

# CHAPTER 10-1

## TEMPERATURE: EFFECTS

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# CHAPTER 10-1

## TEMPERATURE: EFFECTS



Figure 1. Snow on the peak of Mount Edith Cavell, Canadian Rockies, in Jasper National Park, Alberta, Canada. Few plants can grow in this harsh, rocky habitat, but lichens and bryophytes may be found in microsites. Photo by Janice Glime.

### Temperature

The temperatures experienced by various microhabitats on the Earth vary widely, from volcanic lava to exposed rock in the Antarctic. Temperatures at which bryophytes exist also vary widely, from those of geothermal fields to glacial polsters (Figure 1). But the daily temperature of a bryophyte may vary more than we had imagined. Gabriel (2000) points out the importance of microclimate temperatures to the growth rate for Azorean forest bryophytes. And on a single sunny afternoon in the Keweenaw Peninsula of Michigan, with an air temperature of  $\sim 28^{\circ}\text{C}$ , we measured moss leaf temperatures up to  $41^{\circ}\text{C}$ , whereas a nearby black rock, also in the sun, registered only  $31^{\circ}\text{C}$ ! (Hribljan & Glime, unpublished data).

Proctor (2014) includes cooling as one of basic needs of plants on land. Emphasizing the importance of scale, he contends that for large plants (tracheophytes) convective cooling is most important. For low-growing plants such as bryophytes, evaporative cooling is sufficient.

As  $C_3$  plants, bryophytes are adapted to have a net photosynthetic gain at a relatively low temperature, some (e.g. *Racomitrium lanuginosum*; Figure 2-Figure 3) as low as  $-10^{\circ}\text{C}$  (Kallio & Heinonen 1973), but would seldom be expected to do as well at temperatures above  $25^{\circ}\text{C}$ . Even tropical bryophytes seem to do poorly above  $25^{\circ}\text{C}$  (Frahm 1990), where their net assimilation rate decreases drastically, respiration rates are high, and they fail to reach their compensation point (Frahm 1987). Those bryophytes that typically experience cool weather during the growing season, as for example *Hylocomium splendens* (Figure 4) from Swedish Lapland, fail to benefit by enhanced growth from a mean increase of  $1.5\text{--}3^{\circ}\text{C}$  during the growing season (Jägerbrand *et al.* 2003). It seems that at high temperatures, most bryophytes may become dormant, suffer reversible depression of photosynthesis (Weis *et al.* 1986), or die; irreversible damage to photosynthesis can result from damage to photosystem II (Weis *et al.* 1986).





Figure 2. *Racomitrium lanuginosum* forming large mounds in Iceland. Photo by Janice Glime.



Figure 3. *Racomitrium lanuginosum* showing the awns that help reflect light and reduce the temperature while reducing water loss. Photo by Michael Luth, with permission.

Temperature and seasonal changes can play a significant role in determining the distribution of bryophytes. For example, when comparing bryophyte floras of the French Alps and Britain, Pentecost and Zhang (2002) found that the distribution of *Palustriella commutata* (= *Cratoneuron commutatum*; Figure 5) is influenced more by temperature than by water chemistry, despite the need for free CO<sub>2</sub>. Dilks and Proctor (1975) have shown that most bryophytes have a relatively narrow range of temperatures for net photosynthetic gain, experiencing a sharp decline just past the optimum. Indeed, for most bryophytes, the optimum is near 20°C, and for many it is much lower.



Figure 4. *Hylocomium splendens* from British Columbia, Canada. Photo by Des Callaghan, with permission.



Figure 5. *Palustriella commutata* in one of its common habitats (Upper) and closeup (Lower). Photos by Michael Luth, with permission.

## Bryophyte Alteration of Temperature

The temperature of a bryophyte is not necessarily the temperature we would feel as we walk by. Often it is quite different in the nearby niches, cooled by air from a rockhouse or warmed by a spot of sun on the absorbing bryophyte tissues. It is the temperature of the microclimate that often determines the growth rate and distribution of the bryophytes (Gabriel 2000).

Not only do cushions retain water, but they moderate the temperature (Rod Seppelt, Bryonet 27 June 2022). In the Antarctic, when the temperature drops below 0°C, the moss cushions likewise drop in temperature. However, when the cushion begins to freeze, latent heat begins to elevate the temperature to as much as 2°C. This delays the denaturation of the cellular proteins.

Imagine a moss sitting in the forest, still hydrated because of the protection of the forest. Yet as the Earth moves and the position of the sun changes, sunflecks dance about the forest floor like butterflies. One minute the hydrated moss is in the cool shade of the forest, but the next it is beset by the heat of the sun. Proctor (1982) reported sunfleck temperatures up to 39°C when the air temperature was a mere 20°C.

In his treatment on the upper temperature limit of life, Kempner stated that there could be "no defense against high temperatures unless the laws of thermodynamics were violated." But the literal meaning of that is simply not true. Animals sweat, taking advantage of evaporative cooling. Tracheophytes transpire, pumping water from below ground to their leaves, then to the atmosphere, cooling by



the heat absorbed as liquid water changes to gas. And bryophytes, too, can take advantage of transferring water from lower parts to their upper parts where it evaporates and cools the growing tips. And plants, like animals, can reflect the sun by presenting white, reflective surfaces to prevent absorption of the sun's rays. In bryophytes, this reflection may be achieved by **hyalocysts** (hyaline cells), as in *Sphagnum* (Figure 6-Figure 8) and *Leucobryum* (Figure 9-Figure 11), white hair tips on the leaves, as in *Racomitrium* (Figure 3), *Tortula/Syntrichia* (Figure 12-Figure 13), and *Polytrichum piliferum* (Figure 16), or possibly even by the refractive nature of papillae (Figure 14-Figure 15) that give the moss a dull appearance to our eyes.



Figure 6. *Sphagnum papillosum*, a species that lives in full sun that protects its living cells by hyaline cells (hyalocysts). Photo by David Holyoak, with permission.

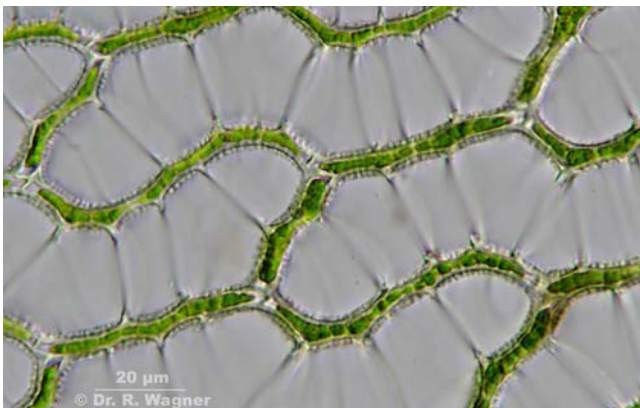


Figure 7. *Sphagnum papillosum* leaf cells showing the large hyaline cells that nearly hide the small photosynthetic cells. Photo by Ralf Wagner <[www.drralf-waner.de](http://www.drralf-waner.de)>, with permission.



Figure 8. *Sphagnum papillosum* leaf cross section showing hyaline cells that nearly surround the photosynthetic cells. Photo from Botany Website, UBC, with permission.



Figure 9. *Leucobryum glaucum* showing its cushion growth form and whitish color. Photo by Janice Glime.

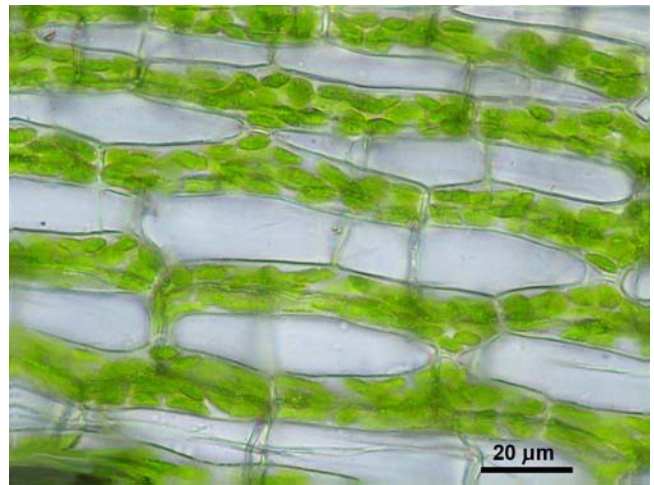


Figure 10. *Leucobryum glaucum* leaf cells showing hyaline and photosynthetic cells. Photo by Ralf Wagner <[www.drralf-waner.de](http://www.drralf-waner.de)>, with permission.

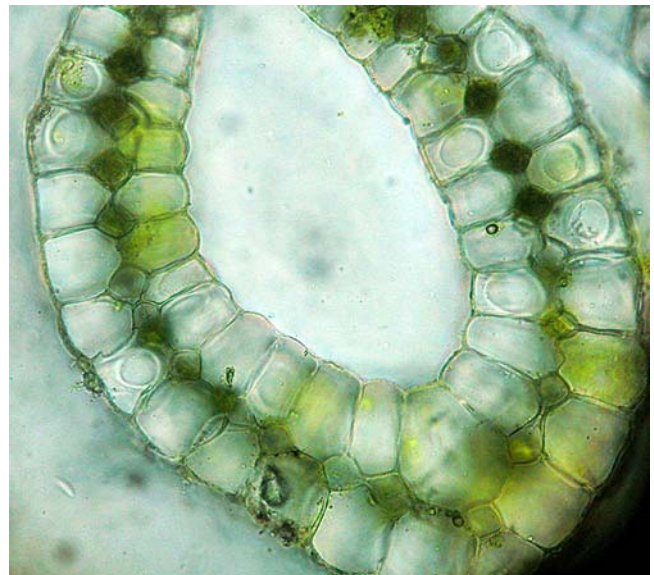


Figure 11. *Leucobryum glaucum* leaf cs showing large hyaline cells surrounding the green photosynthetic cells. Photo by Walter Obermayer, with permission.





Figure 12. *Tortula muralis* wet, showing awns. Photo by Christophe Quintin, through Creative Commons.

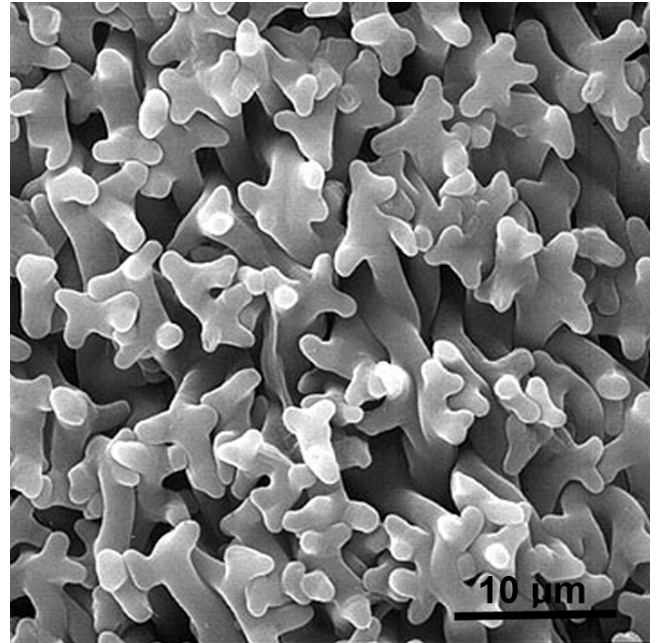


Figure 15. *Tortula muralis* leaf SEM image showing branched papillae that reflect and refract light, helping to keep the leaf cool. Photo from Botany Website, UBC, with permission.



Figure 13. *Tortula muralis* dry, showing the twisting of leaves and awns that help to reflect light and protect chlorophyll. Photo by Kristian Peters, with permission.



Figure 16. *Polytrichum piliferum* exhibiting the hyaline hair tips that help to reflect light and hence aid in cooling the moss in the hot sun. Photo from Botany Website, UBC, with permission.



Figure 14. *Tortula muralis* leaf CS showing branched papillae. Photo from Botany Website, UBC, with permission.

Even as ectothermic animals can modify their temperature by such activities as basking, changing cell shapes, and rearranging scales, bryophytes can survive at sub-zero air temperatures by their own ability to alter the temperature. Lewis Smith (1988) found that in Antarctica the temperature at the surface of a *Schistidium* cushion (Figure 17) could vary from  $-9.2^{\circ}\text{C}$  to  $42.8^{\circ}\text{C}$  on a single day in January, whereas only 1 m away the temperature 10 cm down into a *Ceratodon* turf (Figure 17) had almost no variation (Figure 19). He attributed the lack of change in the *Ceratodon* turf to reduction of heat transfer by the moist turf. However, the nearby but typically near-black *Schistidium* could operate as a black body that would absorb daytime heat, then re-radiate it at night.





Figure 17. *Ceratodon purpureus* (left) in depression that maintains a near constant temperature. *Schistidium antarctici* (right) on ledge where dark color absorbs heat in its dry state. Photo courtesy of Rod Seppelt.

A good example of temperature differences is that of temperatures in the Snowy Mountains of southeastern Australia (Körner & Cochrane 1983). On midsummer days, the maximum leaf-air temperature difference in the trees was a mere 7°C, rising to 13°C in the shrubs, 21°C in the dwarf shrubs, and 24°C in the grass tussocks and rosette plants. But in an isolated moss cushion, the temperature was 30°C higher than the air temperature! The differences were less severe at high elevations except for the low plants, where the moss cushion set the record. Temperatures change quickly within the moss cushion, with deeper portions exhibiting less extreme conditions, as seen in the Antarctic (Figure 18-Figure 19). The bare soil, however, reached 81.9°C! Obviously the mosses must germinate and get established well enough to control their own temperatures before that kind of heat is reached.

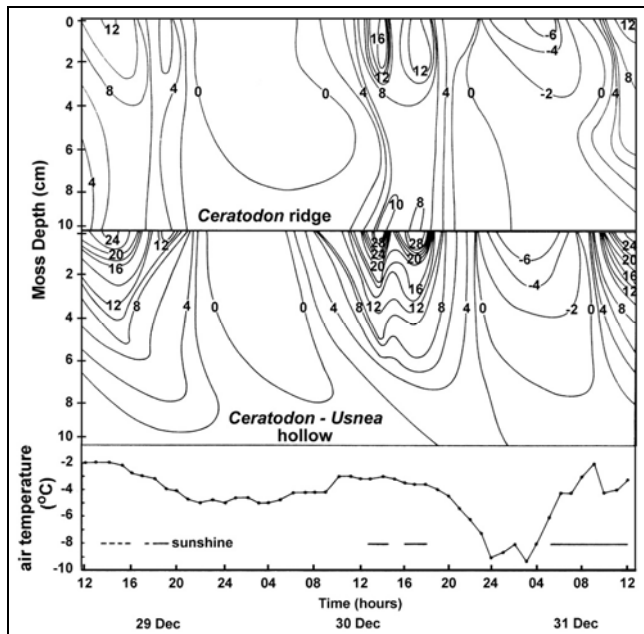


Figure 18. Isotherms for two days in December through a *Ceratodon* turf down to 10 cm and a *Ceratodon* turf covered by dense *Usnea antarctica*. Redrawn from Lewis Smith 1988.

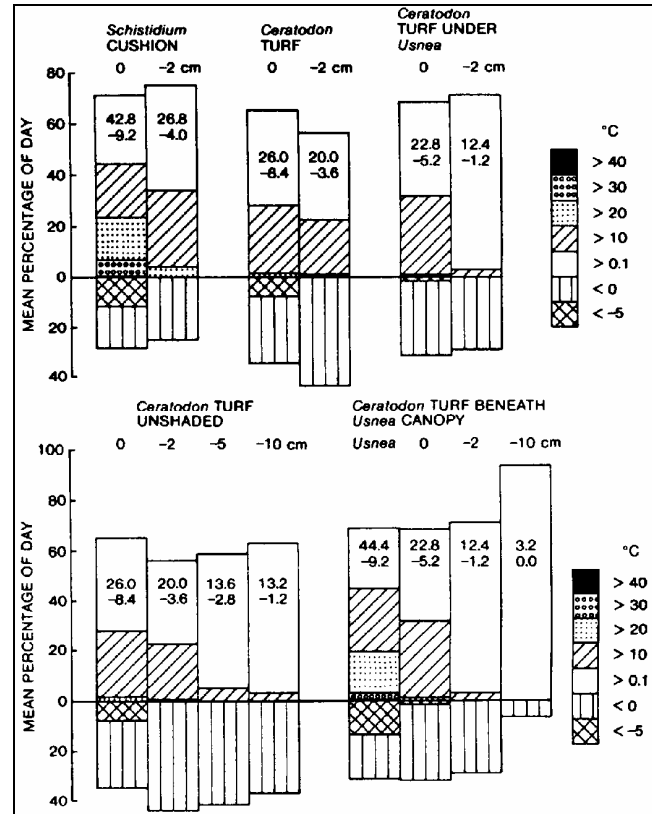


Figure 19. Differences in summer temperatures of surface and subsurface parts of Antarctic moss communities during 13-day period, expressed as mean percentages per day. Absolute maxima and minima for 13-day period appear in bars. From Lewis Smith 1988.

On Mount Fuji, Japan, *Racomitrium lanuginosum* (Figure 2-Figure 3) experiences as much as a 42°C daily temperature range while *Grimmia elongata* (Figure 20) nearby has only a 26°C range. Maruta (1986) suggests that the difference lies in the less dense mat of *R. lanuginosum*.



Figure 20. *Grimmia elongata*, illustrating the dense mat that insulates and maintains less temperature variation than loose mats. Photo by Michael Luth, with permission.

The state of hydration, as we might expect, plays a major role in temperature. Water is slow to change its temperature, compared to air, so it is not surprising that Rydin (1984) found the highest temperatures among



*Sphagnum* (Figure 6) species when they were completely dry. Even shade had little effect on the temperature except when the moss was dry, and under any given set of conditions, there was no difference among *Sphagnum* species.

### Soil Temperatures

Bryophytes are likewise important in altering the soil temperature. This same ability to act as a black body can add warmth to the soil, but in other cases, the moss could absorb or reflect the heat (or light) and prevent it from reaching the soil beneath.

In the tundra, the bryophytes can prevent warming of the soil. In permafrost areas, mosses contribute to maintaining the permafrost in shallower soils (Van Der Wal & Brooker 2004) compared to bare areas. Van Der Wal and Brooker found that herbivore grazing and trampling by barnacle geese and reindeer reduce the growth of the mosses and hence their depth. This, in turn, increases the soil temperatures. Enclosures that prevented this animal activity and permitted the moss mat to become thicker caused a 0.9°C decrease in the soil temperature in just seven years (Van der Wal *et al.* 2001). This cooling caused a 50% reduction in biomass of the grass *Poa arctica* and the polar cress *Cardamine nymanii*.

Thick moss cover acts as insulation, preventing the warmth of the sun from reaching the soil. Under cryptobiotic crusts in the alpine tundra basin of the Olympic Mountains, Washington, USA, the soil surface and immediate subsurface was 5-8°C cooler at midday under moss-dominated crusts (Gold *et al.* 2001) than where crusts were absent. Lichens were even more effective, lowering the temperature by 10-11°C compared to bare soil. In alpine areas, this lower temperature could deprive roots of needed heat, but in prairies and deserts where cryptogamic crusts occur, it could prove to be essential for root survival. Konis (1949) found the upper thermal limit for normal plant cell activity to range from 45 to 55°C, although some cells could survive up to 59°C. Therefore, in the hot climates of prairies and deserts, the bryophyte and lichen crusts could be essential to root survival by ameliorating the soil temperature.

In southern Africa, the crusts are important in providing a habitat where nitrogen fixation occurs, and Aranibar *et al.* (2003) suggest that these crusts permit the survival of these N-fixing systems at high temperatures and through long droughts, providing resilience to the ecosystem.

In the Antarctic, the bryophytes perform the opposite function for the Cyanobacteria. Huntley (1971) reported that they maintained a temperature that was typically more than 10°C higher than the ambient temperature, often reaching 20°C during the middle of the day, and providing a suitable temperature for nitrogen fixation activity of the Cyanobacteria. In a Russian study, nitrogen fixation by bacteria in peat did best in the lower layers (20-30 cm) than in the green portion, but could proceed in a range of 5 to 35°C (Kravchenko & Doroshenko 2003).

The role of the bryophytes in ameliorating soil temperature varies with the ecosystem. For example, in geothermal areas, the bryophytes confine the heat, making soil surface temperatures up to 10°C higher than it is with them removed (Glime & Iwatsuki unpublished data). In a

"moss-lichen pine forest" in Russia, Ipatov and Tarkhova (1983) found that the mosses "soften" the temperature fluctuations more than do lichens and also maintain a higher moisture content, contrasting with the alpine tundra study of Gold *et al.* (2001) where the lichens seemed to do more.

It is no wonder the BOREAS temperature model predicted somewhat poorly until the mosses were added to the model (Pauwels & Wood 1999; Litzgus & Brooks 2000). Moss thickness and moisture content turned out to be important parameters in the sensitivity analysis. But it is complicated. Betts *et al.* (1998) contend that the moss layer makes soil temperature dynamics and water dynamics difficult to track because the moss layer is such a good insulator of the soil. It makes it difficult to predict the temperature of the soil or the thaw date.

### Degree Days

Plants often respond to the cumulative effects of temperature, known as **degree days**. That is a measure of the product of the number of days times the mean temperature (°C) on those days. We know for tracheophytes that these degree days are a factor in germination of seeds, breaking dormancy in bulbs, and ability to reach fruit maturity before the first frost terminates the growing season.

Degree days are seldom mentioned for bryophytes, as few studies have approached their temperature needs in that way. Bates (1989) found that *Leucobryum glaucum* (Figure 9) cushions in Great Britain had their highest growth rate in summer, and unlike most bryophytes, growth was more related to temperature than to precipitation. Rather, it seemed to be related to degree days above 5°C.

While degree days are not mentioned specifically, many studies imply their importance. Callaghan *et al.* (1997) found that the growth of circumpolar populations of *Hylocomium splendens* (Figure 21) depends greatly on the early summer temperatures and the length of the growing season (degree days for sure).



Figure 21. The staircase moss, *Hylocomium splendens*, exhibiting its steps. Its growth is dependent on a sufficient growing season. Photo by Janice Glime.

Bryophytes can have a profound effect on the **soil degree days (SDD)**, which are important for root growth and storage organ dormancy, among other things. When moss cover and the canopy were removed from boreal

forests of interior Alaska, the soil warmed, on average, by 345 and 408 soil degree days, respectively (Bonan 1991). These were the two parameters having the highest effect on soil temperature, which normally averaged 851 soil degree days, with elevation and soil drainage patterns being of secondary importance, with deviations of 71 and 66 soil degree days.

### Safe Sites

Even turtles can benefit from the ability of the mosses to buffer temperatures. In Georgian Bay, Ontario, Canada, some members of the spotted turtle (*Clemmys guttata*; Figure 22) spend their winter under *Sphagnum* (Figure 6) hummocks (Litzgus *et al.* 1999). They enter in early autumn with body temperatures of 12-16°C and stay there until spring (mid to late April) when the air temperature is 1-5°C. Within the safety of the hummock, the turtle's body temperature stays 0.3-3.9°C while air temperatures drop to as low as -35°C. Such data indicate that *Sphagnum* greatly buffers the temperature and creates a very different environment.



Figure 22. *Clemmys guttata* hatching amid mosses. Photo courtesy of Steve Soldan.

Mosses may provide safe sites for seed germination. On iron mine tailings in New York, USA, the turf moss *Polytrichum piliferum* (Figure 23) became a safe seed bed for a variety of grasses (Delach & Kimmerer 2002). It was especially important for those species that germinate early and become established in cool weather. At that time, the mosses can protect the plants from a late frost and even warm the daytime temperatures due their black-body action. However, they can do little to cool the site sufficiently for continued success on the hot tailings rock during the heat of summer.

### Life Cycle Effects

Temperature plays a role in all stages of the life cycle of plants. It potentially affects the physiology of a bryophyte in several ways: photosynthetic rate, respiratory rate, reproductive timing, growth, development, and productivity. These together affect its survivorship. Whereas many animals can maintain a relatively constant internal temperature either through physiological means or by behavioral changes, plants are restricted in their positions and very few have any physiological means by which to change their internal temperatures. Thus, plants, including bryophytes, must adapt structurally,

physiologically, or by life cycle alterations to survive periods of extremes of hot and cold. On the other hand, these temperature changes can also signal and initiate changes in life cycle stages (Grime *et al.* 1990), as discussed in the chapters on development and phenology.



Figure 23. *Polytrichum piliferum*, a moss that becomes a safe site for grass seed germination. Reddish cups are antheridial splash cups. Photo by Janice Glime.

**Spore germination** is often attuned to temperature. In *Mnium hornum* (Figure 24) and *Plagiomnium undulatum* (Figure 25), spore germination is dependent on temperature, with more germinating at 20°C than at 10°C (Newton 1972). Not surprisingly, it also affects regeneration of fragments, but the surprise is that 77% of the female regenerants survived while all the male regenerants of these two species died.



Figure 24. *Mnium hornum* with capsules, a species for which spore germination is best at ~20°C. Photo by Michael Lüth, with permission.



Figure 25. *Plagiomnium undulatum* with capsules, a species for which spore germination is best at ~20°C. Photo by Michael Lüth, with permission.



McLetchie (2001) also found a temperature sex bias in *Sphaerocarpus texanus* (Figure 26), where the spores (Figure 27) that lost dormancy (germinated; Figure 28) on a 25°C day: 15°C night schedule were female biased (Figure 29). McLetchie (1999) found a degree-day type of response in spore germination (Figure 28) of *Sphaerocarpus texanus*, with loss of dormancy increasing with length of time held at a suitable temperature (16/10°C) and germination conditions. But the interesting thing that he found is that spores held at 35/20°C during dormancy lost their dormancy more quickly at 16/10°C than those held at 30/15°C or at 25/15°C, whereas those given the moist conditions needed for germination failed to germinate at all at 35/20°C or 30/15°C. Low temperatures could induce the spores back into a secondary dormancy, much as occurs in seeds of obligate winter annuals.



Figure 26. *Sphaerocarpus texanus*, a species that changes its development based on temperature. Photo by Martin Hutten, with permission.

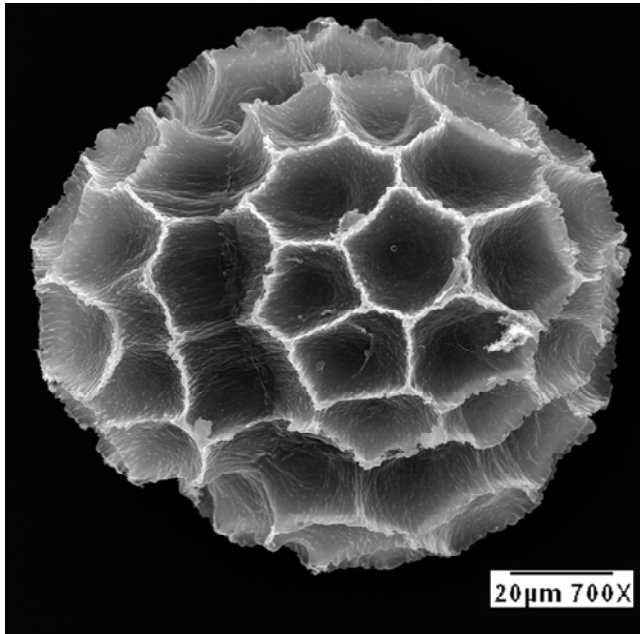


Figure 27. *Sphaerocarpus texanus* spore SEM. Dermination is dependent on temperature and with a 25°C day: 15°C night the spores that germinate are female biased. Photo courtesy of Karen Renzaglia.



Figure 28. *Sphaerocarpus texanus* developing protonema. Germination is dependent on degree days. Photo from Plant actions, with permission.



Figure 29. *Sphaerocarpus texanus* female with archegonia. A temperature regime of 25°C day: 15°C night creates a female bias in spore germination. Photo by Paul Davison, with permission.

The **protonema** may be affected differently by temperature. Dietert (1980) found that the optimum temperature for germination (Figure 30) of both *Funaria hygrometrica* (Figure 31) and *Weissia controversa* (Figure 32) was 30°C, but the optimum for the growth of the protonema was only 25°C. This higher requirement for germination is not unusual among plants because it insures a smaller probability that a killing frost will occur and kill all the young plants. Thus, a few warm days with spores on a dark soil surface can be sufficient for germination, but the green and hydrated protonema will hopefully enjoy a lower temperature.

**Growth** is more than just adding biomass and length. It involves producing buds, branches, rhizoids, and vegetative propagules. Most of these were discussed in the chapter on development, but a brief additional discussion is in order here.



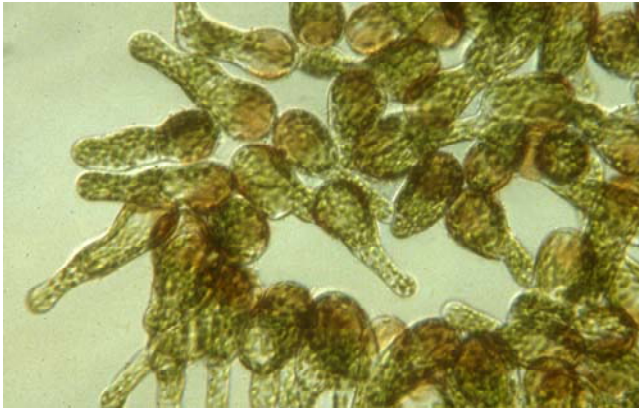


Figure 30. *Funaria hygrometrica* spore germination, a stage for which optimum conditions are at 30°C. Photo by Janice Glime.



Figure 31. *Funaria hygrometrica*, a species whose life cycle is temperature dependent. Photo by Michael Lüth, with permission.



Figure 32. *Weissia controversa* with capsules, a species whose life cycle is temperature dependent. Photo by Michael Lüth, with permission.

**Gametangia** have their own set of temperature requirements as well. In her study on *Funaria hygrometrica* (Figure 31) and *Weissia controversa* (Figure 32), Dietert found that cooler temperatures were needed for gametangia development than those for germination. Monroe (1965) likewise found that a low temperature (10°C) stimulated the production of sex organs in *Funaria* (Figure 33) and showed that day length had no effect on their timing.



Figure 33. *Funaria hygrometrica* young sporophytes, a stage that follows low temperatures needed to stimulate development of archegonia and antheridia. Photo by Michael Lüth, with permission.

The **perennial** moss *Brachythecium rutabulum* (Figure 34) had its maximum relative growth rate, shoot length, and leaf area at ~19°C (Figure 35), but these are related to each other and would be expected to increase concurrently (Furness & Grime 1982a).



Figure 34. *Brachythecium rutabulum*, a common forest floor taxon. Photo by Des Callaghan, with permission.

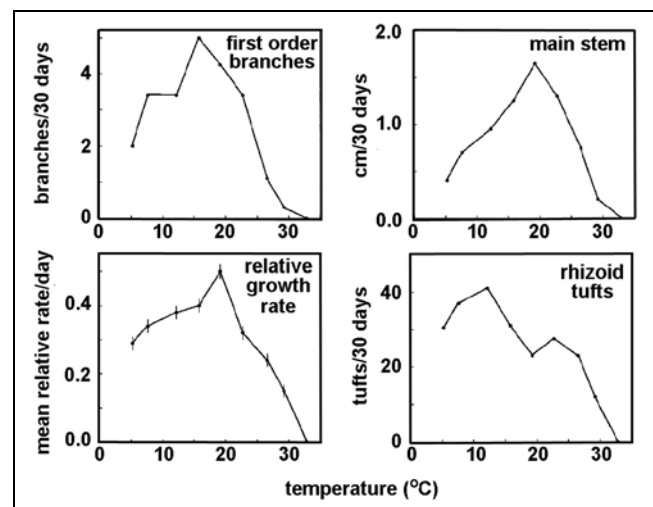


Figure 35. *Brachythecium rutabulum* growth at various temperatures. Redrawn from Furness & Grime 1982a.



**Rhizoids**, on the other hand, do not necessarily develop at the same time as stem and leaf biomass. For *Fontinalis hypnoides* (Figure 36), the number of rhizoid clumps (Figure 37) produced increased with temperature in the range of 1-20°C in both flowing water and pool conditions (Figure 39) (Glime 1980). For *Fontinalis novae-angliae* (Figure 38), it increased up to 15°C in flowing water conditions, but dropped sharply at 20°C, whereas in pool conditions it continued to rise. The **growth optimum** for these species from the same localities, however, is lower, at 15°C, for both species (Glime 1987a). **Branching** rose sharply from 1 to 5°C in *F. hypnoides* but exhibited little increase with temperature above that (Figure 39) (Glime 1982).



