

CHAPTER 11-3

PHOTOSYNTHESIS: LIMITING FACTORS

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Figure 1. *Schistidium maritimum* growing on rocks where desiccation and salt spray exceed the limits of most bryophytes. Photo by Michael Lüth, with permission.

Limiting Factors

"The actual magnitude of assimilation in a leaf at any moment is determined by one or other of the main controlling conditions, light, temperature, or CO₂-supply, acting as a limiting factor." That was the conclusion of Blackman and Smith (1910-1911) in the ninth of their series of papers on vegetable assimilation and respiration. We know that water is another important parameter, but we are still trying to understand completely just how these parameters limit bryophyte photosynthesis. Perhaps Blackman and Smith again best sum it up in their statement that studies on photosynthesis "are more harmoniously interpreted from the point of view of interacting limiting factors than by the conception of optima."

Gerdol *et al.* (1998) illustrated this principle of interacting factors in their study of *Sphagnum capillifolium* (Figure 2). They found that low nighttime temperatures could lower growth five-fold, that nutrients limited growth when nighttime temperatures were high, that N and P limited growth at optimum temperatures. Different enzymes are turned on at different temperatures and different pH levels, and Gerdol *et al.* suggested that

enzymatic reactions could be limited at unfavorable temperatures.



Figure 2. *Sphagnum capillifolium*, a species in which productivity is affected by nighttime temperatures, nutrients, and N and P at optimum temperatures. Photo by Li Zhang, with permission.

Compensation Point

The **compensation point** is that point at which plant assimilation and respiration are compensated, so that gas exchange is null (Harder 1923). The compensation point can be expressed in terms of temperature, CO₂, or light. When plants are at their compensation point, they have reached a limiting factor for that parameter.

Water Availability

Water as a limiting factor is probably the best understood. Productivity on a worldwide scale seems to be correlated with water availability, at least in *Polytrichum strictum* (Figure 3) (Longton 1994). *Sanionia uncinata* (Figure 4) in Svalbard, Norway, living on the glacial foreland of the high Arctic, has its highest photosynthetic activities only on rainy days or soon after, indicating that it is not light, but water, that limits the productivity (Uchida *et al.* 2002). Collins (1976) related net productivity to water content in these two species, likewise demonstrating its importance (Figure 5).



Figure 3. *Polytrichum strictum* with capsules, a species in which water limits productivity. Photo by Michael Lüth, with permission.



Figure 4. *Sanionia uncinata*, a species in which water limits productivity. Photo by Janice Glime.

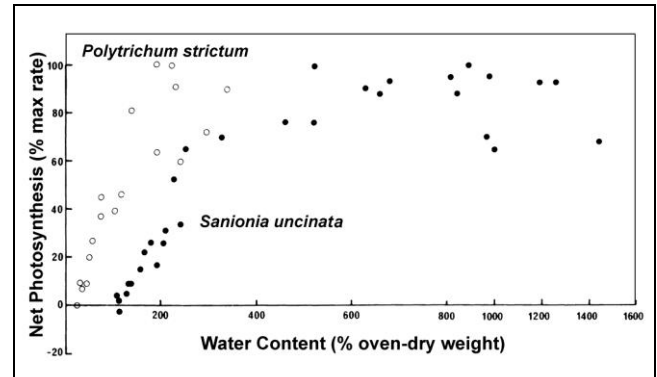


Figure 5. Effect of water content on the net productivity of two mosses from Signy Island. Measurements were at 10°C, 500 $\mu\text{e m}^{-2} \text{s}^{-1}$ (400-700 nm). Redrawn from Collins 1976.

Even in bogs, moisture is limiting. Backéus (1988) found that moisture conditions in August explained about 60% of the variation in *Sphagnum* growth the following year. He concluded that the distribution of moisture within the growing season was more important than the mean values. The importance of water in the growth of various *Sphagnum* species is well documented (Asada *et al.* 2003). Rydin and McDonald (1985b) examined the WC₅₀ (% water content at which 50% of the plants would recover if dried to their compensation point) in several *Sphagnum* species (Table 1). These ranged from 198% for *S. balticum* (Figure 6) to 283% for *S. tenellum* (Figure 7). *Sphagnum* typically requires more than 100% water content for photosynthesis.

Table 1. WC₅₀ values for *Sphagnum*. Based on references given in Rydin & McDonald 1985b.

Species	% WC ₅₀	Reference
<i>S. fuscum</i>	227	Rydin & McDonald 1985b
<i>S. fuscum</i>	400	Silvola & Aaltonen 1984
<i>S. balticum</i>	198	Rydin & McDonald 1985b
<i>S. tenellum</i>	283	Rydin & McDonald 1985b
<i>S. nemoreum</i>	400-620	Titus <i>et al.</i> 1983
<i>S. fallax</i>	250-470	Titus <i>et al.</i> 1983
<i>S. angustifolium</i>	600	Silvola & Aaltonen 1984
<i>S. nemoreum</i>	520	Grace 1970



Figure 6. *Sphagnum balticum*, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.



Figure 7. *Sphagnum tenellum*, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.

The strange phenomenon in *Sphagnum* is that there seems to be no correlation between habitat (hummock vs hollow) and photosynthetic rate at low water contents. Titus *et al.* (1983) found the expected relationship was reversed in *S. fallax* (Figure 8) and *S. capillifolium* (*S. nemoreum*, Figure 9), with the hollow-dwelling *S. fallax* having the higher photosynthetic rates at low water content. Silvola and Aaltonen (1984), on the other hand, found that the hummock species *S. fuscum* (Figure 10) was less desiccation-sensitive than the hollow species *S. angustifolium* (Figure 11). Rydin and McDonald (1985a) found that the hollow species *S. balticum* (Figure 6) and *S. tenellum* (Figure 7) cannot grow in hummocks, but that the hummock species *S. fuscum* and *S. rubellum* (Figure 12) can tolerate the wet hollows. It appears that some species have wide niches for water availability.



Figure 8. *Sphagnum fallax*, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.



Figure 9. *Sphagnum capillifolium*, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.



Figure 10. *Sphagnum fuscum*, a hummock species that is less desiccation-sensitive than are hollow species. Photo by Michael Lüth, with permission.



Figure 11. *Sphagnum angustifolium*, a desiccation-sensitive hollow species. Photo by Michael Lüth, with permission.



Figure 12. *Sphagnum rubellum*, a hummock species that can tolerate wet hollows. Photo by Michael Lüth, with permission.

Part of this dependency on water relates to the contact the plant is able to make with its substratum, or at least the water level below its capitulum. Schipperges and Rydin (1998) found that contact between capitula and the basal portion of the moss is essential to the survival of the moss, with isolated capitula being unable to recover from complete desiccation. They determined that the limit seems to be 10-20% of the water content of the compensation point. Maintenance of this level is accomplished by avoidance of desiccation through high capillarity and dense growth forms.

Hanslin *et al.* (2001) examined the effects of plant density on growth rate and water relationships. Increasing the density negatively impacted the relative growth rate and production of green biomass in both boreal forest mosses examined [*Dicranum majus* (Figure 13), *Rhytidiadelphus loreus* (Figure 14)]. However, in the mid-density range and low relative humidity, some of the watering treatments resulted in the best relative growth rates and green biomass production. Although there were no consistent patterns for most treatments, the length of the wet-dry cycle positively affected the relative growth rate when the number of wet-dry days remained equal. This is most likely due to the high cost of repair, with the longer cycles providing more time for positive productivity after the repair. The length of the dry cycle is far less important than having the needed time for repair and gain.



Figure 13. *Dicranum majus*, a species in which density impacts growth. Photo by Janice Glime.



Figure 14. *Rhytidiadelphus loreus* with capsules, a species in which density impacts growth. Photo by David Holyoak, with permission.

Alpert and Oechel (1987) studied the responses of bryophytes on granitic boulders in the chaparral of San Diego County, California, USA. Even in this dry habitat, the various bryophyte species had significantly different responses to water content, desiccation, and light. Those species in microsites with low water availability achieved maximum net photosynthesis at lower water contents and had a greater ability to recover from prolonged desiccation. Species from microsites with lower light availability achieved higher net photosynthetic rates at lower light intensities. Such studies illustrate the adaptability of bryophytes to a variety of conditions. In this chapter we will examine those limiting factors and the ways that bryophytes cope with them.

Bryophytes adapted to xeric habitats can regain photosynthesis upon rewetting in incredibly short periods of time. In *Grimmia montana* (Figure 15), this occurs in 6-10 minutes (McKay 1935). Equilibrium is reached in 30-40 minutes.



Figure 15. *Grimmia montana*, a xeric species that can regain photosynthesis in 6-10 minutes of rewetting. Photo by Michael Lüth, with permission.

Loss of water can affect not only photosynthesis, but the actual photosynthetic apparatus. As a result, those bryophytes with the ability to achieve non-photochemical quenching have a better chance of survival. In their study of three mosses, Csintalan *et al.* (1999) found that the two rock-dwelling mosses *Grimmia pulvinata* (Figure 16) and

Anomodon viticulosus (Figure 17) had a sharp peak of non-photosynthetic quenching when rewet, whereas quenching seemed to recover slowly in the less desiccation-tolerant *Rhytidiadelphus loreus* (Figure 14). On the other hand, Deltoro *et al.* (1998) suggested that loss of membrane integrity and subsequent loss of potassium might account for the inability to recover its photosynthetic rate.



Figure 16. *Grimmia pulvinata*, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Michael Lüth, with permission.



Figure 17. *Anomodon viticulosus*, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Janice Glime.

The moss *Rhizomnium punctatum* (Figure 18) experiences damage to PS II at 85% relative humidity (Bartosková *et al.* 1999). This is followed by a functional disconnection of the P680 reaction center from the antenna systems that is evident at higher rates of disconnection.



Figure 18. *Rhizomnium punctatum*, a species in which PS II is damaged at a reduction to 85% relative humidity. Photo by Jan-Peter Frahm, with permission.

Water Excess

Silvola (1991) demonstrated that the water needed for photosynthesis varies widely among species. Even within a single boreal forest and peatland system, the minimum water content before net photosynthesis declines ranges from 170% to 500%. On the other hand, these mosses, except for *Polytrichum commune* (Figure 19), also had an upper limit at which photosynthesis would also decline. This limit was imposed by the difficulty of absorbing CO₂ through a water barrier, a phenomenon also observed in *Sphagnum* (Murray *et al.* 1989). Presumably *P. commune* managed to maintain internal air spaces in its leaves among the photosynthetic lamellae (Figure 20), hence permitting it to continue photosynthesis.



Figure 19. *Polytrichum commune* with capsules, a species that maintains photosynthesis at high moisture contents. Photo by David T. Holyoak, with permission.

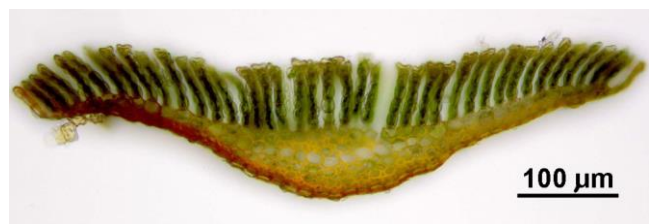


Figure 20. *Polytrichum commune* leaf cross section showing spaces between lamellae. Photo by Amelia Merced, with permission.

Liu *et al.* (2001b) found that in the mosses *Thuidium cymbifolium* (Figure 21) and *Chrysocladium retrorsum* (Figure 22) photosynthesis increased in the range of 20-70% water content. Their optimum water content was 70-80%, but then decreased from 80-95%. *Plagiomnium acutum* (Figure 23) had a somewhat broader range, increasing photosynthesis in the water content range of 20-80%, maintaining its highest photosynthetic level in the 80-95% range.



