

CHAPTER 9-1

LIGHT: THE SHADE PLANTS



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

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.

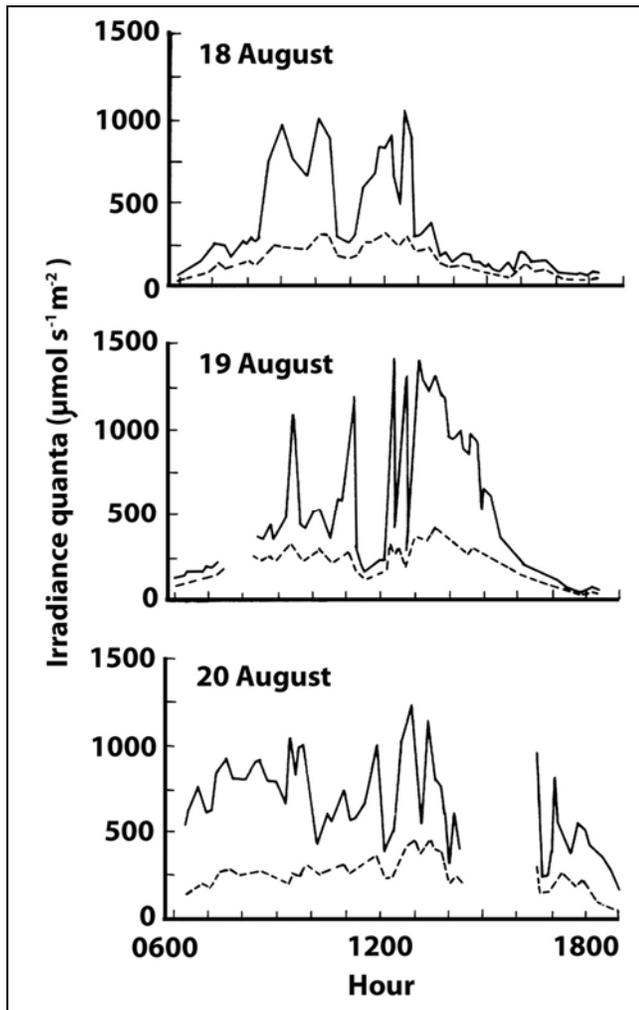


Figure 2. Irradiance at the moss surface - - - and total solar irradiance — in PAR units for three consecutive days in central Alaska in a black spruce forest. Figure redrawn from Skré *et al.* 1983.

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.

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 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 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 $\sim 640 \text{ W m}^{-2}$. 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 $\sim 1 \text{ kW m}^{-2}$, with PAR intensities of $\sim 400 \text{ W m}^{-2}$. Full sunlight ranges $\sim 70,000$ - $100,000$ 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 $1800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ 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 3) occurring in cell walls, cytoplasm, and plastids. Furthermore, cell shape can bend and focus or scatter light, depending on cell wall structure. 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.