Figure 36. *Fontinalis hypnoides*, a species that develops rhizoids in the range of 1-20°C. Photo by Ivanov, with permission.



Figure 37. *Fontinalis hypnoides* rhizoids. Photo by Janice Glime.

The general pattern, however, for branches and total branch and stem growth in *Fontinalis* (Figure 36) is that they occur together (Glime 1980). This is reasonable, as in *B. rutabulum* (Figure 34), because new branches create a greater total branch and stem length, and in most of these species new branches need new rhizoids (Glime & Raeymaekers 1987). The rhizoids, however, tend to have a strong peak at 15°C for most of these aquatic species (Figure 39).

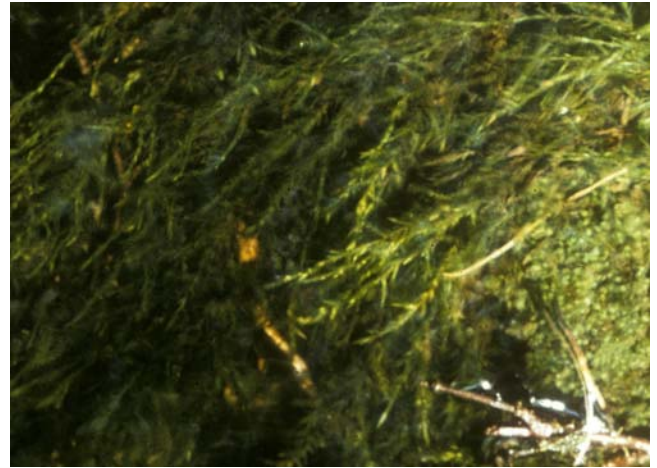


Figure 38. *Fontinalis novae-angliae* with capsules. Photo by Janice Glime.

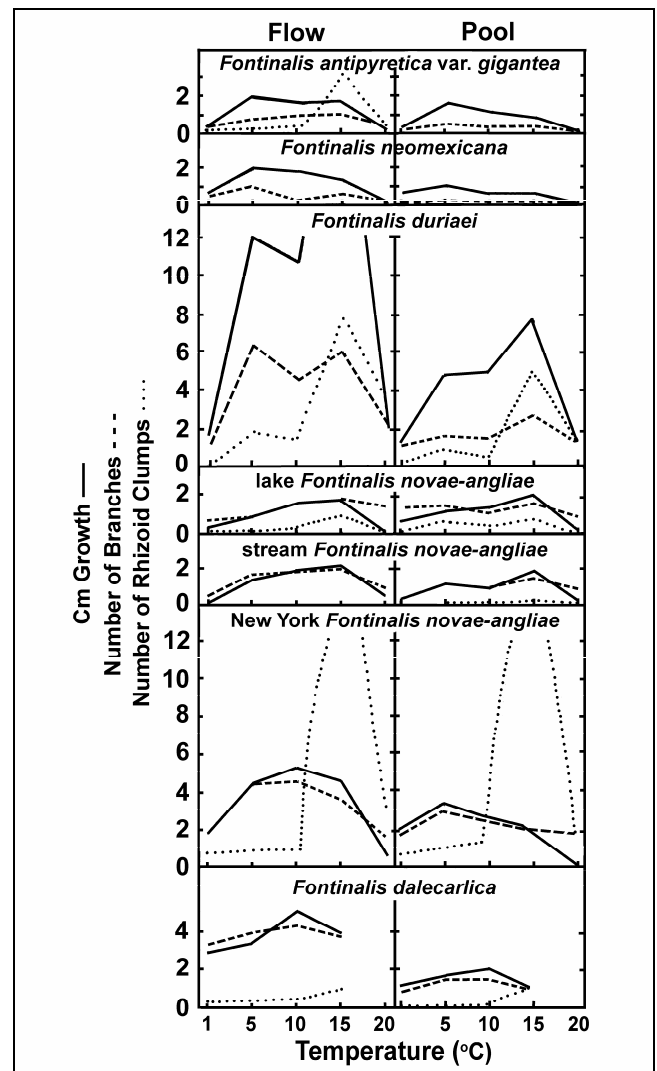


Figure 39. Response of rhizoid clumps, branches, and growth in flowing water (flow) and standing water (pool) conditions to temperatures in the range of 1-20°C for 15 weeks. Populations at 20°C were changed to 13°C after 5 weeks to look for recovery. Numbers represent means of 40 stems. All collections are from the Upper Peninsula of Michigan except the population from New York. Redrawn from Glime & Raeymaekers 1987.



Archegonia of *Fontinalis* seemed to respond more like a threshold existed, with the highest production at 15°C in flowing water, but in pool conditions, that temperature produced the fewest archegonia, with the most at 10° and 15°C, so few conclusions can be drawn. In an experiment on *F. dalecarlica* (Figure 40), production of archegonia (Figure 41) was related to photoperiod (Glime 1984), so temperature may not be an important controlling factor.

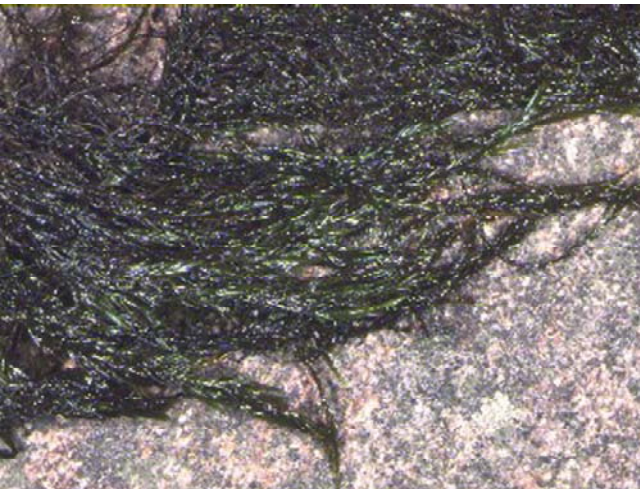


Figure 40. *Fontinalis dalecarlica*, a species in which different life stages are triggered by different temperatures. Photo by Jan-Peter Frahm.

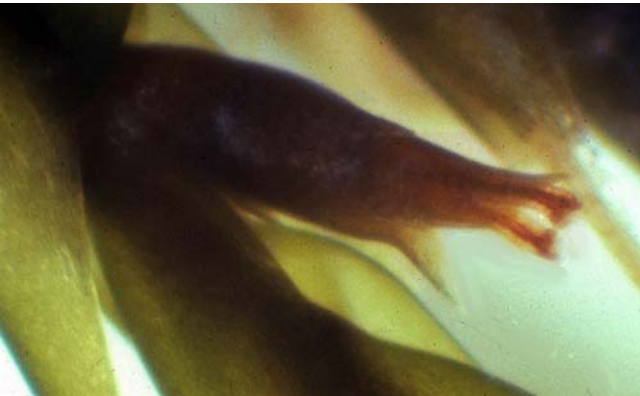


Figure 41. *Fontinalis dalecarlica* archegonia produced in greatest numbers at 15°C. Photo by Janice Glime.

Bopp and Bhatla (1990) determined the mean temperatures required for induction of gametangia in several taxa (Table 1). But they also concluded that several of the species were controlled by photoperiod, including *Pogonatum aloides* (Figure 42-Figure 43).

Table 1. Mean temperature (°C) at which gametangia are induced. From Bopp & Bhatla 1990.

<i>Pogonatum aloides</i>	21
<i>Funaria hygrometrica</i>	10
<i>Physcomitrella patens</i>	15
<i>Physcomitrium pyriforme</i>	7
<i>Philonotis turneriana</i>	18



Figure 42. *Pogonatum aloides*, a species in which photoperiod and temperature trigger life cycle stages. Photo by Michael Luth, with permission.



Figure 43. *Pogonatum aloides* with capsules. Photo by Michael Lüth, with permission.

The success of the **sporophyte** first depends on the success of the gametangia, then on the actual fertilization, and finally the requirements for its own development. Hohe *et al.* (2002) found that the highest number of sporophytes in *Physcomitrella patens* (Figure 44) were produced at 15°C, with numbers dropping greatly at 25°C. Bopp and Bhatla (1990) had similar results, finding the optimal temperature for capsule production to be at 15-19°C, with production dropping by 80% at 19-21°C. Vegetative growth, on the other hand, was best at 25°C. Thus we can understand that temperature is one of the factors that can keep the various energy-requiring activities of the moss, like reproduction and growth, from occurring at the same time.

*Bryum argenteum* (Figure 45) required 25°C for capsule development. Bopp and Bhatla (1990) were surprised to find that in *Funaria hygrometrica* (Figure 31), capsules were produced at 10-15°C in 12-16 hours light, but a shorter photoperiod permitted development at higher temperatures.





Figure 44. *Physcomitrella patens* with capsules that are produced in greatest numbers at 15°C. Photo by Michael Luth.



Figure 45. *Bryum argenteum* with capsules. Production of capsules can occur in a range of 10-15°C in 12-16 hours light per day. Photo by Bob Klips, with permission.

One of the more subtle life cycle effects of temperature is the initiation of **dormancy**. For example, the thallose liverwort *Lunularia cruciata* (Figure 46) can be induced into dormancy by temperatures of 24°C in continuous light, or other high temperature combinations with long days. Since this set of conditions is likely to be a harbinger of forthcoming drought, or already coupled with it, it provides a good signal to go dormant.



Figure 46. *Lunularia cruciata*, a species than can be induced into dormancy by high temperatures and long days. Photo from <[www.aphotofauna.com](http://www.aphotofauna.com)>, with permission.

Several species of *Sphagnum* [*S. magellanicum* (Figure 47), *S. capillifolium* (Figure 48), and *S. fallax* (Figure 49)] have a quite different dormancy trigger (Gerdol 1995). They are able to grow in summer temperatures if there is sufficient moisture, but they are triggered into dormancy by low night temperatures.



Figure 47. *Sphagnum magellanicum*, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by Michael Luth, with permission.



Figure 48. *Sphagnum capillifolium*, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by J. C. Schou, with permission.



Figure 49. *Sphagnum fallax*, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by David T. Holyoak, with permission.



Even fragments may have their optimum for **regeneration**. Although *Sphagnum* (Figure 47-Figure 49) species typically occur in the sun, go dormant in the fall, and grow when enough moisture is available in summer, their fragments do not seem to survive well in heat. Sagot and Rochefort (1996) tested *S. angustifolium* (Figure 50), *S. fallax* (Figure 49), *S. fuscum* (Figure 51), *S. magellanicum* (Figure 47), *S. capillifolium* (= *S. nemoreum*; Figure 48), and *S. papillosum* (Figure 6) and found that only *S. fallax* survived temperatures as high as 30°C for 48 hours of oven drying. The conditions of oven drying may have dried them too quickly, preventing them from entering dormancy. However, the implications are that harvesting peat in the summer may prevent regeneration from fragments that could dry and heat up too quickly once disconnected from the capillary stream of the plants.



Figure 50. *Sphagnum angustifolium*, a species that does not survive above 30°C of oven drying – perhaps preventing them from the physiological changes normally made during drying. Photo by Michael Luth, with permission.



Figure 51. *Sphagnum fuscum*, a species that does not survive above 30°C of oven drying – perhaps preventing them from the physiological changes normally made during drying. Photo by Michael Luth, with permission.

Growth of any organism is a competition for energy and nutrients. This is especially true for plants that continue to grow throughout their lifetimes or over a long expanse of years. Bryophytes include both **annual** (regrowing from spores every year) and **perennial**

(continuing growth of the same plant for a number of years) growth strategies. This means that some must start the growing season from spores and others simply continue growth from existing plants. Hence we should expect different signals for these two growth processes.

## Normal and Extremes for Growth

Aside from these life cycle changes, bryophytes respond physiologically to temperature differences that affect their growth and productivity (Furness & Grime 1982a, b). Most bryophytes have their optimum temperature for growth in the range of 15-25°C (Furness & Grime 1982b). Yet some bryophytes can have an optimum of less than 10°C (Furness & Grime 1982b), as in some species of *Fontinalis* (Glime 1987a). It is likely that this low temperature optimum, at least in *Fontinalis*, results from a cumulative effect of increased respiration at higher temperatures. In experiments where the mosses were acclimated to the test conditions for three weeks, the aquatic species *Fontinalis duriaei* (Figure 52) exhibited optimum net photosynthesis at 10°C (Glime & Acton 1979).



Figure 52. *Fontinalis duriaei*, a species that has optimum photosynthesis at 10°C in the Keweenaw Peninsula of Michigan. Photo by Michael Luth, with permission.

Furness and Grime (1982a) suggested that bryophytes may be able to compete with tracheophytes because the bryophytes are able to grow over a wider temperature range and to exploit the cool months of spring and autumn for growth. They supported this suggestion by showing that while the optimum temperature for growth, shoot length, and leaf area was 19°C in *Brachythecium rutabulum* (Figure 34), the reduction in relative growth was less than 40% at 5°C. In southern Finland, *Sphagnum fuscum* (Figure 51) had a net productivity gain at any temperature above 0°C, provided there was sufficient water (Lindholm 1990). This water limit at higher temperatures seems to be a principle for many bryophytes, although *Sphagnum* generally has a higher temperature optimum than other bryophytes (Koskimies-Soininen & Nyberg 1987; Li & Glime 1990; Li *et al.* 1992).

A number of factors can affect the optimum temperature for growth, and it is likely that a number of physiological races exist. In *Fontinalis novae-angliae* (Figure 38) collected from New Hampshire, USA, the optimum temperature for growth when placed in a common garden was 10°C, whereas the population from the Upper Peninsula of Michigan had its greatest growth at 15°C (Glime 1987b; Figure 53). Furthermore, the New



Hampshire populations had considerably more growth at all temperatures below 20°C than did the Michigan populations. Optima also differed between pool and flowing water conditions, with the New Hampshire population exhibiting its best growth at 5°C in pool conditions. On the other hand, *F. hypnoides* (Figure 36) had almost no difference in growth between pool and flowing water conditions except at 20°C, where the flowing water conditions produced the best growth (Figure 54). In Japan, Saitoh *et al.* (1970) found the optimum for photosynthesis in *F. hypnoides* at 20°C.

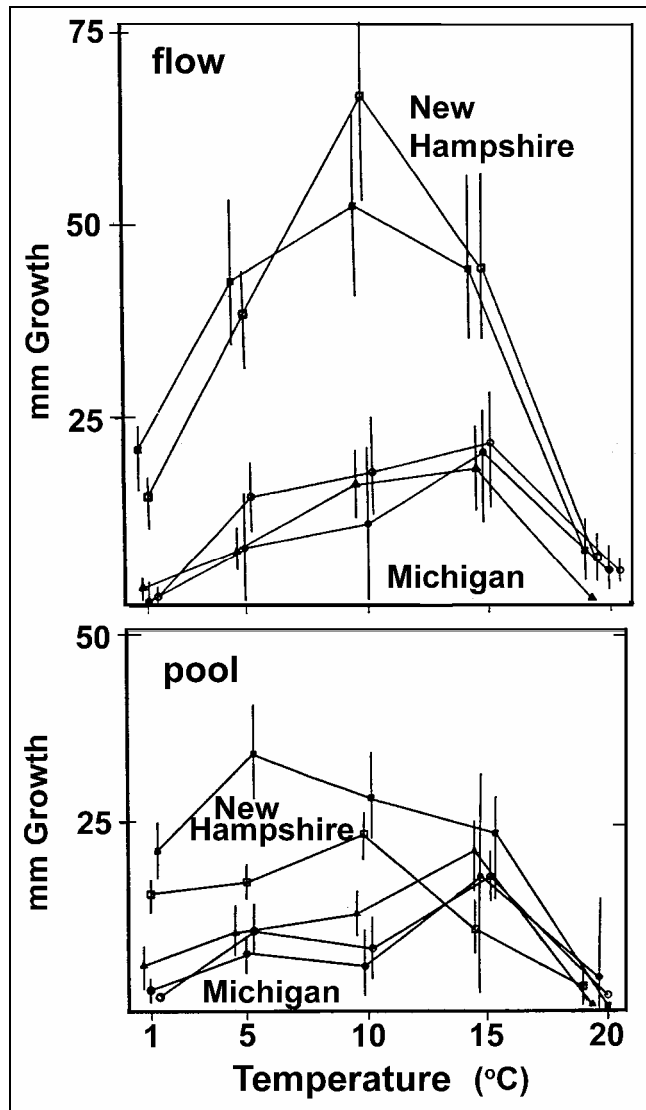


Figure 53. Comparison of growth in flowing water (flow) and standing water (pool) conditions after 15 weeks for *Fontinalis novae-angliae* from two geographic areas. Redrawn from Glime 1987b.

*Fontinalis novae-angliae* (Figure 38) most likely holds the record for high temperature survival of wet mosses. Glime and Carr (1974) boiled it for 14 or more hours a day for two weeks. A year after it was returned to its native stream, a new green leaf appeared on one of the marked stems that had been in the boiling treatment. All the former leaves were gone or brown.

Short-term studies can be misleading, and past history of the bryophyte can influence the temperature for optimum growth. In *Fontinalis hypnoides* (Figure 36), spring-collected (June) mosses grew best at 15-20°C, whereas plants of the same population collected in September ceased growth after 2-3 weeks at 20°C (Glime 1982). It appears that degree days are at work here.

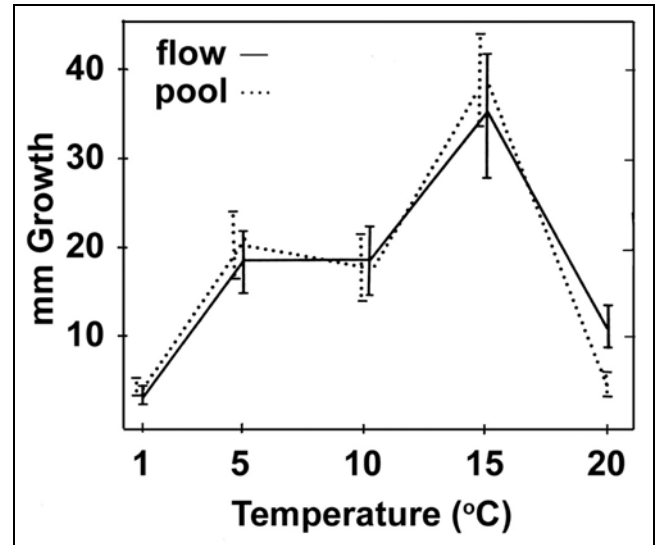


Figure 54. Growth after 15 weeks for *Fontinalis hypnoides* from Isle Royale, Michigan, USA, in flowing water (flow) and standing water (pool) conditions. Redrawn from Glime 1982.

Mosses seem to have the ability to withstand and even take advantage of high temperatures for short periods of time. Liu (2000) showed that *Plagiomnium acutum* (Figure 72), *P. maximoviczii* (Figure 55), *Thuidium cymbifolium* (Figure 56), and *Chrysocladium retrorsum* were able to maintain optimum photosynthetic output at 20-35°C. They actually had a positive net photosynthesis at -15°C and maintained a net photosynthetic gain for 10-30 minutes at 40-45°C. However, the 50% injury temperature ( $IT_{50}$ ) occurred at 44.8°C for *Thuidium cymbifolium* and at 45.3°C for *Plagiomnium acutum*. But even at temperatures less than 45°C, damage to cells and death of the shoot increased with exposure time. None of them survived above 50°C.



Figure 55. *Plagiomnium maximoviczii*, a species that exhibits optimum photosynthetic output at 20-35°C. Photo from Hiroshima University Digital Museum of Natural History, with permission.





Figure 56. *Thuidium cymbifolium* with capsules, a species that exhibits optimum photosynthetic output at 20-35°C. Photo by Li Zhang, with permission.

A measurement of air temperature does not present an accurate picture of actual moss temperatures, so both field measurements, which seemingly represent long-term exposure, and lab measurements, which represent only a short-term duration, present problems in realizing the actual tolerances of bryophytes. For example, Kappen and Smith (1980) found that the geothermal moss *Campylopus praemorsus* tolerated temperatures up to 29.8°C in its active parts, while soil temperatures were much higher. We have seen how bryophytes alter the temperature of both the environment and of themselves relative to ambient air temperature. It is important that field measurements reflect the temperature of the leaves in question through the use of microprobes. And laboratory photosynthetic measurements need to mimic temperatures at which the moss has been maintained if they are to tell us the optimum sustained temperature. Nevertheless, these short-term measurements are useful to tell us short-term tolerances that bryophytes may need to sustain in the field. With a soil temperature reaching 81.9°C in the desert (Körner & Cochrane 1983), they could certainly be subjected to a wide range.

Some more tropical elements of the bryophyte flora seem to find refuge in **rockhouses** (Farrar 1998). These are deep recesses in cliffs and maintain a much buffered temperature regime, but under very low illumination. Although they typically do not get very warm, they seem to be refugia for tropical species that persist there in the absence of extreme winter cold. Perhaps, too, these species are adapted to the low light levels in the lower strata of tropical forests. Although the ferns are more conspicuous in these special habitats, the bryophytes are the most numerous.

## Compensation Point

The **temperature compensation point** is that temperature at which photosynthetic gain equals respiratory loss, *i.e.*, net photosynthesis is zero. It is this compensation point, whether for light, temperature, CO<sub>2</sub>, or other factor that determines whether a plant is capable of surviving over the long term. While some plants may have a negative gain for a short period of time, they must have a net gain over the annual cycle. In the tropics, low light intensity and high temperatures are major factors in preventing lowland forest bryophytes from reaching their compensation point (Frahm 1987). For most bryophytes, this temperature compensation point is reached somewhere above 20-25°C,

with lowland tropical forest bryophytes having drastic drops in net assimilation above 25°C, soon reaching and surpassing their temperature compensation point (Frahm 1990). We can assume that if 25°C is the upper temperature limit for tropical bryophytes in lowlands, this is most likely the upper limit for bryophytes in general, with the exception of those taxa adapted to special habitats like deserts and geothermal areas.

The lower temperature compensation point most likely varies considerably. For two snowbed bryophytes, this limit is not much below freezing, with *Anthelia* (Figure 57) reaching it at -4°C and *Polytrichum* (Figure 58-Figure 59) at -5°C (Loesch *et al.* 1983). Their high temperature compensation point is 30°C and 32°C, respectively. It is not surprising that they have a relatively high compensation point at the low end because they are protected by snow during the periods when other bryophytes would most likely be in danger of a late or early season cold spell. Such snowbed habitats seem to be refugia for more northern taxa most likely left behind by the glacier (see Belland 1983).



Figure 57. The whitened branches of *Anthelia juratzkana* that most likely protect it from the intense UV light at high elevations while it is still at freezing temperatures from melting snow. Photo by Michael Lüth, with permission.



Figure 58. *Polytrichum sexangulare* in late snowbeds. Photo by Michael Lüth, with permission.





Figure 59. *Polytrichum sexangulare*, a late snowbed moss that continues to photosynthesize down to  $-5^{\circ}\text{C}$ . Photo by Martin Hutten, with permission.

Rütten and Santarius (1993) found productivity temperatures in *Plagiommium affine* (Figure 60) and *P. undulatum* (Figure 25) with lower limits in the summer at  $-10$  to  $-15^{\circ}\text{C}$ . For Antarctic bryophytes, even lower temperatures are likely for positive photosynthesis. One must wonder what they could achieve if they could be tested in the Antarctic winter.



Figure 60. *Plagiommium affine*, a species that can survive temperatures of  $-10$  to  $-15^{\circ}\text{C}$  in the summer. Photo by Janice Glime.

As the temperature rises, so do the  $\text{CO}_2$  and light compensation points and saturation points (Joliffe & Tregunna 1968). *Bryum argenteum* (Figure 45) has a compensation point of 58 ppm at  $20.5^{\circ}\text{C}$  (Rastorfer 1970). In the moss *Sanionia uncinata* (Figure 61), temperatures of  $5^{\circ}\text{C}$ ,  $15^{\circ}\text{C}$ , and  $25^{\circ}\text{C}$  have corresponding  $\text{CO}_2$  compensation points of 32, 50, and 82 ppm ( $\text{mg L}^{-1}$ ), respectively (Rastorfer 1971). In other words, as the temperature rises, the moss uses more  $\text{CO}_2$  to achieve a net gain. This rise in  $\text{CO}_2$  requirement is predicted, because these  $\text{C}_3$  plants have photorespiration, which increases more rapidly than photosynthesis as the temperature rises. Hence, more fixation would be required to overcome the photorespiratory losses.



Figure 61. *Sanionia uncinata* with capsules, a species that is able to use more  $\text{CO}_2$  as the temperature rises. Photo by Michael Lüth, with permission.

Compensation points among tracheophytes are generally considered low at approximately 5 ppm or less (Jackson & Volk 1970) and high at 32-122 ppm in moderately bright light and temperatures of  $20$ - $30^{\circ}\text{C}$  (Heath 1962; Goldsworthy & Day 1970).

## Antarctic and Arctic

Even Antarctic mosses seem to survive well at higher temperatures. Rastorfer and Higginbotham (1968) reported that the ratio of photosynthesis to respiration in *Roellia roellii* (Figure 62) ranged 11-27:1 in the temperature range of  $4$ - $24^{\circ}\text{C}$ , dropping to lower values at  $34^{\circ}\text{C}$ . Nevertheless,  $34^{\circ}\text{C}$  is a relatively high temperature. Ino (1990) found that the maximum rate of net photosynthesis at saturating light levels occurred at approximately  $10^{\circ}\text{C}$  in East Antarctic populations of *Ceratodon purpureus* (Figure 63) and *Bryum pseudotriquetrum* (Figure 64-Figure 65). These were one- or three-day measurements.



Figure 62. *Roellia roellia*, an Antarctic species that has an abrupt drop in photosynthesis at temperatures of  $34^{\circ}\text{C}$  and higher. Photo by Martin Hutten, with permission.





Figure 63. *Ceratodon purpureus*, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Janice Glime.



Figure 64. *Bryum pseudotriquetrum* in the Antarctic. Photo courtesy of Catherine Beard.



Figure 65. *Bryum pseudotriquetrum*, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Michael Luth, with permission.



Figure 66. *Marchantia polymorpha* with gemmae cups, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Brenda Dobbs, through Creative Commons.

*Racomitrium lanuginosum* (Figure 67), on the other hand, had its photosynthetic optimum in high light intensities at 5°C, with a minimum net gain at -8 to -10°C (Kallio & Heinonen 1973). In short-term experiments the maximum temperature was generally 25-30°C. Furthermore, even though the moss was not productive at -30°C, it quickly became active, reaching 60% activation within three hours of warming.

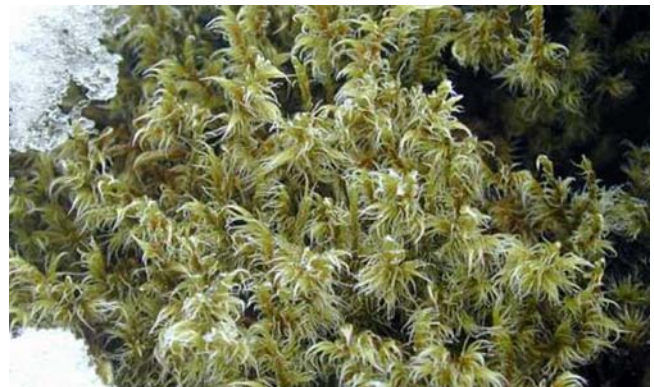


Figure 67. Spring melt reveals *Racomitrium lanuginosum* ready to photosynthesize. Photo by Michael Luth, with permission.

## Acclimation

**Acclimation** is the gradual and reversible adjustment of an organism to environmental fluctuations, not to be confused with **adaptation**, which is a persistent genetic change that provides the organism with a better ability to survive its environmental conditions. The adjustment to winter cold or summer heat is a result of acclimation.

Many bryophytes seem to be pre-adapted to low temperatures, but have some degree of ability to adjust to high temperatures. Antropova (1974) suggested this for species in seven genera of bryophytes [*Atrichum* (Figure 68), *Calliergon* (Figure 69), *Chiloscyphus* (Figure 70), *Funaria* (Figure 31), *Marchantia* (Figure 66), *Mnium* (Figure 24), *Riccia* (Figure 71), based on ability to **plasmolyze**. Loss of plasmolysis is an indication of membrane damage. As might be expected, incubation at



their tolerant temperatures (10 and 20°C) does not affect their thermostability or cold resistance. However, incubation for three hours at temperatures above their optimum does result in increased thermostability. Unlike typical cold acclimation, this increased thermostability is not accompanied by increased cold hardiness. This response is similar to that of flowering plants but different from that of algae.



Figure 68. *Atrichum undulatum*, in a genus that seems to be pre-adapted to low temperatures. Photo by Brian Eversham, with permission.



Figure 69. *Calliergon cordifolium*, in a genus that seems to be pre-adapted to low temperatures. Photo by Janice Glime.



Figure 70. *Chiloscyphus polyanthos*, in a genus that seems to be pre-adapted to low temperatures. Photo by Michael Lüth, with permission.



Figure 71. *Riccia gougetiana* var. *armatissima*, in a genus that seems to be pre-adapted to low temperatures. Photo by Michael Lüth, with permission.

Rütten and Santarius (1993) defined **frost tolerance** as the lowest temperature at which no more than 50% irreversible damage occurred in net photosynthetic activity relative to unfrozen plants. They found that optimum productivity temperatures in *Plagiomnium affine* (Figure 60) and *P. undulatum* (Figure 25) ranged 10-20°C with lower limits in the summer at -10 to -15°C. Their hardiness to cold increased progressively during autumn, reaching temperatures below -35°C by winter. And, as already known from seed plants, the increase in cold hardiness was coupled with an increase in thermostability at high temperatures. But there was no correlation with an increase in total sugar content (sucrose, glucose, and fructose) of the shoots, despite the considerably higher sucrose content than that of less frost-hardy plants. Rütten and Santarius suggest that the accumulation of sucrose may contribute to frost hardiness of these two species, but felt that the seasonal differences could not be accounted for solely by the alterations in sugar concentrations.

Using *Plagiomnium acutum* (Figure 72) and *P. maximoviczii* (Figure 55) from China, Liu *et al.* (2001) showed that the optimum temperature for photosynthesis rose from winter to summer, ranging 20-35°C; the mosses could maintain positive net photosynthesis for 20-30 minutes at -10 to -15°C and from 40-45°C. Their  $Q_{10}$  (change in rate of reaction per 10°C change in temperature) in the range of 0-20°C was only 1.15-1.23. The "average" for non-biological chemical reactions is 2.0. Uchida *et al.* (2002) found that the photosynthetic  $Q_{10}$  for the moss *Sanionia uncinata* (Figure 61) was nearly 1 in the range of 7 to 23°C, whereas the respiratory  $Q_{10}$  was 3.0, causing net photosynthetic loss as the temperature rose.



Figure 72. *Plagiomnium acutum* from China. Photo by Yingdi Liu, with permission.



But bryophytes apparently do have at least limited ability for short-term heat acclimation. Using chlorophyll *a* fluorescence and electrolyte leakage (evidence of membrane damage) to indicate thermal stability, Meyer and Santarius (1998) showed short-term acclimation of hydrated shoots of *Atrichum undulatum* (Figure 68) and *Polytrichastrum formosum* (Figure 73) to elevated, sublethal temperatures within a few hours. This acclimation lasted several days. Declining water content, on the other hand, caused a dramatic rise in heat resistance.



Figure 73. *Polytrichastrum formosum* 1 Des Callaghan, with permission.

Hicklenton and Oechel (1976) found that the moss *Dicranum fuscescens* (Figure 72) 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 75), but its dark respiration rates showed no evidence of acclimation. 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 productivity. At the other end, net productivity was negative at temperatures above 15°C on 5 June.



Figure 74. *Dicranum fuscescens*, a species that raises its temperature optimum as summer progresses from June to July in the subarctic. Photo by Michael Lüth, with permission.

In a field study, Oechel (1976) found a close correlation between the minimum temperature at which 85% of maximum photosynthesis was achieved and the mean maximum tissue temperature for the five days preceding the measurement, further supporting an acclimation to the temperature.