Figure 21. *Thuidium cymbifolium* with capsules, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Li Zhang, with permission.



Figure 22. *Chrysocladium retrorsum*, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Yao Kuiyu, through Creative Common.



Figure 23. *Plagiomnium acutum*, a species that maintains its highest photosynthetic level in the 80-95% water content. Photo by Show Ryu, through Creative Commons.

In *Sphagnum*, needed water content is much higher. The limiting water level depends on habitat and associated construction of the leaf. For example, in the hummock species *S. fuscum* (Figure 10), optimum conditions for

photosynthesis occurred at 600-1000% water content, with higher water levels causing a decline in photosynthesis (Silvola & Aaltonen 1984). *Sphagnum angustifolium* (Figure 11), which occurred in wetter locations, had its optimum at a wetter 900-1300%. Nevertheless, it often was too wet for optimum CO₂ absorption, whereas in *S. fuscum* it rarely was. But the relationship is never so simple. Using *Sphagnum*, Jauhianen *et al.* (1998) demonstrated that the negative effect of high water content on photosynthesis disappears at higher CO₂ concentrations, with the optimum water concentration increasing as the CO₂ level increases. At 3000 ppm (10X normal atmospheric CO₂ concentrations), there is no decrease in photosynthetic rate with increasing water content in *S. fuscum* (Figure 10) (Silvola 1990), supporting the conclusion that greater water content creates a barrier to the entry of CO₂.

Similar water content responses occur in *Sphagnum* species from New Zealand (Maseyk *et al.* 1999). Green plants of *S. cristatum* (Figure 24) had an optimum water content of 1200-2000%, whereas brown mosses had a higher optimum content of 1400-3000%. Brown coloration in mosses occurs in response to high light intensity, which usually is accompanied by higher temperatures. This suggests that there is a coordinated suite of responses.



Figure 24. *Sphagnum cristatum*, a species with an optimum water content of 1200-2000%. Photo by Janice Glime.

Seasonal Water Differences

In the tundra of the foothills north of the Brooks Range, Alaska, USA, up to two-thirds of the annual precipitation occurs during summer thunderstorms. In the boreal spruce (*Picea*) forest (Figure 25) in Manitoba, Canada, evapotranspiration was lowest in spring when the ground was still frozen (Betts *et al.* 1999). It was highest in the summer, dropping again in autumn after frost. Evaporation is, predictably, higher when the surface is wet, but it falls with an increase in light level at all temperatures in the summer because of the transpiration resistance of the forest system (*i.e.* guard cells close). But mosses also play a major role in the water evaporation. A wet moss surface lowers the vegetation resistance to water loss at its midmorning minimum by factor of 4. Mosses keep the soil wet and the atmosphere dry by inhibiting evaporation, particularly when they cover pools of standing water.



Figure 25. *Picea mariana* forest in Northern Alberta, Canada, with *Pleurozium schreberi* and *Hylocomium splendens* on the forest floor. Photo by Richard Caners, with permission.

Photosynthetic rate can be directly related to the length of dehydration period (Davey 1997a, b). However, even some bryophytes from very wet habitats in the Antarctic can exhibit some desiccation tolerance. Hydrophytic mosses were more likely to be harmed by repeated wet-dry cycles than were mesophytic or xerophytic bryophytes. Particularly in hydrophytic bryophyte species, the increase in percentage loss of photosynthetic rate following these wet-dry cycles occurred from spring to summer and from summer to autumn sampling periods. Nevertheless, Davey (1997a) could find only broad scale relationships to water availability and drew the same conclusion as Blackman and Smith (1910-1911), that other factors must be important in explaining the distributions of individual species.

Species differ in their responses to humidity. *Plagiomnium acutum* (Figure 23) has higher photosynthetic rates on cloudy and rainy days than does *Herpetineuron toccoeae* (Figure 26), but lower rates on sunny days (Li *et al.* 1999). *Herpetineuron toccoeae* has a lower rate of transpiration and higher water use efficiency than does *P. acutum*, permitting it to have a higher photosynthetic rate on sunny days. It also has a higher temperature tolerance. Interestingly, both species decrease their dark respiration with increases in temperature and decreases in relative humidity.



Figure 26. *Herpetineuron toccoeae*, a species that has reduced photosynthesis in low light. Photo by Li Zhang, with permission.

Nighttime Absorption

Nighttime can be an important time for water absorption in bryophytes. Condensation resulting in dew provides moisture on the surfaces of these small plants and can rehydrate them from the desiccation of daytime. Such moistening will reach its maximum just before dawn, preparing the bryophytes to take advantage of the cool temperatures in the early morning light.

Csintalan *et al.* (2000) demonstrated this phenomenon in the desert moss *Syntrichia ruralis* (Figure 27). They found that water was absorbed progressively by this moss throughout much of the night. This provided sufficient water for the moss to have positive net photosynthesis for about 1.5 hours immediately after dawn. Although the cumulative carbon balance between dark and light on the day of measurement was negative, on those days with greater dew the balance would be positive. They suggested that this short time period was sufficient to permit repair following long-term desiccation damage.



Figure 27. *Syntrichia ruralis*, a species that absorbs moisture from the atmosphere at night. Photo by Des Callaghan, with permission.

CO₂

With all the talk about the greenhouse effect due to elevated CO₂ in the atmosphere, it is hard to think in terms of CO₂ limits on plant productivity. But indeed it is often what limits productivity. In aquatic systems, CO₂ is usually limiting, except perhaps in deep water where sediment decomposition provides CO₂ but light levels are low (Maberly 1985; Wetzel *et al.* 1985).

Zotz *et al.* (2000) found that gas exchange of CO₂ is negatively correlated with cushion size in *Grimmia pulvinata* (Figure 16). Larger cushions have lower rates of photosynthesis and dark respiration, but alternating dark and light periods cause a complicated response that depends at least in part on the state of hydration.

Despite our increasing CO₂ concentrations in the atmosphere, this gas is often limiting to plants, including bryophytes. For this reason, gas spaces associated with the photosynthetic tissue is important (Raven 1996).

Compensation Point

The bottom line on the CO₂ limit for a species is its CO₂ compensation point. But this changes with the water content, temperature, and light intensity. A plant cannot use more CO₂ if there is insufficient excitation of electrons

due to low light levels. Dilks and Proctor (1975) reported compensation points from published studies (Table 2).

Table 2. CO₂ compensation points for bryophytes.

	μM	
<i>Pellia epiphylla</i>	75	Egle & Schenk 1953
<i>Conocephalum conicum</i>	70-105	Egle & Schenk 1953
<i>Bryum argenteum</i>	58	Rastorfer 1970
27 species	25-145	Dilks & Proctor 1975

Hanson *et al.* (2002) compared bryophytes with pyrenoids (hornworts) with *Marchantia polymorpha* (Figure 28), a liverwort with no pyrenoids. Pyrenoids are known for their ability to concentrate CO₂, permitting them to store inorganic carbon for later use when levels may diminish. The CO₂ compensation points of the two hornworts with pyrenoids was 11-13 ppm CO₂, whereas in *M. polymorpha* it was 64 ppm, a difference consistent with C₃ photosynthesis in the latter.



Figure 28. *Marchantia polymorpha* with archegoniophores, a species with much higher CO₂ compensation points than hornworts with pyrenoids. Photo by Rudolf Macek, with permission.

CO₂ Environment

The CO₂ environment around a terrestrial plant may be different from that generally found in the atmosphere. Soil bryophytes benefit from CO₂ emitted from soil decomposition. For example, in a New Zealand temperate rainforest where bryophytes blanket the forest floor, those bryophytes had an annual net uptake of carbon of 103 g m⁻², whereas the carbon emitted from the forest floor by bryophytes plus soil respiration was 1010 g m⁻² (Delucia *et al.* 2003). This meant that the bryophytes used only about 10% of the CO₂ coming from the forest soil microbes. The bryophyte contribution to carbon fixation would be considerably higher in the boreal forest.

Bryophytes can actually affect the turbulent fluxes of CO₂ in the forest. The combined effects of moss photosynthesis and respiration reduced those fluxes by a mean of 0.6 $\mu\text{M m}^{-2} \text{s}^{-1}$ (Janssens *et al.* 2001).

For the ground-dwelling *Hylocomium splendens* (Figure 25, Figure 29) in a subarctic habitat, the CO₂

concentration around the plants was 400-450 ppm during the hours when the light intensity was above the compensation point (30 $\mu\text{M m}^{-2} \text{s}^{-1}$) (Sonesson *et al.* 1992). Throughout the growing season, it is light, temperature, and water availability that limit the CO₂ uptake.



Figure 29. Ground-dwelling *Hylocomium splendens*. Photo by Michael Lüth, with permission.

Epiphytes compete with tree leaves for limited CO₂ in the canopy. But wherever the bryophytes are growing, no individual limiting factor is able to work alone. The photosynthetic limits of one are dependent on the levels of the others. Examples of this can be seen in a variety of habitats.

The aquatic moss *Fontinalis antipyretica* (Figure 30) has an especially low CO₂ compensation point, but it was consistent with that of C₃ plants (Maberly 1985). The relationship between the photosynthetic rate and the CO₂ concentration showed a photosynthetic increase as the temperature was increased, typical of plants suffering from boundary layer resistance. It is puzzling that this species had a higher assimilation rate in bicarbonate than in pure CO₂ at the same partial pressure (James 1928). This seems to contradict the studies by Bain and Proctor (1980) that indicate its inability to use bicarbonate. Allen and Spence (1981) independently determined this once more for *Fontinalis antipyretica*. Therefore, in aquatic systems at higher levels of pH, when the CO₂ equilibrium shifts toward bicarbonate or carbonate, CO₂ becomes less available to almost non-existent. In these conditions, perhaps the CO₂ is transformed from bicarbonates in some taxa by lower pH values at the moss-water interface, but no experimental evidence has verified this hypothesis. Thus, the number of mosses growing in alkaline waters is limited, and it seems that many of the ones that do occur in alkaline waters are adapted to grow in the highly aerated water of waterfalls and rapids, as, for example, *Fissidens grandifrons* (Figure 31) (pers. obs.). Others are restricted to the splash zone at the edge of the water, where CO₂ is trapped as the water moves through the air, as in *Cratoneuron* (Figure 32) species (Vitt *et al.* 1986; Glime & Vitt 1987).



Figure 30. *Fontinalis antipyretica*, a species with a low CO₂ compensation point. Photo by Andrew Spink, with permission.

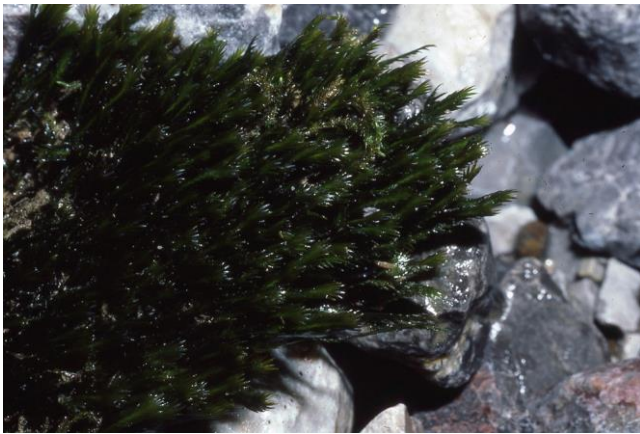


Figure 31. *Fissidens grandifrons*, a species able to live in alkaline waters. Photo by Janice Glime.

