CHAPTER 9-3

LIGHT: EFFECTS OF HIGH INTENSITY

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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.
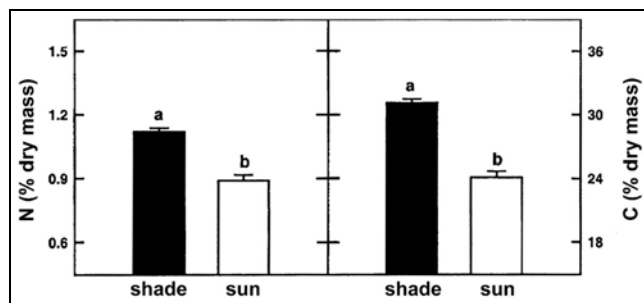

Figure 3. Comparison of N and C content of *Syntrichia ruralis* grown in shade and sun in Kiskunság National Park near Budapest, Hungary. Vertical bars indicate 1 SE; letters indicate significant differences ($p<0.05$). Redrawn from Hamerlynck *et al*. 2002.

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.
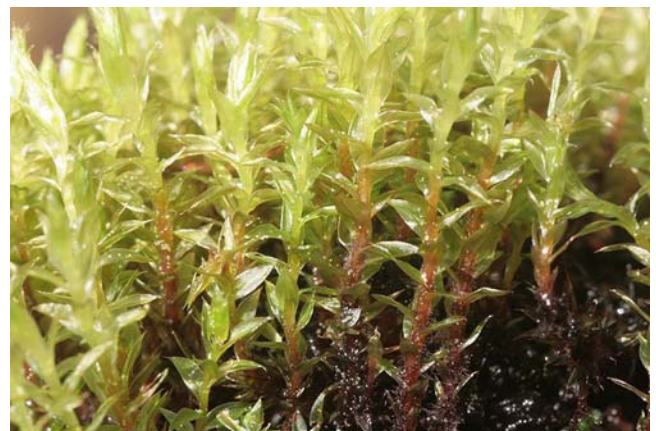

Figure 5. *Bryum pseudotriquetrum*, a species limited by moisture. Photo by Hermann Schachner, through Creative Commons.

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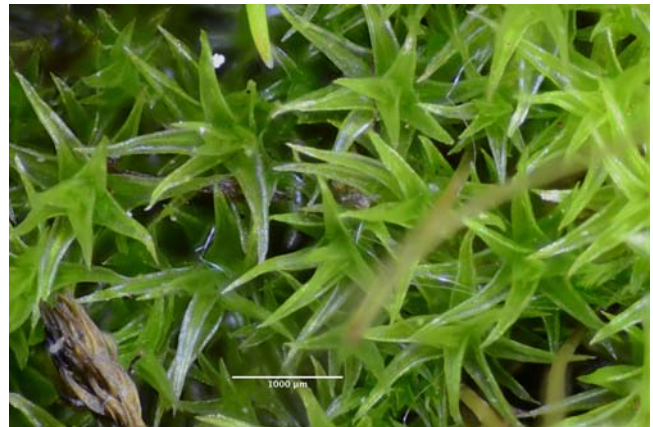
Figure 9. *Ceratodon purpureus* leaves, a species tolerant of high light. Photo by Don Loarie, through Creative Commons.

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

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

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

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

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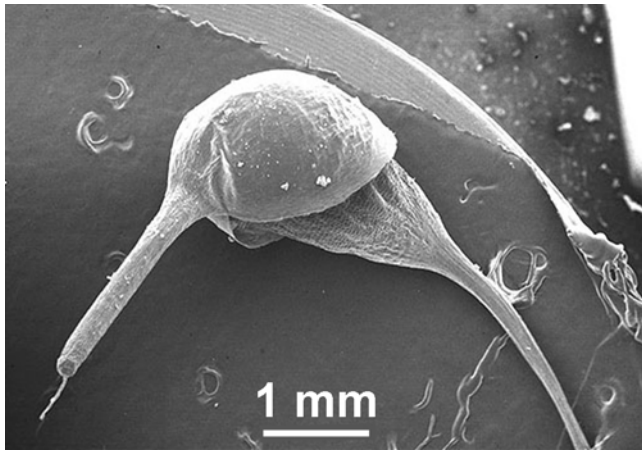
Figure 35. *Funaria hygrometrica* capsule SEM showing calyptra that is split on one side, possibly influencing the curved shape of the capsule. The upper side of the capsule is covered as it completes development. Photo from Botany Website, UBC, with permission

