CHAPTER 10-1

TEMPERATURE: EFFECTS

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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 experiences 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 ~28ºC, we measured moss leaf temperatures up to 41ºC, whereas a nearby black rock, also in the sun, registered only 31ºC! (Hribljan & Glime, unpublished data).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°C (Kallio & Heinonen 1973), but would seldom be expected to do as well at temperatures above 25°C. Even tropical bryophytes seem to do poorly above 25°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 1.5-3°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_2. 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 Lüth, 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.
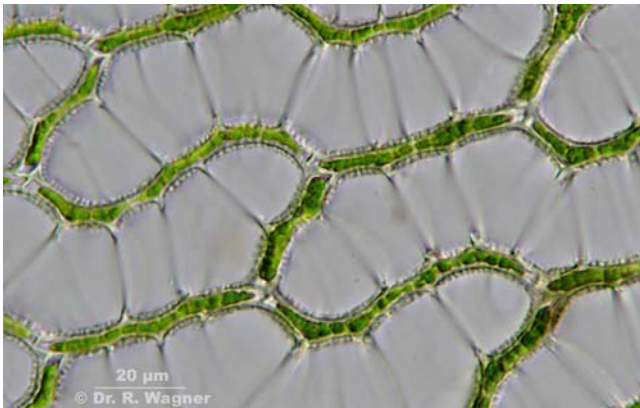

Figure 7. *Sphagnum papillosum* leaf cells showing the large hyaline cells that nearly hide the small photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with perission.

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.
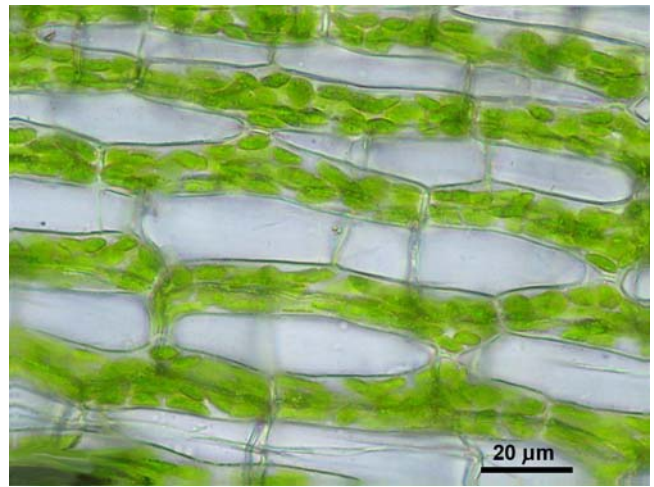

Figure 10. *Leucobryum glaucum* leaf cells showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.
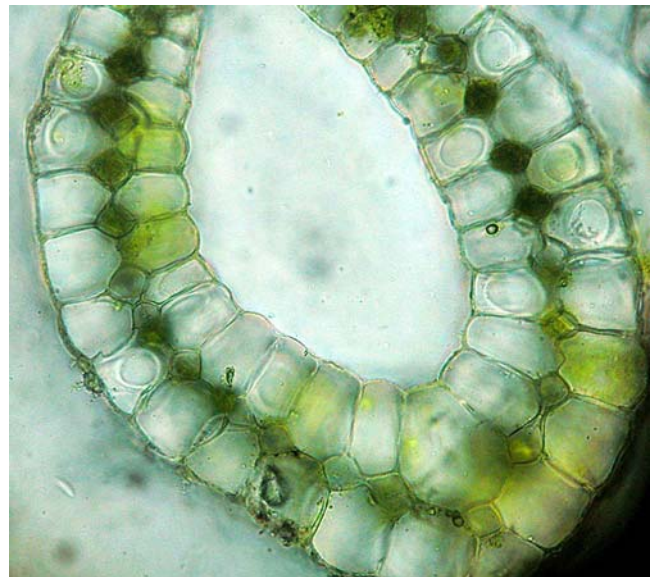

Figure 11. *Leucobryum glaucum* leaf cs showing large hyaline cells surrounding the green photosynthetic cells. Photo by Walter Obermayer, with permission.