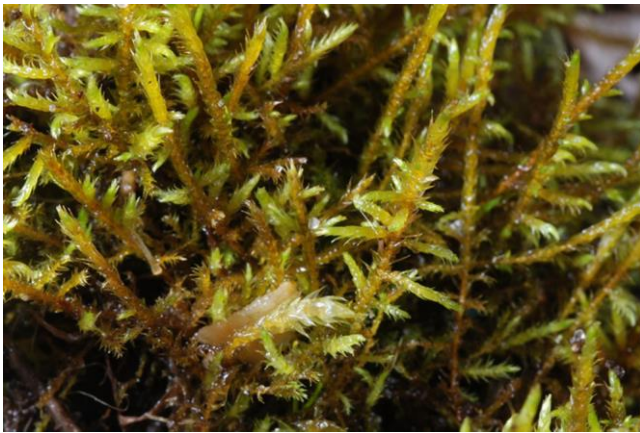


Figure 32. *Cratoneuron filicinum*, in a genus in alkaline areas is restricted to the splash zone. Photo by J. C. Schou, with permission.

Silvola (1990) examined the effects of CO₂ on the hummock moss *Sphagnum fuscum* (Figure 10) productivity and determined that maximum productivity occurred at 600-800% dry mass water content at ambient CO₂ levels of about 380 mg L⁻¹, but that at the saturating CO₂ level of 8000 mg L⁻¹, a saturated water content was needed (Figure 33). Since a CO₂ level of 8000 mg L⁻¹ is unrealistic in nature, the curves for 300-1200 mg L⁻¹ CO₂ are more instructive. One might speculate that the present success of *Sphagnum* in full sun and a temperature of

35°C, where most other bryophytes cannot survive, might be related to the elevated CO₂ emitted from peat.

The conclusion from all these studies is that one cannot look at the limits of CO₂, or any other factor, in absolute terms. They must be examined as they are affected by the other potential limiting factors (Maberly 1985). So what does that mean for a statement like the title of a paper by Adamson *et al.* (1990), "Photosynthesis in *Grimmia antarctica* (= *Schistidium antarcticum*; Figure 34), an endemic Antarctic bryophyte, is limited by carbon dioxide"? When considering limits, it is appropriate to consider the range of the natural conditions of the plant and to express the limits that affect those plants under those conditions. Thus, a plant that is limited by CO₂ in the Antarctic might be limited by light if it were growing in England.

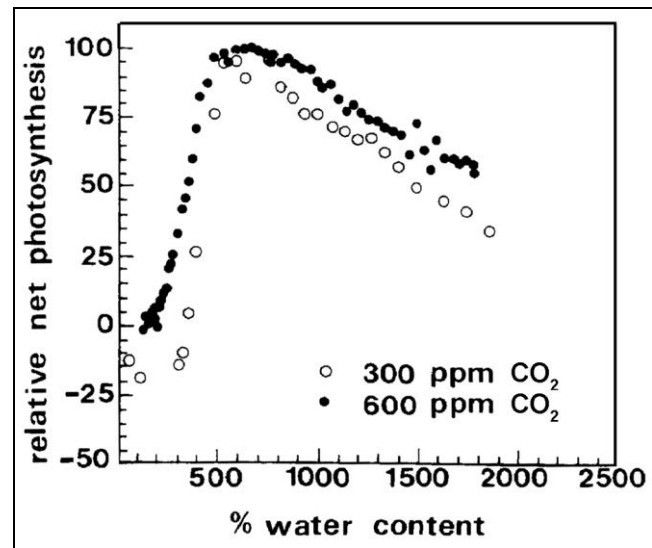


Figure 33. The relationship between net photosynthesis and water content (as percent dry mass) in *Sphagnum fuscum* (Figure 10) at two CO₂ concentrations. Constant conditions were maintained at 20°C, 300 μmol m⁻² s⁻¹ PAR photon flux density, and drying at 70% relative humidity. Redrawn from Silvola 1990.



Figure 34. Saturated *Schistidium* (formerly *Grimmia*) *antarctica* with *Ceratodon purpureus* between the hummocks. Photo courtesy of Rod Seppelt.

Silvola (1985) showed that bryophytes can be limited by CO₂ in their natural habitat. In the light range of 70-500 μM m⁻² s⁻¹, raising the CO₂ concentration from 320 ppm to

640 ppm caused a 1.6-2.6-fold increase in the net daily CO₂ exchange.

But short-term studies in the lab or the field may be misleading. Van der Heijden *et al.* (2000) found that initially photosynthesis of *Sphagnum fallax* (= *Sphagnum recurvum* var. *mucronatum*) (Figure 8) was stimulated by elevated CO₂ (700 µL L⁻¹), but that after only three days it had returned to the levels of the controls. Furthermore, at low N deposition levels (6 g m⁻² yr⁻¹) and elevated CO₂, these plants had 17% more biomass after six months, but at high N deposition levels (up to 23 g m⁻² yr⁻¹), there was little effect on biomass increase. High levels of CO₂ caused a suppression of dark respiration, resulting in an accumulation of soluble sugars in the capitulum. Doubling the CO₂ also reduced the total nitrogen content of the capitula, but not the stems, possibly as a result of the increased sugar content. This reduction was seen in reduced amino acid content, but not in protein content. Such shifts in the carbohydrate to amino acid content has sobering implications for the food web, necessitating that more of the same food be eaten to gain the same amino acid content, and consequently increasing the sugar content. Can invertebrates get diabetes?

Within the bryophyte layers, the CO₂ environment differs from ambient. The forest floor efflux of CO₂ beneath *Sphagnum* (Figure 53) and feather mosses such as *Hylocomium splendens* (Figure 25, Figure 29) in the boreal black spruce forest (Figure 25) is ~7 M m⁻² s⁻¹, a loss from the forest floor of 255.4 g C m⁻² during May-October (Swanson & Flanagan 2001). In *H. splendens*, the upper parts may have 400-450 ppm CO₂ while the light conditions are above the compensation point (*i.e.*, while photosynthesis is occurring), but light levels below saturation during most of the growing season limit CO₂ uptake (Sonesson *et al.* 1992). Nevertheless, the higher than normal atmospheric levels of CO₂ that occur within the mat permit the plants to have photosynthetic levels that are higher than would normally occur at the reduced (below saturating) light levels.

As the CO₂ concentration of the atmosphere increases, productivity of various groups of plants are likely to be affected differently. The rate of net photosynthesis in the hummock peatmoss *Sphagnum fuscum* (Figure 10) increases as the CO₂ concentration increases in the range of 350-2000 ppm CO₂ during half-hour exposures (Jauhiainen & Silvola 1999). The rate at light saturation likewise increases. The effect of radiation fluxes, however, is independent of the level of CO₂. When the exposure to high CO₂ is maintained for longer times, the rates of net photosynthesis gradually decrease compared to those at 350 ppm. On the other hand, at high CO₂ levels, the depression of net photosynthesis found at high water contents is no longer present.

Tropical forests have huge competition for CO₂ in the canopy, but so little light reaches the forest floor that competition is greatly reduced. In a submontane tropical rainforest in Panama, diel variations in water content of six studied bryophytes were great, with both high and low water content limiting photosynthesis (Zotz *et al.* 1997). Low photon flux density is less important in limiting CO₂ exchange. More than half of the carbon gained in the daytime (2.9 mg C per g plant) is lost at night as respiration. If the productivity of this study is

representative, the bryophytes gain 45% of their initial carbon content in a year in this environment.

CO₂-Concentrating Mechanisms

Since CO₂ is frequently a limiting resource, a means of concentrating CO₂ for use later or for grabbing it from water is a useful mechanism. Although bryophytes are known only as C₃ plants (Smith & Griffiths 1996), at least some seem to have such mechanisms. Furthermore, both **Cyanobacteria** and many algae are able to accumulate dissolved inorganic carbon through CO₂-concentrating mechanisms (Smith & Griffiths 1996). In the green algae (**Chlorophyta**), this is accomplished by a proteinaceous structure associated with chloroplasts, the **pyrenoid**. And indeed, this structure is present in the phylum **Anthocerotophyta** (Figure 35), but not in all genera.

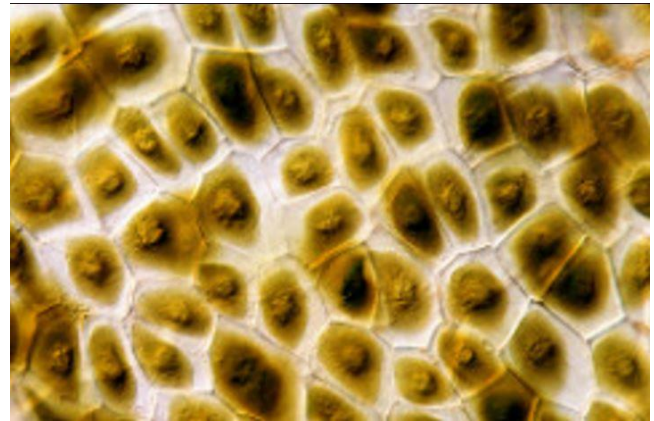
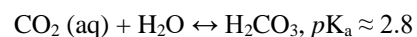
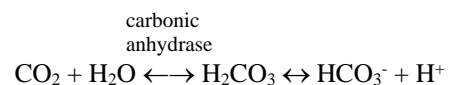


Figure 35. *Phaeoceros* cells with pyrenoids associated with chloroplasts. Photo by George Shepherd, with permission.

I find it interesting that it is a primarily terrestrial group that has this mechanism. Living on the soil permits bryophytes to take advantage of CO₂ emitted through soil respiration. But living in the water, attaining CO₂ can be a severe problem for some bryophytes not receiving CO₂ from the sediments and unable to use the carbonates and bicarbonates in water with non-acid pH. Something is working to permit some bryophytes to live in these conditions, and the mechanism remains unknown.

pH

On land it is likely that pH has only minimal influence on the uptake of CO₂ from the atmosphere. However, in the aquatic system, pH can be a serious limiting factor. The CO₂ that is dissolved in water seeks equilibrium with the bicarbonate and carbonate. This equilibrium is dependent on pH:



where the pK values are those at 25°C

The pK is the pH at which the dissociated and undissociated forms have the same activity, *i.e.*, the two sides of the arrows in the above equations. It is the equilibrium between the two forms. From this we can derive the level at which inorganic carbon exists in the bicarbonate state. At pH 6.35, the solution would be expected to have half CO_2 and half bicarbonate. Above that it becomes predominately bicarbonate. At even higher levels of 10.3, the bicarbonate and carbonate levels are equal. Above pH 10.3, the carbon is predominately in the form of carbonate. Allen and Spence (1981) calculated that at pH 4.4, 99% of the inorganic carbon is present as H_2CO_3 (making free CO_2 available); only 1% is HCO_3^- , and there is virtually no CO_3^{2-} . At pH 8.4, this reverses and 99% of the total inorganic carbon is HCO_3^- ; less than 1% is in H_2CO_3 ; less than 0.03% is in CO_3^{2-} . At any given moment, some CO_2 will exist as biological and chemical reactions occur to release CO_2 into the water, but as time continues, those small amounts will enter into the equilibrium. Nevertheless, metals and other buffering acids and bases can alter the concentrations.

In aquatic systems, CO_2 is spontaneously hydrated to H_2CO_3 , but this hydration occurs about 2 orders of magnitude slower than the hydration which occurs in the carbonic anhydrase-catalyzed reaction. But remember that the carbonic anhydrase is in the cell where the pH is generally above 6.5. Or is it? There is evidence that carbonic anhydrase acts extracellularly in some algae (Hobson *et al.* 2001), including *Chlamydomonas* (Figure 36) and some diatoms. Thus it is possible that there is extracellular activity in some aquatic mosses. Furthermore, the pH of the cell wall is typically lower than that of the cell, ranging 3-6.

