

# CHAPTER 10-3

## TEMPERATURE: HEAT



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

### Heat Stress and Heat Resistance

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



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

Most bryophytes seem to have a heat tolerance of 39-45°C (Scheibmair 1938; Dirckson 1964; Nörr 1974). When

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

We can consider two major types of heat-related environmental parameters. In one case, the environment is characterized by permanently high temperatures, and in the other, the plants are subjected to thermal extremes (Kappen 1981). For those plants surviving constant heat, the mode of survival must be physiological. However, for those that must survive heat stress only occasionally when extremes arrive, the plant adaptations may require some degree of physiological tolerance, coupled with mechanisms for avoiding the heat. For many plants, this latter avoidance mechanism often involves a dormant life cycle stage that is metabolically inactive, permitting it to survive physiologically. For bryophytes, this could be accomplished by spores or vegetative diaspores that survive underground or on the surface as inactive tissue. This does in fact aid some flood plain species and other ephemerals that disappear for long periods of time and appear only when conditions are suitable. But for the vast majority of bryophytes, their slow growth makes this annual strategy impractical and they more typically survive in a state of desiccation (in dormancy) in which their temperature tolerance is typically much higher (Hearnshaw & Proctor 1982). If neither of these strategies is possible, as in wetland bryophytes, their adaptations must include a physiological tolerance to heat, whether it be for short daily periods in summer or for longer duration, or a cooling mechanism. For example, many species of *Sphagnum* have their optimum temperature for growth at 30-35°C (Li & Glime 1990), whereas most bryophytes have an optimum near 20°C (Dilks & Proctor 1975). The cosmopolitan *Bryum argenteum* populations, living from the continent of Antarctica through the hot lowland tropics, exhibits heat stress at 30°C, exhibiting its optimum at 22°C day/15°C night (Hedderson & Longton 1999). But air temperature is not indicative of bryophyte temperature, and emergent bryophytes may in fact lower their temperature through evaporative cooling. When that water is no longer available, the bryophyte is approaching a state of desiccation in which it can become dormant.

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

well as the day-night differences in their environments and to sustain short periods of hot weather in summer.

## Heated Habitats

Tropical areas and geothermal habitats present special constraints on bryophytes due to their persistent high temperatures. One would therefore expect that such bryophytes would possess unique adaptations to permit their survival. However, even tropical bryophytes seem to do poorly above 25°C (Frahm 1990). Such high (but not uncommon) temperatures cause their net assimilation rate to decrease drastically, their respiration rates to rise to high levels, and they fail to reach their compensation point (Frahm 1987).

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

## Plant and Cellular Responses

Effects of heat stress can include loss of membrane integrity (Liu *et al.* 2003), color change to brown (Keever 1957), shoot damage (Liu *et al.* 2004), and enzyme and pigment destruction (Larcher 1995; Meyer & Santarius 1998; Liu *et al.* 2004). Liu *et al.* (2004) found that *Plagiomnium acutum* survived well at 35-40°C, exhibiting no cellular damage, but at 45°C both wet and dry moss cells were damaged (Figure 3). They could find no differences with leaf age, as assessed by position on stem.

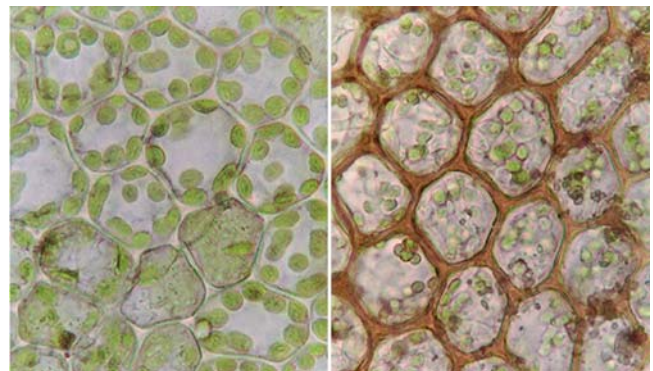


Figure 3. Cells of *Plagiomnium acutum* following wet heat treatment. **Left:** 35°C for 8 hours. **Right:** 45°C for 1 hour. Photos by Yingdi Liu.

