar (*Populus*, Figure 95) with 6% mean cover on 16 quadrats. Then he compared the densities of the trees on these and other plots in an attempt to correlate the light availability with decrease in moss cover. To his surprise, no correlation existed. To explain this anomaly, he considered the fact that poplar is lacking leaves for eight months of the year, whereas spruce is never without leaves. While Brunkman seemed uncomfortable with the lack of correlation, he still considered that tree density was important above 0.5, and he concluded that densities above 0.8 have high moss cover, the lowest being 59%. He noted that in light gaps, the moss cover would be moderate to high, and the flora of flowering plants would include a "decidedly larger number of individuals."

Larsen (1980) contends that if a gap occurs in a boreal spruce forest (Figure 53), the spaces are occupied to a greater extent by herbaceous species and moss cover will diminish. It appears that the relationship of moss cover to light availability may be complicated by the availability of suitable species and the length of time since the light became available. In any event, the species occupying the lighted gap will be different from those occupying the forest before the opening was created (Larsen 1980).

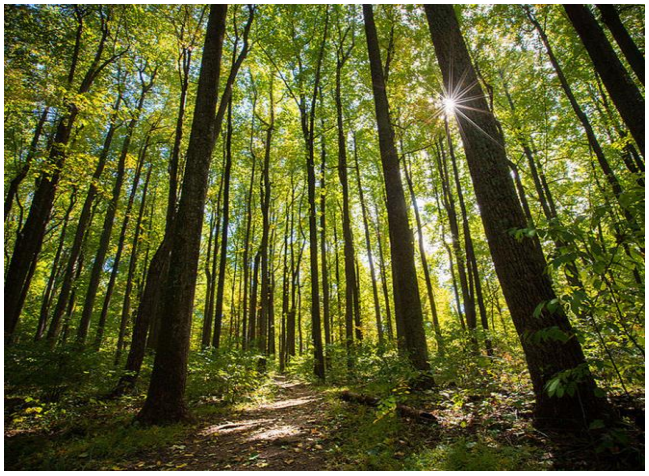

Figure 95. ***Populus*** forest showing sunflecks on the forest floor. Photo from Shenandoah National Park, through Creative Commons.

In an attempt to determine the importance of "reserve trees" to forest management, Shields (2006) examined not only the woody and herbaceous plants in openings with a single central tree (reserve tree) to those of the forest matrix in uneven-aged northern hardwood forests (Figure 96) in the Upper Peninsula of Michigan, but also the bryophytes. He found that bryophyte cover in the opening was only one-third that of the forest matrix, with four species [***Marchantia polymorpha*** (Figure 88), ***Pleurozium schreberi*** (Figure 13), ***Ptilidium pulcherrimum*** (Figure 97), ***Sphagnum*** sp. (Figure 98)] disappearing completely. ***Brachythecium*** spp. (Figure 99) and ***Atrichum undulatum*** (Figure 100) both decreased in importance as the opening size increased. These disappearances most likely involved several factors. Not only did the light increase in the opening, but temperature increased and moisture decreased. Furthermore, substrate availability changed, with coarse woody debris being less available in the cutover openings than in the forest matrix.

Figure 96. Northern hardwood forest in northern Michigan. Photo by Janice Glime.

Figure 97. ***Ptilidium pulcherrimum***, a species sensitive to sun exposure, on a log. Photo by Michael Lüth, with permission.

Figure 98. ***Sphagnum girgensohnii*** in spruce forest, a species that disappears in forest openings. Photo by Michael Lüth, with permission.

Figure 99. ***Brachythecium salebrosum***, a species that decreases in importance in forest gaps. Photo by Michael Lüth, with permission.

Figure 100. ***Atrichum undulatum***, a species that decreases in importance in forest gaps. Photo by Michael Lüth, with permission.

Sunflecks

Sunflecks (Figure 95; Figure 101), those tiny patches of bright light that dance about on the forest floor, have reached a new level of importance in our understanding of forest floor dynamics. Skré *et al*. (1983) found that up to 35% of the forest floor in a black spruce (*Picea mariana*, Figure 53) forest in central Alaska could experience sunflecks at the midday soil surface. These flecks usually had an intensity ~76% that of the light reaching the forest canopy and were the major source of light for bryophytes there. Such sunflecks are known to provide for photosynthesis in exposed parts of clones with the resultant photosynthate translocated to shaded parts of the connected clone internally.

For bryophytes, sunflecks have an advantage over full sunlight because of that intermittence (remember how we measure Vmax? The least disturbance of the canopy changes their position, thus striking different branches or patches of bryophytes. For a photosynthetic bryophyte leaf, this means relief from the constant bombardment of light energy on the chlorophyll molecules and prevents these low-light adapted plants from suffering from excitation damage. The light dances about from ramet to ramet as it does from leaf to leaf on the trees. Rincòn and Grime (1989) found sunflecks to be very important for six bryophytes from a variety of habitats and referred to the ability of bryophytes to be plastic in rate and direction of shoot proliferation as a "foraging" mechanism that permitted them to exploit resources where they became available, in this case, sunflecks. Bergamini and Peintinger (2002) found a similar foraging behavior in ***Calliergonella cuspidata*** (Figure 102) and contended that pleurocarpous mosses have a morphological strategy comparable to the "spacer and branching" strategy of some stoloniferous tracheophytes. Even such upright mosses as ***Polytrichum*** are known to have interconnected ramets that translocate photosynthate to one another.

Figure 101. ***Hylocomium splendens*** in a sunfleck. Photo courtesy of Carrie Andrew.

In the heavily shaded sites of New Zealand, the hornwort ***Megaceros pellucidus*** (Figure 103) experiences a maximum photon flux density of less than 10 μmol m^{-2} s^{-1} (Watkins *et al*. 2011). Daylight sees only weak variation in intensity. The dense canopy provides little opportunity for sunflecks. Interestingly, hornworts from low light conditions (0.2 μmol m^{-2} s^{-1}) had the same carotenoid concentrations as those from higher light conditions (6.9 μmol m^{-2} s^{-1}), but the chlorophyll content of high light plants was approximately 2X that of low light plants, whereas the chlorophyll *a*/*b* ratio was the same in both low and higher light conditions. A significant difference is that in low light the hornworts exhibited an absorbance band at 340 nm that was not present in the higher light conditions.

Figure 102. ***Calliergonella cuspidata*** with lateral branching pattern that permits foraging of the sunlight. Photo by Michael Lüth, with permission.

Figure 103. ***Megaceros pellucidus***, a species that lives in very low light levels in New Zealand forests. Photo by Scott Zona, through Creative Commons.

Figure 104. ***Cryptothallus mirabilis*** with sporophytes protruding from its peat substrate. This liverwort completely lacks chlorophyll and depends on a fungus to obtain its energy. Photo by Michael Lüth, with permission.

Litter Burial

Of course the most drastic effect of the forest canopy on the bryophytes of the forest floor is the virtually total loss of light caused by leaf litter (Figure 1). Although there may be allelopathic effects from the decomposition of leaves that leads to the release of tannins, loss of light is ultimate death to nearly every plant. Johnsen (1959) demonstrated the severity of litter on bryophytes by showing that raking away litter can greatly increase both number of species and cover of bryophytes on the forest floor. It is the leaf litter that relegates the bryophytes to the steep slopes, tip-up mounds, and other places where leaf litter cannot easily accumulate.

The Partnership Choice

While many bryophytes suffer from self-shading that prevents the lower leaves from photosynthesizing, one species actually lives in that shaded habitat, receiving little or no light due to the surrounding moss vegetation. This species is the thallose liverwort ***Cryptothallus mirabilis*** (Figure 104). Its name tells much of its story, for it is indeed a hidden thallus, growing beneath the surface in peat, raw humus, or moss carpets (Schofield 1985), yet miraculously surviving in the darkness there. It is totally lacking in chlorophyll (Potemkin 1992); even its spores lack chlorophyll (Hill 1969). It obtains its carbon through a fungal partnership (Malmborg 1933; Airy Shaw 1949; Ligrone *et al*. 1993; Bidartondo *et al*. 2003), although it may not contribute anything to the relationship. It appears that it subsists much like the flowering Indian pipe (*Monotropa uniflora*, Figure 105), actually being a third member in a parasitic relationship with trees, including *Betula* (Figure 89-Figure 90), that reach the canopy to convert light energy into stored energy in the photosynthate (Bidartondo *et al*. 2003). The photosynthate is transferred from the tree to the fungus to the liverwort.

Figure 105. ***Monotropa uniflora***, a hemiparasitic flowering plant that uses a fungus to connect to carbon sources. Photo by Magellan, through Creative Commons.

Summary

In general, bryophytes are adapted to low light, relative to other land plants. Bryophyte cells may act as lens cells, at least in some cases, focussing light on the chloroplasts or even on leaves beneath them. Branches may behave like leaves in scattering, focussing, and reflecting light while providing air spaces that give access to CO_2. Papillae may serve to scatter light when the leaves are dry or to channel it like a fiber optic when wet. But these are all speculations.

The **leaf area index** (**LAI**) of bryophytes appears to be enormous compared to that of tracheophytes (44-129 compared to 3.8 for the forest floor taxa). Perhaps

the branch should be considered instead of the leaves of bryophytes. This same density of leaves results in considerable self-shading, with rapid light extinction within a moss cushion. Light often penetrates deeper in dry mosses, in some cases reaching a level where sufficient hydration exists for photosynthetic activity. Chlorophyll likewise diminishes with depth in a cushion, but this may be a function of age rather than light intensity, at least in some species. Dense packing of stems does not usually seem to deter vertical growth and may actually enhance it through greater conservation of water, despite the attenuation of light. On the other hand, densely overlying mosses seem to benefit from thinning that exposes underlying branches to more light. It appears that light is more important than hydration at determining optimal density.

As in tracheophytes, leaf morphology may respond to shade by such changes as broader leaves. Even leaf weight may decrease as less light becomes available. Other responses to low light are similar to those of tracheophytes, with increased chlorophyll *b* and antenna pigments, depressed light saturation and compensation points, and deeper green color. However, some bryophytes at least do not have a lower chlorophyll *a*:*b* ratio in low light compared to high light, as would the typical tracheophyte. Rather, bryophytes in general have a lower chlorophyll *a*:*b* ratio in all light conditions than do tracheophytes. This suggests that the bryophyte, with its chlorophyll *a* concentrations maintaining proportionality to chlorophyll *b* concentrations, would be ready for brief opportunities when bright light becomes available. Such a strategy would adapt these plants well to the forest habitat where so many are residing, permitting them to take advantage of changing positions of the sun as it filters through trees and brief bursts of light as **sunflecks** when angle of the sun changes or the wind changes the arrangement of the overarching canopy. These same adaptations would likewise permit mosses intertwined with grasses to one day be covered by a stem, but a few weeks later have grown past it to receive full light. Accessory antenna pigments such as carotenoids increase with chlorophyll *b*.

Some species have chloroplasts that move in response to direction of light, maximizing light absorption. In ***Physcomitrella patens***, chloroplasts accumulate on the side of the protonema where contact is made, presumably giving them maximum protection from light.

Reduction in photosynthesis in low light has its price in reduced storage of photosynthate. In bryophytes, storage can occur without growth, with growth occurring later based on stored reserves. Low light can also increase storage of lipids and temperature can alter the types of lipids being stored. Such adaptations differ among species, especially between sun and shade species.

Sunflecks provide bryophytes with bursts of bright light without the damaging effects of continuous bombardment of UV light and high light intensity on shade-adapted plants. Particularly in pleurocarpous mosses, the many branches provide "**foraging**" opportunities that permit production of photosynthate that can be translocated to other parts of the clone. Even the upright ***Polytrichum*** is able to translocate photosynthate from one stem to another in ramets of one connected clone.

Litterfall can completely bury bryophytes and put them in nearly total darkness. However, some bryophytes may benefit from litter in low-light conditions by forming fungal partnerships that acquire photosynthate from the surrounding leaf litter through this the fungus.

Acknowledgments

My appreciation to all the photographers who have given me permission to use their images, or who have put them in Creative Commons.

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CHAPTER 9-3

LIGHT: EFFECTS OF HIGH INTENSITY

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CHAPTER 9-3
LIGHT: EFFECTS OF HIGH INTENSITY

Figure 1. ***Encalypta rhabdocarpa*** in the alpine region where high-intensity UV light can damage chlorophyll and DNA. Photo by Michael Lüth, with permission.

Effects of High Light Intensity

Exposure to UV light has been hypothesized as a major deterrent of evolution to land. Both chlorophyll and DNA are easily damaged by high intensities of direct sunlight (Figure 1). In fact, it has been suggested that a major role of lignin, absent in bryophytes, is to protect cells against UV light. But it appears that the crafty bryophytes have a number of tools at their disposal.

Light and Moisture Relations

One danger of high light intensity in bryophytes is damage it can do to chlorophyll when the moss is dry. In experiments with a number of species, Churchill and Nelson (unpubl. report 1994; pers obs.) have found that the light intensity transmitted through a wet moss leaf is about twice that transmitted through a dry leaf. Takács *et al*. (2000) found that the non-chlorophyll blue-green fluorescence of ***Syntrichia ruralis*** (Figure 2) and two lichens increased by an order of magnitude upon drying. They attributed these changes in blue-green fluorescence to altered optical properties, not to any change in pigment or phenolic concentration. Lovelock and Robinson (2002) likewise found that the state of hydration affects the ability of the moss to absorb or reflect light. This increased reflection and decreased absorption by the dry leaf should provide at least some protection from damaging effects of UV radiation that could destroy chlorophyll and damage DNA. It suggests that there may be internal and/or external scattering of light by dry moss, whereas wet moss has a

more homogeneous surface and interior, permitting light to travel with less scattering.

Figure 2. ***Syntrichia ruralis*** showing hyaline hair points that are drawn close to the stem when the moss is dry and leaves are twisted around the stem. Photo by Michael Lüth, with permission.

Hamerlynck and coworkers (2002) hypothesized that because of its strong desiccation tolerance characters, the moss ***Syntrichia ruralis*** (Figure 2) would be unable to acclimate to different light intensity regimes. However, they found that in this species sun plants had lower biomass, and lower tissue N, C, and chlorophyll concentrations than shade plants of the species (Figure 3). Interestingly, while the carotenoid:chlorophyll ratios of sun plants were typical of sun plants, they found that as in most bryophytes the chlorophyll *a*:*b* ratios were typical of shade plants. When transplanted to shade, sun plants were able to adjust to the lower light level by increasing their photosystem II yields; these yields decreased in shade plants transplanted to the sun. Conversely, sun plants transplanted to shade continued to be out-performed there by non-transplanted shade plants. They suggest that in this species, shade plants may be able to adjust relatively quickly to disturbance that exposes them to greater light and desiccation.

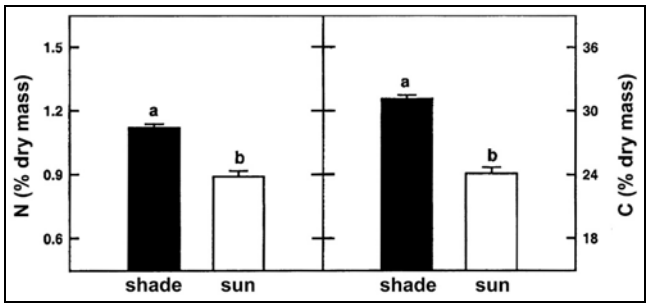

Figure 3. Comparison of N and C content of ***Syntrichia ruralis*** grown in shade and sun in Kiskunság National Park near Budapest, Hungary. Vertical bars indicate 1 SE; letters indicate significant differences ($p<0.05$). Redrawn from Hamerlynck *et al*. 2002.

Photoinhibition

Because high light intensities can damage chlorophyll, they can cause photoinhibition. Even sun plants like ***Sphagnum*** (Figure 49) are vulnerable. Shaded ***Sphagnum*** plants from temperate and Alaskan populations were given more light following removal of tracheophytes, and plants from full sun were shaded (Murray *et al*. 1993). Previously shaded mosses from both locations in the high-light treatment (800 μM m^{-2} s^{-1}) lost significant photosynthetic capacity in just two days and did not recover in the next 14 days. Increased variation in chlorophyll fluorescence relative to maximum fluorescence suggested this was a result of photoinhibition. By contrast, mosses that were moved from full sun to shade grew at a rate 2-3 times as great as that of those in control plots. Murray and coworkers suggested that the inability to acclimate might relate to low tissue N content of these mosses from low-nutrient habitats.

Bryophytes are limited on both ends of the light scale. At low intensities, they have insufficient energy to replace that lost by dark respiration and photorespiration, but on the other end they suffer chlorophyll damage and photoinhibition. Cleavitt (2002) demonstrated that this photoinhibition in ***Mnium spinulosum*** (Figure 4) restricted its occurrence to deeply shaded conifer stands, whereas ***Bryum pseudotriquetrum*** (Figure 5) was limited by its lack of desiccation tolerance. ***Mielichhoferia macrocarpa*** (Figure 6), on the other hand, occurred in the darkest and wettest sites, yet was tolerant of both high light intensities and desiccation. She showed that what we perceive to be narrow physiological limits that we would expect to limit rare species may not tell the whole story. It appears that our knowledge of light limits and adaptations, coupled with physiological responses of bryophyte tissues, needs additional study.

Figure 4. ***Mnium spinulosum***, a species restricted to deep shade. Photo by Jan-Peter Frahm, with permission.

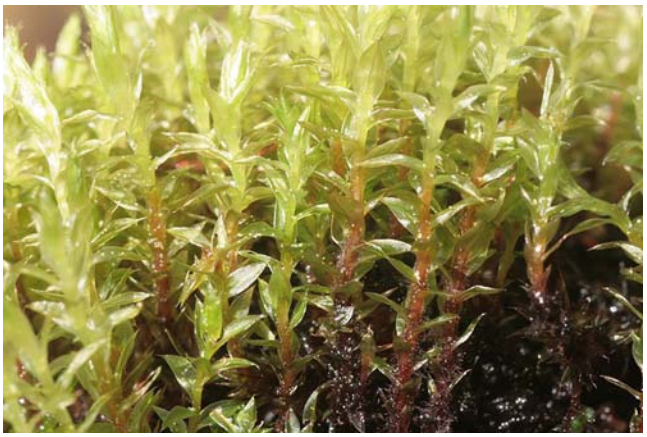

Figure 5. ***Bryum pseudotriquetrum***, a species limited by moisture. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Mielichhoferia macrocarpa***, Robin Bovey, with permission from Dale Vitt.

In Antarctica, the bryophytes experience full exposure to sunlight in summer, but are at least partially protected by ice in winter (Post *et al*. 1990). This high summer exposure causes photoinhibition to be a major factor limiting productivity in these ecosystems. Post and co-workers have documented the damaging effects of low temperatures and high light on the bryophytes in this exposed polar environment. ***Schistidium antarctici*** (Figure 7) experiences daily changes in photosynthetic capacity, resulting from the changing environmental variables of light and temperature. (See also Chapter 11-2 of this volume.

Figure 7. ***Schistidium antarctici***, a species that changes its photosynthetic capacity daily in response to the variable Antarctic weather. Photo courtesy of Rod Seppelt.

Adaptations to High Light

When working with ***Pohlia wahlenbergii*** (Figure 8) from a subalpine area, Coxson and Mackey (1990) were surprised to find that it had a peak of photosynthesis at 8 mg CO_2 g^{-1} h^{-1} in the morning, declined to 5 mg CO_2 g^{-1} h^{-1} by late afternoon, then fully recovered by late evening. They considered that it might have full recovery from photodestruction of pigment complexes, but such a degree of photosensitivity would be unusual for plants living in high light environments. However, this would seem to be consistent with observations on ***Ceratodon purpureus*** (Figure 9) (Rintamaki *et al*. 1994). One of its mechanisms to tolerate high light is its rapid turnover of the D1 reaction center protein in photosystem II. In mosses such as ***Ceratodon purpureus***, this permits rapid replacement of light-damaged protein, thus serving as protection against photoinhibition. Once again, it seems the bryophytes have outdone the tracheophytes.

Figure 8. ***Pohlia wahlenbergii***, a species tolerant of high light. Photo by Michael Lüth, with permission.

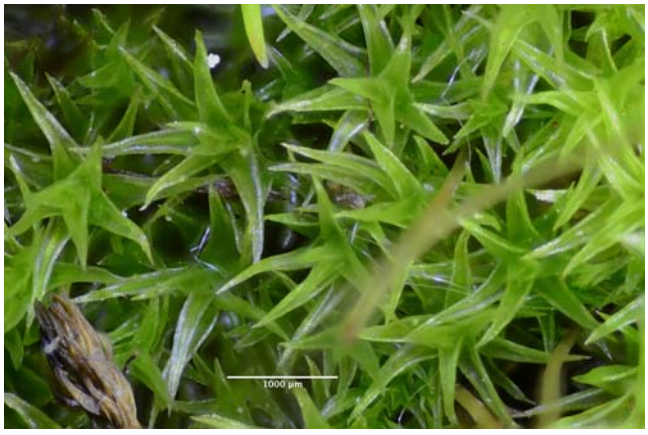

Figure 9. ***Ceratodon purpureus*** leaves, a species tolerant of high light. Photo by Don Loarie, through Creative Commons.

Plants adapt to high light either by structural adaptations or by protective pigments. Tracheophytes have protective epidermal layers, and in most groups there is a palisade layer beneath that epidermis that further serves to absorb light before it reaches the photosynthetic tissue of the spongy mesophyll. Bryophytes lack this structure. Hence, bryophytes must invest more in cellular level

protection to mitigate the damaging effects of high light intensity (Robinson & Waterman 2014). In some cases, the bryophytes use mechanisms already known in algae, such as thermal energy dissipation that is associated with the LHCSR protein, a mechanism no longer present in tracheophytes.

Structural Adaptations

Waite and Sack (2010) found that ten Hawaiian mosses did not demonstrate a correlation between habitat irradiance and light-saturated photosynthetic rate per biomass. However, they found that other photosynthetic parameters and structural traits (leaf area, cell size, cell wall thickness, and canopy density) were aligned with microhabitat irradiance. Furthermore, internally, high light can cause a decrease in thylakoid stacking (Post 1990).

Bryophytes often have filters that help to protect them from high light intensity. For example, several ***Polytrichum*** (Figure 10) species have **lamellae** (Figure 11) that are enclosed by the inrolled **lamina** (Figure 11) of the leaf, thus rendering the leaf a structure that is not very different from that of a deciduous tree. Others have leaves with **filaments** [***Crossidium*** (Figure 12-Figure 13)], **hyaline tips** [***Hedwigia ciliata*** (Figure 14-Figure 16), ***Bryum argenteum*** (Figure 17-Figure 18)], and **awns** [***Tortula*** (Figure 19-Figure 22), ***Syntrichia*** (Figure 2)] that overlap the next leaf and help to deflect light before it reaches the cell interior. Hyaline hair tips, partially covering adjoining leaves when dry (Figure 14, Figure 20), are spread out of the way of the photosynthetic tissue upon hydration (Figure 15, Figure 21).

Figure 10. ***Polytrichum juniperinum***, a species with lamellae and rolled over leaf edges. Photo by Janice Glime.

Figure 11. Leaf cross section of ***Polytrichum juniperinum*** showing leaf edge rolled over lamellae. Photo from Botany Website, UBC, with permission.

Figure 12. ***Crossidium aberrans***, a species with filaments on the leaves. Photo by Michael Lüth, with permission.

Figure 13. ***Crossidium aberrans*** leaves showing filaments on costa. Photo by Michael Lüth, with permission.

Figure 14. ***Hedwigia ciliata*** dry. Photo by Janice Glime.

Figure 15. ***Hedwigia ciliata*** wet. Photo by Robert Klips, with permission.

Figure 16. ***Hedwigia ciliata*** leaf showing transparent awn. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 17. ***Bryum argenteum*** showing tight leaves that overlap and protect each other from light damage. Note the white tips of each leaf. Photo by Michael Lüth, with permission.

Figure 18. ***Bryum argenteum*** leaves showing the hyaline upper half. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Figure 19. ***Tortula brevissima*** showing partially appressed leaves in its dry habitat. Photo by Michael Lüth, with permission.

Figure 20. ***Tortula brevissima*** dry with twisted leaves and appressed. Photo by Michael Lüth, with permission.

Figure 21. ***Tortula brevissima*** wet, with spreading leaves. Photo by Michael Lüth, with permission.

Figure 22. ***Tortula brevissima*** leaf tip and awn. Photo by Heike Hofmann ©swissbryophytes <swissbryophytes.ch>, with permission.

Frey and Kürschner (1991) have demonstrated a correlation between "glass hairs" (Figure 13, Figure 18, Figure 16, Figure 22) and increasing aridity, suggesting that they could be useful as UV shields as aridity, and correlated light exposure, increase. Many taxa curl their leaves (Figure 23), wrap their leaves around the stem (Figure 20), or appress leaves (Figure 20) when dry, causing each leaf to help protect at least part of the next leaf. Structures such as papillae become more transparent when wet, typically doubling their ability to transmit light (Glime, unpubl. data). Short turfs likewise help to protect mosses from high light intensity through self-shading (Schofield 1985).

Epiphytes like ***Octoblepharum*** (Figure 24-Figure 25) and ***Leucobryum*** (Figure 26-Figure 27) have numerous hyaline cells that might help to filter the light before it reaches the photosynthetic cells. But I have seen no experiments that demonstrate if this really alters the light intensity. They could, instead, focus the light on the interior photosynthetic cells while serving as a water reservoir to maintain photosynthesis in a dry atmosphere.

Figure 23. ***Atrichum altecristatum*** drying, showing curling leaves compared to more moist expanded leaves in the background. Photo by courtesy of Eric Schneider.

Figure 24. ***Octoblepharum albidum***, a moss that shields its photosynthetic cells with hyaline cells. Photo by Janice Glime.

Figure 25. Cross section of ***Octoblepharum albidum*** leaf. Photo courtesy of Noris Salazar Allen.

Figure 26. ***Leucobryum glaucum*** with its typical whitish color due to hyaline cells in an upper and lower layer. Photo by James K Lindsey, with permission.

Figure 27. ***Leucobryum glaucum*** leaf cs showing hyaline cells surrounding the photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.

In boreal wetlands, bryophytes have distinct spectral characteristics compared to those of tracheophytes in the visible, near-infrared (NIR), and short-wave infrared (SWIR, 1.50-2.50 µm) regions (Bubier *et al*. 1997). In the visible portion of the spectrum, these mosses exhibit typical absorption in the blue and red regions but differ from the tracheophytes in having a "green" peak reflective of the color (red, brown, or green) of individual species. The reflectance in the NIR region of mosses is usually less than in the tracheophytes, with strong water absorption features at ~1.00 and 1.20 µm, causing distinct reflectance peaks at ~0.85, 1.10, and 1.30 µm. These are diagnostic of the three groups of mosses – ***Sphagnum*** (Figure 48-Figure 49), feather mosses (Figure 28), and brown mosses (Figure 29). Bubier and coworkers suggested that these may indicate different cellular characteristics. The high water content causes the overall reflectance of the mosses in the SWIR region to be lower than that found in tracheophytes.

Figure 28. ***Pleurozium schreberi***, a common feather moss in boreal forests. Photo by Janice Glime.

Figure 29. ***Scorpidium revolvens***, one of the rich fen brown mosses. Photo by Michael Lüth, with permission.

For aquatic bryophytes, water depth affects light intensity and quality. Mártínez Abaigar *et al*. (1993) found that ***Scapania undulata*** (Figure 30-Figure 31) had a Leaf Specific Area (LSA) of 317 cm^2 g^{-1}DW at 5 cm depth, but at 45 cm depth, the LSA increased to 399 cm^2 g^{-1}DW. Concomitantly, Leaf Specific Weight was reduced from 3.16 mg cm^{-2} to 2.50 mg cm^{-2}. These differences can be interpreted as a response to lower light availability at 45 cm and parallel the kinds of changes that occur in tracheophyte leaves. Canopy leaf fall likewise causes an increase in accessory pigments relative to chlorophyll *a* in this liverwort by increasing the light coming through the canopy.

Figure 30. ***Scapania undulata*** with just a hint of red color, suggesting sun exposure (or nutrient deficiency?). Photo by David T. Holyoak, with permission.

Figure 31. ***Scapania undulata*** showing red coloration that can be stimulated by high light intensity. Photo by Michael Lüth, with permission.

Some structural timing changes are likely to help in protecting developing tissues from high light damage. In tracheophytes, bud scales and leaf primordia can prevent desiccation and most likely prevent light damage to developing tissues when the canopy is free of leaves in the spring (Budke *et al*. 2012). But mosses have no such mechanism. Nevertheless, in the moss ***Funaria hygrometrica*** (Figure 32-Figure 35), there are indications that the **calyptra** plays this role for the developing sporophyte. Not only does the calyptra remain on the developing tip of the young sporophyte until the capsule begins to form, but as the calyptra develops, it produces its cuticle before any cuticle develops on the young capsule. In fact, the calyptrae are covered by four layers of cuticle at all stages. Although Budke and co-workers emphasized the importance of the cuticularized calyptra in preventing desiccation, I would consider it likely that this structure also serves as a filter to protect the developing apical cells from UV-B.

Figure 32. ***Funaria hygrometrica*** archegonia (developing calyptrae) and young sporophytes. At this stage, the cuticle has already formed on the calyptra. Photo by Andrew Spink, with permission.

Figure 33. ***Funaria hygrometrica*** with developing capsules covered by calyptrae. Photo courtesy of Steve Juntika.

Figure 34. ***Funaria hygrometrica*** with nearly mature capsules, showing calyptrae split on lower side of capsule. Photo by Li Zhang, with permission.

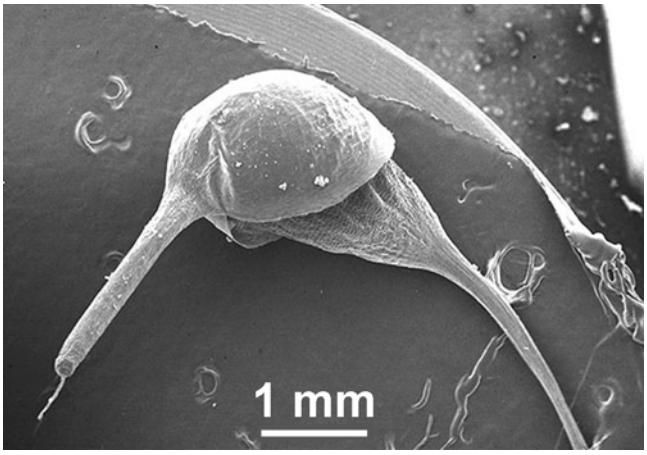

Figure 35. ***Funaria hygrometrica*** capsule SEM showing calyptra that is split on one side, possibly influencing the curved shape of the capsule. The upper side of the capsule is covered as it completes development. Photo from Botany Website, UBC, with permission

Pigmentation

Plant leaves and plant cells are much like a system of filters and lenses. We have already discussed the use of cell structure (lenses) to focus light on a particular location or to alter its intensity. Another way to protect chlorophyll and DNA from high light intensity is through colored pigments (filters) that absorb light.

Increased levels of chlorophyll *b* and xanthophylls, both antenna pigments, are consistent with the suggestion that it is the antenna pigments that dissipate light energy in ***Rhytidiadelphus squarrosus*** (Figure 36); specifically, **zeaxanthin** strongly enhances **light quenching** (dissipation of light energy) in an atmosphere of 20% CO_2 (Bukhov *et al*. 2001a). This appears to be fundamentally different from mechanisms in tracheophytes, as represented by spinach and *Arabidopsis* (Figure 37), where the reaction center appears to be important in quenching. In ***R. squarrosus***, it requires only a few short light pulses, separated by a prolonged dark period, to stimulate the production of additional zeaxanthin (Bukhov *et al*. 2001b). But that was in 20% CO_2! What can it do in the more normal 0.04% CO_2? The interaction of zeaxanthin with thylakoid protonation permits the effective thermal dissipation of light energy in the chlorophyll antenna system of photosystem II in this bryophyte, but not in the two tracheophytes.

It appears that there is a physiological mechanism that facilitates pigment production in response to high light. The gaseous hormone **ethylene** inhibits the synthesis of carotenoids and chlorophyll (Kang & Burg 1972), but stimulates the production of red pigments. Ultimately, its production is inhibited by red light, a convenient feedback mechanism to stop production when the cells have enough red pigment. Ethylene is inhibited by CO_2 and requires O_2 for its formation.

Red pigments become more common in mosses at low temperatures. In our experiments with ***Fontinalis squamosa*** (Figure 38-Figure 40) (Glime & Rohwer 1983), a water-soluble red pigment (anthocyanin derivative?) was produced as a wall pigment in aborted apical buds (Figure 41) and some of the older leaves under treatment with ACC, an ethylene precursor.

Figure 36. ***Rhytidiadelphus squarrosus***, a species that produces zeaxanthin to dissipate strong light. Photo by Michael Lüth, with permission.

Figure 37. ***Arabidopsis thaliana***, a tracheophyte that uses the reaction center of photosynthesis to quench excessive light. Photo by Nicole Hanley, through Creative Commons.

Figure 38. ***Fontinalis squamosa*** in alpine water, showing a healthy green color. Photo from <www.aphotofauna.com>, with permission.

Figure 39. ***Fontinalis squamosa*** stranded above water in the low water levels of summer. Photo by Janice Glime.

Figure 40. ***Fontinalis squamosa*** showing dark pigmentation out of water. Photo by Michael Lüth, with permission.

Figure 41. ***Fontinalis squamosa*** broken-branch buds showing dark pigmentation. Photo by Janice Glime.

In ***Fontinalis antipyretica*** (Figure 42), red leaves were present in a population growing in cold mountain water in full sun (Figure 43-Figure 44) (Glime & Rohwer 1983). A similar response occurred when shoots were kept out of the water under fluorescent light (Figure 45). A similar response is present in ***Ceratodon purpureus*** (Figure 46) in the Antarctic (Post 1990). In high light, the leaves become ginger-colored, a color caused largely by an increase in anthocyanin and decrease in chlorophyll concentrations (Figure 60).

Figure 42. ***Fontinalis antipyretica*** var ***antipyretica*** with reddening that can be caused by exposure to high light. Photo by David Holyoak, with permission.

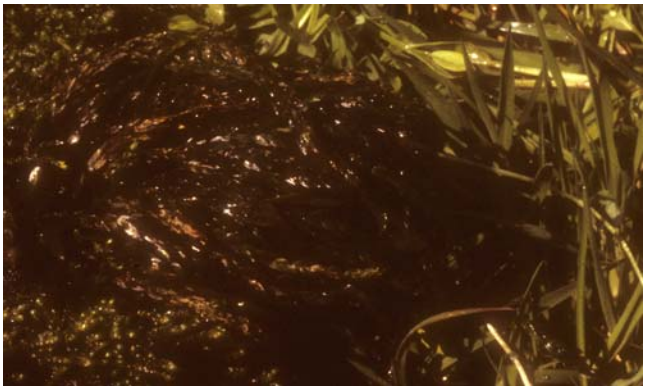

Figure 43. Red ***Fontinalis antipyretica*** in response to bright light of full sun in shallow, cold water emerging from an underground stream in Germany. Photo by Janice Glime.

Figure 44. ***Fontinalis antipyretica*** cells of red plants that were exposed to bright light in cold water (see Figure 43). Photos by Janice Glime.

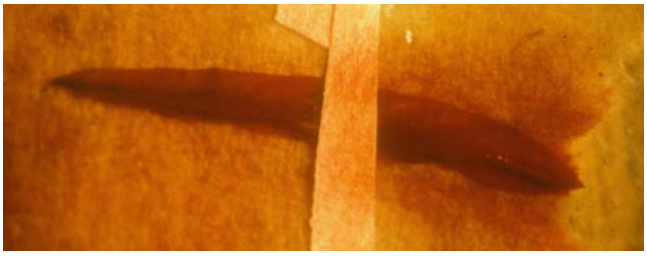

Figure 45. Red ***Fontinalis antipyretica*** in response to bright lights on stem kept out of water under fluorescent light in an experiment. Photo by Janice Glime.

Figure 46. ***Ceratodon purpureus*** on Antarctica, showing red pigmentation in this exposed site. Photo courtesy of Rod Seppelt

In intense light and cold these C_3 bryophytes would have a high photosynthesis/photorespiration ratio due to the fact that photorespiration is low at low temperatures, whereas photosynthesis, while lowered at these temperatures, will not be lowered as much as photorespiration (Zelitch 1971). This high ratio will result in a high O_2/CO_2 ratio that will favor an increase in ethylene production; ethylene will then inhibit production of carotenoids and chlorophyll while stimulating anthocyanin production. The resulting pigmentation will then reflect, scatter, and transmit red light. Since red light should inhibit ethylene production (Kang & Burg 1972), it appears that this system should be self-limiting, with intense red pigment reducing or turning off ethylene production and protecting chlorophyll from overexcitation in intense light (Figure 47). However, this assumes that the red pigment behaves like anthocyanin.

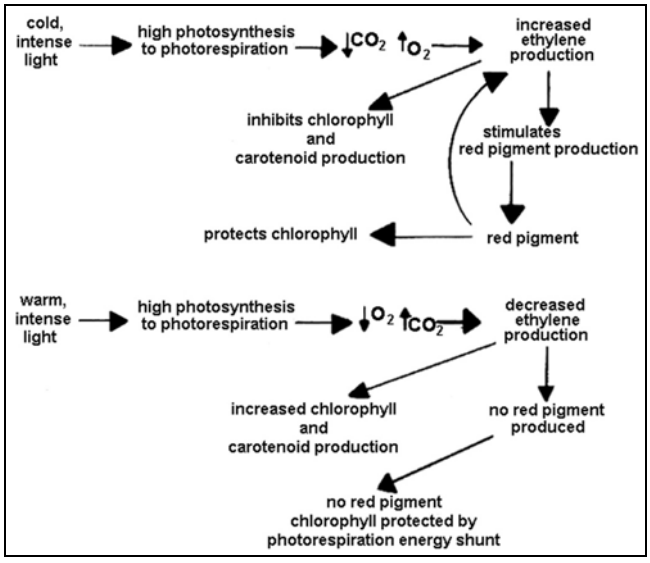

Figure 47. Proposed role of intense light in the production of ethylene and red pigment under cold and warm conditions.

Maseyk *et al*. (1999) compared New Zealand samples of ***Sphagnum cristatum*** (Figure 48) of different colors to determine the effects of pigmentation on photosynthetic response. Brown mosses required higher light intensities (photon flux densities, PFD) than did green samples, had lower quantum efficiencies, and had higher light compensation points, all suggesting that the pigments played a role in filtering out light. An interesting correlation to this was that brown moss samples had a wider range of optimum water content (1400-3000%) than did green mosses (1200-2000%).