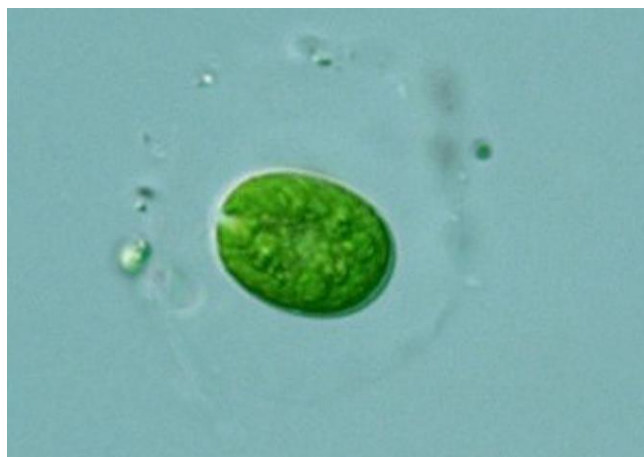


Figure 36. *Chlamydomonas*, a genus that uses carbonic anhydrase extracellularly. Photo by Yuuji Tsukii, with permission.

I am aware of no evidence that this carbonic anhydrase is able to act on water outside the cell in any bryophyte, but then, no one seems to have looked. With such an elevated pH within the cell, the H_2CO_3 is rapidly converted to bicarbonate and the level of carbonic acid is miniscule. But the enzyme RUBISCO is present in the plant photosynthetic cell, ready to place the CO_2 into the photosynthetic pathway where it is bound into the 3-carbon compound, PGA (Rintamäki 1989). Thus, the problem is getting the miniscule amounts of CO_2 from the water in

systems where the pH is too high for the equilibrium to shift toward free CO_2 or H_2CO_3 .

Sphagnum (Figure 7-Figure 12) and other bryophytes have the ability to lower the pH through cation exchange, thus keeping more CO_2 in their environment in readily usable form. Consequently, low pH values in the proximity of bryophytes with polyuronic acid in the cell walls are most likely common, and the cation exchange properties of these acids would provide H^+ ions in the immediate surroundings. This could provide the free CO_2 needed for photosynthesis. In plants living in cool water and low light, such as many aquatic bryophytes, even such low levels of CO_2 are probably adequate. As discussed in the nutrient chapter, this cation exchange and pH -lowering ability have a number of ecological and physiological implications in the peatland habitat. The pH -lowering ability and requirements differ with *Sphagnum* species, with hummock species tending to have requirements for the lowest pH (Haraguchi 1996; Haraguchi *et al.* 2003). After all, it is difficult to have much effect on the pH of an entire lake, but having an effect on the immediate microenvironment of a hummock is not.

Limits to Entry

Water limits the entry of CO_2 into cells. For *Sphagnum fuscum* (Figure 10), Silvola (1990) found the optimal water content at ambient CO_2 levels to be 600-800%. However, if the CO_2 level was raised, that optimal water content increased, an observation consistent with the difficulty of getting CO_2 into a wet cell through the water boundary. By increasing the concentration of CO_2 , more of it is able to penetrate the barrier. At 3000 ppm CO_2 , there was no decrease in the photosynthetic rate with increasing water content.

In aquatic habitats, bryophytes may gain CO_2 from that evolved from sediment respiration. Wetzel *et al.* (1985) found that 25-40% of the CO_2 fixed in leaves of tracheophytes comes from the **rhizosphere** (root area). Bryophytes do not have the **lacunae** (minute cavities) to transmit gases in the manner used by many aquatic tracheophytes, but due to their small size, they are able to incorporate the evolving CO_2 as it escapes from the sediments and before it reaches the awaiting phytoplankton.

Methane

Sphagnum (Figure 7-Figure 12) seems to have an alternative source for gaining carbon (Raghoebarsing *et al.* 2005). It is able to obtain carbon through a symbiotic relationship with endophytic methanotrophic bacteria living in the hyaline cells of both stems and leaves. These bacteria oxidize the carbon from the methane to CO_2 that is then used by the *Sphagnum*. This appears to supply about 10-15% of the carbon used by *Sphagnum*. This and other processes in the peatland system recycle the methane in ways that cause little of the methane to reach the atmosphere.

Light

The majority of bryophytes grow in habitats where the light intensity is less than that of full sunlight. Therefore, it is not surprising that Rincón (1993) found that six forest floor bryophytes all increased their biomass relative to

controls when the light intensity was increased for 36 days. But shoot elongation can have the opposite response. In this study, all species [*Brachythecium rutabulum* (Figure 37), *Eurhynchium praelongum* (Figure 38), *Plagiomnium undulatum* (Figure 39), *Pseudoscleropodium purum* (Figure 40), *Thuidium tamariscinum* (Figure 41)] but *Lophocolea bidentata* (Figure 42) had greater elongation in the lower light intensities. *Dicranum majus* (Figure 13) likewise had its greatest elongation at the lowest light level tested ($20 \mu\text{M m}^{-2} \text{s}^{-1}$) (Bakken 1995).



Figure 37. *Brachythecium rutabulum*, a species with greater elongation in lower light. Photo by J. C. Schou, with permission.



Figure 38. *Eurhynchium praelongum*, a species with greater elongation in lower light. Photo by Blanka Shaw, with permission.



Figure 39. *Plagiomnium undulatum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 40. *Pseudoscleropodium purum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 41. *Thuidium tamariscinum*, a species with greater elongation in lower light. Photo by Janice Glime.



Figure 42. *Lophocolea bidentata*, a leafy liverwort that exhibits greater elongation in low light. Photo by Michael Lüth, with permission.

Murray *et al.* (1993) found a similar elongation response among Alaskan Arctic tundra *Sphagnum* (Figure 7-Figure 12) species. They experimented by removal of tracheophytes in some plots and by use of shade cloth of others, compared to controls. Moss growth in shaded plots was 2-3 times that of mosses in control plots, whereas significant growth reduction was evident in the canopy removal plots. They suggested that those mosses in the canopy removal plots suffered from photoinhibition. In the

laboratory, such inhibition occurred after only two days of high light treatment and the photosynthetic capacity did not recover during the 14 days of the experiment. They suggested that the low tissue nitrogen levels may have prevented the *Sphagnum* from acclimating to the high light intensity.

Compensation and Saturation Points

Bryophytes in general are shade-adapted plants with low light compensation points and low saturation levels. Gabriel and Bates (2003) showed that bryophytes of the evergreen laurel forest in the Azores were likewise shade-adapted plants that reached their light saturation at $30 \mu\text{M m}^{-2} \text{s}^{-1}$. *Andoa berthelotiana* (Figure 43) had the lowest compensation point at $20 \mu\text{M m}^{-2} \text{s}^{-1}$ and *Myurium hochstetteri* (Figure 44) had the highest at $68 \mu\text{M m}^{-2} \text{s}^{-1}$. The deep shade species *Fissidens serrulatus* (Figure 45) had the extremely low compensation point of $7 \mu\text{M photons m}^{-2} \text{s}^{-1}$. With leaves remaining on the trees, the low light levels of winter often limit the photosynthetic activity of these bryophytes. Contrasting with these evergreen forest species, the pendulous moss *Pilotrichella ampullacea* (Figure 46) in Uganda has a saturating light intensity of $400 \mu\text{M m}^{-2} \text{s}^{-1}$ (Proctor 2002).



Figure 43. *Andoa berthelotiana*, a shade-adapted moss in the Azores with the lowest light compensation point there. Photo by Jan-Peter Frahm, with permission.



Figure 44. *Myurium hochstetteri*, a shade-adapted moss in the Azores with the highest light compensation point there. Photo by Michael Lüth, with permission.



Figure 45. *Fissidens serrulatus*, a deep-shade-adapted moss in the Azores with the lowest light compensation point there. Photo by David Holyoak, with permission.



Figure 46. *Pilotrichella ampullacea*, a pendulous moss with a very high light saturation point. Photo by Jan-Peter Frahm, with permission.

It is difficult to compare results from different studies because the units cannot easily be converted to other forms of measure, as discussed in the chapter on light. Older measurements were typically in foot candles or lux, whereas more recent ones are in energy units or PAR (photosynthetically active radiation) units. Conversion is complicated by the composition of the wavelengths of light. For example, Vashistha and Chopra (1989) determined that the optimal growth of the disturbed habitat liverwort *Riccia frostii* (Figure 47) occurred at 3500 lux of continuous light in the lab. But lab light quality differs considerably from that in the field and under fluorescent lights it typically lacks the normal proportion of red light that achieves the highest level of photosynthesis. A light level of 3500 lux is quite low when one considers that full

sunlight is about 70,000 lux. It is likely that at that level of light some other factor became limiting in the lab, perhaps CO_2 .



Figure 47. *Riccia frostii*, a species of disturbed habitats. Photo by Rosemary Taylor, with permission.

The interplay of limiting factors becomes the means of niche partitioning in many of the bryophytes. *Plagiomnium acutum* (Figure 23) and *Herpetineuron toccoeae* (Figure 26) occupy different niches because of this interplay. In *P. acutum*, photosynthesis is lower on sunny days but higher on cloudy and rainy days than that of *H. toccoeae*, indicating its greater ability to absorb and use weak light while having a higher CO_2 assimilation efficiency (Li *et al.* 1999). The greater water use efficiency of *H. toccoeae* and lower rate of transpiration permits that species to tolerate higher temperatures and desiccating conditions. One reason for this is the higher respiratory rate of *P. acutum*.

The mosses *Plagiomnium acutum* (Figure 23) and *P. maximoviczii* (Figure 48) have light compensation points of 20-40 $\mu\text{M m}^{-2} \text{s}^{-1}$ and saturation points of 200-400 $\mu\text{M m}^{-2} \text{s}^{-1}$, with lower values in winter and higher ones in summer (Liu *et al.* 2001a). Thus it appears that they acclimate to the conditions of light or temperature or both.

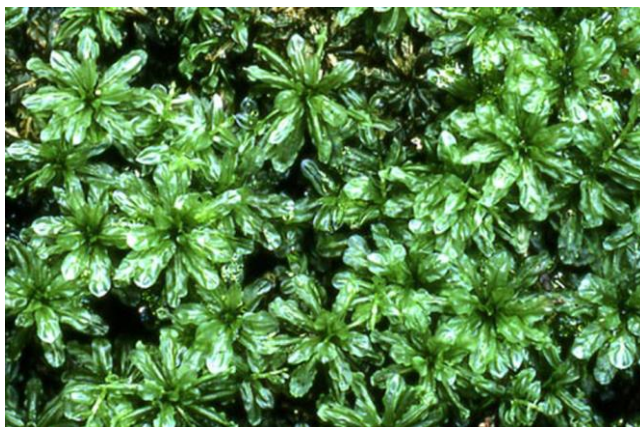


Figure 48. *Plagiomnium maximoviczii*, a species with lower compensation and saturation points in winter. Photo from Hiroshima University Digital Museum of Natural History, with permission.

It is intuitively obvious that light intensity will decrease as one penetrates further into the moss layer. In a

study on Antarctic mosses, Davey and Ellis-Evans (1996) found that not only did the light intensity decrease, but the attenuation maxima were at the wavelengths where chlorophyll has the greatest absorption peaks (675 nm and <450 nm). That again seems intuitive, since it is the green plant that is blocking the light penetration, and that green is the result of the chlorophyll pigments. But it is not quite that simple. Species differ in their absorption spectra, with stem orientation, stem density, leaf size, orientation, and pigment content all affecting absorption. While bryophytes all tend to have similar pigments, the relative proportions differ. Drying causes the wavelength variation to disappear and light to penetrate further into the clump or mat. These light penetration and wavelength changes resulted from both structural changes in the cells and pigment changes. This is adaptive, permitting deeper layers to carry out photosynthesis as the upper parts of the plants dry beyond the point where they can photosynthesize.

