CHAPTER 10-3

TEMPERATURE: HEAT

TABLE OF CONTENTS

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

Heat Stress and Heat Resistance

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

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

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

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

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

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

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

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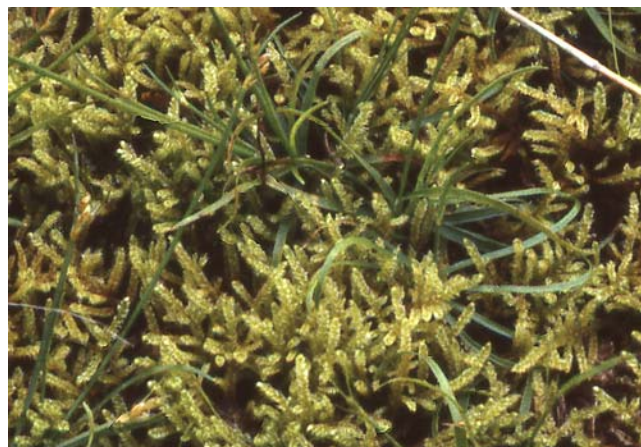

Figure 6. *Hypnum plumaeforme* from a geothermal site near Lake Wakoto, Japan. Photo by Janice Glime.

If neither of these strategies is possible, as in wetland bryophytes, their adaptations must include a physiological tolerance to heat, whether it be for short daily periods in summer or for longer duration, or a cooling mechanism. For example, many species of *Sphagnum* (Figure 19-Figure 23) have their optimum temperature for growth at 30-35ºC (Li & Glime 1990), whereas most bryophytes have an optimum near 20ºC (Dilks & Proctor 1975). The cosmopolitan *Bryum argenteum* (Figure 7) populations, living from the continent of Antarctica through the hot lowland tropics, exhibits heat stress at 30ºC, exhibiting its optimum at 22ºC day/15ºC 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.

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

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

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

Heated Habitats

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

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

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

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

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

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

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

Sporophyte Stress

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

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

Plant and Cellular Responses

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

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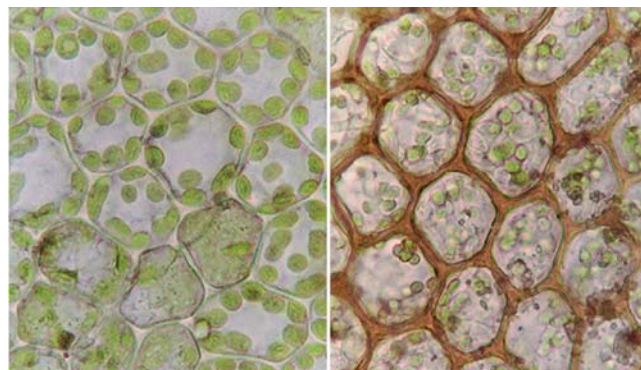

Figure 15. Cells of *Plagiomnium acutum* following wet heat treatment. **Left:** 35°C for 8 hours. **Right:** 45°C for 1 hour. Photos by Yingdi Liu, with permission.

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

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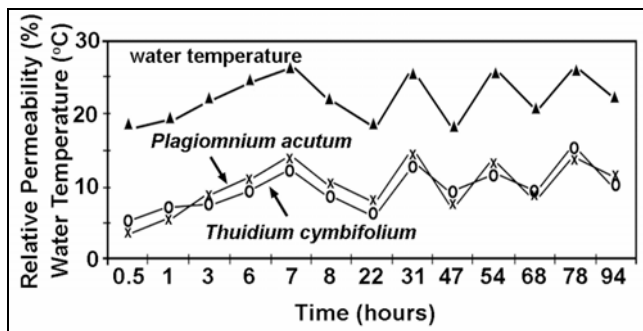

Figure 17. Effect of surrounding temperature on the membrane permeability of two mosses. Redrawn from Liu *et al*. 2003.

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

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

when Carballeira *et al*. (1998) transplanted the moss from a normal river site (16ºC) to the heated river (34ºC), 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 16ºC river to 30ºC, then back to 16ºC, these parameters recovered to 50% of their normal values within 10 days. Photosynthesis and respiration both recovered more slowly than did the pigment ratios.

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

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

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

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

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

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

Li and Glime (1990), on the other hand, demonstrated an optimum growth temperature of 30-35ºC for clumps of *S. magellanicum* (Figure 20) and *S. papillosum* (Figure 23) from the Keweenaw Peninsula of Michigan, USA. Rydin (1984) found no temperature-tolerance differences among *Sphagnum* species from Europe. It is likely that the rate of drying differed among these studies so that moisture state may have contributed to the contrasting results, but geographic races may also have been involved in these distant populations. *Sphagnum fuscum* (Figure 21) responded to summer warming with enhanced length increment (42-62%) and greater biomass increase, while bulk density decreased (Dorrepall *et al*. 2004). Added snow in winter increased the biomass gain by 33%, but growth in length and bulk density did not change significantly. These changes suggest that not only is the health of the plant affected by temperature, but the structure and moisture-holding capacity are altered, potentially having a major impact on the ecosystem.