It appears that membrane permeability varies with temperature even within a normal range of daily temperature fluctuations. Liu *et al.* (2003) demonstrated a temporal fluctuation in cell membrane permeability for *Thuidium cymbifolium* and *Plagiommium acutum* submersed in water through a 94-hour period. The permeability tracked the temperature almost perfectly (Figure 4).

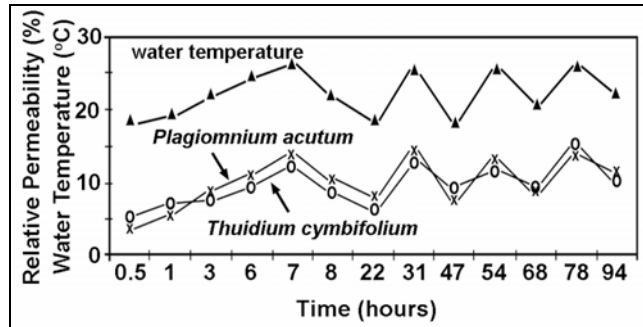


Figure 4. Effect of surrounding temperature on the membrane permeability of two mosses. Redrawn from Liu *et al.* (2003).

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

It appears that even the aquatic moss *Fontinalis antipyretica* may have physiological races adapted to high temperatures. Long exposures to a high temperature could eliminate all but the hardy, and eventually develop a population that is able to withstand the higher temperatures. Such might seem to be the case for this moss growing in a river with abnormally high temperatures due to heated water from hot springs. But when Carballeira *et al.* (1998) transplanted the moss from a normal river site (16°C) to the heated river (34°C), there was no notable change in pigment ratio, photosynthetic rate, or respiratory rate after 25 days at the new high temperature. Furthermore, after 2, 4, and 10 days of exposure of mosses from the 16°C river to 30°C, then back to 16°C, these parameters recovered to 50% of their normal values within 10 days. Photosynthesis and respiration both recovered more slowly than did the pigment ratios.

Sagot and Rochefort (1996) showed that species of *Sphagnum* from eastern Canada differed in their heat tolerance. Among *S. angustifolium*, *S. fallax*, *S. fuscum*, *S. magellanicum*, *S. nemoreum*, and *S. papillosum* oven dried for 48 hours in the range of 20-70°C, only *S. fallax* survived up to a temperature of 30°C. Li and Glime (1990), on the other hand, demonstrated an optimum growth temperature of 30-35°C for *S. magellanicum* and *S. papillosum* from the Keweenaw Peninsula of Michigan,

USA. Rydin (1984) found no temperature-tolerance differences among *Sphagnum* species from Europe. It is likely that the rate of drying differed among these studies so that moisture state may have contributed to the contrasting results, but geographic races may also have been involved in these distant populations. *Sphagnum fuscum* responded to summer warming with enhanced length increment (42-62%) and greater biomass increase, while bulk density decreased (Dorreball *et al.* 2004). Added snow in winter increased the biomass gain by 33%, but growth in length and bulk density did not change significantly. These changes suggest that not only is the health of the plant affected by temperature, but the structure and moisture-holding capacity are altered, potentially having a major impact on the ecosystem.

## Biochemical Responses

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

## Isoprene

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

Although isoprene emission is common among mosses and ferns, it is absent in liverworts and hornworts and less predictable among other tracheophytes (Hanson *et al.* 1999). It may be especially useful in certain habitats. Bryophytes growing in the open, such as many *Sphagnum* species, are more likely to suffer from thermal stress. This stress could be particularly important when these mosses, with their lower parts in water, may still be in a hydrated state. *Sphagnum capillifolium* (Figure 5) from a northern Wisconsin, USA, bog is subject to these large temperature fluctuations and enjoys the benefits of isoprene as a means of increasing its thermotolerance (Hanson *et al.* 1999).

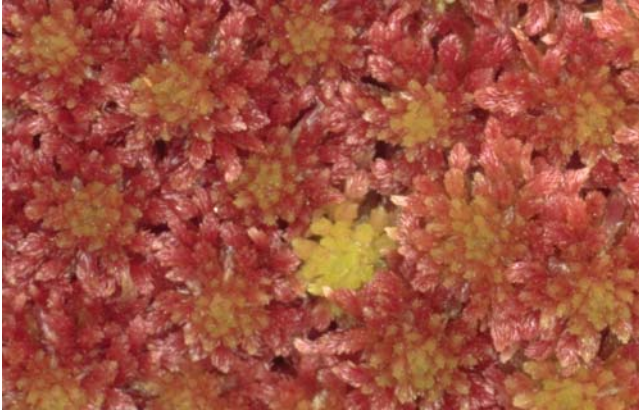


Figure 5. *Sphagnum capillifolium*. Photo by Jan-Peter Frahm.