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.
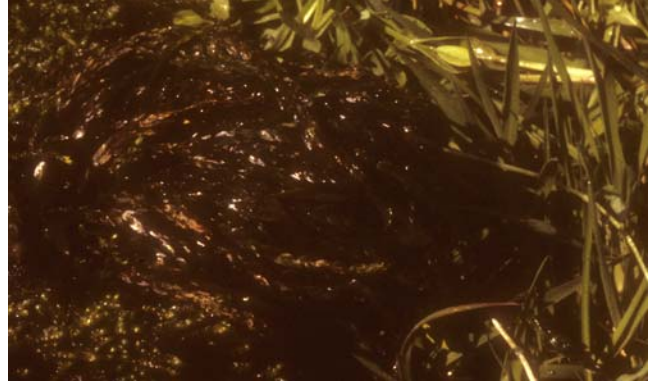

Figure 43. Red *Fontinalis antipyretica* in response to bright light of full sun in shallow, cold water emerging from an underground stream in Germany. Photo by Janice Glime.

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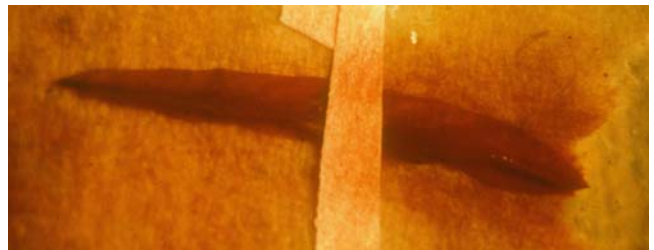

Figure 45. Red *Fontinalis antipyretica* in response to bright lights on stem kept out of water under fluorescent light in an experiment. Photo by Janice Glime.

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.
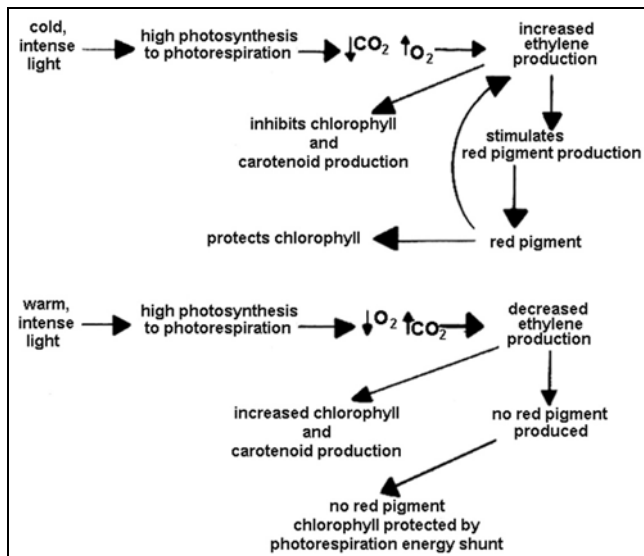

Figure 47. Proposed role of intense light in the production of ethylene and red pigment under cold and warm conditions.

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 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.

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 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.

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. Furthermore, the Fv/Fm, 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).
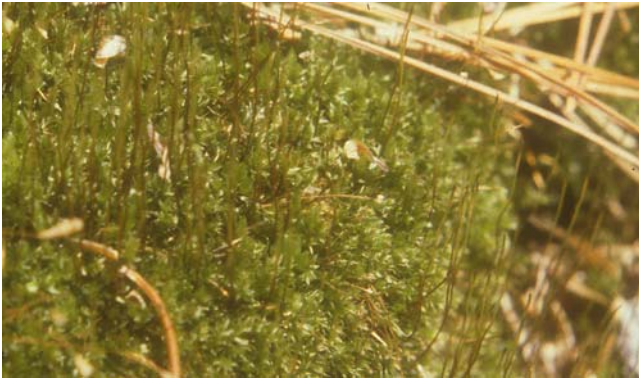
Figure 59. *Ceratodon purpureus* green form as it appears when the snow melts. Photo by Janice Glime.

