

CHAPTER 9-4

LIGHT: SEASONAL EFFECTS



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

Bryophyte View of Light

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

High Light and Low Temperatures

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

the major factor in limiting production of Antarctic bryophytes.

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

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

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



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

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



Figure 3. *Nowellia curvifolia* demonstrating its red leaves of fall. Photo by Jan-Peter Frahm.

Light Effects on Reproduction

Humans don't think in terms of high light intensities for reproduction, but it appears that at least some mosses

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

To confound the issue further, Hughes and Wiggin (1969) found that in *Phascum cuspidatum* (Figure 4), light had just the opposite effect. Plants grown in culture in the shade had significantly more antheridia, more antheridial dehiscence, and larger antheridia than plants grown with light from the north sky. They did find more archegonial heads on plants grown in the light, but the success of fertilization was greater for plants grown in the shade (11%) than in the light (6%). However, they suggested that some of these differences could be accounted for by differences in population sizes.



Figure 4. *Phascum cuspidatum* with capsules. Photo by Michael Lüth.

Seasonal Effects on Pigments

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

Hicklenton and Oechel (1977) found that *Dicranum fuscescens* from northern Canada exhibited an increase in the light required to saturate photosynthesis from early season until mid summer, with the trend reversing later in

the season. They suggest that ability to photosynthesize at low light levels is an advantage to mosses that are still under the snow in early spring. Mosses exposed to high light when they are acclimated to low light actually experience damage, and it appears that the continuous light of summer in the Arctic may likewise be deleterious (Kallio & Valanne 1975). However, the continuous light damage occurred in laboratory experiments and it may be that plants living in the Arctic may acclimate to the seasonal change in photoperiod (Richardson 1981).

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

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

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

There is sufficient indirect evidence that we might expect chlorophyll differences with seasons. For example, we know that photosynthetic capacity changes between summer and winter in at least some mosses. In *Plagiomnium acutum* (Figure 5) and *P. maximoviczii*, photosynthetic capacity diminishes from 126 and 95 $\mu\text{M CO}_2 \text{ kg}^{-1} \text{ dw s}^{-1}$ in summer to 58 and 62 in winter, respectively (Liu *et al.* 2001). On the other hand, the light compensation point of 40 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in summer drops to 20 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in winter while the light saturation point drops similarly from 400 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in summer to 200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in winter. This can most likely be attributed to the lower respiration rate in winter.



Figure 5. *Plagiomnium acutum*, a moss that changes chlorophyll concentrations and light compensation points between summer and winter. Photo by Yingdi Liu.

Although Raeymaekers and Glime (1986) found similar chlorophyll content in the 2 cm terminal parts of *Pleurozium schreberi* in August (2.1 mg/g dw), end of September (2.1), and end of October (2.2) in Baraga County, Michigan, I have observed that *Fontinalis* becomes pale by the end of summer and bright to dark green by February, remaining deep green until June, in New Hampshire and the Upper Peninsula of Michigan. Martínez Abaigar *et al.* (1993) found distinct differences in chlorophyll *a* with season in two species of *Fontinalis* (Figure 8). There is no reason to expect all species to behave the same way, nor to expect the same species to behave the same way in all parts of its distribution.

In their study of 13 aquatic bryophytes, Martínez Abaigar *et al.* (1993) found considerable differences among species in the chlorophyll concentration changes with seasons (Figure 8). For example, *Fontinalis antipyretica* had its highest content in summer, whereas *F. squamosa* had its highest in spring with summer exhibiting the second lowest (the lowest being in autumn). She reported that the greatest chlorophyll content occurred in the immersed species (*Fontinalis antipyretica*, *F. squamosa*, *Fissidens grandifrons* – Figure 6) from San Pedro, *Jungermannia cordifolia*, and *Rhynchostegium riparioides*. The emergent *Cratoneuron commutatum* (Figure 7) had the least. This relationship to water is very likely correlated with light availability; the submerged taxa should produce more chlorophyll.

