

CHAPTER 11-2

PHOTOSYNTHESIS: PHOTOINHIBITION



Figure 1. *Conostomum tetragonum* exposed to the high light intensity of an alpine area. Photo by Michael Lüth.

Photoinhibition

In high light intensities, chlorophyll can be damaged by the enhanced activity of electrons beyond that which it can process. This results in **photoinhibition** by decreasing the photosynthetic capacity. In tracheophytes, this is particularly pronounced in dehydrated plants, but in bryophytes, it seems the pattern is quite different.

Seel *et al.* (1992) compared the desiccation-tolerant moss *Syntrichia ruralis* var. *arenicola* (= *Tortula ruraliformis*) (Figure 2) with the desiccation-intolerant moss *Dicranella palustris* (Figure 2). It appeared that desiccation in the dark had no effect on total concentrations of chlorophylls or carotenoids in either moss, but in *D. palustris* it resulted in loss of protein and accumulation of TBA, suggesting lipid peroxidation. *Dicranella palustris* was unable to recover its photosynthesis during rehydration, whereas photosynthesis of *Syntrichia ruralis* var. *arenicola* had only marginal depression in photosynthesis upon rehydration, and only at the highest irradiance. In the light, *D. palustris* likewise lost not only protein, but also chlorophyll and carotenoids, while lipid peroxidation increased. Again, *S. ruralis* var. *arenicola* suffered little damage. Greater damage occurred to this species when hydrated and exposed to high irradiance. Thus we can include that desiccation tolerance affords some protection to the chlorophyll in the presence of high light intensities, at least in some bryophyte species.



Figure 2. **Upper:** *Syntrichia ruralis* var. *arenicola*. **Lower:** *Dicranella palustris*. Photos by Michael Lüth.

Temperature plays a major role in photoinhibition and light damage. At low Antarctic temperatures with exposure to high light intensity, *Grimmia antarctici* experienced reduction in its **photosynthetic capacity** (light-saturated rate), **photosynthetic efficiency** (photon yield of oxygen), ratio of **variable to maximum fluorescence**, and rate of **fluorescence quenching** when exposed to moderate light (Adamson *et al.* 1988). Adamson *et al.* suggested that photoinhibition may play a major role in limiting photosynthesis and productivity in the Antarctic region. On the other hand, Alpert (1988) showed that *Grimmia laevigata* exhibits no chlorophyll damage during 20 months of desiccation if it is shielded from potential photodamage.

Quenching

Two means, known as **quenching**, seem to be available to plants, or at least to bryophytes, to reduce excessive activation energy and avoid damage from high light activity. In higher plants and bryophytes, this can be done by the reaction center itself. But bryophytes seem to behave somewhat differently from tracheophytes. For example, the leafy liverwort *Bazzania trilobata* exhibits no decrease in quantum yield in its open reaction centers when oversaturated with light, whereas both peas and barley do (Horton *et al.* 1988), suggesting that the behavior of the reaction center is not essential to prevent photoinhibition in at least some bryophytes. Rather, at least some bryophytes seem to be able to accomplish photoquenching by use of accessory pigments (Paulsen 1998).

One might expect such quenching activities to be especially important in alpine bryophytes. Fluorescence in bryophytes in alpine areas with high UV light intensity can result in different effects from those on tracheophytes (Heber *et al.* 2000). When dehydrated, alpine populations of *Grimmia alpestris* had very low chlorophyll fluorescence while alpine tracheophytes had high levels. On the other hand, mosses and lichens increase their chlorophyll fluorescence upon rehydration, whereas tracheophytes experience a decrease. Heber *et al.* considered this increase in mosses and lichens to relate to their lack of photodamage in a dry state. Nevertheless, tracheophytes, bryophytes, and lichens all can form chlorophyll fluorescence quenchers as a response to desiccation, but only the bryophytes and lichens exhibit a decrease in fluorescence in response to light energy transfer while dehydrated. Thus, among the alpine taxa they examined, only the bryophyte *Grimmia alpestris* used deactivation to avoid photodamage in both its hydrated and dehydrated states.

Zeaxanthin

One explanation for photo-protective quenching is that in high intensity light, the carotenoid violaxanthin, which itself inhibits quenching, is de-epoxidized to form **zeaxanthin** (Paulsen 1998). The theory is that this transformation to zeaxanthin lowers the energy level sufficiently to permit it to trap energy from the chlorophyll excited state. However, **auroxanthin**, a diepoxy xanthophyll, has an even higher energy level than that of violaxanthin, but it promotes fluorescence quenching and aggregation in isolated major light-harvesting complex II,

similar to the effect of zeaxanthin. Ruban *et al.* (1998) have challenged this interpretation of trapping chlorophyll energy because auroxanthin behaves similarly to zeaxanthin as a stimulator of quenching. Rather, Ruban *et al.* contend that it is the flat shape of zeaxanthin and auroxanthin, compared to the perpendicular shape of violaxanthin, that permits them to perform their quenching function.