Figure 48. Multi-colored capitula of ***Sphagnum cristatum***. Photo by Janice Glime.

Gerdol (1996) found that ***Sphagnum magellanicum*** (Figure 49) had its greatest growth rates in the shade in plants with the highest chlorophyll *b* concentrations and that a high ratio of chlorophyll to carotenoids was also beneficial in the shade. In the open, growth rates were negatively correlated with the chlorophyll *a*:*b* ratio. Gerdol suggested that this negative relationship is due to the greater ease with which chlorophyll *a* is degraded under environmental stress.

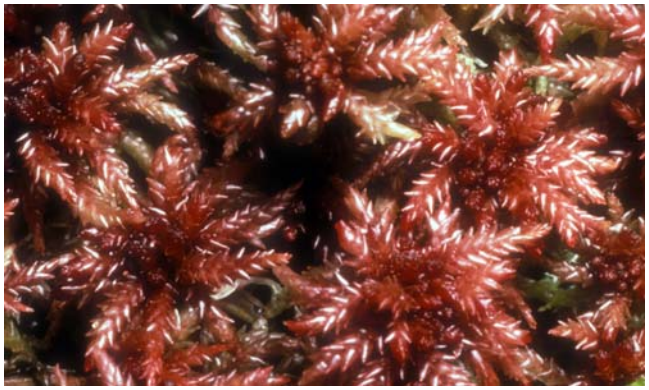

Figure 49. Red ***Sphagnum magellanicum*** resulting from **sphagnorubin** produced when nights are cold and days are bright in the autumn. Photo by Janice Glime.

Light quality matters. In the thallose liverwort ***Marchantia polymorpha*** (Figure 50-Figure 51) the red/far-red ratio matters. De Greef and Fredericq (1969) tested this liverwort in a series of R/FR ratios in 10-minute exposures at the end of the day. In a decreased R/FR ratio, there was a decrease in chlorophyll content. The growth of this liverwort was similar to that shown for seedlings of tracheophytes. The researchers concluded that high levels of the Pfr form of phytochrome were necessary to maintain optimal chlorophyll content in these thalli.

Figure 50. ***Marchantia polymorpha*** demonstrating the pale color of sun plants. Photo by James K. Lindsey, with permission.

Figure 51. ***Marchantia polymorpha*** demonstrating the dark color of shade plants. Photo by Walter Obermayer, with permission.

Sphagnorubin

As with anthocyanin, concentration of **sphagnorubin**, a red wall pigment in some species of ***Sphagnum*** (Figure 49), was also highest in the open (Gerdol 1996). However, the sphagnorubin concentration was not correlated with chlorophyll concentration and growth rate.

Sphagnorubin is a flavonoid related to anthocyanin (Rudolph *et al.* 1977). Schmidt-Stohn (1977) found that in ***Sphagnum magellanicum*** (Figure 49), its synthesis is related to rapid changes in chlorophyll concentration. When Gerdol (1996) did not find the expected negative correlation with chlorophyll concentration, he assumed that the timing of the chlorophyll and sphagnorubin metabolic pathways were different. Sphagnorubin is produced when nights are cold (5°C) and daytime light is intense, but not when both nights and days are warm (18°C) (Rudolph *et al*. 1977; Gerdol *et al* 1998).

Chlorophyll Ratios in Aquatic Bryophytes

Whereas the brook moss ***Fontinalis antipyretica*** (Figure 42-Figure 45) likewise can be brilliant red in nature in intense light and cold water (Glime 1984), on the other end of the scale, aquatic bryophytes alter pigment concentrations as light attenuation occurs with increasing depth. In ***Scapania undulata*** (Figure 30-Figure 31) populations, plants growing at 5 cm depth gained chlorophyll *a* in summer (from 3.43 to 3.69 mg g^{-1} dw) while losing chlorophyll *b* (from 1.17 to 0.87 mg g^{-1} dw), suggesting that they had a much higher light availability in summer (Mártínez Abaigar *et al*. 1993). At 45 cm depth, they lost chlorophyll *a* in summer (from 4.08 to 3.41 mg g^{-1} dw) and likewise lost chlorophyll *b* (from 1.47 to 1.15 mg g^{-1} dw). The increase in chlorophyll *b* with depth was significant ($p<0.01$) in both spring and summer, whereas chlorophyll *a* had a significant increase with depth in spring ($p<0.01$) but not in summer ($p>0.05$). The resulting chlorophyll *a*:*b* ratio was significantly less at 45 cm in both seasons. Variance in carotenoid ratios was extremely small, causing differences of less than 5% between the two depths to be significant for spring samples.

Martínez-Abaigar *et al*. (2003) subjected the aquatic moss ***Fontinalis antipyretica*** (Figure 42) and aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 52) to 3 different radiation regimes for 36 days in the laboratory. In ***F. antipyretica***, UV-A had little biological effect. UV-B caused decreases in both chlorophyll and carotenoid concentrations, chlorophyll *a*/*b* ratios, chlorophyll/phaeopigment ratios, net photosynthetic rates, light saturation point, maximum quantum yield of photosystem II, and apparent electron transport rate, along with increases in their **sclerophyll index** and dark respiration rates. Most of these changes were indicative of plant stress. In the liverworts, however, UV-B caused only an increase in the concentration of UV-absorbing compounds and a decrease in F_v/F_m. The researchers concluded that these differences would permit the liverwort to tolerate higher levels of UV-B radiation. But in my observations of ***Fontinalis antipyretica*** growing near the surface in cold water in full sun, the mosses were a deep red-green, protected by red pigments (Figure 42-Figure 44).

Figure 52. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a species that produces more UV-absorbing compounds in response to high light. Photo by Michael Lüth, with permission.

The **sclerophyll index** has rarely been applied to bryophytes. It was developed to compare features of Australian sclerophyllous plants (literally, hard-leaved plants) and included broad, leathery leaves; reduced leaf size; needle leaves; winged stems; spiny stems; sunken stomata; cutinization and lignification of leaves; development of tannins and resinous substances; strong

development of palisade mesophyll and weak development of spongy mesophyll; and presence of hairs, scales, or waxy bloom on leaf surface (Grieve 1955). Few of these can be applied to bryophytes, but instead **sclerophyll index in bryophytes** is defined as ratio of dry mass to shoot area (Monteforte López 2014), including reduced leaf size, cutinization of leaves, development of tannins (phenolic compounds), thicker leaves, presence of awns or papillae, and waxy bloom might be instructive.

Using 17 species of bryophytes from low light habitats of Yuan-Yang Lake at 1760 m elevation in northern Taiwan, Yang *et al*. (1994) found that the mean chlorophyll *a*/*b* ratio was 2.41, with all mean ratios equalling or exceeding 2.17. Two hydrophytes used for comparison had a mean of 3.08. Nevertheless, these 17 bryophytes had a higher chlorophyll *a*/*b* ratio than most mosses reported in the literature, suggesting that they were adapted (or acclimated) to the intense illumination of that elevation (250 μmol m^{-2} s^{-1}).

UV Absorption

Bryophytes are able to produce pigments that absorb UV-A and UV-B while permitting most of the photosynthetically active radiation to penetrate (Jorgensen 1994). These pigments are primarily **phenylpropanoids** and **flavonoids**. Jorgensen suggests that these pigments may have evolved along with the high biosynthetic activity that is needed for UV protection. One of the necessary components of this evolution was to provide a means of sequestering these protective compounds that would otherwise be toxic. Clarke and Robinson (2008) demonstrated that the Antarctic moss ***Ceratodon purpureus*** (Figure 46) produced cell wall-bound UV protective compounds, an effective place to sequester them to protect their own cells. These UV-B protective compounds not only protect against damaging radiation, but at least some are also important in antiherbivory and antimicrobial activity (Davidson *et al*. 1989; Graham *et al*. 2004).

Unlike the popular perception, some mosses are able to grow in large numbers in full sun. How do these mosses cope with high light and UV-B radiation? ***Physcomitrella patens*** (Figure 53) is one of these sun-dwelling mosses. This remarkable tiny moss actually has greater ability to survive UV-B stress than the flowering sun plant *Arabidopsis thaliana* (Figure 37) (Wolf *et al*. 2010). This moss has ~400 genes that are expressed in response to UV-B radiation! Its response pathways are also distinct.

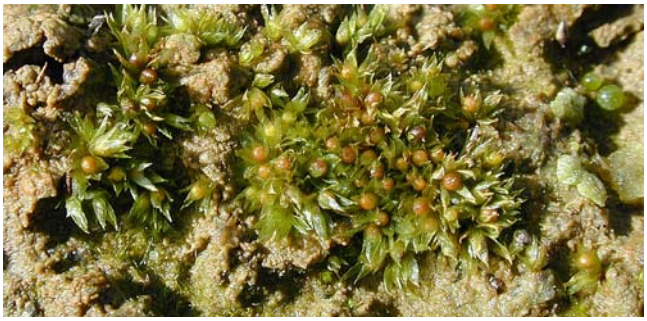

Figure 53. ***Physcomitrella patens***, a tiny sun-dwelling moss that survives high light better than the weedy tracheophyte *Arabidopsis thaliana* (Figure 37). Photo by Michael Lüth, with permission.

In Norway, Wilson *et al*. (1998) found that the growth of ***Hylocomium splendens*** (Figure 54-Figure 55) was strongly stimulated by UV-B when provided with extra water, but under its natural water conditions, UV-B displayed no effect on growth or appearance. On the other hand, leaves of the shrub *Vaccinium vitis-idaea* (Figure 56) became thicker, whereas those of deciduous dwarf shrubs became thinner.

Figure 54. ***Hylocomium splendens*** with its typical forest floor color. Photo by James K. Lindsey, with permission.

Figure 55. ***Hylocomium splendens*** showing the yellowish color typical when the tree canopy is cut. Photo by John Game, through Creative Commons.

Figure 56. ***Vaccinium vitis-idaea***, a species that develops thicker leaves in high light intensity. Photo by Jonas Bergsten, through public domain.

Frey and Kürschner (1991) found a correlation between black pigmentation and increasing aridity in mosses. This most likely is an adaptation to protect the moss from UV light during periods of drought. Normally, water helps to protect chlorophyll from UV light, but during periods of drought, this is not possible. The dark color could serve as a filter against the UV, becoming more transparent to light when water returns. Certainly the color should not be needed for warmth by absorbing heat rays since it is during the warmest periods that high light intensity and desiccation provide the greatest problems.

Many members of the leafy liverwort genus ***Frullania*** (Figure 57) possesses red coloration, grading into nearly black. This genus typically lives on trees and boulders, often at high elevations or high in the canopy. Deeply pigmented species can actually require high light, and account for the presence of this species at high elevations above timberline or high in the canopy of the tropics. On Barro Colorado Island, Panama, epiphyllous liverworts grow more quickly in high light intensities than in the shade, attesting to their adaptations to high light intensity (Coley *et al*. 1993). But these locations also often have higher UV-B light, so the pigmentation may serve as an in important filter against UV damage.

Figure 57. Red coloration of ***Frullania tamarisci***. Photo by Michael Lüth, with permission.

Searles *et al*. (2002) examined the responses of peatland mosses in southern South America to near-ambient (90%) and reduced (20%) UV-B radiation for three growing seasons. The reduction of UV-B cause an increased height growth in ***Sphagnum magellanicum*** (Figure 49), but the plant density decreased. Hence, there was no net influence on biomass production. ***S. magellanicum*** experienced a 10-20% decrease in UV-B-absorbing compounds under the low UV-B regime, but there were no effects on chlorophyll or carotenoid concentrations.

UV radiation is much more intense in terrestrial habitats because in aquatic habitats water quickly absorbs it. It appears that aquatic mosses and liverworts may differ from each other in their UV-absorbing spectra. In ten mosses and four liverworts from a mountain stream at 2,000 m elevation, only the liverworts had high levels of methanol-extractable UV-absorbing compounds, with the exception of ***Polytrichum commune*** (Figure 58) (Arróniz-Crespo *et al*. 2004). Accumulations of such compounds could protect liverworts against the high UV-B light on stream rocks above and near the surface.

Figure 58. ***Polytrichum commune***, a species that produces high levels of methanol-extractable UV-absorbing compounds in high light. Photo by Michael Lüth, with permission.

In their study of aquatic bryophytes, Mártínez Abaigar *et al*. (1993) found very little seasonal or species-specific differences in carotenoid ratios, suggesting that the carotenoids responded little to changes in light intensity in these bryophytes. We know that UV-B quickly loses energy in water, converting to longer wavelengths, and perhaps reducing the danger of UV-B damage in aquatic bryophytes.

UV-B penetration changes throughout the day as the Earth turns and the sunlight travels through less atmosphere as time approaches 12:00 hours, then decreases as the rays strike at a greater angle, once again having to penetrate more atmosphere. The aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 52) exhibited significant **diel** (within 24 hours) changes, responding within a few hours to changes in radiation levels (Fabón *et al*. 2012). The strongest response was to UV-B. High levels of photosynthetically active radiation (PAR), UV-A, and UV-B radiation elicited significant and rapid diel changes in the components of the **xanthophyll cycle** (process of enzymatic removal of epoxy groups from xanthophylls, *e.g.* violaxanthin, antheraxanthin, diadinoxanthin) to create so-called de-epoxidised xanthophylls). Furthermore, the F_v/F_m, phi PSII (absolute quantum yield of CO_2 fixation in photosystem II), and non-photochemical quenching likewise responded quickly to the changes in radiation levels. These changes provided dynamic photoinhibition and protection of PSII, with the xanthophyll cycle providing protection from the excess radiation.

Accessory pigments such as carotenoids can serve to protect chlorophyll from damage by high intensity UV light (Siefermann-Harms 1987) such as that in the Antarctic. The three mosses examined by Siefermann-Harms all had sustained high levels of xanthophyll pigments, especially at exposed sites (Lovelock & Robinson 2002). Among these was an increase in **violaxanthin** (Post 1990). These pigments are photoprotective and indicate that the moss most likely is subjected to continual high levels of photochemical stress (Lovelock & Robinson 2002). ***Ceratodon purpureus*** (Figure 59-Figure 60) had a higher carotenoid:chlorophyll ratio in high light intensities (0.55) than in low ones (0.35).

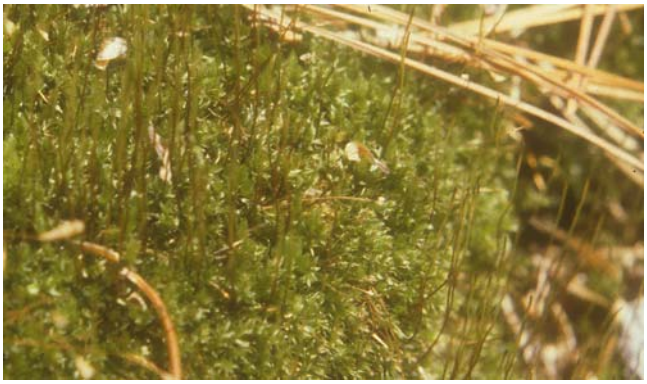

Figure 59. ***Ceratodon purpureus*** green form as it appears when the snow melts. Photo by Janice Glime.

Figure 60. ***Ceratodon purpureus*** in its golden form that has been subjected to high light intensity. Photos by Janice Glime.

Since the Antarctic has received much publicity due to the ozone hole and resulting increase in UV-B penetration through the atmosphere, many of our studies on bryophyte responses to increased UV-B radiation have involved Antarctic bryophytes. Responses are seasonal, resulting in an increase in photoprotective pigments as the ice melts and the mosses become exposed (Dunn & Robinson 2006). One interesting result of these studies is finding that the two cosmopolitan mosses ***Bryum pseudotriquetrum*** (Figure 5) and ***Ceratodon purpureus*** (Figure 46, Figure 59-Figure 60) appear to be better protected against UV-B radiation than is the Antarctic endemic ***Schistidium antarctici*** (Figure 7). Of these three mosses, ***B. pseudotriquetrum*** accumulates the highest concentration of UV-B protective pigments, exhibiting a positive correlation between UV-B radiation and both UV-B-absorbing and anthocyanin pigments. Under desiccating conditions, this species has greater concentrations of these protective pigments than in well-hydrated conditions. This combination would mean that at low temperatures and low moisture, the moss would have limited physiological activity and thus be protected from potential UV-B damage.

Ceratodon purpureus (Figure 59-Figure 60) is the most exposed species of the three studied (Dunn & Robinson 2006). It uses a different strategy of protection, with concentrations of UV-B absorbing pigments being stable through varying light and moisture conditions (Dunn & Robinson 2006). Dunn and Robinson suggested that this is evidence that the protective pigments are constitutive in this species. On the other hand, the anthocyanin pigments were responsive, providing increased antioxidant protection during exposure to high levels of UV-B radiation.

The endemic ***Schistidium antarctici*** (Figure 7), unlike these two cosmopolitan species, is poorly protected, showing no evidence of pigment production in response to UV-B stimulation (Dunn & Robinson 2006). This raises an interesting question of survival, since this species grows along side ***Ceratodon purpureus*** (Figure 59-Figure 60). Are there physiological mechanisms that permit its survival, or is it indeed more vulnerable to a diminished ozone layer, as suggested Dunn and Robinson?

A study by Proctor and Smirnoff (2011) may explain the survival of ***Schistidium antarctici*** (Figure 7). Mosses typically saturate at moderate light levels. Light intensities above those levels can therefore be harmful because of more excited electrons than the photosynthetic apparatus can handle. These saturating levels are similar to those of shade species, demonstrated by the moss ***Plagiomnium undulatum*** (Figure 61) and leafy liverwort ***Trichocolea tomentella*** (Figure 62). But what about bryophytes that live in exposed sites with no shade to protect them? ***Andreaea rothii*** (Figure 63-Figure 64), ***Schistidium apocarpum*** (Figure 65), many ***Sphagnum*** species (Figure 48-Figure 49), and ***Frullania dilatata*** (Figure 66) show a non-saturating electron transfer rate at high light levels, accompanied by high non-photochemical quenching (protection from the adverse effects of high light intensity by dissipating excess excitation energy). ***Plagiomnium undulatum*** and ***Schistidium apocarpum*** can use oxygen and carbon dioxide interchangeably as **electron sinks** (in this case, binding the electrons so they cannot do damage). These two moss species have a high capacity for oxygen photoreduction when CO_2 assimilation is limited. But when the atmosphere is reduced to 1% O_2 with normal levels of CO_2, non-saturating electron flow is not suppressed. Nitrogen + saturating CO_2 causes a higher relative electron transport rate while depressing the non-photochemical quenching. These high abilities of supporting the electron transport by oxygen photoreduction may be a mechanism to permit such mosses as the Antarctic ***Schistidium antarctici*** to survive the high UV-B levels in the Antarctic.

Figure 61. ***Plagiomnium undulatum***, a shade species. Photo by Janice Glime.

Figure 62. ***Trichocolea tomentella***, a shade species. Photo by Michael Lüth, with permission.

Figure 63. ***Andreaea rothii*** wet, from the Black Forest Germany, a sun species. Photo by Michael Lüth, with permission.

Figure 64. ***Andreaea rothii*** dry, living in an exposed site. Photo by Michael Lüth, with permission.

The moss ***Hennediella heimii*** (Figure 67) from Southern Victoria Land, Antarctica, is provided with glacial melt water during the summer. When Pannewitz *et al*. (2003) monitored this moss for 18 days in summer, they found that it had a constant potential photosynthetic activity during that entire period. It grew in the predicament of high light and low temperatures. Nevertheless, it showed no sign of photoinhibition or light saturation, and its electron transport rate response to photosynthetic photon flux densities remained linear at all temperatures. The researchers speculated that it must have a highly effective non-photochemical quenching system.

Figure 65. ***Schistidium apocarpum***, a species that physiological adaptations in addition to its color, awns, and ability to wrap leaves around its stem, all of which aid it in living in exposed sites. Photo by Michael Lüth, with permission.

Figure 66. ***Frullania dilatata***, a desiccation-tolerant leafy liverwort. Photo by Michael Lüth, with permission.

Figure 67. ***Hennediella heimii***, a species that shows no sign of photoinhibition even in the high UV-B light of the Antarctic continent. Photo by Michael Lüth, with permission.

When the snow melts on the Antarctic Peninsula, bryophytes are suddenly exposed to high UV-B levels while still at near-freezing temperatures. Post and Vesk (1992) studied the only continental Antarctic liverwort,

Cephaloziella varians (Figure 68-Figure 69). It occurs in full sun once its ice cover melts. The researchers compared plants from sun-exposed and shaded sites. Those from full sun exhibited dark purple leaves with an anthocyanin-like pigment in thick cell walls. These purple plants grew in dense turfs, were larger, had more closely spaced leaves, and had a higher carotenoid to chlorophyll ratio than did the shaded green plants. The shaded green plants, on the other hand, contained more chlorophyll per unit weight. Like a number of other bryophyte studies, this one showed no variation in the chlorophyll *a*/*b* ratio with differences in light intensity. In low light levels the green plants exhibited higher photosynthetic oxygen evolution rates. The two colors of leaves in similar positions on the plants had more appressed thylakoids in green leaves than did the purple leaves. These differences are the same as expected under varying light exposure.

Figure 68. ***Cephaloziella varians*** amid **Polytrichaceae**. This Antarctic endemic produces red pigments in high light. Photo by Kristian Peters, with permission.

Figure 69. ***Cephaloziella varians*** showing red coloration typical in high light. Photo by Kristian Peters, with permission.

Snell *et al*. (2007) experimented with the same leafy liverwort species, ***Cephaloziella varians*** (Figure 68-Figure 69), by covering it with screens containing Mylar polyester for 44 days. This treatment resulted in changes in thalli, which are normally black, to exhibit a green color. This was the result of reduced concentrations of the anthocyanidin **riccionidin A** in the plant tips. These plants were then exposed to an abrupt increase in their UV-B radiation when the screens were removed. Within only 48 hours the plants were visibly darker. This color change was due to *de novo* synthesis of riccionidin A that reached the same concentrations as that in plants that had not been covered during those 44 days. This synthesis required an equivalent of 1.85% of the carbon fixed during those 48 hours. The F_v/F_m and photochemical quenching were likewise the same in both groups of plants. Nevertheless, the level of chlorophyll fluorescence indicated that non-photochemical quenching was higher in the plants that had just experienced the sudden increase in UV-B.

Otero *et al*. (2008) examined five liverworts and ten mosses from open aquatic habitats of Tierra del Fuego on the southern tip of Argentina, where the atmosphere is thinner than in temperate regions, to determine their responses to UV radiation. They found that the species differed in spectra form and area under the absorbance curve (AUC). The spectra had one, two, or no defined peaks. They suggested that phenolic derivatives might be responsible for the differences in peaks among the species. These phenolic derivatives could serve not only as screening compounds, but also as antioxidants. The AUC values for most of the liverworts were higher than those for most of the mosses. The liverworts ***Noteroclada confluens*** (Figure 70) and ***Triandrophyllum subtrifidum*** (Figure 71) had much higher bulk UV-absorption capacity of the methanolic extracts (BUVACME) than did any other bryophyte in the study. The researchers concluded that "accumulation of UV-absorbing compounds might often increase protection against UV radiation in liverworts, but rarely in mosses." Could this difference be related to their location in southern Argentina? But Otero and coworkers did not find the BUVACME of these aquatic bryophytes to differ significantly from that found elsewhere on the planet.

Figure 70. ***Noteroclada confluens***, a species with an unusually high bulk UV-absorption capacity. Photo by Michael Lüth, with permission.

Figure 71. ***Triandrophyllum subtrifidum***, a species with an unusually high bulk UV-absorption capacity. Photo by Shirley Kerr, with permission.

Huttunen *et al*. (2005) compared the UV-absorbing compounds in herbarium specimens of terrestrial and peatland mosses collected from 1926 to 1996 from the sub-Arctic to see if it had changed as fluorines in the atmosphere increased the ozone hole, permitting greater penetration of UV light. They found that the average amount of total compounds (sum of A280-320 nm absorption) per mass from the lowest to the highest was ***Polytrichum commune*** (Figure 58), ***Pleurozium schreberi*** (Figure 28), ***Hylocomium splendens*** (Figure 54-Figure 55), ***Sphagnum angustifolium*** (Figure 72), ***Dicranum scoparium*** (Figure 73), ***Funaria hygrometrica*** (Figure 32-Figure 35), ***Sphagnum fuscum*** (Figure 74), ***Sphagnum warnstorfii*** (Figure 75), ***Sphagnum capillifolium*** (Figure 76), and ***Polytrichastrum alpinum*** (Figure 77). The amount of UV-B-absorbing compounds per specific surface area correlated with the summertime daily global radiation and latitude, but they found no trend in concentration of UV-B-absorbing compounds from 1920 to 1990 except in ***Sphagnum capillifolium***, which showed a significant decreasing trend in concentrations. Huttunen and coworkers suggested that this lack of correlation with the increasing size of the ozone hole could be the result of degradation of the protective compounds or the difficulty in extracting the wall-bound pigments p-coumaric acid and ferulic acid (Davidson *et al*. 1989) and the sphagnorubins (Geiger *et al*. 1997).

Figure 72. ***Sphagnum angustifolium***. Photo by Kristian Peters, through Creative Commons.

Figure 73. ***Dicranum scoparium*** on forest floor. Photo by Janice Glime.

Figure 74. ***Sphagnum fuscum***, sun-dwelling sun species. Photo by Michael Lüth, with permission.

Figure 75. ***Sphagnum warnstorfii***, exhibiting its sun-exposed red pigments. Photo by Michael Lüth, with permission.

Figure 76. ***Sphagnum capillifolium***. Photo by Li Zhang, with permission.

Figure 77. ***Polytrichastrum alpinum*** with capsules, a species of exposed, usually cold, habitats. Photo by David T. Holyoak, with permission.

Caldwell *et al.* (1998) concluded that some of the most important consequences of elevated UV-B might be indirect effects. In tracheophytes, these include changes in susceptibility of plants to attack by pathogens (fungi & bacteria) and insects, changes in the competitive balance among plants, and altered nutrient cycling. More direct effects seem to occur through altered gene activity rather than direct damage. These changes may be exacerbated or diminished by other changes that are coupled with increased UV-B, such as temperature and CO_2 level changes. Although these indirect effects would seem to be critical, if forest trees and other tracheophyte examples are indicative, we should look for these effects in bryophytes.

Early land plants faced high levels of UV light and at the same time water scarcity from their beginnings on land (Martínez-Abaigar & Núñez-Olivera 2022). Through time, they have developed various physiological and structural adaptations to minimize the effects of UV light on the cell contents. These adaptations vary among the species, with mosses being more UV-tolerant that liverworts.

Desiccation Effects and Light

High light intensities are often coupled with desiccating conditions. Yet, it appears that the mosses that live in such desiccating conditions seldom suffer light damage during their dehydrated periods, and photosynthesis is able to resume immediately upon rehydration, not requiring synthesis of new chlorophyll to resume (Di Nola *et al*. 1983). For example, the desiccation-tolerant moss ***Syntrichia ruralis*** (Figure 2) retains all its pigments upon drying, thus rapidly recovering its photosynthetic functions upon rehydration (Hamerlynck *et al*. 2002). This species permits recovery on a daily basis by a thermal dissipation of the excess light energy as the moss dehydrates in the morning, and recovery upon rehydration depends on light conditions and the rapidity of drying.

Tracheophytes do not enjoy this pigment conservation (Heber *et al*. 2001) and rapidly lose their photosystem II capability under desiccation conditions (Hamerlynck *et al*. 2002). In desiccation-tolerant bryophytes, protein protonation, coupled with the presence of high levels of zeaxanthin, seems fully capable of dissipating excess light energy (Heber *et al*. 2001). A similar rise in zeaxanthin with dehydration occurs in the desiccation-tolerant tracheophyte *Selaginella lepidophylla* (Figure 78Figure 79) (Casper *et al*. 1993). This rise occurs during the dehydration process, and Casper *et al*. hypothesized that zeaxanthin-related protection is engaged in response to the dehydrating conditions, even in low light levels. Nevertheless, chlorophyll fluorescence is lost during drying of predarkened desiccation-tolerant mosses, suggesting that energy dissipation in the dry state is not related to protonation and high levels of zeaxanthin.

Deltoro *et al*. (1998a) found that desiccation-tolerant bryophytes [***Hedwigia ciliata*** (Figure 14-Figure 16), ***Hypnum cupressiforme*** (Figure 80), ***Leucodon sciuroides*** (Figure 81-Figure 82), ***Orthotrichum cupulatum*** (Figure 83), ***Pleurochaete squarrosa*** (Figure 84), ***Porella platyphylla*** (Figure 85), and ***Syntrichia ruralis*** (Figure 2)] were able to resume photosynthesis rapidly upon rehydration, whereas desiccation-intolerant bryophytes [***Barbula ehrenbergii*** (Figure 86-Figure 87), ***Cinclidotus aquaticus*** (Figure 88), ***Conocephalum conicum*** (Figure 89), ***Lunularia cruciata*** (Figure 90), ***Palustriella commutata*** (Figure 91-Figure 92), ***Philonotis calcarea*** (Figure 93), and ***Platyhypnidium riparioides*** (Figure 94)] from mesic and hydric habitats were unable to resume their photosynthetic activity.

Figure 78. *Selaginella lepidophylla* showing the edges curling up as it dries and exposing the white ventral surface that helps to reflect high light. Photo through Creative Commons.

Figure 79. *Selaginella lepidophylla* dry, illustrating its mechanical response to drying. Photo by Nicole Koehler, through public domain.

Figure 80. ***Hypnum cupressiforme***, a widespread, desiccation-tolerant species. Photo by J. C. Schou, with permission.

Figure 81. ***Leucodon sciuroides*** wet, a desiccation-tolerant epiphyte. Photo by Michael Lüth, with permission.

Figure 82. ***Leucodon sciuroides*** dry, showing appressed leaves and decreased surface area. Photo by Michael Lüth, with permission.

Figure 83. ***Orthotrichum cupulatum***, a xerophytic epiphyte. Photo by Michael Lüth, with permission.

Figure 84. ***Pleurochaete squarrosa***, a desiccation-tolerant moss. Photo by Michael Lüth, with permission.

Figure 85. ***Porella platyphylla***, a desiccation-tolerant leafy liverwort epiphyte. Photo by Michael Lüth, with permission.

Figure 86. ***Barbula ehrenbergii***, a desiccation-intolerant moss. Photo by Michael Lüth, with permission.

Figure 87. ***Barbula ehrenbergii***, a species that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

Figure 88. ***Cinclidotus aquaticus***, a species of wet habitats that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

Figure 89. ***Conocephalum conicum***, a species of damp, usually shaded, habitats that is unable to resume photosynthesis after desiccation. Photo by Janice Glime.

Figure 90. ***Lunularia cruciata***, a species that is unable to resume photosynthesis after desiccation. Photo by David Holyoak, with permission.

Figure 91. ***Palustriella commutata***, a species of wet habitats. Photo by J. C. Schou, through Creative Commons.

Figure 92. ***Palustriella commutata***, a species of wet habitats that is unable to resume photosynthesis after desiccation. Photo by David T. Holyoak, with permission.

Figure 93. ***Philonotis calcarea***, a species of wet habitats that is unable to recover photosynthesis after desiccation. Photo by Michael Lüth, with permission.

In examining the xanthophyll content of a desiccation-tolerant leafy liverwort, ***Frullania dilatata*** (Figure 66), they found an increase in de-epoxidized xanthophylls in response to dehydration (Deltoro *et al*. 1998b), whereas this did not occur in the desiccation-intolerant ***Pellia endiviifolia*** (=***Apopellia endiviifolia***; Figure 95), and the latter species had less ability to dissipate the light while dry. Upon rehydration, ***Frullania dilatata*** resumed full photosynthetic capability rapidly, whereas ***P. endiviifolia*** suffered irreversible damage to photosystem II. They suggested that ***F. dilatata*** likewise possesses a desiccation-induced production of zeaxanthin, but they were unable to rule out the loss of K^+ from damaged membranes in ***P. endiviifolia*** as a causal factor for its demise.

Figure 94. ***Platyhypnidium riparioides***, a species of submersed and wet habitats that is unable to recover photosynthesis after desiccation. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Pellia endiviifolia***, a species with weak ability to dissipate light when dry. Photo by Michael Lüth, with permission.

Bartoskova *et al*. (1999) offer a somewhat different explanation for observed changes in chlorophyll fluorescence during drying. Working with leaves of ***Rhizomnium punctatum*** (Figure 96), they found a 50% decrease in the F685/F735 ratio in the chlorophyll fluorescence spectrum during drying. No changes occurred in the E475/E436 bands of fluorescence. They could find no functional changes resulting from desiccation at the energy transfer level and suggested that the change in fluorescence ratio is the result of a rearrangement of chloroplasts into groups that enhance the effect of chlorophyll reabsorption. My own experience in extracting chlorophyll from dry mosses is that they extract better if they are rehydrated first. This would be consistent with the grouping of chloroplasts, hence preventing the solvent from reaching the interior of the clump. In a conversation with Zoltan Tuba, I learned that he had experienced a similar response.

Figure 96. ***Rhizomnium punctatum***, a species that may rearrange its chloroplasts upon drying. Photo by Michael Lüth, with permission.

At least in alpine areas, where UV light may be more intense, desiccation can affect moss (and lichen) fluorescence differently from its effects on tracheophytes. In its dehydrated state, the moss ***Grimmia alpestris*** (Figure 97) had very low chlorophyll fluorescence, whereas it was high in the alpine tracheophytes tested (Heber *et al*. 2000). Conversely, upon rehydration, the mosses and lichens experienced increased chlorophyll fluorescence, whereas the tracheophytes experienced a decrease. This is because, unlike their tracheophyte counterparts, the mosses and lichens do not experience photodamage in their dry state. Both groups of plants form potential chlorophyll fluorescence quenchers as a response to desiccation, but only the dehydrated mosses and lichens responded to the energy transfer from light by exhibiting a decrease in fluorescence. It appears that among these alpine taxa, only the poikilohydric ***Grimmia alpestris*** has a deactivation pathway that enables it to avoid photodamage both in its hydrated and dehydrated states.

Figure 97. ***Grimmia alpestris***, a species that has a deactivation pathway that permits it to live in high light conditions. Photo by Jan-Peter Frahm, with permission.

Beckett *et al.* (2005) found that **hardening** (process of increasing resistance) of the moss ***Atrichum androgynum*** (Figure 98) during drying permitted it to recover fully from dehydration, whereas lack of time for this preparation did not (Figure 99). That is to say, mosses that hardened by slow drying before the silica gel desiccation treatment had a better recovery than mosses that were placed immediately into the desiccation treatment from full hydration. More importantly, hardening greatly increased the photochemical quenching during the first few hours of rehydration. In these early stages photophosphorylation occurs, but not carbon fixation. Thus, it is in these early stages that photoprotection is most important, and the moss experiences reduced efficiency during drying in order to accomplish photoprotection during rehydration.

Figure 98. ***Atrichum androgynum***, a species that recovers fully from dehydration if it is able to undergo hardening during drying. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

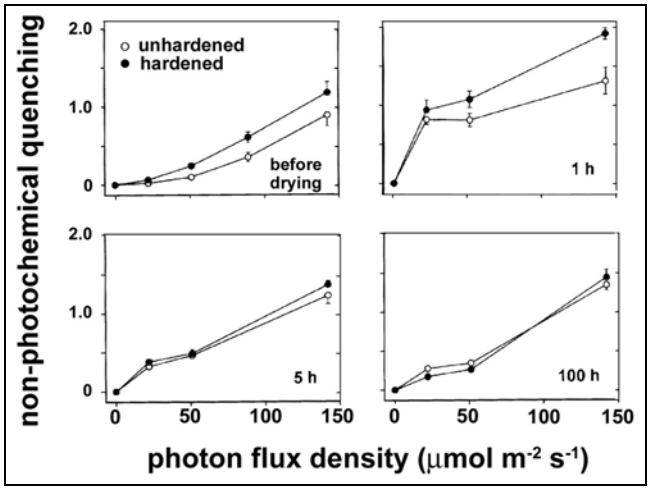

Figure 99. The effect of hardening on the non-photochemical quenching upon rehydration of 1, 5, and 100 hours compared to quenching prior to desiccation in ***Atrichum androgynum***. Redrawn from Beckett *et al*. 2005.

Mosses, as in the tracheophyte resurrection plant *Selaginella lepidophylla* (Figure 78-Figure 79), often have mechanical responses that help to protect them from the damaging effects of light. Lebkuecher and Eickmeier (1991, 1993) have shown that the rolling of the fronds of *S. lepidophylla* serves to protect the plant from light and thermal damage that could be expected in the dry state. In that species, some damage occurs during the drying phase before the curling is complete. It is likely that mosses like ***Hedwigia ciliata*** (Figure 14-Figure 16) and ***Syntrichia ruralis*** (Figure 100) might accomplish the same thing. Might the smaller bryophytes curl quickly enough to avoid that early damage? In ***Hedwigia ciliata***, an appression of

leaves against the stem is realized, and the tips of the branches tend to curve upward, reducing exposure. In ***S. ruralis***, the drying leaves twist (Figure 100) and become more vertically oriented. Hamerlynck *et al*. (2000) suggested that ***S. ruralis*** has a "coordinated suite of architectural and physiological characteristics maintaining the photosynthetic integrity of these plants." These include not only their ability to change the positions of their leaves, but also to alter the surface reflectance as water leaves the leaf cells. This alteration causes more reflectance from a dry surface than from a wet one.

Figure 100. Dry ***Syntrichia ruralis*** exhibiting dark color and twisted leaves that protect it from high light intensity. Photo by Janice Glime.

In the Antarctic, where desiccation is frequent, Lovelock and Robinson (2002) also found significant differences among species and the sites they occupied based on their surface reflectance properties, especially at ~700 nm, whereas pigment concentration did not seem to be important.

Avoidance – Hiding under Rocks

Imagine a light so intense that you must hide under a rock to avoid damaging your pigments. The only light you ever see is that which comes through the rock, or occasionally reflects off the ground around that rock. There are some mosses that take just such a refuge. Using the rock as a filter, ***Syntrichia inermis*** (Figure 101) survives the intense light (and dryness) of the Californian desert by living beneath a piece of translucent rock (Werger & During 1989).

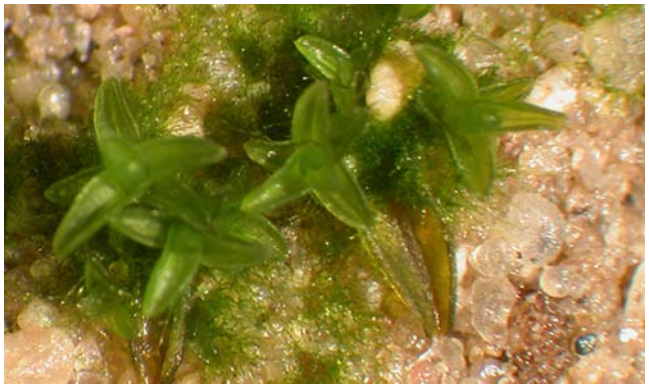

Figure 101. ***Syntrichia inermis***, a moss capable of living under quartz pebbles in the desert. Photo courtesy of Lloyd Stark.

