

CHAPTER 7-10

WATER RELATIONS: SNOW ECOLOGY

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Figure 1. Late snowbeds in an alpine habitat in the Khibiny Mountains, Russia. *Bucklandiella microcarpum* is in the foreground. Photo by Michael Lüth, with permission.

Snow Effects

Snow can contribute in multiple ways to enhance the productivity. We know little about productivity of bryophytes under snow. What we do know is that light can penetrate snow, but that the light quality is altered. We know that snowmelt provides moisture, and that this melt can occur while the snow pack is still present, even in the middle of winter. We know that the snow can buffer the temperature, maintaining it close to 0°C. Dorrepall *et al.* (2004) demonstrated that *Sphagnum fuscum* (Figure 2) experienced an enhancement of 33% in productivity as a result of winter snow addition, while, nevertheless, not increasing growth in length.

Even in areas with considerable snow, bare areas exist, often as a result of winds that clear the snow. Some of these surfaces are rock surfaces that protrude, making them vulnerable to those wind movements of the snow (John 1990). One moss species capable of living in such exposed areas is *Grimmia longirostris* (Figure 3) in the Canadian Rocky Mountains.



Figure 2. *Sphagnum fuscum*, a moss that experiences greater productivity as a result of winter snow. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.



Figure 3. *Grimmia longirostris*, a species of exposed areas. Photo by Michael Lüth, with permission.

I have long suspected that at least some bryophytes are able to carry out photosynthesis under snow as long as it is not too deep for sufficient light penetration. Pannowitz *et al.* (2003) demonstrate that photosynthesis under the snow occurs in lichens. The snow cover provides effective insulation against the bitter cold of the Antarctic atmosphere, protecting both the mosses and the lichens. But in spring, this insulation proves to be detrimental. It retains the severe cold of winter and prevents the bryophytes from benefitting from the early warming of the air. This delay can last 10-14 days. Furthermore, the hydration provided to the lichens by the snow lasts only briefly once the snow disappears, providing only a brief period for photosynthetic activity. Is this same shortening of the photosynthetic period in effect for bryophytes, or are they able to retain the water longer?

In our study of the bryophytes on trees in the Keweenaw Peninsula of Michigan, USA, we found that those about 1 m above the ground were most common on the south sides of the trees (Trynoski & Glime 1982). We attributed this to a combination of winds from the north and sufficient light and moisture for these bryophytes to have photosynthesis in winter. Trees always have a narrow funnel of space between them and the snow (Figure 4). In this area where snow on the ground reaches a meter or more depth, the snow is an insulator. Dark-colored bark is able to absorb heat and the funnel remains somewhat humid. Light is able to penetrate. I have no measurements of growth or photosynthetic activity for these epiphytes – that needs to be done.



Figure 4. Snow-covered forest showing space between snow and tree trunk. Photo by Janice Glime.

Snow can affect the distribution of species. For example, in Japan *Bazzania trilobata* (Figure 5-Figure 7) grows on ground that is well drained all year and is typically sunny (Shirasaki 1987). *Bazzania yoshinagana* (Figure 8), on the other hand, grows on the forest floor in densely shaded coniferous forests. It spends its winter covered with deep snow that insulates it from freezing and provides it with moisture.



Figure 5. *Bazzania trilobata* habitat where it lives in well-drained locations. Photo by Dick Haaksma, with permission.



Figure 6. *Bazzania trilobata*, a species of well-drained locations. Photo by Michael Lüth, with permission.



Figure 7. *Bazzania trilobata* leaf cells showing spherical oil bodies that may help in surviving desiccation. Photo by Walter Obermayer, with permission.



Figure 8. *Bazzania yoshinagana*, a species of dense forest shade where it spends its winter under steep snow. Photo by Li Zhang, with permission.

Snowbed Communities

"Areas which experience prolonged snowlie and possess a distinctive bryophyte-dominated vegetation are termed snowbeds" (Woolgrave & Woodin 1996). Snowbeds (Figure 9) create their own unique characters. They shorten the growing season but can extend the period of hydration. Some bryophytes are dependent on these sources of hydration. On the Antarctic peninsulas the snow cover and site exposure seem to define the plant distribution (Melick *et al.* 1994).



Figure 9. Late snowbed at Bjoerndalen, Spitzbergen. Photo by Michael Lüth, with permission.

