CHAPTER 10-2
TEMPERATURE: COLD

Low Temperature Limits

In general, bryophytes seem able to withstand cold in the leafy state much better than their tracheophyte counterparts. Ochi (1952) found that most mosses (18 species tested) were resistant to cold to -20°C. Seven of these species were resistant to -27°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, a cosmopolitan moss, is pre-adapted to its abode in the Arctic and Antarctic (see Table 1; Figure 7) and suggest that such pre-adaptation may be a common feature of bryophytes. This contention is supported by the low lethal temperatures for bryophytes in the tropics (Table 2).

Surprisingly, Arctic liverworts are not so cold resistant. Among the nine species tested by Biebl (1968), seven were mostly dead at -16°C, with only Lophozia hatcheri and Chandonanthus setiformis surviving well. The moss Aulacomnium turgidum also survived at -16°C. All species survived -6°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°C for half an hour, but twelve-hour exposures killed parts of most of them, the same seven, at 38°C. Aulacomnium turgidum survived up to 48°C for half an hour and up to 40°C for twelve hours. This supports the hypothesis that low temperature survival is coupled with high temperature survival.

Tropical mosses seemed little different. After 24 hours of exposure, Homaliodendron flabellatum and Leucoloma amoenervis survived -14°C and Schistochila commutata survived -11°C (Biebl 1967). Plagiochila, Metzgeria (Figure 2), and Bryum species each survived to at least -4°C. Try doing that to a tropical Maranta.
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Figure 2.  The tropical thalloid liverwort, *Metzgeria claviflora*.  Photo by Michael Lüth.

Table 1.  Temperature limits for net photosynthesis under natural CO₂ and light saturation.  From Larcher (1983), compiled from many authors; *Liu et al. (2001).

<table>
<thead>
<tr>
<th>Plant group</th>
<th>Low-temp limit for CO₂ uptake °C</th>
<th>Temp opt of Pn °C</th>
<th>High-temp limit for CO₂ uptake °C</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbaceous flowering plants</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C₄ plants of hot habitats</td>
<td>+5 to -7</td>
<td>35-45</td>
<td>(50) 50-60</td>
</tr>
<tr>
<td>Sun plants (temperate zone)</td>
<td>-2 to 0</td>
<td>20-30</td>
<td>40-50</td>
</tr>
<tr>
<td>Shade plants (temperate zone)</td>
<td>-2 to 0</td>
<td>10-20</td>
<td>-40</td>
</tr>
<tr>
<td>Desert plants</td>
<td>-5 to 5</td>
<td>20-35 (45)</td>
<td>45-50 (56)</td>
</tr>
<tr>
<td>CAM plants (CO₂ fixation at night)</td>
<td>-2 to 0</td>
<td>5-15</td>
<td>25-30</td>
</tr>
<tr>
<td>Winter annuals, spring-flowering</td>
<td>-2 to 0</td>
<td>10-20</td>
<td>30-40</td>
</tr>
<tr>
<td>and alpine plants</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><strong>Woody plants</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evergreen trees of the tropics</td>
<td>0 to 5</td>
<td>25-30</td>
<td>45-50</td>
</tr>
<tr>
<td>and subtropics</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Winter-deciduous trees of the</td>
<td>-3 to -1</td>
<td>15-25</td>
<td>40-45</td>
</tr>
<tr>
<td>temperate zone</td>
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<td></td>
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<tr>
<td>Evergreen conifers</td>
<td>-5 to -3</td>
<td>10-25</td>
<td>35-42</td>
</tr>
<tr>
<td>Dwarf shrubs of heath and tundra</td>
<td>~3</td>
<td>15-25</td>
<td>40-45</td>
</tr>
<tr>
<td>and alpine plants</td>
<td></td>
<td></td>
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<tr>
<td><strong>Cryptogams</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic and subarctic mosses</td>
<td>~8</td>
<td>~5</td>
<td>~30</td>
</tr>
<tr>
<td><em>Racomitrium lanuginosum</em></td>
<td>-8 to -10</td>
<td>5</td>
<td>25-30</td>
</tr>
<tr>
<td><em>Pleurozium schreberi</em></td>
<td>-5</td>
<td>10-15</td>
<td>20-35</td>
</tr>
<tr>
<td><em>Plagiomnium acutum</em></td>
<td>-10 to -15</td>
<td>20-35</td>
<td>40-45</td>
</tr>
<tr>
<td><em>Plagiomnium maximoviczii</em></td>
<td>-10 to -15</td>
<td>20-35</td>
<td>40-45</td>
</tr>
<tr>
<td>Lichens of cold regions</td>
<td>(-25)-15 to -10</td>
<td>5-15</td>
<td>20-30</td>
</tr>
<tr>
<td>Desert lichens</td>
<td>~10</td>
<td>18-20</td>
<td>38-40</td>
</tr>
<tr>
<td>Tropical lichens</td>
<td>-2 to 0</td>
<td>-20</td>
<td></td>
</tr>
<tr>
<td>Snow algae</td>
<td>~5</td>
<td>0-10</td>
<td>30</td>
</tr>
<tr>
<td>Thermophilic algae</td>
<td>20 to 30</td>
<td>40-55</td>
<td>65-70</td>
</tr>
</tbody>
</table>

Table 2.  Comparison of temperature resistance of leaves of plants from different climatic regions.  Limiting temperatures are for 50% injury (TL₅₀) 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).