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

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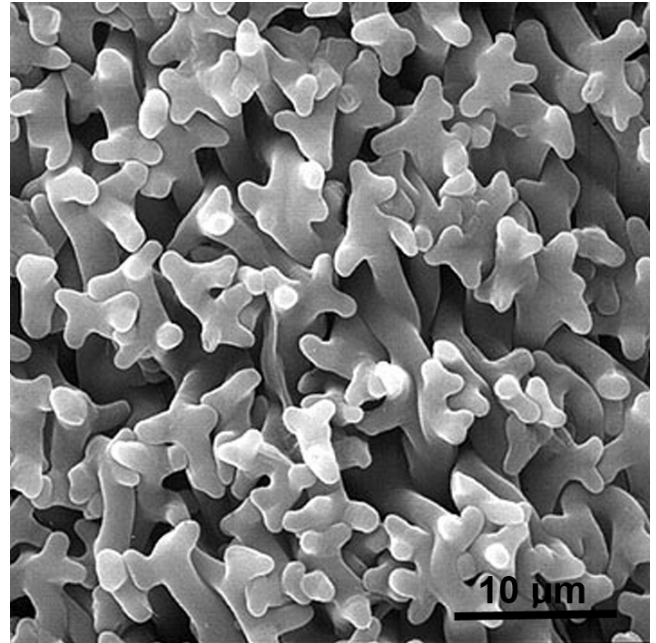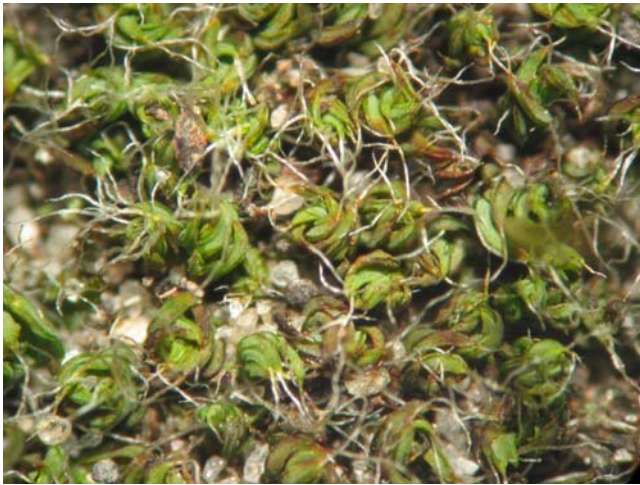

Figure 15. *Tortula muralis* leaf SEM image showing branched papillae that reflect and refract light, helping to keep the leaf cool. Photo from Botany Website, UBC, with permission.

Figure 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.

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°C to 42.8°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 7ºC, rising to 13ºC in the shrubs, 21ºC in the dwarf shrubs, and 24ºC in the grass tussocks and rosette plants. But in an isolated moss cushion, the temperature was 30ºC 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 81.9ºC! Obviously the mosses must germinate and get established well enough to control their own temperatures before that kind of heat is reached.

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 42ºC daily temperature range while *Grimmia elongata* (Figure 20) nearby has only a 26ºC range. Maruta (1986) suggests that the difference lies in the less dense mat of *R. lanuginosum*.
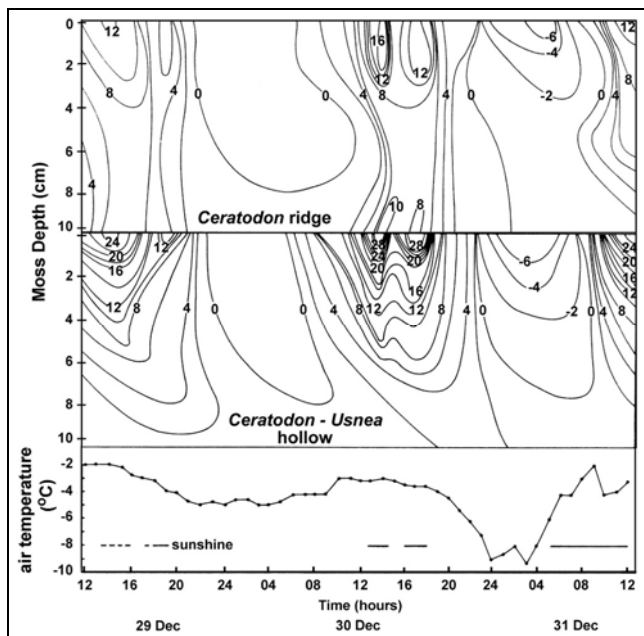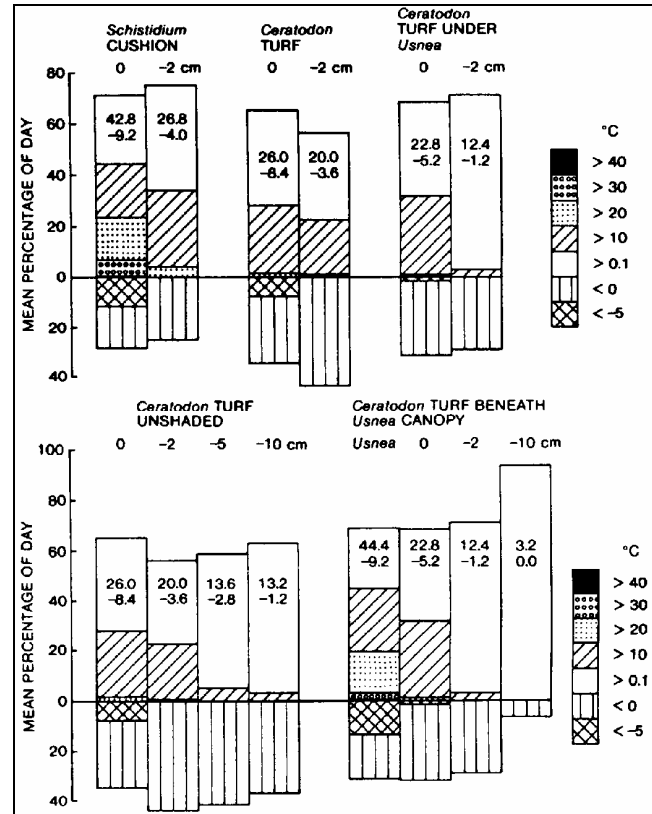