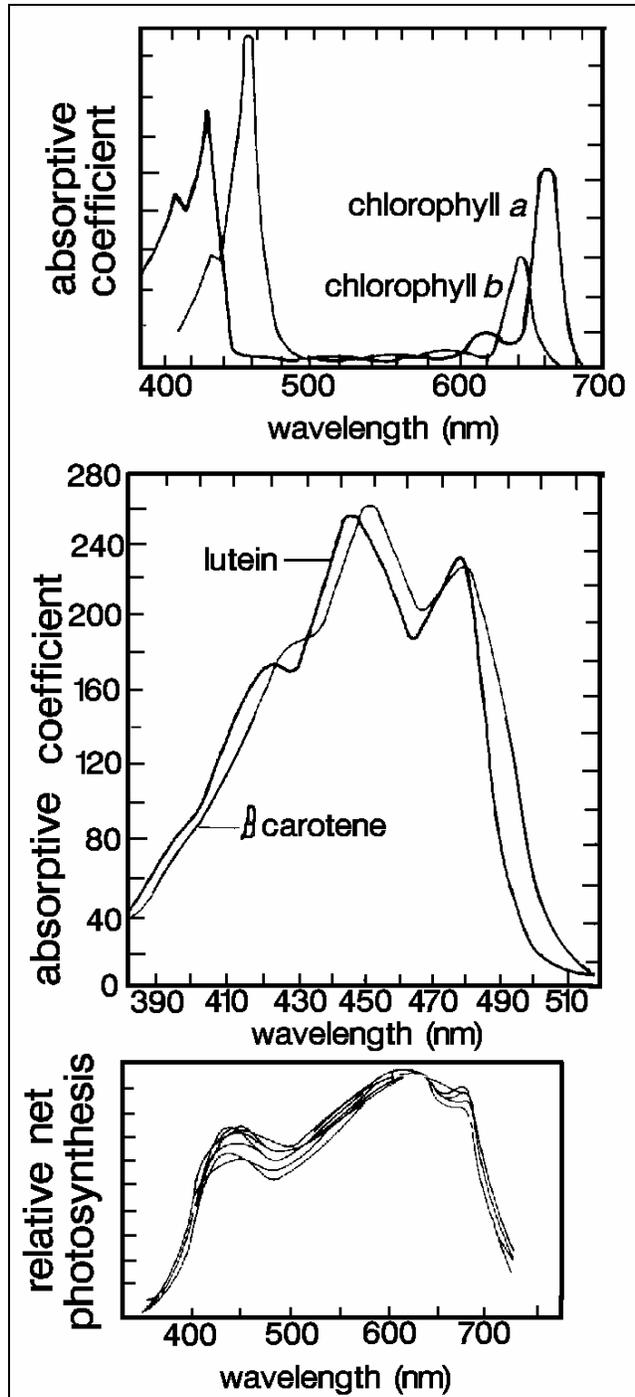


Figure 3. Top: Absorption spectra of chlorophylls *a* and *b*, dissolved in diethyl ether. Middle: Absorbance spectra of lutein and β carotene in ethanol. Bottom: Action spectra of 22 species of crop plants. From Salisbury & Ross (1978).

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

To convert from: Multiply by factor in column to obtain $\mu\text{M m}^{-2} \text{s}^{-1}$	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 4. Only thallose liverworts like *Marchantia* have an arrangement somewhat similar to spongy mesophyll (Figure 5), and a few mosses like the Polytrichaceae have a folded-over leaf margin surrounding leaf lamellae (Figure 6, 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 4. **Upper:** Leaves of *Mylia anomala*. **Lower:** Cells showing chloroplasts in one-cell-thick leaf of the leafy liverwort *Mylia anomala*. Photo by Michael Lüth.

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* 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 5. 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 with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

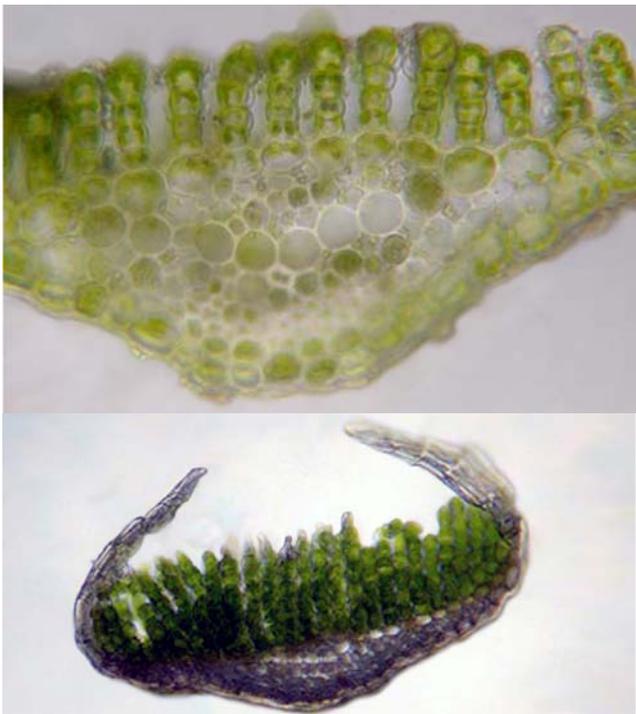


Figure 6. **Upper:** Leaf lamellae of *Pogonatum contortum*, typical of those found in all members of the Polytrichaceae. **Lower:** Leaf lamellae with leaf lamina rolled over them in *Polytrichum piliferum*. Photos with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