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

Biochemical Responses

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

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

Isoprene

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

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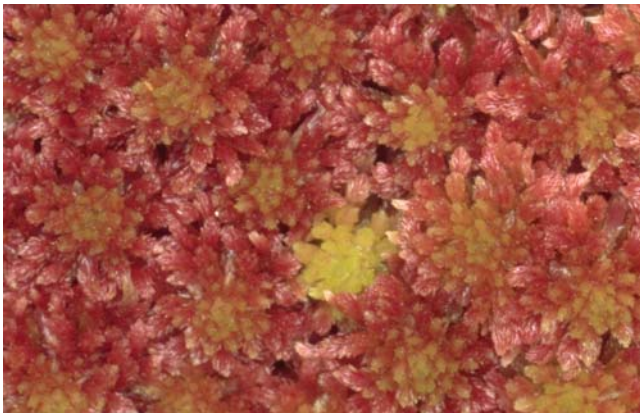

Figure 25. ***Sphagnum capillifolium***. Photo by Jan-Peter Frahm, with permission.

Sugars

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

Peroxidase

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

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

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

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

Heat Shock Proteins

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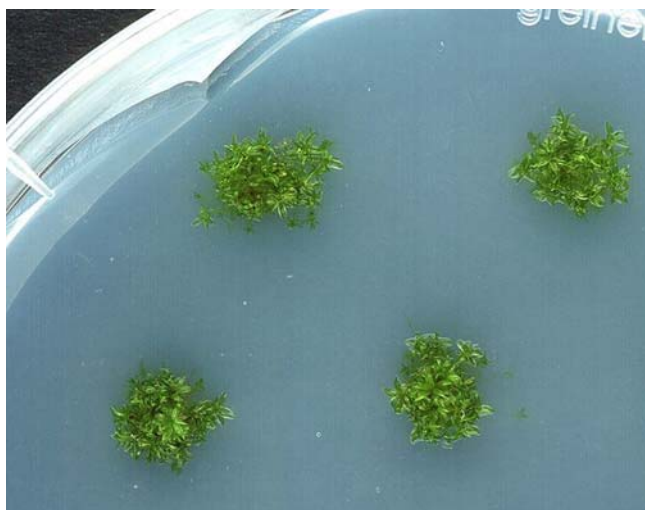

Figure 28. ***Physcomitrella patens*** culture where at least two heat shock proteins were revealed. Photo by Anja Martin in Ralf Reski Lab, through Wikimedia Commons.

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

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

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

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

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

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

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

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

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

Light vs Dark

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

Acclimation

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

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

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

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

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

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

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

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

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

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

Night Temperature

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

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

Hydration State

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

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

Table 1. Wet and dry 50% lethal temperatures (LT_{50} – ºC) for various mosses, based on Nörr 1974 and Kappen 1981.

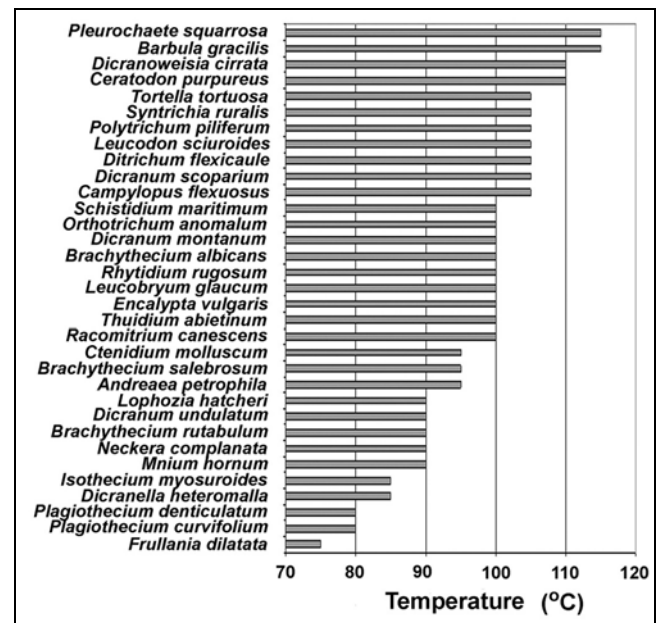|	wet	dry
Hylocomium splendens	43	91
Rhytidiadelphus loreus	42	92
Mnium hornum	44	99
Pleurozium schreberi	42	92
Hypnum cupressiforme	44	102
Dicranum scoparium	45	103
Racomitrium lanuginosum	48	105
Sphagnum capillifolium	46	
mosses	41-51	85-110
liverworts	39-45	70-110