Snowbeds form in crevices and depressions in alpine regions (Figure 9). These are among the last areas to lose their snow, often near the end of the growing season. Nevertheless, some species grow only in these areas (Björk & Molau 2007). One such species that indicates a location with late snowbeds is the liverwort *Anthelia* (Figure 10), a genus whose fossils also indicate areas of late-lying snow in the late-Pleistocene landscape (Miller 1989). These snowbeds provide both a steady water supply and a steady nutrient supply to the adjacent plant communities. Because of this dependence, these communities are particularly vulnerable to climate warming.



Figure 10. *Anthelia juratzkana*, an indicator of late snowbeds. Photo by Hermann Schachner, through Creative Commons.

Many of the alpine bryophytes display adaptations that make their snowbed habitats tenable. *Andreaea nivalis* (Figure 11-Figure 12) is a reddish moss that hangs where snow water glides over the rocks and cliffs (Bailey 1933). Even its name (*nivalis*) means snow-covered. *Brachymerium erectum* (Figure 13) grows in snow water in alpine areas and disintegrates so rapidly after maturity that it is easy to miss it altogether. *Pohlia ludwigii* (Figure 14-Figure 15) lives in or near snow water. *Pohlia filum* (Figure 16) grows in snow water on the south side of Mount Rainier, Washington, USA, and produces brood bodies (Figure 17) in the snow water. *Polytrichastrum sexangulare* (Figure 18-Figure 20) likewise lives near the snow. Its setae begin to elongate before the snow is completely gone and as a result they become trailing and twisted (Figure 20). *Bryum muehlenbeckii* (Figure 21) has deep red leaves and stems, probably protecting it from UV radiation, and possibly increasing its temperature in its cold habitat near the snowbeds. *Pohlia wahlenbergii* var. *glacialis* (Figure 22-Figure 23), by contrast, has whitish leaves. On Mt. Rainier it covers large expanses that are wet with snow water. *Meiotrichum lyallii* (Figure 24) becomes visible at high elevations as soon as the snow disappears and is common on the higher slopes of Mt. Rainier. All of these bryophytes are acrocarpous mosses. Only *Isopterygiopsis pulchella* (Figure 25) is a pleurocarpous snow lover associated with these snowbeds. In all cases, it is likely that these bryophytes are non-competitors with tracheophytes and that take advantage of their C_3 photosynthesis to grow in the cold temperatures when adequate moisture is available.



Figure 11. *Andreaea nivalis* in its alpine habitat. Photo by Michael Lüth, with permission.



Figure 12. *Andreaea nivalis* in a location where it receives water that glides over rocks and cliffs. Photo by Michael Lüth, with permission.



Figure 15. *Pohlia ludwigii*, a moss that thrives in snowmelt water. Photo by Michael Lüth, with permission.



Figure 13. *Brachymerium* in India. *Brachymerium erectum* is short-lived in alpine snowbed runoff. Photo by Michael Lüth, with permission.



Figure 16. *Pohlia filum* growing in wet soil from snowmelt. Photo by Michael Lüth, with permission.



Figure 14. *Pohlia ludwigii* in its late snowmelt water habitat. Photo by Michael Lüth, with permission.



Figure 17. *Pohlia filum* showing the bulbils that are produced while it grows in snowmelt water. Photo by Michael Lüth, with permission.



Figure 18. *Polytrichum sexangulare* at alpine lake in Europe. Photo by Michael Lüth, with permission.



Figure 19. *Polytrichastrum sexangulare*, a late snowbed bryophyte. Photo by Martin Hutten, with permission.



Figure 20. *Polytrichastrum sexangulare* showing crooked and twisted setae from developing under snow. Photo by Michael Lüth, with permission.



Figure 21. *Bryum muehlenbeckii* in snowmelt water on rock. Note the red color, a common character of alpine bryophytes. Photo by Michael Lüth, with permission.