Because of its thin ozone layer, the Antarctic has some of the highest UV intensities on Earth. Among fourteen species of mosses, the light saturation level was 30-270 $\mu\text{M m}^{-2} \text{s}^{-1}$ (Davey & Rothery 1997). Nevertheless, these shade-adapted bryophytes exhibited no photoinhibition at any light intensity tested, up to 700 $\mu\text{M m}^{-2} \text{s}^{-1}$.

The thallose liverwort *Marchantia polymorpha* (Figure 28) is generally a shade plant, but tolerates at least some direct sun. Nevertheless, its light saturation level was only 2000-3000 lux, with inhibition occurring at higher levels (Mache & Loiseaux 1973). This is a very low saturation level when one considers that full sunlight in the temperate zone is typically about 70,000 lux. Isolated chloroplasts had a rate of photosynthesis about one tenth that of those in whole plants, suggesting that the plant may reduce the light level considerably to achieve its optimum low light level. Furthermore, high light stimulates changes in the chloroplast structure, inducing formation of continuous grana instead of the more typical small grana. By contrast, *Hypnum cupressiforme* (Figure 49), an epiphyte, had not reached saturation at any temperature (0-15°C) at light intensities of 12,000 lux (Kallio & Kärenlampi 1975).



Figure 49. *Hypnum cupressiforme* epiphytic habitat, a species with a wide range of temperatures without reaching light saturation. Photo by Dick Haaksma, with permission.

Rastorfer and Higginbotham (1968) measured the light saturation of *Bryum sandbergii* from Idaho, USA, at 20°C in 3% CO_2 and found that photosynthesis attenuated at

about 8 m watts per cm^2 (Figure 50). However, at 4°C , the photosynthetic rate declined at 8 m watts per cm^2 , suggesting photoinhibition at that low temperature (Figure 51).

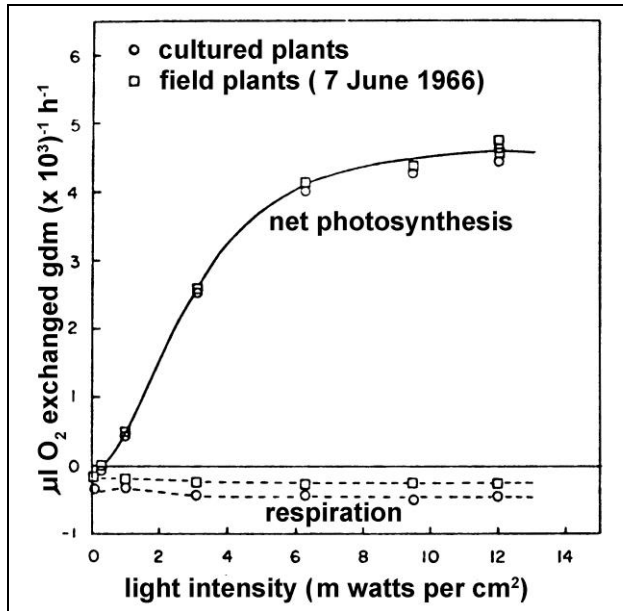


Figure 50. Mean effects of light intensity on net photosynthetic rates of *Bryum sandbergii* in the lab and field at 20°C , 3% CO_2 . $n=5$. Redrawn from Rastorfer and Higginbotham 1968.

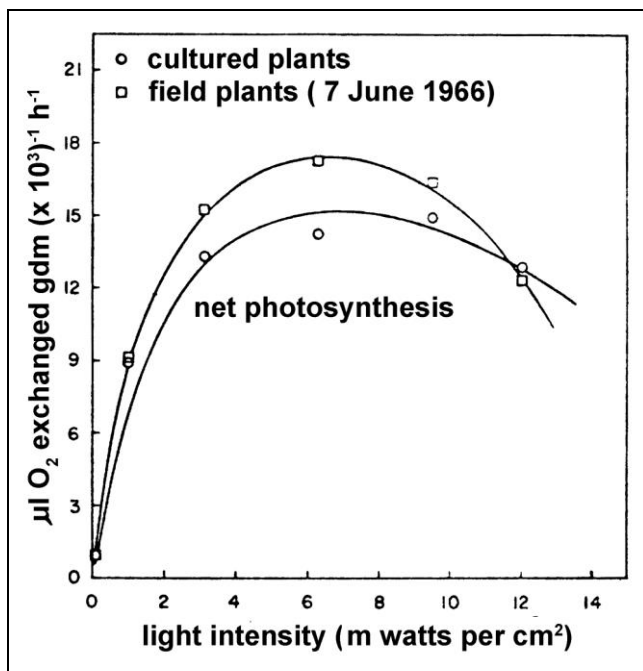


Figure 51. Mean effects of light intensity in the lab and field on net photosynthesis of *Bryum sandbergii* at 4°C , 3% CO_2 . $n=5$. Redrawn from Rastorfer and Higginbotham 1968.

In *Sphagnum cristatum* (Figure 24) and *S. australe* (Figure 52) from New Zealand, the light saturation point ranges from 111 to $266 \mu\text{M m}^{-2} \text{s}^{-1}$ (Maseyk *et al.* 1999). Color affected the saturation point of *S. cristatum*, with brown coloration causing an elevated saturation point. This, in turn, resulted in lower photosynthetic rates, lower

quantum efficiencies, and higher light compensation points than those of green plants.



Figure 52. *Sphagnum australe*, a species with a wide range of light saturation points. Photo by Tom Thekathyl, with permission.

In the Alaskan foothills of the Philip Smith Mountains, *Sphagnum angustifolium* (Figure 11) has a light compensation point of $37 \mu\text{M m}^{-2} \text{s}^{-1}$ and light saturation between 250 and $500 \mu\text{M m}^{-2} \text{s}^{-1}$ at 10°C (Harley *et al.* 1989). At 20°C , this relationship shifted upward, with the compensation point increasing to $127 \mu\text{M m}^{-2} \text{s}^{-1}$ and the saturation point to $500 \mu\text{M m}^{-2} \text{s}^{-1}$. *Sphagnum squarrosum* (Figure 53) experienced decreased photosynthetic capacity and chlorophyll bleaching when the tracheophyte cover was removed.



Figure 53. *Sphagnum squarrosum* 1 J. C. Schou, with permission.

Shade mosses have a light compensation point of 20-400 lux and sun species of 1000-2000 lux (Bazzaz *et al.* 1970). Saturation points generally run 10,000-30,000 lux for sun bryophytes (Proctor 1981). The epiphytic *Ulota crispata* (Figure 54) has a saturation point of 40,000 lux (Miyata & Hosokawa 1961). Thus, sun species of bryophytes have compensation and saturation levels about ten times as high as those of shade mosses. In Kansas, USA, the saturating light level for *Dicranum scoparium* (Figure 55), *Leucobryum glaucum* (Figure 61), and *Thuidium delicatulum* (Figure 62) is $200 \mu\text{M m}^{-2} \text{s}^{-1}$ (McCall & Martin 1991).



Figure 54. *Ulota crispa*, an epiphyte with a high light saturation point. Photo by Janice Glime.



Figure 55. *Dicranum scoparium*, a forest floor species. Photo by Janice Glime.

Aquatic plants from deep water are likely to have the lowest compensation points due to the low levels of light penetrating to depths. *Fontinalis* (Figure 30) exhibited a compensation point of 150 lux at 20°C, but this declined to 40 lux at 5°C (Burr 1941). Wetzell *et al.* (1985) found extremely low light compensation points for *Sphagnum auriculatum* var. *inundatum* (Figure 56) and *Juncus bulbosus* (a seed plant; Figure 59) from deeper water and higher values for the red alga *Batrachospermum* (Figure 60) from shallower areas.



Figure 56. *Sphagnum auriculatum*, a species with a very low light compensation point. Photo by Jan-Peter Frahm, with permission.

More recent measurements have put light measurements in terms of energy units or photosynthetically active radiation (PAR). Using energy units, Krupa (1978) found a compensation point of 0.6 and saturation point of 15 W m⁻² for the shade plant *Rhizomnium punctatum* (Figure 18). For the sun plants *Polytrichum piliferum* (Figure 57) and *Funaria hygrometrica* (Figure 58), the compensation points were 1.8 and 1.4 W m⁻², respectively, and the saturation points 55 and 100 W m⁻², respectively.

Even the bryophytes seem to operate below their light saturation points for most of the growing season. *Hylocomium splendens* (Figure 29) in the subarctic had a compensation point of 30 μM m⁻² s⁻¹ and a saturation point of 100 μM m⁻² s⁻¹ during the growing season, but it only experienced its light saturation level 65% of the time in July, 76% in August, and 96% in September (Sonesson *et al.* 1992).



Figure 57. *Polytrichum piliferum*, a sun species showing its hyaline hair points. Photo by Michael Lüth, with permission.



Figure 58. *Funaria hygrometrica*, a sun species. Photos by Michael Lüth, with permission.



Figure 59. *Juncus bulbosus*, a species with low light compensation point in deep water. Photo by Krzysztof Ziarnek, Kenraiz, through Creative Commons.

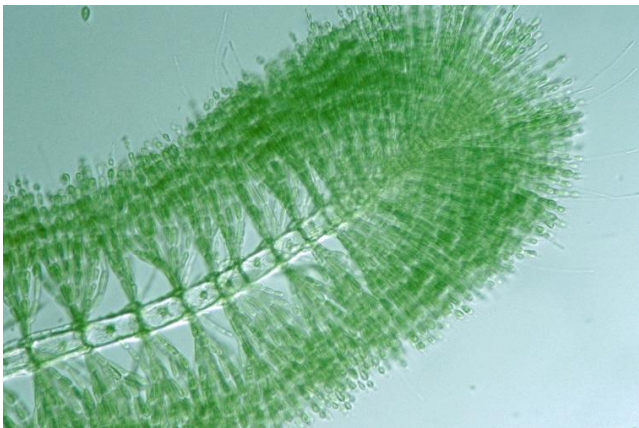


Figure 60. *Batrachospermum*, a shallow-water red alga with a high light compensation point. Photo by Yuuji Tsukii, with permission.

Light intensity, coupled with air humidity, seems to be a limiting factor for distribution of tropical epiphytic bryophytes in the Amazon (Frahm 1987). The low light intensities, coupled with high temperatures in the lowland forests, do not permit the bryophytes to reach their compensation points. Energy lost to respiration at such temperatures is greater than that gained in the low light levels of the lowlands. This relationship accounts for the increasing number of taxa and biomass with increased elevation.



Figure 61. *Leucobryum glaucum*, a forest floor species. Photo by Janice Glime.



Figure 62. *Thuidium delicatulum*, a species of open and forest. Photo by Janice Glime.

Excess Light

Excess light can limit bryophyte productivity by causing photoinhibition and damage to the chlorophyll. Dehydration usually protects the bryophytes from this damage by making the plants dormant. When dehydrated, *Grimmia alpestris* (Figure 63) from an alpine habitat had little chlorophyll fluorescence when subjected to high UV light intensity, whereas tracheophytes had high levels of fluorescence under the same conditions (Heber *et al.* 2000). When these mosses were rehydrated, their fluorescence increased, but that of the tracheophytes decreased upon rehydration. These mosses typically do not experience photodamage while dry, apparently using the same protective mechanism while dry as they are able to use successfully while hydrated.



Figure 63. *Grimmia alpestris*, a species that loses its chlorophyll fluorescence at high light intensities. Photo by Michael Lüth, with permission.

Experiments in canopy removal consistently indicate that high light intensities are not favorable to moss growth. In the Alaskan Arctic tundra, Murray *et al.* (1993) found that *Sphagnum*-dominated moss growth (Figure 53) increased by 2-3 times in shaded plots, but had a significant growth reduction in plots where the tracheophyte canopy had been removed. They suggested that the reduced growth was due to photoinhibition.