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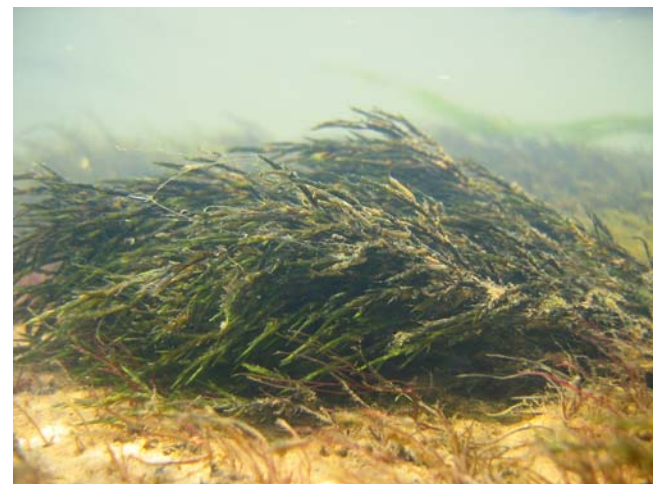

Figure 36. *Fontinalis novae-angliae*, a species in which some stem tissues survived being in intermittent boiling for more than one week. Photo by John Parker, with permission.

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

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

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

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

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

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

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

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

Figure 41. *Plagiochila asplenioides*, a species that exhibits plasmolysis when pretreated with a sugar solution and heated to 55°C, but exhibits loss of membrane integrity when pretreated with salt. Photo by Michael Lüth, with permission.
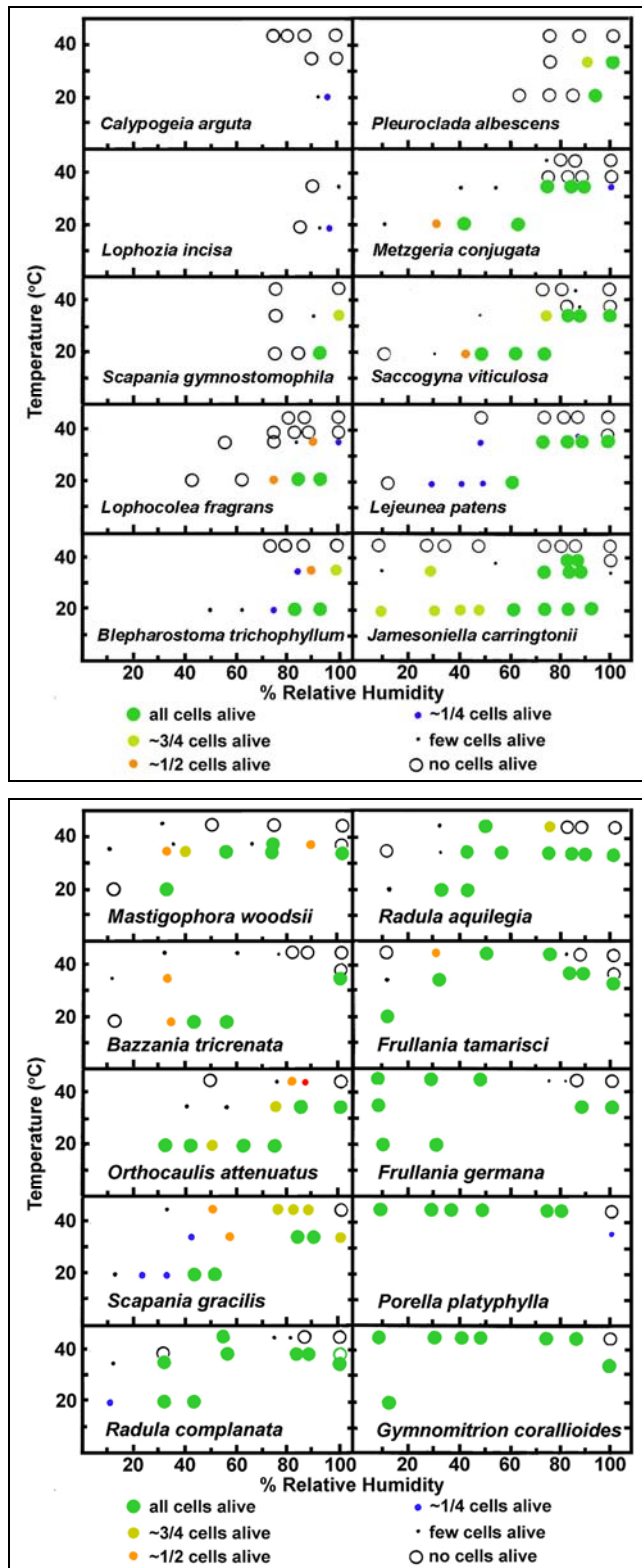
Figure 42. Effects of temperature and state of hydration on 20 leafy liverworts from Europe. Redrawn from Clausen 1964.

