

# CHAPTER 9-3

## LIGHT: EFFECTS OF HIGH INTENSITY



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

### 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.

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 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 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.

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) 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* 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.

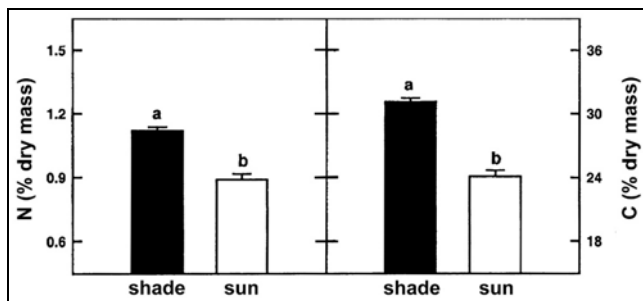


Figure 3. Comparison of N and C content of *Syntrichia ruralis* grown in shade and sun in Kiskunság National Park near Budapest, Hungary. Vertical bars indicate 1 SE; letters indicate significant differences ( $p < 0.05$ ). Redrawn from Hamerlynck *et al.* (2002).

Because high light intensities can damage chlorophyll, they can cause photoinhibition. Even sun plants like *Sphagnum* 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 ( $800 \mu\text{M m}^{-2} \text{s}^{-1}$ ) 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 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. Internally, high light can cause a decrease in thylakoid stacking (Post 1990).

Thus, 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* restricted its occurrence to deeply shaded conifer stands, whereas *Bryum pseudotriquetrum* was limited by its lack of desiccation tolerance. *Mielichhoferia macrocarpa*, 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

### Adaptations to High Light

When working with *Pohlia wahlenbergii* from a subalpine area, Coxson and Mackey (1990) were surprised to find that it had a peak of photosynthesis at  $8 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$  in the morning, declined to  $5 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$  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* (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.

### Structural Adaptations

Bryophytes often have filters that help to protect them from high light intensity. For example, the **lamellae** of several *Polytrichum* species are enclosed by the inrolled lamina of the leaf (Figure 6), thus rendering the leaf a structure that is not very different from that of a deciduous tree. Others have leaves with **filaments** (*Crossidium*), **hyaline tips** (*Hedwigia ciliata*, *Bryum argenteum* – Figure 4), and **awns** (*Tortula*; *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, are spread out of the way of the photosynthetic tissue upon hydration. Frey and Kürschner (1991) have demonstrated a correlation between "glass hairs" and increasing aridity, suggesting that they could be useful as UV shields as aridity, and correlated light exposure, increase. Many taxa curl their leaves, wrap their leaves around the stem, or appress leaves 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. Short turfs likewise help to protect mosses from high light intensity through self-shading (Schofield 1985).

Epiphytes like *Octoblepharum* and *Leucobryum* have numerous hyaline cells (Figure 5) 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, contrarily, focus the light on the interior photosynthetic cells while serving as a

water reservoir to maintain photosynthesis in a dry atmosphere?

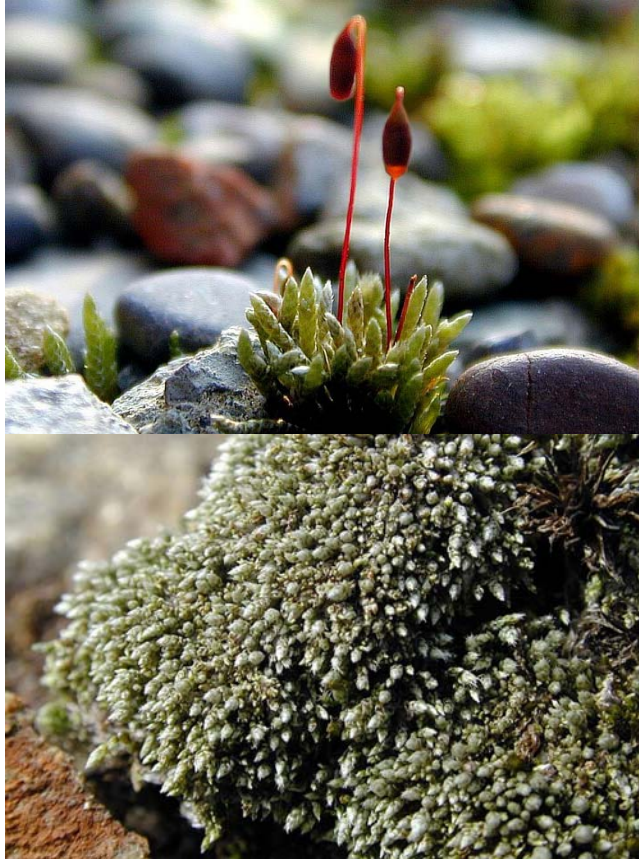


Figure 4. *Bryum argenteum*. **Upper** showing tight leaves that overlap and protect each other from light damage. **Lower** showing white tips of each leaf. Photos by Michael Lüth.