It is not uncommon for bryophytes to become pale in bright sunlight. Others develop red or other energy-absorbing pigments. But some of the effects of greater exposure to light, such as that seen in canopy removal experiments, is that the temperature and moisture conditions change. More of the daylight hours are at temperatures above that which is suitable for C_3 photosynthesis, forcing the plants to become dormant. And the added light and heat cause a greater loss of water by evaporation.

Continuous Light

As already discussed in Chapter 9-4, we know that continuous light may be deleterious to photosynthesis, causing 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, the continuous light damage observed by Kallio and Valanne occurred in laboratory experiments. Plants living in Polar Regions may acclimate to the seasonal change in continuous photoperiod (Richardson 1981).

It appears that continuous light alters the proportions of sugars and lipids. Sakai *et al.* (2001) found that green portions of the moss *Racomitrium barbuloides* (Figure 64) initially increased their storage of both sugars and lipids, but then they decreased. This decrease was accompanied with a significant decline in photosynthetic capacity. They suggested that the green tissue plays a major role in photoassimilate storage. It appears that accumulation of photoassimilates inhibits photosynthesis, but that such accumulation is unlikely under natural conditions.



Figure 64. *Racomitrium barbuloides*, a species that stores sugars and lipids, depending on environmental conditions. Photo from Digital Museum, Hiroshima University, with permission.

Bryophyte Canopy Structure

A bryophyte canopy is constructed differently from that of tracheophytes. Yet, while the leaf structure is very different, the mat structure may in many ways resemble the leaf structure of a tree leaf. Rice *et al.* (2008) investigated the trait relationships in ten species of *Sphagnum* (Figure 7-Figure 12). They found no relationship between N content and maximum photosynthesis per mass or area, differing from relationships in tracheophytes. Only capitulum area seemed to be relevant to N storage and maximum photosynthesis. Water content and carotenoid

concentration were the strongest predictors of maximum photosynthesis.

Tobias and Niinemets (2010) noted the large variation of light availability within the moss canopy. Furthermore, the lowest light levels are in the lower portions where the oldest tissues reside. Variation within the temperate-boreal forest moss *Pleurozium schreberi* (Figure 25, Figure 65) canopy can be greater than that between locations. Chl, Chl/N, and Chl/Carotenoid ratios increase with decreasing light availability between locations. Upper layers of the moss within habitat vary similarly, but after the light diminishes to 50-60% of the above-canopy levels, the layers demonstrate characteristics of senescence. At these depths, pigment and N concentration and photosynthetic capacity decrease with light availability. Thus, younger tissues are able to acclimate, but older ones do not.



Figure 65. *Pleurozium schreberi*, a common boreal feather moss. Photo by Janice Glime.

Waite and Sack (2010), in studying ten Hawaiian moss species, found that the moss species had low leaf mass per area and low gas exchange rates. The light-saturated photosynthetic rate per mass did not correlate with light levels in the habitat. Rather, microhabitat irradiance had the greatest influence on other photosynthetic parameters and structural traits, causing correlations of traits of leaf area, cell size, cell wall thickness, and canopy density. Costa size, canopy height, and light-saturated assimilation rate per mass correlated with structural allocation. N concentration correlated negatively with canopy mass per area (replacing leaf mass per area used in tracheophytes). The structures are different from those of tracheophytes, but the leaf size and function have been replaced with canopy mass and function.

Photoperiod Effects on Physiology

The effects of photoperiod as an event trigger are well known, but their effects on physiology of vegetative plants has been largely ignored (Cvetić *et al.* 2009). In the forest moss *Atrichum undulatum*, day length had no noticeable effect on photosynthetic pigments in the lab. Protein content and malate dehydrogenase activity were both higher in long day (16h light/8h dark) than in short day (8h light/16h dark) growth conditions. Long days produced higher concentrations of total phenolic compounds, greater peroxidase activity, and higher total antioxidative capacity.

Temperature

Once again we see evidence that limiting factors do not act alone. In *Fontinalis antipyretica* (Figure 30), photosynthesis increases with CO₂ concentration, but the level achieved is further dependent upon temperature (Maberly 1985). As the temperature goes up, boundary layer resistance decreases, permitting more CO₂ to enter the plants.

Aquatic mosses seem to be especially sensitive to high temperature, failing to sustain a healthy state for a prolonged period. Their lethal temperature can be quite low, as illustrated by *Leptodictyum riparium* (Figure 66) with a photosynthetic optimum at 23°C and death at 33°C (Sanford 1979). Several *Fontinalis* (Figure 30) species can do well at 20°C for a period of time; then they lose their green color and stop growing (Fornwall & Glime 1982; Glime 1982, 1987a, 1987b, 1987c, Glime & Acton 1979).



Figure 66. *Leptodictyum riparium*, a species that dies at 33°C. Photo by David Holyoak, with permission.

Interestingly, cold resistance seems to be related to heat resistance, as shown by Balagurova *et al.* (1996) for *Sphagnum* species. For *S. subsecundum* (Figure 67), the lethal temperature of cells was 60.3°C. Lethal cold temperatures ranged -16.1°C to -21.8°C.



Figure 67. *Sphagnum subsecundum*, a species that demonstrates both low and high temperature tolerance. Photo by Michael Lüth, with permission.

But temperature seems to have less detrimental effect on photosynthesis in bryophytes than we might expect from its role in other processes and organisms. While bryophytes have little ability to control temperature physiologically, they do have the ability to respond through

alteration of color that may be induced by day length, light intensity, or temperature itself. Could it be that the red color of the antheridial splash cups of *Polytrichum piliferum* (Figure 68) keeps the sperm warm on cool days in spring?

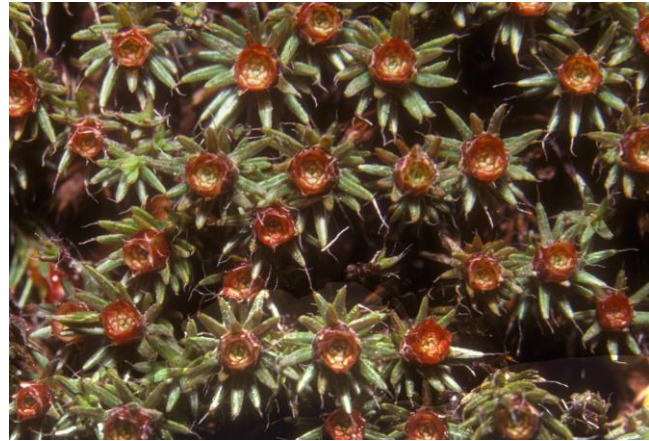


Figure 68. Antheridial splash cups of *Polytrichum piliferum*. Photo by Janice Glime.

Photosynthetic levels in some Arctic mosses seem to be similar over a wide temperature range. Vilde (1988) interpreted the mosses of the Arctic to be well adapted to their temperature regime. He found that photosynthesis has little temperature limitation and even high light intensity has little effect on these Arctic mosses. Uchida *et al.* (2002) found that the net photosynthetic rate in *Sanionia uncinata* in the high Arctic of Svalbard, Norway, was nearly constant at near-saturating light levels across the range of 7 to 23°C, but these same plants exhibited the extraordinarily high Q₁₀ of 3.0 for respiration in that range. This means that the gross photosynthesis must likewise have experienced a large increase with temperature in that range, with respiration using an increasing differential of that newly fixed carbon.

Temperature can have a threshold effect on bryophyte productivity. Asada *et al.* (2003) found that *Sphagnum* (Figure 7-Figure 12) species in a coastal British Columbia, Canada, peatland had lower temperature thresholds than did *Pleurozium schreberi* (Figure 25, Figure 65) and *Racomitrium lanuginosum* (Figure 69). Winter growth was important in this community, most likely because of greater availability of water; growth was more strongly correlated with precipitation than with temperature.



Figure 69. *Racomitrium lanuginosum*. Photo by Michael Lüth, with permission.

Kallio and Heinonen (1973) found that *Racomitrium lanuginosum* (Figure 69) could photosynthesize at -10°C (compensation point) and that it returned to 60% of its normal photosynthetic rate within three hours after storage at -30°C . Its optimum was at 5°C . They interpreted this moss to be pre-adapted to the wide range of temperatures in which it exists, lacking any clear physiological races with respect to temperature response.

Bryophytes acclimate to temperature, altering their optimum temperature for photosynthesis. This is likely to be accompanied by a shift in the light saturation level. However, the respiration rate does not necessarily acclimate at the same time. Both lowland and highland *Dicranum fuscescens* (Figure 70) showed photosynthetic acclimation to higher temperatures of mid summer, with highland plants having maximum rates of $2.1 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$ and lowland plants having only $0.74 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$ (Hicklenton & Oechel 1976). The optimum temperature shift can occur in as little as 48 hours in this species. The light saturation levels increased from spring to midsummer, then lowered again toward autumn. Dark respiration, however, did not acclimate.



Figure 70. *Dicranum fuscescens*, a species that acclimates to the higher temperatures of summer. Photo by Michael Lüth, with permission.

But even within the normal range of temperatures, bryophytes perform poorly at higher temperatures that favor most tracheophytes, as shown by the rapid drop in growth rate of the temperate pleurocarpous moss *Brachythecium rutabulum* (Figure 37) at temperatures above 15°C (Furness & Grime 1982). On the other hand, at only 5°C their growth is still 40% of their maximum rate at $\sim 19^{\circ}\text{C}$. This moss achieved a growth rate exceeding the maximum reported for seedlings of ten tracheophytes. Furness and Grime show the strong seasonal effects of temperature that help to explain some of the phenology of bryophytes. These results are consistent with its peaks of growth in spring and autumn, allowing it to compete with its tracheophyte neighbors in the British tall herb communities where they grow.

Frahm (1990) determined that high temperatures in tropical lowlands result in high respiration rates. Consequently, at temperatures above 25°C , net assimilation drops sharply. It is that high respiratory loss that limits much of bryophyte distribution in the tropics.

In the New Zealand species *Sphagnum cristatum* (Figure 24) and *S. australe* (Figure 52), the optimum temperatures for photosynthesis are 20 to 25°C (Maseyk *et al.* 1999). Liu *et al.* (2001a) found that *Plagiommium*

acutum (Figure 23) and *P. maximoviczii* (Figure 48) could maintain net photosynthetic gain for 10-30 minutes from -15°C to 45°C . Despite their cold climate, fourteen bryophytes in the Antarctic have a temperature optimum for gross photosynthesis of $10-20^{\circ}\text{C}$ and of $0-20^{\circ}\text{C}$ for net photosynthesis (Davey & Rothery 1997). With the relatively high Antarctic light intensity, these bryophytes are usually temperature limited during the growing season.

Like the experiments on *Fontinalis duriaei* (Figure 71) of Glime and Acton (1979), Dilks and Proctor found that prolonged exposure to high temperatures caused a drop in productivity (Figure 72), thus demonstrating that duration of an experiment would influence the determined optimum temperature. While these curves may indicate the general trend of the response, we must exercise caution because the higher than atmospheric level of CO_2 used would most likely push the temperature optimum to a higher level.



Figure 71. *Fontinalis duriaei*, a species that experiences a drop in productivity after prolonged high temperatures. Photo by Michael Lüth, with permission.