Sunflecks can initiate rapidly reversible photoprotection within minutes to elicit non-photochemical chlorophyll fluorescence quenching (Matsubara *et al.* 2005). This is vitally important to bryophytes living in forests where low light is supplemented by these ephemeral bursts of bright light. Detectable conversion of the violaxanthin pigment to the protective antheraxanthin or zeaxanthin takes longer, suggesting that there may be more than one mechanism for photoprotection.

In prolonged strong light, photoprotection is usually stabilized within hours of exposure through this reversible violaxanthin cycle, but there is also a slowly reversible conversion of the pigment lutein epoxide to lutein. Matsubara *et al.* suggested that the lutein "locks in" a primary photoprotective mechanism in some species, causing light-harvesting antenna pigments to serve as centers for dissipating excitation energy in high light. Czezug (1985) found that lutein epoxide accumulated in *Marchantia polymorpha* thalli in late summer, autumn, and after winter. However, thus far we have no evidence of the specific role of lutein or lutein epoxide in bryophytes.

Bukhov *et al.* (2001a) found that light quenching of chlorophyll fluorescence in the moss *Rhytidiadelphus squarrosus* (Figure 3) apparently originated in the pigment antenna system, but in the tracheophytes *Arabidopsis thaliana* and *Spinacia oleracea* it appeared to originate in the reaction center. The quenching in *R. squarrosus* was strongly enhanced by the pigment **zeaxanthin** (Bukhov *et al.* 2001b). Short bursts of light were sufficient to cause an increase in levels of zeaxanthin in this moss, albeit in a 20% CO₂ atmosphere. In fact, only one molecule of zeaxanthin was needed to quench the efficiency of charge separation in Photosystem II by 50%.



Figure 3. *Rhytidiadelphus squarrosus*, a moss that quenches high light energy with the pigment **zeaxanthin**. Photo by Michael Lüth.

Heber *et al.* (2001) concluded that the absence of ATP consumption in reactions associated with the coupled electron transport of PS II permitted the acidification needed in the thylakoids for binding zeaxanthin to the chlorophyll-containing thylakoid protein. These form energy-dissipating traps in the antennae of PS II. Furthermore, the competition for energy capture decreases the activity of PS II. Both mosses and lichens benefit from the protein protonation and zeaxanthin availability in the dissipation of energy in PS II, whereas this is not the case in tracheophytes. The energy dissipation in mosses and lichens in the dry state is not related to protonation and zeaxanthin availability, as indicated by the absence of chlorophyll fluorescence. For mosses and lichens, the big advantage is that excitation of PS II by sunlight is not destructive when they are dry, whereas dry leaves of tracheophytes rapidly lose their PS II activity under strong illumination.

Rintamäki *et al.* (1994) found that strong light induced the PS II centers to increase their capacity for repair of photochemical damage in the moss *Ceratodon purpureus*. This increased tolerance was associated with a rapid turnover of the D1 protein, apparently mediated by lincomycin. In the absence of lincomycin, strong light resulted in a net loss of this D1 protein, suggesting that the rapid degradation of the protein was independent of the resynthesis of polypeptide. They interpreted this to mean that synthesis was the limiting factor in the turnover of the D1 protein during photoinhibition. Furthermore, the initial level of fluorescence was correlated with the production of inactive PS II reaction centers that were depleted of the D1 protein. The higher the fluorescence level, the greater the depletion of the D1 protein. Addition of lincomycin facilitated the recovery of the D1 protein, and the rate of D1 protein synthesis after photoinhibition exceeded that of control plants during the first hours under recovery conditions.

Deltoro *et al.* (1998) compared a desiccation-tolerant (*Frullania dilatata*, Figure 4) and desiccation-intolerant (*Pellia endiviifolia*, Figure 4) liverwort to examine the effects of desiccation and light on non-photochemical quenching. In *F. dilatata*, there was a rise in the concentration of de-epoxidized xanthophylls that can protect the cells from chlorophyll damage when photosynthesis cannot occur to trap the excited electrons. Dry *Pellia endiviifolia*, on the other hand, experienced less dissipation of electron activity and did not experience a rise in de-epoxidized xanthophylls. The increase in de-epoxidized xanthophylls appears to be induced by desiccation and mediated by zeaxanthin.

Chloroplast Position

The position of the chloroplasts plays a role not only in maximizing the light capture by the cell in low light, as in *Schistostega pennata*, but also in minimizing chlorophyll fluorescence during desiccation. Grouping of the plastids during drying may enhance the effect of chlorophyll reabsorption, causing a notable decrease in the F685/F735 ratio in the chlorophyll fluorescence spectrum, as shown in *Rhizomnium punctatum* leaves (Bartosková *et al.* 1999).