Duration

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

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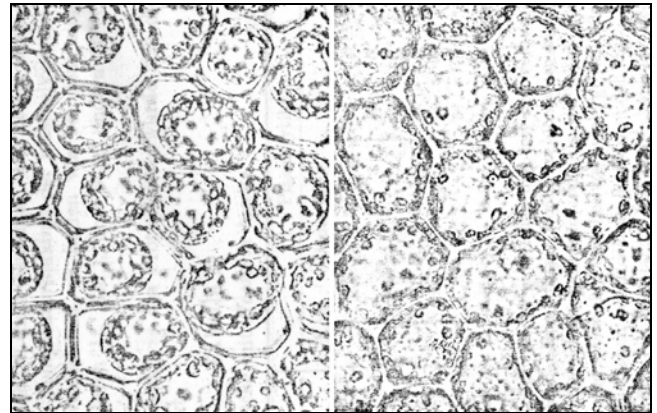

Figure 43. Leaf cells of ***Plagiochila asplenioides*** (Figure 41) demonstrating the effect of heat on desiccated cells. **Left:** Cells plasmolyzed, indicating intact membranes, in 2.5 M sugar solution at 55°C for 1.5 minutes. **Right:** Cells after 1.5 minutes at 55°C with no pretreatment in the salt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

Figure 44. ***Homaliodendron flabellatum***, a species that can tolerate temperatures up to 50ºC in water. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.
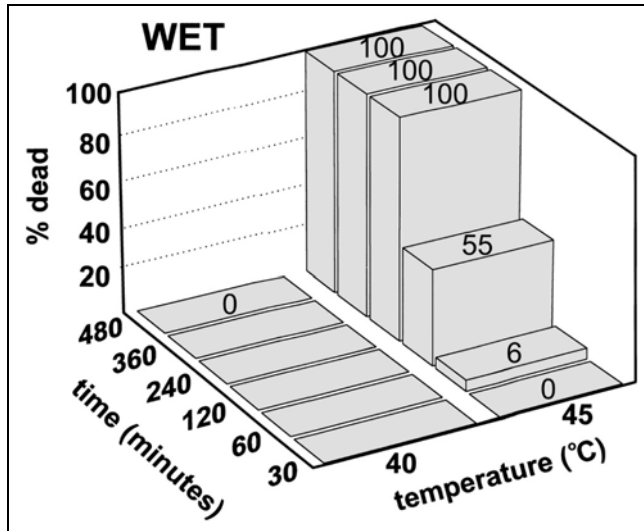
Figure 45. Effect of time on the lethality of temperature in *Plagiomnium acutum* (Figure 14). n=30. From Liu *et al.* 2004.

Age and Structure

In some cases, age is a factor in temperature tolerance of tissues, as shown for two **Plagiomnium** species in response to low temperatures, with mature tissues being more tolerant than young or senescent ones (Rütten & Santarius 1992, 1993). Yet there seems to be no effect of age on the lethal high temperature of **Plagiomnium acutum** (Figure 14) treated wet at 30-60°C for up to 240 minutes (Liu *et al.* 2004). Known cellular damage of high temperatures on bryophytes mainly includes destruction of the plasma membrane as evidenced by loss of electrolytes (Liu *et al* 2003), loss of differential permeability, chemical disorganization, and death of cells or tissue (Liu 20044), all factors where one might expect young and old tissues to respond differently. In studying **Plagiochila asplenioides** (Figure 41), Scheibmair (1938) did indeed find that young leaves survived better than older leaves. The older cells died, protoplasm became deformed, and the membrane and cytoplasm became colored. The young leaves survived up to 53°C for 10 hours, whereas the older leaves died after 6 hours at 48°C.

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

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

HP

Reversible Effects

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

Decomposition

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

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

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

Summary

Although the air temperature seldom exceeds 40ºC, bryophyte temperatures can reach 60-70ºC in some circumstances. Most bryophytes have a hydrated tolerance limit of 45ºC 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 25ºC, 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 50ºC, although *Fontinalis* stem tissue survived more than a week of intermittent boiling. Colors, evaporative cooling, and physical properties can alter the temperature of the growing region of a bryophyte, so air and substrate temperature data may not reflect tissue temperatures.

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

It appears that heat 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 100ºC. 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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