### Sugars

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

### Peroxidase

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

### Heat Shock Proteins

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

It appears that these ancient bryophyte heat shock proteins have been largely ignored, at least if Cambridge

Scientific Abstracts is a good test. We know from the fungus *Phycomyces blakesleeianus* that blue light and high heat will induce them in that organism (Rodríguez-Romero & Corrochano 2004). Perhaps light, as well as temperature, also plays a role in the photosynthetic bryophytes. But what is that role?

### Photosynthetic Apparatus

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

### Acclimation

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

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

Based on laboratory studies, there is evidence that at sublethal temperatures acclimation to high temperatures occurs (*e.g.* *Fontinalis duriaei*, Figure 6, Glime & Acton 1979; Fornwall & Glime 1982; *Polytrichum commune*, Sveinbjörnsson & Oechel 1983), but results are conflicting. Weis *et al.* (1986) found that the thallose liverworts *Preissia quadrata*, *Conocephalum conicum*, and *Marchantia polymorpha* survived mild heat treatment with a reversible depression of photosynthesis. However, more severe heat caused irreversible damage to photosystem II, much as in higher plants. Nevertheless, these thalli did not have any significant increase in thermal stability of their photosynthetic apparatus as a result of exposure to high sublethal temperatures. Contrasting with the delayed response of temperature acclimation in *Pohlia wahlenbergii* (Sandvik & Heegaard 2003), Antropova (1974) found that exposure of only 3 hours at temperatures above their optimum increased heat resistance in bryophytes in a manner similar to that of flowering plants, whereas incubation within their optimum range of 10-20°C had no effect. Whereas Carballeira and coworkers (1998)

found that when exposed to 30°C *Fontinalis antipyretica* showed little difference in pigment ratio, photosynthetic rate, or respiration rate between populations previously grown at normal river temperatures and those grown in a river with abnormally high temperatures resulting from hot springs. Glime (1987) found that this species (collected in Houghton, Michigan, USA) became chlorotic after several weeks of exposure to temperatures above 15°C.



Figure 6. *Fontinalis duriaei* in a stream in Japan. Photo by Janice Glime.

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

### Night Temperature

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

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

### Hydration State

The state of hydration is of great importance in the thermal tolerance of bryophytes and their ability to acclimate (Table 1). Dry bryophytes have much greater thermal tolerance than hydrated ones (Figure 7; Figure 8). Alpert (2000) contended that desiccated plants are able to endure temperatures from -272 to 100°C. But hydrated *Fontinalis novae-angliae* had at least some stem tissue that survived intermittent boiling for more than one week (Glime & Carr 1974). In the moss *Homalothecium lutescens*, a decrease in the water content was responsible

for an increase in heat tolerance (Dulai *et al.* 2002). An osmotic treatment of only 30 minutes shifted the lethal temperatures upward. But if the plants were kept in the dark, the curves did not shift upward as the water deficit increased, suggesting that the thermal stability of PS II may occur only in the energized photosynthetic membranes. On the other hand, Li *et al.* (1999) found that dark respiration decreased as temperature increased (and hydration state decreased) in *Herpetineuron toccoeae* and *Plagiomnium acutum*, perhaps explaining part of the greater heat tolerance of dry mosses.