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 Fv/Fm 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 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 72. *Sphagnum angustifolium*. Photo by Kristian Peters, through Creative Commons.

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.

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.

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.

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

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

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

Figure 81. ***Leucodon sciuroides*** wet, a desiccation-tolerant 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 88. *Cinclidotus aquaticus*, a species of wet habitats that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

Figure 86. *Barbula ehrenbergii*, a desiccation-intolerant moss. 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 87. *Barbula ehrenbergii*, a species that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

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.
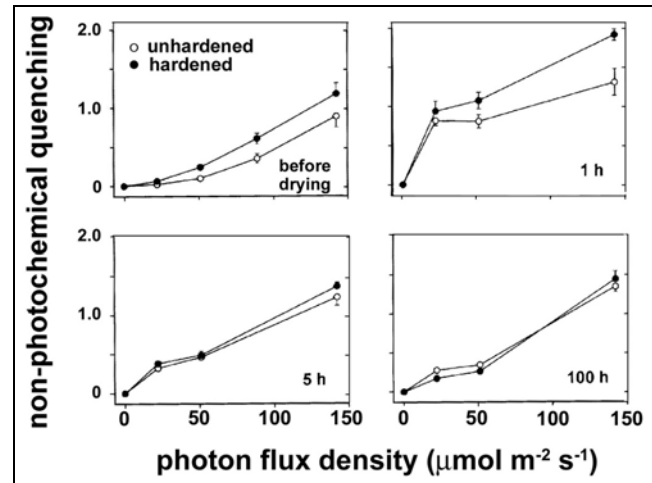

Figure 99.   The effect of hardening on the non-photochemical quenching upon rehydration of 1, 5, and 100 hours compared to quenching prior to desiccation in *Atrichum androgynum*. Redrawn from Beckett *et al*. 2005.

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).
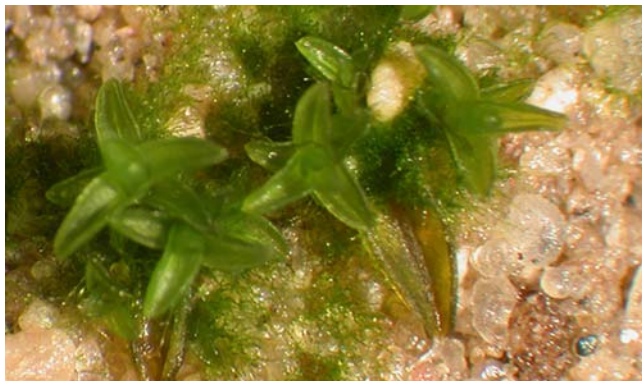

Figure 101. *Syntrichia inermis*, a moss capable of living under quartz pebbles in the desert. Photo courtesy of Lloyd Stark.

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."
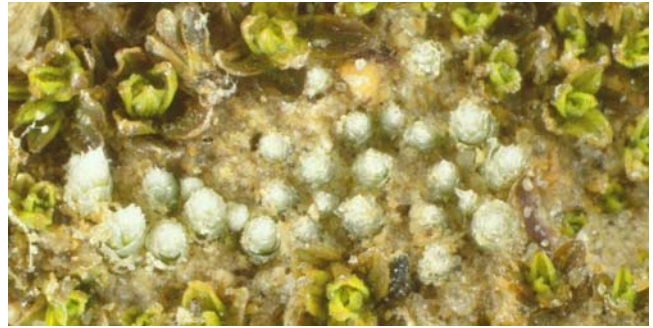

Figure 105. *Gigaspermum* sp, a genus that can occur under translucent quartz rocks in bright sun. Photo by Jan-Peter Frahm, with permission.

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.

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.

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