Figure 4. **Upper:** The desiccation-intolerant *Pellia endiviifolia* lacking any visible protective pigments. **Lower:** The desiccation-tolerant *Frullania dilatata* exhibiting colored protective pigments. Photos by Michael Lüth.

Sun and Shade Plants

Photosynthetic organs of plants typically adjust their chlorophyll concentrations as light conditions change (Martin & Churchill 1982). Hence, those organs in high light intensity tend to have lower concentrations of chlorophyll *b* and total chlorophyll than those in the shade (Valanne 1977; Martin & Churchill 1982). The chlorophyll *b* serves as one of the antenna pigments to trap light energy and transfer it to the chlorophyll *a* reaction center.

Within the bryophytes, there are both chlorophyll and plastid structural differences between plants typical of shade and those of sun, but these may not necessarily be accompanied by photosynthetic differences (Aro *et al.* 1981). For example, *Marchantia polymorpha* has a plastid structure characteristic of shade plants, and *Ceratodon purpureus* of sun plants, but both have the photosynthetic kinetics of shade plants.

Chlorophyll Concentration

Bryophytes in general have chlorophyll concentrations typical of shade plants (Tieszen & Johnson 1968; Table 1). Deora and Chaudhary (1991) examined the chlorophyll content in a number of Indian bryophytes and reported the ranges. Chlorophyll *a* ranged 0.402 ± 0.052 to 2.002 ± 0.700 mg g⁻¹ dry mass. Chlorophyll *b* ranged 0.265 ± 0.067 to 1.634 ± 0.070 mg g⁻¹ dry mass. The highest level of chlorophyll was in the cave moss *Cyathodium tuberosum* (3.636 mg g⁻¹ dw) and the lowest in *Entodon prorepens* (0.667 mg g⁻¹ dw). They found that, like the tracheophytes, high solar irradiances corresponded with low chlorophyll content and high *a:b* ratios. Martínez Abaigar and Núñez Olivera (1998) compiled data from a number of studies to show that on either a weight or areas basis, bryophytes have lower chlorophyll concentrations than do

tracheophytes (Figure 5). They attributed this higher level in tracheophytes to the more complex structure of these plants.

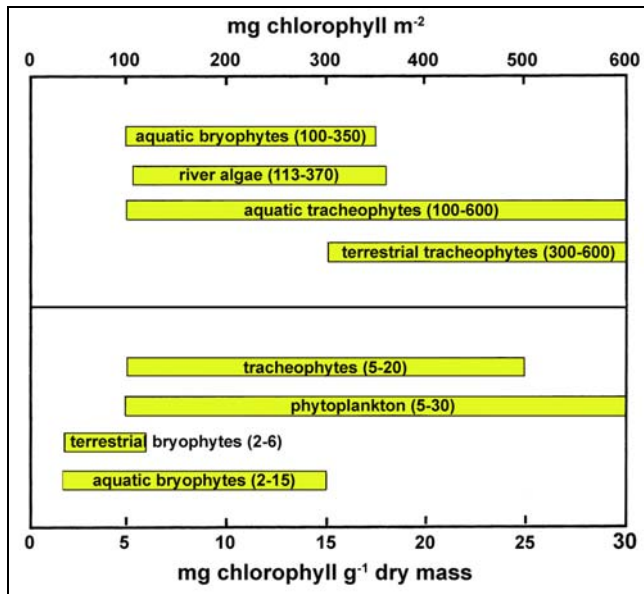


Figure 5. Comparisons of chlorophyll concentrations on an area (**upper**) and biomass (**lower**) basis. Redrawn from Martínez Abaigar and Núñez Olivera (1998), based on data from Martínez Abaigar *et al.* (1994).

Marschall and Proctor (2004) examined 39 moss and 16 liverwort species to compare chlorophylls and carotenoids in relation to light intensity and light saturation. They found a median total chlorophyll concentration of 1.64 mg g⁻¹ for mosses and 3.76 mg g⁻¹ for liverworts. Mean chlorophyll *a*:*b* ratios were 2.29 and 1.99, respectively. The chlorophyll:carotenoid ratio mean was 4.74 for mosses and 6.75 for liverworts. Light saturation values were low, with almost all less than 1000 μmol m⁻² s⁻¹; the median for mosses was 583 and for liverworts 214 μmol m⁻² s⁻¹. These numbers suggest that liverworts, in general, are more shade-adapted than are mosses. Deora and Chaudhary (1991) reached the same conclusion in their study of Indian bryophytes. Pande and Singh (1987) also compared mosses and liverworts during the rainy season in Nainital, Kumaun Himalaya, finding the liverworts to be more prominent in the shade and mosses in the sun, likewise having more chlorophyll and carotenoids in the liverworts. However, they found no chlorophyll:carotenoid differences between liverworts and mosses.