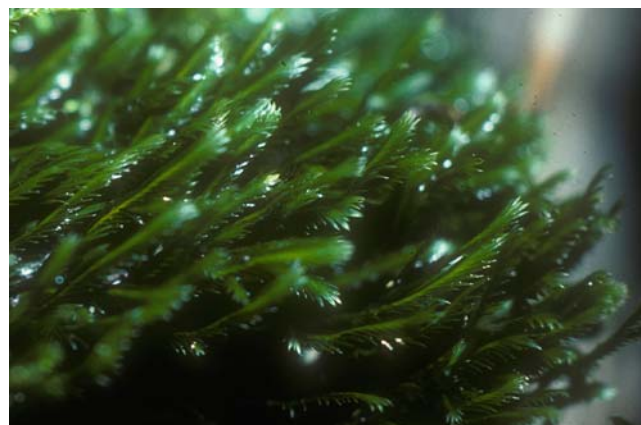


Figure 6. *Fissidens grandifrons* exhibiting dark coloration due to high chlorophyll concentrations. Photo by Janice Glime.



Figure 7. *Cratoneuron commutatum* exhibiting a low concentration of chlorophyll. Photo by Michael Lüth.

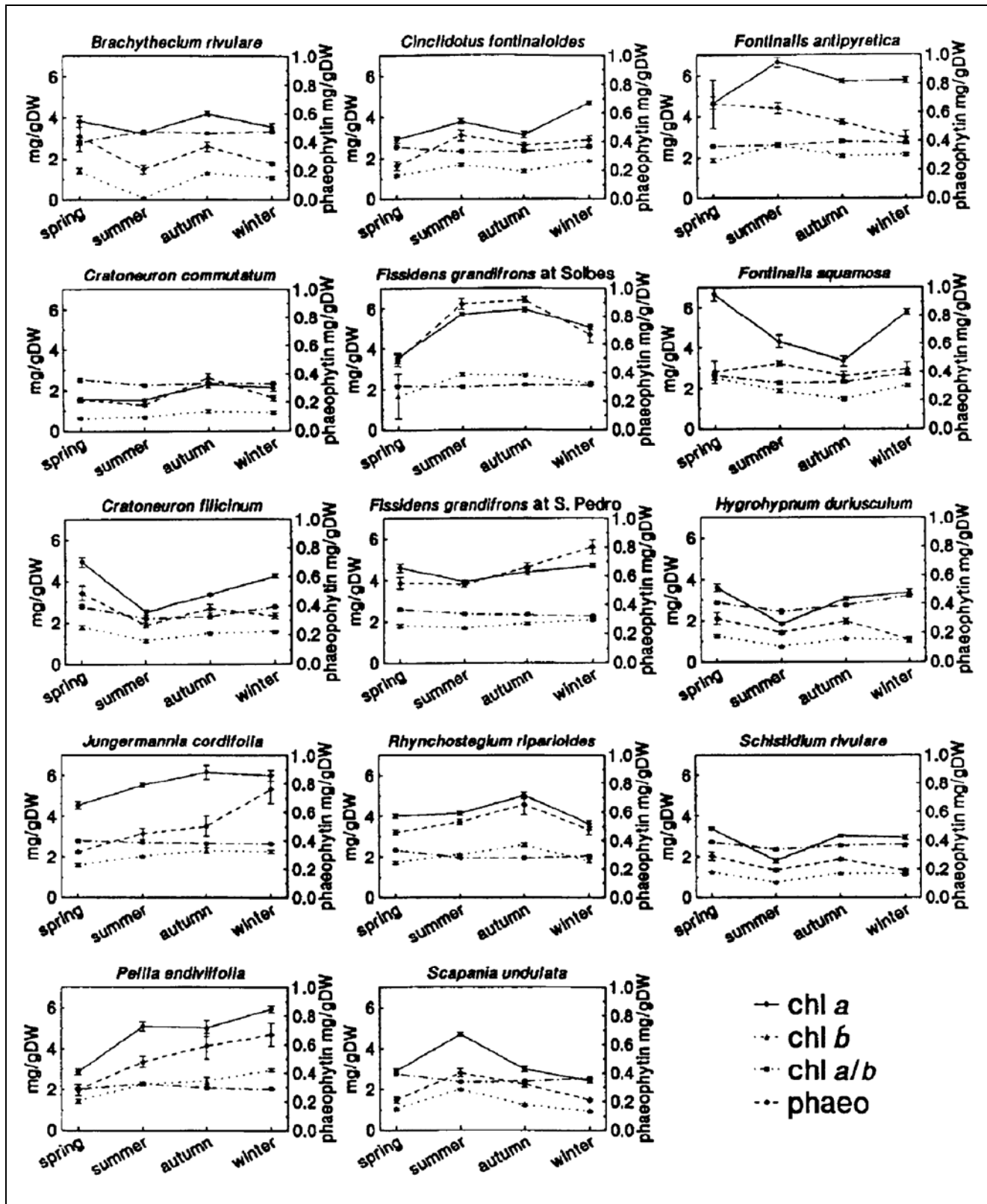


Figure 8. Seasonal changes in chlorophyll (left axis) and phaeophytin (right axis) concentrations (mg/gDW) in 13 species of aquatic bryophytes. Based on Martínez Abaigar *et al.* (1993).

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

We cannot rule out light intensity as the cause for these observed seasonal differences. In their study on *Brachythecium rutabulum*, Kershaw and Webber (1986) found that total chlorophyll increased from 1.70 mg chl g^{-1} on 8 May to 11.1 mg chl g^{-1} on 11 October, corresponding with full canopy conditions that reduced the light intensity

reaching the moss. Concomitantly, light saturation declined from $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the light compensation point declined from $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $4 \mu\text{mol m}^{-2} \text{s}^{-1}$.

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

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

Colors of Light

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

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

Lakes present a similar problem, but for different reasons. Water, both liquid and as snow, is an effective filter against both UV light and the low-energy red wavelengths. Hence, the deeper into the water, or snow, the less of these wavelengths available to the moss. Older, crystalline snow is almost completely opaque to infra-red light. While this water medium is good as protection against UV light, it is detrimental in providing appropriate wavelengths for maximal photosynthesis. Nevertheless, bryophytes, with their single layer of cells, are well adapted, compared to tracheophytes, to capture what little light is able to penetrate, and they benefit from the blue and green