Figure 5. Cross sections of *Octoblepharum* leaves. **Upper:** *O. albidum*. **Lower:** *O. cylindricum*. Photos by Noris Salazar Allen.

For aquatic bryophytes, water depth affects light intensity. Martínez Abaigar *et al.* (1993) found that *Scapania undulata* had a Leaf Specific Area of  $317 \text{ cm}^2 \text{ g}^{-1} \text{ DW}$  at 5 cm depth, but at 45 cm depth, the LSA increased

to  $399 \text{ cm}^2 \text{ g}^{-1} \text{ DW}$ . Concomitantly, Leaf Specific Weight was reduced from  $3.16 \text{ mg cm}^{-2}$  to  $2.50 \text{ mg cm}^{-2}$ . 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 caused an increase in accessory pigments relative to chlorophyll *a*.



Figure 6. Leaf cross section of *Polytrichum juniperinum* showing leaf edge rolled over lamellae. Photo with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

### 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.

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. Ethylene is inhibited by  $\text{CO}_2$  and requires  $\text{O}_2$  for its formation. Red pigments are particularly common in mosses at low temperatures. In our experiments with *Fontinalis* (Glime & Rohwer 1983), a water-soluble red pigment (anthocyanin derivative?) was produced as a wall pigment in aborted apical buds and some of the older leaves under treatment with ACC, an ethylene precursor. In *Fontinalis antipyretica*, red leaves were present in a population growing in cold mountain water in full sun (Figure 7). A similar response is present in *Ceratodon purpureus* 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 11).

In intense light and cold there would be 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  $\text{O}_2/\text{CO}_2$  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 8). However, this assumes that the red pigment behaves like anthocyanin.



Figure 7. Red *Fontinalis antipyretica* in response to bright light. **Top:** Plants in full sun and cold water emerging from an underground stream in Germany. **Middle:** Stem kept out of water under fluorescent light in an experiment. **Bottom:** Cells of red plants. Photos by Janice Glime.

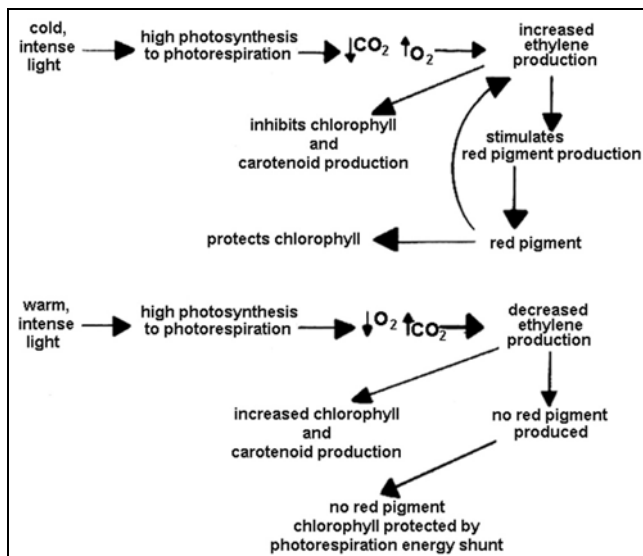


Figure 8. Proposed role of intense light in the production of ethylene and red pigment under cold and warm conditions.

Maseyk *et al.* (1999) actually compared New Zealand samples of *Sphagnum cristatum* (Figure 9) 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 9. Multi-colored capitula of *Sphagnum cristatum*. Photo by Janice Glime.

Gerdol (1996) found that *Sphagnum magellanicum* 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.

### Sphagnorubin

Likewise, concentration of **sphagnorubin**, a red wall pigment (Figure 10), was also highest in the open (Gerdol 1996). However, the sphagnorubin concentration was not correlated with chlorophyll concentration and growth rate.



Figure 10. Red *Sphagnum magellanicum* when nights are cold and days are bright in the autumn. Photo by Janice Glime.