Marschall and Proctor (2004) concluded that bryophytes are **not** "inherently" shade plants and do include sun plants. For example, species of *Polytrichum* have lamellae that provide additional surface area for gas exchange, permitting greater CO₂ uptake; these species had the highest **photosynthetic photon flux density (PPFD)**. Masarovičová and Eliás (1987) supported this conclusion by showing that *Polytrichum commune* (Figure 6), with well-developed lamellae, had a higher saturation photosynthetic rate (3.67-5.62 mg CO₂ g⁻¹ dry mass h⁻¹) and higher photosynthesis per chlorophyll concentration (0.53 mg CO₂ Chl h⁻¹) than did *Atrichum undulatum* (which has less-well-developed lamellae; Figure 6) (3.41 mg CO₂

g⁻¹ dry mass h⁻¹) or *Hypnum cupressiforme* (which has no lamellae) (2.56 mg CO₂ g⁻¹ dry mass h⁻¹). Marschall and Proctor found that chlorophyll concentration, chlorophyll *a*:*b* ratios, and chlorophyll:carotenoid ratios all were significantly correlated with PPFD at 95% saturation in the bryophytes tested. Nevertheless, the light saturation levels of all bryophytes were lower than those for tracheophytes of open sun habitats. Marschall and Proctor attributed the lower saturation levels to the difficulty of obtaining CO₂ into the cells of bryophytes.

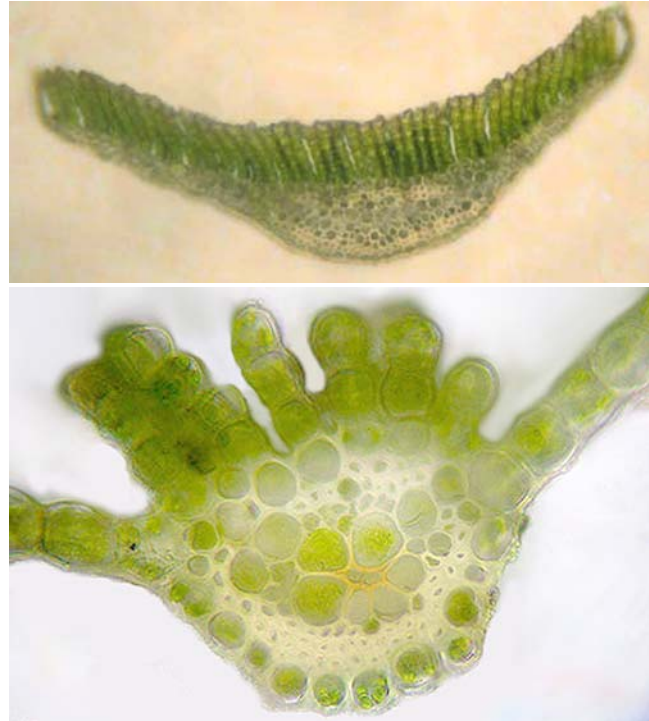


Figure 6. **Upper:** *Polytrichum commune* showing tall lamellae over entire cross section of leaf. **Lower:** *Atrichum selwynii* leaf cross section showing low lamellae over part of leaf. Photos with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

Chlorophyll degrades into phaeophytin. Chlorophyll *a* degrades more easily than does chlorophyll *b*; hence, phaeophytin *a* has been used as an indication of chlorophyll damage that can result from pollution or other stress. Bastardo (1980) suggests that a chlorophyll *a* to phaeophytin ratio of less than 1.0 in the aquatic moss *Fontinalis* indicates irreversible damage to the chlorophyll component. However, in their study of submerged mosses, Martínez Abaigar *et al.* (1994) found that chlorophyll of aquatic mosses did not degrade into phaeopigments.

Deep lakes provide some of the darkest habitats for bryophytes. Fully hydrated, bryophytes are able to take advantage of the CO₂ emitted from the sediments for a slow but steady growth without competition from other macrophytes. These plants are highly shade adapted and have a low light saturation level. The leafy liverwort *Chiloscyphus rivularis* in Crystal Lake, Wisconsin, USA, is saturated at ~50 μM photons m⁻² s⁻¹ (Farmer *et al.* 1988). This leafy liverwort has high concentrations of chlorophylls *a* and *b* as well as carotenoids. The carotenoids produced consist mostly of **lutein**, a yellow-orange pigment that has

most of its absorption at 470-500 nm (blue light). The light energy is transferred through the pigment antenna system to chlorophyll *a*.

In seemingly sharp contrast to this deep-water lutein production, Czezcuga (1987) grew bryophyte leaves under various light intensities with seemingly conflicting results.