wavelengths that have greater penetration through water and ice. One adaptation to this blue and green light environment is that green light can cause major increases in content of chlorophylls and carotenoids in aquatic bryophytes (Czeczuga 1987). The yellow carotenoids are able to capture the blues and greens that penetrate to the greatest depths. Carotenoids, like chlorophyll *b*, serve as antenna pigments, creating additional surfaces for trapping

light and transferring it to the active site of chlorophyll *a*. Might a similar change occur in terrestrial bryophytes, adapting them to life beneath the green filter created by the canopy?

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

Few studies have examined the effects of the wavelength of light, *i.e.* its color, on the growth or physiology of bryophytes. Most of these have been laboratory studies on tropisms, germination, or growth (see chapter on development). However, Jägerbrand and During (2005) experimented with Icelandic *Hylocomium splendens* and *Racomitrium lanuginosum* in the greenhouse using shade cloth (black netting; green plastic film) compared to colorless plastic film to alter the light quality and intensity in a manner consistent with forest shade. The reduced light of both shade types caused greater elongation, reduced biomass growth, and a lower biomass:length ratio in new growth for both species, but the number of branches, branch density, and biomass:length ratio were higher for *H. splendens* (Figure 9). Both shade treatments caused similar increases in length (etiolation) and decreases in the biomass:length ratio. Branch density was significantly decreased by the reduction in red:far red ratio in *Racomitrium lanuginosum*, typically a sun species. Such a response to shade would permit greater light penetration and reduce self-shading. Similar behavior is seen in the needles of balsam fir (*Abies balsamea*), in which the arrangement of needles on branches is relatively flat on shade branches but go all the way around the upper half of the branch on sun branches.