Fornwall and Glime (1982) found evidence of acclimation to cold vs warm in *Fontinalis duriaei* (Figure 52). Using mosses that were collected in the same section of stream every eight weeks from 27 November until 3 December of the following year, they demonstrated that those individuals that were collected in January at 0-1°C had their peak assimilation rate at 10°C. Those mosses collected in June, before the heat of summer, had a peak at 35°C, the highest optimum found in the 1-40°C temperature range of the experiments. These mosses had already reached an optimum of 30°C by 3 April, even though the stream temperature was only 1°C. This suggests that something other than temperature is triggering the change in photosynthetic response to temperature. For aquatic bryophytes, this could be a nutrient pulse during spring runoff, increasing photoperiod, or both.

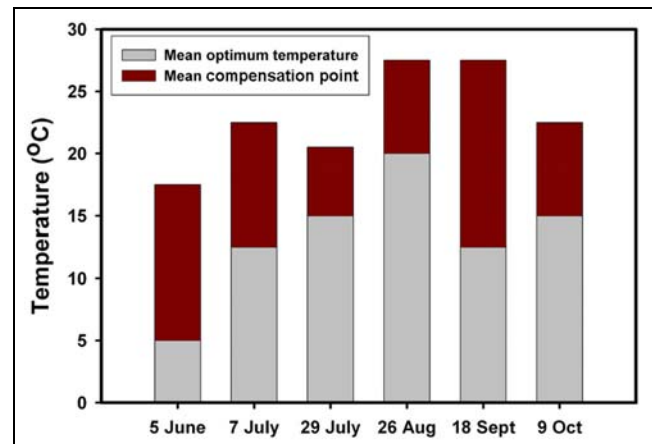


Figure 75. Mean optimum temperatures and upper temperature compensation points for *Dicranum fuscescens* photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel 1976.

In the Antarctic populations of *Sanionia uncinata* (Figure 61) and *Polytrichum strictum* (Figure 76), Collins (1976) demonstrated a shift in the photosynthetic curve depending on the acclimation temperature. Those previously growing at a lower temperature had positive productivity at a lower temperature, had a higher optimum, and had lower productivity at higher temperatures in *Polytrichum strictum* (Figure 77). *Sanionia uncinata* had a similar low temperature response to that of *Polytrichum strictum*, with the same optimum in both treatments, but the ones acclimated at higher temperatures exhibited a more rapid photosynthetic decline above the optimum (Figure 77).





Figure 76. *Polytrichum strictum*, a species whose temperature optimum depends on the previous optimum temperature. Michael Luth, with permission.

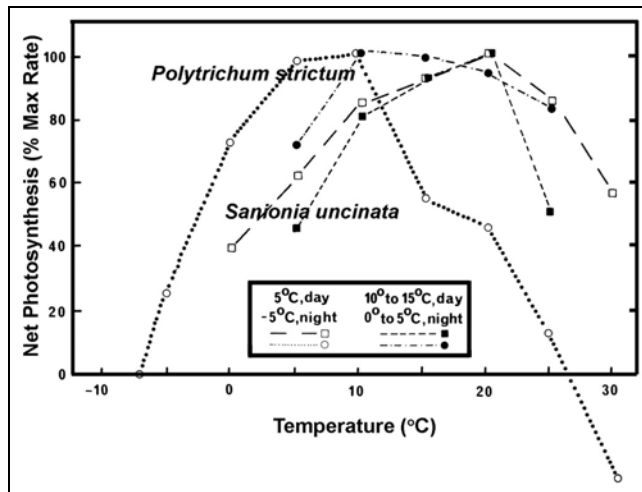


Figure 77. Acclimation responses of two Antarctic moss species at radiant flux density of  $500 \mu\text{Einsteins m}^{-2} \text{s}^{-1}$ . Redrawn from Collins 1976.

### Cold vs Heat

As seen for the polar regions, those factors that help plants adapt to the cold often incur heat resistance as well. Just as antifreeze in a car keeps it from freezing in winter, it keeps it from boiling in the summer. Such "antifreeze" effects work as well in plants.

In their study of temperature resistance in *Sphagnum* (Figure 47-Figure 51), Balagurova *et al.* (1996) found that differences between species were greater for heat resistance than for cold resistance, but there was, nevertheless, a correlation between the two kinds of resistance.

### Acclimation Triggers

One factor that could play a role in acclimation is light intensity, although I don't know what physiological mechanisms might be involved. We know that at 140 lux light intensity *Fontinalis* sp. (see Figure 40) reaches its compensation point at 20°C, but when only 40 lux is present, it reaches compensation at 5°C (Burr 1941). While this should not have been a factor during the lab experiments of Fornwall and Glime (1982), who kept the light intensity constant at 4500 lux, the previous field history of light and photoperiod might have played a role in the temperature performances.

It is often difficult to recognize whether differences are the result of physiological races or of acclimation. For example, Asakawa *et al.* (1991) found that most of the high elevation/high latitude members of several *Frullania* taxa synthesized **tamariscol** (*F. tamarisci* subspecies – Figure 78) and *F. nepalensis*, whereas those in lower altitudes and latitudes did not. (**Tamariscol** imparts intense "mossy" or pleasant odor.) But we have no evidence that this provides any advantage in cooler climates and may be a geographic variant that travels with a gene that is adaptive. On the other hand, particular conditions of the climate at higher elevations and latitudes (in the north) might cause the gene to be expressed, whereas these triggers may be absent at the time of collection from lower latitudes and altitudes.



Figure 78. *Frullania tamarisci*, a high elevation species that produces tamariscol. Photo by Michael Luth, with permission.

Kallio and Saarnio (1986) actually transplanted mosses [*Hylocomium splendens* (Figure 21), *Pleurozium schreberi* (Figure 79), and *Racomitrium lanuginosum* (Figure 2-Figure 3)] from 60°55'N to 69°45'N and from 69°45'N to 78°13'N to determine their adaptations to cold. The physiological stress of these mosses increased as they were moved northward. Kallio and Saarnio concluded that their adaptations were largely due to their ability to acclimate. Day length and temperature served as important environmental cues to acclimation, and these signals changed as mosses were moved to more extreme latitudes.



Figure 79. *Pleurozium schreberi*, a species that is apparently able to acclimate when moved to more northern sites. Photo by Janice Glime.



## Summary

Bryophytes may experience temperatures far greater than the ambient temperature due to their dark color and ability to act as a black body. Generally bryophytes are only able to tolerate temperatures up to about 40°C before the temperature becomes lethal. Their optimum, however, is usually much lower than that. They often are able to have photosynthetic gain at temperatures as low as -10°C, but seldom have a net gain at temperatures above 25°C. Rather, they typically become dormant in summer heat and drought. For many species, the optimum is 15-25°C, although it seems to be much lower for stream bryophytes. Even tropical bryophytes have an upper limit of 25°C.

Bryophytes can alter not only their own temperature, but also the temperature of the soil. Evaporative cooling may lower it, but dark color may raise it. They can protect the root zone of the soil from high temperatures on hot prairies and deserts by shading and insulating. In geothermal areas they can raise the soil temperature by trapping the geothermal heat beneath them. With an atmospheric temperature of 20°C, a sunfleck may warm a moss to 39°C. In some locations they may have a temperature 30°C or more higher than ambient. Their insulating role in the Arctic has a major role in the Arctic temperatures, delaying the thaw cycle by absorbing the heat that would have gone to the soil and decreasing the number of **soil degree days**, and making them essential to the BOREAS temperature model.

Bryophytes can transfer water from lower parts to growing tips and use evaporative cooling much as in tracheophytes. **Awns**, **hyalocysts**, and **papillae** can reflect light to maintain cooler temperatures (See Chapter 7-4). Mosses such as *Sphagnum* retain considerable water, and experience little temperature change. They provide safe sites for small animals such as overwintering turtles and for germinating seeds.

Temperature affects photosynthetic rate, respiratory rate, reproductive timing, growth, development, and productivity. Spore germination temperature is often set higher than that of protonema growth to prevent germination when freeze damage is still likely. Branches, rhizoids, and stem growth may have similar requirements to keep them in consort or may have different temperature requirements to spread out the energy needs or take advantage of suitable conditions for attachment. Gametangia typically have different temperature (or photoperiod) requirements that avoid the competition for energy and to place gametangial maturity at a time when water is available. Sporophyte development may be cued by temperature to delay until after dangers of winter cold. Dormancy is typically triggered by temperature, protecting plants in summer from drought or from being hydrated at a lethal temperature. Even successful development of fragments is dependent on temperature.

Bryophytes seem able to grow over a wider temperature range than tracheophytes, particularly at the low end of the scale. Changes in temperature below their optimum have only modest effects on their productivity, demonstrated by their relatively low **Q<sub>10</sub>**

in that range, but net productivity drops off rapidly above their optimum. Physiological races exist within species that can give them quite different temperature responses and optima. However, recent past history of temperatures may be responsible for their **acclimation** rather than their **adaptation**. Optimum temperatures for photosynthesis are typically lower in winter than in summer and may actually rise before the ambient temperature rises, suggesting that temperature is not necessarily the signal.

Some tissues are more resilient than others and may even survive extensive boiling for several weeks, giving rise to new tissues at a later time. Short-term studies may be misleading for testing lethality and optima because of the importance of acclimation and internal tissue protection. Nevertheless, they can tell us the **compensation point** under a specific set of conditions if the recent history is known.

Low temperature acclimation seems to prepare mosses for high temperatures as well, giving Antarctic bryophytes the ability to survive high temperatures. Lack of proper signals for acclimation can prevent bryophytes from extending their ranges into new latitudes.

## Acknowledgments

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# CHAPTER 10-2

## TEMPERATURE: COLD

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## CHAPTER 10-2

# TEMPERATURE: COLD



Figure 1. *Racomitrium heterostichum* mostly imbedded in ice while some branches are free and available for photosynthesis. Photo by Michael Lüth, with permission.

### Low Temperature Limits

In general, bryophytes seem able to withstand cold in their leafy state much better than their tracheophyte counterparts. Ochi (1952) found that most mosses (18 species tested) were resistant to cold to  $-20^{\circ}\text{C}$ . Seven of these species were resistant to  $-27^{\circ}\text{C}$ . He was unable to find any trend in relationships to osmotic value, permeability, or seasonal fluctuations. Ochi's results support the later statement of Kallio and Heinonen (1973), that *Racomitrium lanuginosum* (Figure 2), a cosmopolitan moss, is pre-adapted to its abode in the Arctic and Antarctic (see Table 1) and suggest that such pre-adaptation may be a common feature of bryophytes. This contention is supported by the low temperatures that become lethal for bryophytes in the tropics (Table 2).



Figure 2. *Racomitrium lanuginosum*, a species pre-adapted to living in the polar regions with long, white hair tips. Photo by Janice Glime.



Surprisingly, Arctic liverworts do not seem to be so cold resistant. Among the nine species tested by Biebl (1968), seven were mostly dead at  $-16^{\circ}\text{C}$ , with only the leafy liverworts *Barbilophozia hatcheri* (Figure 3) and *Chandonanthus setiformis* (Figure 4) surviving well. The moss *Aulacomnium turgidum* (Figure 5-Figure 6) also survived at  $-16^{\circ}\text{C}$ . All species survived  $-6^{\circ}\text{C}$ . But these were July responses in Greenland; a quite different picture might emerge in winter. On the other hand, all of them survived up to  $42^{\circ}\text{C}$  for half an hour, but twelve-hour exposures killed parts of most of them, the same seven, at  $38^{\circ}\text{C}$ . *Aulacomnium turgidum* survived up to  $48^{\circ}\text{C}$  for half an hour and up to  $40^{\circ}\text{C}$  for twelve hours. This supports the hypothesis that low temperature survival is coupled with high temperature survival.



Figure 3. *Barbilophozia hatcheri*, a leafy liverwort that survives to  $-16^{\circ}\text{C}$ . Photo by Michael Lüth, with permission.



Figure 4. *Chandonanthus setiformis*, a leafy liverwort that survives to  $-16^{\circ}\text{C}$ . Photo by Michael Lüth, with permission.

Tropical mosses seemed rather similar. After 24 hours of exposure, *Homaliodendron flabellatum* (Figure 7) and *Leucoloma amoene-virens* survived  $-14^{\circ}\text{C}$  and *Schistochila commutata* (Figure 8) survived  $-11^{\circ}\text{C}$  (Biebl 1967). Tropical *Plagiochila* (Figure 9), *Metzgeria* (Figure 10), and *Bryum* (Figure 11) species each survived to at least  $-4^{\circ}\text{C}$ . Try doing that to a tropical *Maranta* (Figure 12).



Figure 5. *Aulacomnium turgidum* in a mountainous habitat. Photo by Michael Lüth, with permission.

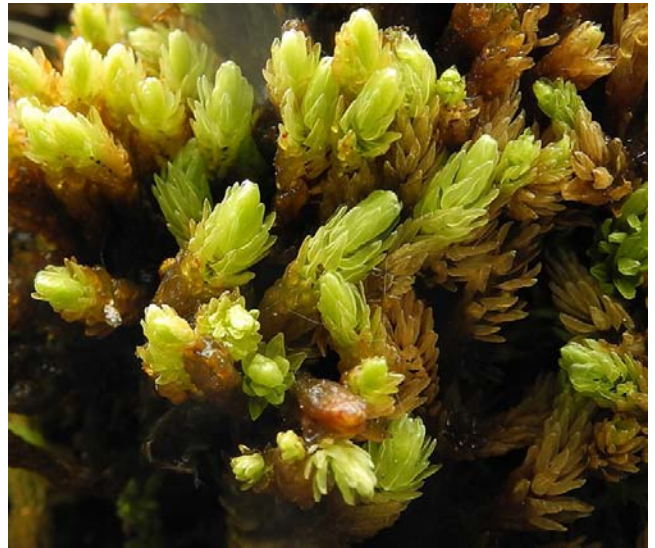


Figure 6. *Aulacomnium turgidum*, a moss that survives to  $-16^{\circ}\text{C}$ . Photo by Michael Lüth, with permission.



Figure 7. *Homaliodendron flabellatum*, a tropical species that can survive to  $-14^{\circ}\text{C}$ . Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.





Figure 8. *Schistochila* sp, a tropical species that survives to -12°C. Photo by Jan-Peter Frahm, with permission.



Figure 9. *Plagiochila* sp. from the Neotropics. Some tropical members of this genus survive to -4°C. Photo by Michael Lüth, with permission.



Figure 10. The tropical thalloid liverwort, *Metzgeria claviflora*. Photo by Michael Lüth, with permission.



Figure 11. *Bryum apiculatum* from the Neotropics. Some tropical members of this genus survive to -4°C. Photo by Michael Lüth, with permission.

Table 1. Temperature limits for net photosynthesis under natural CO<sub>2</sub> and light saturation. From Larcher 1983, compiled from many authors; \*Liu *et al.* 2001.

Plant group	Low-temp limit for CO <sub>2</sub> uptake °C	Temp opt of P <sub>n</sub> °C	High-temp limit for CO <sub>2</sub> uptake (°C)
<b>Herbaceous flowering plants</b>			
C <sub>4</sub> plants of hot habitats	+5 to 7	35-45	(50) 50-60
Sun plants (temperate zone)	-2 to 0	20-30	40-50
Shade plants (temperate zone)	-2 to 0	10-20	~40
Desert plants	-5 to 5	20-35 (45)	45-50 (56)
CAM plants (CO <sub>2</sub> fixation at night)	-2 to 0	5-15	25-30
Winter annuals, spring-flowering and alpine plants	-7 to -2	10-20	30-40
<b>Woody plants</b>			
Evergreen trees of the tropics and subtropics	0 to 5	25-30	45-50
Winter-deciduous trees of the temperate zone	-3 to -1	15-25	40-45
Evergreen conifers	-5 to -3	10-25	35-42
Dwarf shrubs of heath and tundra	~-3	15-25	40-45
<b>Cryptogams</b>			
Arctic and subarctic mosses	~-8	~-5	~-30
<i>Racomitrium lanuginosum</i>	-8 to -10	5	25-30
<i>Pleurozium schreberi</i>	-5	10-15	28-33
<i>Plagiomnium acutum</i> *	-10 to -15	20-35	40-45
<i>Plagiomnium maximoviczii</i>	-10 to -15	20-35	40-45
Lichens of cold regions	(-25)-15 to -10	5-15	20-30
Desert lichens	~-10	18-20	38-40
Tropical lichens	-2 to 0	~20	
Snow algae	~-5	0-10	30
Thermophilic algae	20 to 30	45-55	65-70





Figure 12. *Maranta leuconeura*, a tropical plant that dies in cool temperatures well above freezing. Photo by Stickpen, through public domain.

Table 2. Comparison of temperature resistance of leaves of plants from different climatic regions. Limiting temperatures are for 50% injury (TL<sub>50</sub>) after exposure to cold for 2 or more hours, or after exposure to heat for 0.5 h. Bryophytes appear in **bold**. Tracheophyte data from Larcher 1983, based on data from many authors; cold tracheophytes had been cold-hardened. Data marked by \* from Biebl 1967; Data marked by + from Liu *et al.* 2003.

Plants	°C for cold injury	°C for heat injury in growing season
<b>Tropics</b>		
Trees	+5 to -2	45-55
Forest undergrowth	+5 to -2	45-48
Mountain plants	-5 to -10	~45
<i>Schistochila commutata</i> *	-14	<b>44</b>
<i>Plagiochila</i> sp.*	-7	<b>44</b>
<i>Homaliodendron flabellatum</i> *	<-14	<b>52</b>
<i>Leucoloma amoenervis</i> *	<-14	
<i>Bryum</i> sp.*	-11	<b>52</b>
<b>Subtropics</b>		
Sclerophyllous woody plants	-8 to -12	50-60
Subtropical palms	-5 to -14	55-60
Succulents	-5 to -10	58-65
C <sub>4</sub> grasses	-1 to -3(-8)	60-64
<b>Temperate zone</b>		
Evergreen woody plants of coastal regions with mild winters	-6 to -15 (-25)	50-55
<i>Plagiomnium acutum</i> <sup>+</sup>		<b>45 (50 dry)</b>
<b>Arcto-tertiary relict trees</b>	-10 to -25 (-15 to -30)	
Dwarf shrubs of Atlantic heaths	-20 to -30	45-50
Winter-deciduous trees and widely distributed shrubs	(-25 to -40)	~50
<b>Herbs</b>		
Sunny habitats	10 to -20 (-30)	48-52
Shady habitats	40-45	
Water plants	~10	38-42
<b>Cold-winter areas</b>		
Evergreen conifers	-40 to -90	44-50
Boreal broad-leaved trees	(-196)	42-45
Arctic and alpine dwarf shrubs	-30 to -70	48-54
Herbs of the high mountains and arctic	(-30 to -196)	44-54

## Stress Protection

Bryophytes are well known for their secondary compounds. These defend against competition, microbes, and herbivory, while often protecting against UV radiation, providing drought tolerance, and freezing survival (Xie & Lou 2009). These latter protections can all be associated with cold temperatures. Specifically, bibenzyls and bis(bibenzyls) have provide desiccation tolerance; fatty acid derivatives and phenylpropanoids provide freeze tolerance.

But bryophytes seem to have a large arsenal of protectors against cold stress. They are able to accumulate soluble sugars and abscisic acid (ABA) (Bhyan *et al.* 2012). The latter increases freezing tolerance in plant cells and also is important in desiccation tolerance – a likely consequence of ice crystal formation. During acclimation in *Physcomitrella patens* (Figure 13) that was developed to be insensitive to ABA, the cells accumulated sucrose to levels similar to those found in ABA-normal plants. But the trisaccharide theandrose did not accumulate in the ABA-deficient plants. Furthermore, these deficient plants had very limited accumulation of LEA-like boiling-soluble proteins. On the other hand, Minami *et al.* (2005) found an accumulation of several transcripts for LEA proteins and boiling-soluble proteins during freeze-tolerance acclimation. Bhyan *et al.* (2012) concluded that cold acclimation requires an ABA-dependent signalling system. Cold-induced sugar acclimation, however, may or may not be dependent on the ABA system. This ABA dependence is in contrast to the study by Minami *et al.* (2005), which concluded that ABA had no role in cold hardening in *P. patens*.



Figure 13. *Physcomitrella patens* with young sporophytes. Photo by Michael Lüth, with permission.

## Freezing

As the external temperature is depressed, the bryophyte cell cools rapidly, presenting a rather different pattern from that of tracheophytes. In tracheophytes, leaf hairs, thick cuticle, and epidermis all serve to insulate the internal leaf cells from rapidly changing temperatures. Bryophyte leaves have none of these.

Freezing presents a number of problems for cells. Formation of crystals can cause physical damage by poking holes in the cell membrane or distorting the cell so that solutes can leak out more easily. Crystals are hygroscopic, attracting the water molecules from the cells to the cell



surface or intercellular spaces where the crystals may reside. This loss of water from the cells causes them to dehydrate. And cell membranes may be damaged or not function properly as fatty acids with higher solidification points become nonpliable.

Despite being perennial above ground, many, perhaps most, bryophytes survive freezing. Fletcher (1982) provided representative species from New Zealand [*Papillaria crocea* (Figure 14), *Hypopterygium* spp. (Figure 15), *Hymenodontopsis bifaria*, *Cyathophorum bulbosum* (Figure 16), *Calyptrochaeta brownii* (Figure 17)], South Africa [*Hypopterygium* sp. (Figure 15)], Australia [*Gigaspermum repens* (Figure 18), *Goniomitrium acuminatum* subsp. *enerve* (Figure 19)], and from Florida, USA [*Rhizogonium spiniforme* (Figure 20)] that survive freezing. In addition, Fletcher demonstrated that *Takakia lepidozoides* (Figure 21-Figure 22) remained healthy, as did *Sphagnum* spp. (Figure 24) and *Mnium* spp. (Figure 23). That number only provides us proof that some species survive, but gives us no idea of the world picture.



Figure 14. *Papillaria crocea* in a cloud forest at Mt Budawang, Australia, a species that is able to survive freezing. Photo by Peter Woodard, through Public Domain.



Figure 15. *Hypopterygium arbuscula*, in a New Zealand and South African genus in which some species are able to survive freezing. Photo by Scott Zona, with permission.



Figure 16. *Cyathophorum bulbosum*, a New Zealand species that is able to survive freezing. Photo by Peter Woodard, through Creative Commons.



Figure 17. *Calyptrochaeta brownii*, a South African species that is able to survive freezing. Photo by Tom Thekathiyil, with permission.



Figure 18. *Gigaspermum repens*, an Australian species that is able to survive freezing. Photo by David Tng, with permission.





Figure 19. *Goniomitrium acuminatum* subsp. .enerve, a species that survives freezing in Australia. Photo by David Tng, with permission.



Figure 22. *Takakia lepidozoides*, a high elevation species that survives freezing. Photo by Rafael Medina, through Creative Commons.



Figure 20. *Rhizogonium spiniforme*, a Florida species that is able to survive freezing. Photo by Janice Glime.



Figure 23. *Mnium thomsonii* from the Khibiny Mountains, Apatity, Murmansk, member of a genus in which some species survive freezing. Photo by Michael Lüth, with permission.



Figure 21. *Takakia lepidozoides* habitat, Japan. Photo from Digital Museum, University of Hiroshima, with permission.



Figure 24. *Sphagnum capillifolium*, a species that does not show frost damage above  $-16^{\circ}\text{C}$ . Photo by Michael Lüth, with permission.

*Sphagnum capillifolium* (Figure 24) exhibits a critical freezing temperature threshold for photosystem II that is identical to its ice nucleation temperature ( $-1.1^{\circ}\text{C}$ ) (Buchner & Neuner 2010). But frost damage ( $\text{LT}_{50}$ ) is not visible until the temperature reaches  $-16.1^{\circ}\text{C}$ . The  $\text{LT}_{50}$  is the condition/level at which the condition is lethal to 50% of the population.

Something is going on in nature that does not seem to be mimicked in the lab. *Haplomitrium hookeri* (Figure 25) from New Zealand and *H. mnioides* (Figure 26) from Japan are able to grow in winter in their native habitats, but in cultivation all plants were unhealthy after being subjected to frost (Fletcher 1982). *Moerckia blyttii* (Figure 27), *Symphogyna* sp. (Figure 28), *Corsinia coriandrina* (Figure 29), and *Asterella* sp. (Figure 30-Figure 31) became severely bleached by frost in cultivation, but



*Corsinia coriandrina* remained healthy on an exposed wall top and in an unheated greenhouse down to a temperature of  $-5.5^{\circ}\text{C}$ . Blackening occurred in *Dumortiera hirsuta* (Figure 32), but the plants survived. *Asterella* and *Monoclea forsteri* (Figure 33) likewise were blackened by frost in the greenhouse. *Fossombronia* (Figure 34) and *Anthocerotophyta* (Figure 35-Figure 36) experienced thallus decay, a phenomenon that they exhibited commonly in winter in nature. Plants of the hornworts *Anthoceros punctatus* (Figure 35) and *Phaeoceros laevis* (Figure 36) remained healthy in the greenhouse. Likewise, *Lunularia* (Figure 37), *Pellia* (Figure 38), *Preissia* (Figure 39), *Riccardia* (Figure 40), *Riccia* (Figure 41), and *Marchantia polymorpha* (Figure 42) showed no frost damage in the lab.



Figure 25. *Haplomitrium hookeri*, a species that survives frost in nature, but not in the lab. Photo by Štěpán Koval, with permission.



Figure 26. *Haplomitrium mnioides*, a species that survives frost in nature, but not in the lab. Photo by Yang, Jia-Dong, through Creative Commons.



Figure 27. *Moerckia blyttii*, a species that became severely bleached by frost in the lab. Photo by Michael Lüth, with permission.



Figure 28. *Symphyogyna brasiliensis* female plant. A species in this genus became severely bleached by frost in the lab. Photo by George J. Shepherd through Creative Commons.



Figure 29. *Corsinia coriandrina*, a species that became severely bleached by frost in the lab but remained healthy in nature. Photo by Michael Lüth, with permission.





Figure 30. *Asterella lindenbergiana*, a genus in which some species are blackened by frost in the greenhouse. Photo by Michael Lüth, with permission.



Figure 31. *Asterella lindenbergiana*, a frost-sensitive genus in the lab. Photo by Martin Hutten, with permission.



Figure 32. *Dumortiera hirsuta*, a species that survives frost in the lab, but it is blackened. Photo by Michael Lüth, with permission.



Figure 33. *Monoclea forsteri*, a species that is blackened by frost in the lab. Photo by Jan-Peter Frahm, with permission.



Figure 34. *Fossombronia angustata*. This genus commonly exhibits winter thallus decay. Photo by Michael Lüth, with permission.



Figure 35. *Anthoceros punctatus*, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Tab Tannery, through Creative Commons.





Figure 36. *Phaeoceros laevis* with capsules, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Michael Lüth, with permission.



Figure 39. *Preissia quadrata*, member of a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Janice Glime.



Figure 37. *Lunularia cruciata*, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Des Callaghan, with permission.



Figure 40. *Riccardia*, a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Li Zhang, with permission.



Figure 38. *Pellia epiphylla*, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Li Zhang, with permission.



Figure 41. *Riccia nigrella*, member of a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Jan-Peter Frahm, with permission.





Figure 42. *Marchantia polymorpha* with red edges, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Brenda Dobbs, through Creative Commons.

This raises the question of how do these exposed bryophytes survive. Why don't they suffer structural damage from internal ice crystals? How are they protected from severe desiccation as crystals on the outsides of leaves draw water from the cells?

Melick and Seppelt (1992) investigated these questions in *Schistidium antarctici* (Figure 43), *Ceratodon purpureus* (Figure 43, Figure 50), *Bryum pseudotriquetrum* (Figure 44-Figure 45), and *Cephaloziella exiliflora* (Figure 46) that were collected in late summer in the Antarctic Wilkes Land. Following 16 days of immersion, the plant loss of the carbohydrates glucose and fructose was relatively low (ca. 10-29% of the sugar content) in healthy mosses. However, in the senescing tissues of *S. antarctici* 69% of these sugars were lost. Following 16 freeze-thaw cycles the bryophytes experienced a sugar loss 2-3 times as great as in non-frozen controls in all but the dead brown tissue. *Bryum pseudotriquetrum* lost 65% of its total sugar content after a freeze-thaw cycle, whereas the other species lost less than 28%. Freezing points varied from  $-8.3^{\circ}$  to  $-3.5^{\circ}\text{C}$ , with dead material having the highest freezing temperatures. Freezing temperatures and sugar loss did not correlate and there was no change in the freezing point temperature of tissues after the sugar loss.



Figure 43. *Schistidium antarctici* hummock with *Ceratodon purpureus* in hollows. Photo courtesy of Rod Seppelt.



Figure 44. *Bryum pseudotriquetrum* in Antarctica, a species that loses considerable sugar after a freeze-thaw cycle. Photo by Rod Seppelt, through Creative Commons.



Figure 45. *Bryum pseudotriquetrum* in Norway, a species that loses little sugar following 16 days of immersion. Photo by Michael Lüth, with permission.



Figure 46. *Cephaloziella exiliflora*, a species that loses little sugar following 16 days of immersion. Photo by Tom Thekathyl, with permission.

On Windmill Islands of continental Antarctica, there was almost no seasonal change in the soluble carbohydrate content of the bryophytes and lichens (Melick & Seppelt 1994). The researchers considered that this lack of change



may be the result of the extreme climate and rapid temperature fluctuations.

### Desiccation Tolerance

One of the consequences of freezing is dehydration. Consider the loss of moisture from your meat in the freezer when ice crystals form on the meat surface. Ice crystals are hygroscopic, pulling moisture from adjacent tissues. Furthermore, ice within the cell deprives the cell of the use of that water. The desiccation tolerance of bryophytes, therefore, helps them to survive freezing (Segreto *et al.* 2010). In their study of cryopreservation of bryophytes, Segreto and coworkers found that this natural desiccation tolerance negated the need for pretreatment or use of cryoprotectants before preserving live bryophyte tissues through freezing. They also found that longer or larger shoots of the leafy liverwort *Herbertus* (Figure 47) were able to regenerate more easily than smaller fragments, a phenomenon that suggests they are either able to transport from healthy cells to those that have been harmed, or that the greater amount of tissue helps to protect some of the cells.



Figure 47. *Herbertus hutchinsiae*; longer and larger shoots regenerate more easily in this genus. Photo by Michael Lüth, with permission.

Much like their resistance to hot temperatures, at least some bryophytes (*Syntrichia ruralis* – Figure 48-Figure 49) are more likely to survive freezing if they are dehydrated first (Bewley & Thorpe 1974). Those that were frozen in the hydrated state had lower rates of respiration and showed signs of freeze damage when rehydrated. Nevertheless, the respiration of desiccated mosses and of those desiccated and immersed in liquid nitrogen (frozen) was much higher on recovery than that of the controls that had remained hydrated at room temperature.

Desert species should be particularly adapted to freezing. They are endowed with various adaptations to survive desiccation, and they have a high probability of being desiccated when they experience freezing temperatures. But winter is the active season for the semi-desert grassland mosses in Hungary, with overwintering green shoots that are frequently exposed to temperatures below zero at night (Tuba *et al.* 2008). Daytime temperatures reach 0-5°C, and the dark-colored mosses (*Tortula/Syntrichia* – Figure 48-Figure 49) are even warmer (-2.1° to 6.9°C). The bryophytes were among the

18 out of 20 species that exhibited positive net photosynthesis. The abrupt increase in temperature in March did not affect the productivity rate of the mosses.



Figure 48. *Syntrichia ruralis*, a species that survives freezing better if it is dry first. Photo by David Holyoak, with permission.



Figure 49. *Syntrichia ruralis* dry, showing twisting leaves and awns that help to slow drying and protect at least some leaf cells from UV damage. Photo by Misha Ignatov, with permission.

Lenne *et al.* (2010) found that the ubiquitous moss *Ceratodon purpureus* (Figure 50) did not accumulate ice within the moss tissues during freezing. However, external ice induced desiccation. The water-filled hydroid cells cavitated at -4°C. Parenchyma cells of the stem's inner cortex lost 20% of their original volume and exhibited **cytorrhysis** (permanent and irreparable damage to cell wall after complete collapse of plant cell due to water loss and consequent loss of internal positive pressure) at the lowest temperature of -20°C. Nevertheless, following freezing at -20°C, chlorophyll fluorescence showed no damage to the chlorophyll. Once again, desiccation played a major role. In hydrated mosses, internal ice nucleation occurred at -12°C, but desiccated mosses showed no evidence of freezing at the lowest temperature of -20°C. There was nothing left to freeze.