As in other studies, in the shade the total carotenoid content and β -carotene increased, along with chlorophyll, but in the sunlight there was a marked increase in the lutein content of the leaves. Why should these leaves increase their antenna pigments, particularly lutein, in the sunlight? Is it serving as a filter, unconnected to the antenna function?

Table 1. Chlorophyll concentration (mg g⁻¹ dry mass) in a variety of bryophytes.

Species	<i>a</i>	<i>b</i>	Total	<i>a/b</i>	Date/ Intensity	Location	Reference
<i>Polytrichum commune</i>	7.74	3.82	11.56	2.14	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Polytrichum formosum</i>	6.37	2.67	9.04	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Polytrichum piliferum</i>				3.63			Krupa 1984
<i>Atrichum undulatum</i>	6.06	2.27	8.34	2.67	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Atrichum angustatum</i>				1.5			Martin 1980
<i>Plagiomnium undulatum</i>	7.21	2.62	9.82	2.75	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Rhizomnium punctatum</i>			14				Krupa 1984
<i>Ditrichum flexicaule</i>	2.66	1.06	3.72	2.51	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Hypnum cupressiforme</i>	4.87	1.91	6.60	2.44	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Pohlia</i> sp.	8.22	3.46	11.68	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
<i>Cyathodium tuberosum</i>	2.002	1.630	3.636	1.225	10 klux		Deora & Chaudhary 1991
<i>Plagiochasma appendiculatum</i>	1.934	1.231	3.165	1.571	12 klux		Deora & Chaudhary 1991
<i>Plagiochasma articulatum</i>	1.651	1.112	2.763	1.485	12 klux		Deora & Chaudhary 1991
<i>Riccia billardieri</i>	1.465	0.897	2.362	1.632	12-14 klux		Deora & Chaudhary 1991
<i>Tortula muralis</i>	1.801	1.388	3.189	1.297	50-70 klux		Deora & Chaudhary 1991
<i>Hyophila involuta</i>	1.210	0.713	1.923	1.697	50 klux		Deora & Chaudhary 1991
<i>Gymnostomiella vernicosa</i>	1.102	0.687	1.789	1.604	60 klux		Deora & Chaudhary 1991
<i>Fissidens geminiflorus</i> var <i>nagasakinus</i>	1.060	0.663	1.723	1.598	55 klux		Deora & Chaudhary 1991
<i>Fissidens curvato-involutus</i>	0.969	0.552	1.521	1.755	45-55 klux		Deora & Chaudhary 1991
<i>Fabronia minuta</i>	0.956	0.891	1.847	1.068	40-50 klux		Deora & Chaudhary 1991
<i>Fissidens diversifolius</i>	0.913	0.645	1.558	1.424	50 klux		Deora & Chaudhary 1991
<i>Bryum cellulare</i>	0.889	0.629	1.518	1.413	50 klux		Deora & Chaudhary 1991
<i>Funaria hygrometrica</i>	0.837	0.587	1.424	1.425	70 klux		Deora & Chaudhary 1991
<i>Bryum capillare</i>	0.544	0.514	1.098	1.058	70 klux		Deora & Chaudhary 1991
<i>Entodon myurus</i>	0.544	0.371	0.915	1.613	80-90 klux		Deora & Chaudhary 1991
<i>Funaria nutans</i>	0.514	0.479	1.020	1.129	70 klux		Deora & Chaudhary 1991
<i>Philonotis revoluta</i>	0.964	0.864	1.828	1.115	75 klux		Deora & Chaudhary 1991
<i>Barbula vinealis</i>	0.406	0.279	0.685	1.455	90 klux		Deora & Chaudhary 1991
<i>Entodon prorepens</i>	0.402	0.265	0.667	1.516	80-90 klux		Deora & Chaudhary 1991
<i>Marchantia polymorpha</i>			0.462*	1.23			Rao et al. 1979
<i>Marchantia polymorpha</i> tips	7.7	2.33	10.03	3.30			Fredericq & De Greef 1968
<i>Marchantia polymorpha</i> bases	6.25	1.88	8.13	3.32			Fredericq & De Greef 1968
<i>Marchantia palmata</i>			0.207*	1.07			Rao et al. 1979
<i>Reboulia hemisphaerica</i>			0.234*	1.11			Rao et al. 1979
<i>Ceratodon purpureus</i>			6.8	2.2	rhythmic lt, 1400 μ W cm ²		Valanne 1977
<i>Ceratodon purpureus</i>			3.0	2.0	contin lt, 1400 μ W cm ²		Valanne 1977
<i>Ceratodon purpureus</i>			8.5	2.0	rhythmic lt, 200 μ W cm ²		Valanne 1977
<i>Ceratodon purpureus</i>			8.1	1.9	contin lt, 200 μ W cm ²		Valanne 1977
<i>Dicranum scoparium</i>			1.7				Martin 1980
<i>Brachythecium velutinum</i>			1.8				Martin 1980
<i>Grimmia laevigata</i>			1.6				Martin 1980
<i>Leucobryum glaucum</i>			1.4				Martin 1980
<i>Leucodon julaceus</i>			1.9				Martin 1980
<i>Plagiomnium cuspidatum</i>			1.6				Martin 1980
<i>Polytrichum ohioense</i>			1.8				Martin 1980
<i>Sphagnum lescurii</i>			1.8				Martin 1980
<i>Thelia asprella</i>			1.9				Martin 1980
<i>Thuidium delicatulum</i>			2.1				Martin 1980