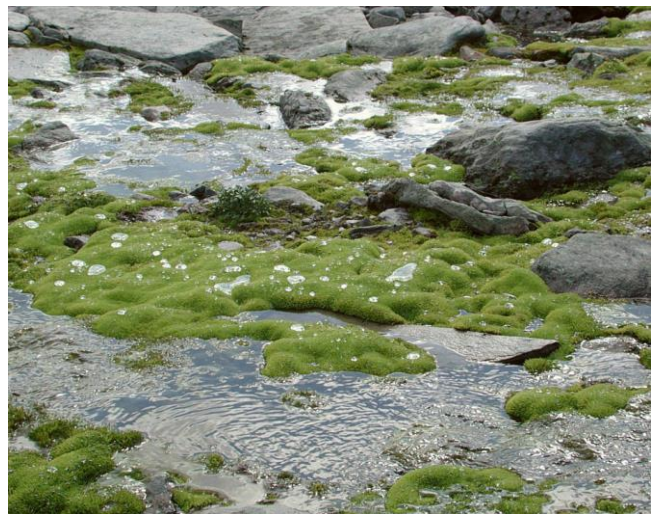


Figure 22. *Pohlia wahlenbergii* var. *glacialis* in its snowmelt habitat. Photo by Michael Lüth, with permission.



Figure 23. *Pohlia wahlenbergii* var. *glacialis*, a species that thrives in snow water. Photo by Michael Lüth, with permission.



Figure 24. *Meiotrichum lyallii* with capsules, looking somewhat flattened after snowmelt. Photo by Paul Wilson, with permission.



Figure 25. *Isopterygiopsis pulchella*, the only pleurocarpous moss living in late snowbeds on Mt. Rainier, USA. Photo by Jan-Peter Frahm, with permission.

In Scotland, some of these same species are dependent on the snowbeds (Rothero 2007). These include *Andreaea nivalis* (Figure 11-Figure 12), *Polytrichum sexangulare* (Figure 18-Figure 20), *Kiaeria falcata* (Figure 26-Figure 27), *Anthelia juratzkana* (Figure 10), and *Pohlia ludwigii* (Figure 14-Figure 15). Additionally, snowbeds in the UK are habitats for *Racomitrium heterostichum* (Figure 28), *Marsupella brevissima* (Figure 29-Figure 30), *Kiaeria starkei* (Figure 31), *Moerckia blyttii* (Figure 32), *Pleurocladula albescens* (Figure 33-Figure 34), *Marsupella arctica*, and *Marsupella condensata* (Figure 35). The flushes and mires resulting from melting snowbeds also support growths of *Pohlia wahlenbergii* var. *glacialis* (Figure 22-Figure 23), *Scapania paludosa* (Figure 36), and occasionally *Sphagnum riparium* (Figure 37) and *S. lindbergii* (Figure 38-Figure 39).



Figure 26. *Kiaeria falcata* habitat where snowbeds are important to this species. Photo by Michael Lüth, with permission.



Figure 27. *Kiaeria falcata*, a moss dependent on snowbeds. Photo by Michael Lüth, with permission.



Figure 28. *Racomitrium heterostichum*, a snowbed species. Photo by J. C. Schou, through Creative Commons.



Figure 29. *Marsupella brevissima* habitat. Photo by Michael Lüth, with permission.



Figure 33. *Pleuroclada albescens* in a snowmelt bed in Norway. Photo by Michael Lüth, with permission.



Figure 30. *Marsupella brevissima*, a snowbed liverwort. Photo by Jan-Peter Frahm, with permission.



Figure 34. *Pleuroclada albescens*, a snowbed liverwort. Photo by Michael Lüth, with permission.



Figure 31. *Kiaeria starkei* with capsules, a late snowbed moss. Photo by Rosemary Taylor, with permission.



Figure 32. *Moerckia blyttii*, a snowbed bryophyte. Photo by Michael Lüth, with permission.



Figure 35. *Marsupella condensata*, a species that lives in snowbeds in the UK. Photo by Andrew Hodgson, with permission.



Figure 36. *Scapania paludosa*, a species that benefits from snowmelt flushes. Photo by Michael Lüth, with permission.



Figure 37. *Sphagnum riparium*, a species sometimes found in late snowbeds. Photo by Jan-Peter Frahm, with permission.



Figure 38. *Sphagnum lindbergii* where it gains water from spring flushes. Photo by Michael Lüth, with permission.



Figure 39. *Sphagnum lindbergii*, a species that sometimes benefits from snowbed water. Photo by Michael Lüth, with permission.