<table>
<thead>
<tr>
<th>Plants</th>
<th>°C for cold injury</th>
<th>°C for heat injury in growing season</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tropics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trees</td>
<td>+5 to -2</td>
<td>45-55</td>
</tr>
<tr>
<td>Forest undergrowth</td>
<td>+5 to -2</td>
<td>45-48</td>
</tr>
<tr>
<td>Mountain plants</td>
<td>-5 to -10</td>
<td>~45</td>
</tr>
<tr>
<td><em>Schistochila commutata</em></td>
<td>-14</td>
<td>44</td>
</tr>
<tr>
<td><em>Plagiochila sp.</em></td>
<td>-7</td>
<td>44</td>
</tr>
<tr>
<td><strong>Homalidendron flabelatum</strong></td>
<td>&lt;-14</td>
<td>52</td>
</tr>
<tr>
<td><strong>Leucoloma amoennervis</strong></td>
<td>&lt;-14</td>
<td>52</td>
</tr>
<tr>
<td><strong>Bryum sp.</strong></td>
<td>-11</td>
<td>52</td>
</tr>
<tr>
<td><strong>Subtropics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sclerophyllous woody plants</td>
<td>-8 to -12</td>
<td>50-60</td>
</tr>
<tr>
<td>Subtropical palms</td>
<td>-5 to -14</td>
<td>55-60</td>
</tr>
<tr>
<td>Succulents</td>
<td>-5 to -10</td>
<td>58-65</td>
</tr>
<tr>
<td>C₄ grasses</td>
<td>-1 to -3(8)</td>
<td>60-64</td>
</tr>
<tr>
<td><strong>Temperate zone</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evergreen woody plants of coastal</td>
<td>-6 to -15 (-25)</td>
<td>50-55</td>
</tr>
<tr>
<td>regions with mild winters</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Plagiomnium acutum</em></td>
<td></td>
<td>45 (50 dry)</td>
</tr>
<tr>
<td><strong>Arcto-tertiary relict trees</strong></td>
<td>-10 to -25</td>
<td>(-15 to -30)</td>
</tr>
<tr>
<td>Dwarf shrubs of Atlantic heaths</td>
<td>-20 to -30</td>
<td>45-50</td>
</tr>
<tr>
<td>Winter-deciduous trees and widely</td>
<td>(-25 to -40)</td>
<td>~50</td>
</tr>
<tr>
<td>Distributed shrubs</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Herbs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sunny habitats</td>
<td>10 to -20 (-30)</td>
<td>48-52</td>
</tr>
<tr>
<td>Shady habitats</td>
<td>40-45</td>
<td></td>
</tr>
<tr>
<td>Water plants</td>
<td>~10</td>
<td>38-42</td>
</tr>
<tr>
<td><strong>Cold-winter areas</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evergreen conifers</td>
<td>-40 to -90</td>
<td>44-50</td>
</tr>
<tr>
<td>Boreal broad-leaved trees</td>
<td>(-196)</td>
<td>42-45</td>
</tr>
<tr>
<td>Arctic and alpine dwarf shrubs</td>
<td>-30 to -70</td>
<td>48-54</td>
</tr>
<tr>
<td>Herbs of the high mountains and arctic</td>
<td>-30 (-196)</td>
<td>44-54</td>
</tr>
</tbody>
</table>

**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*, *H. revolutum*, and *Abietinella abietinum* (Figure 3) among the pleurocarpous mosses ventured into the dry areas with little snow.  Lichens dominated the rocks.  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.

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, Pannenwitz 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 northern 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.

**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). Yet it is amazing that we have all but ignored winter ecology for all plants and are now beginning to realize that changes in climate that shorten winter and decrease snow depth could have major impacts on the ways plants complete their life cycles (Campbell et al. 2005). Our assumption that plants are dormant in winter has misled us into ignoring some of the dynamic events that influence their future.

**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⁻¹ 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* 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 4 suggests that they don’t. How little we know of their winter ecology!