Figure 18. Isotherms for two days in December through a *Ceratodon* turf down to 10 cm and a *Ceratodon* turf covered by dense *Usnea antarctica*. Redrawn from Lewis Smith 1988.

Figure 20. *Grimmia elongata*, illustrating the dense mat that insulates and maintains less temperation 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. Exclosures that prevented this animal activity and permitted the moss mat to become thicker caused a 0.9ºC 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 5-8ºC 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 10-11ºC 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 55ºC, although some cells could survive up to 59ºC. 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 10ºC higher than the ambient temperature, often reaching 20ºC 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 35ºC (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 10ºC 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 (ºC) 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 5ºC.

While degree days are not mentioned specifically, many studies imply their importance. Callaghan *et al.* (1997) found that the growth of circumarctic 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 stairstep 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 12-16ºC and stay there until spring (mid to late April) when the air temperature is 1-5ºC. Within the safety of the hummock, the turtle's body temperature stays 0.3-3.9ºC while air temperatures drop to as low as -35ºC. 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 20ºC than at 10ºC (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 Luth, with permission.

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

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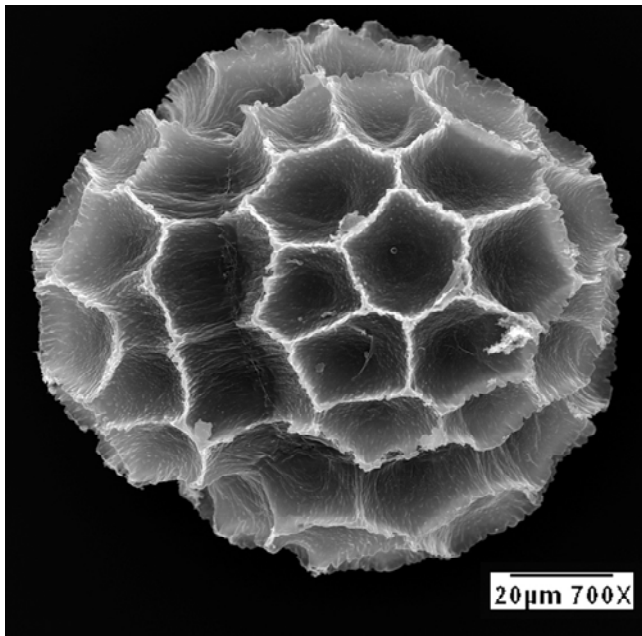

Figure 27. *Sphaerocarpos texanus* spore SEM. Dermination is dependent on temperature and with a 25ºC day: 15ºC night the spores that germinate are female biased. Photo courtesy of Karen Renzaglia.