In snowbeds, more than 40% of the cover is often comprised of bryophytes (Jägerbrand 2011). This may be as little as 3% of the exposed area during early melt to 80% in the late-melting areas. Björk (2007) found 26 species that grow mostly in snowbeds, 13 of which are found only in those areas. In a late snowbed in western Newfoundland, Canada, Belland (1983) found some of the same species associations as named above for the UK. In particular, *Andreaea nivalis* (Figure 11-Figure 12) was common in late snowbeds. Belland found 49 bryophyte species in the eight late snowbeds he investigated. Other dominant species included *Kiaeria falcata* (Figure 26-Figure 27), *Moerckia blyttii* (Figure 32), and a species of *Trematodon* (Figure 40). The uniqueness of this habitat is demonstrated by the disjunct distribution for 13 of these species between western and eastern North America. Eleven of the species are characteristic of snowbed habitats throughout most of the world.



Figure 40. *Trematodon longicollis*, in a genus represented in snowbeds in Newfoundland, Canada. Photo by Michael Lüth, with permission.

The unique combination of temperature regime and moisture support some of the rare species of the world. On Mt. Washington, New Hampshire, USA, Slack *et al.* (2013) found *Haplomitrium hookeri* (Figure 41), *Aulacomnium turgidum* (Figure 42-Figure 44), *Dicranum elongatum* (Figure 43), and *Pseudocalliergon trifarium* (Figure 45) – all rare species in the northeastern USA.



Figure 41. *Haplomitrium hookeri* in a late snowbed in Wales. Photo by Janice Glime.



Figure 44. *Aulacomnium turgidum*, a rare species that survives on Mt. Washington, New Hampshire, USA. Photo by Michael Lüth, with permission.



Figure 42. *Aulacomnium turgidum* in an alpine area of Norway. Photo by Michael Lüth, with permission.



Figure 43. *Dicranum elongatum*, a rare species on Mt. Washington, NH, USA. Photo by Hermann Schachner, through Creative Commons.



Figure 45. *Pseudocalliergon trifarium*, a rare species that survives the harsh climate on Mt. Washington, NH, USA. Photo by Andrew Hodgson, with permission.

Growth Form Variability

Snowbeds can create unusual growth forms. For example, in the high Arctic of Spitsbergen, the fellfield type of *Sanionia uncinata* (Figure 46-Figure 48) had few branchless shoots and formed dense colonies, leading to better desiccation avoidance (Ueno *et al.* 2001). The snowbed type had many branchless shoots and more sparse colonies. Furthermore, there were fewer branches in the upper part of the shoot than in the lower part in the snowbeds. Was this a response to the snow, possibly damaging branch buds, or was the more dense branching in the fellfield an adaptation selected to permit survival in the drier climate there?



Figure 46. *Sanionia uncinata* alpine habitat in Europe. Photo by Michael Lüth, with permission.



Figure 47. *Sanionia uncinata* with capsules in runoff area. Photo by Michael Lüth, with permission.



Figure 48. *Sanionia uncinata* with capsules and showing pinnate growth form. Photo by Michael Lüth, with permission.

The multiple growth forms of some species in the Antarctic seem to be a response to submersion (Seppelt & Selkirk 1984). For example, *Bryum pseudotriquetrum* (Figure 49-Figure 50) was originally named as *Bryum algens* there due to its different growth form. *Calliergon sarmentosum* (Figure 51-Figure 52) assumes a different morphology when shoots develop under water or in damp conditions (Priddle 1979). *Bryum argenteum* (Figure 53-Figure 54) in the Antarctic assumes longer and narrower leaves with increased cell size in etiolated shoots (Longton 1981; Seppelt & Selkirk 1984), perhaps due to submersion,

or possibly due to growth in the reduced light under snow. *Ceratodon purpureus* (Figure 55-Figure 60) lives in shallow lakes in the Antarctic and was originally known as *Ceratodon minutifolius* there, differing in leaf shape and leaf apex (Horikawa & Ando 1963; Seppelt & Selkirk 1984).



Figure 49. *Bryum pseudotriquetrum* in the Antarctic, a moss with many growth forms. Photo courtesy of Catherine Beard.



Figure 50. *Bryum pseudotriquetrum* beside a stream, showing a typical growth form in the North Temperate Zone. Photo by Michael Lüth, with permission.



Figure 51. *Calliergon sarmentosum* mountain habitat in Europe. Photo by Michael Lüth, with permission.