![Figure 4. Racomitrium lanuginosum emerges from the snow unfrozen and in good health. Photo by Michael Lüth.](image)

**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 & Gliine 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 is separated by a small funnel of air, I assume caused in part by the reradiation of heat from the dark trunk of the tree. 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.

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 physiologists 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$^{-3}$ (very fresh snowfall) would completely buffer most temperature fluctuations. When the density increases to 0.2 g cm$^{-3}$, 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 5), 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$^{-3}$, typical of the upper part of the snow pack in late winter, only 2 - 3% of the surface light reached 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$^{-3}$, 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$^{-3}$, the late season snow provides an insulating source of water as it melts, increasing the transmission of light.

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 impliable.

Melick and Seppelt (1992) showed that freeze-thaw cycles in the Antarctic bryophytes would greatly increase the rates of sucrose leakage from the cell to a magnitude 2-3 times that under non-freeze-thaw conditions. The moss *Bryum pseudotriquetrum* lost 65% of its sucrose following 16 freeze-thaw cycles, while other mosses studied lost only 28%. There appeared to be no change in the freezing point temperature of tissues after this loss, with tissue freezing points varying from -3.5 to -8.3°C. The highest freezing temperatures occurred in dead tissues.
Desiccation Tolerance

Much like their resistance to hot temperatures, at least some bryophytes (*Syntrichia ruralis*) 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.

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 7) 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).

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 *Grinnia antarctica* 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.

Pannewitz et al (2003b) showed similar protection for *Hennediella heimiti* 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 acclimatized by building up non-photochemical quenching systems.

Figure 7. *Racomitrium lanuginosum*. **Upper**: growing with alpine plants in the mountains in New Zealand. **Lower**: Demonstrating the long, white hairtips that help protect it from high light intensities when dry or in cold temperatures. Photos by Janice Glime.

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 sciuroides* (Figure 8), 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 CO₂ fixation, hence protecting their photosynthetic system from excess excitation. This temporary reduction in CO₂ fixation is quickly returned to normal after freezing.

One protection against high light intensity is development of red pigments. Just as high elevation mosses may be red, like those discussed as living in late snowbeds, and snow algae such as *Chlamydomonas nivalis* 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. Several species of *Sphagnum* have this color response, wherein cold temperatures induce production of the red cell wall pigment *sphagnorubin*, a flavonoid (Tutschek 1982).

The activity and thermosensitivity of superoxide dismutase (SOD) is highly sensitive to ions of Ca$^{++}$ and Zn$^{++}$ (Christov & Bakardjieva 1999). In *Mnium affine*, calcium was most important for the 1 cytosolic and mitochondrial SOD's, whereas zinc was more important for the chloroplastic and 2 cytosolic SOD's.

**Abscisic Acid**

ABA (abscisic acid) is produced in tracheophytes in preparation for cold temperatures and permits plants to survive to lower temperatures, something like antifreeze. Nagao *et al.* (2005) have shown that media containing ABA does indeed lower the LT$_{50}$ (temperature at which 50% of cells die) for *Physcomitrella patens* 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. That only tells us what ABA can do. Next we need to determine that moses dos 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* 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 *Physcomitrella 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.

**Transporter Proteins, ABA, and Ca**

Further studies on *Physcomitrella patens* 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 *Physcomitrella 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

Figure 8. *Leucodon sciuroides* on a tree trunk where it is exposed to atmospheric temperatures all year. Photo by Michael Lüth.

Figure 9. *Physcomitrella patens* with young sporophytes. Photo by Michael Lüth.
enhancement of freezing tolerance in Physcomitrella patens. The LT$_{50}$ dropped from -2ºC to -10ºC when the protonemata were grown in a medium with enhanced ABA (Nagao et al. 2003). 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 (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, Arrichum undulatum, Plagiomnium undulatum (Figure 10), P. affine (Figure 10), and Mnium hornum, and the thallose liverwort Pellia epiphylla. The frost resistance between summer and winter differed by more than 25ºC 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 and Hynnum cupressiforme were highly frost tolerant in summer and at that time had high sucrose levels. Furthermore, as sucrose levels declined during exposure to higher temperatures, cold hardiness declined.

However, they 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 10) and P. undulatum (Figure 10) (Rütten & Santarius 1993a). Sucrose seemed to contribute in some way to the tolerance, increasing from summer to winter, while temperature limits increased from -10ºC in summer to less than -35ºC 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 40ºC 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 (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. 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?

Figure 10. Upper: Plagiomnium undulatum. Lower: Plagiomnium affine. Photos by Michael Lüth.

Aro and Karunen (1988), in studying protonemata of Ceratodon purpureus, 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 (6ºC) caused an increased incorporation of $^{14}$C into the neutral lipid fraction and decreased its incorporation into the glycolipid fraction in Dicranum elongatum, suggesting a preferential accumulation of acetylenic tricylglycerols. Such responses, when adaptive, can permit the moss to prepare for the drought of winter through the signal of low temperature.