As we have seen, polar deserts are unfriendly habitats due to the damaging effects of UV radiation. For **Cyanobacteria** (Figure 102) and algae, living under translucent rocks is a way to escape that damaging radiation (Thomas 2005). These assemblages can be as productive as their neighbors that are not protected by rocks. Is seems likely to me that some members of these microbial communities might enhance the habitat for the few species of bryophytes that live there. For example, **Cyanobacteria** can convert atmospheric nitrogen to a form usable by the bryophytes. Non-photosynthetic bacteria can provide CO_2. This remains another microecosystem begging for ecological study.

Figure 102. **Cyanobacteria** under quartz rock. Photo by Michael Wing, public domain through NSF funds.

Williams (1943) described a "moss peat" under translucent pebbles in the American Great Plains, but there seems to be no publication of the actual species. The rare moss ***Aschisma kansanum*** is known only from this unique habitat, where it occurs at the base of nearly clear quartz pebbles (Cridland 1959). The thick, leathery protonema, which is persistent, covers the buried part of the pebbles overlying sandy Pleistocene gravels. And in the Antarctic, where mosses must "worry" about the effects of UV light – what better place to hide than behind glass, in the form of quartz. And there one might also find the tiny ***Hennediella heimii*** (Figure 103) beneath the rock (Fife 2005).

Figure 103. ***Hennediella heimii***, a moss that lives under quartz rocks in the Antarctic. Photo by Michael Lüth, with permission.

Marchand (1998) determined that about 1.5% of the full sunlight hitting a milky quartz rock penetrated through about 2.5 cm of rock, comparing this to the light reaching a potted plant in a well-lit office. In some cases, visible light can reach a depth of 5 cm. The rock offers the added advantage of reflecting much of the heat and registering temperatures ~7ºC less than under a dark-colored volcanic rock.

Terry Hedderson (Bryonet 22 February 2005) tells of quartz-field bryophyte communities beneath stones in the Knersvlakte area of Namaqualand and from the inselbergs of Bosmansland, both in South Africa. He provides this anecdotal account: "The bryophyte assemblages seem to come in two forms: In some areas where there are extensive and relatively deep patches of translucent small quartz pebbles, one can find entire communities comprising ***Bryum argenteum*** (Figure 17-Figure 18), ***Riccia*** spp. (Figure 104), ***Hennediella longipedunculata***, other small **Pottiaceae**, ***Chamaebryum***, ***Gigaspermum*** (Figure 105) and others, buried to a depth of a few centimetres (3-10 say). These often occur with various Aizoaceae seedlings, as mentioned by a previous contributor. Some of the best examples that I've seen of these are on the summits of Ghamsberg and Pellaberg in Bosmansland. In areas where the pebble cover is less continuous (like in the Knersvlakte), I have found communities under flattish single stones that are imbedded in a clay matrix. Here they often occur with lots of blue-greens, with the main bryophyte component comprising ***Archidium dinteri***, ***Bryum argenteum***, various ***Riccias*** and small ***Fissidens*** spp (Figure 106). The vast majority of stones have only blue-greens and it is not at all clear what determines whether bryophytes are present or not. In both cases the plants are often quite vigorous and healthy looking, and not the least bit etiolated, so I imagine that they receive sufficient light."

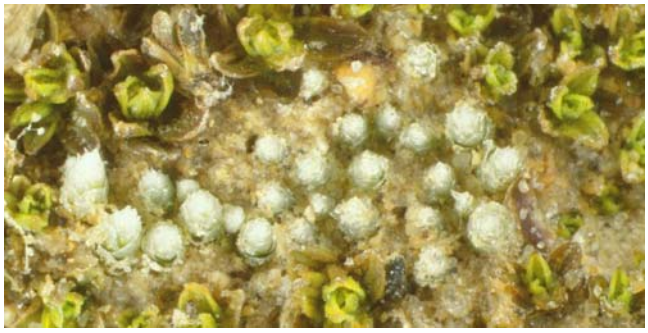

Figure 105. ***Gigaspermum*** sp, a genus that can occur under translucent quartz rocks in bright sun. Photo by Jan-Peter Frahm, with permission.

Figure 106. ***Fissidens bryoides*** with capsules, a tiny species such as those that might occur under flat stones in high light. Photo by Janice Glime.

But records of these sequestered mosses are far more rare than those of algae. This intriguing habitat has led a number of bryologists to overturn numerous rocks in places like the Namib Desert, so far only to find more algae.

In the Antarctic, bryophytes (and algae) occur beneath rocks, stones, and sand (Lewis-Smith 2000). Seppelt (2005) finds buried mosses there occupying ephemeral riverbeds and other places where they have been buried by sand carried by wind or water. ***Bryum pseudotriquetrum*** (Figure 5) and ***B. subrotundifolium*** (Figure 107) can be uncovered by sweeping away the sand. In these habitats, as in sand dunes and volcanic tephra, the acrocarpous mosses are able to grow upward and eventually emerge into the light. For those buried by sand, refracted and reflected light may help to sustain them through photosynthesis as they wend their way to the top.

Figure 104. ***Riccia sorocarpa***. Members of this genus are known from under quartz rocks. Photo by Michael Lüth, with permission.

Figure 107. ***Bryum subrotundifolium*** with Collembola among sand grains on Antarctica. Photo courtesy of Catherine Beard.

Lava fields often provide cracks through which rays of light may penetrate. Yojiro Iwatsuki (the finder), Zen Iwatsuki, and I were surprised in Iceland to uncover a miniature moss garden, predominately ***Saelania glaucescens***, hidden under a fissure in the lava rock (Figure 108). Juana María González-Mancebo related an experience in the Canary Islands (Bryonet, 22 February 2005) where the researchers found 69 species of bryophytes living among the second layer of rock, under the rocks of the first layer of lava, in lava tubes, and in volcanic pits. Even the epiphyte ***Neckera intermedia*** (Figure 109) can grow in the more humid lava flows of Tenerife.

Figure 108. ***Saelania glaucescens*** exposed by our removal of several pieces of the broken volcanic rock above it. Photo by Janice Glime.

Figure 109. ***Neckera intermedia***, an epiphyte that can grow in lava flows. Photo by Jan-Peter Frahm, with permission.

If you are a moss in the Mojave Desert, you can have a rough life. The sunlight is intense and hot. Moisture is all but non existent most of the time. But ***Syntrichia caninervis*** has found an unusual way of coping. It lives under white, translucent quartz rocks (ScienceFriday.com 2020). On those rare occasions when it does rain, the moss begins rehydrating immediately and remains moist long enough to replenish its energy supply. Undoubtedly the rock helps to maintain a longer hydration period, but it also filters the intense light.

Figure 110. ***Syntrichia caninervis*** growing under white quartz rock, Mojave Desert, California, USA. Photo by Kirsten Fisher, with permission.

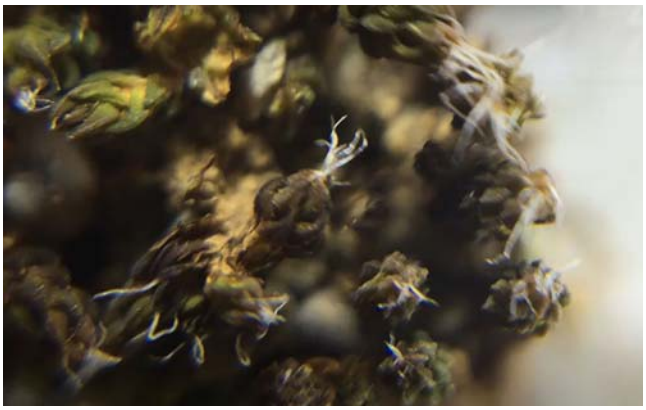

Figure 111. ***Syntrichia caninervis*** dry, from under quartz rock, Mojave Desert, California, USA. Photo by Kirsten Fisher, with permission.

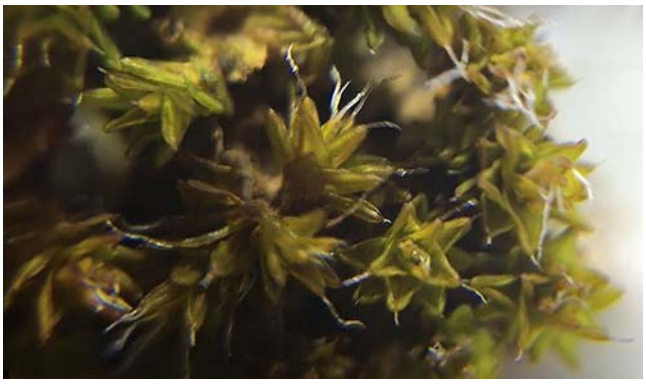

Figure 112. ***Syntrichia caninervis*** from under quartz rock, 50 seconds after wetting. Photo by Kirsten Fisher, with permission.

Summary

Due to their one-cell-thick leaves, bryophytes are especially susceptible to damage by UV light. Dry plants are especially vulnerable to chlorophyll and DNA damage due to the lack of protective water. Some have altered optical properties that reduce the light penetration into cells. Bryophytes can suffer photoinhibition due to overstimulation of chlorophyll in high light, which can result in a decrease in thylakoid stacking.

Some mosses have **lamellae**, **inrolled leaf lamina**, **filaments**, **hyaline tips**, and **awns** that partially cover the leaf and protect it from light. Others curl the leaves or wrap them around the stem. Aquatic mosses are protected by their water medium.

In response to high light intensities, bryophytes experience a decrease in chlorophyll. By having a relatively high amount of chlorophyll *a* compared to chlorophyll *b* in their shade plants, they are ready for sunflecks and other short periods of light availability, thus making up for the low productivity that is possible in the shade.

Pigments can filter light and reduce its energy, thus protecting the chlorophyll and DNA. Ethylene stimulates the production of red pigments, which are particularly common at low temperatures and in bright light. In ***Sphagnum***, this red pigment is a cell wall pigment, **sphagnorubin**. **Violaxanthin** is known to increase in response to high light. **Zeaxanthin** responds by disabling the chlorophyll antenna pigments (**quenching**), thus reducing the energy reaching the chlorophyll *a*.

Bryophytes are superior to tracheophytes in preserving their chlorophyll during desiccation and are thus ready for photosynthesis upon rehydration. This may be due to a rearrangement of the chloroplasts into protective groups. **Hardening** is important in this preparation.

Some bryophytes avoid the intense radiation by growing under translucent rocks. These locations are especially important in deserts where light is intense and desiccation is a major problem, As see in ***Syntrichia caninervis***..

Acknowledgments

Thank you to Rod Seppelt for helping me resolve which liverwort name belonged to species from the Antarctic continent.

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CHAPTER 9-4

LIGHT: SEASONAL EFFECTS

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CHAPTER 9-4
LIGHT: SEASONAL EFFECTS

Figure 1. Winter condition of *Thuidium tamariscinum*, when the canopy is gone and the temperature is cold. Photo by Michael Lüth, with permission.

Bryophyte View of Light

Light is a constantly changing parameter in the world of the bryophytes. They experience long and short periods (**photoperiod**) as the seasons change. They experience high intensity and low intensity as the leaves grow on the trees. They experience changes from white light to green light as the canopy closes. And each of these changes is coupled with changes in temperature and available moisture. Each of these requires its own set of adaptations to permit the bryophyte to survive. But bryophytes can also take advantage of these changes as signals to them of the upcoming series of climatic events.

High Light and Low Temperatures

When plants are metabolically slowed by low temperatures (ca. 1ºC) and light intensity is high (Figure 1), photo-oxidation damage can occur in cells (Kuiper 1978). This can result in such responses as rupture of the chloroplast envelope, formation of vesicles in thylakoids, and rapid degradation of linolenic acid. Adamson and coworkers (1988) suggest that such photoinhibition may be the major factor in limiting production of Antarctic bryophytes.

Blue light seems to be especially effective in the photo-oxidation of unsaturated fatty acids, indicating that carotenoids (yellow pigments absorb blue light) contribute to the process. One of the causes of the breakdown of chlorophyll can be attributed to the degradation of its complexing lipid, monogalactose diglyceride (Kuiper 1978). Ironically, it is the unsaturated fatty acids that are susceptible to this oxidation, causing a risky condition for plants preparing for the cold of winter while sustaining the bright light of autumn. However, presence of tocopherol, an anti-oxidant, can nullify this photo-oxidation process (Kuiper 1978) and may play a key role in protection of chlorophyll during autumn and spring when such low temperature and bright light conditions prevail.

When days are bright and nights are cold, ***Sphagnum magellanicum*** (Figure 2) produces **sphagnorubin** and becomes a deep wine red (Gerdol 1996). When the plants occur in the open, where higher light intensities are expected, the concentration of sphagnorubin is greater.

However, in intense light and warm temperatures ***Sphagnum magellanicum*** does not produce much red pigmentation (Rudolph *et al*. 1977). In this case the photorespiration/ photosynthesis ratio would be high due to the fact that photorespiration has a $Q_{10} = 3$ with very little damping at higher temperatures. Photosynthesis, however, is observed to reach an optimum and then decrease its rate rapidly (Zelitch 1971). This would result in a high CO_2/O_2 ratio that would decrease ethylene production and stimulate chlorophyll and carotenoid synthesis. Anthocyanin (and sphagnorubin?) production would not be enhanced and so no red pigmentation would be found. In the case of warm temperatures, the red pigment would convey no adaptive advantage since the greatly increased photorespiration would serve as an energy shunt to protect the chlorophyll from overexcitation by the intense light (Bidwell 1979).

Figure 2. ***Sphagnum magellanicum*** colored by sphagnorubin. Photo by Michael Lüth, with permission.

A second function of red pigment at low temperatures could be the heat absorption and warming of the moss, a mechanism already known to warm flowers, such as those enclosed in a red spathe in ***Symplocarpus foetidus*** (Figure 3), and to increase respiration in cold-adapted copepods (Byron 1982). Zehr (1979) has suggested that the red color of the leafy liverwort ***Nowellia curvifolia*** (Figure 4), induced by exposure to light when leaves fall, increases the temperature of the liverwort to allow greater photosynthesis and respiration in winter.

Figure 3. ***Symplocarpus foetidus*** showing red spathe that creates a warm space, attracting flies that pollinate the flowers inside. Photo by Sue Sweeney, through Creative Commons.

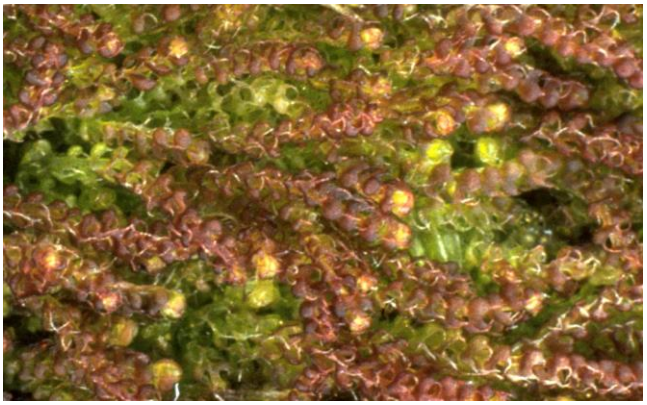

Figure 4. ***Nowellia curvifolia*** demonstrating its red leaves of fall. Photo by Jan-Peter Frahm, with permission.

Light Effects on Reproduction

Humans don't think in terms of high light intensities for reproduction, but it appears that at least some mosses do. ***Hylocomium splendens*** (Figure 26) had poor reproduction in all populations except those that had received extra light as the result of removal of stems (Rydgren & Økland 2001). Those that were merely clipped to remove all growing tips and provide extra light did no better than the controls, suggesting that it was not the stimulus of the wounding or the extra energy diverted away from growing buds that caused the greater reproduction. In the second year of the experiment, the removal group had ten times as many sporophytes as the other treatment groups. But is this an indication of good or of bad conditions? Many algae and even flowering plants go into a sexual stage when growing conditions are poor, providing a means for the species to survive through its offspring.

To confound the issue further, Hughes and Wiggin (1969) found that in ***Phascum cuspidatum*** (Figure 5), light had just the opposite effect. Plants grown in culture in the shade had significantly more antheridia, more antheridial dehiscence, and larger antheridia than plants grown with light from the north sky. They did find more archegonial heads on plants grown in the light, but the success of fertilization was greater for plants grown in the shade (11%) than in the light (6%). However, they suggested that some of these differences could be accounted for by differences in population sizes.

Figure 5. ***Phascum cuspidatum*** with capsules. Photo by Michael Lüth, with permission.

In the Antarctic, bryophytes are frozen in winter, but in summer they are fully exposed to the polar sun. In fact, Post *et al*. (1990) found that the major limiting factor to

Antarctic bryophyte productivity is photoinhibition. This would not be unusual for C_3 plants such as bryophytes growing at low temperatures in high light. Nevertheless, this topic has rarely been studied in bryophytes.

Seasonal Effects on Pigments

Light intensity changes with the seasons, and at least some plants are adapted to respond to those changes. Tracheophytes change their chlorophyll concentration based on the amount of light reaching the leaf. Plants grown in low light will increase their chlorophyll *b* concentration, and thus their chlorophyll *a*:*b* ratio decreases. Those plants kept indoors in low light will suddenly turn red or become bleached if they are put out in bright sunlight, and the photosynthetic apparatus will become permanently damaged. Leaves growing on the shady side of a tree will be thinner and darker, while those in the sun put on extra layers of palisade tissue. Bryophytes cannot change their leaf thickness in response to light changes, but it is possible for them to change the chlorophyll concentration and the ratio of shoot area to biomass. A bryophyte branch can effectively operate like a leaf of a seed plant and thus some of the same size ratio responses are possible.

Hicklenton and Oechel (1977) found that ***Dicranum fuscescens*** (Figure 6) from northern Canada exhibited an increase in the light required to saturate photosynthesis from early season until mid summer, with the trend reversing later in the season. They suggest that ability to photosynthesize at low light levels is an advantage to mosses that are still under the snow in early spring. Mosses exposed to high light when they are acclimated to low light actually experience damage, and it appears that the continuous light of summer in the Arctic may likewise be deleterious (Kallio & Valanne 1975). However, the continuous light damage occurred in laboratory experiments and it may be that plants living in the Arctic may acclimate to the seasonal change in photoperiod (Richardson 1981).

Figure 6. ***Dicranum fuscescens***, a species that changes its light saturation point as the season changes. Photo by Michael Lüth, with permission.

Van der Hoeven *et al*. (1993) found that shoot area to dry weight ratio increased from September to December in three pleurocarpous bryophytes, but they could offer no explanation for the shift (Table 1). They assumed chlorophyll per gram dry weight would not change seasonally, based on a study of ***Pleurozium schreberi*** (Figure 7) (Raeymaekers & Glime 1986). But if these species are more active in summer, a decrease in chlorophyll might be expected in December. On the other hand, if they store photosynthate in the summer and have maximum growth during the cooler autumn and early winter, the loss of weight per shoot length might be expected.

Figure 7. ***Pleurozium schreberi***, a species that does not have seasonal changes in chlorophyll content. Photo by Janice Glime.

Table 1. Shoot area to dry weight ratio of mosses in September (n=20) and December (n=25). From van der Hoeven *et al*. (1993).

	September	**December**
Calliergonella cuspidata	143±12	302±45
Rhytidiadelphus squarrosus	140±10	230±30
Ctenidium molluscum	147±11	226±43

There is sufficient indirect evidence that we might expect chlorophyll differences with seasons. For example, we know that photosynthetic capacity changes between summer and winter in at least some mosses. In ***Plagiomnium acutum*** (Figure 8) and ***P. maximoviczii*** (Figure 9), photosynthetic capacity diminishes from 126 and 95 µM CO_2 kg^{-1} dw s^{-1} in summer to 58 and 62 in winter, respectively (Liu *et al.* 2001). On the other hand, the light compensation point of 40 µmol m^{-2} s^{-1} in summer drops to 20 µmol m^{-2} s^{-1} in winter while the light saturation point drops similarly from 400 µmol m^{-2} s^{-1} in summer to 200 µmol m^{-2} s^{-1} in winter. This can most likely be attributed to the lower respiration rate in winter.

Figure 8. ***Plagiomnium acutum***, a moss that changes chlorophyll concentrations and light compensation points between summer and winter. Photo by Yingdi Liu, with permission.

Figure 9. ***Plagiomnium maximoviczii***, a species that changes chlorophyll concentrations and light compensation points between summer and winter. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Although Raeymaekers and Glime (1986) found similar chlorophyll content in the 2 cm terminal parts of ***Pleurozium schreberi*** (Figure 7) in August (2.1 mg/g dw), end of September (2.1), and end of October (2.2) in Baraga County, Michigan, I have observed that ***Fontinalis*** becomes pale by the end of summer (Figure 10) and bright to dark green by February (Figure 11), remaining deep green until June, in New Hampshire and the Upper Peninsula of Michigan. Mártínez Abaigar *et al*. (1993) found distinct differences in chlorophyll *a* with season in two species of ***Fontinalis*** (Figure 15). There is no reason to expect all species to behave the same way, nor to expect the same species to behave the same way in all parts of its distribution.

Figure 10. ***Fontinalis antipyretica*** exhibiting typical late summer and autumn colors. Photo by Malcolm Storey, through Creative Commons, with online permission.

Figure 11. ***Fontinalis antipyretica*** exhibiting typical late winter to early spring colors. Photo by Malcolm Storey, through DiscoverLife, with online permission.

In their study of 13 aquatic bryophytes, Mártínez Abaigar *et al*. (1993) found considerable differences among species in the chlorophyll concentration changes with seasons (Figure 15). For example, ***Fontinalis antipyretica*** (Figure 11) had its highest content in summer, whereas ***F. squamosa*** (Figure 12) had its highest in spring with summer exhibiting the second lowest (Figure 13), the lowest being in autumn. They reported that the greatest chlorophyll content occurred in the immersed species [***Fontinalis antipyretica***, ***F. squamosa***, ***Fissidens grandifrons*** (Figure 14) from San Pedro, ***Jungermannia cordifolia*** (Figure 16), and ***Platyhypnidium riparioides*** (Figure 17-Figure 18)]. The emergent ***Cratoneuron commutatum*** (Figure 19) had the least. This relationship to water is very likely correlated with light availability; the submerged taxa should produce more chlorophyll.

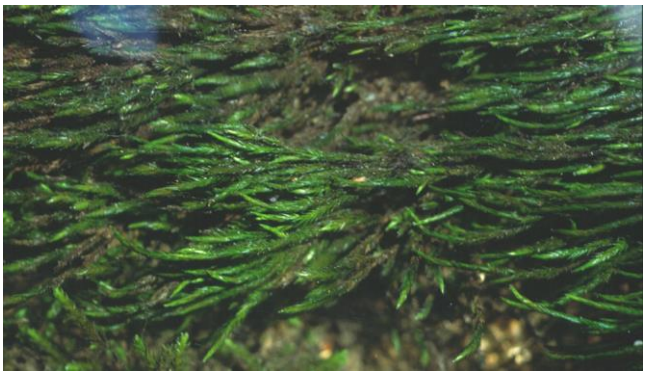

Figure 12. ***Fontinalis squamosa*** with a healthy spring color. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Fontinalis squamosa*** on rock above water near Swallow Falls Wales in mid-summer. Photo by Janice Glime.

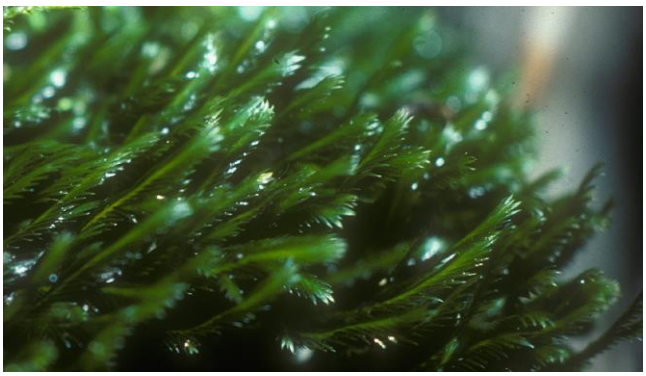

Figure 14. ***Fissidens grandifrons*** exhibiting dark coloration due to high chlorophyll concentrations. Photo by Janice Glime.

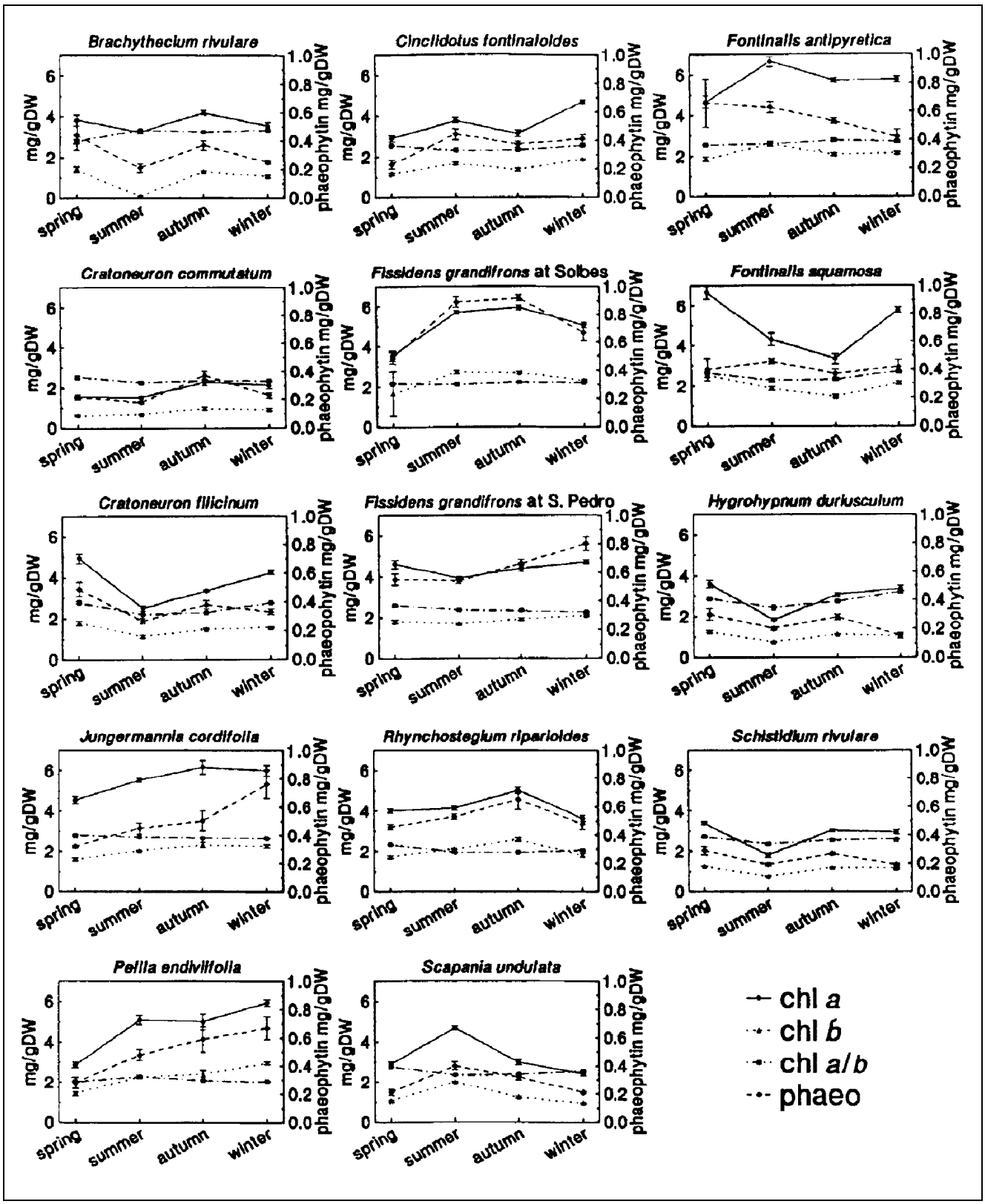

Figure 15. Seasonal changes in chlorophyll (left axis) and phaeophytin (right axis) concentrations (mg/gDW) in 13 species of aquatic bryophytes. Based on Mártínez Abaigar *et al*. 1993.

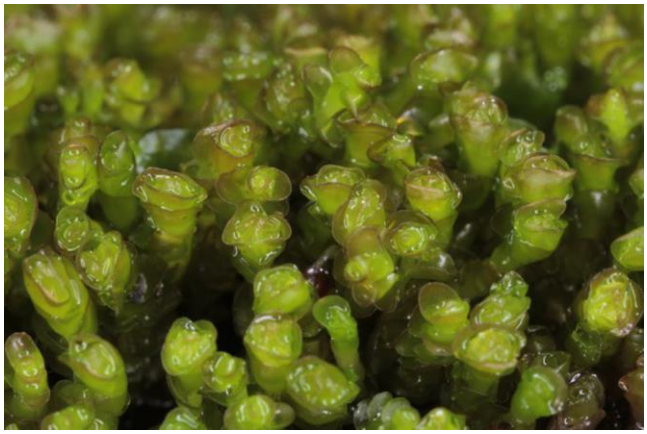

Figure 16. ***Jungermannia cordifolia***, one of the species with the highest chlorophyll content among aquatic species. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Platyhypnidium riparioides*** showing its habitat and green color. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Platyhypnidium riparioides*** showing its bright green color. Des Callaghan, with permission.

Chlorophyll is not the only pigment to respond to seasons. In ***Rhytidiadelphus squarrosus*** (Figure 20), ***R. triquetrus*** (Figure 21), and ***Mnium hornum*** (Figure 22), the biflavonoid and coumestane concentrations likewise showed seasonal variation, with concentrations increasing with periods of active growth (Brinkmeier *et al*. 1999). These concentrations were also affected by light intensity, independent of season.

Figure 19. ***Cratoneuron commutatum*** exhibiting a low concentration of chlorophyll. Photo by Michael Lüth, with permission.

Figure 20. ***Rhytidiadelphus squarrosus***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo by Michael Lüth, with permission.

Figure 21. ***Rhytidiadelphus triquetris***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo courtesy of Carrie Andrew.

We cannot rule out light intensity as the cause for these observed seasonal differences. In their study on ***Brachythecium rutabulum*** (Figure 23), Kershaw and Webber (1986) found that total chlorophyll increased from 1.70 mg chl g^{-1} on 8 May to 11.1 mg chl g^{-1} on 11 October, corresponding with full canopy conditions that reduced the light intensity reaching the moss. Concomitantly, light saturation declined from 200 µmol m^{-2} s^{-1} to 30 µmol m^{-2} s^{-1} and the light compensation point declined from 65 µmol m^{-2} s^{-1} to 4 µmol m^{-2} s^{-1}.

Figure 22. ***Mnium hornum***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo by Michael Lüth, with permission.

Figure 23. ***Brachythecium rutabulum***, a species that increases its chlorophyll content as the tree canopy reduces its available light. Photo by Michael Lüth, with permission.

Mishler and Oliver (1991) found that the amount of green tissue and concentration of chlorophyll per dry weight were higher in summer than in winter or early summer in the xerophytic moss ***Syntrichia ruralis*** (Figure 24). The chlorophyll *a:b* ratios, however, did not follow any seasonal pattern.

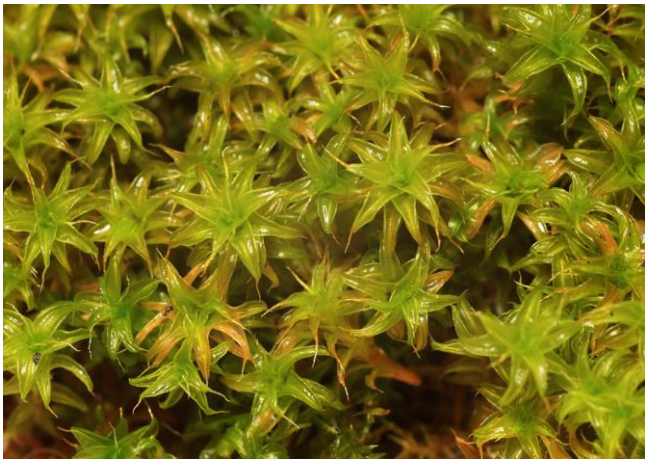

Figure 24. ***Syntrichia ruralis***, a species in which chlorophyll content in summer in the Organ Mountains of southern New Mexico, USA. Photo by Barry Stewart, with permission.

But what do bryophytes do in total darkness, as found under deep snow in winter? Only 3-4 mm of older crystalline snow is required for snow to become opaque (Gates 1962), rendering photosynthesis impossible. It appears that at least some of them should have no problem. When grown in total darkness for four months, the leafy liverwort ***Plagiochila asplenioides*** (Figure 25) rapidly lost starch, but exhibited little loss of chlorophyll (Suleiman & Lewis 1980). Once revived, the tissues were photosynthetically viable immediately. Thus, we should expect that many bryophytes might become photosynthetically active as soon as the snow recedes. Furthermore, low light levels penetrating the snow prior to total melt are sufficient to initiate photosynthesis.

Figure 25. ***Plagiochila asplenioides***, a species that loses almost no chlorophyll in the dark, but does lose starch. Photo by Michael Lüth, with permission.

Colors of Light

Those bryophytes living on the forest floor receive quite a different light quality from those in the open. The canopy, with its massive quantity of green leaves, serves as an effective filter against red light, the part of the spectrum creating the greatest photosynthetic activity. Thus, bryophytes on the forest floor must succeed in light that is weighted toward green and diminished in red wavelengths.

But the color of light is a seasonal attribute. When the canopy is gone from a deciduous forest in winter, light quality is nearly that of full sunlight, whereas in summer it is highly displaced toward the green end of the spectrum when red light is filtered out by the canopy. And the quality of light changes at the two ends of the photoperiod as well as light penetrates a greater distance through the atmosphere when it arrives nearly parallel to the Earth's surface.

Lakes present a similar problem, but for different reasons. Water, both liquid and as snow, is an effective filter against both UV light and the low-energy red wave lengths. Hence, the deeper into the water, or snow, the less of these wavelengths available to the moss. Older, crystalline snow is almost completely opaque to infra-red light. While this water medium is good as protection against UV light, it is detrimental in providing appropriate wavelengths for maximal photosynthesis. Nevertheless, bryophytes, with their single layer of cells, are well adapted, compared to tracheophytes, to capture what little light is able to penetrate, and they benefit from the blue and

green wavelengths that have greater penetration through water and ice. One adaptation to this blue and green light environment is that green light can cause major increases in content of chlorophylls and carotenoids in aquatic bryophytes (Czeczuga 1987). The yellow carotenoids are able to capture the blues and greens that penetrate to the greatest depths. Carotenoids, like chlorophyll *b*, serve as antenna pigments, creating additional surfaces for trapping light and transferring it to the active site of chlorophyll *a*. Might a similar change occur in terrestrial bryophytes, adapting them to life beneath the green filter created by the canopy?

Turbidity of water can have other effects on the light quality. Algae will act much like the canopy and absorb red light with their chlorophyll pigments. Detrital and suspended matter also block and filter the light, altering the quality and the intensity. These can have physiological effects on the bryophytes.

Few studies have examined the effects of the wavelength of light, *i.e.* its color, on the growth or physiology of bryophytes. Most of these have been laboratory studies on tropisms, germination, or growth (see chapter on development). However, Jägerbrand and During (2006) experimented with Icelandic ***Hylocomium splendens*** (Figure 26) and ***Racomitrium lanuginosum*** (Figure 27) in the greenhouse using shade cloth (black netting; green plastic film) compared to colorless plastic film to alter the light quality and intensity in a manner consistent with forest shade. The reduced light of both shade types caused greater elongation, reduced biomass growth, and a lower biomass:length ratio in new growth for both species, but the number of branches, branch density, and biomass:length ratio were higher for ***H. splendens*** (Figure 28). Both shade treatments caused similar increases in length (etiolation) and decreases in the biomass:length ratio. Branch density was significantly decreased by the reduction in red:far red ratio in ***Racomitrium lanuginosum***, typically a sun species. Such a response to shade would permit greater light penetration and reduce self-shading. Similar behavior is seen in the needles of balsam fir (*Abies balsamea*), in which the arrangement of needles on branches is relatively flat on shade branches but go all the way around the upper half of the branch on sun branches.

Figure 26. ***Hylocomium splendens***, a species in which a reduction in the red:far red ratio cause a decrease in branch density. Photo by Sheila, through Creative Commons.

Figure 27. ***Racomitrium lanuginosum***, a species in which a reduction in the red:far red ratio cause a decrease in branch density. Photo by Michael Lüth, with permission.

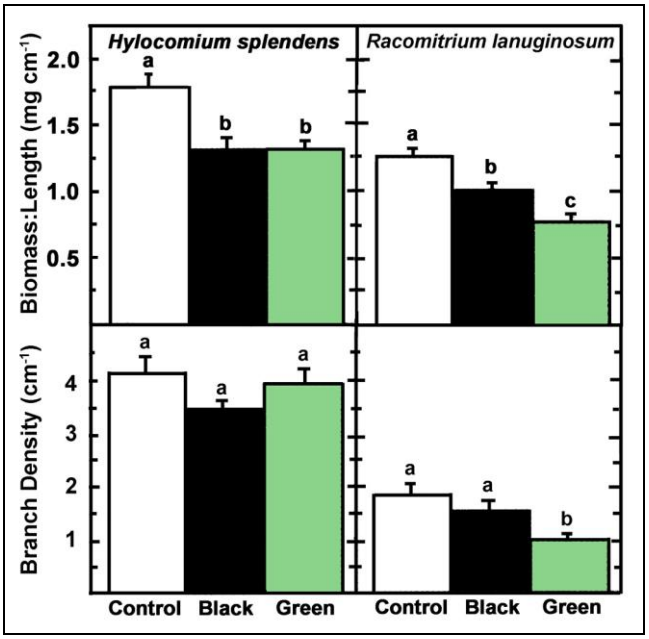

Figure 28. Effects of simulated shade on branch density and biomass to length ratio in two bryophytes. Bars indicate ± SE. Bars with different letters within treatment indicate significant differences (Tukey-Kramer post-hoc-tests, $p<0.05$ except ***Racomitrium lanuginosum*** branch density at $p<0.10$). Redrawn from Jägerbrand & During 2006.

Photoperiod Effects

An alternation of day and night has been with plants since their inception. Thus, we should expect that most species have taken advantage of this alternation in various ways. Continuous light over a long period of time can cause 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, many moss taxa flourish in the continuous light of summer in the Arctic, so destruction in this way must not be universal. Or does it depend on the wavelengths?