*Fresh weight

Chlorophyll *a:b* Ratio

Chlorophyll *a:b* ratios can vary considerably, depending on the light available, time of year, and the adaptations of the bryophytes. Martin and Churchill (1982) reported a mean of 2.69 (2.29-2.99) for 20 moss species in an oak-hickory (*Quercus-Carya*) woods in Kansas, USA. But in his study of North Carolina, USA, Martin (1980) reported only 1.14-2.1 for 11 moss species. Masarovičová and Eliás (1987) found a range of 2.14-2.85 for woodland mosses in SW Slovakia in July.

The genus *Riccia* frequents a variety of disturbed habitats as well as living on the water surface of lakes and ponds. Patidar *et al.* (1986) found that within this genus, the highest chlorophyll concentrations occurred in shade-grown *Riccia discolor*. The lowest concentrations occurred in *Riccia fluitans*, a species that floats on the water surface, often in direct sunlight. But surprisingly, the chlorophyll *a:b* ratios did not differ among the species in these different habitats.

An increase in irradiance will cause an increase in productivity up to the point where light saturation is reached. In a 36-day laboratory experiment using seven different light levels, Rincón (1993) demonstrated this concept with six bryophyte species (*Brachythecium rutabulum*, *Eurhynchium praelongum*, *Lophocolea bidentata*, *Plagiomnium undulatum*, *Pseudoscleropodium purum*, *Thuidium tamariscinum*); all responded to the higher light intensities with greater biomass increase. But they also demonstrated (except for *Lophocolea bidentata*) that lower light intensities resulted in greater shoot length increase, a response suggesting that IAA was being inhibited by the greater intensity of light. Like Patidar *et al.* (1986), they found that all species had higher chlorophyll levels at low irradiances, but there were no distinct changes in chlorophyll *a:b* ratios with light intensity.

Tieszen and Johnson (1968) pointed out the importance of bryophytes in tundra ecosystems by examining the chlorophyll distribution within several communities. Those communities with the lowest overall chlorophyll had the greatest amount of it in their moss and ericaceous components. In the Dry Sedge tundra, about one-third of the chlorophyll was in the moss component. However, in the Wet Sedge tundra, only about 2% was in the moss component. Like other studies discussed earlier, they found that the moss layer had the lowest chlorophyll *a:b* ratio, which ranged 1.5-2.5 for all plants. These are relatively low chlorophyll *a:b* ratios overall and correspond with the lower light intensities of Arctic latitudes.

Yang *et al.* (1994) compared bryophyte chlorophyll *a:b* ratios in 17 species from Yuan-Yang Lake. The minimum ratio was 2.17, with a mean of 2.41. This mean was lower than that found for the two aquatic tracheophytes (3.08), but was nevertheless somewhat higher than most bryophyte values reported (Table 1).

Age Differences

Masarovičová and Eliás (1987) showed that chlorophyll concentrations differ with age. One need only look at bryophytes in the spring to observe that older parts

are typically dark and new growth is a light, almost chartreuse, green. However, storage of other substances in senescing parts contributes to their dark color.

Seasonal Differences

As light intensity changes, antenna pigments, cytoplasmic water-soluble pigments, and wall pigments change. This results in seasonal changes in the color of the bryophytes.

Martin and Churchill (1982) found that total chlorophyll content of woodland mosses increased from early spring (1.45 mg g⁻¹ dry mass) before canopy closure to that attained after full canopy closure (4.36 mg g⁻¹ dry mass), demonstrating the wide range of plasticity in the chlorophyll content in these plants. Kershaw and Webber (1986) found a similar relationship in *Brachythecium rutabulum*, with chlorophyll concentrations increasing from 1.70 mg g⁻¹ on 8 May to 11.1 mg g⁻¹ on 11 October. During this time, light saturation declined from 200 μM m⁻² s⁻¹ to 30 μM m⁻² s⁻¹ by 6 July, with the light compensation point likewise falling from 65 μM m⁻² s⁻¹ to 4 μM m⁻² s⁻¹. It is clear that at least some bryophytes have a large capacity to adjust to changing light levels.