Figure 50. *Ceratodon purpureus*, a species that experiences **cytorrhysis** due to desiccation that results from freezing, but chlorophyll remains undamaged. Photo by Janice Glime.

Tolerance to desiccation is one feature that helps bryophytes to survive freezing. Since leaves are generally only one cell thick, and most other parts only a few cells thick, water is easily drawn from the tissues during the slow cooling that occurs in nature. This increases the solute concentration and lowers the freezing point. Hence, intracellular freezing does not occur (Mazur 1969, in Smith 1982). In fact, some mosses are able to photosynthesize at temperatures below 0°C. In **nunataks** (area escaping glaciation) of Queen Maud Land, Antarctica, the air temperature rarely exceeds 0°C, yet moss photosynthesis occurs during the summer as long as there is sufficient water availability (Gjessing & Ovstedal 1989). Narrow clefts and stone blocks shield the mosses from desiccation and maintain less heat loss, but they are also shielded from direct solar radiation most of the time. Nevertheless, short-term periods of warming, even to -2°C, can greatly increase the moss temperature. These microsites permit mosses growing in such severe habitats to have the highest photosynthetic rates.

In the Arctic, *Racomitrium lanuginosum* (Figure 2) has an optimum temperature of 5°C at high light intensities (12,000-15,000 lux), but can sustain photosynthesis down to -10°C (Kallio & Heinonen 1973). Even after exposure to -30°C this moss is able to activate quickly (60% within 3 hours) when warmed. Thus, the bryophytes that exist in such harsh environments as the Antarctic and Arctic must have high freezing resistance, a high resistance to light stress, and a low photosynthetic temperature optimum (Alberdi *et al.* 2002).

In *Marchantia berteroana* (Figure 51), an Antarctic liverwort, freezing greatly reduces photosynthesis, but the author suggested that photosynthesis was also possible at temperatures below freezing (Davey 1997). Rather than temperature, this species is greatly limited by desiccation stress.

### Protection of Photosynthetic System from Light

High light intensities at low temperature levels can be extremely damaging to bryophytes that have leaves only one cell thick. Nevertheless, it appears that many, and perhaps most, bryophytes have mechanisms that protect them. In the Antarctic, where such conditions are common, the reversible inhibition present during freezing suggests that mosses such as *Schistidium antarctici* (Figure 43)

have processes that protect them from such photoinhibitory damage (Lovelock *et al.* 1995a) and thus do not require the repair processes that would require temperatures favorable for such repair enzyme activity. Rather, these mosses, when subjected to snow removal, suffered photoinhibition that was reversed when the temperature became warmer (Lovelock *et al.* 1995b). Nevertheless, the greatest recovery occurred in low light. Lovelock and coworkers (1995b) suggest that the photoinhibition during freezing is a protective process that down-regulates photosystem II when photosynthesis cannot keep up with the light-stimulated excitation of electrons.



Figure 51. *Marchantia berteroana*, a species limited by desiccation stress, but freezing only reduces photosynthesis. Photo by Andrew Hodgson, with permission.

Pannewitz *et al.* (2003b) showed similar protection for *Hennediella heimii* (Figure 52) at Canada Flush in Antarctica. Constant meltwater in the summer kept this moss continuously hydrated at near-freezing temperatures while light levels were frequently high. Yet there were no signs of either light saturation or photoinhibition. Rather, the electron transport rate response to light was linear at all temperatures. Pannewitz and coworkers suggested that the moss might be acclimated by building up non-photochemical quenching systems.



Figure 52. *Hennediella heimii*, a very cold-tolerant moss while continuously hydrated. Photo by Barry Stewart, with permission.



For those bryophytes that are epiphytes, it is unlikely that enough mechanisms exist to avoid freezing entirely. But living on a dark tree trunk is likely to mean frequent freeze-thaw cycles. This not only presents problems of desiccation, but also presents potential light damage to the photosynthetic system. Working with the Mediterranean epiphytic moss *Leucodon sciurioides* (Figure 53), Deltoro *et al.* (1999) found that one aspect of bryophyte freeze-thaw survival could be their ability to enhance their non-radiative dissipation of absorbed light energy by freeze-induced decrease in CO<sub>2</sub> fixation, hence protecting their photosynthetic system from excess excitation. This temporary reduction in CO<sub>2</sub> fixation is quickly returned to normal after freezing.



Figure 53. *Leucodon sciurioides* on a tree trunk where it is exposed to atmospheric temperatures all year. Photo by Michael Lüth, with permission.

Rütten and Santarius (1992a) found that photosynthetic apparatus in mature tissues of *Plagiomnium* (Figure 55) species was more frost tolerant than that of either young or old leaves. As freezing stress increased, fluorescence decreased and the photosystem II-mediated electron transport system became inactivated. This resulted in inhibition of electron donations to the photochemical reaction of photosynthesis, differing little from the pattern in tracheophytes. Nevertheless, there was little decrease in transfer of excitation energy through antenna pigments to reaction centers of photosystem II as a result of lethal freezing stress.

### Role of Calcium

Calcium seems to play a role in cold tolerance through its role in regulation of membrane transport. In *Physcomitrella patens* (Figure 13), wild type plants respond to cold shock (0-10°C) by increasing cellular content of calcium (Russell *et al.* 1996). It is most likely not calcium itself, but its effect on membrane permeability and other processes in the cell that provide actual protection. In the thallose liverwort *Conocephalum conicum* (Figure 54), Krol *et al.* (2003) likewise found that calcium played a role in climate response. A sudden drop in temperature causes it to generate all-or-none action potentials that appear to be the result of membrane potential changes due to influx of Ca<sup>++</sup> derived from both internal and external sources.



Figure 54. *Conocephalum conicum*, a species in which membrane potentials change in response to freezing. Photo by Janice Glime.

The activity and thermosensitivity of superoxide dismutase (SOD) is highly sensitive to ions of Ca<sup>++</sup> and Zn<sup>++</sup> (Christov & Bakardjieva 1999). In *Plagiomnium affine* (Figure 55), calcium was most important for the one cytosolic and mitochondrial SOD's, whereas zinc was more important for the chloroplastic and two cytosolic SOD's.

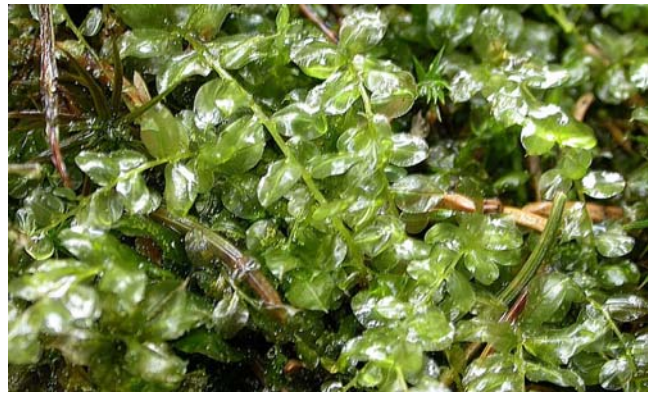


Figure 55. *Plagiomnium affine*, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.

### Abscisic Acid

*Physcomitrella patens* (Figure 13), as in many studies, has contributed to our understanding of freezing protection in bryophytes. When this species was grown on ABA agar, it accumulated up to 22% of its dry weight as sucrose, compared to 3.7% in control (non-ABA) tissues (Davey 1997). Sucrose serves as a protectant during both freezing and drying, but is insufficient as the only agent for freezing protection. When subjected to temperatures down to -80°C, it survived a freeze-cycle only when provided with the cryoprotectant DMSO, a compound that makes membranes more permeable. This species can only survive slow drying, which it does down to 0.02 g H<sub>2</sub>O per g DW. Sugar composition and glass transition temperatures differed little between slow and fast drying. Nevertheless, the strength of the hydrogen bonding in the cell's glassy matrix was greater in the slow-drying conditions.

ABA (abscisic acid) is produced in tracheophytes in preparation for cold temperatures and permits plants to survive to lower temperatures, somewhat like antifreeze.



Nagao *et al.* (2005) have shown that media containing ABA does indeed lower the LT<sub>50</sub> (temperature at which 50% of cells die) for *Physcomitrella patens* (Figure 13) from -2°C to -10°C and even lower. They observed that there was a "dramatic" alteration in the appearance of the organelles, manifest in slender chloroplasts with reduced starch grains. The vacuoles became segmented rather than the typical single large vacuole. ABA also protected the cells from membrane lesions that occurred in controls at -4°C. One of the mechanisms of protection stimulated by the ABA treatment was an increase in the osmotic concentration of cells of the protonema, most likely due to the increased sugar concentration that accompanied the ABA treatment. But that only tells us what ABA can do. Next we need to determine that mosses do indeed produce it or increase its production at the right time, what stimuli cause this production, and can lunularic acid (ABA analog in liverworts) do the same for liverworts.

But the story does not appear to be straight-forward. Although they reported ABA-induced freezing tolerance in *Physcomitrella patens* (Figure 13) in 2003, Minami *et al.* (2003, 2005) reported that freezing tolerance was not associated with an increase in the level of endogenous abscisic acid in *P. patens*, but that it was associated with increases in the expression of stress-related genes. It seems that the role of ABA is to induce the genes, not to offer protection itself (Nagao *et al.* 2001; Minami *et al.* 2003, 2005). When they subjected protonemata of *P. patens* to -4°C, following normal growth conditions, more than 90% of the cells died, indicating that protonema cells are freezing-sensitive (Minami *et al.* 2003, 2004). ABA treatment resulted in a significant increase in the expression of all PPAR genes within 24 h. These genes are known to participate in the increase of freezing tolerance, and indeed, the death rate decreased significantly.

Minami *et al.* (2005) likewise studied freeze tolerance in *Physcomitrella patens* (Figure 13). They found that in the temperature range of 10°C and 0°C, and especially at 0°C, freeze tolerance increased significantly. But they found that internal tissue levels of ABA did not increase during that acclimation period. Furthermore, removal of ABA by activated charcoal did not affect the developing freeze tolerance. Hence, they concluded that ABA is unimportant in freeze tolerance. I would guess that it is, however, important in surviving the accompanying desiccation.

### Transporter Proteins, ABA, and Ca

Further studies on *Physcomitrella patens* (Figure 13) support this conclusion. Two novel transporter-like proteins increase dramatically with low temperature treatment, among other stresses, and increase the cellular tolerance to freezing stress (Takezawa & Minami 2004). It is likely that calmodulin is used by the cell to regulate these novel proteins, and that ABA serves to induce the expression of the necessary genes. However, in *P. patens*, slow freezing to -4°C caused death of more than 90% of the protonema cells (Minami *et al.* 2003). ABA treatment for 24 hours caused a dramatic increase in the freezing

tolerance of this plant, but cold treatment had little effect. This seems to contradict the earlier findings of Nagao *et al.* (2001). They found that both ABA and low temperatures caused an increase in gene expression with concomitant enhancement of freezing tolerance in *Physcomitrella patens*. The LT<sub>50</sub> dropped from -2°C to -10°C when the protonemata were grown in a medium with enhanced ABA (Nagao *et al.* 2005). It appears that ABA might be the agent needed to effect expression of the freeze-tolerance genes, but how much advance notice does it require?

### Sugars and Plasmolysis

But it appears that ABA also is associated with the increase of soluble sugars in the protonemata of *Physcomitrella patens* (Figure 13) (Nagao *et al.* 2003). Such sugars increase freezing tolerance, most likely by depressing the freezing point.

Rütten and Santarius (1992b) found an increase in cold tolerance from summer to winter in the mosses *Polytrichastrum formosum* (Figure 56), *Atrichum undulatum* (Figure 57), *Plagiomnium undulatum* (Figure 61), *P. affine* (Figure 55), and *Mnium hornum* (Figure 58), and the thallose liverwort *Pellia epiphylla* (Figure 38). The frost resistance between summer and winter differed by more than 25°C in some species, but *Pellia epiphylla* showed little hardening. Concomitant with this increase in frost tolerance, they found a rise in sucrose concentration (except in *Mnium hornum*), and those mosses that were highly frost resistant had a total sugar concentration of 90-140 mM, 80% of which was sucrose. The mosses *Brachythecium rutabulum* (Figure 59) and *Hypnum cupressiforme* (Figure 60) were highly frost tolerant in summer and at that time had high sucrose levels. Furthermore, as sucrose levels declined during artificial exposure to higher temperatures, cold hardiness declined.



Figure 56. *Polytrichastrum formosum*, a species that increases its frost tolerance from summer to winter. Photo by Michael Lüth, with permission.





Figure 57. *Atrichum undulatum*, a species that increases its frost tolerance from summer to winter. Photo by Michael Lüth, with permission.



Figure 58. *Mnium hornum*, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.



Figure 59. *Brachythecium rutabulum*, a species that is highly frost tolerant in summer. Photo by Michael Lüth, with permission.



Figure 60. *Hypnum cupressiforme*, a species that is highly frost tolerant in summer. Photo by Michael Lüth, with permission.



Figure 61. *Plagiomnium undulatum*, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.

However, Rütten and Santarius (1993a) found that different levels of sucrose, glucose, and fructose at the cellular level had no bearing on the frost tolerance of leaves of *Plagiomnium affine* (Figure 55) and *P. undulatum* (Figure 61). Sucrose seemed to contribute in some way to the tolerance, increasing from summer to winter, while temperature limits increased from  $-10^{\circ}\text{C}$  in summer to less than  $-35^{\circ}\text{C}$  in winter, but there was no correlation between increased sugar content of shoots and frost resistance. They concluded that other factors were also necessary to the increased frost tolerance.

Studies on membrane permeability suggest that sugar uptake and release may be altered as mosses prepare for winter (Rütten & Santarius 1993b). Liu (2000) showed that as the temperature increased above  $40^{\circ}\text{C}$  in these and other species, the membrane permeability increased. At the cold end of the scale, it appears that protection against an increase in membrane permeability may be a necessary step in cold hardiness. Greater retention of sugars could account for the higher concentrations in cold temperatures.



On the other hand, reversible plasmolysis can protect cells by permitting water loss and preventing crystal damage.

This relationship to membrane permeability is supported by studies on *Physcomitrella patens* (Figure 13) (Minami *et al.* 2003). Minami and coworkers subjected protonema cells to hyperosmotic concentrations of NaCl and mannitol, causing an increase in freezing tolerance. They interpreted this increase to indicate that ABA and cold stress trigger the expression of cryoprotectant genes. Oldenhof *et al.* (2006) suggested that sucrose might act as an osmotic spacer in membranes, while at the same time ABA mediates the synthesis of proteins, strengthening the cellular glasses. But we know that ABA can cause membranes to leak. Might there still be a more direct role for ABA than simply a trigger for genes, or is its usual role in membrane leakage one of triggering genes that cause this response?

Aro and Karunen (1988), in studying protonemata of *Ceratodon purpureus* (Figure 50), found that the content and unsaturated level of membrane lipids increased significantly in low growth temperatures, apparently contributing to frost hardiness. Hakala and Sewón (1992) found that both drought and low temperatures (6°C) caused an increased incorporation of  $^{14}\text{C}$  into the neutral lipid fraction and decreased its incorporation into the glycolipid fraction in *Dicranum elongatum* (Figure 62), suggesting a preferential accumulation of acetylenic triacylglycerols. Such responses, when adaptive, can permit the moss to prepare for the drought of winter through the signal of low temperature.



Figure 62. *Dicranum elongatum*, a subarctic moss. Photo by Michael Lüth, with permission.

The protonema stage is often ignored in understanding the ecology and physiology of bryophytes. Yet if it is unable to reach a mature state of development and produce gametophores, the species will be greatly limited in its establishment survival. Nagao *et al.* (2006) demonstrated that like the leafy plant, the protonema responds to ABA application, increasing its freezing tolerance. This response includes the accumulation of low-molecular-weight soluble sugars, including theanderose (G6- $\alpha$ -glucosyl sucrose). This accumulation was inhibited by an inhibitor of nuclear-encoded protein synthesis (cycloheximide), resulting in a marked decrease in freezing tolerance. Theanderose is

promoted by cold acclimation and by treatment with hyperosmotic solutes, both of which increase cellular freezing tolerance.

### Freezing Longevity

Just how long can a bryophyte remain frozen and survive? In the Antarctic on Signy Island, *Chorisodontium aciphyllum* (Figure 63-Figure 64) and *Polytrichum strictum* (= *P. alpestre*; Figure 65) form a major part of the vegetation. Recently, Roads and Longton (2013) reported *C. aciphyllum* that was extracted from a core at 138 cm depth. This depth remains permanently frozen. There was no great surprise that regrowth occurred from specimens of *C. aciphyllum* retrieved from depths of 0-30 cm, but three new shoots grew from specimens extracted from 110 cm! And in addition the leafy liverwort *Cephaloziella varians* (Figure 66) regenerated new shoots from the muddy base of that core at 123-138 cm. Based on radiocarbon dating, these plants had been there ~1750 years and had been frozen a good portion of that time!



Figure 63. *Chorisodontium aciphyllum* in Antarctica, a species that apparently can remain viable in a frozen state for more than 1700 years! Photo from the Polar Institute through Creative Commons.



Figure 64. *Chorisodontium aciphyllum*, a species that regenerated from a frozen state after more than 1700 years! Photo from the Jan-Peter Frahm, with permission.





Figure 65. *Polytrichum strictum*, a major component of the Antarctic flora. Photo by Michael Lüth, with permission.



Figure 66. *Cephaloziella varians*, a species that regenerated from 1750 year old cores in Antarctica, here nestled among *Polytrichaceae*. Photo by Kristian Peters, with permission.

### Internal Cushion Temperatures

The internal temperatures in bryophyte cushions follow the ambient temperature until the cushion temperature drops below 0°C and the water there begins to freeze (Rod Seppelt, Bryonet 27 June 2022). When the cushion begins to freeze, latent heat is released, elevating the cushion temperature ~2°C. This slows freezing and provides more time for physiological processes to acclimate, including that of protein partial denaturing. These physiological modifications reduce tissue damage.

### Freezing Effects

Freezing can have many consequences on cells of plants. In bryophytes, it can cause disorganization of the chloroplast lamellae, thus damaging the photosynthetic system (Pihakaski & Pihakaski 1979), damage the cell membranes, and cause desiccation and loss of solutes. In the thallose liverwort *Pellia epiphylla* (Figure 38) that had been chilled and hardened at -22°C, ultrastructural changes occurred. Vacuoles contained a fine granular substance in hardened tissues. Those that had only been chilled had large electron-dense particles embedded in a finer granular substance. The oil bodies changed, with abundant lipid-

like bodies in the cytoplasm. These resembled the oil globules of oil bodies, with oily-looking flecks in the vacuoles. Large starch grains were present in the chloroplasts and the lamellar system lost some of its organization. Interestingly, the net photosynthesis was highest in material that had spent the longest time at -22°C.

### Supercooling Intracellular Water

But what is it that permits plants to survive the sub-zero temperatures of winter? One of the first requirements for survival at below freezing temperatures is supercooling of intracellular water (George & Burke 1977). If the water in the cells were to freeze, ice crystals and expansion of water in its frozen state could cause mechanical damage to the cell. We can observe that many trees have as their northern limit the line where -40°C is rarely reached. This is significant since the lower limit for supercooling of water is -41°C (Kuiper 1978), and George and Burke (1977) have observed ice formation in xylem at -30 to -40°C.

### Ice Crystals Increase Solutes

Although ice crystals outside the cells can kill plants by desiccation, as in the case of the Florida orange trees, they can also be a means of "winterizing" cells by increasing internal solute concentrations. Molecules have vibrational energy. When an ice crystal forms, the vibrational energy is much reduced, creating an energy gradient between the liquid water molecules in the cell and the crystallized ones outside it (Marchand 1991). The result is that the more active liquid molecules migrate toward the area of less energy on the outside of the cell, adding to the mass of the crystals. Of course the result inside the cell is an increase in concentration of cytoplasmic solutes, thus lowering its freezing point, just as antifreeze does in a car battery. The process of protein denaturation, discussed below, causes the membranes to be leaky, facilitating this emigration of water. In many cells, there seems to be a second change as the temperature continues to decrease, and that change seems to correspond with cell death. One theory suggests that this may be accompanied by failure of water to leave the cell, resulting in internal crystallization and membrane destruction. Even in the absence of internal crystallization, cells still face another problem as the temperature decreases. As additional water is lost, irreversible dehydration may occur and toxic concentrations of solutes may accumulate (Weiser 1970).

### Crystal Damage

It is the formation of crystals, not the low temperature itself, that damages cells irreparably, whether it is external crystals that cause dehydration and toxicity, or internal crystals that physically disrupt cell membranes (Schmitt *et al.* 1985). Therefore, another possibility exists for at least some plants to survive the cold, a process called **glass formation** (Marchand 1991). Glass formation results from **vitrification**, in which water solidifies without reorienting into a crystal (Figure 1). This process occurs when we immerse tissue in liquid nitrogen and thus permits us to preserve tissues without ice crystal damage. Balsam poplar trees are known to "form glass" at temperatures below -28°C (Hirsh *et al.* 1985). This means that the contents of



the cell are solid, thus preventing crystal damage, desiccation, and concentration of solutes to toxic levels.

### Preventing Ice Crystals

Growers protect oranges by spraying non-nucleating bacteria on them, thus out-competing the bacteria that form the centers for ice crystals on the oranges. Some frogs make tiny proteins that become the centers of small crystals rather than large ones. And it appears that bryophytes and algae may also form special proteins that diminish crystal damage to cells.

One of the means by which plant cells are able to protect themselves from freeze damage is to modify or prevent ice crystals. Crystals form around tiny "nuclei" such as dust particles and bacteria. Being hygroscopic, these crystals grow by taking moisture from their surroundings, including cells. On the outside of the cell, they can desiccate a cell by extracting the water and binding it to the crystal. Inside the cell, they can not only desiccate the cell, but can also cause physical harm by protruding through a cell membrane.

In the Antarctic, Cyanobacteria, algae, and mosses form macromolecular substances that modify growing ice crystals, causing pitting of the crystals, and that cause them to go through an ice phase during freezing (Raymond & Fritsen 2000) – **glass formation** (Figure 67). One Antarctic species of *Bryum* (Figure 68) can modify these crystals by using this macromolecular substance to modify the shape of the growing crystals, and it may be that the mechanism of these macromolecules is to prevent recrystallization of ice (Raymond & Fritsen 2001). These substances are absent in temperate Cyanobacteria and mosses, but do occur in mosses from cold North American habitats. Their actual role is unknown, but their ability to be destroyed by temperatures of 45-65°C suggests that they are protein. It is possible that they may be non-nucleating proteins that reduce crystal formation.



Figure 67. *Hedwigia ciliata* with glass formation (ice) on the surface rather than ice crystals. Photo by Michael Lüth, with permission.



Figure 68. *Bryum cryophilum*, showing the red pigments common in polar regions. One species of *Bryum* can modify ice crystals, somehow reducing damage to the plant cells. Photo by Michael Lüth, with permission.

### Rate of Freezing

The effectiveness with which these mechanisms can protect the cell are dependent upon the rate of freezing. White and Weiser (1964) found that leaves on the southwest side of a tree could drop in temperature by 9.5°C per minute across the freezing point of cell water at sunset! The result of this rapid freezing was cell death due to crystallization of water trapped inside the cell. Yet the same species was able to tolerate temperatures as low as -87°C when the temperature decreased slowly. Marchand (1991) contends that slow cooling of 10°C per hour is common in nature and permits time for the removal of water from cells by exterior crystal formation.

But what do all these tracheophyte scenarios mean for bryophytes? In 1912 Irmischer reported that at least some mosses were tolerant to desiccation and cold. Antropova (1974) found that temperatures above optimum for 3 hours did not affect cold resistance of moss cells, nor did temperatures within the optimum range influence either thermal stability or cold resistance. From these experiments he deduced that bryophytes respond similarly to tracheophytes but differently from algae to changes in temperature.

But the cooling process in bryophytes is different from that of tracheophytes (Dilks & Proctor 1975). If a tracheophyte cell is cooled rapidly, the cell contents freeze, and this usually causes fatal damage to the cell. However, the normal condition in nature is slow cooling. Because mosses and liverworts lack protective cells or thick, waxy cuticles, and are mostly one cell thick, this process is much more rapid. As the ambient temperature cools to below freezing, bryophyte cell contents will supercool and lose water to the surroundings, depending on the water-potential gradient. Levitt (1972) found that the injurious freezing rate for cell sections of tracheophytes is 60 times as rapid as for whole plants. Since bryophytes are much like a section of tracheophytes, they could experience a similar rapid freeze, one that could occur during a sudden drop in temperature, making bryophytes more vulnerable than tracheophytes. However, as water freezes outside bryophyte cells, the internal freezing point decreases due to loss of water and increasing concentration of cell sap (Dilks & Proctor 1975). And here tracheophytes have a disadvantage compared to bryophytes. Rather, they are



inhibited from water loss by a hydrophobic cuticle, and even if they accomplished this loss, their cells are more likely than those of bryophytes to be damaged by desiccation. Hence, cells high in water content and having little waxy cuticle for protection, like those of lettuce, turn to mush when frozen.

Among the bryophytes compared in Figure 69, the mosses *Hookeria lucens* (Figure 70) and *Plagiothecium undulatum* (Figure 71) are the most like wet filter paper, with a plateau in cellular cooling as the cell reaches the freezing temperature of water and water leaves the cell. The thallose liverwort (*Conocephalum conicum*, Figure 54), on the other hand, is more similar to the tracheophyte *Arbutus unedo* (Figure 72), with a slow decline in temperature below the freezing point of water.

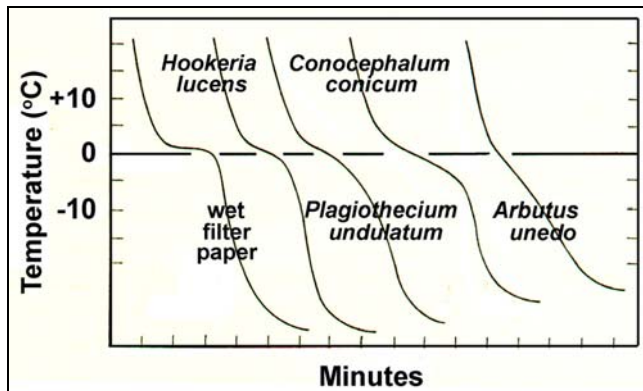


Figure 69. Temperature drop of bryophyte leaf cells compared to that of filter paper and a tree species (*Arbutus unedo* – the strawberry tree). Redrawn from Dilks and Proctor 1975.



Figure 70. *Hookeria lucens*. Photo by Michael Lüth, with permission.



Figure 71. *Plagiothecium undulatum*. Photo by Michael Lüth, with permission.



Figure 72. *Arbutus unedo* (strawberry tree). Photo by Richie Steffen, courtesy Great Plant Picks, with online permission.

### Hydration State

The state of hydration is an important consideration in the tolerance of bryophytes to temperature. It is well-known that they tolerate much higher temperatures in the dry state, but they also often tolerate lower temperatures in the dry state as well. This is predictable because of the danger of water forming crystals that can harm membranes.

Dilks and Proctor (1975) subjected nine moss species and one thallose liverwort species to sub-zero temperatures in a desiccator at 32% relative humidity. All survived to -30°C in this dry state except the cushion moss *Leucobryum glaucum* (Figure 73) and leafy liverwort *Plagiochila asplenoides* (Figure 74) var. *major*, both of which died in the desiccator with and without the cold treatment. In the wet state, however, of the 27 mosses tested, 20 had 50% or more death at -10°C and lower. For three of the taxa (*Andreaea* spp., Figure 75), the status could not be determined. *Hylocomium splendens* (Figure 76), *Racomitrium aquaticum* (Figure 77), *R. lanuginosum* (Figure 78), and *Scorpiurium circinatum* (Figure 78) survived to -10°C. *Hookeria lucens* (Figure 71), *Leucobryum glaucum* (Figure 73), *Mnium hornum* (Figure 58), and *Plagiopus oederianus* (Figure 79) were dead or mostly dead at -5°C. Among the liverworts, none of the thallose liverworts survived at -5°C. Among the leafy liverworts, four species survived as well as the mosses, but two had more than 50% mortality at -5°C. Only *Plagiochila spinulosa* (Figure 80) survived to -10°, with 50% survival. It is interesting that such epiphytes as *Porella platyphylla* (Figure 81) had poor survival when moist at -5°C, because that leafy liverwort lives in northern habitats where it is likely to experience such conditions in the winter, but perhaps acclimation and physiological races differ.





Figure 73. *Leucobryum glaucum*, a species that died in the desiccator (32% RH) in a cold treatment to  $-30^{\circ}\text{C}$ . Photo by Janice Glime.



Figure 76. *Hylocomium splendens*, a species that survived to  $-10^{\circ}\text{C}$  in the lab. Photo by Michael Lüth, with permission.



Figure 74. *Plagiochila asplenioides*, a species that died in the desiccator (32% RH) in a cold treatment to  $-30^{\circ}\text{C}$ . Photo by Michael Lüth, with permission.



Figure 77. *Racomitrium aquaticum*, a species that survived to  $-10^{\circ}\text{C}$  in the lab. Photo by Michael Lüth, with permission.



Figure 75. *Andreaea nivalis*. In experiments to  $-30^{\circ}\text{C}$  and 32% RH, effects on three species in this genus were inconclusive. Photo by Michael Lüth, with permission.



Figure 78. *Scorpiurium circinatum*, a species that survived to  $-10^{\circ}\text{C}$  in the lab. Photo by Michael Lüth, with permission.





Figure 79. *Plagiopus oederianus*. Photo by Michael Lüth, with permission.

These data suggest that mosses are more tolerant of wet cold than liverworts and that the thallose liverworts are the most vulnerable.

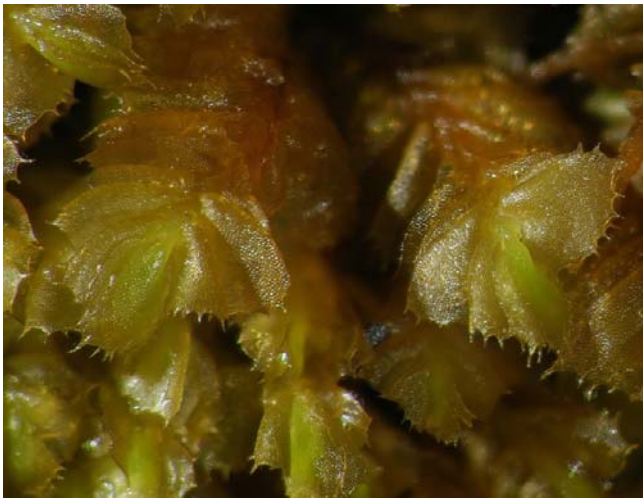


Figure 80. *Plagiochila spinulosa* in Scotland, a species with more than 50% survival at -10°C. Photo by Michael Lüth, with permission.



Figure 81. *Porella platyphylla*, a species that has poor survival if moist at -5°C. Photo by Michael Lüth, with permission.

## Lipids in Membranes and Protein Denaturation

We know that bryophytes are able to exist farther north (and south) than woody plants and yet lack the insulating effects of a thick layer of bark. Furthermore, the plasma membrane must remain intact if cellular nutrients and other solutes are to be contained upon thawing. As the temperature drops, the lipid matrix of a plasma membrane can crystallize, and the degree of crystallization depends upon the types of lipids. Saturated lipids crystallize first, with less saturated ones crystallizing at lower temperatures. The crystallization causes membrane proteins to aggregate, setting off a chain reaction. These aggregated proteins make possible the oxidation of sulfhydryl groups of the protein molecules because the close contact permits the formation of disulfide bridges (Levitt 1969). This denaturation of the membrane protein is irreversible and results in membrane destruction, often leading to cell death. It seems then that bryophytes must have some means to prevent this series of events from occurring.

Tracheophytes typically increase their lipid content in response to decreasing temperatures, resulting in winter hardiness. The lipids phosphatidyl choline and phosphatidyl ethanolamine in particular seem to contribute to increased resistance to cold (Kuiper 1970; Yoshida 1974; Siminovitch *et al.* 1975; De La Roche *et al.* 1972, 1975; Willemot 1975). The unsaturated fatty acid linolenic acid likewise seems to play a major role in reducing frost damage (Kuiper 1978).