**Sphagnorubin** is a flavonoid related to anthocyanin (Rudolph *et al.* 1977). Schmidt-Stohn (1977) found that in *Sphagnum magellanicum*, 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 light is intense, but not when both nights and

days are warm (18°C) (Rudolph *et al.* 1977; Gerdol *et al.* 1998).

### Chlorophyll Ratios

Whereas the brook moss *Fontinalis antipyretica* 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* populations, plants growing at 5 cm depth gained chlorophyll *a* in summer (from 3.43 to 3.69 mg g<sup>-1</sup> dw) but lost chlorophyll *b* (from 1.17 to 0.87 mg g<sup>-1</sup> dw), suggesting that they had a much higher light availability in summer (Mártinez Abaigar *et al.* 1993). At 45 cm depth, they lost chlorophyll *a* in summer (from 4.08 to 3.41 mg g<sup>-1</sup> dw) and likewise lost chlorophyll *b* (from 1.47 to 1.15 mg g<sup>-1</sup> 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.

Using 17 species of bryophytes from low light habitats 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  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

### UV Absorption

It appears that mosses and liverworts may differ 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 (MEUVAC), with the exception of *Polytrichum commune* (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.

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. In the Antarctic, the three mosses examined all had sustained high levels of xanthophyll pigments, especially at exposed sites (Lovelock & Robinson 2002). Among these is 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 11) had a higher carotenoid:chlorophyll ratio in high light intensities (0.55) than in low ones (0.35).



Figure 11. *Ceratodon purpureus*. **Upper:** Green form as it appears when the snow melts. **Bottom:** Golden form that has been subjected to high light intensity. Photos by Janice Glime.

On the other hand, in their study of aquatic bryophytes, Márquez 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.

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*; specifically, **zeaxanthin** strongly enhances **light quenching**, *i.e.* dissipation of light energy, in an atmosphere of 20% CO<sub>2</sub> (Bukhov *et al.* 2001a). This appears to be fundamentally different from mechanisms in tracheophytes, as represented by spinach and *Arabidopsis*, 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<sub>2</sub>! What can it do in the more normal 0.04% CO<sub>2</sub>? 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.

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.

The leafy liverwort genus *Frullania* possesses red coloration (Figure 12), grading into nearly black. 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, this genus grows more quickly in high light intensities than in the shade, attesting to its adaptations to high light intensity (Coley *et al.* 1993).



Figure 12. Red coloration of *Frullania tamarisci*. Photo by Michael Lüth.

## 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* 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* (Casper *et al.* 1993). This rise occurs during the dehydration process, and Casper *et al.* hypothesized that zeaxanthin-related protection is engaged in response to the dehydrating conditions, even in low light levels. Nevertheless, chlorophyll fluorescence is lost during drying of predarkened desiccation-tolerant mosses, suggesting that energy dissipation in the dry state is not related to protonation and high levels of zeaxanthin.

Deltoro *et al.* (1998a) found that *Hedwigia ciliata*, *Hypnum cupressiforme*, *Leucodon sciuroides*, *Orthotrichum cupulatum*, *Pleurochaete squarrosa*, *Porella platyphylla*, and *Syntrichia ruralis*, all desiccation-tolerant bryophytes, were able to resume photosynthesis rapidly

upon rehydration, whereas desiccation-intolerant bryophytes (*Barbula ehrenbergii*, *Cinclidotus aquaticus*, *Conocephalum conicum*, *Lunularia cruciata*, *Palustriella commutata*, *Philonotis calcarea*, and *Rhynchostegium riparioides*) from mesic and hydric habitats were unable to resume their photosynthetic activity. In examining the xanthophyll content of a desiccation-tolerant leafy liverwort, *Frullania dilatata* (Figure 13), 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*, and the latter species had less ability to dissipate the light while dry. Upon rehydration, *Frullania dilatata* resumed full photosynthetic capability rapidly, whereas *Pellia 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<sup>+</sup> from damaged membranes in *Pellia endiviifolia*.



Figure 13. *Frullania dilatata*, a desiccation-tolerant leafy liverwort. Photo by Michael Lüth.

Bartoskova *et al.* (1999) offer a somewhat different explanation for observed changes in chlorophyll fluorescence during drying. Working with leaves of *Rhizomnium punctatum*, 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.

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* 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.

Beckett *et al.* (2005) found that **hardening** (process of increasing resistance) of the moss *Atrichum androgynum* during drying permitted it to recover fully from dehydration, whereas lack of time for this preparation did not (Figure 14). That is to say, mosses 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.