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

Figure 29. *Sphaerocarpos texanus* female with archegonia. A temperature regime of 25ºC day: 15ºC 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 30ºC, but the optimum for the growth of the protonema was only 25ºC. 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.
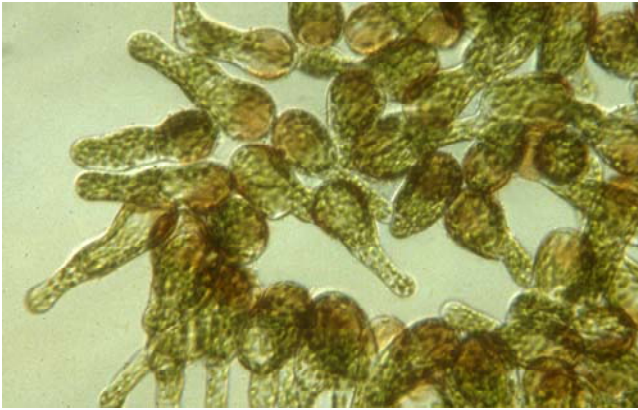
Figure 30. *Funaria hygrometrica* spore germination, a stage for which optimum conditions are at 30ºC. Photo by Janice Glime.

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 Luth, 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 (10ºC) 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 Luth, with permission.

The **perennial** moss *Brachythecium rutabulum* (Figure 34) had its maximum relative growth rate, shoot length, and leaf area at ~19ºC (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.
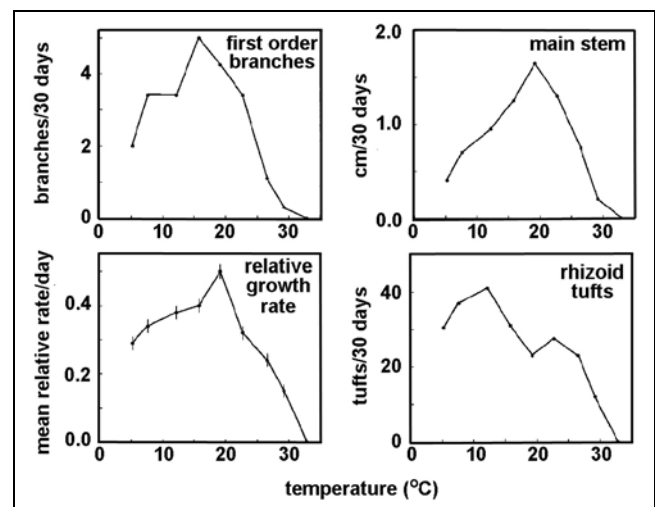

Figure 35. *Brachythecium rutabulum* growth at various temperatures. Redrawn from Furness & Grime 1982a.

