

CHAPTER 10-4

TEMPERATURE: SPECIES AND ECOSYSTEMS

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CHAPTER 10-4

TEMPERATURE: SPECIES AND ECOSYSTEMS



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

Species and Distributions

Importance of Climate

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

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

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



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



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

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

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



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



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

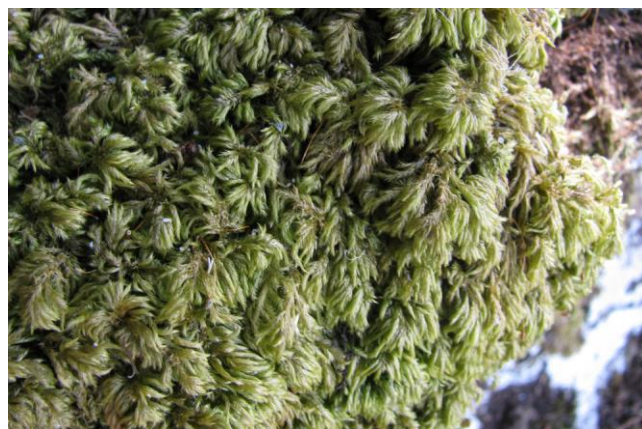


Figure 6. *Isoetecium myosuroides* near Swallow Falls, Wales, where warmer temperatures and sufficient moisture permit it to live. Photo by Janice Glime.



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



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



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



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



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



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



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



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



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

Warming Studies

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

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



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

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



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



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

Seasonal Fluctuations

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

Species Differences

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



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



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



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

Cryptic Species

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

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



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

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

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



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



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



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

Ecosystem Relationships

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

Altering Ecosystems

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

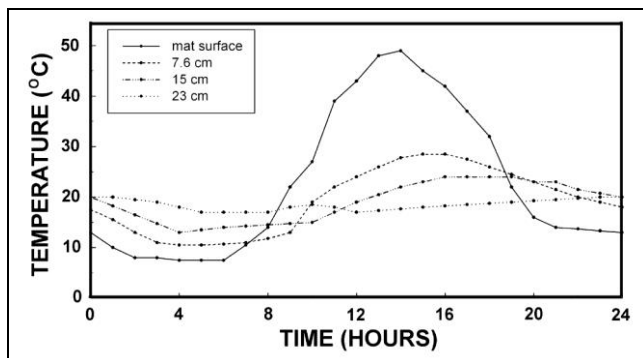


Figure 26. Effects of moss mat on soil temperature. Modified from Richardson 1958.

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

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

Disturbed Habitats

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



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

Grassland

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

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



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



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



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



Figure 31. *Lophocolea bidentata*, a species that decreased in the United Kingdom with winter warming. Photo from <www.aphtofauna.com>, with permission.

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



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

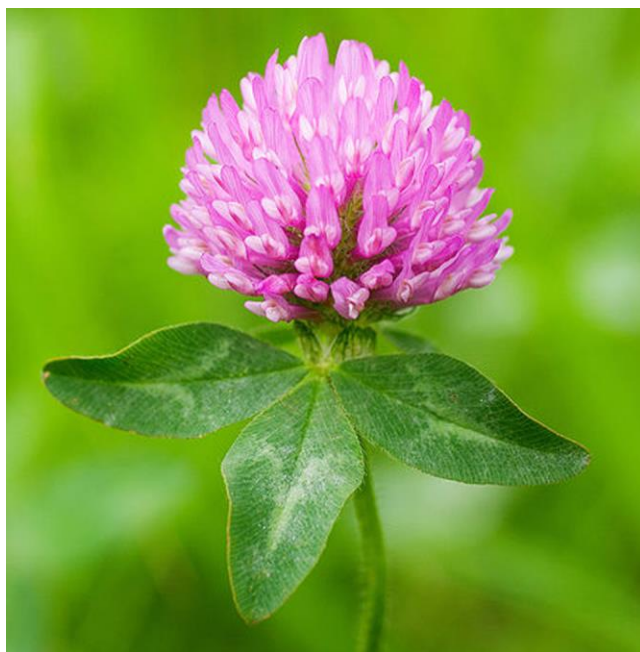


Figure 33. *Trifolium pratense*, a species that increases bryophyte cover in pots. Photo by Masaki Ikeda, through Creative Commons.



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



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



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



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

Tropics

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

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

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

Polar and Alpine

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

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



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



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



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

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



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



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

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



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



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

Predictions of the effects of warming on the cold tundra have varied from increasing productivity of the bryophyte heath to decreasing productivity, and from increasing CO₂ loss to the atmosphere to increasing it. Johnson *et al.* (1996) found that elevated temperature alone did not change the net CO₂ storage because losses of CO₂ from respiration were offset by gains in photosynthetic uptake. However, methane (CH₄) losses are temperature-dependent and could be a substantial source of transfer from carbon sinks to the atmosphere, further amplifying global warming. Such predictions are further complicated by the availability of water and the type of vegetation.

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



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



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

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



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



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

Lakes

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

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

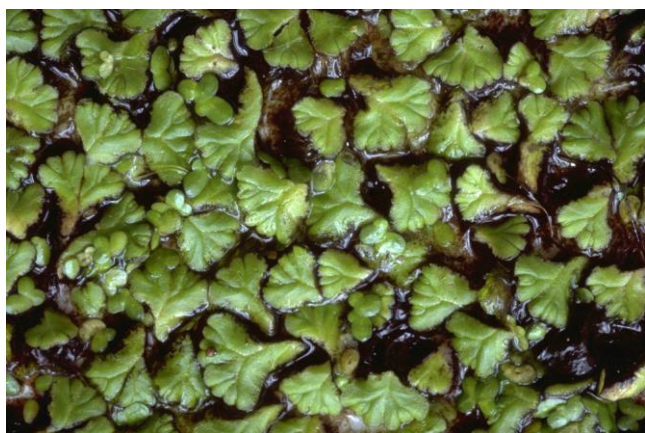


Figure 49. *Ricciocarpus natans*, a species that can survive winter in ice or under snow. Photo by Jan-Peter Frahm, with permission.



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

Streams

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



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

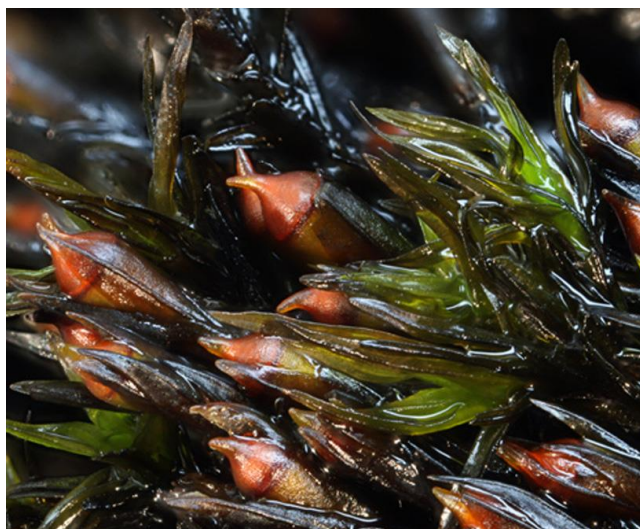


Figure 52. *Schistidium agassizii*, a species that recovers well from desiccation but is inhibited by high temperatures. Photo by Des Callaghan, with permission.



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



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



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

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

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

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



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

Peatlands

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



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



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



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



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



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

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

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

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



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

Summary

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

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

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

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

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

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

Acknowledgments

I appreciate the many photographers, and especially Michael Lüth, who have contributed to the images in this chapter.

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