## Unsaturated Lipids

Gellerman and coworkers (1972) reported highly unsaturated lipids in several genera of bryophytes. When Al-Hasan and coworkers (1989) examined *Bryum bicolor* (Figure 82) to determine the effects of temperature on cold hardening, they found that the lipids of this species contained higher proportions of digalactosyldiacyl glycerols and sulfoquinovosyldiacyl glycerols when incubated at 5°C than when plants were incubated at 25°C. An interesting and seemingly non-adaptive aside is the greater production of linolenic acid under continuous illumination at 5°C, since low temperatures generally coincide with short days.



Figure 82. *Bryum bicolor*, a species that has higher concentrations of digalactosyldiacyl glycerols and sulfoquinovosyldiacyl glycerols when incubated at 5°C than when incubated at 25°C. Photo by Michael Lüth, with permission.



## Fatty Acid Alterations

One of the means by which organisms prepare for changes in temperature is to alter fatty acid components to those with lower solidification points. Lemmings change the fatty acids in their foot pads by eating bryophytes that contain lots of arachidonic acids, thus providing these tissues with cell membranes that are more pliable at low temperatures (Prins 1981). Meanwhile, the bryophytes are also preparing for winter in a different way.

The protonema of the common moss *Ceratodon purpureus* (Figure 50) prepares for winter by increasing its content and unsaturated level of membrane lipids (Aro & Karunen 1988). The galactolipids typically found in chloroplast membranes increased; phospholipids nearly doubled when plants were acclimated at 4°C vs 20°C. But this seems to have little effect on the frost hardness. Rather, it permits these acclimated protonemata to retain a high phospholipid content. If, as is typical of unhardened protonemata, the phospholipids had been lost, that would have caused irreversible damage to CO<sub>2</sub> fixation following freezing and thawing. Aro and Karunen concluded that while the changes in membrane lipids were themselves not an important component of hardening, they were somehow involved in other factors that contributed to frost hardness.

In *Sphagnum fimbriatum* (Figure 83-Figure 84), when the temperature decreases in the range of 5-15°C, the amounts of linoleic,  $\alpha$  linolenic, and arachidonic acids in their glycolipids [both monogalactosyldiacyl glycerols (MGDG) and digalactosyldiacyl glycerols (DGDG)] also decrease (Koskimies-Soininen & Nyberg 1991). These are replaced with increased proportions of palmitic, stearic, and oleic acids, especially in MGDG. However, if light intensity also decreases, as it would as winter approaches, this species exhibits an increase not only of palmitic and stearic acids, but also of linolenic and arachidonic acids, in MGDG, while oleic and  $\alpha$ -linolenic acids decrease. But this pattern is certainly not universal. Even the related *S. magellanicum* (Figure 85) responds differently (Koskimies-Soininen & Nyberg 1987). It had its largest changes in fatty acid composition at lower temperatures (0-5°C) and short photoperiods (3-6 hrs daylight). But, unlike *S. fimbriatum*, in decreasing light and temperatures, *S. magellanicum* exhibited a decrease in linolenic acid.



Figure 83. *Sphagnum fimbriatum* frozen in its habitat. Photo by Dick Haaksma, with permission.



Figure 84. *Sphagnum fimbriatum*, a species that decreases its concentrations of various fatty acids, including arachidonic acids, when the temperature decreases in the range of 5-15°C. Photo by Michael Lüth, with permission.



Figure 85. *Sphagnum magellanicum*, a species that has its largest changes in fatty acids at 0-5°C. Photo by Michael Lüth, with permission.

There are indications that the fatty acid composition of bryophyte cells change as the temperatures do (Saruwatari *et al.* 1999). *Marchantia polymorpha* (Figure 42) exhibited changes in the percentages in linolenic acid, arachidonic acid, and eicosapentaenoic acid when the temperature was changed from 25°C to 15°C. Both linolenic acid and eicosapentaenoic acid increased greatly. However, the changes were not equal throughout the cell. Arachidonic acid and eicosapentaenoic acid increased in the chloroplast fraction but not in the rest of the cell, while the level of linolenic acid was increased in both fractions. We need to understand this in the context of the high levels of arachidonic acids known in bryophytes and the suggestion that some animals eat bryophytes to prepare for winter because of these high levels. Prins (1982) has proposed that they provide more fluid fat pads for animals that run around on frozen ground in winter.

One study on lichens might help us predict the way in which bryophytes could respond (Dertien *et al.* 1977). In forested areas, both bryophytes and lichens can be found on tree trunks as well as on the forest floor and in open soil areas. In their study of lichens, Dertien and coworkers (1977) found that lichens of tree trunks contained high levels of the unsaturated linoleic and linolenic acids; however, nearby sand dune species had large quantities of cyclic acids rather than unsaturated acids. This may relate



to the greater likelihood of low temperatures on the tree trunks.

### Fatty Acids and N

Using *Ctenidium molluscum* (Figure 86), *Pogonatum urnigerum* (Figure 87), *Dichodontium pellucidum* (Figure 88), and *Tortella tortuosa* (Figure 89), Al-Hasan *et al.* (1991) demonstrated that increasing the nitrogen concentration of the medium causes a decrease in the dominant unsaturated fatty acids arachidonic acid (in *C. molluscum*), eicosatrienic acid (in *P. urnigerum*), and linoleic acid (*D. pellucidum*, *T. tortuosa*). Nitrogen availability generally decreases as the growing season progresses in forests, so it is possible that such a decrease could serve as a signal for mosses to store more unsaturated fatty acids. Arachidonic acid and eicosapentaenoic acid are widespread in mosses (Hansen & Rossi 1990), but arachidonic acid never occurs in angiosperms (Karunen 1990).



Figure 86. *Ctenidium molluscum* in a rock canyon in Europe. This species seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.



Figure 87. *Pogonatum urnigerum*, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Janice Glime.



Figure 88. *Dichodontium pellucidum*, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.



Figure 89. *Tortella tortuosa*, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.

### Triglycerides

The role of triglycerides in low temperature survival seems yet to be explored. Karunen (1981) found that in the subarctic moss *Dicranum elongatum* (Figure 62) triglycerides commonly increased only at low temperatures of 1-6°C. But what might they do for frost hardiness?

### Polyribosomes

In the desiccation-tolerant moss *Syntrichia ruralis* (Figure 48-Figure 49), temperatures down to 2°C cause a proliferation of polyribosomes, accompanied by a decrease in single ribosomes (Malek & Bewley 1978). The number of ribosomal subunits does not change. Mosses that have not been desiccated exhibit leucine uptake and were able to synthesize protein at 2° and -2.5°C. However, slowly dried mosses do not contain polyribosomes and instead reform them upon rehydration. There seems to be no change in the



rate of protein synthesis in mosses kept at cold temperatures (2°C) or winter collected. Rather, the moss appears to be pre-acclimated or pre-adapted to freezing year-round. Malek and Bewley concluded that this moss does not have any seasonal cold hardening.

### Age Difference to Freezing

Hudson and Brustkern (1965) found that old and young leaves of mosses may differ in their responses to sub-zero temperatures. They found that *Plagiomnium undulatum* (Figure 61) mature leaves experienced extracellular freezing when cooled slowly, thus preventing intracellular freezing. Young shoots, on the other hand, could not tolerate temperatures below 12°C. When subjected to freezing temperatures, young leaves of *P. undulatum* do not experience extracellular ice formation, thus making intracellular freezing more likely. Rütten and Santarius (1992a) found that not only young leaves, but also old leaves of *Plagiomnium*, had much less frost tolerance than mature leaves.

### Freezing Effect on Distribution and Niche

Green *et al.* (2007) reported that freeze-thaw cycles are extremely common in parts of Antarctica, with up to 110 occurring in a single year in the northern maritime. Some lichens adapt to this by growing in the pores of rocks, so we should look for bryophytes that have similar safety mechanisms.

The ability to survive freezing will influence both geographic and habitat distribution of bryophytes. Shirasaki (1984) found that *Bryoxiphium norvegicum* (Figure 90) subsp. *japonicum* is distributed in southern Japan at altitudes of 80 m to 2350 m, whereas further north the upper limit declines. Although this species occurs in areas where there is deep snow for a long period of time, it lives mostly on the vertical faces of overhanging rocks in ravines where it is not likely to be covered directly by snow. However, it is positioned where the overhanging soil and snow protect it from the cold wind.

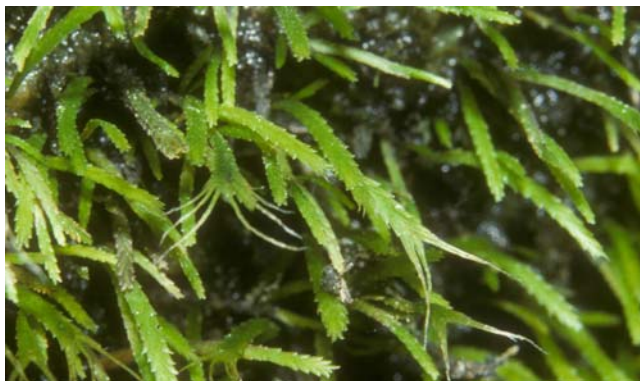


Figure 90. *Bryoxiphium norvegicum* growing on a rock face. Some varieties of this species are able to grow at high elevations. Photo by Janice Glime.

Shirasaki (1987) also found that the distributions of the leafy liverworts *Bazzania trilobata* (Figure 91) and *B. yoshinagana* (Figure 92) in Japan seem to relate to differences in cold and related desiccation tolerance. *Bazzania trilobata* grows on soil that receives sunshine and

good drainage. It is able to survive in areas with little snow where early spring subjects it to severe cold and desiccation. By contrast, *B. yoshinagana* lives primarily on the floor of dense conifer forests where deep snow covers it all winter, thus maintaining moisture and insulating it from the sub-freezing air.



Figure 91. *Bazzania trilobata*, a species that grows in areas that have little snow where early spring subjects it to severe cold and desiccation. Photo by Michael Lüth, with permission.



Figure 92. *Bazzania yoshinagana*, a species is covered by deep snow all winter. Photo by Real thing X 0.3. The copyright of the photograph of this site belongs to the author. Please reprint without permission.

As was seen for *Fontinalis* (Figure 123-Figure 124) species in the previous subchapter on temperature, adaptation to cold can be a contributing difference between species, permitting them to live where they do. It seemed that for centuries we concentrated on morphological differences between species and attempted to see their geographic separations in that perspective. However, physiological differences are much more likely to determine where plants live than are their morphological differences. In some cases, morphology can cause



physiological differences, such as growth forms that alter temperature, but we should not stop there in our quest for niche delineation.

A good demonstration of these physiological differences is seen in the genus *Sphagnum*. In their study of five species, Balagurova *et al.* (1996) found that the photosynthetic leaf cells of *Sphagnum balticum* (Figure 93), *S. subsecundum* (Figure 94), and *S. teres* (Figure 95) were more frost-resistant than were those of *S. magellanicum* (Figure 85) and *S. fuscum* (Figure 96).



Figure 93. *Sphagnum balticum*, a species that is more frost-resistant than the hummock species *S. magellanicum* and *S. fuscum*. Photo by Michael Lüth, with permission.



Figure 94. *Sphagnum subsecundum*, a species that is more frost-resistant than the hummock species *S. magellanicum* and *S. fuscum*. Photo by Michael Lüth, with permission.



Figure 95. *Sphagnum teres*, a species that is more frost-resistant than the hummock species *S. magellanicum* and *S. fuscum*. Photo by Michael Lüth, with permission.



Figure 96. *Sphagnum fuscum*, a hummock species that is somewhat frost-sensitive. Photo courtesy of Andres Baron Lopez.

For the sunny species of *Sphagnum magellanicum* (Figure 85) and *S. papillosum* (Figure 97), short days induce dormancy and long days induce growth (Li & Glime 1990; Gerdol 1995). This corresponds well to their optimum growth temperature of 30-35°C, a high optimum for bryophytes. Nevertheless, *Sphagnum magellanicum* can grow actively whenever it has sufficient moisture and the nighttime temperature exceeds 0°C (Gerdol 1996). It appears that nighttime temperature can be critical to the growth of *Sphagnum* species. *Sphagnum capillifolium* (Figure 24) suffered a five-fold reduction in growth at low nighttime temperatures (Gerdol *et al.* 1998). There seemed to be no alteration in photosynthetic pigments or pigment ratios, but rather enzymatic reactions were limited at low temperatures.



Figure 97. *Sphagnum magellanicum* (red) and *S. papillosum* (olive-green) growing together on a sunny hummock. Those on the right are wet and on the left they are dry. Photo by Janice Glime.

### Regulation of Mammal Reproduction?

There is interesting evidence that some plants stimulate reproductive activity in small mammals that eat them by providing to them their own growth substances. Gibberellic acid, common in germinating seeds, and 6-methoxybenzoxazolinone (6-MBOA, a glycoside derivative) have such an effect. Is it possible that bryophytes, developing under the snow, provide a source of



green food to small mammals, such as voles and lemmings, under the snow pack and help to regulate their reproductive cycle?

## Overwintering under Snow

Snow affords great protection from the ravages of winter, and we might have a very different polar and boreal flora without it. Flock (1978) found that it was the areas with deep, late-season snow where bryophytes reached their highest species indices on the Niwot Ridge of Colorado, USA, an alpine area. An interesting separation of acrocarpous and pleurocarpous mosses occurred, with acrocarpous mosses being the most abundant ones in the dry areas that had only a light snow cover. Pleurocarpous mosses were nearly restricted to the wet sites with deep snow, where they outnumbered the acrocarpous taxa. Only *Hypnum vaucheri* (Figure 98-Figure 99), *H. revolutum* (Figure 100), and *Abietinella abietinum* (Figure 101) among the pleurocarpous mosses ventured into the dry areas with little snow. Liverworts were rare. This distribution may be more one of moisture needs than of temperature, but at least the possibility exists for some mosses to enjoy the greater protection from extreme cold when most of the area may be free of snow.



Figure 98. *Hypnum vaucheri* habitat in Aversal Graubünden, a species that survives winter in areas with little snow. Photo by Michael Lüth, with permission.



Figure 99. *Hypnum vaucheri* in Norway. Photo by Michael Lüth, with permission.



Figure 100. *Hypnum revolutum*, a species that is able to survive in cold but dry areas with little snow. Photo by Michael Lüth, with permission.

On the other hand, snow cover can be a detriment when the growing season is short, preventing sufficient productivity to complete a life cycle. In the Antarctic, Pannewitz *et al.* (2003a) found that indeed the snow cover was a good insulator, but late-lying snow retained the winter cold that kept the bryophytes inactive long after the ambient air temperature was warm enough for activity. Unlike some north temperate areas where the sub-surface soil may be 10°C in the winter (Jiquan Chen, University of Toledo, unpublished data), temperatures under the Antarctic snow were typically less than -10°C while snowmelt was complete in surrounding areas.



Figure 101. *Abietinella abietina*. Photo by Michael Lüth, with permission.

## Snow Temperatures

In the temperate and boreal zones, winter cold and snow can play a major role in ecosystem behavior. Snow cover can be an essential factor in protecting plants from severe cold and wind, while in many cases providing a steady stream of water and nutrients to the soil. Soil temperatures at 5 cm beneath the surface under deep snow in Houghton, Michigan, USA, can remain above freezing for an entire winter while air temperatures plummet to -10°C or lower (Jiquan Chen, University of Toledo, unpublished data). Longton (1979) reported temperatures at the moss level (*Polytrichum strictum*; Figure 65) at Pinawa, Manitoba, Canada, to remain between 0° and -10°C under the winter snow, but in summer sun the diurnal temperatures fluctuated widely. The mosses clearly ameliorate the temperature in spring and autumn, with



fewer freeze-thaw cycles and higher minimum temperatures at moss levels than at 200 cm above the ground.

We have mostly ignored winter ecology in bryophytes. Do they photosynthesize under the snow? How will they respond to shorter winters as the climate warms? Are any or all of them dormant in cold winters? What is the effect of snow depth on their physiological behavior?

Pannewitz *et al.* (2003a) found that it was possible to measure photosynthetic activity of lichens under undisturbed snow. The snow cover provides a good insulator for both lichens and mosses. But this insulation works at both warming and cooling temperatures. These lichens were inactive at subzero temperatures, even when the air temperatures had warmed enough to allow metabolic activity. For lichens, the maximum activity occurred during the 10-14 days following the final disappearance of the snow. But some species were activated at temperatures below -10°C when water became available from the high air humidity. Similar accounts of bryophyte responses are largely lacking in most winter ecosystems.

### Nutrients from Snow

Inputs and losses of soil nutrients change as temperatures slow processes and snow melt leaches nutrients from collected dust. During January to March, nitrate export can increase from 0 to 1 kg ha<sup>-1</sup> as the temperature increases from -10 to -3°C (Park *et al.* 2004 in Campbell *et al.* 2005).

These processes will certainly affect the mosses, positioned at the interface between snow and soil. In her studies on *Sphagnum russowii* (Figure 102) in a Jack pine forest (*Pinus banksiana*), Scafone (unpubl) found that the mosses were frozen in a block of ice under the snow as the melt season began in April. But is this the case all winter? Do the mosses receive nutrients that trickle through the snow, trapping them and sequestering them for an early spring surge of growth? Or do they remain frozen until after the snow is gone, facilitating the movement of nutrients past them to breaks in the ice-covered moss carpet? Figure 103 suggests that they don't. How little we know of their winter ecology!



Figure 102. *Sphagnum russowii*, a species that can freeze in a block of ice and survive. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 103. *Racomitrium lanuginosum* emerges from the snow unfrozen and in good health. Photo by Michael Lüth, with permission.

### Epiphytes

Mosses in the North Temperate Zone seem to appear in the spring in a much fresher condition than they were in the previous fall, and some of them seem to be further developed. Our data on epiphytes in Keweenaw County, Michigan, USA, suggest that perhaps winter affords them an opportunity to grow in a moist, light environment, protected from winter winds (Trynoski & Glime 1982). We suggested this possibility because, contrary to the popular misconception, the mosses were more abundant on the south side of the trees at 1 m above the ground. In Keweenaw County, the winds come predominately from the north and northwest, bringing desiccation to mosses on that side of the tree. Of course, the south side of the tree is subject to the drying heat of the sun in the summer, but only if the canopy allows it to pass. Our conjecture is that in winter the deep snow (1 m or more) provides a haven. Snow cover does not hug a tree all the way to the surface of the snow. Instead, it forms **tree wells**, where snow is separated from the tree trunk by a small funnel of air, caused at least in part by the reradiation of heat from the dark trunk of the tree (Figure 104). Within this funnel, there is little air movement, and if our theory about the reradiation is correct, the temperature must be near melting, *i.e.* 0°C. Under such conditions, we would assume that the funnel must be moist in winter, at least on sunny days. On the south side of the tree, the temperature would be higher, causing more hours of moist air and above freezing temperatures. Furthermore, sun penetration through the snow should provide ample light at this low temperature. Under such circumstances, we conjecture that mosses could achieve a slow but steady growth during 4-5 months of winter.





Figure 104. Tree well at the base of *Acer platanoides*. Although the snow has melted considerably, this shows the funnel that can form. Photo by Janice Glime.

As we pondered the tree funnels, we also considered that mosses on rocks and soil under the snow probably receive a relatively steady moisture supply, ample light, and a 0°C temperature, permitting the cold-adapted ones to achieve photosynthesis, little respiratory loss, and some level of growth during at least part of the winter. This raises the interesting question as to what role the snow on the side of a tree trunk might play in the distribution of mosses, providing moisture and light for growth in winter and probably occurring on the side that receives the most direct rain in summer, assuming the prevailing wind direction does not change seasonally. But how much, if any, light penetrates several feet of snow?

### Light through Snow

Fortunately, Marchand (1993) has provided proof that many of our theories about snow are possible. He was trying to explain how voles managed to be reproductively active just 10 weeks before the snow melted, and when the snow pack was deeper, they delayed their reproductive activity, again being active just 10 weeks before the snow melt, which occurred a full month later. Assuming they had no more ability to see into the future than do we, he began taking measurements under the snow. Some startling facts were discovered (although, I suspect some physicists would not be surprised).

As expected, the more dense the snow at a given depth, the less light penetrated. However, what Marchand did not predict was that as the snow melted and filled in the spaces between the snow crystals, the light penetration increased. (See transparency in Figure 1). Hence, the voles could use light intensity as an indicator of the coming of clear ground, and our bryophytes could carry out photosynthesis and grow or develop well before the snow was gone in the spring.

He found that any combination of depth:density that was greater than 200 gave maximum thermal protection, resulting in a near 0°C temperature under the snow. Thus, 20 cm of snow with a density of 0.1 g cm<sup>-3</sup> (very fresh snowfall) would completely buffer most temperature fluctuations. When the density increases to 0.2 g cm<sup>-3</sup>, twice as much snow is required for the same thermal

protection. This means that additional snowfall can ameliorate the lowered temperature effects of increasing density of compacted older snow.

But what of light? Marchand knew that only a small amount of light, principally in the blue and blue-green range (Figure 105), could penetrate the deep snow pack. Under only 3-4 mm of older, crystalline snow, no infra-red radiation penetrates (Gates 1962).

Photosynthesis is greatest in the red range, with a smaller second peak in the blue range. When the snow density reaches 0.3 - 0.4 g cm<sup>-3</sup>, typical of the upper part of the snow pack in late winter, only 2 - 3% of the surface light reaches a depth of 15 cm. When Marchand's group compacted the snow as much as they could, attaining a density of 0.5 g cm<sup>-3</sup>, the light penetration was nearly zero. That seemed to be the critical density – the density possible by compaction alone. It was following that experiment when they discovered that melting snow actually increased in transmission of light. Instead of refracted, scattered light passing through tiny ice grains, the light was now passing through larger, fused grains that caused much less scattering and absorption. Although less than 0.1% of incident light seems to reach the ground from late December to early April when the snow depth is greater than 40 cm and density > 0.25 g cm<sup>-3</sup>, the late season snow provides an insulating source of water as it melts, increasing the transmission of light.



Figure 105. Ice cave at Athabasca Glacier, Jasper, British Columbia, Canada, demonstrating the blue-green color of light penetrating ice. Photo by Janice Glime.

### Late Snowbeds

Unique communities of bryophytes occur adjacent to summer snowfields, taking advantage of the cooler temperatures and most likely greater moisture. In such cool habitats, one might find red mosses that increase their leaf temperatures by absorbing the light rays and reradiating them as heat. These mosses might have their lower parts in meltwater at 0°C while their growing tips are much warmer in the rays of the sun with this "red body" heating. Such mosses include *Andreaea nivalis* (Figure 106), *Bryum muehlenbeckii* (Figure 107), and *Racomitrium sudeticum* (Figure 108) (Bailey 1933; Belland 1983). Others are white, perhaps being protected from the bright light reflecting from the nearby snow, while



being subjected to temperatures that do not allow rapid use of excited electrons among the chlorophyll antenna pigments (see Figure 2 of *Racomitrium lanuginosum* for an example). The genus that once was *Webera*, and now most likely is *Pohlia* (Figure 109-Figure 110), seems to have several species that thrive in this unique habitat (Bailey 1933; Woolgrove & Woodin 1994). Bailey comments that in the Cascade Range, Washington, USA, all of these taxa are acrocarpous. Only *Isopterygiopsis pulchella* (Figure 111) among these is a pleurocarpous moss.



Figure 106. *Andreaea nivalis*, illustrating the red color of this arctic/alpine species. Photo by Michael Lüth, with permission.



Figure 107. *Bryum muehlenbeckii*, a species that uses "red body" heating in the sun. Photo by Michael Lüth, with permission.



Figure 108. *Racomitrium sudeticum*, a species that uses "red body" heating in the sun. Photo by Michael Lüth, with permission.

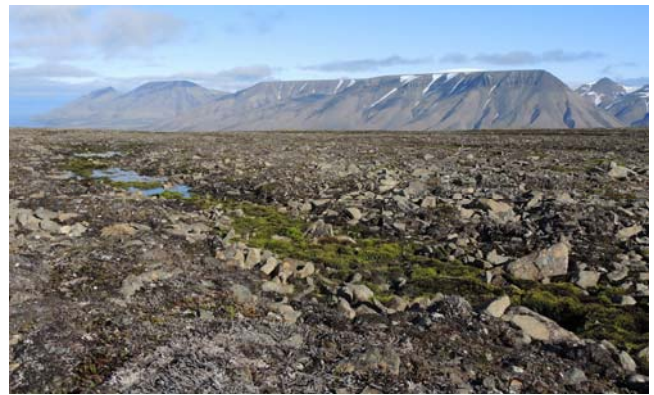


Figure 109. *Pohlia ludwigii*, a late snowbed bryophyte. Photo by Michael Lüth, with permission.



Figure 110. *Pohlia ludwigii*, a late snowbed bryophyte. Photo by Michael Lüth, with permission.

Lösch *et al.* (1983) reported that only the top 4 mm of the late snowbed liverwort *Anthelia juratzkana* (Figure 112-Figure 113) has enough chlorophyll to be capable of net gain in photosynthesis. This species reaches its low temperature compensation point at  $-4^{\circ}\text{C}$ . It easily sustains life in 9 months of darkness, cold, and wetness. However, its respiration rate increases, causing the net photosynthetic rate to decrease following snow melt. In *Polytrichum sexangulare* (Figure 114-Figure 115), also a snowbed moss, the low temperature compensation point is  $-5^{\circ}\text{C}$ . However, this species did not tolerate being wet and cold in



the dark for so long. Both species survive in these snowbed communities because of their ability to use low light intensities at low temperatures (optimum of 6-11°C). *Anthelia juratzkana* is able to grow at the edge of snowbanks at very cold temperatures. *Polytrichum sexangulare* succeeds because of its more rapid growth rate, permitting it to outcompete the seed plants. But this evades the question, how do these bryophytes survive the alternating warm and freezing temperatures at the edge of the snowbeds, or do they?



Figure 111. *Isopterygiopsis pulchella*, a late snowbed pleurocarpous moss. Photo by Michael Lüth, with permission.



Figure 112. *Anthelia juratzkana* in a recently melted late snowbed. Photo by Michael Lüth, with permission.

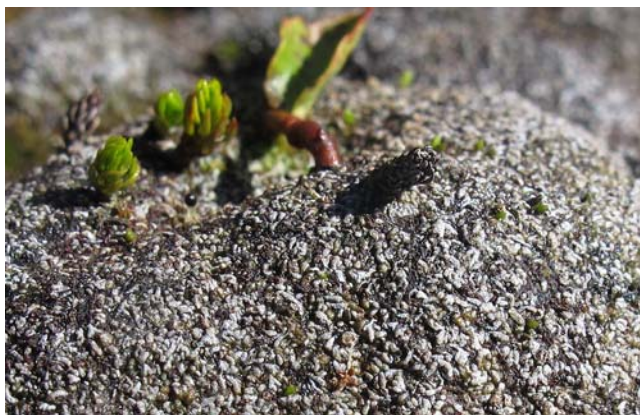


Figure 113. *Anthelia juratzkana*, a late snowbed leafy liverwort that reaches its low temperature compensation point at -4°C and is able to exhibit growth at the edge of a snowbed. Photo by Michael Lüth, with permission.



Figure 114. *Polytrichum sexangulare* with capsules, a late snowbed species. Photo by Michael Lüth, with permission.



Figure 115. *Polytrichum sexangulare*, a species that grows rapidly, permitting it to outcompete other species. Photo by Michael Lüth, with permission.

## Acclimation and Adaptation

Could the Antarctic climate be so severe that the bryophytes are always ready? Melick and Seppelt (1994) found little or no change in soluble carbohydrate levels. However, as already noted, both chlorophyll and carotenoids did respond to seasons. But are bryophytes elsewhere ready both to remain dormant when conditions are too cold and to grow during periods that are warm enough?

### Winter Growth

I have long suspected that a number of bryophyte species are able to grow in cold winter months, perhaps even under the snow. For example, mosses like *Brachythecium rutabulum* (Figure 59) have better growth at temperatures below 18°C in winter collections than those from summer collections (Furness & Grime 1982).

In a study of 40 bryophyte species in Europe, Furness and Grime (1982) found that most species had an optimum growth temperature of 15°-25°C. Nevertheless, many species continued to grow at temperatures less than 10°C.

### Winter Warming Events

What happens to a frozen moss when those sunny days take its temperature above freezing? We know that tracheophytes can be severely damaged when "spring



comes early" and then winter returns. Buds may begin to open, then the tender young leaves killed when frost returns. This expensive energy loss uses stored resources and cannot be tolerated frequently. But what happens to bryophytes under these same circumstances?

Bjerke *et al.* (2011) simulated such events in a sub-Arctic heath using infrared heat lamps and soil warming cables. Among the dominant cryptogamic flora, they subjected the boreal moss *Hylocomium splendens* (Figure 76) to such warming events for three consecutive winters. Unlike the lichen *Peltigera aphthosa* (Figure 116), *H. splendens* exhibited a significant decrease in summertime net photosynthesis (up to 48%) and growth rate (up to 52%). The lichen does not have seasonal life cycle stages, but *H. splendens* has seasonal stages when it produces new branches and leaves. The most critical of these responding to winter warm periods is the initiation of growth. These young shoots are vulnerable if the cold period returns shortly thereafter. Such winter warm periods have been experienced in areas such as my home in the Keweenaw Peninsula of Michigan and are likely to increase in frequency as the global climate changes.



Figure 116. *Peltigera aphthosa*, a lichen that lacks a seasonal life cycle. Photo by Steven K. Sullivan, through Creative Commons.

Snowbed bryophytes are not likely to experience winter melt, but in the spring the bryophytes at the edge of the snowbed may experience alternating warming and freezing periods. We have seen above that late snowbed bryophytes like *Anthelia juratzkana* (Figure 112-Figure 113) and *Polytrichum sexangulare* (Figure 114-Figure 115) survive the short growing season and long period of snow cover because of their ability to have a net photosynthetic gain in low light at low temperatures (Lösch *et al.* 1983). But how do these bryophytes, especially *A. juratzkana*, fare at the edge of the snowbed if it melts, then freezes again? Our knowledge of bryophytes in winter, and especially when experiencing intermittent warming, is extremely meager.

### Pigments and Color Changes

One protection against high light intensity is development of red pigments (Quinn 2008). Just as high elevation mosses may be red, like those discussed as living in late snowbeds, and snow algae such as *Chlamydomonas nivalis* (Figure 117), are red, some bryophytes produce red pigments to provide protection against UV radiation and

may even receive an added bonus of warmer daytime temperatures due to color. Anthocyanins, known in both bryophytes and tracheophytes, convert light to heat; this is especially important in the cooler days at the beginning and end of the growing season (Quinn 2008).

Several species of *Sphagnum* (Figure 102) have this color response, wherein cold temperatures induce production of the red cell wall pigment **sphagnorubin**, a flavonoid (Tutschek 1982).



Figure 117. Pink snow caused by the alga *Chlamydomonas nivalis* in the Arctic. Photo through Creative Commons.

Bendz *et al.* (1962) pointed out that the color of a bryophyte can vary widely, depending on solar radiation and nutrient availability. These red pigments appear to be anthocyanins. *Bryum cryophilum* (Figure 68) exhibits deep red color in the Arctic along stream borders. These proved to be anthocyanins in the cytoplasm. Red cell wall pigments occur in *Sphagnum magellanicum* (Figure 85) and *S. capillifolium* (*S. nemoreum*; Figure 24). Likewise, *Warnstorfia pseudosarmentosa* has red anthocyanin cell wall pigments. One of its pigments chemically resembles those of *B. cryophilum* and the other resembles those of the two aforementioned *Sphagnum* species.

In the Antarctic, Post and Vesik (1992) found that the leafy liverwort *Cephaloziella exiliflora* (Figure 46) was green in shaded sites and dark purple in sunny locations. This red color was due to an anthocyanin-like pigment bound in the thick cell walls of the sun plants. These plants grew in dense turfs and their leaves were larger and more closely spaced, most likely increasing moisture-holding capacity and reducing sun damage. It is interesting that the chlorophyll *a/b* ratio did not vary, but the green shade plants had more chlorophyll per unit weight.

Charlie Campbell (Bryonet 12 December 2013) found that the red *Sphagnum magellanicum* (Figure 85) was more photosynthetically active after freezing than the yellow-brown *S. papillosum* (Figure 97). Others (Quinn 2008) have reported that more highly colored species live in colder mountainous regions, compared to those close to the sea. Other color changes are noted in response to sun. *Hypnum imponens* (Figure 118-Figure 120) and *Thuidium delicatulum* (Figure 121-Figure 122) definitely change from medium green (Figure 119, Figure 121) to yellow-green or vivid yellow tones (Figure 120, Figure 122) when exposed to more sunlight (Annie Martin, Bryonet 12 December 2013).