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 1-20ºC in both flowing water and pool conditions (Figure 39) (Glime 1980). For *Fontinalis novae-angliae* (Figure 38), it increased up to 15ºC in flowing water conditions, but dropped sharply at 20ºC, whereas in pool conditions it continued to rise. The **growth optimum** for these species from the same localities, however, is lower, at 15ºC, for both species (Glime 1987a). **Branching** rose sharply from 1 to 5ºC 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 1-20ºC. 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 15ºC for most of these aquatic species (Figure 39).
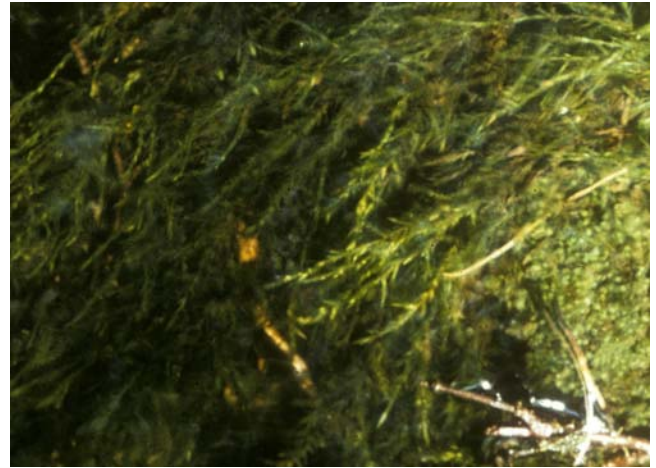
Figure 38. *Fontinalis novae-angliae* with capsules. Photo by Janice Glime.
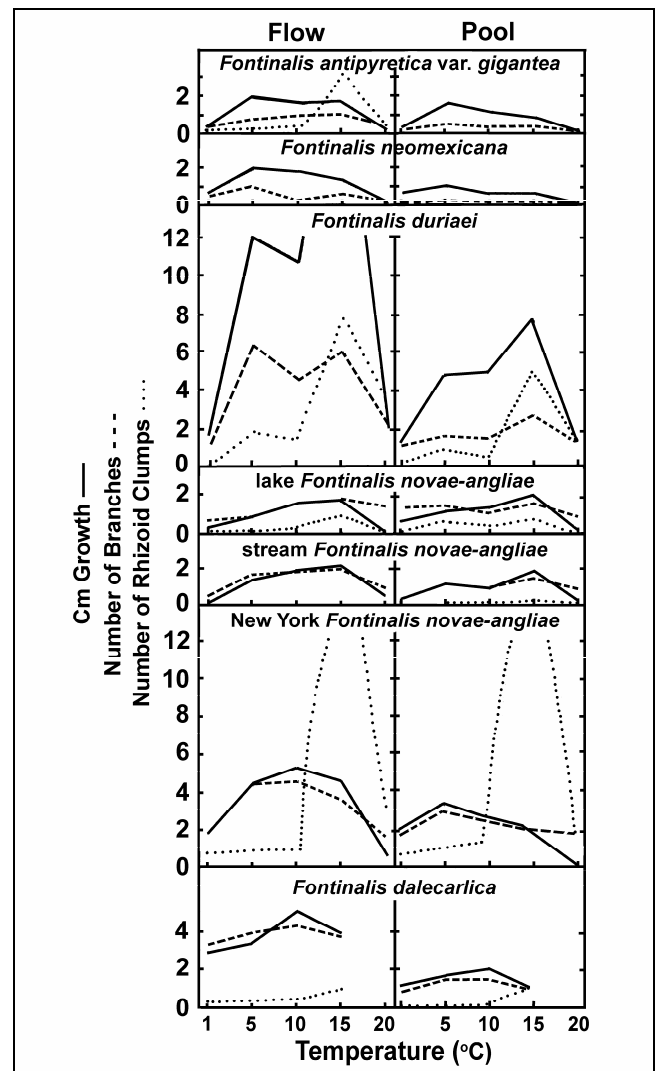
Figure 39. Response of rhizoid clumps, branches, and growth in flowing water (flow) and standing water (pool) conditions to temperatures in the range of 1-20ºC for 15 weeks. Populations at 20ºC were changed to 13ºC after 5 weeks to look for recovery. Numbers represent means of 40 stems. All collections 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 15ºC in flowing water, but in pool conditions, that temperature produced the fewest archegonia, with the most at 10° and 15ºC, 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.
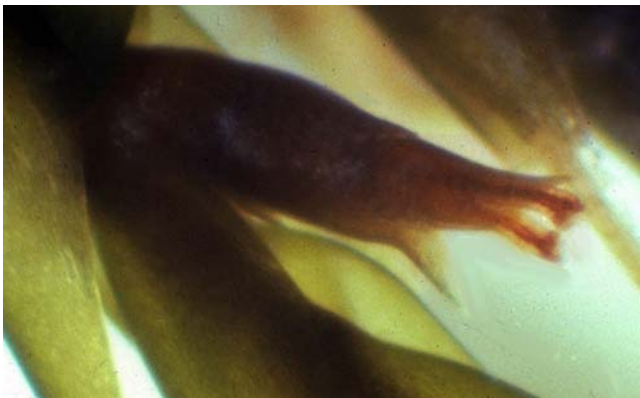

Figure 41. *Fontinalis dalecarlica* archegonia produced in greatest numbers at 15°C. Photo by Janice Glime.

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 (ºC) at which gametangia are induced. From Bopp & Bhatla 1990.