**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.

**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 et al. 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 -40ºC is rarely reached. This is significant since the lower limit for supercooling of water is -41ºC (Kuiper 1978), and George and coworkers (1977) have observed ice formation in xylem at -30 to -40ºC.
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 crystalized 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 above, 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 any cell will 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 11). One Antarctic species of Bryum 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 1. Hedwigia ciliata with glass formation (ice) on the surface rather than ice crystals. Photo by Michael Lüth.

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 Irmscher 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 an advantage 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 12, the mosses Hookeria lucens (Figure 13) and Plagiothecium undulatum (Figure 14) are 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), on the other hand, is more similar to the tracheophyte Arbutus unedo, with a slow decline in temperature below the freezing point of water.

**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 Leucobryum glaucum (Figure 15) and Plagiochila asplenioides (Figure 16) 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.), the status could not be determined. Hylocomium splendens, Racomitrium aquaticum, R. lanuginosum, and Scorpiurium circinatum survived to -10°C. Hookeria lucens (Figure 14), Leucobryum glaucum (Figure 15), Mnium hornum, and Plagiochila oederianus (Figure 17) 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 survived to -10°C, with 50% survival. It is interesting that such epiphytes as Porella platyphylla 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.
These data suggest that mosses are more tolerant of wet cold than liverworts and that the thallose liverworts are the most vulnerable.

**Lipids in Membranes & Protein Denaturation**

We know that bryophytes are able to exist farther north 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.

![Figure 16. Plagiochila asplenioides. Photo by Michael Lüth.](image)

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).

![Figure 17. Plagiopus oederianus. Photo by Michael Lüth.](image)

**Unsaturated Lipids**

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

**Fatty Acid Alteration**

One of the means by which organisms prepare for changes in temperature is to alter their 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* 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 hardiness. 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 CO₂ 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 hardiness.

In *Sphagnum fimбриatum*, when the temperature decreases in the range of 5-15°C, the amounts of linoleic, α linolenic, and arachidonic acids in their glycolipids [both monogalactosyldiacylglycerols (MGDG) and digalactosyldiacylglycerols (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 α-linolenic acids decrease. But this pattern is certainly not universal. Even the related *S. magellanicum* 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. fimбриatum*, in decreasing light and temperatures, *S. magellanicum* exhibited a decrease in linolenic acid.

In the liverwort *Marchantia polymorpha*, cells grown at 25°C contained 18% linolenic acid (18:3 omega 3), 11% arachidonic acid (4 omega 6), and 3% eicosapentaenoic acid (20:5 omega 3) in their fatty acids (Saruwatari et al. 1999). At 15°C, there were large increases in the amounts of 18:3 omega 3 and 20:5 omega 3 acids, with little effect.
on other fatty acid groups. The 20:5 omega 3 group increased only in the chloroplast fraction whereas the 18:3 group increased in the chloroplast and cellular fractions. Only the MGDG and chloroplastic PC of the 20:5 group increased at the lower temperature.

**Fatty Acids**

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 & N**

Using Ctenidium molluscum, Pogonatum urnigerum, Dichodontium pellucidum, and Tortella tortuosa, Al-Hasan's group (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).

**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 18) 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, temperatures down to 2°C caused a proliferation of polyribosomes, accompanied by a decrease in single ribosomes (Malek & Bewley 1978). However, slowly dried mosses do not contain polyribosomes and reform them upon rehydration. There seemed 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 19) 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, had much less frost tolerance than mature leaves.

Figure 19. Plagiomnium undulatum leaves that are mature enough, but are not senescent, permitting them to sustain extracellular freezing. Photo by Michael Lüth.

**Freezing Effect on Distribution and Niche**

The ability to survive freezing will influence both geographic and habitat distribution of bryophytes. Shirasaki (1984) found that Bryoxiphium norvegicum (Figure 20) 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. Shirasaki (1987) also found that the distributions of the leafy liverworts Bazzania trilobata and B. yoshinagana 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.
As seen for *Fontinalis* species in the previous subchapter on temperature, adaptation to cold can be a major 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*, *S. subsecundum*, and *S. teres* were more frost-resistant than were those of *S. magellanicum* and *S. fuscum*.

For the sunny species of *Sphagnum magellanicum* and *S. papillosum* (Figure 21), 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* 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.

**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?

**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.

**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. Ca alters membrane permeability, thus affecting membrane transport. Cold temperatures seem to increase the cellular content of Ca\(^{2+}\), 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. 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

Literature Cited


Chapter 10-2: Temperature: Cold