Continuous darkness will cause bryophytes to use up their reserves. For example, ethanol-soluble sugars and lipids decrease in green portions of ***Racomitrium***

barbuloides (Figure 29) maintained in continuous darkness, whereas senescent brown portions of the moss do not lose these substances (Sakai *et al*. 2001). Starch, on the other hand, is maintained within the cells under continuous dark treatments. When this same moss was subjected to continuous light, the ethanol-soluble sugars and lipids initially increased in the green portions, but then decreased, concomitant with a significant decline in photosynthetic capacity. The maximum sugar and lipid concentrations stored under 12 hours light/12 hours dark were similar to those in continuous light, but this day/night treatment did not result in diminished photosynthetic capacity.

Figure 29. ***Racomitrium barbuloides***, a species in which continuous darkness results a decrease in ethanol-soluble sugars and lipids. Photo from Digital Museum, Hiroshima University, with permission.

This marked diurnal periodicity under a normal light regime is manifest in peak times for photosynthetic activity. Early morning hours provide the best moisture conditions, so it is not surprising that subalpine populations of ***Pohlia wahlenbergii*** (Figure 30) exhibited their highest photosynthetic activity in the early hours of morning. This high rate repeated itself in the early evening, suggesting photosensitivity and repair (Coxson & Mackey 1990), or could it be only a moisture relationship? Another possible explanation for the peak twice a day is an endogenous rhythm (Coxson & Mackey 1990). In any case, this would appear to be an adaptive behavior for bryophytes that must contend with drying in the afternoon sun, particularly in their most active photosynthetic tissues near the tips.

Figure 30. ***Pohlia wahlenbergii*** var. ***glaciale***, whose peaks in photosynthetic activity are early morning and evening. Photo by Michael Lüth, with permission.

In ***Marchantia polymorpha*** (Figure 31-Figure 32), short photoperiod, and not nutrient supply, cause the plants to produce more gemmae cups (Figure 31), whereas on a long photoperiod more gametangiophores (Figure 32) are produced than on plants in a short photoperiod (Voth & Hamner 1940).

Figure 31. ***Marchantia polymorpha*** gemmae cups, a stage that is promoted by a short photoperiod. Photo by Michael Lüth, with permission.

Figure 32. ***Marchantia polymorpha*** archegoniophores, a stage that is promoted by long photoperiods. Photo by Janice Glime.

Photoperiod can play a role in development, productivity, acclimation, and other aspects of the bryophyte life (Kallio & Saarnio 1986). These topics will be discussed in other chapters related to these topics.

Summary

Changes in light quality, duration, and intensity can signal changing seasons and cause physiological changes that prepare bryophytes for winter or summer conditions. But high light intensities can damage chlorophyll and DNA, especially at low temperatures.

When photooxidation occurs under high light intensities, bryophytes can experience photoinhibition in the form of rupture of the chloroplast envelope, formation of vesicles in thylakoids, and rapid degradation of linolenic acid. Some bryophytes respond to the damaging effects of high light intensity

and low temperatures by producing **light-quenching pigments** such as **sphagnorubin**. At warm temperatures, photorespiration provides an energy shunt to protect chlorophyll from overexcitation. Red pigments may also warm the bryophytes by absorbing heat.

Increased light intensity may stimulate the production in gametangia, but in others it inhibits them. Chlorophyll concentrations may change with seasons, with some bryophytes having high concentrations in early spring, enabling them to take advantage of low light under diminishing snow. Shoot area to dry weight increases in some bryophytes during autumn, perhaps likewise permitting the plants to take advantage of diminishing light. Some mosses have diminished capacity for photosynthesis in winter, but their compensation point and saturation points are also depressed. The changes vary with species and are part of what makes them different species. Nevertheless, generally the chlorophyll *b* concentration increases as light diminishes. Bryophytes that have been under the snow for months are generally ready to begin photosynthesis immediately upon receiving enough light.

Forest canopy leaves filter out a large portion of red light and transmit green light to the bryophytes below. Water accomplishes a similar filtering function, but the green light can cause chlorophylls and carotenoids to increase in aquatic taxa.

Reduced light can cause greater elongation, reduced biomass growth, and a lower biomass:length ratio in new growth, while the number of branches, branch density, and biomass:length ratio can be higher. However, greatly reduced light can cause etiolation, thus reducing self-shading. A reduced ratio of red:far red can decrease branch density.

Continuous light is detrimental to some taxa, but bryophytes in polar regions thrive on the added summer light. Continuous dark can cause some mosses to use up their energy reserves, but low polar temperatures minimize this effect. Many, perhaps most, bryophytes have their peak photosynthetic activity in early morning and late evening when the most moisture is available. Moss gardeners, take note!

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CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

JANICE M. GLIME AND MAGDALENA TURZAŃSKA

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CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

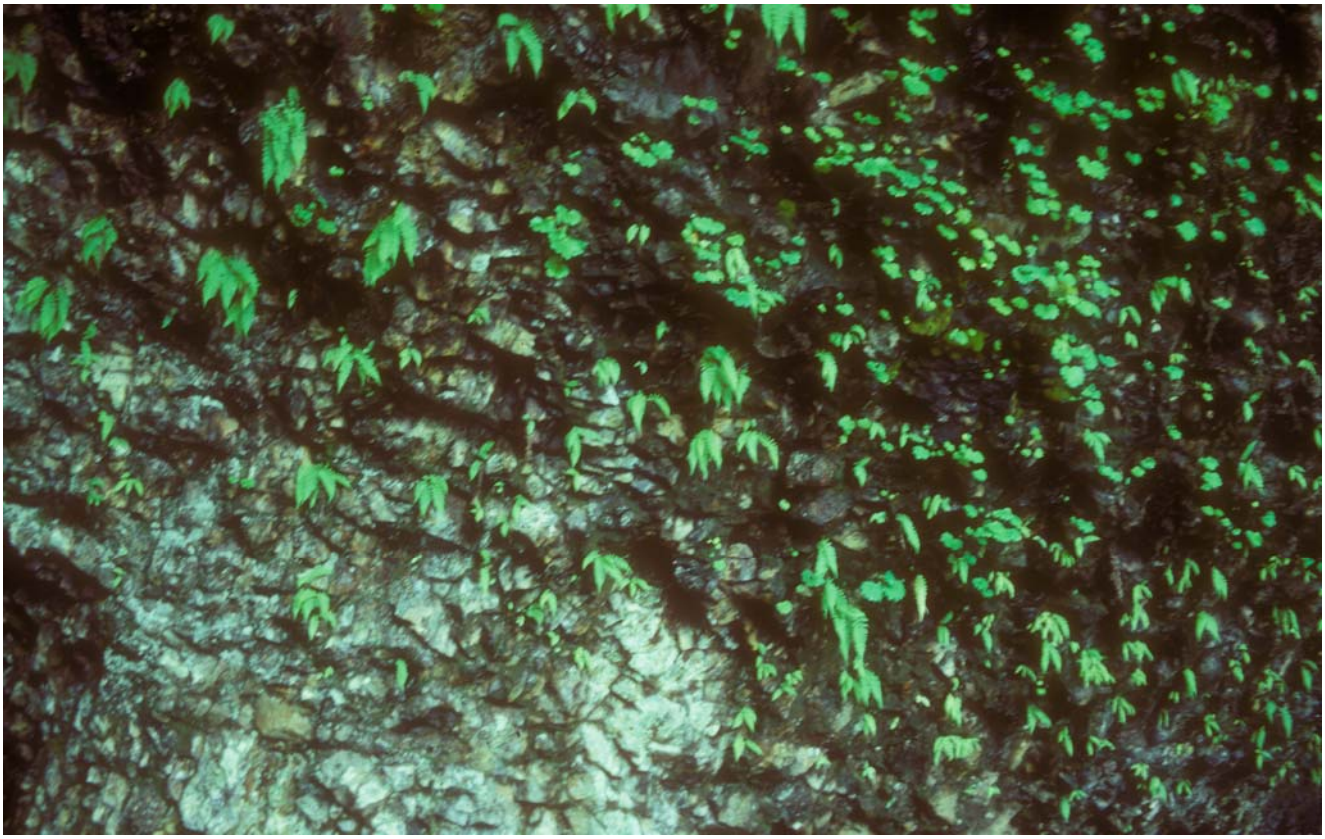

Figure 1. ***Schistostega pennata***, the luminous moss, growing on the roof of a cave in Rausu, Japan. Photo by Janice Glime.

Cave Mosses - Reflectance

Caves provide a classical example of gradients, with diminishing light and temperatures gradually descending or ascending from the mouth to an interior temperature near 10°C. As light diminishes, so does ability of the plant to meet its light compensation point. Thus, through this gradient, we see that flowering plants are the least tolerant, then ferns, followed by bryophytes, and last algae as the most tolerant (Dalby 1966b).

In non-commercial caves where light diminishes rapidly, or in buried lava caves, finding these bryophytes can be difficult and time consuming. Hanley (1982) used an echo sounder to locate bryophytes in caves and other dark areas such as deep lakes. However, in many caves, artificial lights provide sufficient illumination for algae, bryophytes, and ferns to succeed deep within the cave (Boros 1964). In fact, in many commercial caves, bryophytes have been considered to be a nuisance and measures have been taken to remove them, often using sodium hypochlorite. However, to avoid release of chlorine and other dangerous gases into caves, researchers tested hydrogen peroxide. But even the dilute 15% hydrogen peroxide necessary to remove bryophytes is destructive to fragile limestone formations, and the solution must be buffered with bits of limestone rock for at least 10 hours before its application (Faimon *et al*. 2003). I fail to understand why the bryophytes are considered offensive!

Schistostega pennata – Luminous Moss

No moss seems to be revered more than the clandestine cave moss ***Schistostega pennata*** (Figure 1-Figure 3), also known as dragon's gold (Berqvist 1991). Always a delight to find, its protonemata shine like emerald jewels from the darkness of a rock crevice or cave. So intriguing is this moss that the Japanese have a monument to it in Hokkaido (Iwatsuki 1977, Kanda 1988; Figure 2), where it grows in profusion in a cave barely large enough for a child to stand. At just the right position, you can see its marvelous reflections, but move the wrong way and they

are lost. The frond-like gametophyte and terminal sporophyte have none of that ethereal luminescent quality (Figure 3). Ignatov *et al*. (2012) examined the developmental pattern of this species and determined that it has sexual reproduction in September.

Figure 2. Monument to ***Schistostega*** in Hokkaido, Japan. Photo by Janice Glime.

Figure 3. ***Schistostega pennata*** plants showing their frond-like appearance and capsules at the end of the stem. Photo by Martin Hutten, with permission.

This unusual jewel-like property (Figure 4) is the result of the protonema (Gistl 1926). The cells are lens-shaped (Figure 7) and their upper surface is curved in such a way as to focus the light on the interior of the cell (Figure 6; Figure 5). This "normal" form is reached only when they grow in light that comes at all times from the same oblique direction. The chloroplasts orient themselves so that they are always at the most intensely lighted spot on the inner wall of the cell (Figure 7). If a change in the light direction occurs, as may happen seasonally, the chloroplasts can reposition themselves within one to three hours.

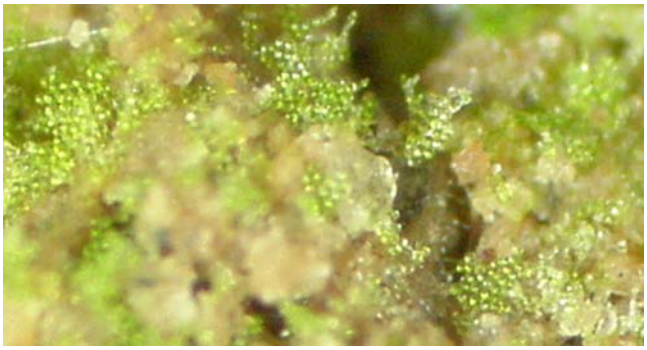

Figure 4. Protonemata of ***Schistostega pennata*** showing upright clumps. Photo courtesy of Misha Ignatov.

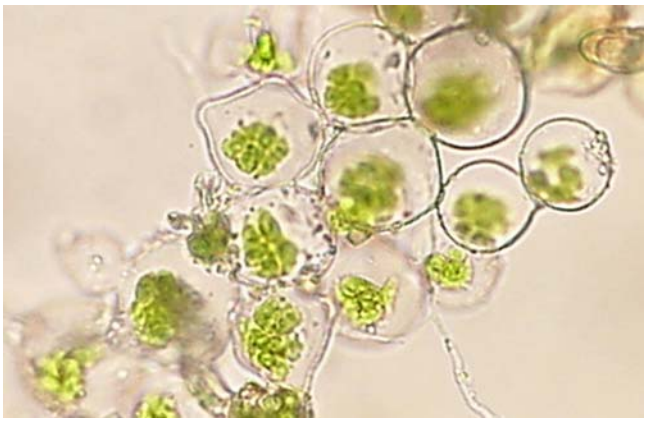

Figure 5. Protonema of ***Schistostega pennata*** showing lens-shaped cells. Photo courtesy of Misha Ignatov.

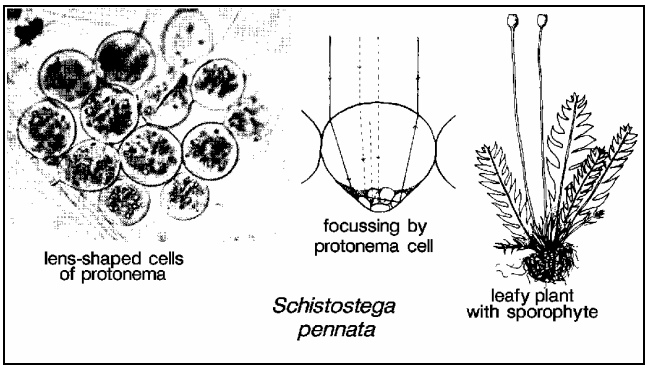

Figure 6. The cave moss, ***Schistostega pennata***, reprinted with permission from Zen Iwatsuki.

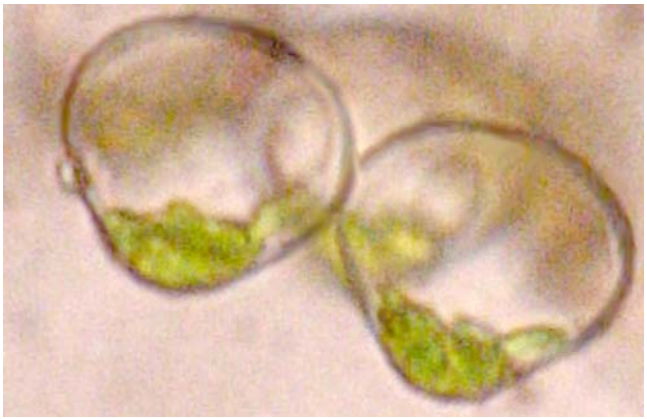

Figure 7. Lens-shaped cells of protonema of ***Schistostega pennata*** with chloroplasts arranged on one side of cell to focus light. Photo courtesy of Misha Ignatov.

Like Crum (1973), we find appeal in retelling the account by Kerner von Marilaun in *Pflanzenleben*, as translated by F. W. Oliver in *The Natural History of Plants*:

> "On looking into the interior of the cave, the background appears quite dark, and an ill-defined twilight only appears to fall from the center on to the side walls; but on the level floor of the cave innumerable golden-green points of light sparkle and gleam, so that it might be imagined that small emeralds had been scattered over the ground. If we reach curiously into the depth of the grotto to snatch a specimen of the shining objects, and examine the prize in our hand under a bright light, we can scarcely believe our eyes, for there is nothing else but dull lusterless earth and damp, mouldering bits of stone of yellowish-grey color! Only on looking closer will it be noticed that the soil and stones are studded and spun over with dull green dots and delicate threads, and that, moreover, there appears a delicate filigree of tiny moss-plants, resembling a small arched feather stuck in the ground [Figure 10]. This phenomenon, that an object should only shine in dark rocky clefts, and immediately lose its brilliance when it is brought into the bright daylight, is so surprising that one can easily understand how the legends have arisen of fantastic gnomes and cave-inhabiting goblins who allow the covetous sons of earth to gaze on the gold and precious stones, but prepare a bitter disappointment for the seeker of the enchanted treasure; that, when he empties out the treasure which he hastily raked together in the cave, he sees roll out of the sacks, not glittering jewels, but only common earth. . . . On the floor of rocky caves one may discern by careful examination two kinds of insignificant-looking plant-structures, one a web of threads studded with small crumbling bodies, and the other bluish-green moss-plants resembling tiny feathers. The threads form the so-called protonema, and the green moss-plants grow up as a second generation from this protonema ... the gleams do not issue from the green moss-plants, but only from their protonema."
>
> "From the much branched threads ... numerous twigs rise up vertically, bearing groups of spherical cells arranged like bunches of grapes. All the cells of a group lie in one plane, and each of these plants is at right angles to the rays of light entering through the aperture of the rocky cleft. Each of the spherical cells contains chlorophyll-granules, but in small number ... and they are always collected together on those sides of the cells which are turned towards the dark background of the cave.... Taken together, these chlorophyll-granules form a layer which under low power of the microscope appears as a round green spot ... the light which falls on such cells through the opening of a rocky cleft behaves like the light which reaches a glass globe at the further end of a dark room. The parallel incident rays which arrive at the globe are so refracted that they form a cone of light, and since the hinder surface of the globe is within this cone, a bright disc appears on it. If this disc, in which the refracted rays of light fall, is furnished with a lining, this also will be comparatively strongly illuminated by the light concentrated on it and will stand out from the darker surroundings as a bright, circular patch.... It is well worthy of notice that the patch of green chlorophyll-granules on the hinder side of the spherical cell extends exactly so far as it is illumined by the refractive rays, while beyond this region, where there is no illumination, no chlorophyll granules are to be seen. The refracted rays which fan on the round green spot are, moreover, only partially absorbed; in part they are reflected back as from a concave mirror, and these reflected rays give a luminous appearance. This phenomenon, therefore, has the greatest resemblance to the appearance of light which the eyes of cats and other animals display in half-dark places, only illumined from one side, and so does not depend upon a chemical process, an oxidation, as perhaps does the light from a glow-worm or of the mycelium of fungi which grow on decaying wood. Since the reflected light-rays take the same path as the incident rays had taken, it is clear that the gleams of the ***Schistostega*** can only be seen when the eye is in the line of the incident rays of light. In consequence of the small extent of the aperture through which the light penetrates into the rock cleft, it is not always easy to get a good view.... If we hold the head close to the opening, we thereby prevent the entrance of the light, and obviously in that case no light can be reflected. It is, therefore, better when looking into the cave to place one's self so that some light at any rate may reach its depth. Then the spectacle has indeed an indescribable charm."

The result of these very reflective chloroplasts in ***Schistostega pennata*** is that the protonema takes on the appearance of "goblin gold" and can create quite eerie effects (Figure 4-Figure 5; Figure 8-Figure 9).

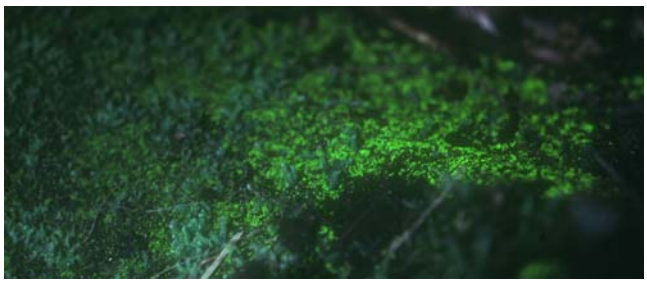

Figure 8. Luminous appearance of ***Schistostega pennata*** protonemata. Photo by Janice Glime.

Figure 9. Luminous protonemata of ***Schistostega pennata*** in natural light. Photo by Martin Hutten, with permission.

Figure 10. A single plant of ***Schistostega pennata*** among its protonemata, the "small arched feather." Photo by Des Callaghan, with permission.

In Japan, there is an opera written about this moss! The opera, written by Ikuma Dan, is based on a book of the same title, "Luminous Moss," by Taijun Takeda (Glime & Iwatsuki 1987). The story relates the tragedy of several sailors who were stranded by a blizzard on the northern island of Hokkaido. With no hope of escaping that remote northern tip of the island before spring to find food and shelter elsewhere, they hid in a cave. As their rations ran out and their fellow sailors died of starvation, they did the only thing they could to survive – they became cannibals. Finally, the captain alone remains. When he is brought to trial for his unthinkable acts, he reflects on the halo of green (the luminous moss) about the heads of each who has been a cannibal, but he tells the courtroom that the halo is visible only to those who have not been cannibals. He alludes to the cannibal in each of us as we struggle to survive among the millions of the world. Today a cave in Hokkaido is set aside as a memorial to protect this unusual moss (Kanda 1971, 1988; Figure 2).

Schistostega pennata (Figure 8-Figure 10) is widespread in the North Temperate Zone. Bowers (1968) and Conard (1938) have reported it from the Upper Peninsula of Michigan, where I have seen it growing on the roof of a cave behind a waterfall. Outside that same cave, I have observed the leafy gametophore, which resembles a tiny fern frond (Figure 11), growing on a small ledge of the rock wall, but protonemata there, if present, did not exhibit their highly reflective property. Bowley (1973) found the moss in several localities in Vermont, Champlin (1969) reported it from Rhode Island, Christy and Meyer (1991) from Wisconsin, Case (1975) found it in Alberta, Canada. Matsuda (1963) reported it in artificial caves in Japan. Perhaps the most unusual report is that of Koike (1989) who reported its culture in empty bottles in urban areas of Japan. Reinoso Franco *et al*. (1994) considered it to be an acidophile, at least on the Iberian Peninsula.

When I went to Germany, I was delighted to find ***Schistostega pennata*** (Figure 8-Figure 11) growing at the base of a boulder where it probably did not get direct sunlight except at sunset and most likely did not get direct rainfall very often either. Perhaps one reason for its success in such habitats is the presence of protonemal gemmae (Edwards 1978). In the Europe, ***Schistostega pennata*** also grows in rabbit holes (Glenny 2020).

Figure 11. ***Schistostega pennata*** showing frond-like branches of leafy gametophyte. Photo with permission from Botany Website, UBC, with permission.

Cyathodium

In the thallose liverwort genus ***Cyathodium*** (Figure 12), some species that grow in caves and similar low-light environments also emit a yellowish luminescence from their thalli (Crum 1973). These liverworts are tropical and subtropical and in China grow in karst caves (Zhang *et al*. 2004).

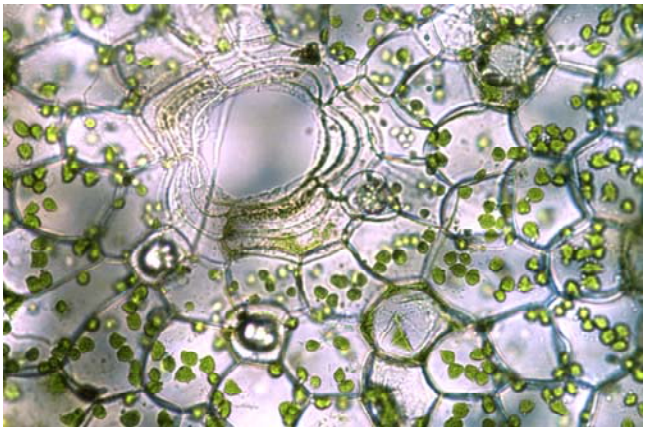

Figure 12. View through pore of ***Cyathodium cavernarum***, a thallose cave liverwort that emits a yellowish luminescence in caves. Photo by Noris Salazar Allen.

Mittenia plumula

In Australia, a similar moss, ***Mittenia plumula*** (Figure 13), lives on dimly lit, clay-covered rock ledges, at the entrances to wombat holes (Figure 14-Figure 15), and on tip-up mounds of fallen trees (Figure 16-Figure 17). The latter habitat makes the moss rather common after cyclone damage that causes trees to topple. In these locations, the moss lives on soil. Stone (1961, 1986) concluded that ***Mittenia*** belongs in the order **Schistostegales** with ***Schistostega*** (Figure 1-Figure 11). Both have a pinnate leaf arrangement, protonemata with similar luminescent properties, similar pale color of the leafy plant, and similar habitats.

Figure 13. ***Mittenia plumula*** showing leaves with bluish tint. Photo courtesy of David Glenny.

Figure 14. ***Mittenia plumula*** in wombat hole in Australia. Photo by Tony Markham, with permission. See <https://www.youtube.com/watch?v=PaXJTcaz1RE>.

Figure 15. ***Mittenia plumula*** growing in a wombat hole in Australia. Photos by Janice Glime.

Figure 16. ***Mittenia plumula*** habitat on tip-up mound. Photo courtesy of David Glenny.

Figure 17. ***Mittenia plumula*** protonemata on tip-up mound. Photo courtesy of David Glenny.

Mittenia plumula differs from ***Schistostega pennata*** by having protonemata with cylindrical filaments instead of spherical cells that act as a lens. Unlike ***Schistostega pennata*** (Figure 1-Figure 11), where the protonemal cells are spherical and are obviously acting as a lens, the

protonema of ***Mittenia plumula*** (Figure 18-Figure 20) is composed of cylindrical filaments and the chloroplasts are not on one side of each cell to take advantage of focused light. Nevertheless, under the compound microscope there is a faintly visible blue luminescence from the filament walls. This luminescence resembles the iridescence seen in some tropical plants of dark forest floors, for instance in ***Selaginella willdenowii*** (Figure 21).

Figure 18. ***Mittenia plumula*** protonemata in rabbit hole. Photo from Wildlife in the Marches at <www.youtube.com> .

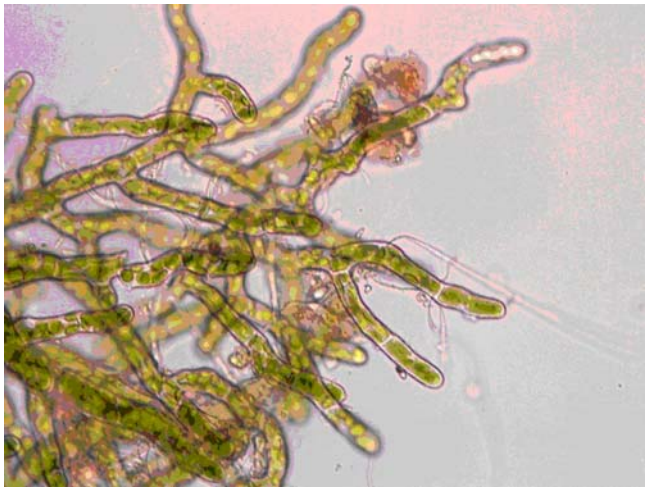

Figure 19. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

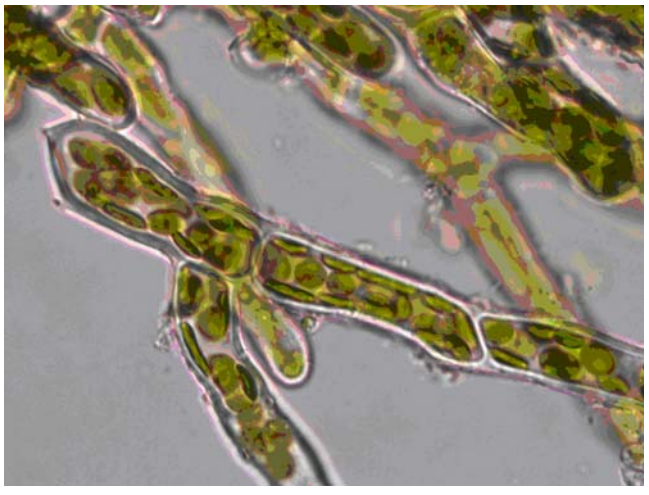

Figure 20. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

Figure 21. ***Selaginella willdenowii*** exhibiting **iridescence**. Photo courtesy of David Glenny.

Cave Communities

Growth of other bryophytes in caves far from a natural light source has been a source of fascination for both bryologists and non-bryologists all over the world, and these bryophytes often form zones around electric lights (Haring 1930). So fascinating are these plants of low light that their descriptions have appeared in non-botanical journals. Boros (1964) was able to publish a paper in the first volume of the *International Journal of Speleology* (**speleology** is the study of caves), reporting on mosses growing around electric light sources deep within a cave. Dalby (1966b) later published a similar article on their growth under reduced light in caves, this time in the first volume of *Studies in Speleology*. Numerous communities have been described from caves around the world: Shiomi (1973) in Japan; Maheu and Guerin (1935) in France; Rajczy (1979) in Greece; Ziober (1981), Komáromy *et al*. (1985), Rajczy *et al*. (1986), and Buczkó and Rajczy (1989) in Hungary; Lo Giudice & Privitera (1984) in Italian grottos; Stefureac (1985) in Romanian grottos; Weber (1989) for both animals and flora, including bryophytes, in two German caves and artificial caverns; Kubešová (2009) in the Czech Republic. Even *Science* has accepted articles on mosses in Virginia (USA) caverns, including the famous Luray Cavern (Lang 1941, 1943), and Prior (1961) again studied Luray Cavern mosses, publishing in *The Bryologist*.

Most cave bryophytes are not specific to these habitats. Reinoso Franco *et al*. (1994) have found ***Schistostega pennata*** with ***Isopterygium elegans*** (Figure 22; low-light species of canyons and crevices), ***Diplophyllum albicans*** (Figure 23; forest epiphyte), ***Calypogeia arguta*** (Figure 24), ***C. azurea*** (Figure 25; also an epiphyte), ***Pogonatum nanum*** (Figure 26), and ***Fissidens curnovii*** at a *p*H of 5.7 in caves.

Figure 22. ***Isopterygium elegans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 23. ***Diplophyllum albicans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 24. ***Calypogeia arguta***, a species that is able to grow in low light. Photo by Des Callaghan, with permission.

Figure 25. ***Calypogeia azurea***, a species that is able to grow in low light. Photo by Hermann Schachner through Creative Commons.

Figure 26. ***Pogonatum nanum***, a species that is able to grow in low light. Photo by J. C. Schou, with permission.

The widespread ***Fissidens taxifolius*** (Figure 27) grew in Crystal Caverns in Virginia, USA, and aroused the curiosity of a visitor who delivered it to Conard (1932). This moss grew on the damp ceiling, forming circles about 8" from several electric light bulbs, having appeared only a few years earlier. The moss looked normal, but the leaves were further apart than in typical specimens, not an unusual trait for a moss of low light.

Figure 27. ***Fissidens taxifolius***, a common moss that can grow on the ceiling of caves. Photo by Jan-Peter Frahm, with permission.

A variety of species seem to be capable of growing in caves. Buczkó & Rajczy (1989) reported nineteen bryophyte taxa from three caves in Hungary. Dalby (1966a) reported the occurrence of the **tufa**-former (rock former resulting in carbonates built upon bryophytes and other plants due to addition of photosynthetic oxygen to dissolved minerals), ***Eucladium verticillatum*** (Figure 39), in a poorly lit cave, also occurring in caves in Hungary (Buczkó & Rajczy 1989). In Crystal Cave, Wisconsin, Thatcher (1949) found ***Barbula unguiculata*** (Figure 28), ***Brachythecium populeum*** (Figure 29), ***Brachythecium salebrosum*** (Figure 30), ***Bryoerythrophyllum recurvirostrum*** (Figure 31), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Ceratodon purpureus*** (Figure 34), ***Fissidens taxifolius*** (Figure 27), ***Leptodictyum riparium*** (Figure 35), ***Marchantia polymorpha*** (Figure 36), ***Plagiomnium cuspidatum*** (Figure 37), and ***Warnstorfia fluitans*** (Figure 38). Like Conard, Thatcher observed the leaves to be more distant than is typical.

Figure 28. ***Barbula unguiculata***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 29. ***Brachythecium populeum*** with capsules, a species that is able to grow in caves. Photo by Janice Glime.

Figure 30. ***Brachythecium salebrosum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 31. ***Bryoerythrophyllum recurvirostrum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 32. ***Bryum caespiticium*** with capsules, a species that is able to grow in caves. Photo by Bob Klips, with permission.

Figure 33. ***Bryum capillare***, a species that is able to grow in caves. Photo by Andrew Spink, with permission.

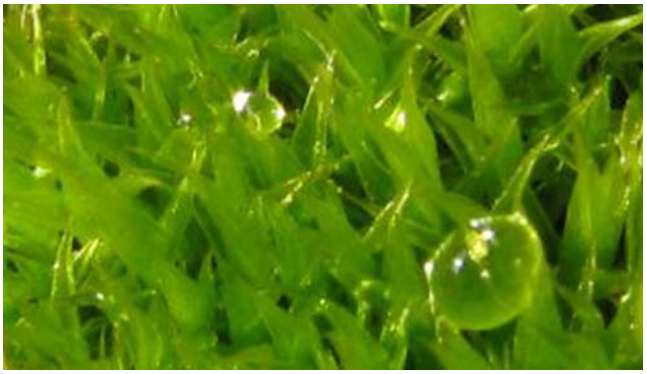

Figure 34. ***Ceratodon purpureus***, a species that is able to grow in caves. Photo by Jiří Kameníček, with permission.

Figure 35. ***Leptodictyum riparium***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 36. ***Marchantia polymorpha***, a species able to grow in caves. Photo from Botany Website, UBC, with permission.

Figure 37. ***Plagiomnium cuspidatum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 38. ***Warnstorfia fluitans***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Komáromy *et al*. (1985) likewise found ***Eucladium verticillatum*** (Figure 39), a ***Brachythecium*** (***B. velutinum***), and two species of ***Fissidens*** [***F. dubius*** (Figure 40), ***F. pusillus*** (Figure 41)] in a cave. Within only one year from its first illumination, Howe Cavern in New York, USA, already was adorned with ***Amblystegium serpens*** (var. ***juratzkanum***; Figure 42), ***Amphidium mougeotii*** (Figure 43), ***Brachythecium rutabulum*** (Figure 44), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Leptobryum pyriforme*** (Figure 45), and ***Marchantia polymorpha*** (Figure 36) encircling its new lights (Haring 1930). Buczkó and Rajczy (1989) found that ***Amblystegium serpens*** (=*A. juratzkanum* var. *juratzkanum*; Figure 42) was the most characteristic moss in several Hungarian caves, extending furthest from the cave entrance that provided the only light, surviving at only 232 lux. Niklas Lönnell reported to Bryonet (3 March 2010) that ***Eucladium verticillatum*** (Figure 39) introduced at an underground station in Stockholm, Sweden, thrives decades later on moist areas of the walls where artificial light is available.

Figure 39. ***Eucladium verticillatum***, a tufa-forming moss. Photo by Michael Lüth, with permission.

Figure 40. ***Fissidens dubius***, a known cave dweller. Photo by Bernd Haynold, through Creative Commons.

Figure 41. ***Fissidens pusillus***, a species known to live in caves. Photo by Michael Lüth, with permission.

Figure 42. ***Amblystegium serpens***, a common cave moss in Hungary. Photo by Michael Lüth.

Figure 43. ***Amphidium mougeotii***, a species that colonized within one year around lights in a cave. Photo by Michael Lüth, with permission.

Figure 44. ***Brachythecium rutabulum*** with capsules, a species that colonized around lights in a cave within one year. Photo by Tim Waters, through Creative Commons.

Figure 45. ***Leptobryum pyriforme***, an invader of bare soil in caves. Photo by Michael Lüth.

Tufa formers such as ***Eucladium*** (Figure 39) (von der Dunk & von der Dunk 1980), ***Barbula*** (Figure 28), and ***Didymodon*** (Figure 46) are found in many of these caves, since the caves are usually limestone, and tufa formers must be adapted to relatively dim light to survive the calcium carbonate covering they must endure.

Figure 46. Tufa-forming ***Didymodon tophaceus***, a former of didymodontoliths. Note carbonates at base encrusted on older stems. Photo by Michael Lüth, with permission.

With all these reports, it is not unexpected then that Koponen (1977) reported mosses at a depth of 176 m in a mine at Vihanti, Finland. The surprising fact is that the mosses he found are the very light-tolerant ***Ceratodon purpureus*** (Figure 34) and ***Pohlia nutans*** (Figure 47). But then, these two mosses seem to do well in extremes, as long as it is not too hot.

Jedrzejko and Ziober (1992) illustrated the effects of light on the species composition of moss communities and the ability of mosses to survive at low light intensities with their study of bryophytes in seven Polish caves. More than 50% of the bryophyte flora occurred where they had full access to daylight. As the investigators went deeper into the caves, the number of species decreased, but with 1.3% of the species occurring only in the darkest zone.

Figure 47. ***Pohlia nutans***, a widespread moss that frequents caves and mines. Photo by Michael Lüth.

Rockhouses

Rockhouses are really just small caves created by deep recesses in bedrock cliffs. But despite their smaller size, they can create conditions much different from those of their surroundings outside the cavity. They tend to be buffered from extremes in both temperature and moisture, with cold blasts emanating in the summer and protection from severely cold winds in the winter. Nevertheless, despite their moderate climate, their low light levels greatly restrict the potential flora. It is therefore interesting that the greatest affinities of these floras are with the tropics (Farrar 1998). While the species in the rockhouses tend to be endemic to the eastern United States, the conditions created for them mimic the low light intensities of the dense rainforests. It is possible that the climatic moderation of the rockhouses might have permitted adapted plant groups to persist here since the time when a tropical/subtropical climate existed in the eastern US during the Pre-Pleistocene. It is in these secluded habitats that a number of endemic ferns reside, but the most numerous plants are the bryophytes. Farrar considered both groups to be preadapted to this habitat by their vegetative reproduction and their ability to have net photosynthetic gain in very low light.

Responses to Low Light in Caves

If you have ever picked up a board from your lawn, you know how thin and long the grass stems can be. This elongation response by plants in low light is termed **etiolation**. Dunham and Lowe (1927) described etiolation of bryophytes in caves and among boulders in New England, USA. But at least some light should be present, right? Nevertheless, Fries (1945) succeeded in growing the mosses ***Funaria hygrometrica*** (Figure 48) and ***Leptobryum pyriforme*** (Figure 45) from protonemata on inorganic media in total darkness. Thus, it would appear that some growth can occur, using the plant's reserves, even in the absence of light.

Rajczy (1978-1979) chose to experiment with growing mosses in total darkness of a cave. He used two common Hungarian species, ***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51), which he planted in flowerpots along with their original soil. These were placed in a cave where the climate is very constant, having a temperature of 9.5 ±1ºC and 95-100% relative humidity. ***Plagiomnium ellipticum*** rapidly became brown and within three months had produced long, fine, vertical, leafless stems of 4-6 cm length. ***Atrichum undulatum***, on the other hand, remained green for two years. Its chloroplasts increased from a mean of 8.8 to 10.3 per cell from May to October. In the cave both species had a much higher ratio of dark CO_2 fixation that did the control samples from normal light (Table 1). One interesting event in Rajczy's experiment was that isopods (***Mesoniscus graniger***; Figure 49) consumed all the dead material of the plants. The mosses soon grew pale, then partly brown.