Epiphytes are subject to almost constant drying in both summer and winter. Their highest chlorophyll production is in the autumn, October to November, in Japan (Miyata & Hosokawa 1961), when autumn rain and temperatures suitable for C₃ plants make photosynthesis possible. Their lowest concentrations are in summer.

Gerdol *et al.* (1994) took a novel approach to determining seasonal differences in pigment concentrations in *Sphagnum capillifolium* (Figure 7). They compared plant segments and found that both chlorophylls were highest in the midsummer segment. Carotenoids were fairly stable except in spring. Chlorophyll degradation products (phaeophytin, pheophorbide, and chloride) accumulated in the autumn capitulum segment. They interpreted this autumn segment to indicate a rapid degradation of chlorophyll coincident with the night chilling of the end of the growing season.



Figure 7. *Sphagnum capillifolium*, exhibiting its colorful pigments. Photo by Jan-Peter Frahm.

Czczuga (1985) quantified the carotenoid pigment concentration in *Marchantia polymorpha* from March until November. Percentage of total pigments were close to or more than double in June, July, and August (17.8-25.0%)

compared to the other sampled months (1.8-9.3%). At the same time, the chlorophyll *a:b* ratio dropped steadily from 1.41 on 1 April to 1.00 by 14 October.

In a study of aquatic bryophytes the chlorophyll *a* and *b* values ranged widely from 1.52 to 6.67 mg chl *a* g⁻¹ dry mass and from 0.61 to 2.70 mg chl *b* (Martínez Abaigar *et al.* 1994; Figure 8). In autumn and winter, chl *a* ranged 2.11-6.27 and chl *b* ranged 0.91 to 2.95. The ranges of *a:b* ratio remained nearly the same in all four seasons (1.95-3.25).

But when the bryophytes were separated by habitat, several patterns emerged. Those from habitats subject to summer desiccation had a low summer concentration of chlorophyll and *a:b* ratio with an increase in the carotenoid portion. Those from under a dense tree canopy increased in chlorophyll content from spring to summer, and some continued that increase into autumn, while others dropped down again. Those that were continuously submerged demonstrated the smallest seasonal pigment variations.