Figure 118. *Hypnum imponens* in forest showing green color. Photo by Janice Glime.



Figure 121. *Thuidium delicatulum* in shaded location at Hocking Hills Ohio, USA. Photo by Janice Glime.



Figure 119. *Hypnum imponens* from forest showing light green color. Photo by Janice Glime.



Figure 122. *Thuidium delicatulum* showing golden color indicative of a sunny location. Photo by David Holyoak, with permission.



Figure 120. *Hypnum imponens* showing typical golden sun colors. Photo by Michael Lüth, with permission.

In *Sphagnum capillifolium* (Figure 24), Gerdol *et al.* (1998) found no trigger for the formation of red wall pigments when nighttime temperatures were 5°C and above

One principle to keep in mind in this discussion is that being cold and in bright light at the same time is a problem for plants, especially bryophytes. The light excites the chlorophyll electrons, but the cold temperature slows down the physiological processes. Hence, pigments that absorb some of that light energy can help to protect the chlorophyll from damage. These should not be part of the chlorophyll antenna system because that would transfer even more energy to the chlorophyll. Rather, they can be cytoplasmic or cell wall pigments. In the chapter on light, I have already discussed the reaction of *Fontinalis antipyretica* (Figure 123-Figure 124) in cold water exiting an underground stream into full sunlight. The moss was crimson!

Exposure to UV-B radiation is often the trigger for higher levels of pigmentation (Robinson *et al.* 2005). However, the Antarctic species *Schistidium antarctici* (Figure 43) did not increase UV-B absorbing pigmentation under higher UV-B radiation, unlike many other species in the Antarctic.



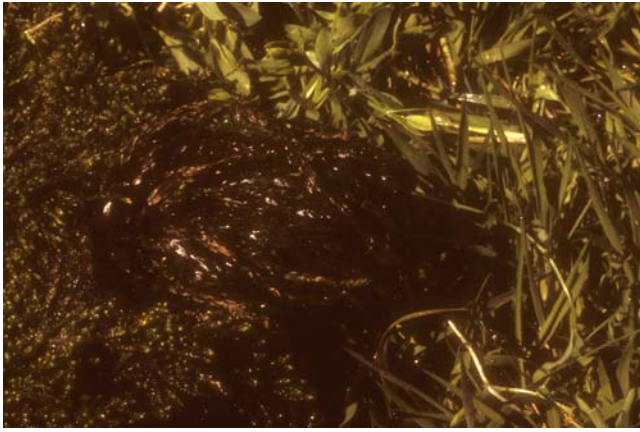


Figure 123. *Fontinalis antipyretica* exhibiting red color from the stress of high light levels and cold temperatures. Photo by Janice Glime.

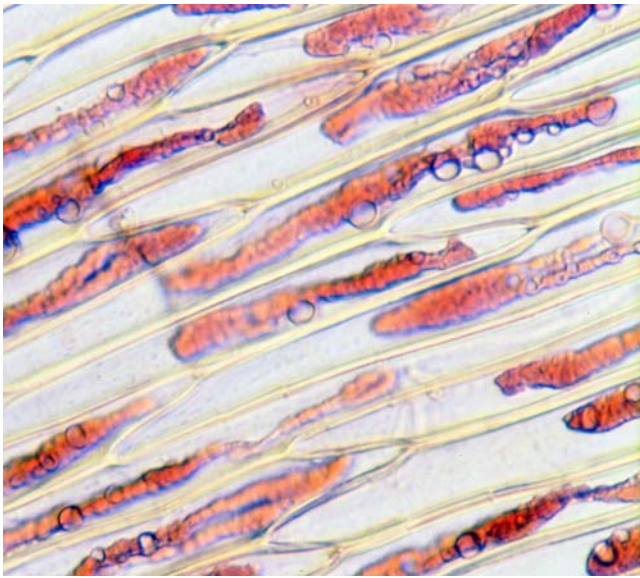


Figure 124. *Fontinalis antipyretica* red cells that result from stress. Photo by Janice Glime.

Dunn and Robinson (2006) suggest that *Bryum pseudotriquetrum* (Figure 44-Figure 45) will have an advantage over other species under conditions of high UV-B radiation that occurs with low temperatures. This will be mediated in *B. pseudotriquetrum* by the presence of UV-B absorbing and anthocyanin pigments that limit physiological activity during periods of low temperatures and desiccation, but also limiting photoprotective and repair mechanisms.

In the same study (Dunn & Robinson 2006), *Ceratodon purpureus* (Figure 50) is intermediate among the three species studied. Rather than responding to high levels of UV-B, it has a stable, constitutive concentration of UV-B- absorbing pigments. However, the anthocyanin pigments in this species were more responsive than those of *Bryum pseudotriquetrum* (Figure 44-Figure 45), most likely providing antioxidant protection during periods of high UV-B radiation (Turnbull & Robinson 2009). *Bryum pseudotriquetrum* did decrease the accumulation of photosynthetic product as the temperature rose. Of the three species, *Schistidium antarctici* (Figure 43) presents the least protection and seems to have no UV-B protective response (Dunn & Robinson 2006).

In a different Antarctic study, Melick and Seppelt (1994) found that pigment levels varied seasonally. Total chlorophyll and the chlorophyll *a/b* ratio dropped during winter. Carotenoids increased in the summer, presumably responding to the higher light intensity.

## Summary

The optimum growth temperature for most bryophytes lies between 15 and 25°C, but it can go much lower in habitats that remain cold for most of the year. The lowest extreme for photosynthesis appears to be about -15°C and the uppermost around 40-45°C. However, it is unlikely that there would be a sustained photosynthetic gain at these higher temperatures.

Snow provides insulation and may serve as a source of nutrients and moisture during the winter. Acrocarpous mosses seem more able to tolerate dry areas with only light snow cover, whereas pleurocarpous mosses are more common on wet sites with deep, long-lasting snow. Some epiphytes may benefit from the moist, protected funnels of air between the snow and tree trunk. Light quality is altered through the snow to principally blue and blue-green and diminishes rapidly from the surface.

Bryophytes near late snowbeds remain cold from melt water while experiencing high light intensities and, like bryophytes from regions of extreme cold, are often red, deriving protection from UV and possibly benefitting from warming. White tips also seem to help in reflecting the bright light. Like the exposed bryophytes, these typically are acrocarpous, with *Isoeterygiopsis pulchella* being a notable exception.

Freezing of cells can result in damage from crystals that poke holes in membranes, loss of solutes, and desiccation. Hence, desiccated cells are more likely to survive freezing than hydrated cells. Some bryophytes have net photosynthetic gain on nunataks and other areas where the temperature rarely exceeds 0°C. Net gain at -10°C is not uncommon.

But low temperature and high light intensity can cause photoinhibition. Bryophytes gain protection through colored pigments and down-regulation of photosystem II to prevent over-excitation of electrons. Mature tissues seem to exceed both young and senescing tissues in their frost tolerance.

Calcium and ABA seem to have a role in cold tolerance, although the mechanism is incompletely understood. ABA stimulates the activity of genes that code for stress proteins. These, in turn, increase freezing tolerance and decrease the death rate. Presence of ABA protects cells from membrane lesions and causes an increase in the sugar concentration of cells, but this may be an indirect effect through activation of genes that code for the production of stress proteins. Calcium alters membrane permeability, thus affecting membrane transport. Cold temperatures seem to increase the cellular content of  $\text{Ca}^{++}$ , which comes from both internal and external sources. An increase in soluble sugars could lower the freezing point or provide energy for rapid repair. Depressed temperatures stimulate the



bryophytes to prepare for winter by activating these mechanisms.

Membrane integrity may be maintained by alteration of fatty acids and lipids, with those having high freezing points being replaced with ones having lower freezing points. There seems to be a change to more unsaturated fatty acids as weather cools. Decreasing N levels may signal this change to occur. Some experiments suggest that arachidonic acids diminish as the temperature cools, but if light intensity decreases, as it would as winter approaches, at least some mosses exhibit an increase not only of palmitic and stearic acids, but also of linolenic and arachidonic acids. Such fatty acids as arachidonic acid may even be important in protecting the footpads of lemmings that eat the mosses prior to the onset of winter.

Bryophytes respond differently from tracheophytes to freezing. Because they are only one cell thick and lack internal air spaces, their external surfaces are able to form ice rather than crystals. This helps to insulate the cell. Furthermore, cellular loss of water in preparation for winter deprives the external surfaces from drawing water from the cells to grow crystals. Presence of macromolecular substances, most likely proteins, help polar and cold region bryophytes to form ice rather than crystals. The rapid cooling achieved by the one-cell-thick leaves also causes water loss from the cell, increasing solute concentration and lowering the freezing point inside the cells. This also contributes to the prevention of internal crystal formation. Thallose liverworts with multiple cell layers are more likely to suffer freezing damage.

The ability to accomplish the various means of surviving freezing plays an important role in the niche width and distribution of closely related species.

## Acknowledgments

I must again acknowledge all the photographers who have made their images available to me either through Creative Commons or by giving me permission.

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# CHAPTER 10-3

## TEMPERATURE: HEAT

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# CHAPTER 10-3

## TEMPERATURE: HEAT



Figure 1. Condensation of moisture in heated air emerging from geothermal vents at Namakolla, Myvatn, Iceland. Note the green covering of bryophytes that endure this warm, moist environment. Photo by Janice Glime.

### Heat Stress and Heat Resistance

Since air temperatures rarely exceed 40°C, it might seem unlikely that bryophytes ever experience the high temperatures often used in experiments. But such levels are not as uncommon as supposed (Larcher 1995). Black mosses on rocks of cliffs and exposed boulders can attain considerable internal heat, and even forest mosses can get hot in sunflecks. When the air temperature is only 20°C, mats of *Mnium hornum* (Figure 2) can reach 39°C. *Sphagnum* can reach a temperature 10°C higher than air temperature (Longton 1979) and habitats such as freshly burned soil can reach 65°C (Larsen 1980). Yet mosses are known to suffer injury when the temperature exceeds 40°C (Larcher 1995), and temperatures in the range of 42-51°C are typically lethal (Nörr 1974; Richardson 1981; Meyer & Santarius 1998; Proctor & Pence 2002). *Grimmia* (probably *Schistidium*; Figure 3-Figure 4) grown at 38°C produced fewer protonemata and shoots, and more plants turned brown than when grown at 27°C (Keever 1957). Hence, it is of ecological interest to understand the effects of high temperatures on bryophytes.



Figure 2. *Mnium hornum* showing the soft leaves that are exposed to the sun and can reach 39°C when the air temperature is 20°C. Photo by Des Callaghan, with permission.





Figure 3. *Schistidium apocarpum* showing its dark color that absorbs heat and protects from UV damage. Photo by Michael Lüth, with permission.



Figure 4. *Schistidium apocarpum* with capsules, showing white awns that help to keep the plants cool and add protection from UV rays. Photo by Michael Lüth, with permission.

Most bryophytes seem to have a heat tolerance of 39–45°C (Scheibmair 1938; Dirckson 1964; Nörr 1974). When they are constantly wet, they have an even lower tolerance for continuous warm temperatures, as for example species of *Fontinalis* (Figure 5) that lose their vitality and chlorophyll at sustained temperatures of 20°C (Dilks & Proctor 1975; Glime 1987b, c). On the other hand, the warm soil of geothermal areas permits a haven for some species such as *Hypnum plumaeforme* (Figure 6), which reaches its northernmost limits in Japan in a geothermal area (Iwatsuki & Glime 1983). In such areas, bryophytes dominate on warmer soils due to high root zone temperatures that are lethal to roots of tracheophytes. By living on the surface, bryophytes are subject to cooling effects of the atmosphere while insulating the soil and causing it to retain more geothermal heat (Glime & Iwatsuki 1997). This heated ground is particularly important to the Antarctic bryophyte flora.

We can consider two major types of heat-related environmental parameters. In one case, the environment is characterized by permanently high temperatures, and in the other, the plants are subjected to thermal extremes (Kappen 1981). For those plants surviving constant heat, the mode of survival must be physiological. However, for those that must survive heat stress only occasionally when extremes arrive, the plant adaptations may require some degree of physiological tolerance, coupled with mechanisms for avoiding the heat. For many plants, this latter avoidance

mechanism often involves a dormant life cycle stage that is metabolically inactive, permitting it to survive physiologically. For bryophytes, this could be accomplished by spores or vegetative diaspores that survive underground or on the surface as inactive tissue. This does in fact aid some flood plain species and other ephemerals that disappear for long periods of time and appear only when conditions are suitable. But for the vast majority of bryophytes, their slow growth makes this annual strategy impractical and they more typically survive in a state of desiccation (in dormancy) in which their temperature tolerance is typically much higher (Hearnshaw & Proctor 1982).



Figure 5. *Fontinalis antipyretica*, a cool temperature species that loses its vitality and chlorophyll at sustained temperatures of 20°C. Photo by Andrew Spink, with permission.

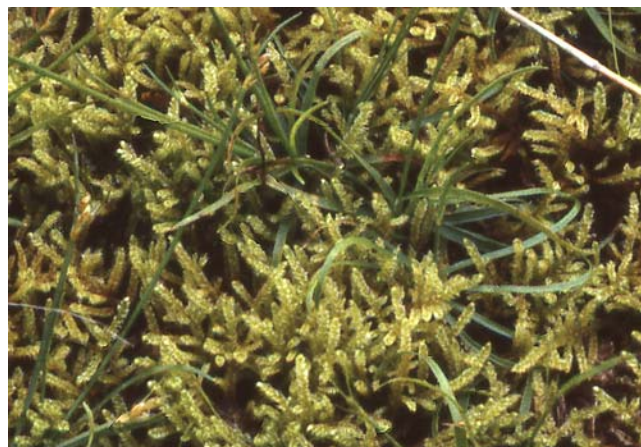


Figure 6. *Hypnum plumaeforme* from a geothermal site near Lake Wakoto, Japan. Photo by Janice Glime.

If neither of these strategies is possible, as in wetland bryophytes, their adaptations must include a physiological tolerance to heat, whether it be for short daily periods in summer or for longer duration, or a cooling mechanism. For example, many species of *Sphagnum* (Figure 19–Figure 23) have their optimum temperature for growth at 30–35°C (Li & Glime 1990), whereas most bryophytes have an optimum near 20°C (Dilks & Proctor 1975). The cosmopolitan *Bryum argenteum* (Figure 7) populations, living from the continent of Antarctica through the hot lowland tropics, exhibits heat stress at 30°C, exhibiting its optimum at 22°C day/15°C night (Hedderston & Longton 1999). But air temperature is not indicative of bryophyte temperature, and emergent bryophytes may in fact lower their temperature through evaporative cooling. When that



water is no longer available, the bryophyte is approaching a state of desiccation in which it can become dormant.



Figure 7. *Bryum argenteum* with capsules, a cosmopolitan species that exhibits heat stress at 30°C. Photo by Keith Bowman, with permission.

Responses to heat are not immediate in bryophytes. In their study of *Pohlia wahlenbergii* (Figure 8), Sandvik and Heegaard (2003) found that the response to nutrient addition was immediate, but that to temperature was delayed. Likewise, *Fontinalis* (Figure 5) species can continue to look healthy for several weeks at temperatures above 15 and even 20°C in the field, but after prolonged additional exposure in the lab, they lose their green color and cease growing (Glime 1987b). Such behavior permits them to weather the daily fluctuations as well as the day-night differences in their environments and to sustain short periods of hot weather in summer.



Figure 8. *Pohlia wahlenbergii*, a species that responds immediately to nutrient addition, but has a delayed response to temperature. Photo by Michael Lüth, with permission.

## Heated Habitats

Tropical areas and geothermal habitats present special constraints on bryophytes due to their persistent high temperatures (see Makinde 1993). One would therefore expect that such bryophytes would possess unique adaptations to permit their survival. However, even tropical bryophytes seem to do poorly above 25°C (Frahm

1990). Such high (but not uncommon) temperatures cause their net assimilation rate to decrease drastically, their respiration rates to rise to high levels, and they fail to reach their compensation point (Frahm 1987).

Bryophytes growing in geothermal areas must be capable of tolerating prolonged high temperatures (Given 1980; Hearnshaw & Proctor 1982). For some, this can be done in a dry state, when heat tolerance is much greater. During periods of rain or dew, evaporative cooling can help to maintain a tolerable temperature and permit photosynthetic activity. *Bryum japonense* has been found growing at 40°C, *Philonotis falcata* (Figure 9) and *Bryum cyclophyllum* (Figure 10) at 38°C (Watanabe 1957), and *Campylopus* (Figure 11) at 53°C (Glime & Iwatsuki 1994), although the temperature of the actively growing apical region may be much less (e.g. 30°C in *Campylopus praemorsus*; Kappen & Smith 1980). Although liverworts are often considered intolerant, Volk (1984) demonstrated tolerance up to 80°C dry and 50°C wet in *Riccia* (Figure 12). Other geothermal taxa, for example *Bryum argenteum* (Figure 7) (Hedderson & Longton 1999) and *Polytrichum* (Figure 33) species (Loesch *et al.* 1983), exhibit a wide latitudinal range, yet exhibit thermal stress at a mere 30°C and 32°C, respectively. One must exercise caution in interpreting temperature data, however, because they may represent only the soil or air temperatures, which can differ significantly from that of the growing tip of the bryophyte.



Figure 9. *Philonotis falcata*, a species that can grow in a geothermal area with a soil surface temperature at 38°C. Photo from Digital Museum, Hiroshima University, with permission.



Figure 10. *Bryum cyclophyllum*, a species that can grow in a geothermal area with a soil surface temperature at 38°C. Photo Janice Glime.





Figure 11. *Campylopus introflexus* with water drops that are typical at geothermal sites. Photo by Michael Lüth, with permission.



Figure 12. *Riccia austinii*, representative of a genus in which some members are able to tolerate temperatures up to 80°C dry and 50°C wet. Photo by Janice Glime.

## Sporophyte Stress

Little attention has been paid to temperature relationships of the sporophyte. But in desert mosses, this can be a limiting part of the life cycle. And it appears that post-embryonic sporophytes in at least some desert mosses can only develop in the cooler, wetter months (McLetchie & Stark 2006). It is the perennial gametophytes that permit these plants to survive from year to year. In the desert species *Microbryum starckeanum* (Figure 13), all gametophytes survived temperatures of 35-75°C for 1-3 hours, subsequently producing protonemata and shoot buds in a 35-day recovery period. Some leaves exhibited symptoms of stress at 55°C, including leaf burning and discoloration of shoots. However, sporophyte recovery was poor, with reduction in growth and maturation. No sporophytes reached meiosis after exposure for one hour at 75°C. Furthermore, maternal shoots suffered more than did those that aborted their sporophytes in the 35° and 55°C treatments. These shoots took longer to regenerate through protonemata. The reason for this susceptibility of the sporophyte remains unknown. It might be simply less thermotolerance in the sporophyte, or it might be that the gametophyte in some way affects the thermotolerance of the sporophyte.



Figure 13. *Microbryum starckeanum*, a xerophyte for which the sporophyte is more likely to be damaged by heat than is the gametophyte. Photo by Richard Zander, with permission.

## Plant and Cellular Responses

Effects of heat stress can include loss of membrane integrity (Liu *et al.* 2003), color change to brown (Keever 1957), shoot damage (Liu *et al.* 2004), and enzyme and pigment destruction (Larcher 1995; Meyer & Santarius 1998; Liu *et al.* 2004). Liu *et al.* (2004) found that *Plagiommium acutum* (Figure 14) survived well at 35-40°C, exhibiting no cellular damage, but at 45°C both wet and dry moss cells were damaged (Figure 15). They could find no differences with leaf age, as assessed by position on stem.



Figure 14. *Plagiommium acutum*, a species that tolerates temperatures up to 40°C, but suffers damage at 45°C. Photo by Show Ryu, through Creative Commons.

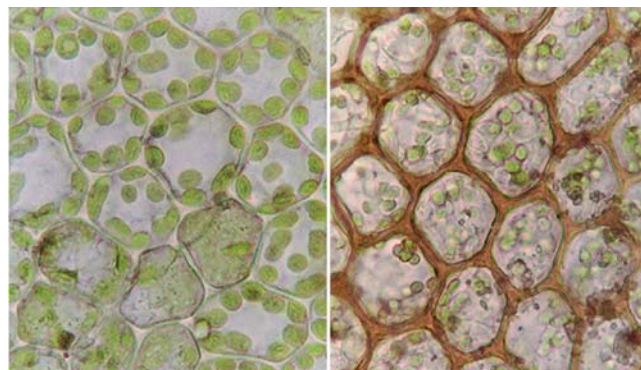


Figure 15. Cells of *Plagiommium acutum* following wet heat treatment. **Left:** 35°C for 8 hours. **Right:** 45°C for 1 hour. Photos by Yingdi Liu, with permission.



It appears that membrane permeability varies with temperature even within a normal range of daily temperature fluctuations. Liu *et al.* (2003) demonstrated a temporal fluctuation in cell membrane permeability for *Thuidium cymbifolium* (Figure 16) and *Plagiomnium acutum* (Figure 14) submersed in water through a 94-hour period. The permeability tracked the temperature almost perfectly (Figure 17).



Figure 16. *Thuidium cymbifolium* with capsules, a species in which cell membrane permeability tracks the temperature. Photo by Li Zhang, with permission.

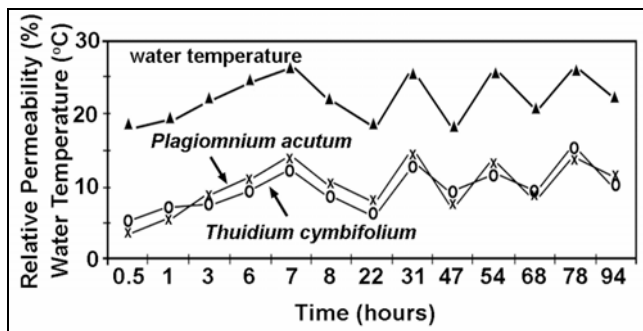


Figure 17. Effect of surrounding temperature on the membrane permeability of two mosses. Redrawn from Liu *et al.* 2003.

In a series of studies, Glime (1980, 1982, 1984, 1987a, b, c) and coworkers (Glime & Knoop 1986; Glime & Raeymaekers 1987) have shown that temperature affects rhizoid production, growth, branching, and gametangia formation in several species of the aquatic moss *Fontinalis* (Figure 5; see subchapter on Temperature Effects). And certainly elevational restrictions imply physiological effects that preclude many taxa from growing at higher elevations. These restrictions may even be gender-specific, as in *Macromitrium* (Figure 18), where the dwarf male plants are restricted to lower latitudes and altitudes (below the 6°C January isotherm in Japan), presumably due to low-temperature stress (Une 1985; Une & Yamaguchi 2001).

It appears that even the aquatic moss *Fontinalis antipyretica* (Figure 5) may have physiological races adapted to high temperatures. Long exposures to a high temperature could eliminate all but the hardy, and eventually develop a population that is able to withstand the higher temperatures. Such might seem to be the case for this moss growing in a river with abnormally high temperatures due to heated water from hot springs. But

when Carballeira *et al.* (1998) transplanted the moss from a normal river site (16°C) to the heated river (34°C), there was no notable change in pigment ratio, photosynthetic rate, or respiratory rate after 25 days at the new high temperature. Furthermore, after 2, 4, and 10 days of exposure of mosses from the 16°C river to 30°C, then back to 16°C, these parameters recovered to 50% of their normal values within 10 days. Photosynthesis and respiration both recovered more slowly than did the pigment ratios.



Figure 18. *Macromitrium microstomum*, member of a genus in which at least some species have dwarf males that are more sensitive to cold temperatures than are females. Photo by Janice Glime.

The ability to tolerate heat is important in dispersal and establishment in a new habitat. Whole colonies can regulate their temperature through insulation. But fragments, often the best means of propagation, lack this protection. When fragments (stem pieces) of several species of *Sphagnum* were air dried at 20°C and a relative humidity of ~60%, they survived up to 14 days without water. *Sphagnum fallax* (Figure 19) and *S. magellanicum* (Figure 20) resisted desiccation better than did *S. fuscum* (Figure 21). As one might expect, desiccation delayed the onset of regeneration, most likely due to the need to repair damaged membranes and recover lost nutrients. Oven drying of for 48 hours at 20°C and above was lethal at all temperatures in *S. angustifolium* (Figure 22), *S. fuscum*, *S. magellanicum*, *S. capillifolium* (= *S. nemoreum*; Figure 25), and *S. papillosum* (Figure 23). Only *S. fallax* was able to survive up to 30°C.



Figure 19. *Sphagnum fallax*, a species in which fragments can survive up to 14 days at 20°C without water. Photo by Michael Lüth, with permission.





Figure 20. *Sphagnum magellanicum*, a species in which fragments can survive up to 14 days at 20°C without water. Photo by Michael Lüth, with permission.



Figure 21. *Sphagnum fuscum*, a species whose fragments can survive up to 14 days at 20°C without water, but that does not resist desiccation as well as *S. fallax* and *S. megellanicum*. Michael Lüth, with permission.



Figure 22. *Sphagnum angustifolium*, a species that dies when dried in an oven at 20°C. Photo by Jan-Peter Frahm, with permission.

Li and Glime (1990), on the other hand, demonstrated an optimum growth temperature of 30-35°C for clumps of *S. magellanicum* (Figure 20) and *S. papillosum* (Figure 23) from the Keweenaw Peninsula of Michigan, USA. Rydin (1984) found no temperature-tolerance differences

among *Sphagnum* species from Europe. It is likely that the rate of drying differed among these studies so that moisture state may have contributed to the contrasting results, but geographic races may also have been involved in these distant populations. *Sphagnum fuscum* (Figure 21) responded to summer warming with enhanced length increment (42-62%) and greater biomass increase, while bulk density decreased (Dorrepall *et al.* 2004). Added snow in winter increased the biomass gain by 33%, but growth in length and bulk density did not change significantly. These changes suggest that not only is the health of the plant affected by temperature, but the structure and moisture-holding capacity are altered, potentially having a major impact on the ecosystem.



Figure 23. *Sphagnum papillosum*, a species that dies when dried in an oven at 20°C. Photo by Janice Glime.

## Biochemical Responses

The observed variations in responses among bryophyte species undoubtedly also result from biochemical differences. Al-Hasan & coworkers (1989) demonstrated a greater concentration of glycerols in *Bryum bicolor* (Figure 24) incubated at 5°C than in those at 25°C. It appears, from work with the tracheophyte *Arabidopsis thaliana*, that a reduction in polyunsaturated lipids enhances the thermal stability of the photosynthetic electron transport system (Hugly *et al.* 1989).



Figure 24. *Bryum bicolor* decreases its concentration of glycerols when incubated at 25°C compared to those plants at 5°C. Photo by Michael Lüth, with permission.



## Isoprene

More recently, Hanson & coworkers (1999) have suggested that heat tolerance in mosses may be due, at least in part, to the production of isoprene, a mechanism of thermal tolerance that seems to have been lost multiple times among more advanced plants. Although little is known thus far about its universality among bryophytes, we do know that at least some bryophytes produce isoprene in response to high temperatures or high light intensities, at considerable cost in carbon – greatly exceeding 2% at temperatures above 30°C (Harley *et al.* 1999). These responses suggest that isoprene may have a role in ameliorating the stresses associated with high temperatures, a role consistent with the physiological evidence. On the other hand, isoprene may contribute to human stress, because it plays a major role in the formation of ozone in forested regions (Harley *et al.* 1999). Isoprene is widespread within the plant kingdom, but it seems to exercise no phylogenetic affinities, is not stored in the leaves, and has no antiherbivory role. Its production in conditions of high light or temperature suggests its protective role in those conditions.

Although isoprene emission is common among mosses and ferns, it is absent in liverworts and hornworts and less predictable among other tracheophytes (Hanson *et al.* 1999). It may be especially useful in certain habitats. Bryophytes growing in the open, such as many *Sphagnum* species, are more likely to suffer from thermal stress. This stress could be particularly important when these mosses, with their lower parts in water, may still be in a hydrated state. *Sphagnum capillifolium* (Figure 25) from a northern Wisconsin, USA, bog is subject to these large temperature fluctuations and enjoys the benefits of isoprene as a means of increasing its thermotolerance (Hanson *et al.* 1999).

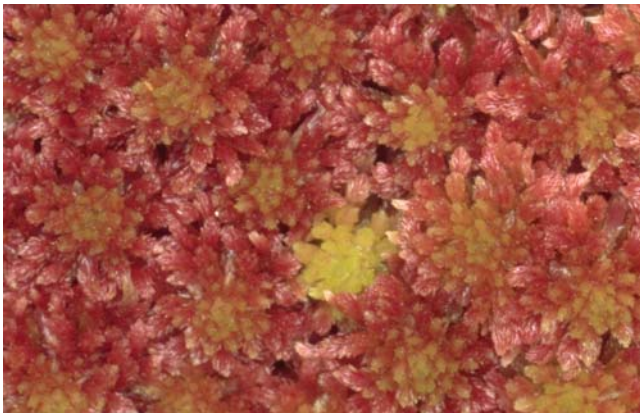


Figure 25. *Sphagnum capillifolium*. Photo by Jan-Peter Frahm, with permission.

## Sugars

In some temperate mosses, sucrose declines upon exposure to high temperatures, resulting in a decline of cold hardiness (Rütten & Santarius 1992), but its loss seems to imply no apparent advantage for heat hardening.

## Peroxidase

*Marchantia polymorpha* (Figure 26) contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase

(Hirata *et al.* 2000). Hirata and coworkers demonstrated that it is able to perform oxidative polymerization of lunularin, the liverwort counterpart of ABA. It may play a role in stabilizing the cell membrane during desiccation events. The thallose liverwort *Marchantia polymorpha* contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase. Little seems to be known about peroxidases in mosses. In *Mnium* sp. (Figure 2), peroxidase appeared to be relatively stable up to 70°C, but then dropped rapidly as the temperature rose (Bakardjieva *et al.* 1996). Addition of Ca helped to stabilize the peroxidase at higher temperatures. Zinc ions helped to stabilize its activity at high temperatures but inhibited the activity at lower temperatures. When these responses were compared to those of the fern *Polypodium vulgare* (Figure 27), zinc had little effect on that plant at 70°C. The stability of peroxidase at relatively high temperatures may help the bryophytes to survive the desiccation occurring as the bryophyte approaches high temperatures.



Figure 26. *Marchantia polymorpha*, a species that produces lunularin that may play a role in stabilizing the cell membrane during desiccation events. Photo by David Holyoak, with permission.



Figure 27. *Polypodium vulgare*, a plant is unresponsive to zinc as a membrane stabilizer at 70°C, unlike the moss *Mnium* sp. Photo by Anneli Salo, through Creative Commons.



## Heat Shock Proteins

Early identification of genes and gene function in *Physcomitrella patens* (Figure 28) revealed the presence of at least two heat shock protein genes (Machuka *et al.* 1999). It appears that heat shock proteins were present early among the bryophytes (Waters & Vierling 1999a). *Funaria hygrometrica* (Figure 29) has at least six such small heat shock proteins (Waters & Vierling 1999a, b). Waters and Vierling considered that genes for these cytosolic proteins must have originated at least 450 million years ago, much earlier than genes for phytochromes. Interestingly, the patterns and rates of evolution in *F. hygrometrica* seem different from those of angiosperms. Some, but not all, of the amino acid sequences are the same in both groups.

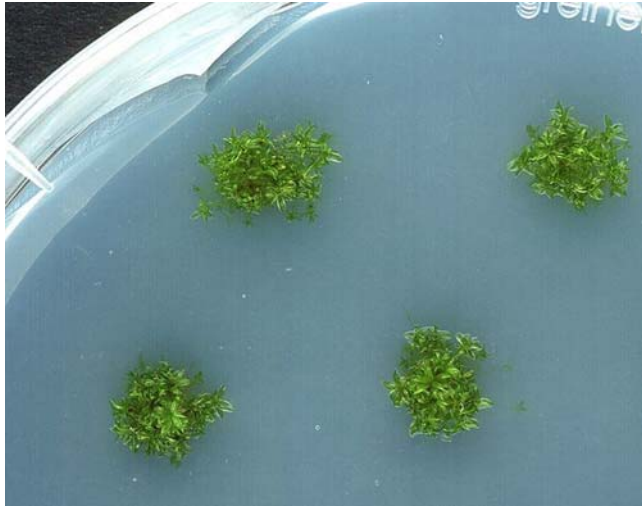


Figure 28. *Physcomitrella patens* culture where at least two heat shock proteins were revealed. Photo by Anja Martin in Ralf Reski Lab, through Wikimedia Commons.