Figure 48. ***Funaria hygrometrica***, a species that is able to grow without a media carbon source in the dark. Photo by Michael Lüth, with permission.

Table 1. Incorporation of CO_2 into moss biomass in caves compared to controls. From Rajczy 1978-1979.

$^{14}CO_2$ Incorporation				
	Net Activity (cmp/leaf)			Contrib dk
	total fix	dark fix	light fix	fix to total fix
Atrichum undulatum				
control	898	85	813	9%
cave sample	174	81	93	47%
Plagiomnium ellipticum				
control	3790	340	3450	9%
cave sample	550	220	330	40%

Figure 49. ***Mesoniscus graniger***, an isopod consumer of dead mosses. Photo by Richard Kovács, through Creative Commons.

When ***Atrichum undulatum*** (Figure 50) cells were examined with the electron microscope after four months of experiment (September), the chloroplasts differed considerably from those of the control plants. The size of the grana had increased but their number decreased and they were arranged mostly at the periphery of the chloroplast. There were no starch grains. Then, in March, there was a most unexpected change. The chloroplasts contained starch once more and the grains appeared to be identical to those of the control plants. Thylakoids (Figure 52) were even thinner than in September, and only 1-2 stroma thylakoids were present. From 3 to 10 broad, low grana were present.

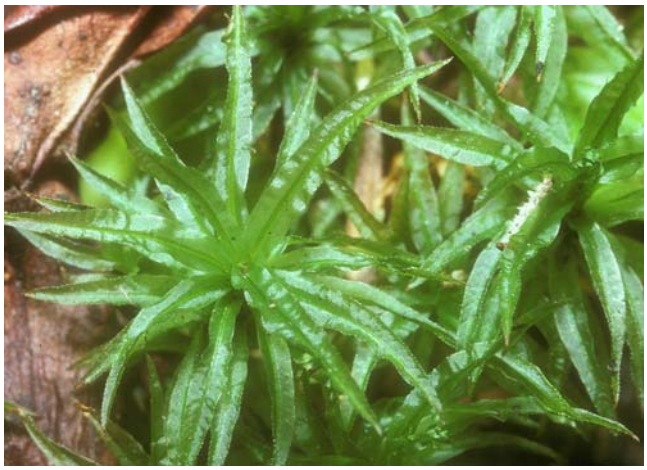

Figure 50. ***Atrichum undulatum***, a species that acclimates to living in caves. Photo by Janice Glime.

Figure 51. ***Plagiomnium ellipticum***, a species that seems unable to live in the low light of caves. Photo by Michael Lüth, with permission.

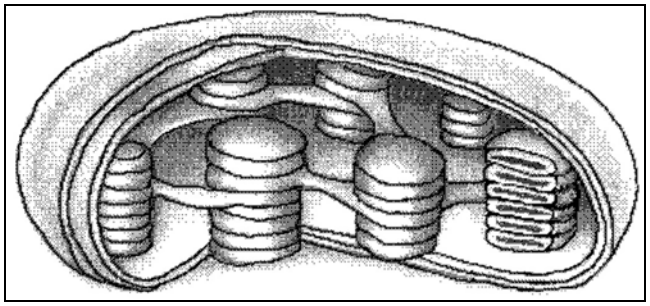

Figure 52. Chloroplast with cutaway view to show inner and outer membrane, stacks of thylakoids that form grana, and connecting stroma. Drawing by Janice Glime

Surprisingly, ***Plagiomnium ellipticum*** (Figure 51) also had starch grains in March. However, these were not like those of their control plants. Some were far larger, and most chloroplasts lacked them. Most of the chloroplast envelopes were torn up.

In April, samples taken from the cave to the lab had measurable photosynthesis, although they had no exposure to light prior to the time of measurement. For ***Atrichum undulatum*** (Figure 50), photosynthesis reached 15-20% of that in the controls. Both species retained some photosynthetic activity for the two years of the experiment, but that of ***Atrichum undulatum*** was greater.

Rajczy (1978-1979) interpreted these results to mean that the mosses were subsisting on heterotrophic energy sources. He could find no other explanation for the sudden appearance of starch after 10 months in the cave. Furthermore, he cited the dark-culturing experiments of Servettaz (1913), Pringsheim and Pringsheim (1935), and Fries (1945) to support his position. Could the mosses be using electromagnetic rays? symbiosis? chemosynthesis? Cave algae are known to subsist using these unusual methods of obtaining energy (Kol 1966; Hadju 1979). And why did both species [***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51)] have starch grains in March when the grains had disappeared earlier? Did some endogenous rhythm, lacking stimulus by photoperiod or temperature, trigger a change in metabolic activity?

Reflectance in the Desert

In desiccation-tolerant species, surface properties often change. This can result in a change in surface reflectance, as exemplified in the xerophytic moss ***Syntrichia ruralis*** (Figure 53) (Hamerlynck *et al*. 2000). In this species, distinct differences occur in the ability to establish thermal dissipation of excess light energy throughout a range of light levels, helping to protect the sensitive chlorophyll and DNA.

Figure 53. ***Syntrichia ruralis***, a species that changes its optical properties when dry vs wet. Photo by Jan-Peter Frahm, with permission.

In the Antarctic, surface reflectance properties differed over a range of water content, but did not correlate with pigment content (Lovelock and Robinson 2002). Nevertheless, the photochemical reflectance was correlated with the concentrations of active xanthophyll-cycle pigments and the photosynthetic light use efficiency as

measured by chlorophyll fluorescence. The water content had a strong influence on both the amplitude and position of the red-edge and may itself cause the differences in reflectance. Continuous high levels of xanthophyll pigments indicate the continual high light levels.

Fluorescence and Other Light Emissions

(coauthored with Magdalena Turzańska)

Definitions

Wikipedia defines **fluorescence** as "emission of light by a substance that has absorbed light or other electromagnetic radiation of a different wavelength." One little-known property of at least some bryophytes is their ability to fluoresce various colors in UV light. Lichenologists are familiar with this property in lichens (Figure 54-Figure 55), using it as an identification tool (Hale 1956). Bees know it in flowers (we call them nectar guides), being attracted to fine lines of marsh marigold (*Caltha palustris* – Figure 56-Figure 57) and black patches of oriental poppy (*Papaver orientale* – Figure 58) petals and by their emission of fluorescence in the UV light of the sun. In fact, Talamond *et al*. (2015) consider **autofluorescence** to be abundant in plant cells. But bryologists seem rarely to use it

Figure 54. The lichen *Xanthoria polycarpa* in natural light. Photo through Creative Commons.

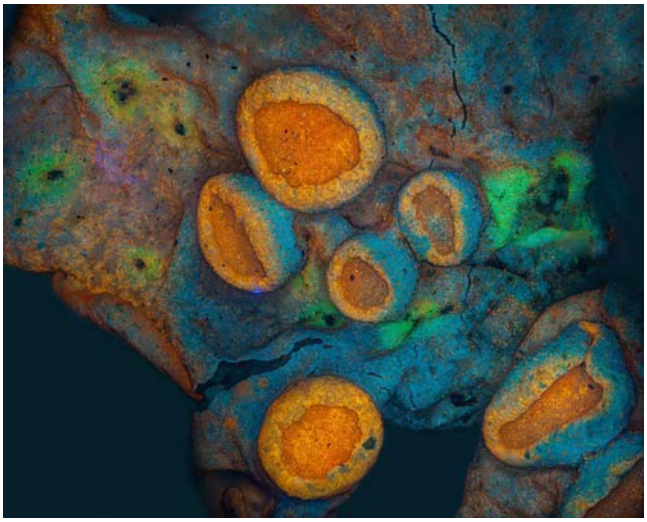

Figure 55. *Xanthoria polycarpa* showing fluorescence in UV light. Photo by Walter Machielsen, with permission.

Figure 56. *Caltha palustris*, a species whose flowers appear yellow to us, but that reflect UV rays seen by bees. Photo by H. Zell, through Creative Commons.

Figure 57. *Caltha palustris* in UV light, showing UV-reflecting lines. Photo courtesy of Dave Kofranek.

Figure 58. The oriental poppy (*Papaver orientale*) has patches that appear black to us, but that reflect UV light that is visible to bees, guiding them to the center of the flower where the pollen and stigma reside. Photo by Janice Glime.

Fluorescence should not be confused with **bioluminescence**. Fireflies have bioluminescence. Some dinoflagellates (think red tides) have bioluminescence. This is a form of chemiluminescence produced by living organisms. It requires a light-emitting molecule (**luciferin**)

and an enzyme (**luciferase**), wherein the enzyme catalyzes the oxidation of the luciferin. The luciferin and its associated enzyme differ among species. The reaction may also require **ATP** (energy-carrying molecule, adenosine triphosphate). In **luminescence**, something adds energy, causing an electron to get bounced from one orbital to another, emitting light, then decaying back down (Jerry Jenkins, Bryonet 23 April 2022). Bioluminescence is not known in land plants, but since it is present in some bacteria, it is possible that we have not discovered it in some bacteria-bryophyte associations. **Triboluminescence** results from mechanical energy such as crushing sugar cubes or rubbing quartz crystals. Heat produces **incandescence** (emitted from hot body as result of high temperature, *e.g.* incandescent light bulb).

Phosphorescence (microsecond decay that changes spin state, causing prolonged emission of light even in darkness) is a form of luminescence that results from the absorption of radiation (such as light or electrons) and continues for a noticeable time after these radiations have stopped. We have seen these in various items that glow in the dark after being exposed to light. I have seen them on cards with a cross or on ceilings to look like stars.

Fluorescence is not seen by the human eye during the day because our eyes are less sensitive to those short wave lengths and the longer "visible" light waves keep us from seeing it. However, with the right equipment, *i.e.* a UV light source, we can detect it. The discovery of a liverwort that was fluorescing precipitated one of the longest running threads on Bryonet.

Jerry Jenkins (Bryonet 23 April 2022) provided us with a detailed description of the light emissions from organisms. For example, he noted that the light emitted by ***Zygodon rupestris*** (=***Zygodon viridissimus* var. *rupestris***; Figure 59), shared by Ken Kellman (Bryonet 21 April 2022), could be **fluorescence** or **phosphorescence**. These cannot be distinguished just by using a UV flashlight.

Figure 59. ***Zygodon rupestris***, a species known for blue fluorescence. Photo by Jonathan Sleath, with permission.

It is intriguing that the ***Zygodon rupestris*** (Figure 59) does not emit this light when dry (Ken Kellman, Bryonet 21 April 2022). Kellman suggested that perhaps in the dry state the UV light is blocked from entering the cells and thus there is no stimulation. This could be possible due to structural changes that make the dry cells less transparent. A second possibility is that UV light is able to enter the cell, but that the change in structure due to drying makes it impossible for the emitted visible light to get out for us to see. Jenkins (Bryonet 23 April 2022) suggested that it is also possible that it is fluorescence that is quenched or red-shifted out of the visible range in the dry moss. This could be caused by neighboring molecules or by binding to membranes [or cell walls?]. Those neighbors can affect the energy levels and frequency of light emission of the excited electrons. (See Wilson & Hastings 2013 for more detail on the mechanism of fluorescence.)

Jerry Jenkins (Bryonet 23 April 2022) ultimately concluded that it was **photoluminescence** (which includes fluorescence) that emitted light from ***Zygodon rupestris*** (Figure 59) when irradiated with UV. The incoming UV photon interacts with an orbiting electron, causing it to achieve an excited state. Some of the photon energy is transferred to the electron. The remainder is used in vibrations and rotation. As the electron decays, it emits a photon, but with less energy than that of the incoming photon. Thus, the light has a longer wavelength and is shifted toward the red end of the spectrum into the visible spectrum.

Compounds That Fluoresce

The specific compounds in bryophytes that fluoresce have not been studied extensively. However, we know more about those in tracheophytes. Wolfbeis (1985) listed the following compounds from leaves that emit blue-green fluorescence: alkaloids (berberine, quinine, lysergic acid), aurones, chalcones, chromones, coumarins (umbelliferone, esculetin, scopoletin), flavones (except 5-hydroxyflavones), flavins (FMN, FAD, riboflavin), flavonols, furocumarins (psoralen), hydroxycinnamic acids (caffeic, ferulic, sinapic), isoflavones, nicotinamides (NADH, NADPH), phenolic acids (salicylic, gentisic, ellagic), polyenes (phytofluen), pterines (folic acid, dihydrofolate), quinones (phyllohydroquinone), stilbenes (resveratrol), other coenzymes (pyridoxal-5'-phosphate), and degradation products (kynurenine, polyadenylic acid).

The internal environment can modify the fluorescent response, including such factors as temperature, viscosity, spatial constraints, *p*H, polarity, and presence of quenchers, such as heavy metals and oxygen, influencing the spectral characteristics and yield (Cerovic *et al*. 1999).

Parts That Fluoresce

Chlorophyll fluorescence is well known in algae and plants, including bryophytes (Shi *et al*. 1992; Proctor & Smirnoff 2011), giving an indication of the health of the plant by its ability to emit light from its active chloroplasts (*e.g.* Csintalan *et al*. 1999; Deltoro *et al*. 1999; Arróniz-Crespo 2008). As in tracheophytes and algae, the chlorophyll of bryophytes fluoresces red in UV light. In the hornwort ***Anthoceros*** sp., the chlorophyll fluoresces a brilliant red whereas the cell walls fluoresce blue (Figure 60-Figure 64). In ***Fontinalis antipyretica***, the cell wall fluoresces yellow, contrasting with the red chloroplasts (Figure 65). A similar contrast is present in ***Sphagnum***, with photosynthetic cells showing red chlorophyll fluorescence and cell walls showing a blue-green fluorescence in UV light (Figure 66-Figure 68). In ***Funaria hygrometrica***, there is a strong chlorophyll fluorescence, but the cell walls seem to lack any

fluorescence visible in the UV light of a microscope (Figure 69).

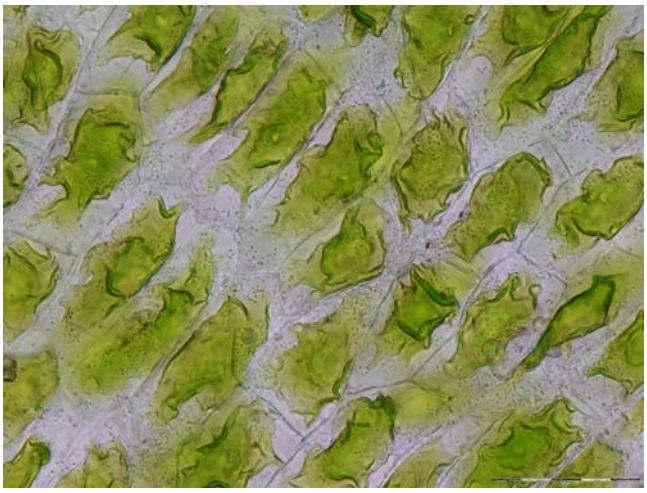

Figure 60. ***Anthoceros*** sp. gametophyte cells in white light. Photo by Magdalena Turzańska.

Figure 61. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

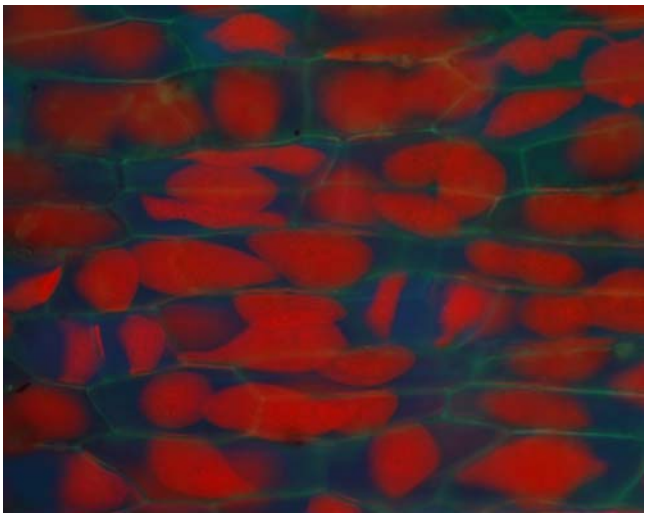

Figure 62. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

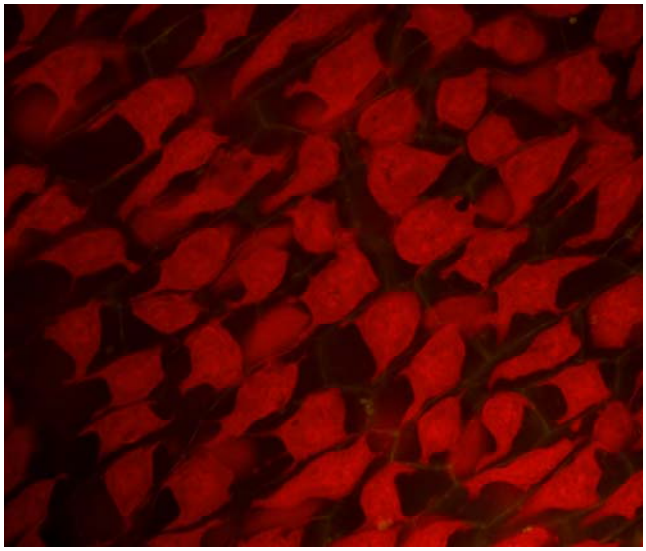

Figure 63. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

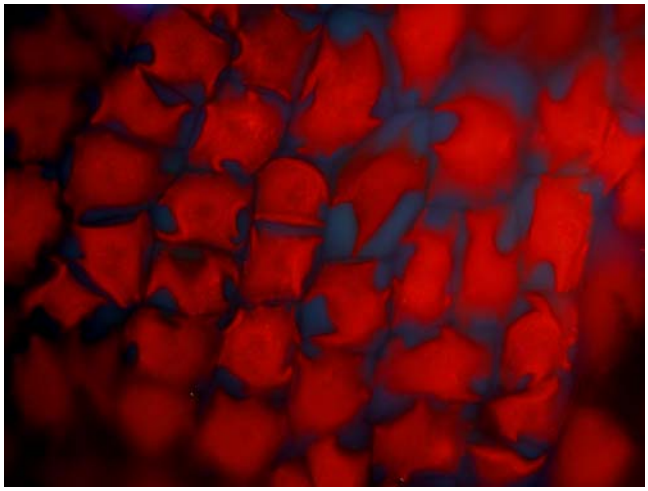

Figure 64. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

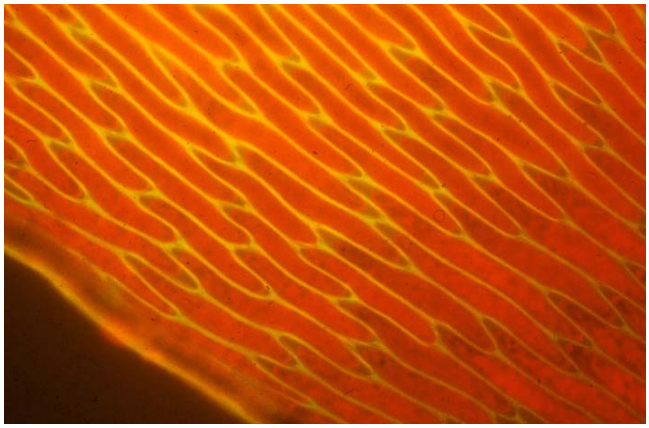

Figure 65. ***Fontinalis antipyretica*** cell wall showing yellow fluorescence, contrasting with the red of the chlorophyll fluorescence. Photo by Janice Glime.

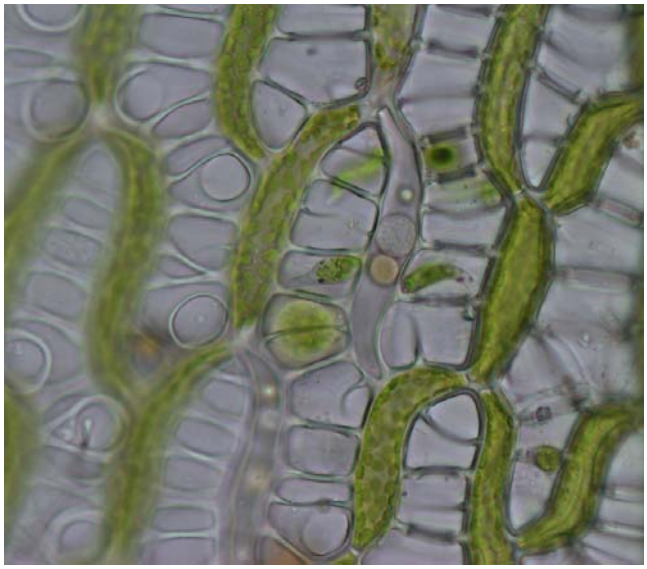

Figure 66. ***Sphagnum*** sp. leaf with algae in hyaline cells. Photo by Magdalena Turzańska.

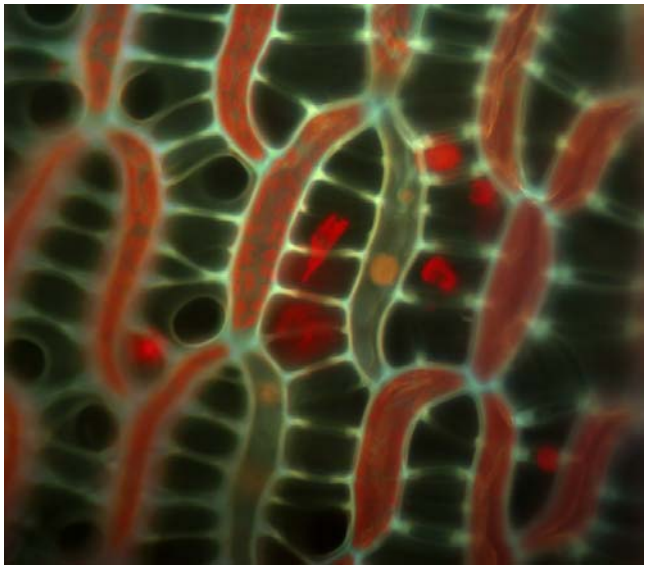

Figure 67. ***Sphagnum*** sp. leaf fluorescence of the leaf in Figure 66 with algae fluorescing red in hyaline cells and cell walls fluorescing greenish. Photo by Magdalena Turzańska.

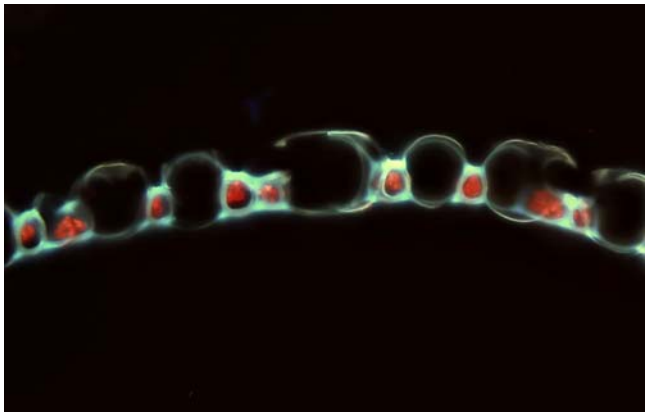

Figure 68. ***Sphagnum*** sp. leaf fluorescence in cross section with chlorophyll fluorescing red and cell walls fluorescing green in UV light. Photo by Magdalena Turzańska.

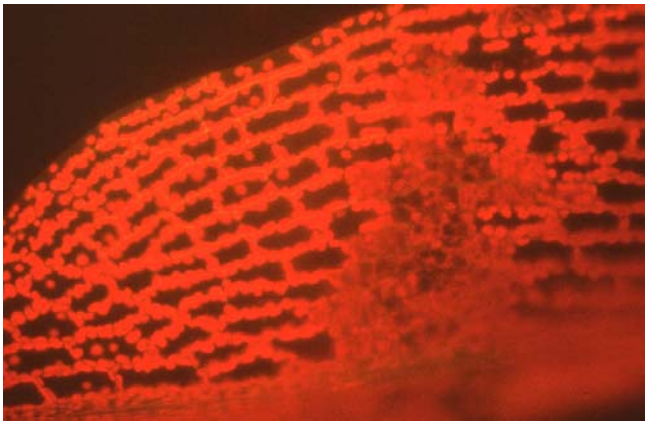

Figure 69. ***Funaria hygrometrica*** leaf chlorophyll fluorescence, showing the typical red fluorescence of that molecule. Note that the cell walls lack fluorescence under the UV light of a microscope. Photo by Janice Glime.

The use of fluorescence to detect the damage to chlorophyll has been established for some time (Proctor 2003). These uses include indication of effects of various intensities of desiccation (Proctor 2003) and of metal contaminant locations within the cell, as shown in ***Fontinalis antipyretica*** (Figure 70-Figure 71) (Chorvatova *et al*. 2021).

Figure 70. ***Fontinalis antipyretica***, an aquatic moss with cell wall fluorescence under UV light and a species where one can trace metals using fluorescence. Photo by Hermann Schachner, through Creative Commons.

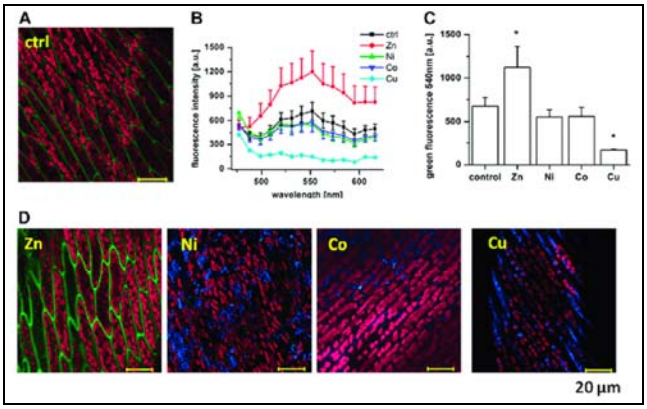

Figure 71. Fluorescence of various metals in ***Fontinalis antipyretica*** located by UV light. From Chorvatova *et al*. 2021.

Various parts of bryophytes are known to fluoresce. Ridgway and Larson (1966) reported on the usefulness of the fluorescence technique to follow sporogenesis in the hornwort ***Anthoceros*** sp. (Figure 72-Figure 76). Similar changes in color seem to occur in ***Riccia*** sp. (Figure 77-Figure 80). Using a UV microscope enables us to examine the development and greening of spores (Figure 78-Figure 79), protonemal bud initiation, callose distribution to find phloem-like elements, callose in cross walls of leptoids, events leading to egg formation, events following fertilization (Sarafis 1971; Brandes 1967), and locating elusive propagules (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

Figure 72. ***Anthoceros punctatus***, member of a genus in which fluorescence permits us to follow development of spores, at least in some species. Photo by Jonathan Sleath, with permission.

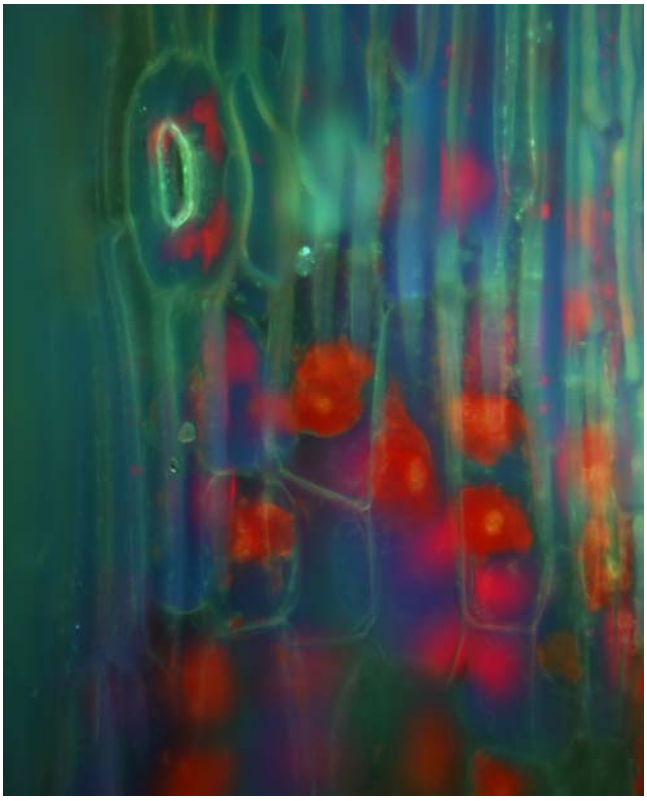

Figure 73. ***Anthoceros*** sp. sporophyte fluorescence showing greenish cell walls and red of chlorophyll in developing spores. Photo by Magdalena Turzańska.

Figure 74. ***Anthoceros*** sp. sporophyte fluorescence. Note the clarity of the stomatal openings. Photo by Magdalena Turzańska.

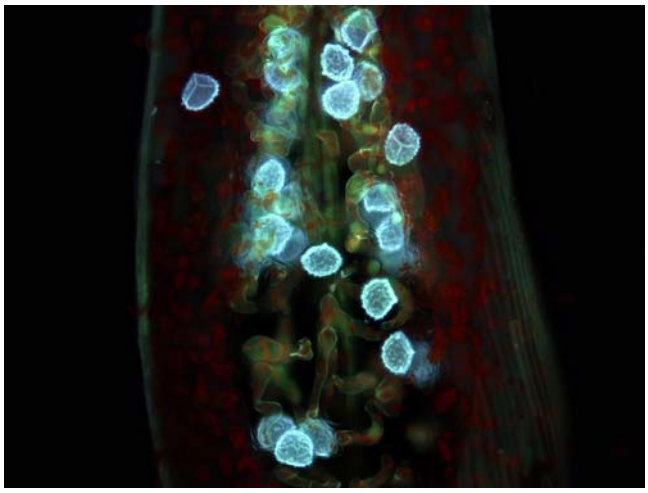

Figure 75. ***Anthoceros*** sp. sporophyte showing blue spore fluorescence. Photo by Magdalena Turzańska.

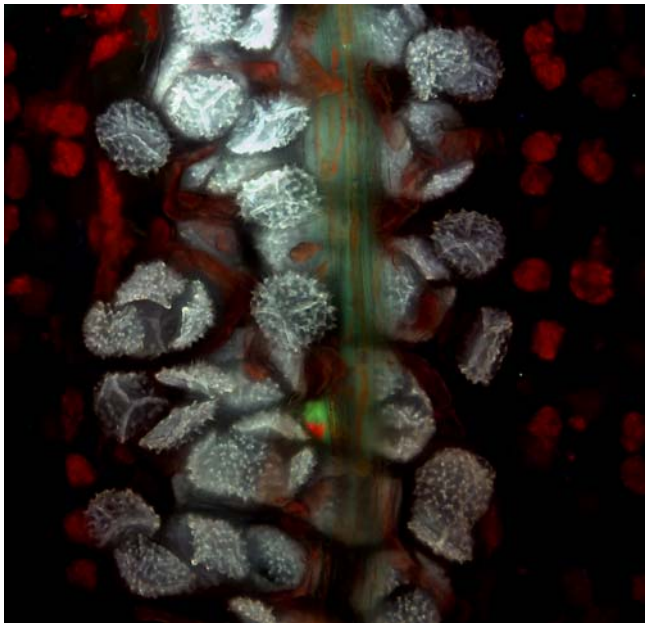

Figure 76. ***Anthoceros*** sp. sporophyte showing pale fluorescence. Photo by Magdalena Turzańska.

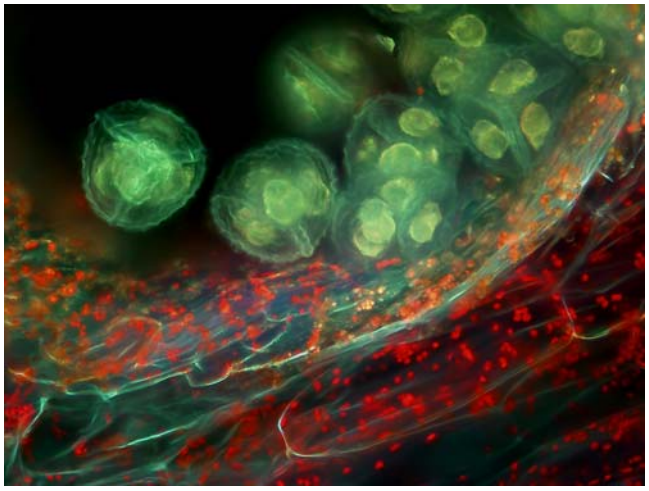

Figure 77. ***Riccia cavernosa*** young sporangium with green fluorescence of young spores. Photo by Magdalena Turzańska.

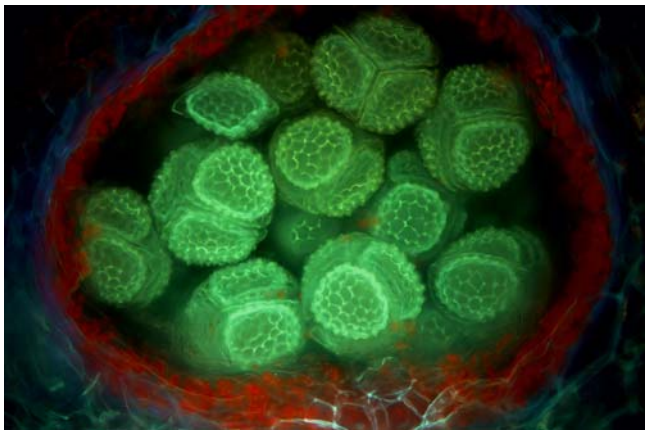

Figure 78. ***Riccia*** sorocarpa sporangium with spore tetrads showing green fluorescence and decoration on the spores and nuclei no longer visible through the spore wall. Photo by Magdalena Turzańska, with permission.

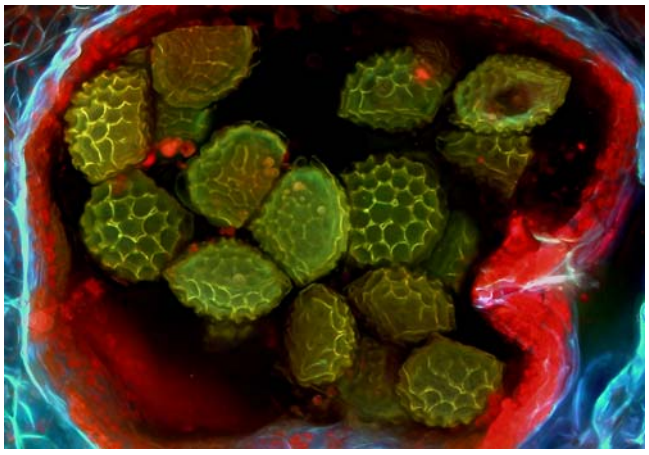

Figure 79. ***Riccia*** sp. mature spores fluorescing differently from younger spores in Figure 78. Photo by Magdalena Turzańska, with permission.

The change in color of the cell walls in spore tetrads to those of the mature spores in ***Riccia*** sp. suggests that the compounds present change with maturity. The sporangia stand out from the coloring of the thallus internal cell walls in ***Riccia*** (Figure 80).

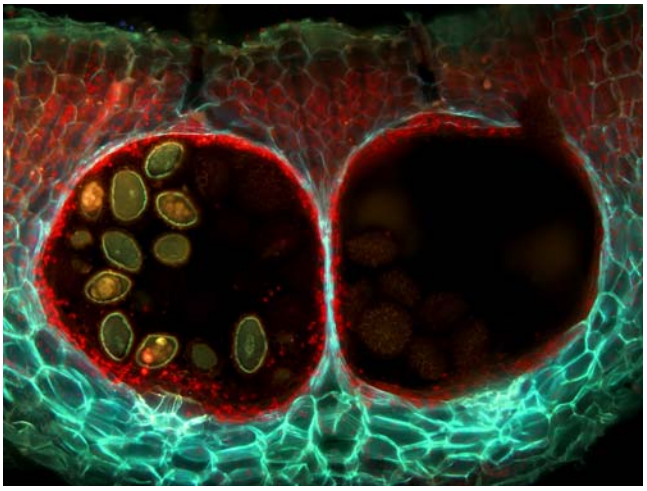

Figure 80. ***Riccia*** sporangia with red chlorophyll fluorescence and blue-green thallus cell wall fluorescence. Spore walls are fluorescing gold. Photo by Magdalena Turzańska.

My first encounter with the phenomenon of **fluorescence** in bryophytes was on a field trip in Europe where I entered in conversation with Gisela Nordhorn-Richter. She had stopped at a display of microscopes at her university just because the poor guys didn't have many visitors. She took her research organisms, members of the genus ***Pohlia*** (Figure 81-Figure 82), to test the quality of the microscopes, one of which had UV light capabilities. To her amazement, gemmae lit up all over the place, displaying far more than she had been able to see without the UV aid. She then looked at other species and found that this was a good tool to help in determining number and shape, enabling her to delineate species more easily (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

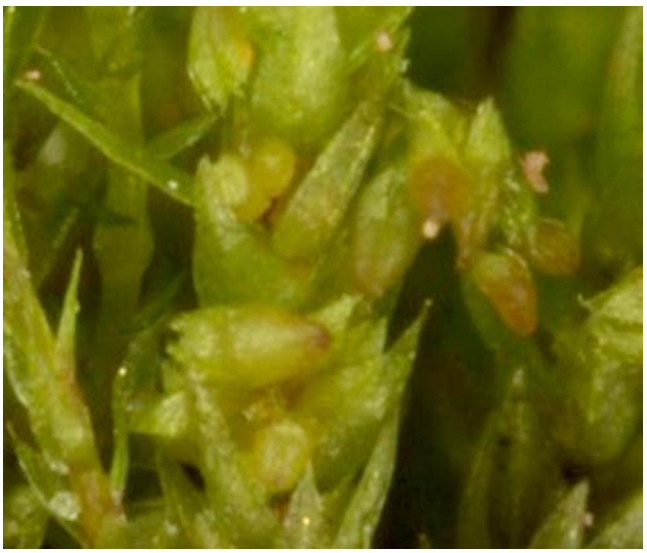

Figure 81. ***Pohlia bulbifera*** showing location of bulbils – structures that can be located in UV light by their fluorescence. Photo by Jan-Peter Frahm, with permission.

Figure 82. ***Pohlia bulbifera*** bulbils that fluoresce, making them easier to locate. Photo by Des Callaghan, with permission.

An image of a gemma of ***Lunularia cruciata*** (Figure 83-Figure 84) from Robin Young indicates that this structure fluoresces blue in UV light. Furthermore, the gemmae of ***Zygodon rupestris*** fluoresce blue (Figure 147). Gemmae can provide multiple colors, including a golden shade in liverworts ***Calypogeia*** sp. (Figure 85), ***Metzgeria*** sp. (Figure 86), and ***Radula complanata*** (Figure 87), and mosses ***Aulacomnium androgynum*** (Figure 88) and ***Tetraphis pellucida*** (Figure 89-Figure 90). The gemmae of ***Tetraphis pellucida*** suggest that the fluorescence color changes with age.