Marschall and Proctor (2004) found that the **PPFD** (photosynthetic photon flux density) at 95% saturation had a median of $583 \mu\text{mol m}^{-2} \text{s}^{-1}$ for mosses and $214 \mu\text{mol m}^{-2} \text{s}^{-1}$ for liverworts, again suggesting that liverworts are adapted to a lower light regime. Not surprisingly, two *Polytrichum* species had the highest values. Their system of lamellae (Figure 6) 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 7) the internal air chambers do little to facilitate photosynthesis compared to *Monoclea forsteri* (Figure 8) 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.

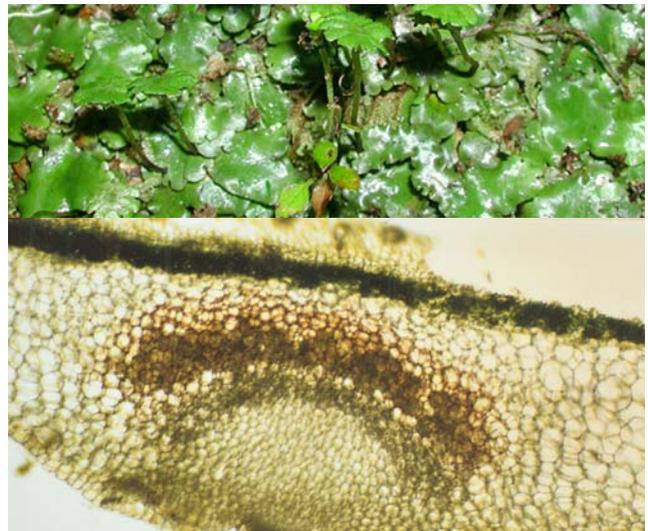


Figure 7. **Upper:** *Marchantia foliacea* thallus. **Lower:** Cross section of thallus of *Marchantia foliacea* showing the nearly solid nature of the thallus. Air chambers occur within the green layer near the upper surface. The brown layer is a layer of arbuscular mycorrhizal fungi. Photos by Julia Russell.



Figure 8. Thallus of *Monoclea forsteri*. Photo by Jan-Peter Frahm.

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 9.

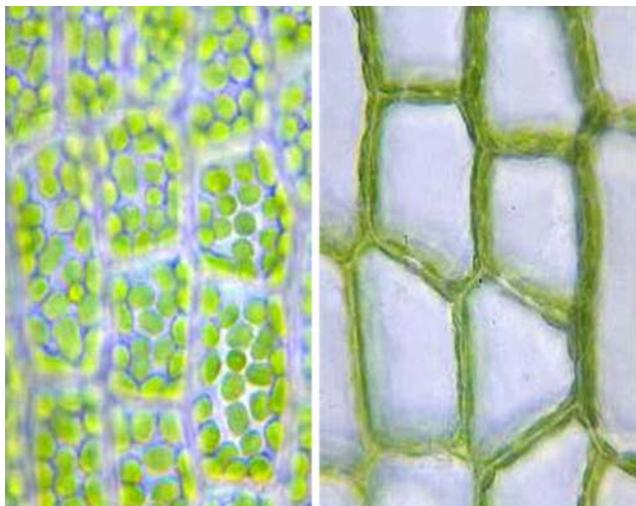


Figure 9. *Funaria hygrometrica* cells from dim light (left) and strong light (right). Photos by Winfried Kasprk.