Figure 29. *Funaria hygrometrica*, a species in which we know at least six small heat shock proteins. Photo by Brian Eversham, with permission.

It appears that these ancient bryophyte heat shock proteins have been largely ignored, at least if Cambridge Scientific Abstracts is a good test. We know from the fungus *Phycomyces blakesleeanus* (Figure 30) that blue light and high heat will induce them in that organism (Rodriguez-Romero & Corrochano 2004). Perhaps light, as well as temperature, also plays a role in the photosynthetic bryophytes. But what is that role?



Figure 30. *Phycomyces blakesleeanus*, a fungal species in which heat shock proteins are induced in blue light and high temperatures. Photo by Phil Bendle, through Creative Commons.

**Heat shock proteins** help the cells to survive the stress induced on other proteins in the cells (Feder & Hofmann 1999). These authors concluded that all species have heat shock proteins and that their expression is correlated with the natural levels of stress they encounter in their environment. From this, it follows that they also are correlated with resistance to stress.

Basile *et al.* (2013) found that heat shock proteins induced by atmospheric pollution cause effects similar to those under the stress of heavy metals in the thallose liverwort *Conocephalum conicum* s.l. (Figure 31), including severe alterations to the organelles. The implication is that it is the heat-shock proteins that make this liverwort tolerant of heavy metals. When subjected to stress, newly translated proteins can be unstable. The heat shock proteins serve as chaperones that remain attached to these unstable proteins for an extended period of time (Kültz 2005). This chaperone permits the correct folding of denatured proteins, thus stabilizing them and providing defense against damage or dysfunction. It is this capability that labelled them as stress proteins (Wang *et al.* 2004). Furthermore, Neumann *et al.* (1995) concluded that small heat shock proteins protected cells against heavy metal and other stresses by creating a more resistant membrane or improved repair mechanisms.



Figure 31. *Conocephalum conicum* s.l., a species in which heat shock proteins are produced in response to heavy metal stress. Photo by Robert Klips, with permission.



Saidi *et al.* (2005) have helped us to understand this role. They found that in *Physcomitrella patens* (Figure 28), a temperature of 38°C promoted expression of heat shock genes over three orders of magnitude, whereas at 25°C there was little expression of the promoter genes. This increase in expression permitted the accumulation of GUS ( $\beta$ -glucuronidase) and demonstrated labelled F-actin cytoskeleton in all cell types in all tissues.

In the aquatic moss *Fontinalis antipyretica* (Figure 5), temperatures between 20° and 30°C induced production of heat shock proteins. The mean annual temperature of this moss is ~9.5°C (Rau *et al.* 2007). When subjected to heavy metals, this moss produced heat shock proteins, but these did not correspond to any known proteins.

But how does the cell "sense" that the temperature is increasing? Using *Physcomitrella patens* (Figure 28), Saidi *et al.* (2011) indicated that physiological and biochemical evidence suggest that the primary sensory role may be  $\text{Ca}^{++}$  ions. The primary sensor seems to relate to the plasma membrane and may result from the fluidity-sensitive  $\text{Ca}^{++}$  channels in plasma membranes.

### Light vs Dark

Light vs dark can affect response to heat, with plants of *Plagiomnium acutum* (Figure 14) in the dark requiring a longer time to exhibit cell damage and death than those in the light, perhaps because of light damage and higher photorespiratory rates at high temperatures (Liu *et al.* 2004).

### Acclimation

Evidence on heat acclimation in bryophytes provides conflicting scenarios and clearly more studies are needed. Some studies indicate that bryophytes have little ability to acclimate to near lethal temperatures and that high temperature hardening may be effectively absent. For example, Meyer and Santarius (1998) found only a 1°C increase for membrane thermal stability from short-term acclimation to sublethal temperatures in two genera. *Fontinalis antipyretica* (Figure 5) exposed to a prolonged near-lethal temperature of 30°C exhibited little difference in response between populations previously grown at normal river temperatures and those grown in a river with abnormally high temperatures resulting from hot springs (Carballeira *et al.* 1998).

Both acclimation temperature range and duration influence the acclimation response. Antropova (1974) found that incubation of bryophytes for 72 hours at tolerance temperatures (10 & 20°C) did not influence thermal stability or cold resistance, but that exposure to above optimum temperatures for only 3 hours did increase heat resistance in a behavior similar to that of flowering plants. Glime (1987) found that members of the genus *Fontinalis* (Figure 32) were able to tolerate elevated temperatures (above 15°C) for several weeks, but that after prolonged exposure of months they ceased growth and become yellow.

Based on laboratory studies, there is evidence that at sublethal temperatures acclimation to high temperatures occurs (*e.g.* *Fontinalis duriaei*, Figure 32, Glime & Acton 1979; Fornwall & Glime 1982; *Polytrichum commune*, Figure 33, Sveinbjörnsson & Oechel 1983), but results are conflicting. Weis *et al.* (1986) found that the thallose

liverworts *Preissia quadrata* (Figure 34), *Conocephalum conicum* s.l. (Figure 31), and *Marchantia polymorpha* (Figure 26) survived mild heat treatment with a reversible depression of photosynthesis. However, more severe heat caused irreversible damage to photosystem II, much as in higher plants. Nevertheless, these thalli did not have any significant increase in thermal stability of their photosynthetic apparatus as a result of exposure to high sublethal temperatures.



Figure 32. *Fontinalis duriaei* in a stream in Japan. Photo by Janice Glime.



Figure 33. *Polytrichum commune*, a species that has demonstrated acclimation to high temperatures. Photo by Michael Lüth, with permission.



Figure 34. *Preissia quadrata*, a species that experiences reversible damage at mild heat treatments, but at higher temperatures it is irreversible. Photo by Michael Lüth, with permission.

Contrasting with the delayed response of temperature acclimation in *Pohlia wahlenbergii* (Figure 8) (Sandvik & Heegaard 2003), Antropova (1974) found that exposure of



only 3 hours at temperatures above their optimum increased heat resistance in bryophytes in a manner similar to that of flowering plants, whereas incubation within their optimum range of 10-20°C had no effect. Whereas Carballeira and coworkers (1998) found that when exposed to 30°C *Fontinalis antipyretica* (Figure 5) showed little difference in pigment ratio, photosynthetic rate, or respiration rate between populations previously grown at normal river temperatures and those grown in a river with abnormally high temperatures resulting from hot springs, Glime (1987) found that this species (collected in Houghton, Michigan, USA) became chlorotic after several weeks of exposure to temperatures above 15°C.

Balagurova *et al.* (1996) found that differences in heat resistance among several *Sphagnum* (Figure 19-Figure 23) species was less than that for their cold resistance, but that those differences were correlated. In the case of *Sphagnum*, environmental conditions strongly affected the thermal resistance. Clearly, the causes and mechanisms of response are complex.

## Night Temperature

It is interesting that it is nighttime temperature that is the limiting factor for growth of *Sphagnum magellanicum* (Figure 20) in the southern Alps of Italy (Gerdol 1996). It exhibited active growth whenever the night temperature was above 0°C. This is consistent with the concept that IAA is inhibited by light and therefore most growth occurs at night. Long-day photoperiod promoted growth of all *Sphagnum* species [*S. capillifolium* (Figure 25), *S. magellanicum*, and *S. fallax* (Figure 19)] in an earlier study, with induction requiring both short days and low nighttime temperatures (Gerdol 1995).

Gerdol *et al.* (1998) likewise found that low nighttime temperature limited the growth of *Sphagnum capillifolium*, causing a five-fold reduction in growth. A nighttime temperature of 5°C triggers production of red wall pigments, which may contribute to reduced productivity by lowering light intensity reaching the chlorophyll. No degradation of the chlorophyll itself occurred.

## Hydration State

The state of hydration is of great importance in the thermal tolerance of bryophytes and their ability to acclimate (Table 1). Dry bryophytes have much greater thermal tolerance than hydrated ones (Figure 35; Figure 42). Alpert (2000) contended that desiccated plants are able to endure temperatures from -272 to 100°C. But hydrated *Fontinalis novae-angliae* (Figure 36) had at least some stem tissue that survived intermittent boiling for more than one week (Glime & Carr 1974). In the moss *Homalothecium lutescens* (Figure 37), a decrease in the water content was responsible for an increase in heat tolerance (Dulai *et al.* 2002). An osmotic treatment of only 30 minutes shifted the lethal temperatures upward. But if the plants were kept in the dark, the curves did not shift upward as the water deficit increased, suggesting that the thermal stability of PS II may occur only in the energized photosynthetic membranes. On the other hand, Li *et al.* (1999) found that dark respiration decreased as temperature increased (and hydration state decreased) in *Herpetineuron toccoeae* (Figure 38) and *Plagiomnium acutum* (Figure 14),

perhaps explaining part of the greater heat tolerance of dry mosses.

Table 1. Wet and dry 50% lethal temperatures (LT<sub>50</sub> – °C) for various mosses, based on Nörr 1974 and Kappen 1981.

	wet	dry
<i>Hylocomium splendens</i>	43	91
<i>Rhytidiadelphus loreus</i>	42	92
<i>Mnium hornum</i>	44	99
<i>Pleurozium schreberi</i>	42	92
<i>Hypnum cupressiforme</i>	44	102
<i>Dicranum scoparium</i>	45	103
<i>Racomitrium lanuginosum</i>	48	105
<i>Sphagnum capillifolium</i>	46	
mosses	41-51	85-110
liverworts	39-45	70-110

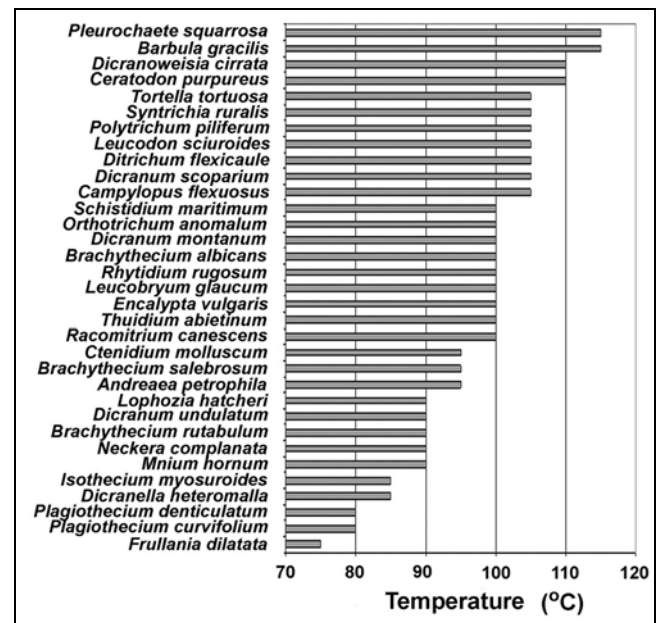


Figure 35. Lethal temperatures for various dry mosses. Based on Lange (1955), using the highest temperature below which most of the mosses first survived for 30 minutes.

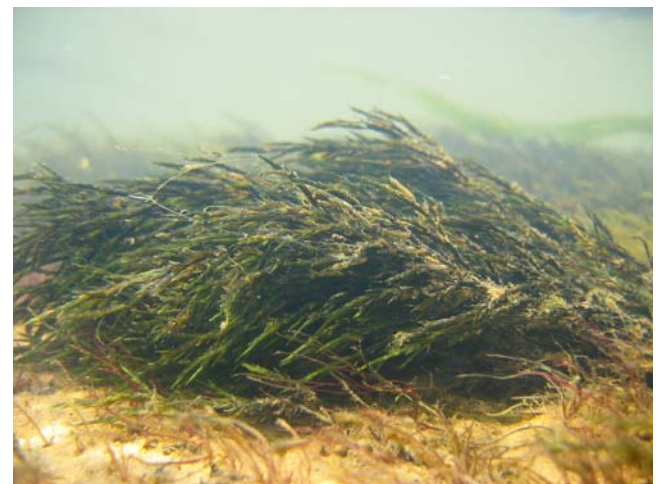


Figure 36. *Fontinalis novae-angliae*, a species in which some stem tissues survived being in intermittent boiling for more than one week. Photo by John Parker, with permission.





Figure 37. *Homalothecium lutescens*, a species that becomes more heat tolerant at lower moisture levels. Photo by Michael Lüth, with permission.



Figure 38. *Herpetineuron toccoae*, a species in which dark respiration decreases at higher temperatures with lower moisture levels. Photo by Michael Lüth, with permission.

In two Polytrichaceae [*Atrichum undulatum* (Figure 39) and *Polytrichastrum formosum* (Figure 40)], short-term acclimation of hydrated shoots occurred within a few hours and provided a small but significant increase in the stability of the cellular membranes and photosynthetic apparatus (Meyer & Santarius 1998). By contrast, it required several days to dehardening the tissues. Contrasting with this minimal resistance of hydrated tissues, the increase of heat tolerance in desiccating tissues was dramatic, with an inverse relationship between hydration and heat tolerance.

As one might expect, water use efficiency (WUE) plays a role in heat tolerance in bryophytes. In the moss *Herpetineuron toccoae* (Figure 38), transpiration usually is lower and water use efficiency higher than that of *Plagiomnium acutum* (Figure 14) in the same habitat (Li *et al.* 1999). This seems to endow *H. toccoae* with a greater capacity for heat tolerance and dry habitats.

Clausen (1964) explored the relationship between temperature and humidity in 20 species of liverworts from a wide range of locations throughout the globe (Figure 42).



Figure 39. *Atrichum undulatum*, a species that is able to acclimate to temperature changes within a few hours. Photo by Brian Eversham, with permission.



Figure 40. *Polytrichastrum formosum*, a species that is able to acclimate to temperature changes within a few hours. Photo by Michael Lüth, with permission.

A common method of drying mosses in the laboratory for temperature experiments has been to place the plants in a sugar or salt solution until they plasmolyze (Figure 43). This pretreatment induces heat resistance, most likely by suspending cellular metabolism.



Figure 41. *Plagiochila asplenoides*, a species that exhibits plasmolysis when pretreated with a sugar solution and heated to 55°C, but exhibits loss of membrane integrity when pretreated with salt. Photo by Michael Lüth, with permission.



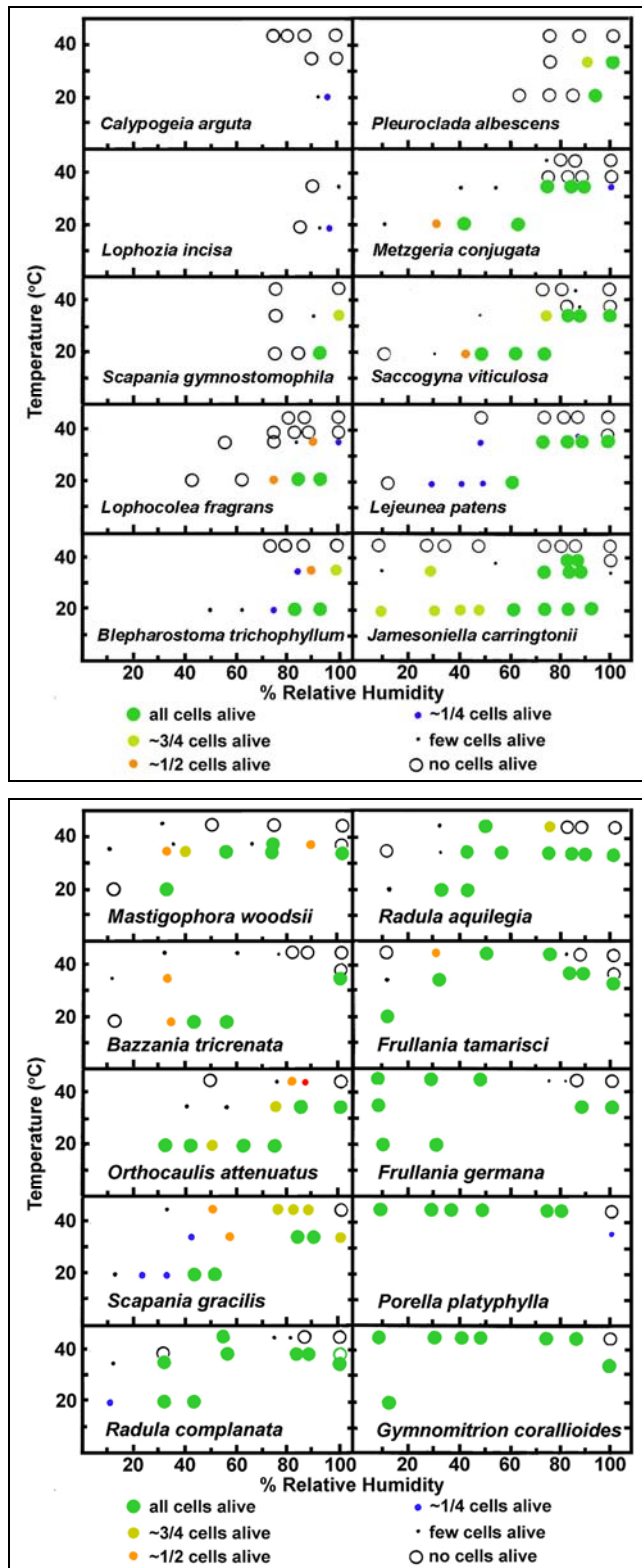


Figure 42. Effects of temperature and state of hydration on 20 leafy liverworts from Europe. Redrawn from Clausen 1964.

## Duration

Not only is the actual temperature important, but the duration is also important. Just as we might walk through a hot boiler room unscathed, but be unable to stay for an hour in there without getting sick, bryophytes likewise are able to tolerate short-term bursts of heat as might come from

dancing sunflecks. For example, the tropical liverwort *Schistochila commutata* dies at 32°C in water with 12 hours exposure, but survives at 42°C (but not 44°C) with only 1/2 hour exposure (Biebl 1967). The tropical mosses *Homaliodendron flabellatum* (Figure 44) and *Bryum* sp. (Figure 7) tolerate temperatures up to 50°C in water for half an hour, contrasting with the 25°C limit for tropical bryophytes reported by Frahm (1990). Figure 45 demonstrates the effect of time in the moss *Plagiomnium acutum* (Figure 14).

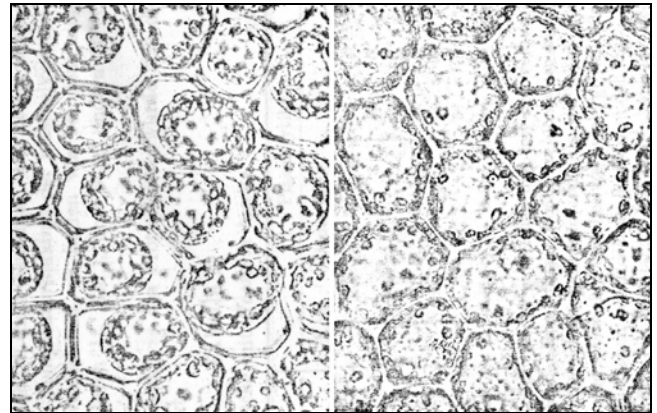


Figure 43. Leaf cells of *Plagiocilia asplenoides* (Figure 41) demonstrating the effect of heat on desiccated cells. **Left:** Cells plasmolyzed, indicating intact membranes, in 2.5 M sugar solution at 55°C for 1.5 minutes. **Right:** Cells after 1.5 minutes at 55°C with no pretreatment in the salt solution. Lack of cell shrinkage upon drying suggests loss of membrane integrity, suggesting that these cells are dead. Photos from Scheibmair 1938.



Figure 44. *Homaliodendron flabellatum*, a species that can tolerate temperatures up to 50°C in water. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.



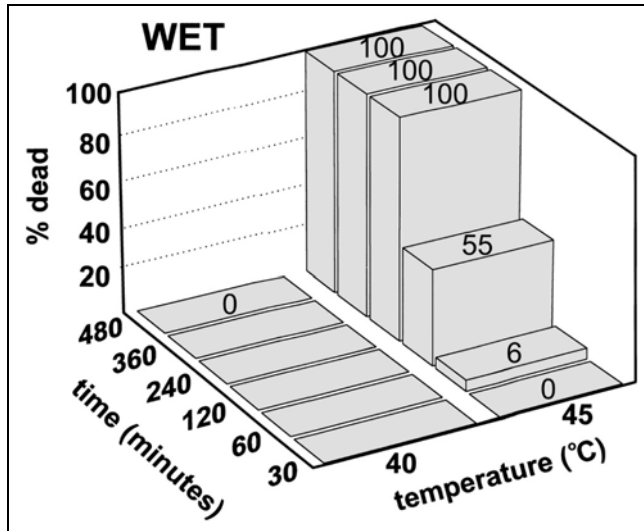


Figure 45. Effect of time on the lethality of temperature in *Plagiomnium acutum* (Figure 14).  $n=30$ . From Liu *et al.* 2004.

## Age and Structure

In some cases, age is a factor in temperature tolerance of tissues, as shown for two *Plagiomnium* species in response to low temperatures, with mature tissues being more tolerant than young or senescent ones (Rütten & Santarius 1992, 1993). Yet there seems to be no effect of age on the lethal high temperature of *Plagiomnium acutum* (Figure 14) treated wet at 30–60°C for up to 240 minutes (Liu *et al.* 2004). Known cellular damage of high temperatures on bryophytes mainly includes destruction of the plasma membrane as evidenced by loss of electrolytes (Liu *et al.* 2003), loss of differential permeability, chemical disorganization, and death of cells or tissue (Liu 2004), all factors where one might expect young and old tissues to respond differently. In studying *Plagiochila asplenioides* (Figure 41), Scheibmair (1938) did indeed find that young leaves survived better than older leaves. The older cells died, protoplasm became deformed, and the membrane and cytoplasm became colored. The young leaves survived up to 53°C for 10 hours, whereas the older leaves died after 6 hours at 48°C.

Although a variety of measures have been used to assess damage in bryophytes, the actual physiological responses of bryophytes to temperature are not well understood. One complication is that optimal temperatures for one aspect of a bryophyte life cycle might be detrimental for another, as shown for example in *Fontinalis* rhizoid production, gametangia formation, growth, and branching (Glime 1984, 1987a, b, c; Glime & Knoop 1986; Glime & Raeymaekers 1987). Chlorophyll content (Miyata & Hosokawa 1961; Melick & Seppelt 1994), photosynthesis (Shimizu *et al.* 1983), growth, weight, and number of branches (Bengtson *et al.* 1982; Bakken 1993) are often used as measures of bryophyte health.

It appears that we know almost nothing about the effect of temperature on the development of the sporophyte. Working with desert bryophytes, Stark (personal communication, April 2005) suggested that stress on the gametophyte might trigger the plant to abort its sporophyte, making it difficult to determine independent stress on the sporophyte itself. It appears that once expansion has been initiated, they are very stress tolerant when dry.

HP

## Reversible Effects

In thallose liverworts, heat-stress depression of photosynthesis can be reversible (Weis *et al.* 1986). *Preissia quadrata* (Figure 34), *Conocephalum conicum* s.l. (Figure 31), and *Marchantia polymorpha* (Figure 26) all were able to recover from mild heat stress, with the recovery period dependent on the extent of the damage. With severe damage, Photosystem II suffered irreversible damage. Nevertheless, unlike in tracheophytes, treatment with high sublethal temperatures had no significant effect on their heat stability.

## Decomposition

Few studies have examined bryophyte decomposition, and many misconceptions occur among ecologists about bryophyte decomposition. It is quite a different thing to be decaying from the bottom up on a live plant than to drop leaves and branches that henceforth decay. By being still connected to living plant tissue, decaying portions of a bryophyte are able to move internal and external constituents upward or outward to living portions. Such movement can be influenced by temperature.

Thormann *et al.* (2004) compared decomposition between the sedge *Carex aquatilis* (Figure 46) and the moss *Sphagnum fuscum* (Figure 21) in the boreal peatlands. They found a 5 to 17-fold decrease in bog *Sphagnum fuscum* litter decomposition with elevated temperature, whereas decomposition of the sedge litter was either enhanced 2- to 30-fold or was unaffected by elevated temperatures. Fungal decay was favored over bacterial decay in elevated temperature conditions. The fungi were able to use polyphenolic polymers as their carbon source, hence favoring their existence over the bacteria in the peat. Nutrient quality seemed to play a major role, favoring the nutrient-rich litter of sedges (8.0–25.7%) over that of bryophytes (0.2%) at higher temperatures. Hence, increases in temperature may not cause the positive feedback to temperature that has been anticipated for all peatlands. Rather, intermediate and rich fens may cause a positive feedback, but poor fens and bogs may actually cause a negative feedback that reduces the input of carbon to the atmosphere.





Figure 46. *Carex aquatilis*, a species with high nutrient content that decomposes much more rapidly at elevated temperatures than does bog litter (which decreases its decomposition rate). Photo by Max Licher, SW Biodiversity, with online permission.

## Summary

Although the air temperature seldom exceeds 40°C, bryophyte temperatures can reach 60-70°C in some circumstances. Most bryophytes have a hydrated tolerance limit of 45°C or less.

Bryophytes can survive the heated periods as spores or other dormant propagules, by becoming dormant (if desiccated), or by physiological adaptations to the elevated temperatures, including desiccation that leads to dormancy. Emergent bryophytes can use evaporative cooling to maintain lower tissue temperatures.

Despite potentially high temperatures, tropical bryophytes typically do poorly above 25°C, due to high respiration rates. Geothermal bryophytes often provide their own insulation, with hot bases but cool growing tips. The record for wet heat tolerance seems to be *Riccia* at 50°C, although *Fontinalis* stem tissue survived more than a week of intermittent boiling. Colors, evaporative cooling, and physical properties can alter the temperature of the growing region of a bryophyte, so air and substrate temperature data may not reflect tissue temperatures.

Heat stress can cause loss of membrane integrity, color changes, shoot damage, enzyme denaturation, pigment destruction, and negative photosynthetic gain. Temperature can promote differential development times for spores, gemmae, rhizoids, branching, growth, gametangia, and sporophyte maturation. Some of these effects are gender specific and may restrict the male and female plants or expression of sexual organs to different elevations or microclimates. **Cryptic species, microspecies, or physiological races** may exist that are not mirrored by differences in morphology, permitting a species to occupy a wide range of climatic conditions.

It appears that heat may damage bryophytes in the light more than in the dark, perhaps due to energy loss to photorespiration. Nighttime temperatures may be important for some taxa, with minimal temperatures required for growth.

Known biochemical responses to elevated temperatures include an increase in **glycerols, isoprenes, and heat shock proteins**, whereas **sugars** decrease, but we know little about any of their roles. **Peroxidase** may play a role in stabilizing cell membranes during thermal stress and desiccation, with Ca and Zn contributing to its stabilization at high temperatures.

Many bryophytes seem to lack the ability to acclimate to high temperatures. Nevertheless, heat resistance can increase in as little as three hours of exposure to above-optimum temperatures, but plants may take several days to **deharden**. It appears that some physiological processes such as photosynthesis may acclimate, but that thermal stability does not change as easily. Even *Sphagnum* exhibited more change in its cold resistance than in its heat resistance, but the two acclimations were correlated.

Desiccated bryophytes have far greater thermal tolerance than hydrated ones, with some apparently surviving the entire temperature range from -272 to 100°C. In fact, one mechanism for increased heat tolerance is for the plant to decrease its water content, whether by changing its osmotic relationships or by coincidence with a drying atmosphere. One explanation for this is that dark respiration can decrease in response to increased temperatures and concomitant drying. Duration is important, with short durations being tolerable when longer ones are not. Greater **water use efficiency** seems to endow mosses with a greater heat tolerance, but may not be helpful to thallose liverworts.

Age plays a role in heat tolerance in some species, with mature tissues being the most tolerant, and young and senescent ones being less so. Sporophyte responses are poorly known, but some evidence suggests that heat may cause embryo abortion in some taxa.

Decomposition may be altered differently among bryophytes compared to that of tracheophytes. Elevated temperatures can favor fungal over bacterial decay, promoting the decay of the polyphenolic polymers in bryophyte cell walls. High nutrient litter increases decay more with temperature increases than does bryophyte litter. This results in some habitats losing bryophyte litter more quickly while others lose it more slowly.

## Acknowledgments

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# CHAPTER 10-4

## TEMPERATURE: SPECIES AND ECOSYSTEMS

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# CHAPTER 10-4

## TEMPERATURE: SPECIES AND ECOSYSTEMS

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Figure 1. Mountainous habitats provide a wide range of temperatures. Here *Ditrichum flexicaule* grows in the foreground. Photo by Michael Lüth, with permission.

### Species and Distributions

#### Importance of Climate

In his study of the Gulf of St. Lawrence region of Canada, Belland (2005) found that climatic variables were the most important factors determining moss species distributions, with warmth of the growing season being the most important. Acebey *et al.* (2003) likewise found that climate accounted for the reduced bryophyte species diversity and changes in growth forms from submontane rainforest in Bolivia to the 4-15-year-old fallows at 500-650 m elevation. In central Belgium, species composition could be predicted based on four life-history traits

(minimum spore size, life expectancy, type of gametophyte, and papillose leaf cell walls) and three ecological traits (indicator values of light, temperature, and soil acidity) (Vanderpoorten & Engels 2002). For bryophytes of the eucalypt-dominated forests in Tasmania, minimum temperature in the coldest month and precipitation were the most important variables predicting bryophyte cover, richness, and composition (Pharo *et al.* 2005). These were reduced by the cover of vascular plants. Certainly temperature plays an important role at all stages of the life cycle.



While some species are limited in their extension toward the poles by cold temperatures, others are unable to survive further away from the poles due to the heat. *Grimmia torquata* (Figure 2-Figure 3) is an arctic-montane moss that reaches its southern limit in Newfoundland, where further southward expansion seems to be limited by high summer temperatures (Hedderson & Brassard 1990). On the other hand, *Aulacomnium androgynum* (Figure 4) and *Isoetecium myosuroides* (Figure 5-Figure 6) reach their northern limit there due to low winter temperatures and water availability.



Figure 2. *Grimmia torquata* in Norway, a species limited by heat south of Newfoundland. Photo by Michael Lüth, with permission.



Figure 3. *Grimmia torquata*, a northern species that is limited in distribution by heat. Photo by Michael Lüth, with permission.

In nearly every study, however, the importance of water availability is the major limiting factor for growth of bryophytes within a region. Temperature may define the bounds of their distribution, but water availability determines their growth rate within that suitable temperature range. For example, in their study of nine bryophytes [*Racomitrium lanuginosum* (Figure 7), *Pleurozium schreberi* (Figure 8), *Sphagnum austini* (Figure 9), *S. fuscum* (Figure 10), *S. rubellum* (Figure 11), *S. papillosum* (Figure 12), *S. lindbergii* (Figure 13), *S. tenellum* (Figure 14), and *S. pacificum* (Figure 15)] in a

coastal peatland in British Columbia, Canada, Asada *et al.* (2003) found that growth was most strongly correlated with precipitation and less so with temperature. Surprisingly, temperature thresholds for *Sphagnum* were lower than those for *Pleurozium schreberi* and *Racomitrium lanuginosum*, and winter growth was important for these *Sphagnum* species. But we must keep in mind that temperature often co-varies with precipitation, with cooler summer temperatures in a suitable range occurring when there is precipitation.



Figure 4. *Aulacomnium androgynum*, a species for which the northern limit is determined by temperature and moisture availability. Photo by Janice Glime.



Figure 5. *Isoetecium myosuroides* on tree at Swallow Falls, Wales, a species that is limited north of Newfoundland by low winter temperatures and water availability.

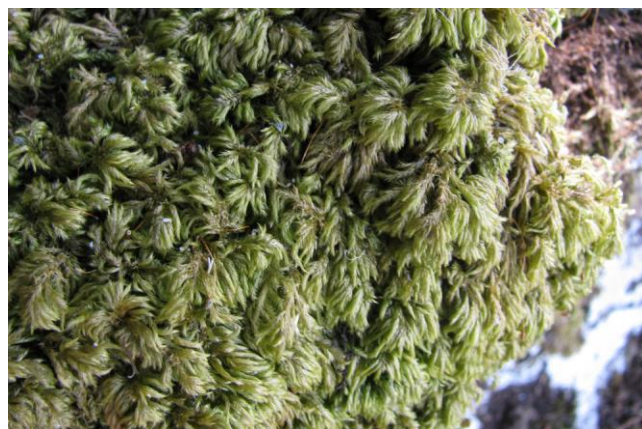


Figure 6. *Isoetecium myosuroides* near Swallow Falls, Wales, where warmer temperatures and sufficient moisture permit it to live. Photo by Janice Glime.