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

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

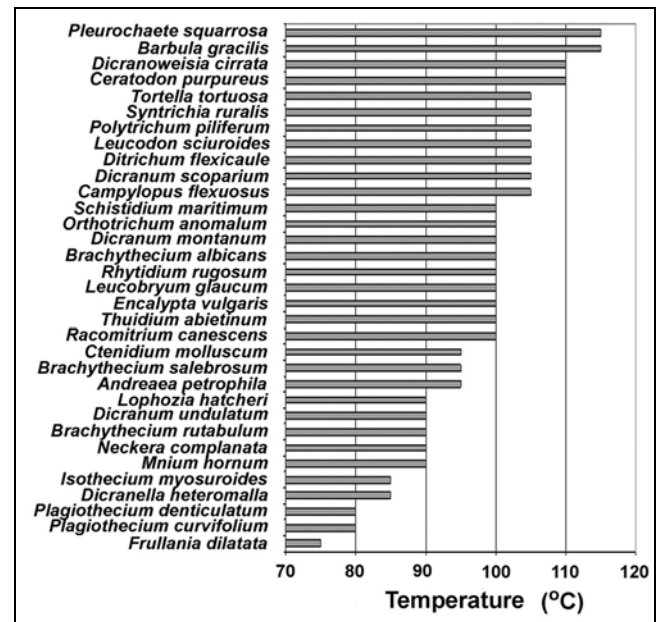


Figure 7. Lethal temperatures for various dry mosses. Based on Lange (1955), using the highest temperature below which most of the mosses first survived for 30 minutes.

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

As one might expect, water use efficiency (WUE) plays a role in heat tolerance in bryophytes. In the moss

*Herpetineuron toccoeae*, transpiration usually is lower and water use efficiency higher than that of *Plagiomnium acutum* in the same habitat (Li *et al.* 1999). This seems to endow *H. toccoeae* with a greater capacity for heat tolerance and dry habitats.

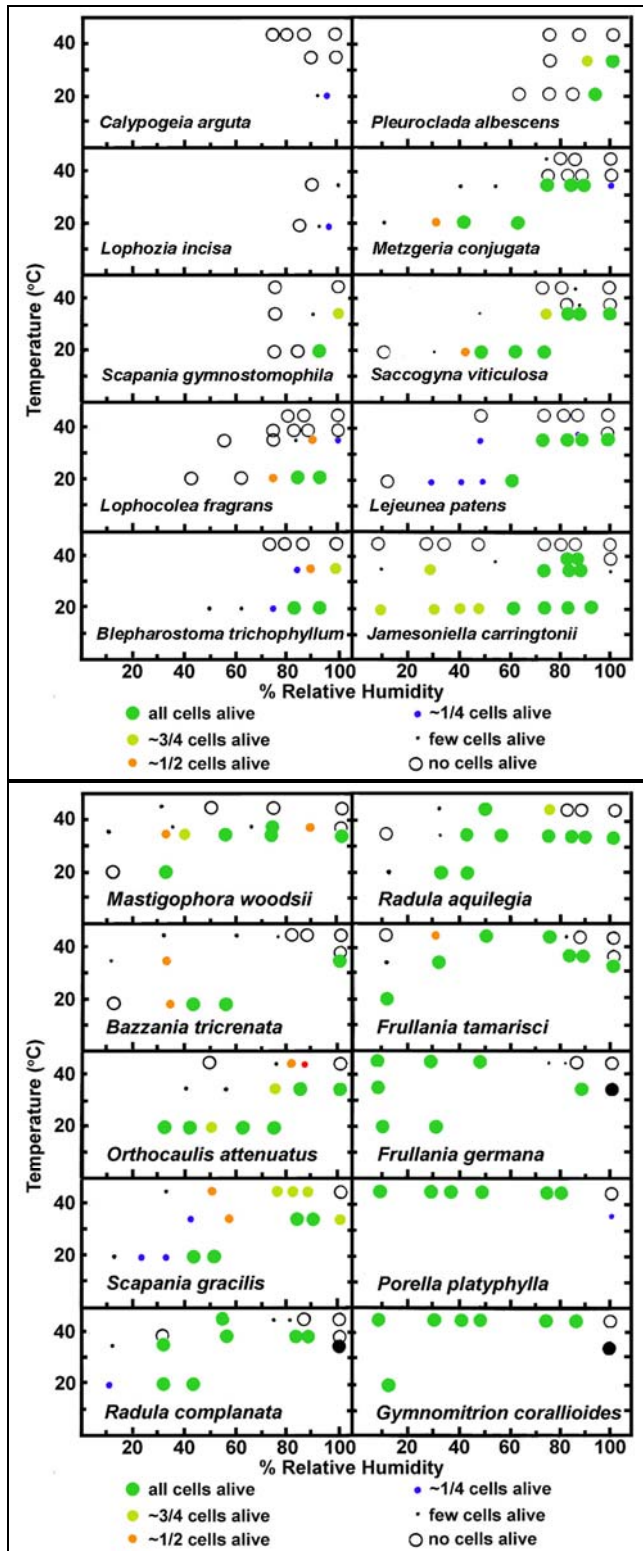


Figure 8. Effects of temperature and state of hydration on 20 leafy liverworts from Europe. Redrawn from Clausen (1964).