Pogonatum aloides	21
Funaria hygrometrica	10
Physcomitrella patens	15
Physcomitrium pyriforme	7
Philonotis turneriana	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 15ºC, with numbers dropping greatly at 25ºC. Bopp and Bhatla (1990) had similar results, finding the optimal temperature for capsule production to be at 15-19°C, with production droping by 80% at 19-21°C. Vegetative growth, on the other hand, was best at 25ºC. 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 25ºC for capsule development. Bopp and Bhatla (1990) were surprised to find that in *Funaria hygrometrica* (Figure 31), capsules were produced at 10-15ºC in 12-16 hours light, but a shorter photoperiod permitted development at higher temperatures.
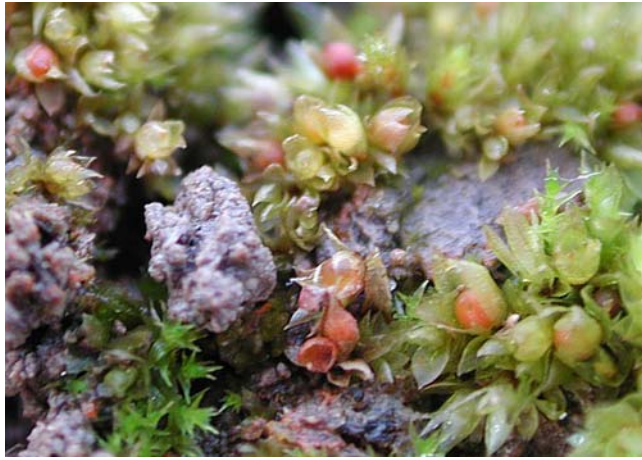
Figure 44. **Physcomitrella patens** with capsules that are produced in greatest numbers at 15°C. Photo by Michael Luth.

Figure 45. **Bryum argenteum** with capsules. Production of capsules can occur in a range of 10-15ºC 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 24ºC 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>, 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 30ºC 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 15-25ºC (Furness & Grime 1982b). Yet some bryophytes can have an optimum of less than 10ºC (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 10ºC (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 Lüth, 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 19ºC in *Brachythecium rutabulum* (Figure 34), the reduction in relative growth was less than 40% at 5ºC. In southern Finland, *Sphagnum fuscum* (Figure 51) had a net productivity gain at any temperature above 0ºC, 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 10ºC, whereas the population from the Upper Peninsula of Michigan had its greatest growth at 15ºC (Glime 1987b; Figure 53). Furthermore, the New

Hampshire populations had considerably more growth at all temperatures below 20ºC than did the Michigan populations. Optima also differed between pool and flowing water conditions, with the New Hampshire population exhibiting its best growth at 5ºC 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 20ºC, 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 20ºC.

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 15-20ºC, whereas plants of the same population collected in September ceased growth after 2-3 weeks at 20ºC (Glime 1982). It appears that degree days are at work here.
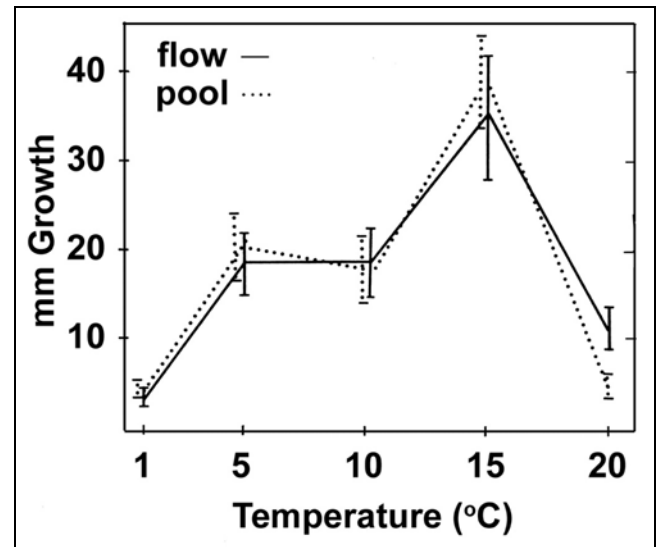
Figure 54. Growth after 15 weeks for *Fontinalis hypnoides* from Isle Royale, Michigan, USA, in flowing water (**flow**) and standing water (**pool**) conditions. Redrawn from Glime 1982.