Figure 7. *Racomitrium lanuginosum*, a species for which growth responds more to precipitation than to temperature. Photo by Juan Larrain, with permission.



Figure 10. *Sphagnum fuscum*, a species for which growth responds more to precipitation than to temperature. Photo by Jutta Kapfer, with permission.



Figure 8. *Pleurozium schreberi*, a species for which growth responds more to precipitation than to temperature. Photo by Bob Klips, with permission.



Figure 11. *Sphagnum rubellum*, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.



Figure 9. *Sphagnum austini* in Scotland, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.



Figure 12. *Sphagnum papillosum*, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.





Figure 13. *Sphagnum lindbergii* in Norway, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.



Figure 14. *Sphagnum tenellum*, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.



Figure 15. *Sphagnum pacificum* in Alaska, a species for which growth responds more to precipitation than to temperature. Photo by Vita Plasek, with permission.

### Warming Studies

Studies on effects of global warming (to be discussed in detail in a later chapter) are helping us to understand how bryophytes are affected by temperature and how they affect the temperatures of the soil beneath them. In a

species-poor Icelandic moss heath where *Racomitrium lanuginosum* (Figure 7) dominated, mean daily surface temperatures were 1-2°C higher under a simulated warming regime, but the soil temperatures tended to be lower than in the control plots (Jonsdottir *et al.* 2005). In several other habitats that were more species-rich, changes were more moderate. In the Arctic, it appears that warming temperatures are likely to decrease bryophyte relative cover as graminoids increase (Hollister *et al.* 2005). Wahren *et al.* (2005) found a similar increase in sedges (*Eriophorum vaginatum* – Figure 16) and decrease in bryophytes in Alaska after eight years of increased temperatures, but even the control plots had a similar response. Ironically, plots with additional snow cover were actually warmer due to the greater insulating effect. They also benefitted by the additional moisture available.



Figure 16. *Eriophorum vaginatum* (cottongrass), a species that increases in abundance after warming for eight years. Photo by Martin Olsson, through Creative Commons.

In northern habitats, the moss *Hylocomium splendens* (Figure 17) has been studied in many contexts, permitting us to understand its biology well. In a study on circumarctic populations, its growth was strongly correlated with both the early summer temperatures and the length of the growing season (Callaghan *et al.* 1997). The mildest of the subarctic sites fostered the greatest annual segment mass increase, growth rates, and degeneration rates, whereas the lowest were at the high arctic site. Conversely, longevity increased as the climate became more harsh at the more northern sites. Growth between years at two contrasting sites correlated significantly with the temperatures of June and July. This moss is tolerant of a wide range of daily temperature variation, so it is not likely to be seriously affected by global warming. However, not all Arctic systems are likely to respond in the same way. Even *Hylocomium splendens* responded negatively to perturbations of climate at a sub-Arctic site, perhaps due to lower humidity and non-equilibrium responses in the relatively short term of the study (Callaghan *et al.* 1999).





Figure 17. *Hylocomium splendens*, a species whose growth responds to early summer temperatures and the length of the growing season. Photo by Daniel Mosquin, Botany Website, UBC, with permission.



Figure 18. *Sphagnum squarrosum* in its typical forest habitat. Photo by J. C. Schou, with permission.

### Seasonal Fluctuations

As seen in the previous chapters, temperature can invoke changes in the biochemical constituents of the bryophyte cells. In a study on bryophytes of Windmill Islands, Antarctica, Melick and Seppelt (1994) found that pigment levels varied seasonally, with total chlorophyll and chlorophyll *a/b* ratios decreasing in winter, most likely as a light response. Total carotenoids increased in summer, primarily in response to the greater light intensity. Water content was greatest in summer. Soluble carbohydrate levels, on the other hand, varied little among seasons, contrasting with fluctuations seen in bryophytes from other polar regions. This lack of change in carbohydrates may be due to the rapid temperature fluctuations seen on a daily basis during the Antarctic growing season.

### Species Differences

Within a genus, the responses of different species to temperature vary (Koskimies-Soininen & Nyberg 1991). For example, in the predominantly sun-adapted *Sphagnum*, the shade-tolerant species *S. squarrosum* (Figure 18-Figure 19) suffered loss in its photosynthetic capacity and chlorophyll content when exposed to the heat and bright light following canopy removal (Harley *et al.* 1989), although this may have been strictly a light response. *Sphagnum fimbriatum* (Figure 20) responded in very different ways from *S. magellanicum* (Figure 21) to changes of temperature (Koskimies-Soininen & Nyberg 1987, 1991). When *Sphagnum* species [*S. austinii* (Figure 9), *S. fuscum* (Figure 10), *S. rubellum* (Figure 11), *S. papillosum* (Figure 12), *S. lindbergii* (Figure 13), *S. tenellum* (Figure 14), and *S. pacificum* (Figure 15)] were compared to other boreal bryophytes, they exhibited lower temperature thresholds than did *Pleurozium schreberi* (Figure 8) or *Racomitrium lanuginosum* (Figure 7) (Asada *et al.* 2003). These differences often relate to habitat in ways that are obvious, such as hummock vs hollow. Despite the tolerance for heat in some *Sphagnum* taxa, winter growth was important for these species.



Figure 19. *Sphagnum squarrosum* with capsules, a shade species that is sensitive to high temperatures and full sun.. Photo by Michael Lüth, with permission.



Figure 20. *Sphagnum fimbriatum*, a species that responds differently to elevated temperature from *S. magellanicum*. Photo by Michael Lüth, with permission.





Figure 21. *Sphagnum magellanicum* hummock, a species that responds differently to elevated temperature from *S. fimbriatum* to elevated temperature. Photo by Michael Lüth, with permission.

### Cryptic Species

Many more species most likely have physiological races (cryptic species, microspecies) that differ in their ability to cope with a variety of environmental differences. It is these physiological races that may some day become different species if they remain isolated from each other long enough to become reproductively isolated. Until then, they confound the ecologist by responding to environmental parameters differently.

Physiological races provide physiological differences among populations that appear to be morphologically identical, permitting them to take advantage of a wider range of ecological conditions. A number of cryptic species permit the cosmopolitan *Grimmia laevigata* (Figure 23) to survive the extremes of temperature, UV light, and desiccation in its rock habitat (Fernandez *et al.* 2006), often fully exposed to the sun where its black color can cause extremely high temperatures.



Figure 22. A green form of *Grimmia laevigata* that may also differ in physiological responses to temperature and desiccation. Photos by Michael Lüth, with permission.

Production of gametangia must be attuned to the growing season, which becomes shorter as one moves toward the poles or to higher elevations. Two species of *Pohlia* [*P. nutans* (Figure 24), *P. cruda* (Figure 25)], widely separated in the sub-Arctic and Britain, exhibited shorter maturation periods for both gametangia and

sporophytes in the Arctic and sub-Arctic than they did in Britain (Clarke & Greene 1970). One cannot rule out, however, the longer days as compensation for the shorter growing season.



Figure 23. A dark, strongly awned form of *Grimmia laevigata* that may also differ in physiological responses to temperature and desiccation from the green form in Figure 22. Photo by Michael Lüth, with permission.



Figure 24. *Pohlia nutans*, a species that has shorter maturation periods for both gametangia and sporophytes in the Arctic and sub-Arctic than they do in Britain. Photo by Michael Lüth, with permission.



Figure 25. *Pohlia cruda*, a species that has shorter maturation periods for both gametangia and sporophytes in the Arctic and sub-Arctic than they do in Britain. Photo by Michael Lüth, with permission.



## Ecosystem Relationships

Even within a small geographic region, **aspect** (compass direction a slope faces) can have significant effects on the microclimate. On the Cushetunk Mountain of New Jersey, USA, the south slope experiences heavy shade with a nearly isothermal air temperature at 2 m (Cantlon 1953). Under light shade, in small openings, and during the leafless season, this same 2 m in height experiences sharp changes in temperature, with the highest daytime temperatures being near the ground. The north slope, on the other hand, has its lowest temperatures near the ground in all seasons. The greatest differences between the two slopes are in the 5 cm zone above the ground, where soil bryophytes would grow. Furthermore, the greatest vegetation differences between the two slopes were seen in the bryophyte layers, with the fewest between tree layers.

## Altering Ecosystems

Bryophytes play a significant role in their ecosystems in altering soil temperatures. Serving as insulation, they keep the soil cooler in summer and warmer in winter. Dark-colored soil serves as a heat-absorbing body, but covered by a moss mat, that soil is protected from the direct radiation that could raise its temperature. In other words, bryophytes buffer the soil temperature (Figure 26).

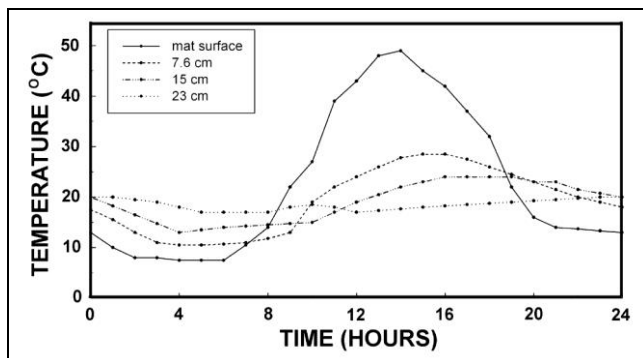


Figure 26. Effects of moss mat on soil temperature. Modified from Richardson 1958.

Especially in northern climates, bryophytes may be instrumental in altering soil temperatures and retarding nutrient turnover, *i.e.*, serving as ecosystem engineers (Eckstein 2000). Not only do they slow the rate of turnover through their insulating effect, but they retard it through their contributions of organic acids and low nutrients that discourage the growth of decomposer microorganisms.

Mosses themselves are very resistant to decomposition, whereas grasses are among the highest (Hobbie 1996). Therefore, any climate change that favors the growth of mosses will reduce the availability of stored nutrients, whereas their decrease will accelerate nutrient turnover and release more carbon to the atmosphere.

## Disturbed Habitats

Liverworts are often colonizers of disturbed habitat such as flood plains, where they are subjected to very high temperatures as the soil dries. Genera such as *Riccia* (Figure 27) can withstand temperatures of more than 80°C dry and up to 50°C wet (Bolk 1984).



Figure 27. *Riccia ciliata*, a drought tolerant species of disturbed habitats. Photo by Michael Lüth, with permission.

## Grassland

Grasslands generally do not have many bryophyte species, but some taxa may be relatively abundant there. Some grasses can buffer temperatures and hold moisture near the ground by providing a canopy.

In a study of limestone grasslands in the southern Pennine Hills of the United Kingdom, Bates *et al.* (2006) subjected bryophytes to 3°C winter warming. Responses were relatively minor. Drought was the greatest problem, with total bryophyte cover and cover of *Calliergonella cuspidata* (Figure 28) and *Rhytidiadelphus squarrosus* (Figure 29) responding negatively. *Fissidens dubius* (Figure 30) increased in drought-simulated plots. Winter warming caused *R. squarrosus* and *Lophocolea bidentata* (Figure 31) to decrease, along with overall species richness, but *Campyllum chrysophyllum* (Figure 32) increased.



Figure 28. *Calliergonella cuspidata* at Swallow Falls, Wales, a species that experiences reduced cover when experiencing drought. Photo by Janice Glime.





Figure 29. *Rhytidiadelphus squarrosus*, a species that experiences reduced cover when experiencing drought. Photo by Michael Lüth, with permission.



Figure 30. *Fissidens dubius*, a drought-tolerant species. Photo by Michael Lüth, with permission.



Figure 31. *Lophocolea bidentata*, a species that decreased in the United Kingdom with winter warming. Photo from <[www.aphotofauna.com](http://www.aphotofauna.com)>, with permission.

In a different grassland study, Ingerpuu *et al.* (2005) found rather different results. They planted typical forbs [*Trifolium pratense* (Figure 33), *Festuca elatior* var. *pratensis* (Figure 34), *Prunella vulgaris* (Figure 35)] in pots with either of two bryophyte species [*Brachythecium rutabulum* (Figure 36), *Rhytidiadelphus squarrosus* (Figure 37)]. Using four different densities of tracheophytes, they found that bryophyte cover increased with tracheophyte density, presumably due to creation of more favorable temperatures.



Figure 32. *Campyllum chrysophyllum*, a species that increased in the United Kingdom with winter warming. Photo by David Holyoak, with permission.

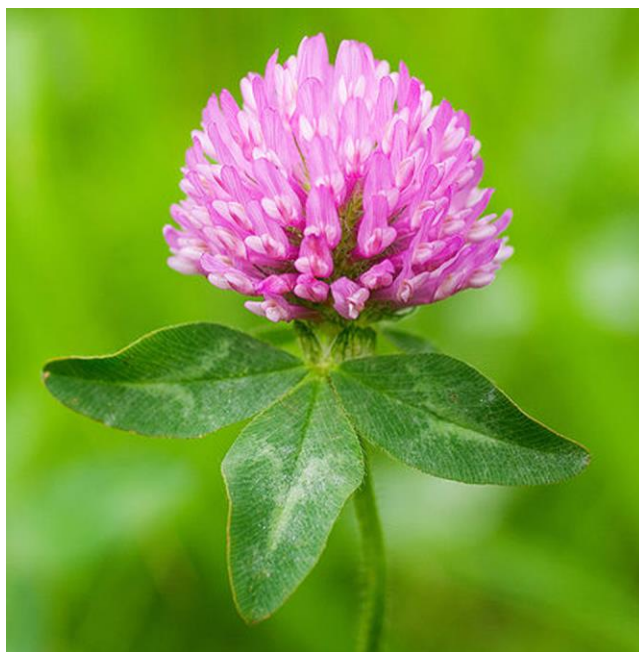


Figure 33. *Trifolium pratense*, a species that increases bryophyte cover in pots. Photo by Masaki Ikeda, through Creative Commons.



Figure 34. *Festuca elatior* var. *pratensis*, a species that increases bryophyte cover in pots. Photo by T. Voekler, through Creative Commons.





Figure 35. *Prunella vulgaris*, a species that increases bryophyte cover in pots. Photo by Zeynel Cebeci, through Creative Commons.



Figure 36. *Brachythecium rutabulum*. Photo by Michael Lüth, with permission.



Figure 37. *Rhytidiadelphus squarrosus*. Photos by Michael Lüth, with permission.

## Tropics

Within a given tropical ecosystem, temperature ranges are less extreme than in most other regions of the world. This homogeneity of temperature makes water and light availability of paramount importance to distributions of many species. But loss of energy to respiration at frequent

high temperatures can be severe. In aquatic habitats, where bryophytes may remain hydrated despite high temperatures, few temperate aquatic taxa are able to survive.

Greater temperature variation is seen when one compares the lowlands with the montane areas. In the tropical areas of Pernambuco State, Brazil, the submontane forest is more favorable for bryophyte growth than is the lowland forest (Cavalcanti Porto 1992). This can be attributed to the lower temperatures of the higher elevations, coupled with additional moisture that results from condensation, despite the lower actual precipitation at the higher elevation. These cooler, more moist conditions favor considerably greater bryophyte diversity than can be found in warmer lowlands.

## Polar and Alpine

Polar and alpine regions maintain cool temperatures favorable to  $C_3$  plants such as bryophytes throughout the growing season. Even on days that may exceed temperatures favoring net carbon gain, most of the day is generally cool enough to favor fixation over respiration. Such temperature conditions, when coupled with sufficient moisture, are highly favorable to the growth of bryophytes.

The dominant bryophytes [*Bryum argenteum* (Figure 38), *B. pseudotriquetrum* (Figure 39), and *Ceratodon purpureus* (Figure 40)] on the Antarctic continent all are cosmopolitan and are widespread in the habitable terrain of Antarctica (Lewis Smith 1999). Each of these species predominates in its specific hydrologic zone. But the hydrologic conditions strongly influence the thermal regime for its moss dwellers. There are frequent long periods of 24-hour sunshine, during which temperatures within the moss turf remain above freezing. These long warming periods can result in more than 3.5 mm annual growth in each of these species. Despite the fact each of these species has an optimum temperature of 15°C for photosynthesis, they are able to maintain significant photosynthesis at 5°C. At 5°, 10°, and 20°C, photosynthetic rates were *B. argenteum* > *B. pseudotriquetrum* > *C. purpureus*.



Figure 38. *Bryum argenteum* with capsules, one of the dominant bryophytes on Antarctica. Photo by Ivanov, with permission.





Figure 39. *Bryum pseudotriquetrum* in Norway, one of the dominant bryophytes on Antarctica. Photo by Michael Lüth, with permission.



Figure 40. *Ceratodon purpureus*, one of the dominant bryophytes on Antarctica. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Jonasson *et al.* (1999) predict that warming trends in the Arctic will elicit positive responses of tracheophytes under a regime of both increased warming and higher nutrient levels, causing a decline of bryophytes. In the Antarctic, however, experiments in which soils were incubated at temperatures ranging 2 to 25°C caused rapid development of algae, mosses, and lichens (Kennedy 1996). Some of the species that grew from these propagule banks at warmer temperatures were species not currently known from Antarctica. Further evidence of the importance of temperature in the Antarctic is the dense cover of bryophytes from temperate areas (e.g. *Campylopus introflexus* (Figure 41), *Marchantia polymorpha* (Figure 42), *Philonotis acicularis*) in the geothermal areas, while other areas support only sparse cover of any vegetation. Continued dominance and increased cover of bryophytes in the Antarctic will, at least initially, be sustained through bryophytic propagules in the soil bank and the near absence of sources of tracheophyte propagules.



Figure 41. *Campylopus introflexus*, a cosmopolitan moss that survives in geothermal areas in Antarctica. Photo by Jan-Peter Frahm, with permission.



Figure 42. *Marchantia polymorpha* with archegoniophores, a species that survives in geothermal areas in Antarctica. Photo by Janice Glime.

Like the polar regions, alpine areas experience extremes of temperature on a single day. On Mt. Fuji, *Racomitrium lanuginosum* (Figure 43) experiences up to 42°C temperature range in a single day, whereas differences in microhabitat permit *Grimmia elongata* (Figure 44) to experience only 26°C difference at the same time. This microhabitat difference is at least in part orchestrated by the moss itself – *R. lanuginosum* has a less dense mat than *G. elongata*, but the former experiences a small increase in storage heat that results in a large increase in its daily temperature.



Figure 43. Exposed habitat with *Racomitrium lanuginosum*. Photo by Michael Lüth, with permission.





Figure 44. Somewhat protected habitat with denser cushions of *Grimmia elongata*. Photo by Michael Lüth, with permission.

Predictions of the effects of warming on the cold tundra have varied from increasing productivity of the bryophyte heath to decreasing productivity, and from increasing CO<sub>2</sub> loss to the atmosphere to increasing it. Johnson *et al.* (1996) found that elevated temperature alone did not change the net CO<sub>2</sub> storage because losses of CO<sub>2</sub> from respiration were offset by gains in photosynthetic uptake. However, methane (CH<sub>4</sub>) losses are temperature-dependent and could be a substantial source of transfer from carbon sinks to the atmosphere, further amplifying global warming. Such predictions are further complicated by the availability of water and the type of vegetation.

The presence of permafrost is strongly influenced by the type of vegetation present (Camill 1999a). Changes in temperature would influence these vegetation patterns and impact the locations of permafrost and availability of surface water. Plateau regions characterized by black spruce (*Picea mariana* – Figure 45) with little *Sphagnum* and high cover of feather mosses (*Pleurozium schreberi* (Figure 8), *Hylocomium splendens* (Figure 17), and *Ptilium crista-castrensis* (Figure 46)] may change considerably in character if their underlying permafrost were to diminish. Cores in these habitats suggest that thawed aquatic habitats progress to aquatic lawn areas, then to hummock communities (Camill 1999b). Such hummock communities can form permafrost in less than 80 years, but such permafrost formation in today's landscape is unlikely due to the climate-warming trend.



Figure 45. *Picea mariana* forest in Northern Alberta, Canada, with the feather mosses *Pleurozium schreberi* and *Hylocomium splendens* Richard Caners, with permission.



Figure 46. *Ptilium crista-castrensis*, a species that is likely to diminish if the permafrost melts. Photo by Janice Glime.

Some mosses that are relatively cosmopolitan extend into the Antarctic. On a continent that is only 2% ice free, 24 species of mosses and 1 of liverworts are known (Seppelt & Ochrya 2008). One such moss, *Hennediella heimii* (Figure 47-Figure 48) finds its southern limit for sporophyte production (Figure 48) in Antarctica (Seppelt *et al.* 1992).



Figure 47. *Hennediella heimii* in a dense turf as one might find in Antarctica. Photo through Creative Commons.



Figure 48. *Hennediella heimii* with capsules, with its southern limit for capsule production in Antarctica. Photo by David T. Holyoak, with permission.



## Lakes

Although being spared the extremes of the Antarctic terrestrial habitats, the Arctic lakes are a less than favorable habitat. They are both cold and nutrient-poor, with a short growing season (Sand-Jensen *et al.* 1999). These conditions provide the advantage of clear water to great depths, but the attenuation of light, especially red light, makes growth of bryophytes on the bottom of these lakes extremely slow. However, slow growth (~10 mm per shoot per year) is accompanied by slow decomposition, giving these bryophytes an "unprecedented" longevity, compared to other macrophytic vegetation. Because of their ability not only to tolerate these extreme conditions, but to persist for long periods of time, bryophytes are often the exclusive macrophytes in these lakes.

Seppelt (pers. comm. 7 April 2015) reports that *Ricciocarpus natans* (Figure 49) and *Riccia fluitans* (Figure 50), both floating aquatic liverworts, are common in Alaskan lakes. They survive winter under a layer of snow or encased in ice. But he points out that under the snow is actually the warmest place in the area. He supports the concept that hot dry adaptations may be the same as those for cold and dry.

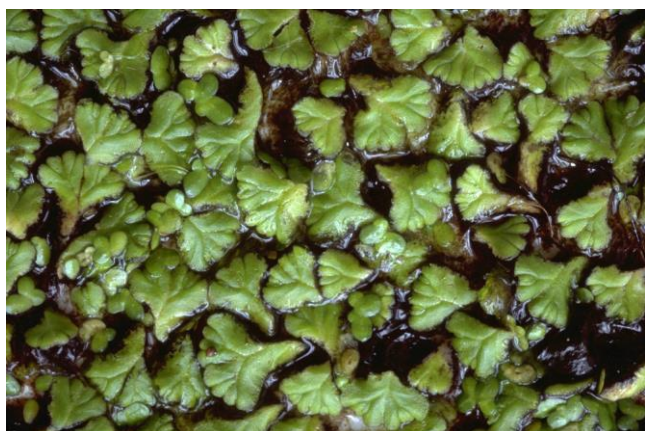


Figure 49. *Ricciocarpus natans*, a species that can survive winter in ice or under snow. Photo by Jan-Peter Frahm, with permission.



Figure 50. *Riccia fluitans*, a species that can survive winter in ice or under snow. Photo through Creative Commons.

## Streams

In riverbeds, strong gradients of temperature and moisture exist, providing excellent testing grounds for hypotheses related to moisture, light, and temperature. Arscott *et al.* (2000) used mosses from Alaska streams to test the hypothesis that *Schistidium agassizii* (Figure 51-Figure 52) would have greater tolerance to desiccation and that *Hygrohypnum* [*H. alpestre* (Figure 53), *H. ochraceum* (Figure 54-Figure 55)] would have greater tolerance to elevated temperatures. *Hygrohypnum* spp. not only had greater tolerance to temperatures above 20°C, but also had significantly higher photosynthetic rates at light saturation at all temperatures measured. *Schistidium agassizii*, on the other hand, had little response to increased light and was inhibited by high temperatures, but recovered rapidly from desiccation. Such studies as these indicate the importance of temperature coupled with other variables, especially light and moisture availability.



Figure 51. *Schistidium agassizii* in Norway, a species that recovers well from desiccation but is inhibited by high temperatures. Photo by Michael Lüth, with permission.

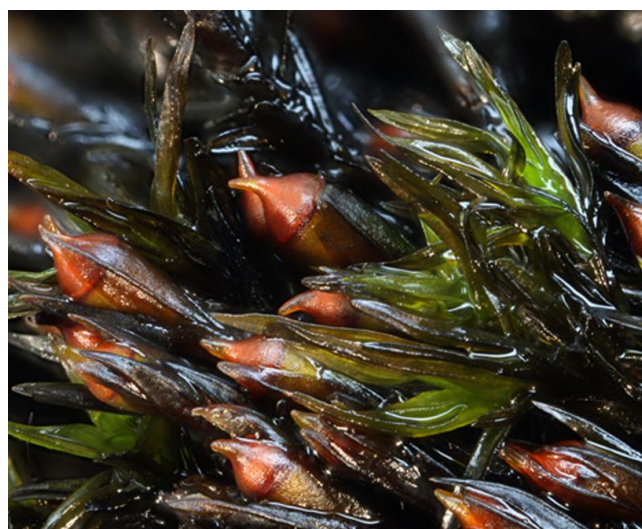


Figure 52. *Schistidium agassizii*, a species that recovers well from desiccation but is inhibited by high temperatures. Photo by Des Callaghan, with permission.





Figure 53. *Hygrohypnum alpestre* in Norway, a species that tolerates temperatures above 20°C and higher photosynthetic rates at light saturation. Photo by Michael Lüth, with permission.



Figure 54. *Hygrohypnum ochraceum* in a typical habitat. Photo by Michael Lüth, with permission.



Figure 55. *Hygrohypnum ochraceum*, a species that tolerates temperatures above 20°C and higher photosynthetic rates at light saturation. Photo by Michael Lüth, with permission.

Warmer temperatures of aquatic habitats not only challenge the carbon gain of photosynthesis over carbon loss to respiration, but they can alter solubility of some contaminants. In an Arctic stream (Alaska, USA), *Hygrohypnum alpestre* (Figure 53) and *H. ochraceum* (Figure 54-Figure 55) were able to take advantage of added

phosphorus by having greater productivity, but *Schistidium agassizii* (Figure 51-Figure 52) was not (Arscott *et al.* 2000). The *Hygrohypnum* had greater tolerance to temperatures above 20°C, with significantly higher productivity at all temperatures, perhaps accounting for its greater P uptake, whereas *S. agassizii* recovered more easily from desiccation but lacked tolerance for high temperatures.

There are most likely differences among species in their response to heavy metals at different temperatures. If a plant is temperature stressed, one might expect it to be more easily damaged by heavy metals, much as humans are more vulnerable to new infections when they are already sick. Nevertheless, Claveri and Mouvet (1995) found that when *Platyhypnidium riparioides* (Figure 56) was moved from 7°C to 29°C, both control and copper-contaminated (80 g L<sup>-1</sup>) mosses exhibited chlorophyll denaturation, but copper uptake kinetics did not change.



Figure 56. *Platyhypnidium riparioides*. Photo by Michael Lüth.

## Peatlands

Peatlands provide a good test for temperature effects because the mosses are so abundant and they are widespread in the northern part of the northern hemisphere. Furthermore, they provide a gradient of microclimates from hollows to hummocks within the same macroclimate (Figure 57). Nicholson *et al.* (1996) examined the climatic relationship of peatlands along a north-south gradient in the Mackenzie River Basin, Canada. Surprisingly, in this system climate was secondary to surface water chemistry, pH, solute concentration, and height above water table. Among the climatic variables, temperature and length of growing season shared importance with precipitation, a major factor in height of water table. Hummock species such as *Aulacomnium palustre* (Figure 58), *Dicranum undulatum* (Figure 59), *Hylocomium splendens* (Figure 17), *Pleurozium schreberi* (Figure 8), *Polytrichum strictum* (Figure 60), *Sphagnum fuscum* (Figure 10), and *Tomenthypnum nitens* (Figure 61) had the widest ecological amplitude (Nicholson & Gignac 1995). Permafrost in northern habitats has created higher peat surfaces, permitting more hummock species to survive. Lawn and hollow species, on the other hand, have narrower ecological amplitude and are therefore less frequent in more northern peatlands due to continuously frozen hollows.





Figure 57. Peatland with *Sphagnum flexuosum*, illustrating the numerous microhabitats available to create varied microclimates. Photo by Michael Lüth.



Figure 58. *Aulacomnium palustre*, a hummock species with wide ecological amplitude. Photo by Kristian Peters through Creative Commons.



Figure 59. *Dicranum undulatum*, a hummock species with wide ecological amplitude. Photo by Jan-Peter Frahm, with permission.



Figure 60. *Polytrichum strictum* with capsules, a hummock species with wide ecological amplitude. Photo by Michael Lüth, with permission.



Figure 61. *Tomentypnum nitens* in Norway, a hummock species with wide ecological amplitude. Photo by Michael Lüth, with permission.

Diversity seems to depend less on climate and more on habitat heterogeneity (Vitt *et al.* 1995). Nevertheless, habitat heterogeneity (46%) and temperature (15%) explain 61% of the variation in peatland diversity in 96 peatlands of continental western Canada. Vitt *et al.* (1995) found that habitat heterogeneity, coupled with pH or temperature, can predict biodiversity in some peatland types. For example, *Sphagnum fuscum* (Figure 10, Figure 57) is a hummock species. For *Sphagnum fuscum* in southern Finland, growth was limited to the time when the temperature was above 0°C, but was further limited to times with ample moisture (Lindholm 1990) and thus would be affected by its height above the water table.

Although we tend to think of *Sphagnum* microhabitats as being defined by moisture, temperature can play an important role in competition between *Sphagnum* species. In a competition experiment among *S. fuscum* (Figure 10, Figure 57) and *S. balticum* (Figure 62) from a site in northern Sweden and *S. magellanicum* (Figure 21) and *S. cuspidatum* (Figure 62) from southern Sweden, all four species grew more in height and biomass production with an increase in temperature, using 11.2°, 14.7°, 18.0°, and 21.4°C, but bulk density decreased (Breeuwer *et al.* 2008). The hollow species *S. cuspidatum* was the least responsive. The hummock species *S. fuscum*, on the other hand, increased biomass production 13-fold from the lowest to highest temperature when in **monoculture** (only one



species in culture). *Sphagnum balticum* proved to be the better competitor against *S. magellanicum* and *S. fuscum*, but it lost its competitive advantage at the highest temperature.



Figure 62. *Sphagnum balticum* (brownish) and *S. cuspidatum* (green), species that increase in height and biomass production with an increase in temperature. Photo by Jan-Peter Frahm, with permission.

## Summary

Climate, and especially temperature and water availability, is the primary determinant in the distribution of bryophytes. Temperature typically defines the boundaries of distribution, but water availability defines their growth and distribution within those boundaries. The ability of a species to cope with these two parameters determines, to a large degree, the breadth of the niche for a species and is often a determining difference among species and among **physiological races (microspecies, cryptic species)**.

Studies on potential effects of global warming have provided us with much of what we know about bryophyte responses to temperature. In polar regions, specific habitats may respond differently, with bryophytes increasing where sufficient water is available, but decreasing where conditions favor tracheophytes. Bryophytes in non-polar regions will most likely increase, whereas those in warmer regions will most likely decrease.

Bryophytes experience seasonal changes in temperature yearly. These usually are accompanied by temperature and light/photoperiod changes. Responses may include concentration changes in chlorophyll and other pigments, soluble carbohydrate content, and in water content. Where daily fluctuations are extreme in the Antarctic, carbohydrate content changes little on an annual basis.

Bryophytes can play a major role in altering the soil temperature of an ecosystem, hence altering nutrient turnover rates. Their own decomposition is slowed by cold temperatures.

Disturbance often exposes bryophytes to intolerable heat, but other taxa, such as *Riccia* species, are adapted to survive in such areas. Grasslands can buffer temperatures enough to permit survival of some species. Tropical habitats are too warm for most

aquatic bryophytes, but high elevations, where it is cooler and usually moist, there may be considerable diversity. Polar and alpine regions generally favor bryophyte growth relative to tracheophyte growth, causing dominance of bryophytes in many areas. Cold Arctic and alpine lakes may be populated exclusively by bryophytic macrophytes that have very slow growth, but exceptional longevity. Cold streams favor the growth of bryophytes, whereas warm ones favor tracheophytes. Peatlands provide a wide range of moisture and temperature combinations that favor a high diversity of species within the genus *Sphagnum*.

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