A common method of drying mosses in the laboratory for temperature experiments has been to place the plants in

a sugar or salt solution until they plasmolyze (Figure 9). This pretreatment induces heat resistance, most likely by suspending cellular metabolism.

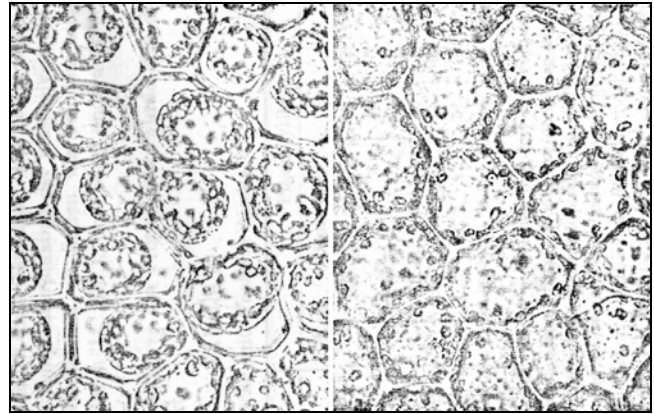


Figure 9. Leaf cells of *Plagiochila asplenioides* demonstrating the effect of heat on desiccated cells. **Left:** Cells plasmolyzed, indicating intact membranes, in 2.5 M sugar solution at 55°C for 1.5 minutes. **Right:** Cells after 1.5 minutes at 55°C with no pretreatment in the salt solution. Lack of cell shrinkage upon drying suggests loss of membrane integrity, suggesting that these cells are dead. (Photos from Scheibmair 1938.)

## Duration

Not only is the actual temperature important, but the duration is also important. Just as we might walk through a hot boiler room unscathed, but be unable to stay for an hour in there without getting sick, bryophytes likewise are able to tolerate short-term bursts of heat as might come from dancing sunflecks. For example, the tropical liverwort *Schistochila commutata* dies at 32°C in water with 12 hours exposure, but survives at 42°C (but not 44°C) with only 1/2 hour exposure (Biebl 1967). The tropical mosses *Homaliodendron flabellatum* and *Bryum* sp. tolerate temperatures up to 50°C in water for half an hour, contrasting with the 25°C limit for tropical bryophytes reported by Frahm (1990). Figure 10 demonstrates the effect of time in the moss *Plagiomnium acutum*.

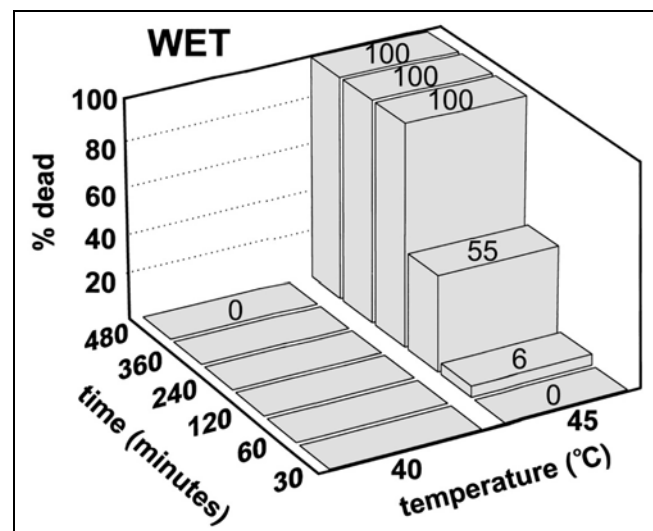


Figure 10. Effect of time on the lethality of temperature in *Plagiomnium acutum*. n=30. From Liu *et al.* (2004).

## Age and Structure

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

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

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

## Reversible Effects

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

## Decomposition

Few studies have examined bryophyte decomposition, and many misconceptions occur among ecologists about bryophyte decomposition. It is quite a different thing to be decaying from the bottom up on a live plant than to drop leaves and branches that henceforth decay. By being still connected to living plant tissue, decaying portions of a

bryophyte are able to move internal and external constituents upward or outward to living portions. Such movement can be influenced by temperature.

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

## Summary

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

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

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

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

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

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

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

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

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

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

## Acknowledgments

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