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 20-35ºC. They actually had a positive net photosynthesis at -15ºC and maintained a net photosynthetic gain for 10-30 minutes at 40-45ºC. 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.
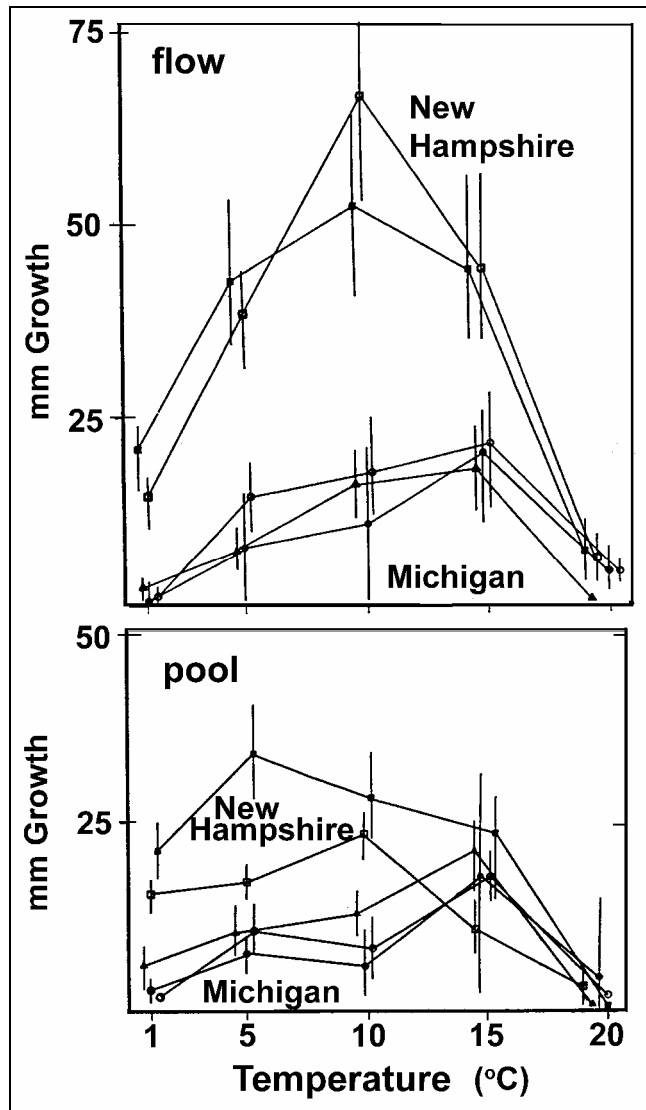

Figure 53. Comparison of growth in flowing water (flow) and standing water (pool) conditions after 15 weeks for *Fontinalis novae-angliae* from two geographic areas. Redrawn from Glime 1987b.

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.

Figure 55. *Plagiomnium maximoviczii*, a species that exhibits optimum photosynthetic output at 20-35ºC. 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 20-35ºC. 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 29.8ºC 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 81.9ºC 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_2, 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 20-25ºC,

with lowland tropical forest bryophytes having drastic drops in net assimilation above 25ºC, soon reaching and surpassing their temperature compensation point (Frahm 1990). We can assume that if 25ºC 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 -4ºC and *Polytrichum* (Figure 58-Figure 59) at -5ºC (Loesch *et al.* 1983). Their high temperature compensation point is 30ºC and 32ºC, 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°C. Photo by Martin Hutten, with permission.

Rütten and Santarius (1993) found productivity temperatures in *Plagiomnium affine* (Figure 60) and *P. undulatum* (Figure 25) with lower limits in the summer at -10 to -15ºC. 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. *Plagiomnium affine*, a species that can survive temperatures of -10 to -15°C in the summer. Photo by Janice Glime.

As the temperature rises, so do the CO_2 and light compensation points and saturation points (Joliffe & Tregunna 1968). *Bryum argenteum* (Figure 45) has a compensation point of 58 ppm at 20.5ºC (Rastorfer 1970). In the moss *Sanionia uncinata* (Figure 61), temperatures of 5ºC, 15ºC, and 25ºC have corresponding CO_2 compensation points of 32, 50, and 82 ppm (mg L^{-1}), respectively (Rastorfer 1971). In other words, as the temperature rises, the moss uses more CO_2 to achieve a net gain. This rise in CO_2 requirement is predicted, because these 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 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 20-30ºC (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 4-24ºC, dropping to lower values at 34ºC. Nevertheless, 34ºC is a relatively high temperature. Ino (1990) found that the maximum rate of net photosynthesis at saturating light levels occurred at approximately 10ºC 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°C and higher. Photo by Martin Hutten, with pernission.