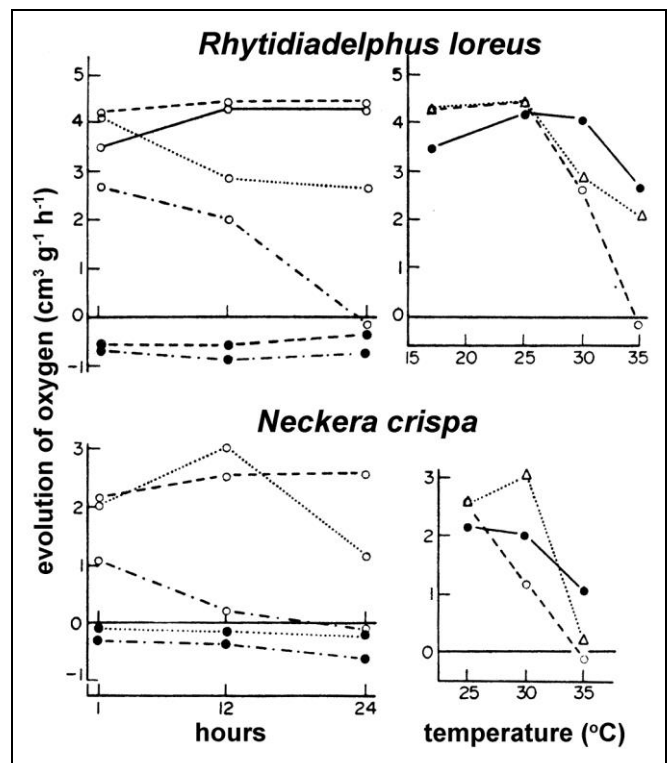


Figure 72. Effect on photosynthesis of prolonged exposure at various temperatures (— 17°C ; - - 25°C ; 30°C ; -.-.- 35°C) and responses for net assimilation after 1 hour (●), 12 hours (Δ), and 24 hours (○). Redrawn from Dilks & Proctor 1975.

Rastorfer and Higginbotham (1968) demonstrated an increase in net photosynthesis of *Bryum sandbergii* in the range of 4-24°C, with a drop at 34°C. Dilks and Proctor (1975) compared twenty-three mosses and five liverworts at temperatures varying 5-45°C. These bryophytes typically exhibited fourth order polynomial curves that rose to an optimum, then dropped abruptly (Figure 73). However, not all species showed such a sudden drop and some exhibited a broad optimum, as seen in Figure 74. It is interesting that the more Arctic *Racomitrium lanuginosum* (Figure 69) exhibits the opposite curve shape – a sharp rise with temperature to its optimum at 5°C, and a slow decline above the optimum (Kallio & Heinonen 1973; Kallio & Kärenlampi 1975). *Pleurozium schreberi* (Figure 25, Figure 65) seems to exhibit a nearly bell-shaped curve with temperature, exhibiting an optimum at 10-15°C (Kallio & Kärenlampi 1975).

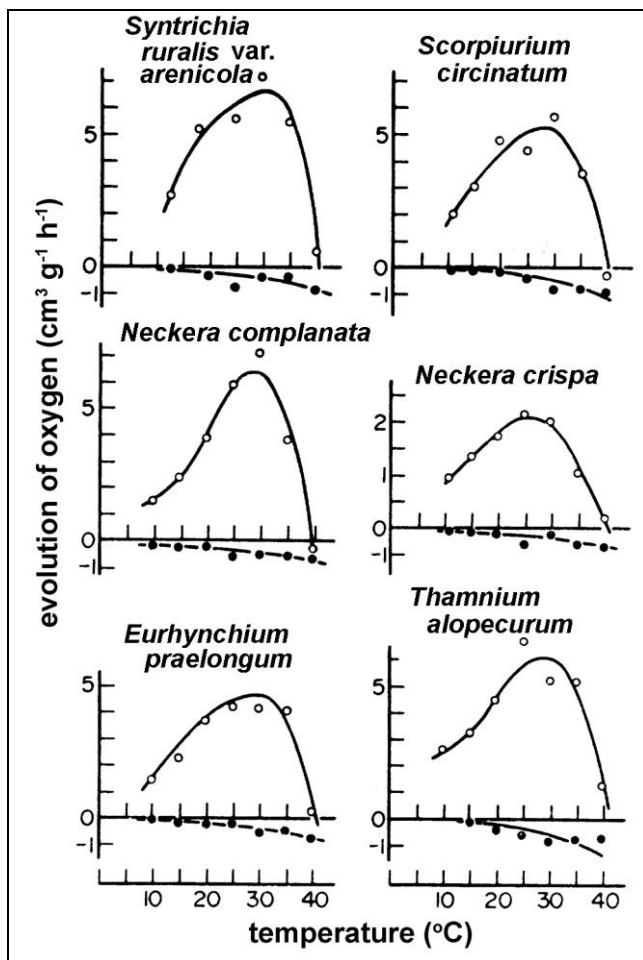


Figure 73. Photosynthesis at various temperatures. O = net assimilation; • = respiration. These responses are modelled with a fourth order curve. Redrawn from Dilks & Proctor 1975.

In the harsh conditions of the Antarctic, we can find some novel responses to temperature and light intensity. The ubiquitous moss *Bryum argenteum* (Figure 75) had a strong dark respiration response to temperature, causing significant changes in CO₂ exchange rates (Green *et al.* 1998). This species had a strong linear correlation between gross photosynthesis and electron-transport rate in PS II. Green and coworkers suggested that this deviation from the curvilinear relationship in tracheophytes might result from

some sort of suppression of dark respiration in the light. In fact, it seems that both bryophytes and C₃ tracheophytes experience photorespiration in the light. Nevertheless, the relationship appears to be different in the bryophytes.

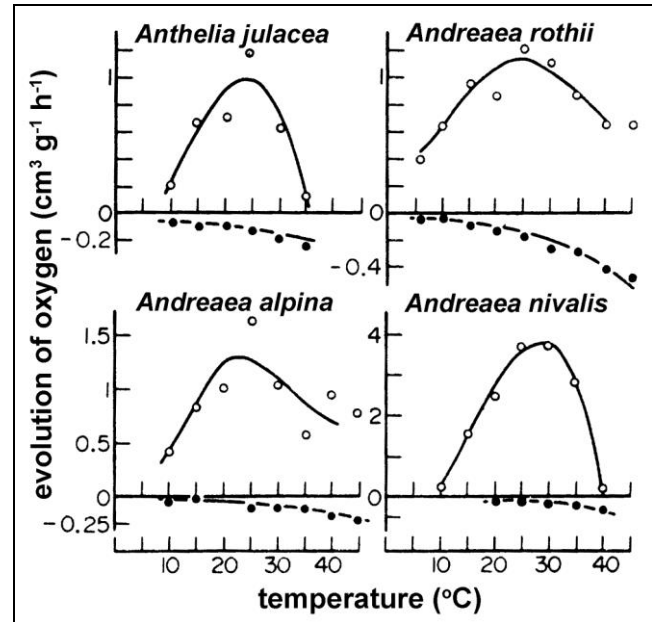


Figure 74. Photosynthesis at various temperatures for several mosses with a northern range. O = net assimilation; • = respiration. These responses are modelled with a fourth order curve but lack the sudden drop seen in Figure 73. Redrawn from Dilks & Proctor 1975.



Figure 75. *Bryum argenteum*, a species with a strong respiratory response to rising temperatures. Photo by Michael Lüth, with permission.

Compensation Point

In studying 27 temperate bryophytes, Dilks and Proctor (1975) found the high temperature compensation point to be about 35-40°C. However, temperature compensation points are affected by both light intensity and CO₂ concentration and vice versa (Rastorfer 1971).

Acclimation

Acclimation is a physiological change that adjusts to new conditions. It differs from adaptation in that the ability to change is programmed in the genetic code and the changes are temporary and non-heritable. For example, low temperatures can slow down the photosynthetic

apparatus, but in some habitats high light intensities may still cause high excitation of the photosynthetic apparatus. There is evidence [in *Leucodon sciurioides* (Figure 76)] that low temperatures may induce non-radiative dissipation of the absorbed light energy (Deltoro *et al.* 1999). This dissipation is necessary to protect the photosynthetic apparatus from excess excited electrons. This ability to dissipate energy and recover photosynthetically almost immediately upon return to temperatures above freezing permits this bryophyte to survive high light intensity at considerably lower temperature limits. The moss has become acclimated to the new temperature. This moss is one of many examples of preadaptation observed in mosses. This Mediterranean moss is capable of surviving light and temperature conditions that might be encountered in the Antarctic.



Figure 76. *Leucodon sciurioides*, an epiphyte, showing dry branches to the left and wet ones in the middle. Photo by Michael Lüth, with permission.

Even changes in CO_2 concentrations can elicit acclimation in bryophytes. *Riccia fluitans* (Figure 77) lives part of its life floating on lakes and ponds. But some of these plants end up stranded on soil out of water. This environment is much higher in both light and CO_2 than the floating environment from which they came. The relative growth rate under low light and low CO_2 was 0.011 day^{-1} , whereas under high light intensity and high CO_2 it was 0.138 day^{-1} (Andersen & Pedersen 2002). Interestingly, maximum photosynthesis decreased with increasing light intensities, but it increased with increasing CO_2 . The CO_2 compensation point was very low at high light and low CO_2 levels, increasing at low light and high CO_2 levels. These shifts in compensation point are an advantage for plants that live in dense mats in the water with low CO_2 availability and high light intensity at the surface and greater CO_2 and lower light intensity on the lower side of the floating mat.



Figure 77. *Riccia fluitans*, a species in which photosynthetic rate decreases in high light. Photo by Jan-Peter Frahm, with permission.

Glime and Acton (1979) used mosses conditioned for three weeks to a range of temperatures in the lab to demonstrate the effect of temperature on the photosynthesis of *Fontinalis duriaei* (Figure 71). These experiments indicated that the prior history of the moss affected its productivity at a given temperature. Maximum growth occurred in spring and fall and peak assimilation occurred at 5400 lux at 10°C .

Fornwall and Glime (1982) approached the same seasonal question by using field-acclimated plants and showed that *Fontinalis duriaei* (Figure 71) altered its maximum temperature for photosynthesis seasonally. When mosses were brought from the field and their photosynthesis measured in the range of $0.5\text{--}40^\circ\text{C}$, optimal temperatures shifted from 10°C in January to 35°C in August. However, these were short-term measurements of photosynthesis with one hour of acclimation to the respirometer flask and two hours of measurement time. Other experiments with growth at these temperatures over a 15-week period showed that the mosses could only sustain this high level of productivity for a short time and that in fact, temperatures above 20°C caused the mosses to cease growth in the lab (Glime 1982, 1987a, b, c). A more thorough discussion of temperature acclimation is in Chapter 10-1.

The color of these mosses changed with the seasons as well, with the most deep green color in March and April and a brown color in September (Fornwall & Glime 1982). The puzzling result of this study is that not only did mosses from a stream with wide seasonal fluctuations show this acclimation, but those mosses that resided in a stream that maintained a summer temperature of 8.5°C likewise shifted their summer optimum temperature to 35°C in the lab photosynthetic experiments. This suggests that the optimum may not result from acclimating to temperature but that it instead may be stimulated by the lengthening photoperiod or other environmental parameter associated with the seasons.

One might expect temperature acclimation in more northern regions. Oechel *et al.* (1975) demonstrated that subarctic populations of *Dicranum fuscescens* (Figure 70) exhibited a high temperature acclimation (Figure 78). Acclimation to warm temperatures caused a higher temperature optimum (similar to mean field temperatures,

ranging 5-15°C), higher maximum net photosynthetic rate, and a lower photosynthetic max at 0°C.