Figure 83. ***Lunularia cruciata***, a species with fluorescing gemmae. Photo by David Holyoak, with permission.

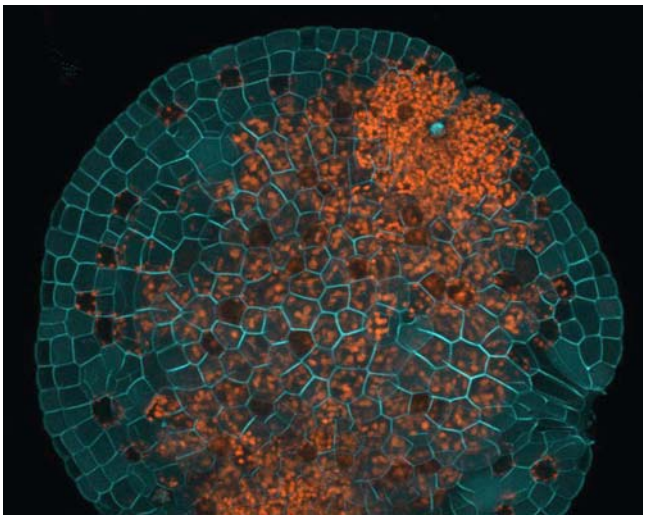

Figure 84. ***Lunularia cruciata*** gemma fluorescing. Photo by Robin Young, with permission.

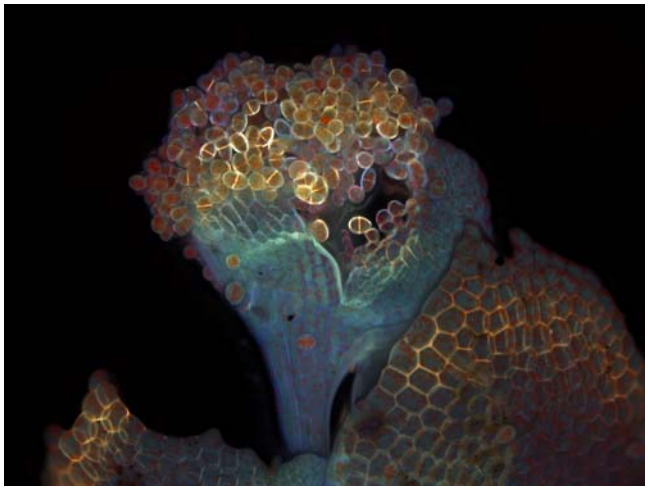

Figure 85. ***Calypogeia*** sp. gemmae with wall fluorescence. Photo by Magdalena Turzańska.

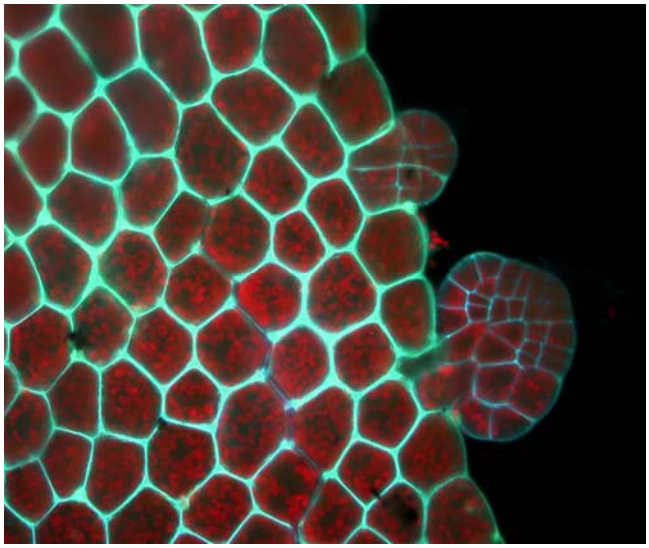

Figure 86. ***Metzgeria*** sp. showing fluorescence of cell walls, including that of marginal gemmae. It appears that the conspicuousness of the gemmae depends on the concentration of the fluorescing substance. Photo by Magdalena Turzańska.

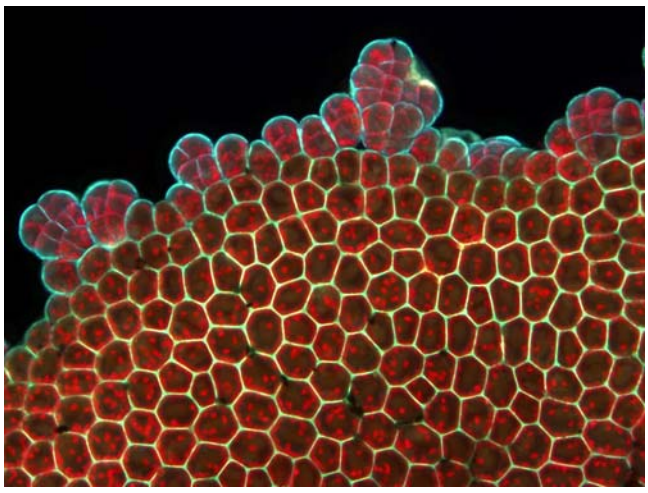

Figure 87. ***Radula complanata*** yellow leaf cell wall fluorescence with blue-green gemma cell wall fluorescence. Photo by Magdalena Turzańska.

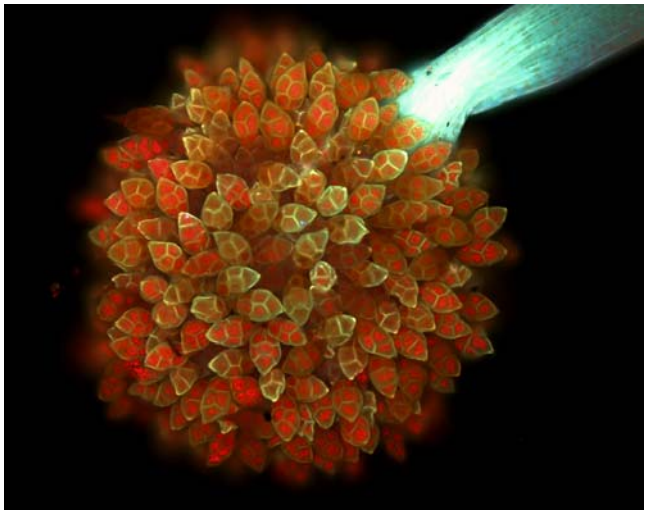

Figure 88. ***Aulacomnium androgynum*** gemmae with wall and chlorophyll fluorescence. Photo by Magdalena Turzańska.

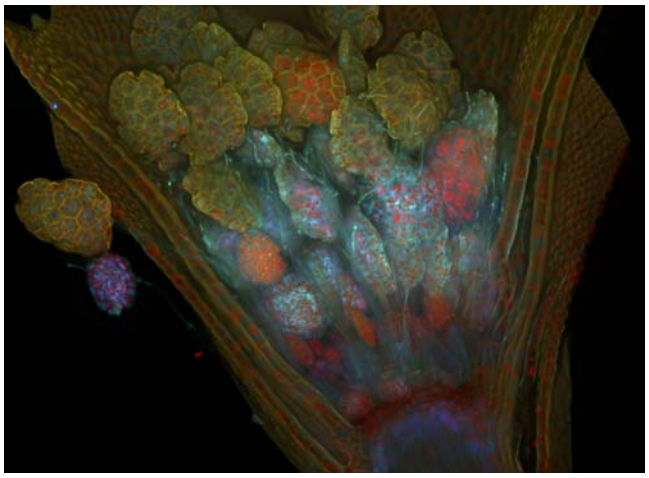

Figure 89. ***Tetraphis pellucida*** gemmae cup fluorescence showing golden cell walls of cup and multiple colors of gemmae, presumably indicating different ages. Photo by Magdalena Turzańska.

Figure 90. ***Tetraphis pellucida*** gemma fluorescence showing golden cell walls, red chloroplasts, and something blue. Photo by Magdalena Turzańska

Even branch buds can become more obvious because of a deep chlorophyll fluorescence. This is illustrated in ***Physcomitrella patens*** (Figure 91).

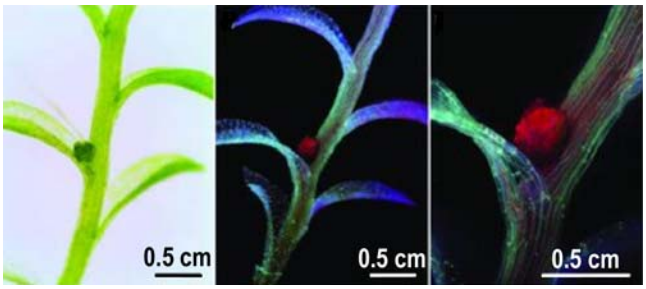

Figure 91. ***Physcomitrella patens*** normallight and fluorescence showing greenish leaf cell walls and bright red of bud due to dense chlorophyll. Photo modified from Beata Zagórska-Marek, with permission; published in American Journal of Botany with Creative Commons attribution <https://creativecommons.org/licenses/by/4.0/#>.

Merced and Renzaglia (2017) used fluorescence as a tool in viewing the stomata of a variety of bryophytes. In a species of ***Bartramia*** (Figure 92-Figure 93) the guard cells fluoresce red due to chloroplasts, but the rest of the capsule has a blue-green color in UV light. They also showed the coloration in UV light for ***Orthotrichum*** sp. (Figure 94-Figure 95), ***Physcomitrium*** sp. (Figure 96-Figure 97), and ***Polytrichum*** sp. (Figure 98).

Figure 92. ***Bartramia pomiformis*** with capsules. Photo by Northern Forest Atlas, with permission through Jerry Jenkins.

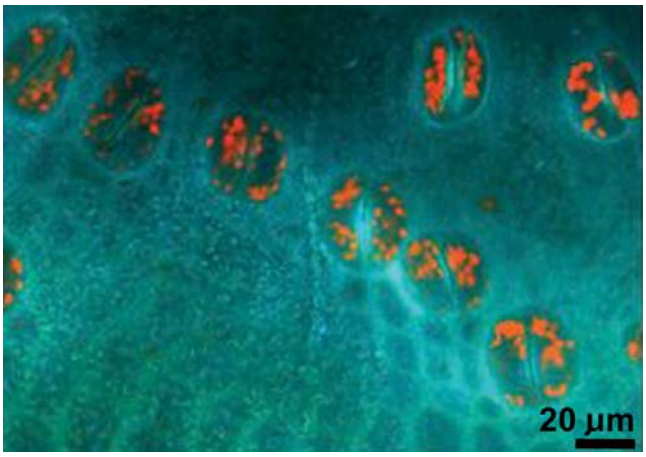

Figure 93. ***Bartramia*** guard cells with chloroplasts and cell walls fluorescing. Photo from Merced & Renzaglia 2017, with permission.

Figure 94. ***Orthotrichum alpestre***, in a genus where guard cells are of taxonomic importance. Photo by Michael Lüth, with permission.

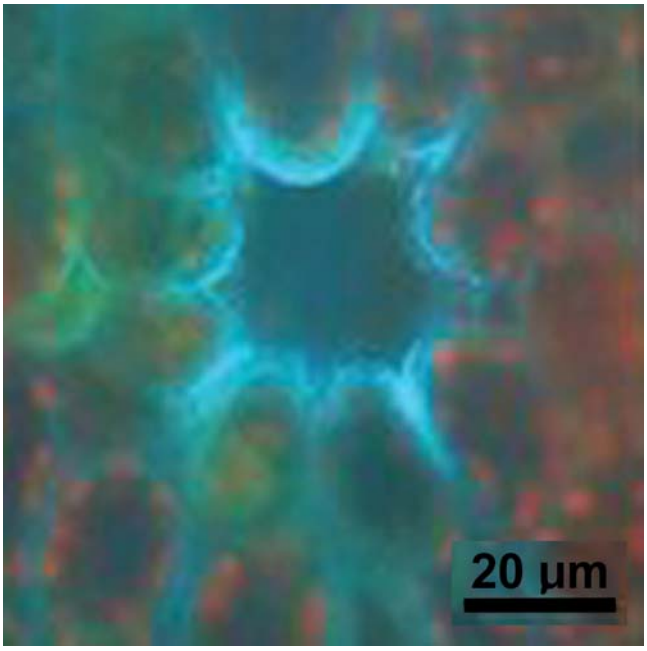

Figure 95. ***Orthotrichum*** guard cells with chloroplasts and cell walls fluorescing in UV light. Photo modified from Merced & Renzaglia 2017, with permission.

Figure 96. ***Physcomitrium patens*** showing capsules Photo by Hugues Tinguy, with permission.

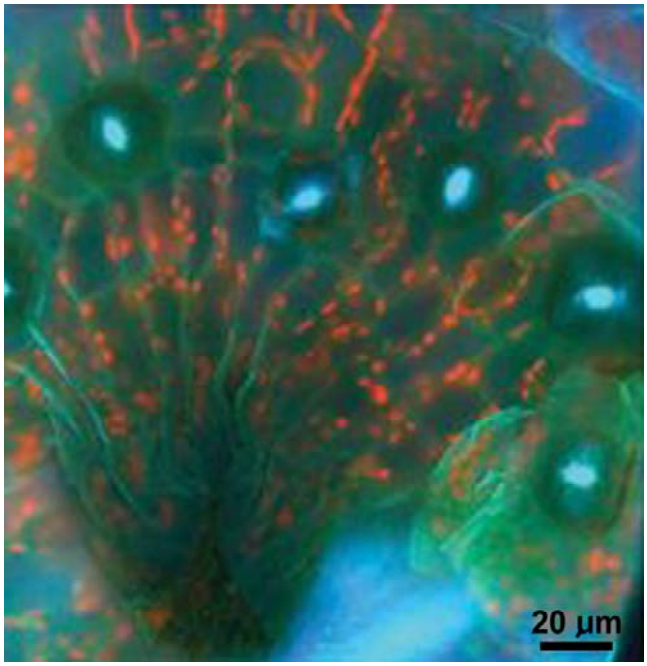

Figure 97. ***Physcomitrium*** guard cells and chloroplasts (**orange**) in fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

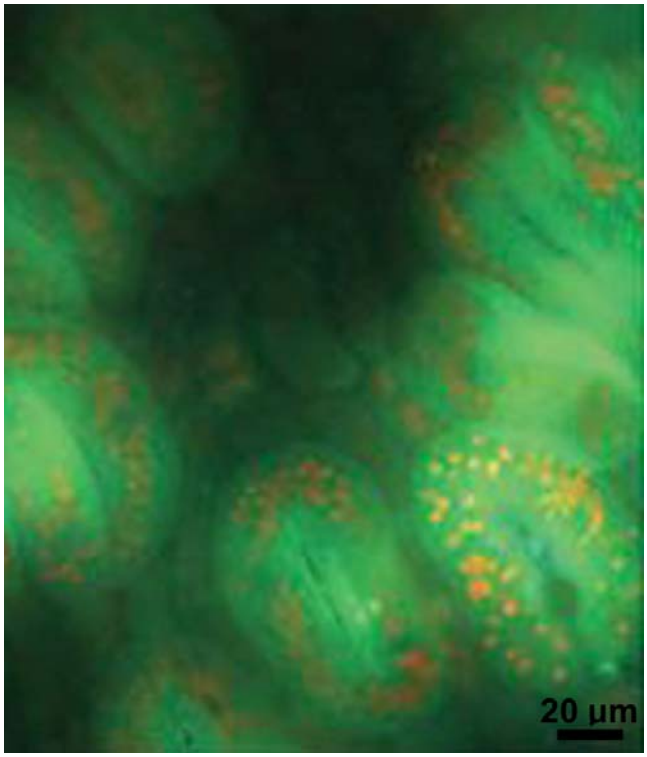

Figure 98. ***Polytrichum*** guard cells with chloroplasts (orange) using fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

In addition to the fluorescence of stomata in the sporophyte, it appears that the gametophyte thallus and the cells surrounding the pores of ***Conocephalum conicum*** (Figure 99-Figure 101) and ***Marchantia polymorpha*** (Figure 102) also exhibit fluorescence.

Figure 99. ***Conocephalum conicum*** showing raised pores. Photo by Dick Haaksma, with permission.

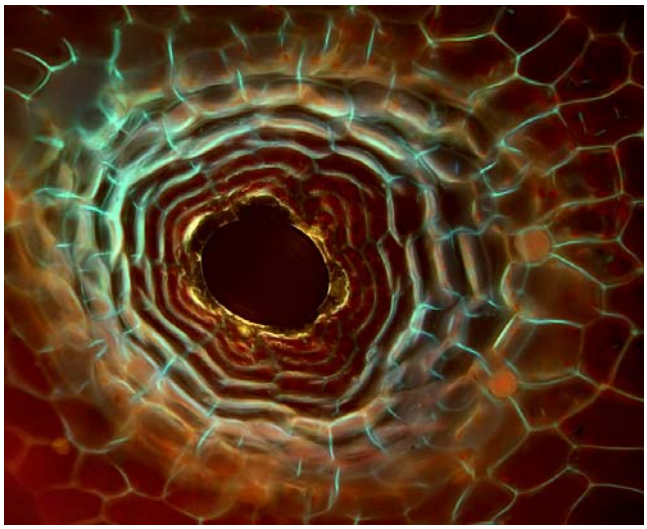

Figure 100. ***Conocephalum conicum*** pore fluorescence. This image has been enhanced by increasing the color contrast using Photoshop. Photo by Magdalena Turzańska, with permission.

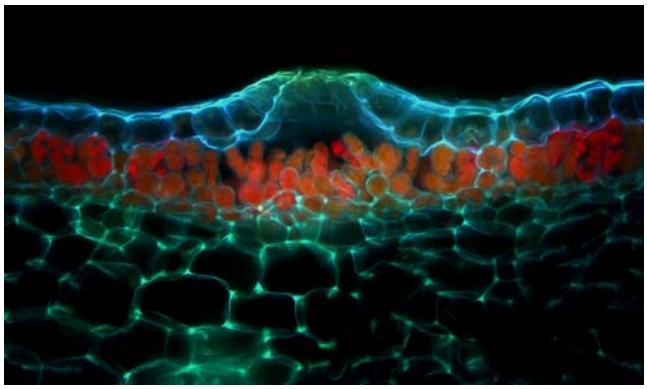

Figure 101. ***Conocephalum conicum*** thallus section showing pore and fluorescence. Note the bright red chlorophyll in photosynthetic cells under the epidermis. Photo by Magdalena Turzańska.

Little has been published about fluorescence of sexual structures. Nevertheless, in her photographic images Magdalena Turzańska illustrates that the antheridia (Figure 103-Figure 108) and archegonia (Figure 109-Figure 110) and associated paraphyses can exhibit a colorful display.

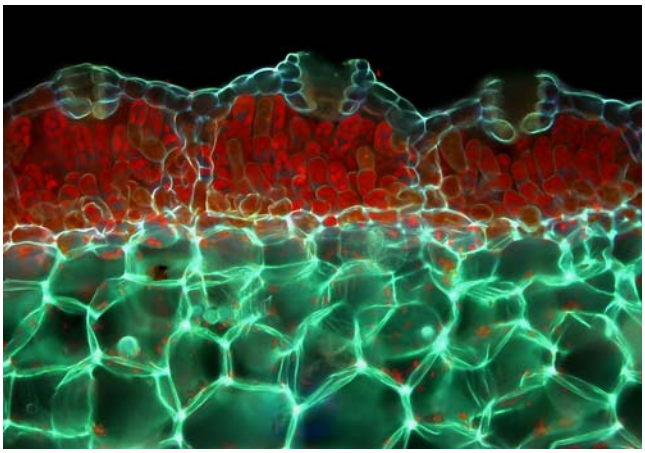

Figure 102. ***Marchantia polymorpha*** thallus section showing fluorescing pore, chlorophyll fluorescence, and fluorescing thallus tissue. Photo by Magdalena Turzańska.

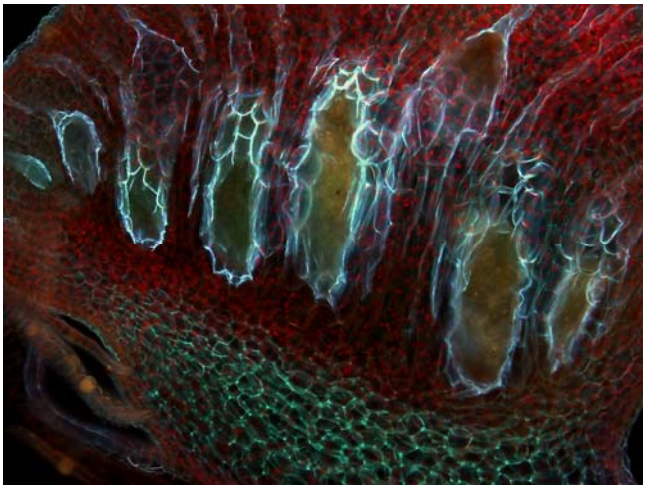

Figure 103. ***Conocephalum conicum*** antheridia showing fluorescence of their walls, chlorophyll in surrounding cells, and green walls of non-photosynthetic thallus cells. Photo by Magdalena Turzańska.

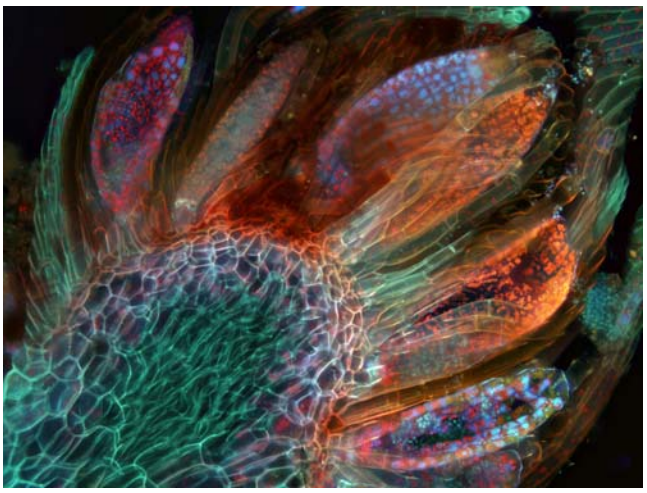

Figure 104. Moss antheridia fluorescence providing a colorful contrast to that of the stem. Photo by Magdalena Turzańska, with permission.

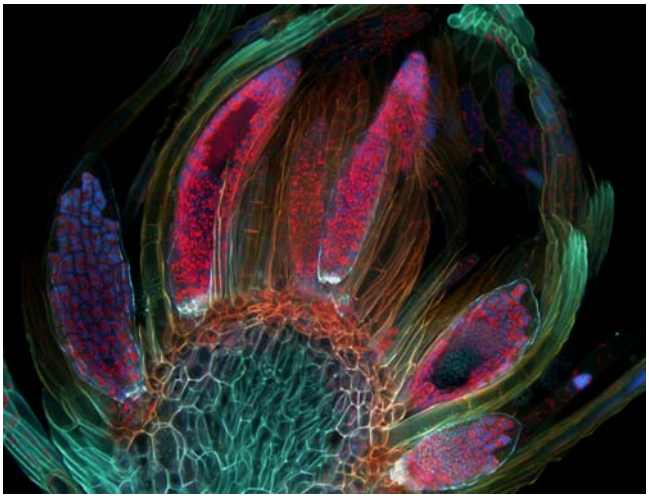

Figure 105. Moss antheridia fluorescence with intense coloration. Photo by Magdalena Turzańska.

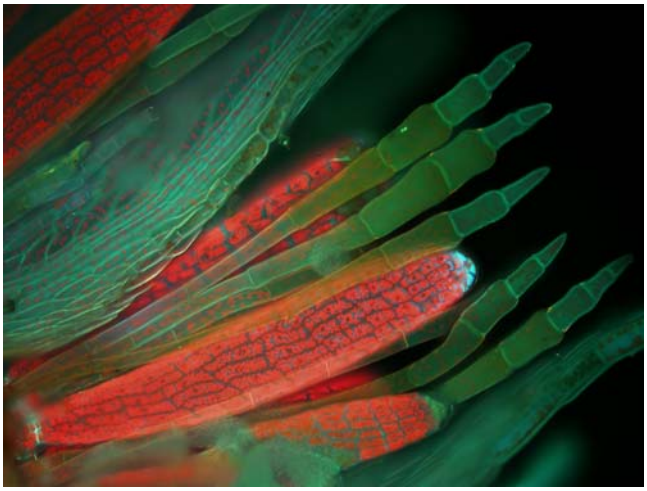

Figure 106. ***Mnium hornum*** antheridia fluorescence barely visible at tips due to chlorophyll fluorescence; paraphyses have strong green fluorescence. Photo by Magdalena Turzańska.

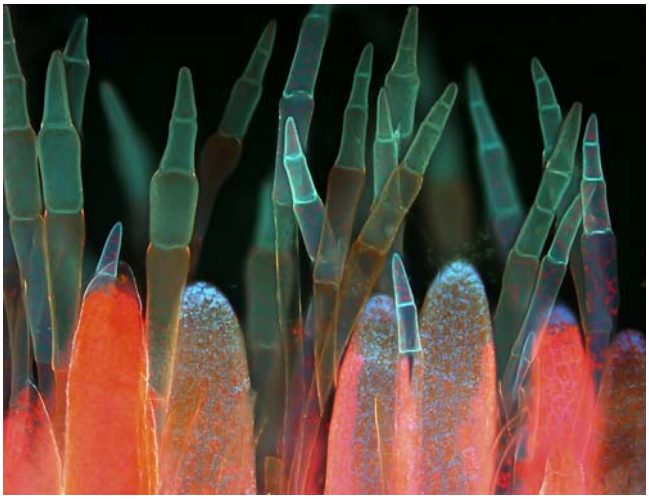

Figure 107. ***Mnium hornum*** antheridia and paraphyses fluorescing. Photo by Magdalena Turzańska, with permission.

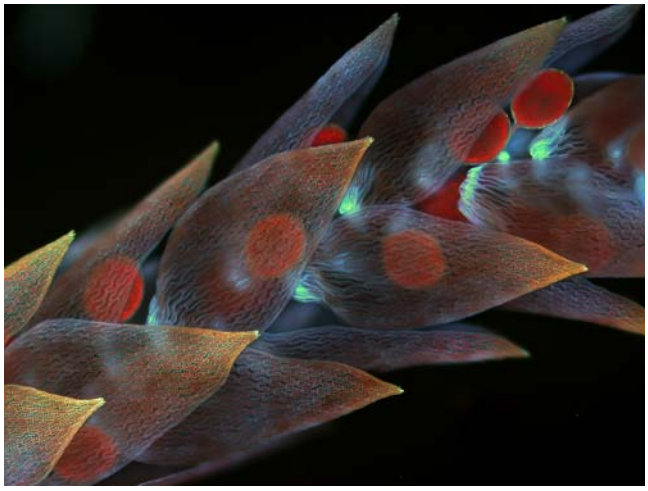

Figure 108. ***Sphagnum*** sp. antheridia showing fluorescence in UV light. Photo by Magdalena Turzańska.

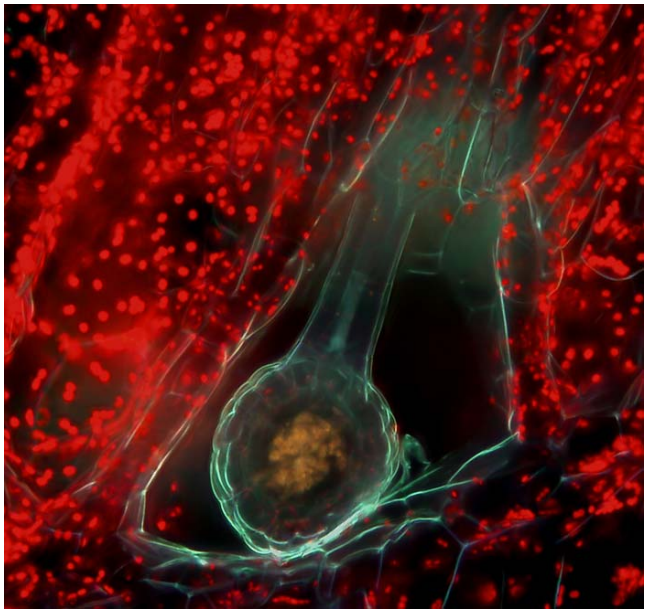

Figure 109. ***Riccia*** sp. archegonium fluorescence, surrounded by chlorophyll fluorescence of the thallus. Photo by Magdalena Turzańska.

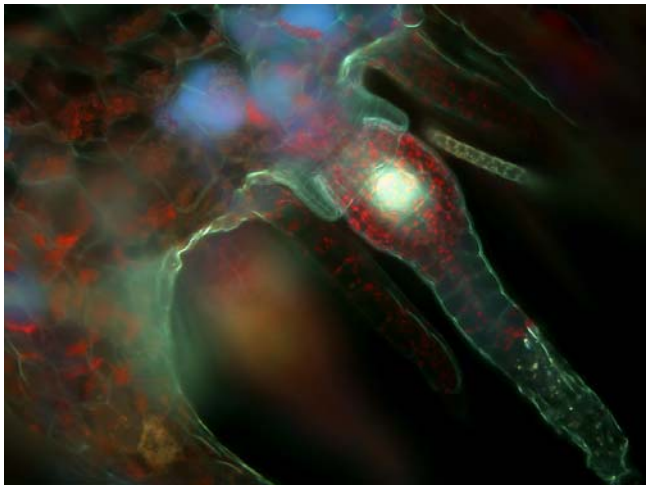

Figure 110. ***Marchantia polymorpha*** archegonium green fluorescence with red chlorophyll fluorescence at base and bright egg. Photo by Magdalena Turzańska.

The fluorescence of sporophytes seems to be largely unknown. The only images I have seen are those of Magdalena Turzańska for ***Phascum*** sp. (Figure 111) and ***Sphagnum*** sp. (Figure 112) The latter appears to lack capsule fluorescence, but exhibits it in the pseudopodium. It would be interesting to see if the fluorescence of spores and capsule are more common in species lacking a peristome, perhaps serving to attract arthropod dispersal vectors.

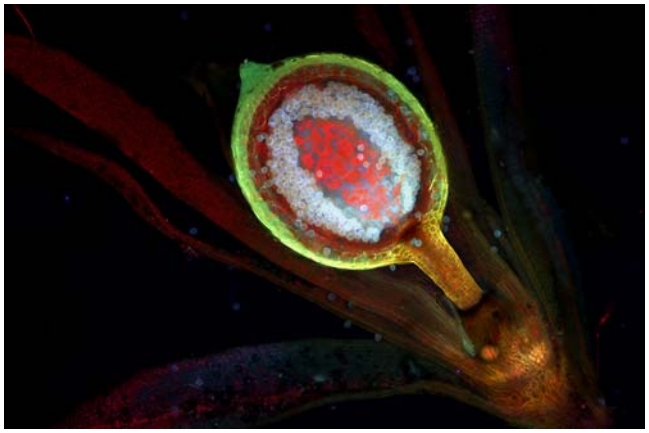

Figure 111. ***Phascum*** sp. fluorescence of capsule and spores in capsule with no peristome. Photo by Magdalena Turzańska.

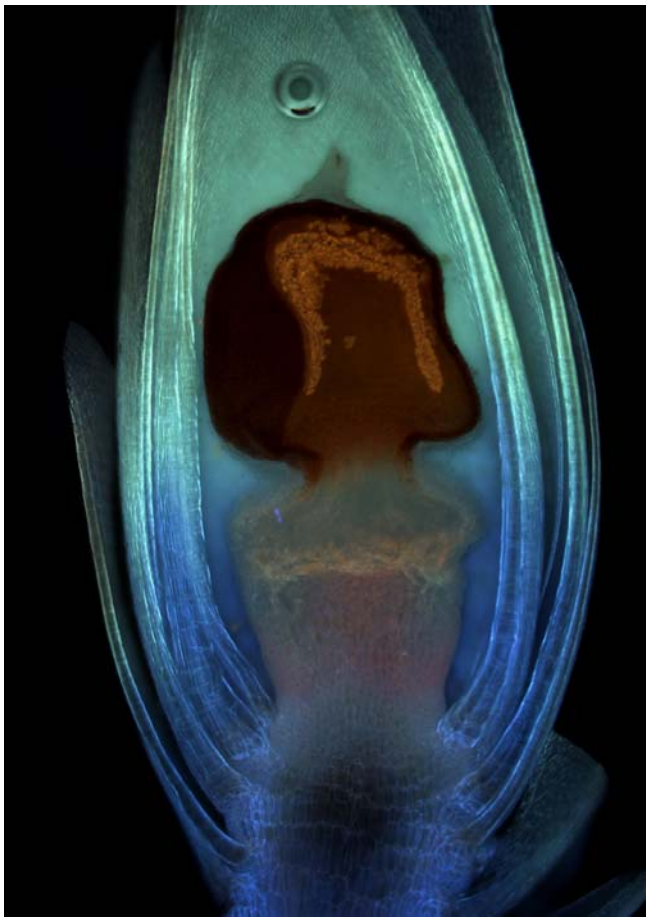

Figure 112. ***Sphagnum*** sp. fluorescence with capsule apparently not fluorescing, but the developing pseudopodium has some pink, green, and greenish fluorescence. Photo by Magdalena Turzańska.

In liverworts, the spores are nestled among elaters that may help to loosten and expel the spores from the capsules. These, too, can fluoresce (Figure 113-Figure 114). Since I have few records, it is too early to determine if this is a common character in liverwort elaters. I have even fewer examples of fluorescence in peristomes (Figure 115).

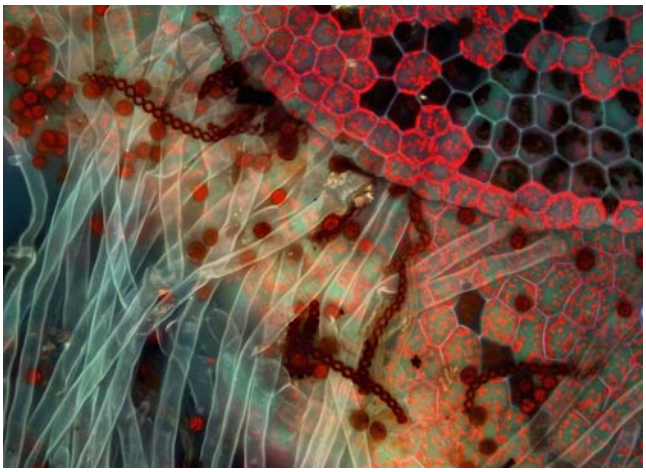

Figure 113. ***Marchantia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

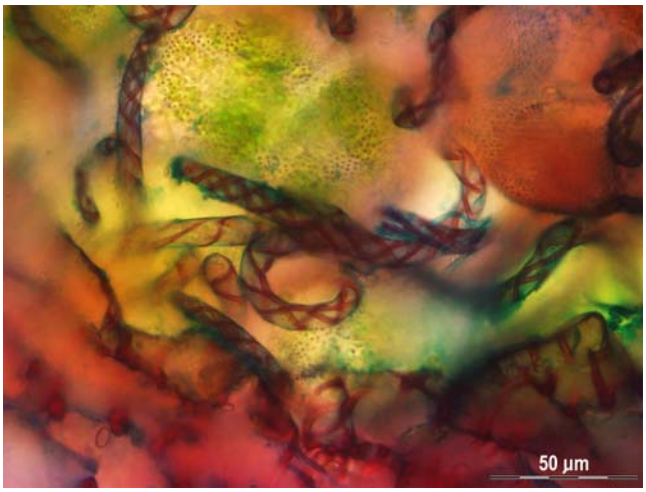

Figure 114. ***Pellia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

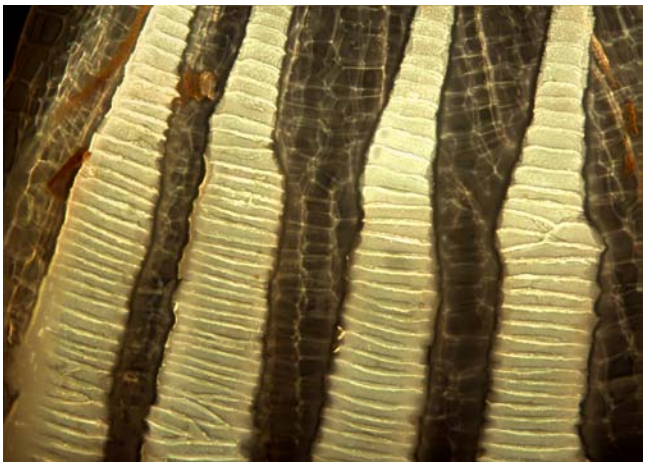

Figure 115. Moss peristome golden fluorescencein UV light. Photo by Magdalena Turzańska.

In addition to the fluorescence of the plant parts, it is often possible to distinguish the presence of epiphytes more easily using UV light. This can be seen in Figure 66-Figure 67 for algae on ***Sphagnum***, in Figure 116-Figure 117 for **Cyanobacteria** on ***Hylocomium splendens***, and ***Blasia pusilla*** (Figure 118-Figure 121). Can it be used as well to detect and help identify bacteria on the bryophytes?

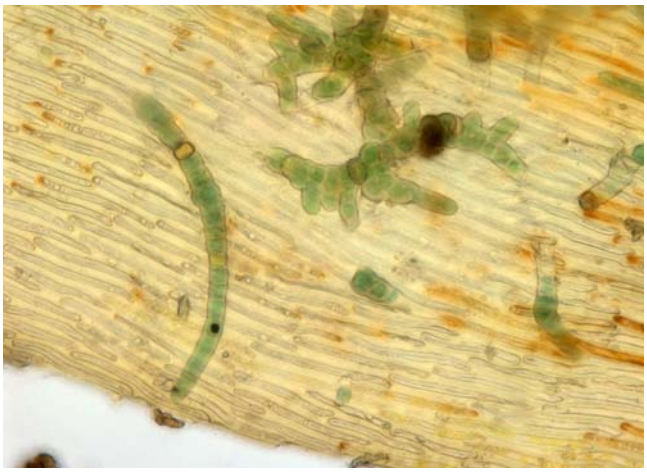

Figure 116. ***Hylocomium splendens*** with ***Stigonema*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

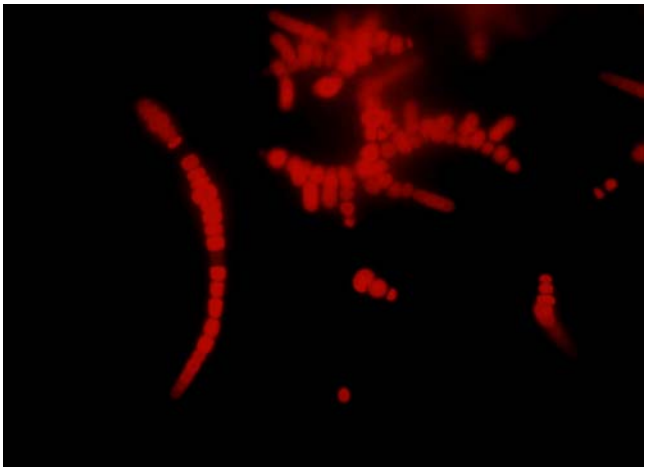

Figure 117. ***Stigonema*** (**Cyanobacteria**) on ***Hylocomium splendens*** fluorescence. Photo by Magdalena Turzańska.