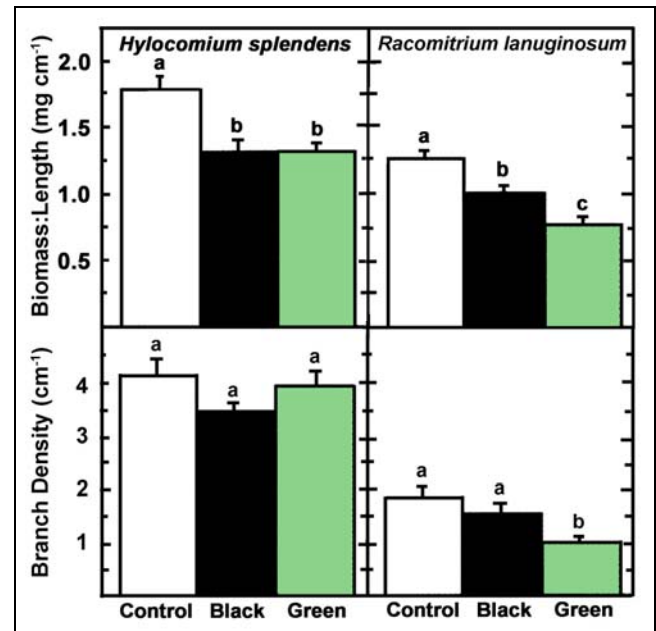


Figure 9. Effects of simulated shade on branch density and biomass to length ratio in two bryophytes. Bars indicate \pm SE. Bars with different letters within treatment indicate significant differences (Tukey-Kramer post-hoc-tests, $p < 0.05$ except *R. lanuginosum* branch density at $p < 0.10$). Redrawn from Jägerbrand & During (2005).

Photoperiod Effects

An alternation of day and night has been with plants since their inception. Thus, we should expect that most species have taken advantage of this alternation in various ways. Continuous light over a long period of time can cause mosses to lose their chlorophyll (Kallio & Valanne 1975). The stroma thylakoids are destroyed, much like the destruction seen in continuous dark in the cave experiments of Rajczy (1982). However, many moss taxa flourish in the continuous light of summer in the Arctic, so destruction in this way must not be universal. Or does it depend on the wavelengths?

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

This marked diurnal periodicity under a normal light regime is manifest in peak times for photosynthetic activity. Early morning hours provide the best moisture conditions, so it is not surprising that subalpine populations of *Pohlia wahlenbergii* (Figure 10) exhibited their highest photosynthetic activity in the early hours of morning. This high rate repeated itself in the early evening, suggesting photosensitivity and repair (Coxson & Mackey 1990), or could it be only a moisture relationship? Another possible explanation for the peak twice a day is an endogenous rhythm (Coxson & Mackey 1990). In any case, this would appear to be an adaptive behavior for bryophytes that must contend with drying in the afternoon sun, particularly in their most active photosynthetic tissues near the tips.



Figure 10. *Pohlia wahlenbergii* var. *glaciale*, whose peaks in photosynthetic activity are early morning and evening. Photo by Michael Lüth.

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

Summary

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

When photooxidation occurs under high light intensities, bryophytes can experience photoinhibition in the form of rupture of the chloroplast envelope, formation of vesicles in thylakoids, and rapid degradation of linolenic acid. Some bryophytes respond to the damaging effects of high light intensity and low temperatures by producing **light-quenching pigments** such as **sphagnorubin**. At warm temperatures, photorespiration provides an energy shunt to protect chlorophyll from overexcitation. Red pigments may also warm the bryophytes by absorbing heat.

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

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

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

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

Acknowledgments

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