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.

Compensation points suggest that there is indeed adaptation within the bryophytes to both low and high light levels (Table 4). For example, in Antarctic lakes, *Drepanocladus (sensu lato)* has a light compensation point similar to that of algal communities (0.11 W m⁻², \approx 0.5 μ M m⁻² s⁻¹), whereas *Calliergon*, which occurs in shallower water, has a compensation point of 0.64 W m⁻², \approx 2.9 μ M m⁻² s⁻¹ (Priddle 1980). *Fissidens serrulatus* (Figure 11) could maintain a positive net photosynthesis down to 7 μ mol 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 12), typical of conifer forests, required 30 μ M m⁻² s⁻¹ to reach its compensation point at natural concentrations of CO₂ 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
<i>Fontinalis</i>	5°C	15		Burr 1941
	20°C	40		
<i>Atrichum undulatum</i>	spring	3000		Baló 1987
	summer	1000	5000	
<i>Polytrichum formosum</i>	spring	4000	10,000	Baló 1987
	summer	1000	25,000	
<i>Plagiommium affine</i>	spring	4000	15,000	Baló 1987
	summer	1000	25,000	
<i>Chiloscyphus rivularis</i>		1750		Farmer <i>et al.</i> 1988
	Condition	Comp μ M m ⁻² s ⁻¹	Sat μ M m ⁻² s ⁻¹	Reference
<i>Pellia borealis</i>		4.6	81	Szewczyk 1978
<i>Fissidens serrulatus</i>	21°C	7	24	Gabriel & Bates 2003
<i>Andoa berthelotiana</i>	21°C	8	20	Gabriel & Bates 2003
<i>Echinodium prolixum</i>	21°C	9	27	Gabriel & Bates 2003
<i>Bazzania azorica</i>	21°C	9	29	Gabriel & Bates 2003
<i>Plagiommium</i> spp.	25°C	10	400	Liu <i>et al.</i> 1999
<i>Frullania tamarsci</i>	21°C	10	36	Gabriel & Bates 2003
<i>Lepidozia cupressina</i>	21°C	12	30	Gabriel & Bates 2003
<i>Myurium hochstetteri</i>	21°C	31	68	Gabriel & Bates 2003
<i>Pilotrichella ampullacea</i>	tropics		100	Proctor 2002
<i>Floribundaria floribunda</i>	tropics		100	Proctor 2002
<i>Hylocomium splendens</i>	summer	30	100	Sonesson <i>et al.</i> 1992
<i>Brachythecium rutabulum</i>	8 May	65	200	Kershaw & Webber 1986
	6 July	4	30	



Figure 10. Thalli and archegoniophores of *Marchantia palacea* var. *diptera* from Japan. Photo by Janice Glime.

A low compensation point and a low light saturation value are typical for C₃ plants, and thus for bryophytes (Table 2). The low light compensation point in tracheophytes is in part due to the ability of C₃ plants to open their stomata quickly to take advantage of CO₂ exchange whenever sufficient light is available. However, lacking stomata, bryophytes are not limited by stomatal opening speed, so response time to take in CO₂ should not impose the same kinds of limits it does in tracheophytes. On the other hand, higher levels of CO₂ 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 CO₂ 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 CO₂ concentration is higher, as already seen for *Hylocomium splendens* (100 μmol m⁻² s⁻¹ at a CO₂ concentration of 400-450 mg L⁻¹) (Sonesson *et al.* 1992). This is a relatively high level of CO₂ (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 CO₂-enriched environment will permit the plants to take advantage of bursts of light (**sunflecks**) 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 11. Gametophyte with sporophyte of *Fissidens serrulatus*. Photo by Michael Lüth.



Figure 12. Side view of the feather moss *Hylocomium splendens*. Photo with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

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*, which was saturated at 68 μmol m⁻² s⁻¹.

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

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

*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.

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 CO₂ are available.

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