Figure 118. ***Blasia pusilla Nostoc*** colonies. Photo by Magdalena Turzańska.

Figure 119. ***Blasia pusilla*** with ***Nostoc*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

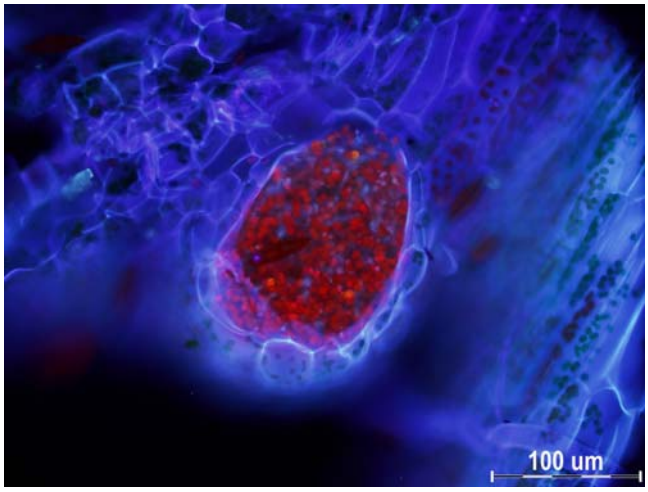

Figure 120. ***Blasia pusilla*** blue fluorescence of thallus and red **Cyanobacteria** fluorescence. Photo by Magdalena Turzańska.

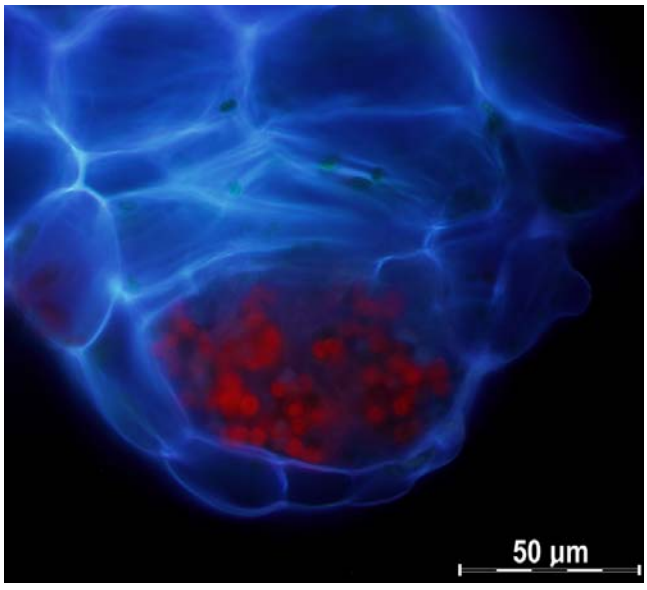

Figure 121. ***Blasia pusilla*** with red fluorescence of **Cyanobacteria** and blue thallus fluorescence. Photo by Magdalena Turzańska.

Which Species Fluoresce?

For some reason, the method of viewing bryophytes with UV light has been neglected. It was not until Dale Kruse inquired about bryophyte fluorescence on Bryonet (25 March 2011) that the subject again surfaced: "I just returned from a trip to Puerto Rico where I visited the rainforests of the Caribbean (El Yunque) National Forest. A 'non-bryological' employee there suggested there were fluorescent mosses in the forests of El Yunque. I did a quick search on the web and found very little information. I have seen fluorescent lichens but not mosses." Bryologists responded with skepticism, suggesting it was a fungus or bacterium (or possibly a lichen). Then Michael Lüth responded (Bryonet 26 March 2011): "We saw a fluorescent ***Frullania dilatata*** (Figure 122-Figure 124) on an excursion, when someone held a fluorescent lamp to a tree searching for some lichens." And Michael was able to show us proof (Figure 123).

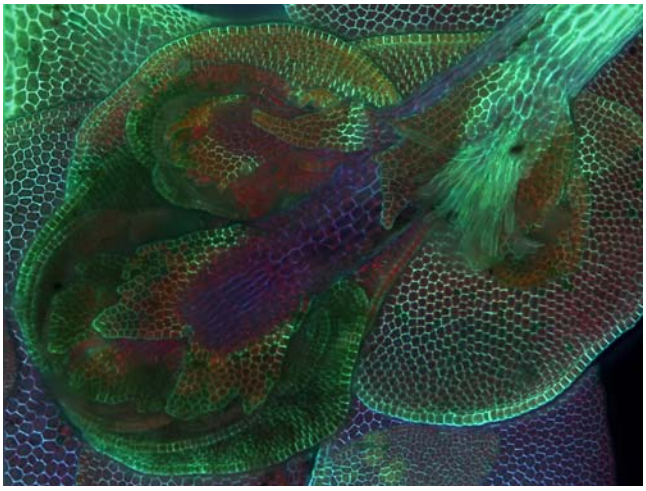

Figure 124. ***Frullania dilatata*** green cell wall fluorescence. Photo by Magdalena Turzańska.

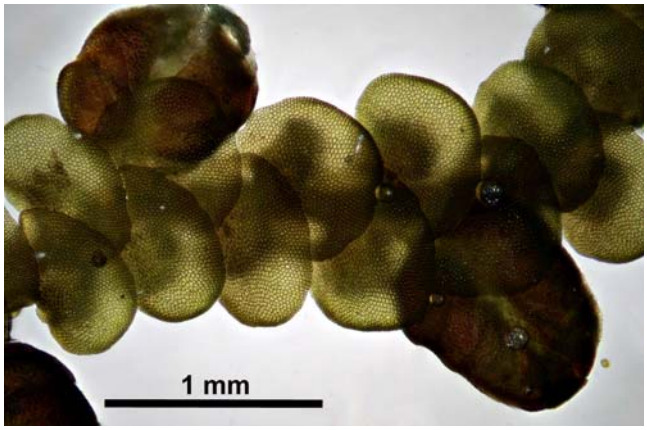

Figure 122. ***Frullania dilatata***, a species that exhibits purple fluorescence. Photo by Claire Halpin, with permission.

In 2022, the topic of fluorescence erupted on Bryonet again. Emmet Judziewicz and Virginia (Bryonet 13 March 2022) reported that on a casual one-hour walk in the Hawaiian rainforest, their UV flashlight revealed a "striking bright red fluorescence" in several leafy liverworts. These included **Cephaloziaceae**: ***Fuscocephaloziopsis connivens*** (Figure 125-Figure 126) **subsp.** ***sandvicensis***, ***Odontoschisma denudatum*** (Figure 127), and **Lepidoziaceae**: ***Lepidozia australis*** (Figure 128), ***Telaranea nematodes*** (Figure 129), but the common ***Bazzania praerupta*** (=***Bazzania cordistipula***; Figure 130-Figure 131) did not exhibit red florescence, nor did the other common leafy liverworts they examined.

Figure 123. ***Frullania dilatata*** demonstrating purple fluorescence under UV light from a special UV-emitting hand lens. Photo by Michael Lüth, with permission.

Figure 125. ***Fuscocephaloziopsis connivens***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

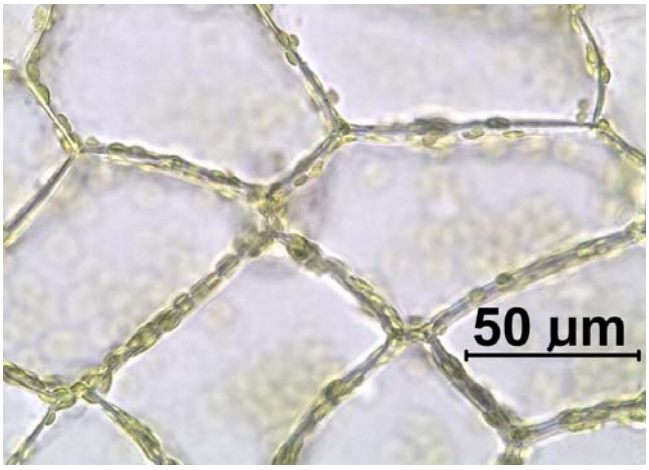

Figure 126. ***Fuscocephaloziopsis connivens*** cells showing chloroplasts clinging to cell walls. Photo by Hugues Tinguy, with permission.

Figure 127. ***Odontoschisma denudatum***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

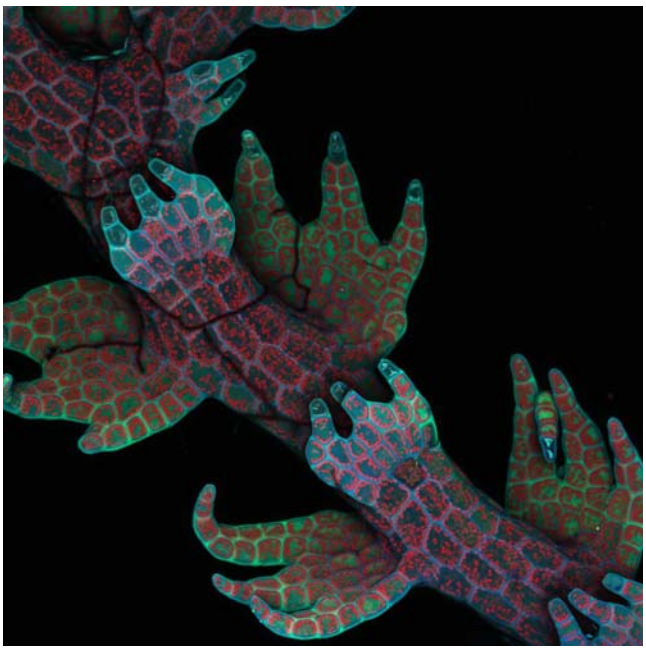

Figure 128. ***Lepidozia australis*** showing fluorescence. Photo by Robin Young, with permission through CC-BY-NC 4.0.

Figure 129. ***Telaranea nematodes***, a member of the **Lepidoziaceae** that exhibits fluorescence in UV light. Photo by Michael Lüth, with permission.

Figure 130. ***Bazzania praerupta***, a species in the **Lepidoziaceae** that does not fluoresce in UV light when viewed macroscopically. Photo by Lin Shanxiong, through Creative Commons.

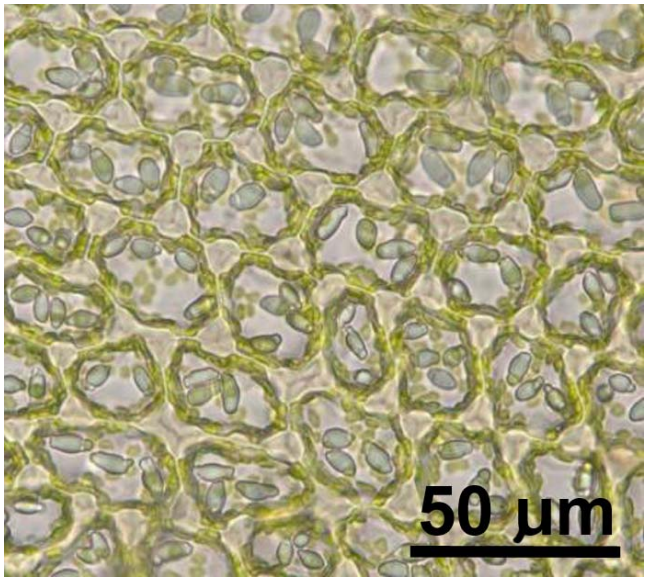

Figure 131. ***Bazzania praerupta*** leaf cells showing large trigones, but lacking papillae. Photo by Lin Shanxiong, through Creative Commons.

Andi Cairns (pers. comm. 27 March 2022) reported ***Bazzania vittata*** (Figure 132-Figure 134, Figure 174) fluorescing blue beside a ***Bazzania corbieri*** (Figure 132-Figure 134, Figure 135) that was not fluorescing. The adjacent mosses ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) and ***Pyrrhobryum paramattense*** (Figure 132-Figure 133, Figure 137) were likewise not fluorescing. Herbarium specimens of ***Bazzania vittata*** from Thornton Peak in North Queensland, Australia, also fluoresced blue even when **dry** (Andi Cairns, pers. comm. 29 March 2022). She explored an additional ~20 specimens of dried leafy liverworts from the Australian Wet Tropics and the only one that fluoresced blue under UV light was ***Bazzania vittata*** (Andi Cairns, pers. comm. 30 March 2022).

Figure 132. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 133. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. ***Bazzania corbieri*** appears to be fluorescing purple in some branches – perhaps dead ones with cells or structures no longer hiding the fluorescence? Photo by Will Cairns, courtesy of Andi Cairns.

Figure 134. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 135. ***Bazzania corbieri***, a non-fluorescing species. Photo by Andrew Franks, with permission.

Figure 136. ***Leucobryum aduncum* var. *aduncum***, a species that lacks fluorescence. Photo by Niels Klazenga, with permission.

Figure 137. ***Pyrrhobryum paramattense*** with capsules, a species that lacks fluorescence. Photo by Peter Woodard, through Creative Commons.

David Glenny found fluorescence of ***Bazzania tayloriana*** (Figure 138) in New Zealand, reported again by John Braggins (Bryonet 18 April 2022) (Figure 139). This is true for specimens from both North and South Islands of New Zealand.

Figure 138. ***Bazzania tayloriana***, a species that exhibits blue fluorescence in UV light. Photo courtesy of John Braggins.

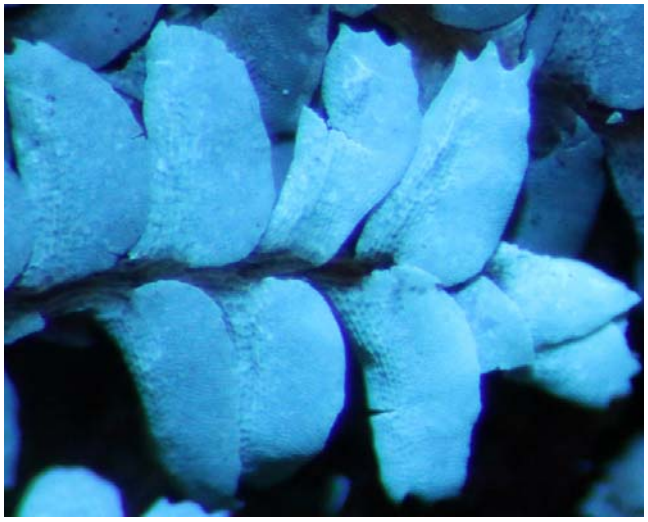

Figure 139. ***Bazzania tayloriana*** showing blue fluorescence. Photo courtesy of John Braggins.

In California, USA, when Ken Kellman (Bryonet 21 April 2022) discovered that the bark of the valley oak (***Quercus lobata***; Figure 140) was fluorescing dark red under the light of a uvBeast V3 MINI, he found that the fluorescence was coming from a tiny moss that proved to be ***Zygodon rupestris*** (Figure 59, Figure 141-Figure 142). But when he used UV light on the dry specimens, there was no fluorescence. Fluorescence appeared again when the moss was rewet. Both the leaves and the gemmae (Figure 143-Figure 144) were glowing red. The nearby mosses ***Antitrichia californica*** (Figure 145) and ***Homalothecium nuttallii*** (Figure 146) did not fluoresce, wet or dry.

Figure 140. ***Quercus lobata***, a species that can serve as substrate for fluorescent ***Zygodon rupestris***. Photo by JKehoe Photos, through Creative Commons.

Figure 141. ***Zygodon rupestris*** on a tree in the UK. Photo by Claire Halpin, with permission.

Figure 142. ***Zygodon rupestris***, a species known to exhibit fluorescence when hydrated but not when dry. Photo by Jonathan Sleath, with permission.

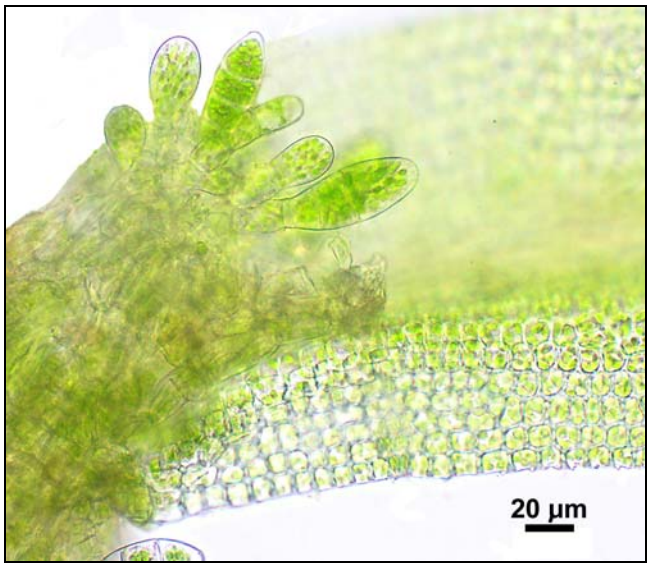

Figure 143. ***Zygodon rupestris*** leaf with gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 144. ***Zygodon rupestris*** gemmae, a plant part that is able to fluoresce. Photo by Claire Halpin, with permission.

Figure 145. ***Antitrichia californica***, a pleurocarpous moss species that seems to lack macroscopic fluorescence capability. Photo by John Game, through Creative Commons.

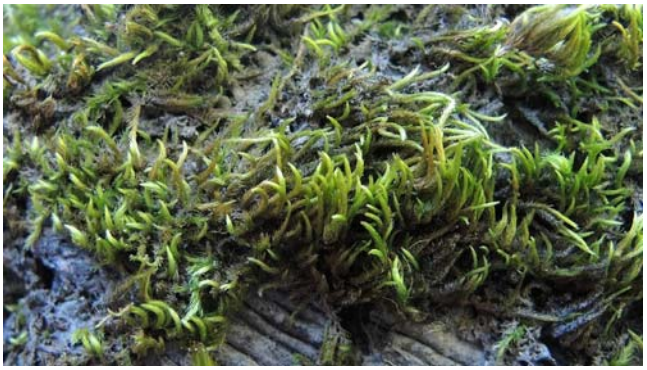

Figure 146. ***Homalothecium nuttallii***, a pleurocarpous species that seems to lack fluorescence capability. Photo by Michael Lüth, with permission.

Tom Ottley (Bryonet 23 April 2022) followed up on these observations with different collections of ***Zygodon rupestris*** (Figure 141-Figure 144). Although it seemed to be that the gemmae were fluorescing, after some difficulty he was able to determine with high power of the microscope that it was an alga that was fluorescing dark red. With the help of a UV microscope, Ottley (Bryonet 5 May 2022) was able to see two sorts of fluorescence in ***Z. rupestris*** (Figure 147). One was the bright whitish-blue from the contents of the gemmae (Figure 147) and the other was red from the chloroplasts of the associated algae (Figure 147). He found no detectable fluorescence in the laminal cells of the moss leaves.

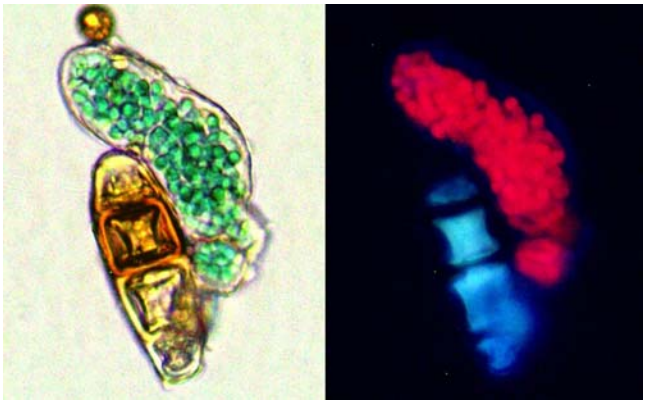

Figure 147. ***Zygodon rupestris*** fluorescence. **Left**: gemma and alga in LED white light. **Right**: gemma and alga fluorescing in UV light. Photo courtesy of Tom Ottley.

Eric Whiting (Bryonet 26 March 2022) was inspired by the Bryonet discussion to re-examine some of his ***Fossombronia*** (Figure 148) samples from semi-arid regions of Australia. Using a hand-held battery unit, he was able to see what appeared to be fluorescence in these, but not in other soil-crust bryophytes from New South Wales, Australia. However, with a stronger UV light he discovered that it was **reflectance** and not fluorescence (Eric Shiting, Bryonet 6 May 2022). He raised the question of whether reflectance could reduce the incoming light energy sufficiently to lower it to a tolerable level. He questioned whether UV light might be equally well reflected.

Figure 148. ***Fossombronia cf wondraczekii*** in Australia, in a genus that seems to lack macroscopic fluorescence. Photo by Bernd Haynold, through Creative Commons.

Magdalena Turzańska has documented the fluorescence of additional species with her photography. These include the liverworts ***Blasia pusilla*** (Figure 149-Figure 150), ***Barbilophozia*** (Figure 151), ***Cephalozia bicuspidata*** (Figure 152), ***Calypogeia*** sp. (Figure 153), ***Gymnocolea inflata*** (Figure 154), ***Lepidozia reptans*** (Figure 155), ***Lophocolea heterophylla*** (Figure 156-Figure 157), ***Marsupella sp***. (Figure 158), ***Metzgeria*** sp. (Figure 160), ***Plagiochila asplenioides*** (Figure 161), ***Radula complanata*** (Figure 162-Figure 163), and ***Trichocolea tomentella*** (Figure 164), and mosses ***Brachythecium*** sp. (Figure 165), ***Mnium hornum*** (Figure 166), ***Polytrichum piliferum*** (Figure 167-Figure 168), ***Tetraphis pellucida*** (), and ***Thuidium tamariscinum*** (Figure 169-Figure 171).

Figure 149. ***Blasia pusilla*** thallus section with **Cyanobacteria**. Photo by Magdalena Turzańska.

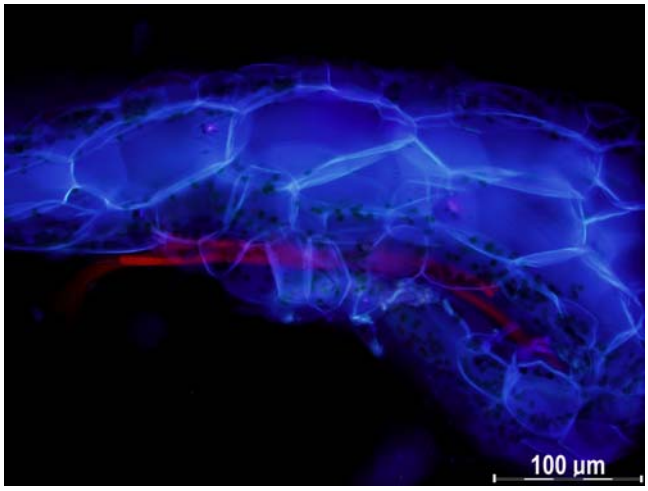

Figure 150. ***Blasia pusilla*** thallus section showing brilliant blue fluorescence. **Cyanobacteria** are fluorescing red. Photo by Magdalena Turzańska.

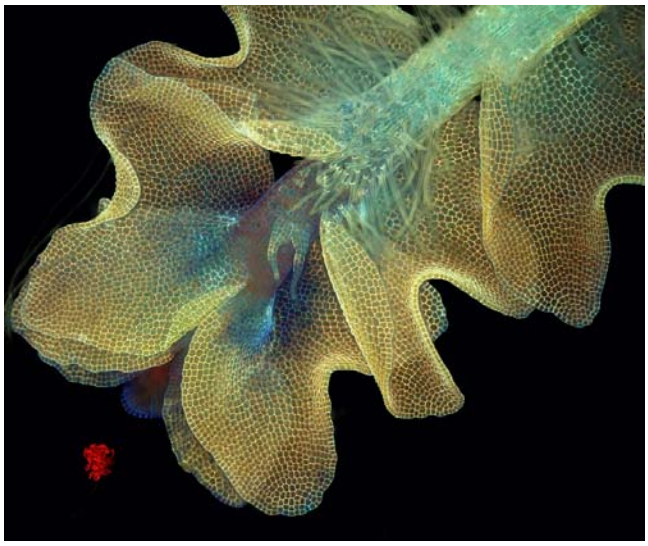

Figure 151. ***Barbilophozia*** sp. showing fluorescence in the leaf cell walls with the base of the leaf glowing blue. The stem has yet another shade of blue. The hair-like filaments are rhizoids. **Cyanobacteria** are fluorescing red in the lower left. Photo by Magdalena Turzańska.

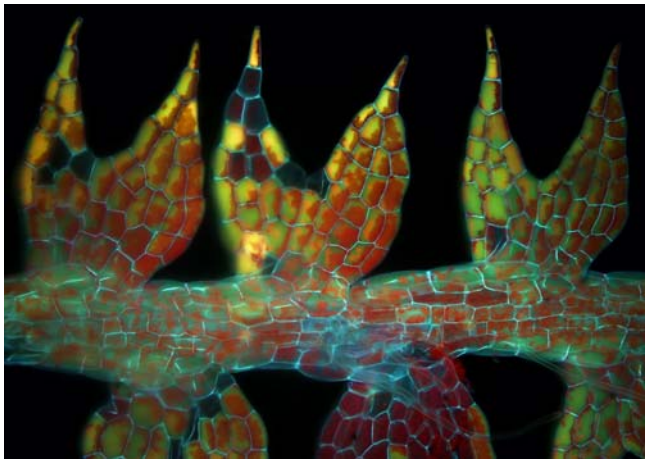

Figure 152. ***Cephalozia bicuspidata*** fluorescence, a tiny species that might be more easily located at night with a UV source. Photo by Magdalena Turzańska.

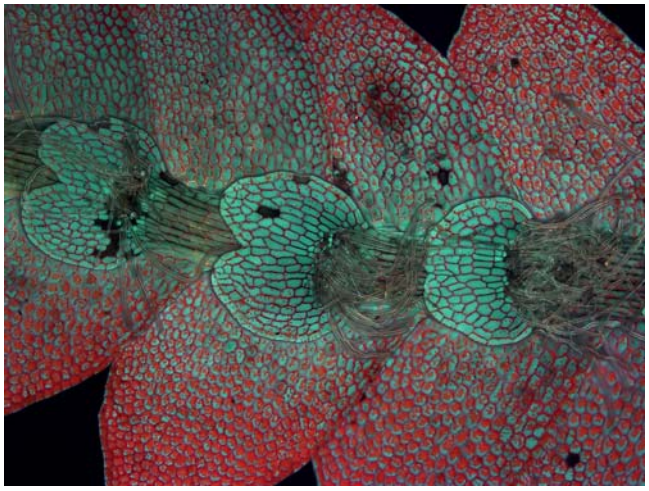

Figure 153. ***Calypogeia*** sp. with cell wall fluorescence; the fluorescence makes it easier to see the underleaves. Photo by Magdalena Turzańska.

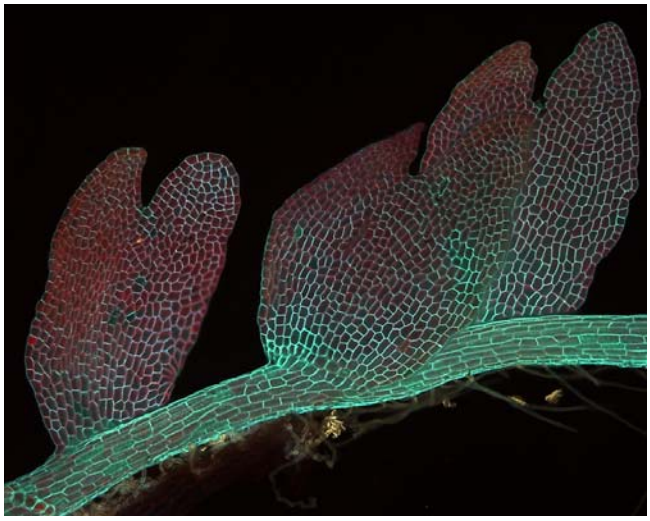

Figure 154. ***Gymnocolea inflata*** with green fluorescence of cell walls. Photo by Magdalena Turzańska.

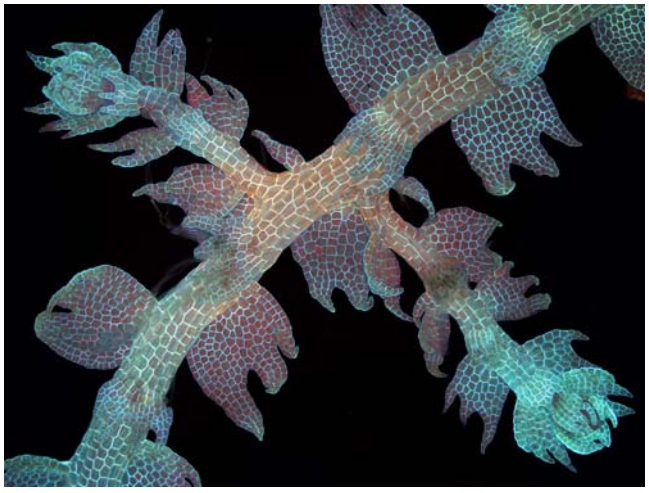

Figure 155. ***Lepidozia reptans*** ventral view showing blue cell wall fluorescence. Photo by Magdalena Turzańska.

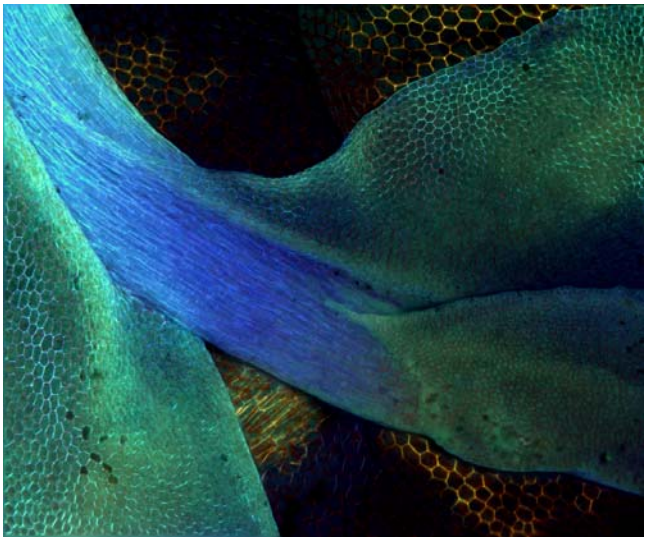

Figure 156. ***Lophocolea heterophylla*** fluorescence showing blue stem cells and greenish leaf cell walls. Photo by Magdalena Turzańska.

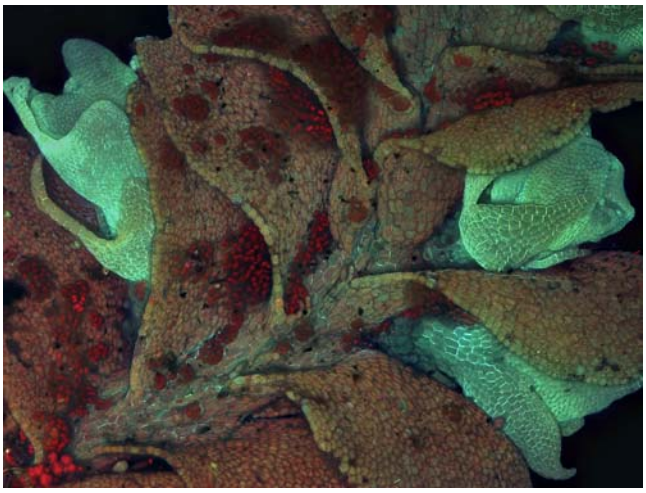

Figure 157. ***Lophocolea heterophylla*** with red patches of **Chlorophyta** fluorescing on leaves that are apparently dead or at a different stage of maturity from the branches with greenish cell wall fluorescence. Photo by Magdalena Turzańska.

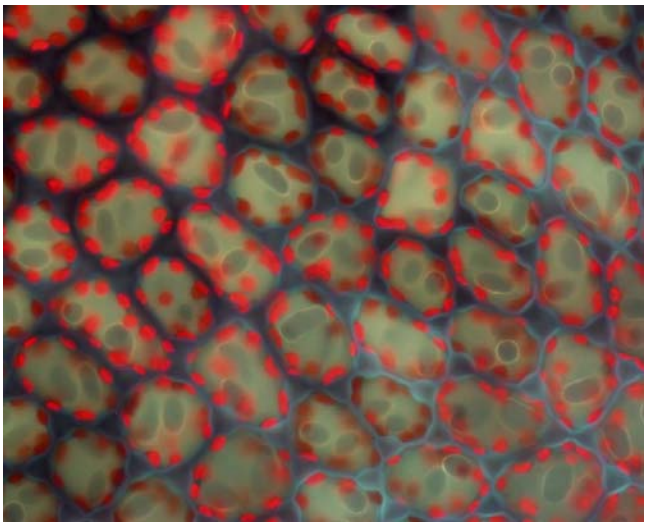

Figure 158. ***Marsupella*** sp. leaf cells fluorescing blue. Photo by Magdalena Turzańska.

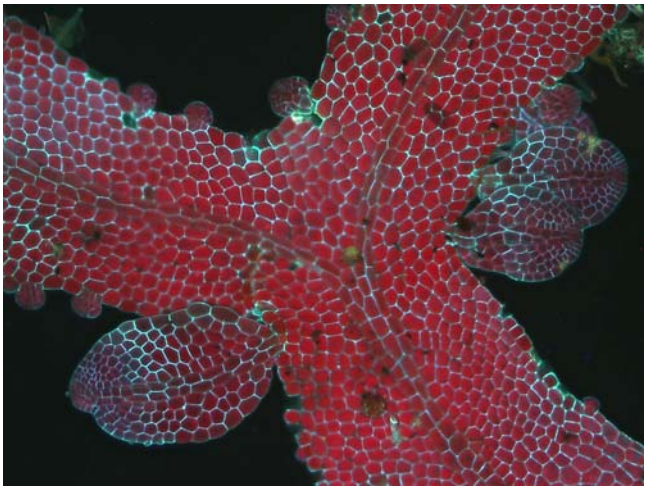

Figure 159. ***Metzgeria*** sp. blue-green fluorescence of cell walls. Photo by Magdalena Turzańska.

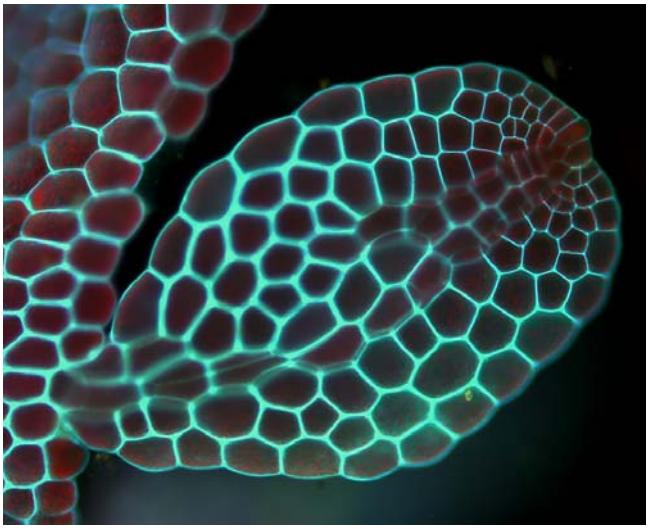

Figure 160. ***Metzgeria*** sp. showing blue-green cell wall fluorescence. Photo by Magdalena Turzańska.

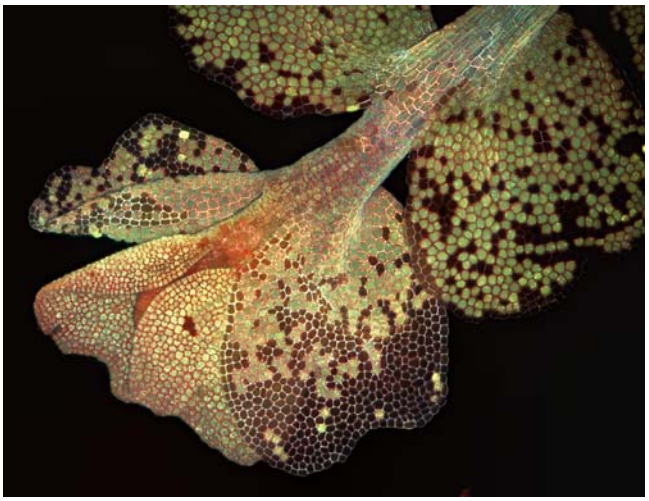

Figure 161. ***Plagiochila asplenioides*** exhibiting golden leaf cell wall fluorescence. Stem cell walls have a more pinkish cast. Photo by Magdalena Turzańska.

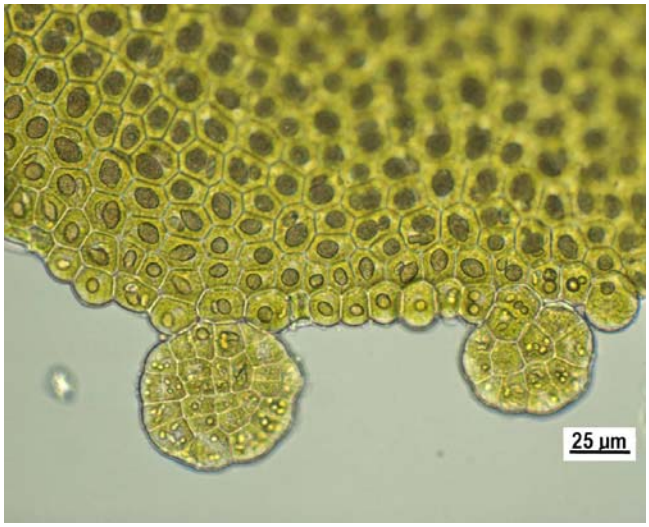

Figure 162. ***Radula complanata*** with gemmae, shown in white light. Photo by Blanka Aguero, with permission.