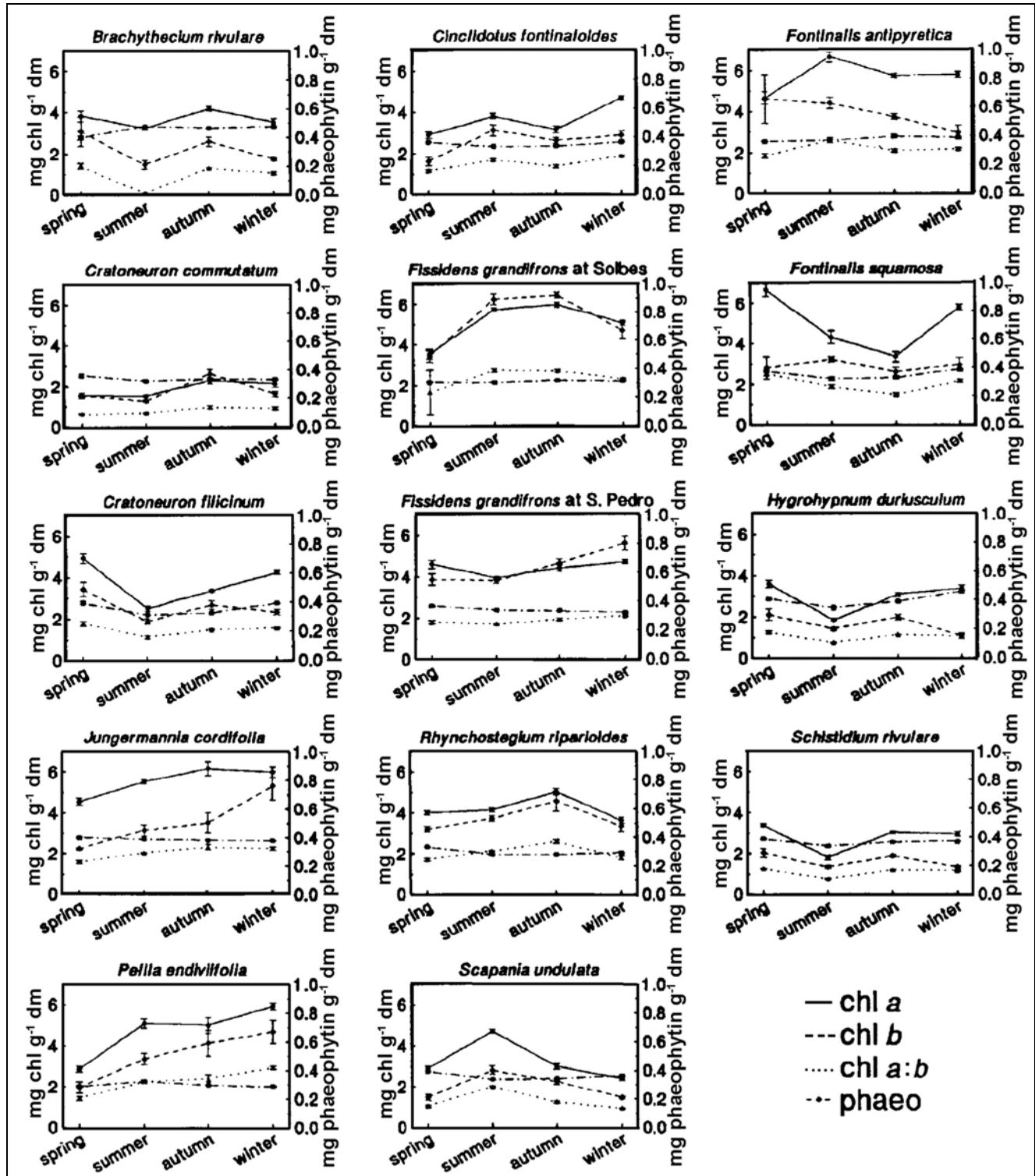


Figure 8. Seasonal changes in chlorophyll in thirteen species of aquatic bryophytes. Based on Martínez Abaigar *et al.* (1994).

Habitat Differences

Desert and Dry Areas

In the desiccation-tolerant *Syntrichia ruralis* from the Organ Mountains of southern New Mexico, Mishler and Oliver (1991) found that the total chlorophyll on a dry weight basis was higher in late summer and winter than in early summer. The chlorophyll *a:b* ratios were relatively low (1.00-2.50), compared to those of tracheophytes, and seemed to have no regular variation pattern.

Aquatic

Martínez Abaigar *et al.* (1994) compared stream bryophytes to tracheophytes and found that the chlorophyll concentrations were higher (2.2-92. mg g⁻¹ dry mass and 97-351 mg m⁻²) than those of terrestrial bryophytes and comparable to those values for epilithic river algae, but lower than for the tracheophytes. The chlorophyll *a:b* ratio of 2.1-2.8 was significantly lower than they found for tracheophytes. Of note is their find that chlorophyll degradation in underwater bryophytes did not produce phaeopigments. This is an important consideration for those persons who would choose a measure of phaeophytin to indicate damage to the bryophytes in pollution studies.

Antarctic

In a habitat where light is obscured by snow for more than six months of the year, it is not surprising that chlorophyll levels diminish. In the Antarctic, bryophyte chlorophyll levels decrease in winter, as does the chlorophyll *a:b* ratio (Melick & Seppelt 1994). In summer the rise in carotenoid levels corresponds to the period of high light intensity. The only Antarctic liverwort, *Cephaloziella exiliflora*, copes with the high light exposure in the Antarctic summer by producing a purple anthocyanin-like pigment (Post & Vesik 1992). Compared to more protected and shaded plants of the species, these plants had higher carotenoid:chlorophyll ratios, more dispersed thylakoids with fewer grana, fewer appressed thylakoids, more closely spaced leaves, and were larger, growing in a dense turf. Shaded plants had more chlorophyll per unit weight, but their *a:b* ratios did not seem to vary much.

Summary

Photoinhibition results from over excitation of electrons under conditions when the plant is unable to use all of those electrons in photosynthesis. It is a common occurrence under high light intensities, especially at low temperatures. This temperature relationship may account for the limitations of some species that prevent their surviving in polar regions. Desiccation-tolerant species seem to be able to dissipate this energy better than the desiccation-intolerant species. Unlike tracheophytes, bryophytes can suffer greater damage when hydrated than when dehydrated.

Quenching is the ability of the plant to redirect the energy in a way that it does not damage the chlorophyll. Accessory pigments can do this by filtering the light or stabilizing the energy level. In bryophytes, the pigment

zeaxanthin has been implicated in this role, along with a number of other pigments that depend on the species, reacting in some cases almost instantaneously and in others taking hours.

In some cases, clumping of chloroplasts and changes in shape permit the plastids to protect each other.

Bryophytes are typical shade plants, although some species do have adaptations to sun. Under low light intensity, bryophytes increase their chlorophyll *b* concentrations, providing more locations for trapping the light energy. Chlorophyll *a:b* ratios generally range between 2 and 3, but can be as low as 1 in some habitats and as high as 3.6 in others.

Lutein is commonly produced in aquatic bryophytes, but also in sunlight, causing its function to be uncertain.

Chlorophyll concentrations change seasonally, with highest concentrations generally being during the rainy growing season.

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