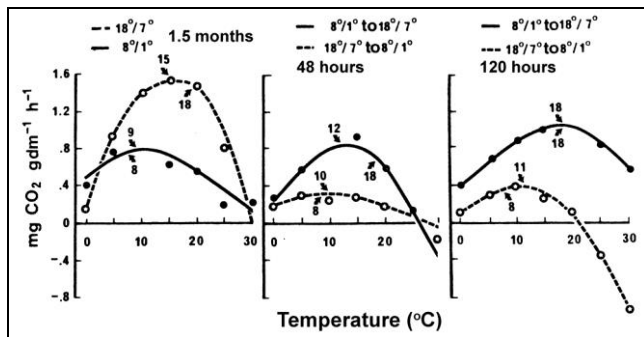


Figure 78. Acclimation responses of net photosynthesis to temperature in *Dicranum fuscescens* (Figure 70) at Schefferville, Quebec (55°N) after cultivation at warm (18°/7°C) and cool (8°/1°C) temperatures for 1.5 months. Modified from Oechel *et al.* 1975.

Dicranum fuscescens (Figure 70) in subarctic Canada raised its temperature optimum for photosynthesis from 0-10°C in the beginning of June to 10-20°C by 7 July, with net productivity dropping drastically by 29 July (Figure 79), but its dark respiration rates showed no evidence of acclimation (Hicklenton & Oechel 1976). The tissue temperatures fluctuated between a low of 3°C and a high of 26°C during that period. The remarkable drop in productivity by the end of July suggests that the moss could not sustain the high temperature respiratory cost and eventually lost net gain in productivity. At the other end, net productivity was negative at temperatures above 15°C on 5 June. On the other hand, Arctic populations had an optimum temperature that was generally higher than the mean maximum tissue temperature with optima ranging from 12-19°C (Oechel *et al.* 1975). This high optimum commonly accompanies tolerance for lower temperatures.

Even short-term adjustments to changing light levels are possible. The drought-tolerant *Syntrichia ruralis* (Figure 27) experienced increases in F_v/F_m , NPQ, and light-adapted PS II yield [ϕ (PS II)] in sun plants transplanted to the shade, and concurrent decreases in shade plants transplanted to the sun (Hamerlynck *et al.* 2002). But these plants also seemed to have a memory of their old habitat; sun plants performed at a consistently lower level in the shade than did non-transplanted shade plants. Nonetheless, the ability to adjust its photosynthetic apparatus to changing light conditions permits this species to take advantage of a habitat in which the canopy above it changes, changing its exposure to sun vs shade.

One of the changes that occurs on a seasonal basis is a change in the light compensation point and light saturation point. In *Plagiommium acutum* (Figure 23) and *P. maximoviczii* (Figure 48) from the temperate zone in China, light compensation points switch from 20 $\mu\text{M m}^{-2} \text{s}^{-1}$ in the winter to 40 $\mu\text{M m}^{-2} \text{s}^{-1}$ in the summer (Liu *et al.* 2001a). Likewise, the light saturation ranges from 200 $\mu\text{M m}^{-2} \text{s}^{-1}$ in winter to 400 $\mu\text{M m}^{-2} \text{s}^{-1}$ in summer. The temperature optimum also ranges from a low of 20°C in winter to a high of 35°C in summer.

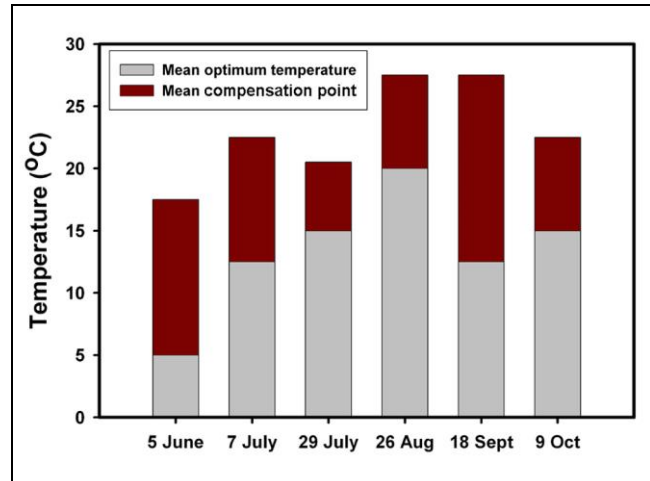


Figure 79. Mean optimum temperatures and upper temperature compensation points for *Dicranum fuscescens* (Figure 70) photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel 1976.

Aquatic Differences

In streams, the availability of CO_2 varies widely, dependent on the temperature, pH, and rate of flow. In standing water, CO_2 can be even more limiting as temperatures rise and the CO_2 goes out of solution and is lost into the atmosphere. These CO_2 conditions are typically limiting to plant growth, including bryophytes (Madsen *et al.* 1993; Rice & Schuepp 1995). However, structural modifications of leaf spacing, leaf size, and exposure of photosynthetic cells among hyaline cells in *Sphagnum* (Figure 80-Figure 81) all contribute to making aquatic taxa less resistant to CO_2 uptake than are non-aquatic taxa (Rice & Schuepp 1995).

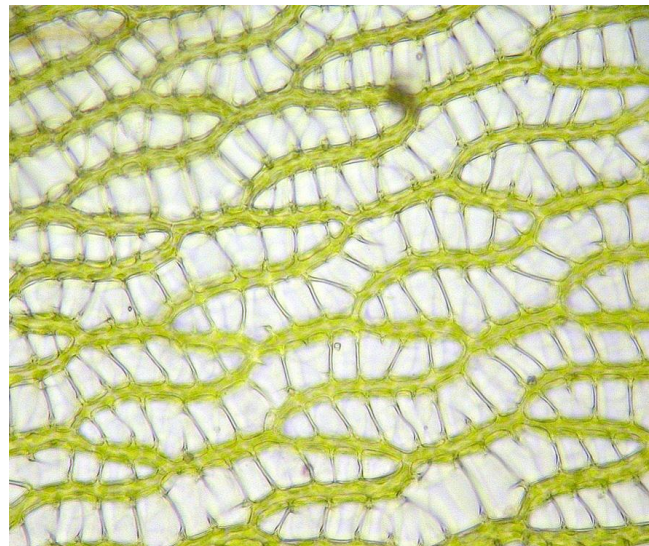


Figure 80. *Sphagnum novo-zelandicum* leaf cells showing hyaline cells and photosynthetic cells. Photo by David Tng, with permission.

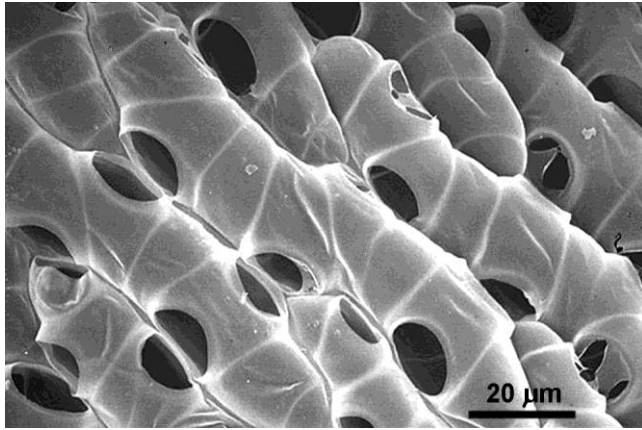


Figure 81. *Sphagnum* hyaline cells and pores. Photo from Botany Website, UBC, with permission.

In the aquatic environment, it is the deep water that has the highest CO₂ concentration (Maberly 1985), a product of microbial activity in the sediments. But deep water has the lowest light intensity. A testimony to the CO₂ limits imposed on aquatic mosses is their ability to grow well at extremely low light levels in the bottoms of lakes. These limits change seasonally, with productivity of *Fontinalis antipyretica* (Figure 30) in the North Bay of Esthwaite Water, England, being limited by light in November and by temperature in March. In August, despite microbial decomposition, intense competition for CO₂ from dense phytoplankton limits the moss productivity.

Another problem for aquatic bryophytes is that not only does the intensity of light decrease, but the spectral quality changes with depth. A reduction in water clarity due to increased load of dissolved organic carbon in Grane Langsoe caused a greater attenuation of blue light, relative to red light (Schwarz & Markager 1999). Photosynthesis is most active in red light, with its second peak in blue. However, red light has long wavelengths with low energy and thus is readily absorbed by water, making it diminish quickly with depth. The additional decrease in blue light, which has a short, high-energy light wave, means that the bryophytes are deprived of both of the most active wavelengths. The most abundant moss (70% of biomass) in these conditions was *Warnstorfia exannulata* (Figure 82), which exhibited its maximum absorption in the young parts that were most highly pigmented.



Figure 82. *Warnstorfia exannulata*, a species with relatively low productivity in deep water. Photo from Biopix, through Creative Commons.

Riis and Sand-Jensen (1997) showed that this species and *Sphagnum subsecundum* (Figure 67) grew faster in deep than in shallow water in a low-nutrient lake in Denmark. Their study supported the hypothesis that supersaturated CO₂ as well as low temperatures and higher nutrient concentrations on the bottom of the lake supported the faster growth, despite the lower light intensity. One advantage of the lower temperature is that gases such as CO₂ stay in solution more easily. *Sphagnum subsecundum* exhibited lower dark respiration (1.3-fold) and higher photosynthesis (3.3-fold) at 9.5 m than at 0.7 m conditions.

In lakes, light attenuates with depth, often creating a photosynthetic desert at the bottom. Bryophytes, already adapted to low light, typically grow to greater depths than their macrophytic tracheophyte counterparts. In the Karelia Republic of northwestern Russia, bryophytes dominate at depths in three acidified lakes (pH of water 5.3-5.9) (Ilyashuk 2002). One lake was dominated by a dense carpet of *Sphagnum denticulatum* (Figure 83) at a depth of 5.0-7.6 m, covering about 50% of the bottom. A second lake had only *Warnstorfia exannulata* s.l. (Figure 82) at 5.0-7.0 m, covering 20% of the bottom. The third had only *Fontinalis hypnoides* (Figure 84) at 4.5-5.5 m, covering 13% of the bottom. In these latter two lakes, the net annual production by the mosses was 32-41 g air-dry mass m⁻² yr⁻¹. In the *Sphagnum*-dominated lake, however, the rate was much higher (157 g m⁻²).



Figure 83. *Sphagnum denticulatum*, a species with a high rate of annual production in deep water. Photo by Michael Lüth, with permission.



Figure 84. *Fontinalis hypnoides*, a species with relatively low productivity in deep water. Photo by Ivanov, with permission.

Summary

Photosynthesis is limited by light intensity, temperature, CO₂ availability, and water availability. The compensation point is the level of any of these variables at which the CO₂ assimilation is equal to the CO₂ respired by the plant. These are influenced not only by the environment and seasons, but also by plant density and the plants themselves.

Limits are at both ends of the scale. There is a minimal level needed for successful net gain, but there are also upper limits beyond which the plants will lose energy. The saturation level is that level at which increase causes no further photosynthetic gain.

During the growing season, water is typically the limiting factor. However, some bryophytes are able to use water from fog and dew. Given enough water, CO₂ is often limiting. However, in some habitats, such as lake sediments, CO₂ emissions from bacteria and various invertebrates may elevate the CO₂ levels above ambient air CO₂. And some bryophytes, especially *Sphagnum*, may use methane, converted to CO₂ by bacteria, to supply their CO₂. Aquatic bryophytes may use cation exchange to lower the pH in their immediate vicinity, permitting the use of bicarbonate by shifting the equilibrium toward free CO₂. Furthermore, it is possible that some may use external carbonic anhydrase to capture bicarbonate, but experiments to support this in bryophytes are lacking. Light may be limiting, but bryophytes seem to have the lowest light compensation point of any plant group. High light intensity can cause photodamage.

Net photosynthetic activity in many, perhaps most, bryophytes exhibits an abrupt drop above its optimum due to the loss of CO₂ through photorespiration.

Bryophytes acclimate to temperature, CO₂ level, and light intensity. This permits changes in the optimum, compensation point, and upper level limit or saturation point.

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