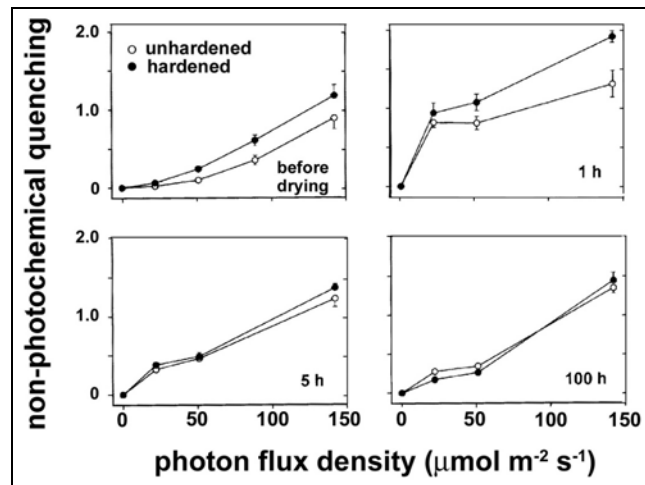


Figure 14. The effect of hardening on the non-photochemical quenching upon rehydration of 1, 5, and 100 hours compared to quenching prior to desiccation in *Atrichum androgynum*. Redrawn from Beckett *et al.* (2005).

Mosses, as in the tracheophyte resurrection plant *Selaginella lepidophylla*, 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* and *Syntrichia ruralis* (Figure 15) might accomplish the same thing. Might the smaller bryophytes that curl respond 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 and become more vertically oriented. Hamerlynck and coworkers (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.

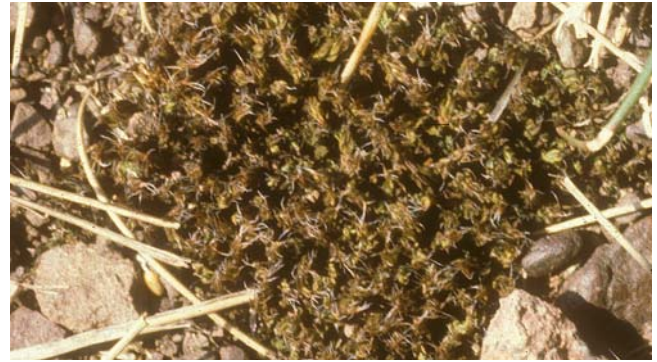


Figure 15. Dry *Syntrichia ruralis* exhibiting dark color and twisted leaves that protect it from high light intensity. Photo by Janice Glime.

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  $\sim 700$  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 in front of that rock. There are some mosses that take just such a refuge. Using the rock as a filter, *Syntrichia inermis* (Figure 16) survives the intense light (and dryness) of the Californian desert by living beneath a piece of translucent rock (Werger & During 1989).

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 can find the tiny *Henediella heimii* (Figure 17) beneath the rock (Fife 2005).

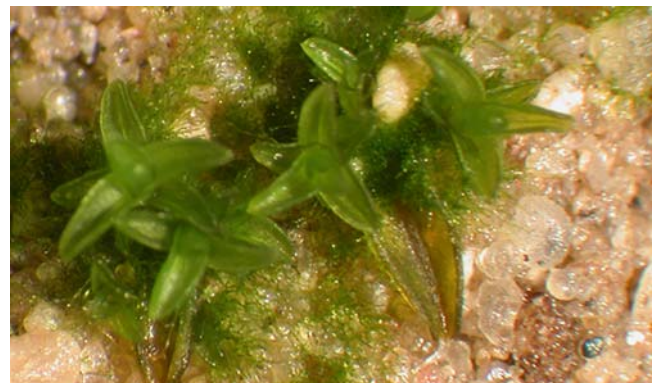


Figure 16. *Syntrichia inermis*, a moss capable of living under quartz pebbles in the desert. Photo by Lloyd Stark.



Figure 17. *Henediella heimii*, a moss that lives under quartz rocks in the Antarctic. Photo by Michael Lüth.

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  $\sim 7^{\circ}\text{C}$  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*, *Riccia* spp., *Henediella longipedunculata*, other small Pottiaceae, *Chamaebryum*, *Gigaspermum* 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. 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."

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* and *B. subrotundifolium* 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.

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 hidden under a fissure in the lava rock (Figure 18). 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* can grow in the more humid lava flows of Tenerife.



Figure 18. *Saelania glaucescens* exposed by our removal of several pieces of the broken volcanic rock above it. Photo by Janice Glime.

## 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.

## Acknowledgments

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