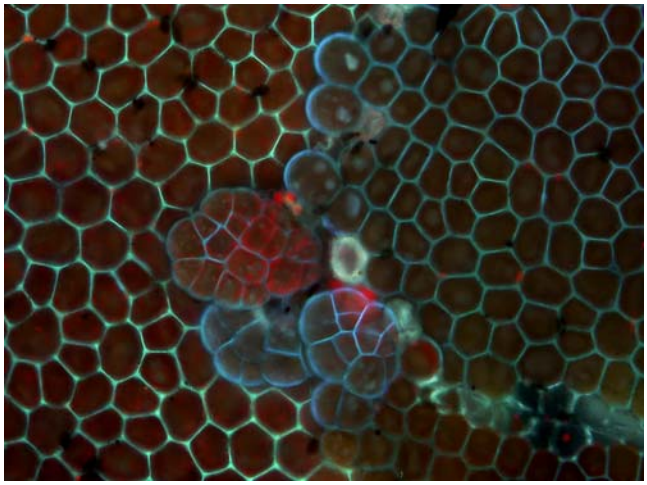

Figure 163. ***Radula complanata*** leaf cell wall and gemmae cell wall fluorescence. Note the difference in color between the blue gemmae cell walls and greenish walls of lamina cells. Photo by Magdalena Turzańska.

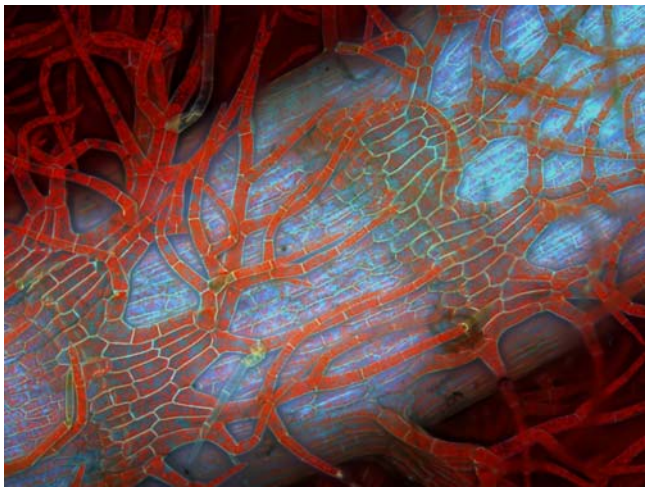

Figure 164. ***Trichocolea tomentella*** with blue cell wall fluorescence. Photo by Magdalena Turzańska.

Figure 165. ***Brachythecium*** fluorescence with leaf cell walls fluorescing aqua and the stems fluorescing bright red. This view makes the leaf bases easy to see. Photo by Magdalena Turzańska.

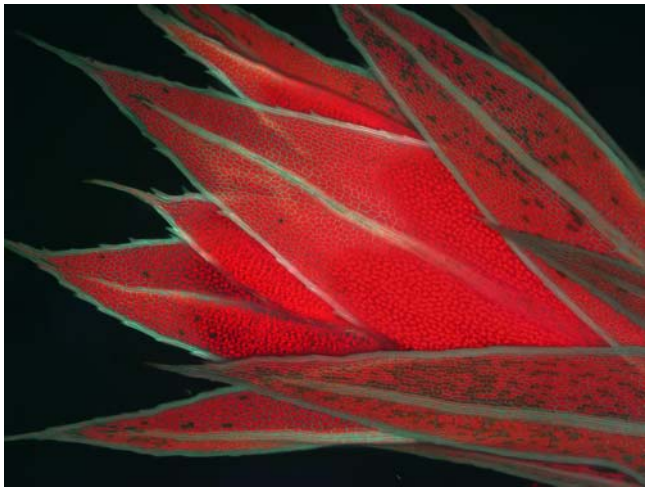

Figure 166. ***Mnium hornum*** leaf border and costa fluorescence with brilliant chlorophyll fluorescence in the leaf cells. Photo by Magdalena Turzańska.

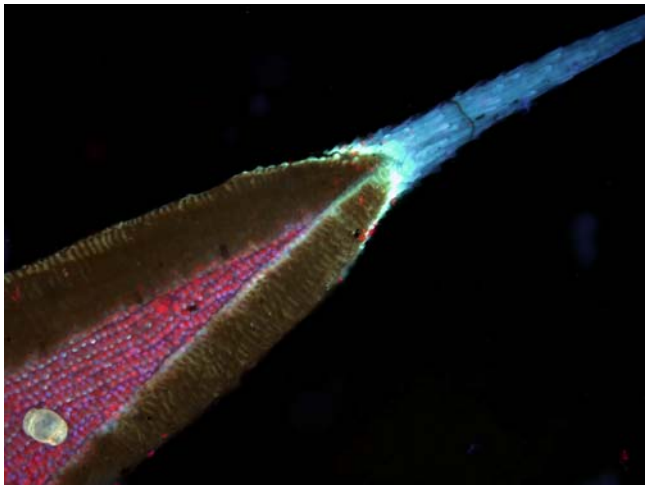

Figure 167. ***Polytrichum piliferum*** leaf fluorescence showing red chlorophyll and blue leaf hair tip. The cell walls of the lamellae can barely be seen fluorescing blue. Photo by Magdalena Turzańska.

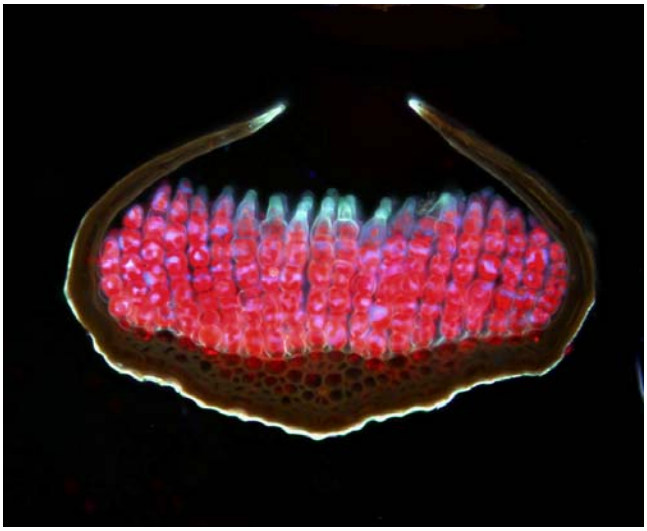

Figure 168. ***Polytrichum piliferum*** leaf cs showing blue fluorescence of the outer cells of lamellae and pale yellow of leaf surface. The lamellae cell walls are fluorescing throughout, but the fluorescence is barely visible due to the strong fluorescence of the chlorophyll. Photo by Magdalena Turzańska.

Figure 169. ***Thuidium tamariscinum*** in sunlight, a species with fluorescent leaf cell walls and contrasting costa fluorescence when illuminated with UV light. Photo by Hermann Schachner, through Creative Commons.

Figure 170. ***Thuidium tamariscinum*** fluorescence in UV light. Photo by Magdalena Turzańska.

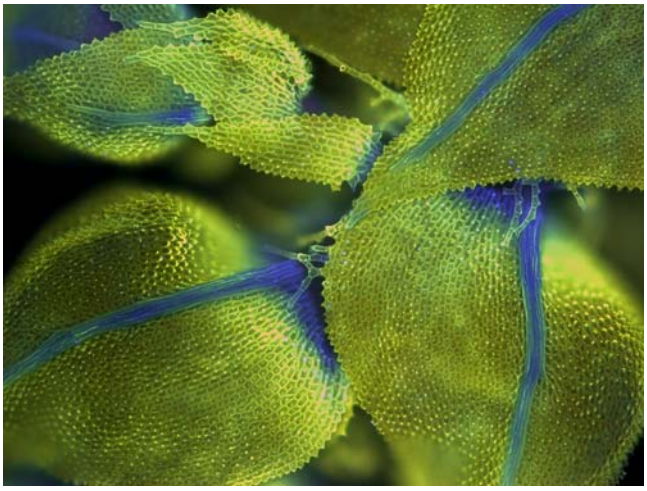

Figure 171. ***Thuidium tamariscinum*** showing a blue fluorescence in the costa and yellow fluorescence in the leaf cell walls, indicating that they have different compounds. These colors have been created by adding berberine to cause the fluorescence. Note the striking difference between the natural fluorescence in Figure 170 and that with berberine stain in this image. Photo by Magdalena Turzańska.

A search of internet images turned up some additional species. One such discovery was a beautiful image of two ***Sphagnum*** species growing together with one (possibly ***Sphagnum divinum***) fluorescing a deep blue-purple and the other lacking fluorescence (Figure 172).

Figure 172. ***Sphagnum*** spp. in white (**upper**) and UV (**lower**) light. The fluorescing moss (**lower**) appears to be ***Sphagnum divinum***, based on its reddish tint (**upper**) and larger, fleshy appearance. Photo ©Damon Noe, with permission.

Sources of Fluorescence

These examples raise the question of the compound(s) causing the fluorescence in bryophytes and why do some have it and others do not. For example, Tamás Pócs (Bryonet 24 March 2022) recalled that ***Bazzania vittata*** (Figure 173-Figure 174) was the only liverwort with fluorescence among those present on the summit of Bellenden Ker in Queensland, Australia.

The two best-known molecules exhibiting fluorescence are chlorophyll and lignin (Donaldson 2020). However, numerous others also exist. These elicit a variety of colors and some (ferulates – one of phenolic compounds) change color with a change in *p*H or chemicals such as Naturstoff reagent (flavonoids). Use of glutaraldehyde as a fixing agent can also induce autofluorescence and permit the imaging of proteins in organelles in the cell protoplast.

It is unclear which structures in bryophytes are responsible for the fluorescence. Andi Cairns (pers. comm. 30 March 2022) suggested that the fluorescence might be due to surface quality. To support this idea, she cited the glaucous surface with minute papillae on both ***Bazzania vittata*** (Figure 173-Figure 174) and ***B. tayloriana*** (Figure 175-Figure 176) (Meagher 2019). ***Zygodon rupestris*** (Figure 59) also has multiple papillae per cell (Figure 177).

Figure 173. ***Bazzania vittata*** in LED light, a species that exhibits fluorescence Photo by Will Cairns, courtesy of Andi Cairns.

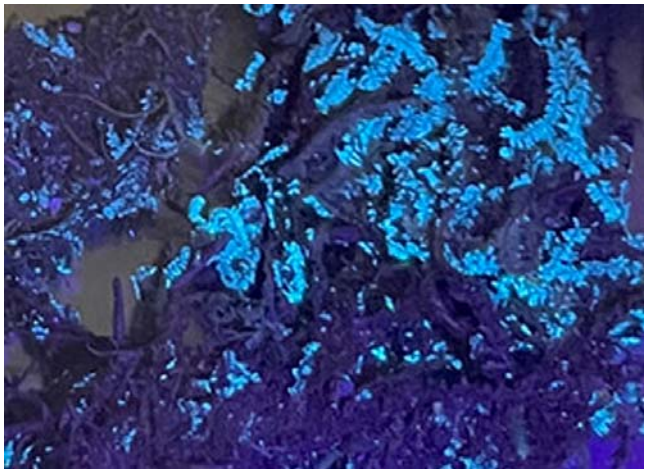

Figure 174. ***Bazzania vittata*** fluorescing. Photo courtesy of Andi Cairns.

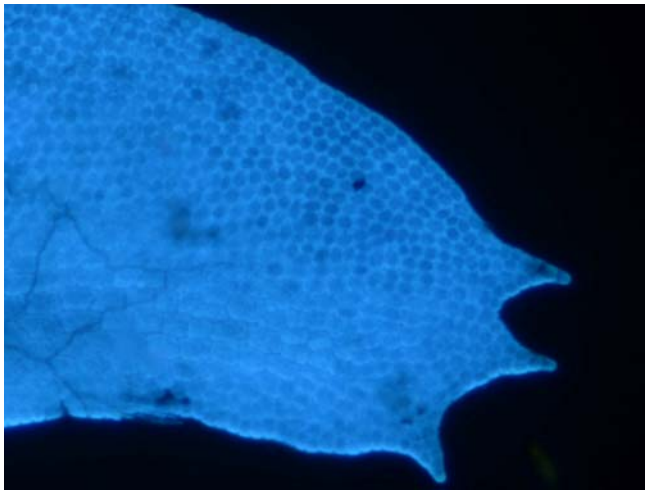

Figure 175. ***Bazzania tayloriana*** leaf showing minute papillae visible on the margins and blue fluorescence. Photo courtesy of David Glenny.

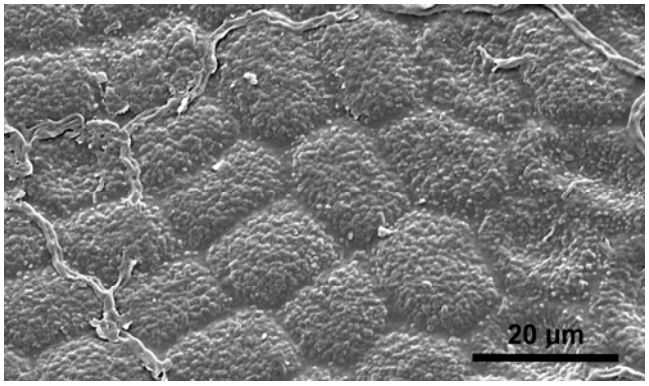

Figure 176. ***Bazzania tayloriana*** dorsal surface cells showing minute papillae. Photo courtesy of John Braggins.

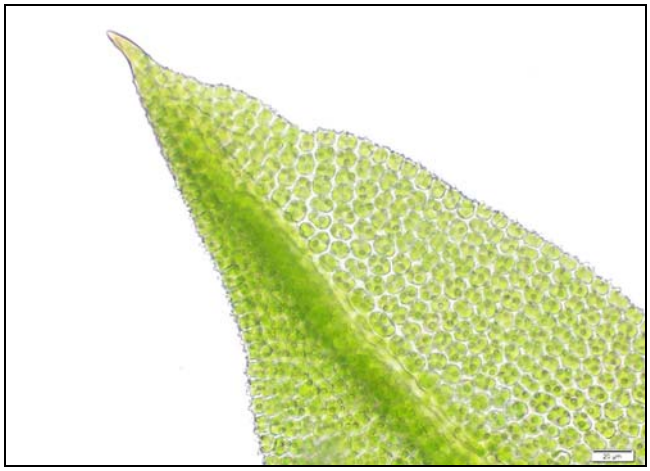

Figure 177. ***Zygodon rupestris*** leaf cells showing papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that McClure and Miller (1967) explored the flavonoids causing fluorescence at such an early date without precipitating more studies on this property in a wider range of bryophytes. They found that most of the fluorescence came from flavonoids and some phenolics, as reported by Dave Kofranek (Bryonet 23 April 2022). It is further interesting that none of the pleurocarpous mosses tested exhibited fluorescence, an observation consistent with that of Ken Kellman (Bryonet 21 April 2022) for ***Antitrichia*** (Figure 145) and ***Homalothecium*** (Figure 146). The study only listed blue and purple reactions, so perhaps there was no testing for those that fluoresce red, yellow, or other colors. There is so much remaining for us to understand.

Magdelena Turzańska has found only weak fluorescence in pleurocarpous mosses, ass seen here in ***Hypnum*** sp. (Figure 178).

Figure 178. ***Hypnum*** sp., a pleurocarpous moss showing a golden cell wall fluorescence. Photo by Magdalena Turzańska.

Role

Fluorescence can help to attract pollinators in flowering plants and thus aid in dispersal, but its role in bryophytes is unknown and unexplored. Andi Cairns speculated on the function of fluorescence in bryophytes as agents of antiherbivory (Andi Cairns, pers. comm. 2 June 2022), and J. K. Oliver suggested that they might just be **spandrels** (phenotypic trait that is byproduct of evolution of some other characteristic, rather than direct product of adaptive selection) – a term introduced by Gould and Lewontin (1979) (Andi Cairns, pers. comm., 24 March 2022).

In tracheophytes, Body *et al*. (2019) found that the yellow fluorescent protein that causes yellow fluorescence was produced in response to **jasmonic acid**, a compound produced in response to herbivory. But we thus far have no evidence that this, or any other fluorescence in bryophytes, is a response to herbivory.

But it is always fun to speculate. It is the start of hypotheses that can be tested. Tom Ottley (pers. comm. 5 May 2022) speculated about the potential role in dispersal of gemmae. Musing that the bryophytes could just make blue pigments instead, he realized that bryophytes are not known to make blue pigments. He suggested that perhaps the compound responsible is able to convert UV light to blue. On the other hand, insects are able to see reflected UV light itself (Turpin 2012). This might be a way of making gemmae and other propagules visible amid the maze of non-emitting leaves, just as it helped Gisela Nordhorn-Richter to locate them for her taxonomic studies. For leafy liverworts, the gemmae are more easily

discernable because of their locations at leaf margins. So far, I have found no information to indicate widespread presence of fluorescence in leafy liverwort gemmae. Perhaps the leaf fluorescence helps the insects to find the plants themselves, with contact with gemmae being almost inevitable.

Lloyd (1924) suggested that the taxonomist could use fluorescent color differences to identify **Cyanobacteria**, especially between closely related species. This seems to be possible with some bryophytes, often being a presence-absence difference. But we need many more UV views of bryophytes to really understand the color variation and its potential use in identification.

Perhaps a more important question needs to be answered. Which of these fluorescent colors can other organisms see? Are the colors we see with UV light under the microscope visible to organisms in nature?

For example, in cross section, a species of ***Leucobryum*** (Figure 179) demonstrated cell wall fluorescence. On the other hand, when viewed in the field with a UV light source, ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) exhibited no fluorescence.

Figure 179. ***Leucobryum glaucum*** leaf cs showing fluorescence of the cell walls. Photo by Magdalena Turzańska.

As I saw the color of fluorescence in more and more species of bryophytes, I was inclined to think that these are indeed spandrels. The compounds that produce them are often secondary compounds that serve in functions of structure, antiherbivory, and antibiotics. The fact that they fluoresce is likely just a product of the class of compounds that have these functions. At the same time, there is no evolutionary rule that a compound cannot have more than one adaptive quality. It would be interesting to see if the various colors have any correlation with habitat conditions and if they are inducible or always present.

Methodology

For most of our purposes, the field equipment can be simple and relatively inexpensive. Andi Cairns and colleagues used an LED white light head torch (ASD $3.00) and a small UV torch (ASD $14.99, no name, made in China). For their photography they used a combination of the two lights to obtain both fluorescence of one species while showing lack of fluorescence in the other species present. The photos were taken with an iPhone.

For microscopic work, Magdalena Turzańska uses UV light and an Olympus BX50 fluorescence microscope with an Olympus DP 71 camera.

Staining bryophytes can help to make fluorescence visible in some weakly fluorescing structures. Magdalena Turzańska uses berberine (extracted from *Chelidonium majus* roots) for cell wall staining. These are shown below in ***Diplophyllum albicans*** (Figure 180) and ***Nowellia curvifolia*** (Figure 181). Other stains can be used for special purposes.

Bryophytes have been used to develop methods for detecting fluorescent compounds present in small quantities (Delépée & Pouliquen 2002; Zhao *et al*. 2007). Delépée and Pouliquen (2002) used ***Fontinalis antipyretica*** (Figure 65, Figure 70-Figure 71) to develop a method for detecting oxolinic acid. Cerovic *et al*. (1999) reviewed the potential of using fluorescence signals for remote sensing of vegetation. Can this application be used for bryophytes?

Figure 180. ***Diplophyllum albicans*** female shoot showing fluorescence of the dye berberine in the leaf and perianth cell walls. This is not natural fluorescence. The fluorescence is too weak to be visible without the dye. Photo by Magdalena Turzańska.

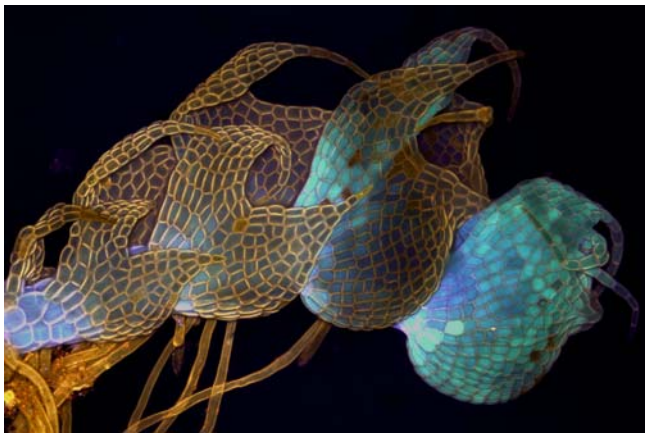

Figure 181. ***Nowellia curvifolia*** showing golden cell wall fluorescence in the leaves after staining with berberine. Photo by Magdalena Turzańska.

Prospects

It appears that fluorescence in bryophytes is a field wide open for study. So many evolutionary questions remain unanswered. How widespread is it among bryophytes? Are the compounds involved the same as those in tracheophytes? Which structures fluoresce? Does this location differ among species or habitats? Which compounds predominate in the bryophytes, and are there phylogenetic patterns to their presence? Can the colors of fluorescence be used to help in identification? Can it help us find some of the tiny species growing among larger species? Does the fluorescence attract arthropods, especially would-be dispersal agents? If so, to what degree does it improve dispersal chances? Does the phenomenon have any adaptive value in particular habitats? Does the fluorescence change with seasons? with temperature? [we know that chlorophyll fluorescence can change with temperature (Deltoro *et al*. 1999)], with drying? Is fluorescence lost over time in herbarium specimens?

Pigments

As in the algae, one can use the chlorophyll-to-phaeophytin ratio to assess physiological stress in bryophytes (Lopez *et al*. 1997). This ratio proved to be a better indicator of environmental stress than presence-absence data for species in 188 stretches of river in northwest Spain. Organic pollution was indicated most strongly, with *p*H also strongly correlated.

As discussed in other chapters, pigments can respond to changes in light intensity. Dark-colored wall or cytoplasmic pigments are present in genera like ***Frullania*** (Figure 123) that are able live high in the canopy or at high elevations (Li *et al*. 1989; Glime *et al*. 1990). Aquatic bryophytes that grow in cold water and full sunlight likewise may produce red cytoplasmic pigments, as seen in ***Fontinalis*** (Figure 182).

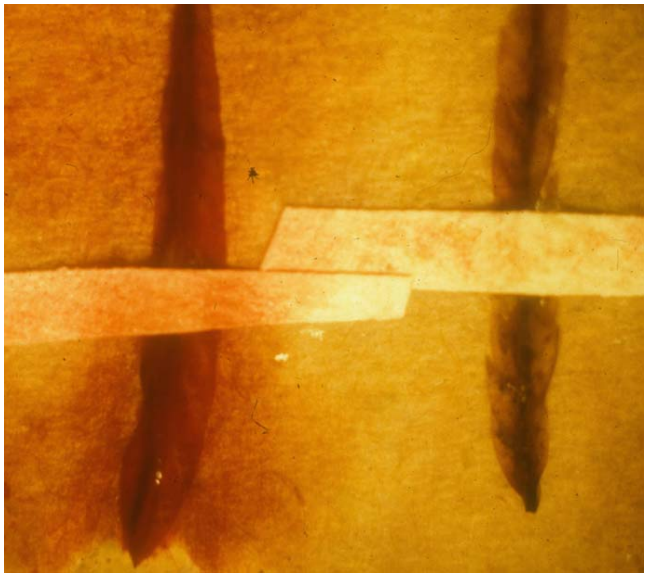

Figure 182. ***Fontinalis antipyretica*** producing red cytoplasmic pigments under water stress in high light. Photo by Janice Glime.

One can only speculate about the advantages of color. Red pigments can be a bit of an enigma. They can respond to both high light and low light. In bright light they are protectors, being positioned between the light source and chlorophyll, often in cell walls where they can protect the entire cell. In low light they seem to work best on the lower surface, or the side away from the light source.

In tropical forests some of the flowering plants have purplish-red coloration on the undersides of leaves. Botanists have considered this to be an adaptation to the low light there. Red algae live in the ocean depths and absorb green light using red pigments (Ritz *et al*. 2000), with most of the red light absorbed by the water itself. These deep water algae are able to activate the red pigments and transfer the energy to the chlorophyll antenna system (photosynthetic light-harvesting antennae) where it activates the chlorophyll electrons (Bag 2021). The chlorophyll antenna system works in bryophytes as well. In bryophytes, thee most frequent of the antenna pigments are α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al*. 1972). See Chapter 11-1 of this volume for a more thorough discussion of the role of antenna pigments in bryophytes.

Deep forest plants such as bryophytes are able to absorb the green light that filters through the canopy (Neill & Gould 2000; Ruberti *et al*. 2012) and reflect it, presumably to the chlorophyll. In the red alga *Rhodella violacea*, the genes for the production of the red and blue-green pigments phycoerythrin and phycocyanin, respectively, are down-regulated in bright light (Ritz *et al*. 2000). Since chlorophyll is most active in the red end of the spectrum (Wang & Folta 2013), such red reflectance could offer a light enhancement under a green canopy. In ***Arabidopsis thaliana***, when both green and blue light are present, the anthocyanin (red) level is lower than when only blue light is present (Bouly *et al*. 2007; Zhang & Folta 2012) and the degree of reduction of the anthocyanin depends on the rate at which the green light is delivered with the blue light (Zhang & Folta 2012). Melati *et al*. (2019) demonstrated that shaded plants of the Luja plant (*Peristhrophe bivalvis*) has a higher red pigment concentration in shade plants than in full light intensity.

More relevant to the purplish liverwort scales is the red coloration on the undersurfaces of rainforest extreme shade plants. Increased anthocyanin coloration on tracheophyte leaf undersurfaces correlates with the increased absorption of light at the upper (violet) end of the photosynthetic action spectrum (Lee & Graham 1986). Whereas increased red pigments can be a stress response to shade plants exposed to high light intensity, it appears that red pigments on the lower surfaces of photosynthetic organs might have a different function in light capture.

Since anthocyanin is often the pigment responsible for a purplish color, it is possible this mechanism is at work in the liverworts as well, reflecting the limited light that manages to penetrate that far and thus increase that which activates the chlorophyll. It is not an antenna pigment because it is not near the chlorophyll. Such a potential advantage has not, to my knowledge, been explored in the liverworts.

Coloration can also be used as a diagnostic tool. In tracheophytes, pigment variations are indicators for several nutrient deficiencies, toxicities, or antagonisms (Martínez-Abaigar & Núñez-Olivera 1998). Little has been done with color as a nutrient status indicator in bryophytes.

We know that the flavonoid pathway is a specialized metabolic pathway in plants (Davies *et al*. 2020). In flowering plants, flavonoids signal pollinators and dispersal organisms, but they also assist in tolerance to abiotic stresses. We have presumed that this pathway arose during the colonization of land, suggesting that it may have arisen in bryophytes as a defense against UV and drought. It is, nevertheless, absent in hornworts. The bryophyte pathway and its regulation are similar in some ways and differ in others when compared to that seen in flowering plants. One proposal is that flavonoids helped early land plants cope with increased exposure to UVB. But they also helped overcome the dangers imposed by desiccation and extreme temperatures (Markham 1988; Jorgensen 1994; Kenrick & Crane 1997; Cockell & Knowland 1999; Rozema *et al*. 2002; Ligrone *et al*. 2012; Mouradov & Spangenberg 2014; Demarsy *et al*. 2017; Davies *et al*. 2018; de Vries & Archibald 2018; Rensing 2018). Alternatively, Stafford (1991) proposed that these compounds regulated auxin action as well as signalling to mycorrhizal and symbiotic fungi, *i.e.*, serving in communication between complementary organisms. Stafford argued against the UVB-screening role because early concentrations would probably have been low, thus limiting their efficiency at a time when UV-B was particularly high.

I have long been confounded by the one-purpose approach of so many biologists, especially ecologists. It seems to me that these compounds could very well have been as Stafford proposed, serving to signal both auxins and fungi, but at the same time contributing to protection from UV-B. As time proceeded, those individuals that produced more flavonoids would have greater survival rates in the face of extreme temperatures, drought, and UV-B, permitting them to occupy habitats not available to those individuals that produced lesser concentrations of flavonoids. Most likely starting as primitive anthocyanins in the liverworts, the flavonoids have kept adding roles and become more effective at them (Berland *et al*. 2019).

Jumping to the 21st Century, researchers have discovered **auronidins** in ***Marchantia polymorpha*** (Berland *et al*. 2019). But Berland and coworkers discovered that the red pigments in the liverwort ***Marchantia*** (Figure 102, Figure 110, Figure 183-Figure 184) are not anthocyanins, but rather are phenylpropanoids that they have named **auronidins**, a previously unknown and distinct flavonoid class. Liverworts produce red cell-wall-bound pigments called **riccionidins** (now known to be auronidins) as a response to stresses, including UV-B, drought, and nutrient deficiency. Berland and coworkers suggest that these may have been the first anthocyanidins formed in the early land plants and distinct from the anthocyanins. They provide red coloration similar to that of anthocyanins, but they also have a strong fluorescence. Their antioxidant properties could be important in several pathways, but they seem to restricted to cell walls.

This suggests that we should look at fluorescence in our consideration of early evolutionary relationships among bryophytes. Martínez-Abaigar and Núñez-Olivera (2022) have reviewed UV effects on bryophytes, noting that these effects depend on species and evolutionary lineage. Mosses are more UV-tolerant than are liverworts. It should be enlightening to discover where fluorescence exists and how it relates to current habitats and that of the ancestors.

The discovery of auronidins raises so many questions for me. What organs have them? What are the adaptive values, if any, in these organs? Can they tell us an evolutionary story? How do they relate to habitats? Does their fluorescence give the plants any advantage, or is it simply a consequence of having the compound be useful for other characteristics? Are the colors seasonal?

Figure 183. ***Marchantia polymorpha*** with gemmae, showing distribution of red pigmentation, presumably auronidins. Photo by Dick Haaksma, with permission.

Figure 184. ***Marchantia polymorpha*** with red archegoniophores, but green thalli, Laxarbakki, Myvatn, Iceland, 26 July 1987. These red pigments are most likely auronidins. Photo by Janice Glime.

Yet another advantage of the auronidins is their ability to enhance resistance to the fungus ***Phytophthora palmivora*** (Carella *et al*. 2019). Hyphae are unable to penetrate in highly pigmented regions of these plants.

Leaf Canopy

It is well known that chlorophyll concentration increases in response to reduced light availability (Niinemets & Tobias 2014). But within the bryophyte canopy, older tissues are lower on the plant and thus receive less light. In this case, the chlorophyll

concentration decreases with not only age, but also with decreasing light availability (Davey & Ellis-Evans 1996; Niinemets & Tobias 2014). Furthermore, in lower light, the plants are less dense and the leaves are usually farther apart, decreasing the density (Niinemets & Tobias 2014). This reduction in density increases the light interception per leaf area. Pleurocarpous mosses are able to acclimate structurally to light levels by adjusting the density of leaves and branches, whereas non-branching acrocarpous mosses lack the ability to change branching density. In addition, mosses under low water conditions have a greater degree of aggregation, thus further reducing light penetration. But as mosses desiccate they have greater light penetration further down the stem than the same mosses when hydrated, increasing productivity in older parts (Davey & Ellis-Evans 1996).

Absorption is not equal throughout the spectrum. Davey and Ellis-Evans (1996) observed that the greatest attenuation occurred at wavelengths corresponding to the peaks of chlorophyll absorption (675 nm and below 450 nm). Other factors that affect absorption include stem orientation, stem density, leaf size and orientation, and pigment content.

Leaf Angle

Angle of incidence (Figure 185) is the angle formed between the direction of light and the vertical (difference from straight on), so a low sun has a higher angle of incidence. **Leaf angle** (Figure 186) is the angle made by the axil of the leaf and the axis. It affects the reflectance of light in plants. Therefore, a small leaf angle (approaching vertical) creates the effect of a large angle of incidence.

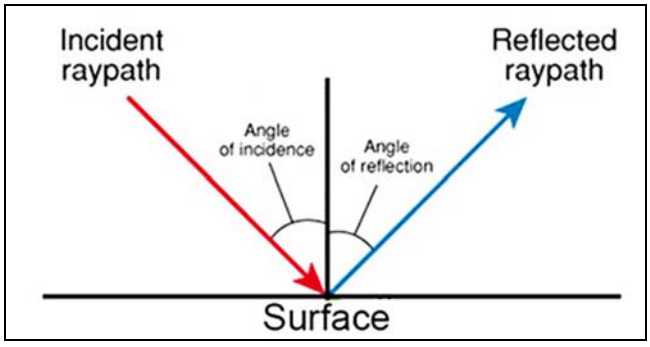

Figure 185. Angle of incidence and reflection pathway. Drawing modified from Clive Dexter at <http://ezbackgrounds.com/blog/ezlighting-guide-angle-incidence.php>.

Howard (1967) demonstrated that leaf angles in four tracheophyte species of 0-30° (=90-60° angle of incidence) made little difference in reflectance, but when the angle of incidence was smaller, the reflectance increased rapidly, consequently rapidly reducing photosynthesis. In the tree leaves of *Eucalyptus regnans*, photosynthesis begins to decrease at ~72° leaf angle, and at 45°, photosynthesis drops to 70% of values of horizontal leaves. At 5° leaf angles it approaches 0% (Kriedmann *et al*. 1964).

In bryophytes, many moss species raise their leaves and wrap them around the stem as they dry, effectively providing greater protection to the chlorophyll by greater overlapping of leaves. In the desert moss ***Syntrichia caninervis*** (Figure 187), leaf angle changes (Figure 188) are an important means of protecting against the effects of high light intensity during long periods of desiccation (Wu *et al*. 2014). First, the leaf movement helps to slow drying, permitting the plant to adjust physiologically in preparation for desiccation (see Chapters 7-5 and 7-6 in Water Relations). Second, the acute leaf angle of only 30° of a dry plant protect the photosynthetic cells. And third, when the leaf rehydrates, it returns in 7 seconds to an angle of 69-84°, with the first leaves reaching normal position in only 1 second. The hyaline cells at the leaf base are thin-walled and facilitate rapid uptake of water, swell, and push the leaf away from the stem. The leaf hair also play a role in reflecting light and reducing its impact on the chlorophyll. But the leaf hairs (**awns**) play another role that thus far has not been explained. They somehow are important in adjusting the leaf angle. When these awns are removed, the angle adjustment is retarded.

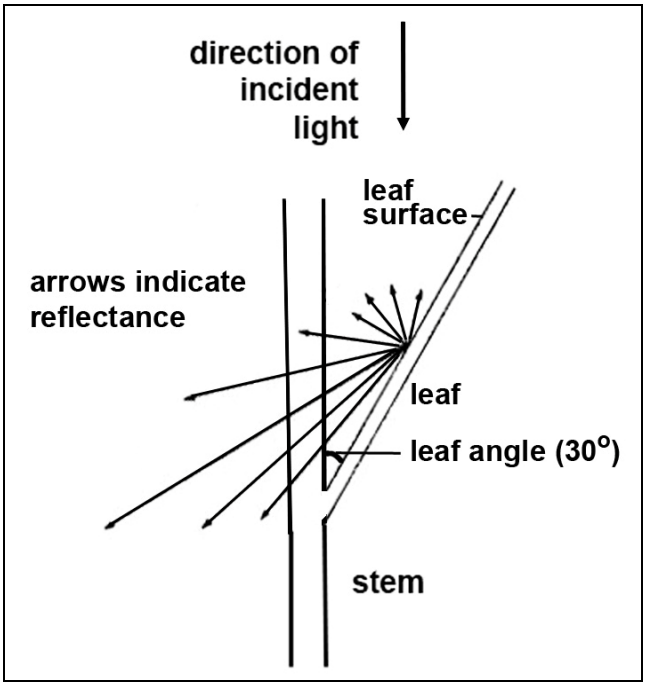

Figure 186. Incidence light and reflectance on a leaf at an acute angle. In this case, the incident light strikes the leaf at an angle of 60° from the straight up light that would strike the leaf from a perpendicular direction. Redrawn from Howard 1967.

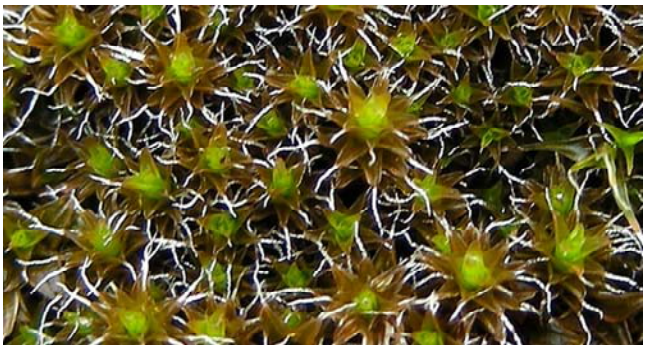

Figure 187. ***Syntrichia caninervis***, a species that changes leaf angles in response to drying. Photo by Michael Lüth, with permission.

Figure 188. ***Syntrichia caninervis*** dry exhibiting twisted leaves with a small leaf angle. Photo by Sheri Hagwood, through public domain.

Xerophytic mosses like ***Syntrichia ruralis*** (Figure 53) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).

Summary

Protonemata of some mosses, such as ***Schistostega pennata***, are able to position their chloroplasts to receive maximum available light and the lens-shaped cells help to focus the light. Their high reflectance provides a luminescence in caves. Similar reflective abilities are present in ***Mittenia plumula*** that lives in wombat holes. ***Cyathodium*** species that live in caves have a similar reflective ability in their thalli.

Some bryophytes are able to live in the dim light surrounding light bulbs in visitor caves, exceeded in their low-light survival only by the algae. Many of the cave bryophytes are also typical of other habitats of greater light intensity, including high-light tolerators like ***Ceratodon purpureus*** and ***Pohlia nutans***. Some are the **tufa formers** that often are so encrusted with limestone that only their tips are able to get sufficient light for photosynthesis. ***Amblystegium serpens*** seems able to live in the lowest light at only 232 lux.

One response to bryophytes in deep caves is **etiolation**, which spaces leaves further apart, thus exposing more surface area to the little light available. In some species, the number of chloroplasts and size of grana can increase and growth can occur even in the dark. Long, thin "exploratory" branches may form. In ***Atrichum undulatum*** the starch disappeared in winter but reappeared in spring, in the dark! When placed in the light, photosynthesis began without delay.

Various plant parts may exhibit fluorescence. So far this ability is known from leaf cell walls, stems, spores, antheridia, archegonia, paraphyses, capsules, peristomes, elaters, gemmae, and bulbils, in addition to the chlorophyll fluorescence known from all photosynthetic organisms. Fluorescence under the microscope has been exhibited in many bryophyte species, but few seem to have been documented in the field. Fluorescence may be caused by a number of compounds, including flavonoids, fatty acids, and lignin-like compounds. Its colors vary widely, but are not visible to the human eye when bright sunlight is present. Nevertheless, many kinds of insects are able to see these colors even in daylight. Its role remains unknown, and it may simply be a property of the cell wall components and antibiotic compounds, but its value in attracting dispersal agents should be explored.

Some mosses develop pigments in response to increased light intensity, although chlorophyll concentrations usually decrease. Others change the leaf angles, decreasing the damage to chlorophyll. Antenna pigments help to transfer light energy to the chlorophyll in low light and pigments on the lower surface may help by reflecting red light back to the chlorophyll.

The light intensity diminishes as it penetrates the bryophyte canopy, but when the leaves dry, more light may reach older portions.

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