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 5ºC, with a minimum net gain at -8 to -10ºC (Kallio & Heinonen 1973). In short-term experiments the maximum temperature was generally 25-30ºC. Furthermore, even though the moss was not productive at -30ºC, it quickly became active, reaching 60% activation within three hours of warming.
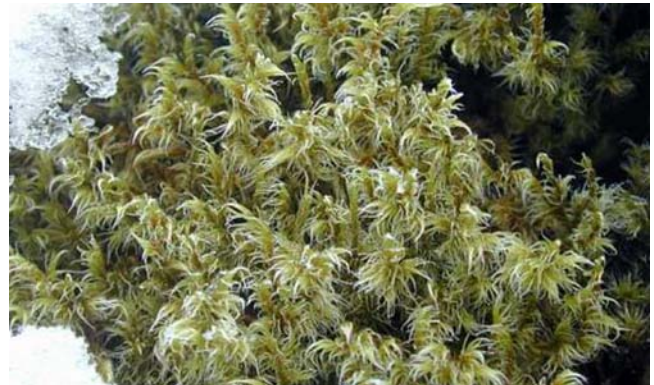

Figure 67. Spring melt reveals *Racomitrium lanuginosum* ready to photosynthesize. Photo by Michael Lüth, with permission.

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 20ºC) 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 10-20ºC with lower limits in the summer at -10 to -15ºC. Their hardiness to cold increased progressively during autumn, reaching temperatures below -35ºC 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 20-35ºC; the mosses could maintain positive net photosynthesis for 20-30 minutes at -10 to -15ºC and from 40-45ºC. Their Q_{10} (change in rate of reaction per 10ºC change in temperature) in the range of 0-20ºC 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 23ºC, 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 0-10ºC in the beginning of June to 10-20ºC 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 3ºC and a high of 26ºC 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 15ºC 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 0-1ºC had their peak assimilation rate at 10ºC. Those mosses collected in June, before the heat of summer, had a peak at 35ºC, the highest optimum found in the 1-40ºC temperature range of the experiments. These mosses had already reached an optimum of 30ºC by 3 April, even though the stream temperature was only 1ºC. 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.
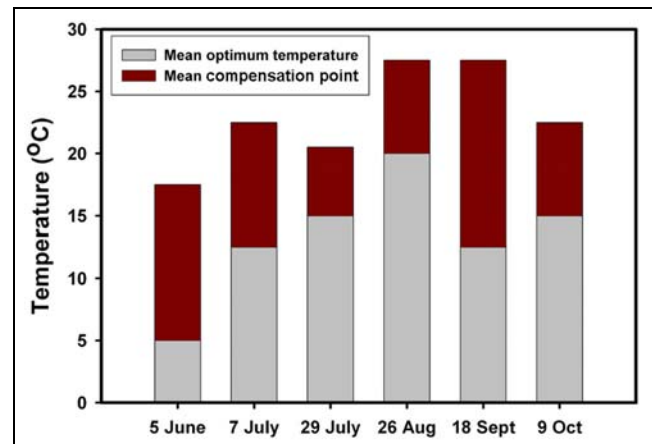

Figure 75. Mean optimum temperatures and upper temperature compensation points for **Dicranum fuscescens** photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel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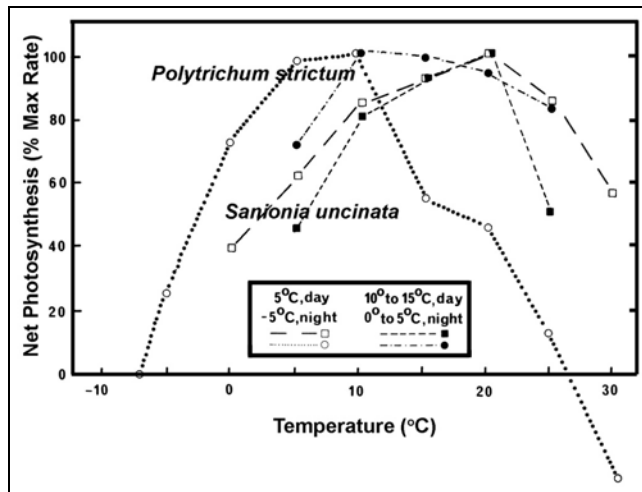

Figure 77. Acclimation responses of two Antarctic moss species at radiant flux density of 500 μeinsteins m^{-2} s^{-1}. Redrawn from Collins 1976.

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 20ºC, but when only 40 lux is present, it reaches compensation at 5ºC (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 60º55'N to 69º45'N and from 69º45'N to 78º13'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 40ºC 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 -10ºC, but seldom have a net gain at temperatures above 25ºC. Rather, they typically become dormant in summer heat and drought. For many species, the optimum is 15-25ºC, although it seems to be much lower for stream bryophytes. Even tropical bryophytes have an upper limit of 25ºC.

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 20ºC, a sunfleck may warm a moss to 39ºC. In some locations they may have a temperature 30ºC 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_{10} 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 that 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.

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