Figure 52. *Calliergon sarmentosum* aquatic growth form. Photo by Michael Lüth, with permission.



Figure 53. *Bryum argenteum* from the Neotropics, exhibiting the broader leaves typical there. Photo by Michael Lüth, with permission.

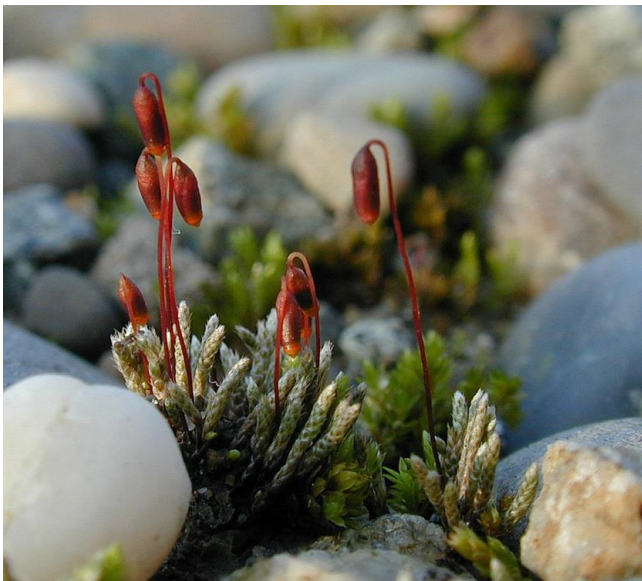


Figure 54. *Bryum argenteum* from alpine area in Europe where it exhibits longer, narrower leaves than plants from the tropics. Photo by Michael Lüth, with permission.



Figure 55. *Ceratodon purpureus* in Antarctica. Photo by Rod Seppelt, with permission.



Figure 56. *Ceratodon purpureus* in Antarctica. (Blackish mosses at right are *Bryum pseudotriquetrum*.) Photo by Rod Seppelt, with permission.



Figure 57. Submerged *Ceratodon purpureus* in the Antarctic. Bubbles from photosynthesis here create a condition known as **pearling**. Photo courtesy of Rod Seppelt.



Figure 58. Open growth of well-hydrated *Ceratodon purpureus*. Photo by Michael Lüth, with permission.



Figure 59. Cushions of *Ceratodon purpureus* in the mountains of Norway. Photo by Michael Lüth, with permission.



Figure 60. *Ceratodon purpureus* dry among rocks in Michigan, USA. Photo by Janice Glime.

Duration of Snowbeds

The duration of the snowbeds separates communities in Scotland (Woolgrove & Woodin 1994). Prolonged

snowlie has negative effects on the *Marsupella-Anthelia* community (Figure 29-Figure 30, Figure 35; Figure 10). On the other hand, the *Polytrichum-Kiaeria* (Figure 18-Figure 20; Figure 26-Figure 27) community is positively affected by its prolongation. *Pohlia* (Figure 14-Figure 16, Figure 22-Figure 23) seems less affected by the duration, but the substrate moisture content is important for it.

Snowmelt

Kaiser (1921) describes his "journey into mossland" during a February thaw in Pennsylvania, USA. So many mosses appeared, bright green, and ready to grow. These winter survivors, especially along streambanks, included *Plagiomnium cuspidatum* (Figure 61-Figure 62), *Leucobryum glaucum* (Figure 63-Figure 67), *Bryoandersonia illecebra* (Figure 68-Figure 69), *Dicranum scoparium* (Figure 70-Figure 71), *Plagiomnium ciliare* (Figure 72), *Rhizomnium punctatum* (Figure 73), *Conocephalum conicum* (Figure 74), *Marchantia polymorpha* (Figure 75), *Pellia epiphylla* (Figure 76), *Atrichum* (Figure 77), *Dicranella* (Figure 78), *Pohlia nutans* (Figure 79-Figure 80), and *Bartramia pomiformis* (Figure 81-Figure 82), among others, all benefitting from the snowmelt moisture.



Figure 61. *Plagiomnium cuspidatum* hydrated, a moss that survives snow cover to regain photosynthesis in spring. Photo by Hermann Schachner, through Creative Commons.



Figure 62. *Plagiomnium cuspidatum* dry. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 63. *Leucobryum glaucum* on edge of crevice where it escapes the leaf litter. This site benefits from runoff, but can also suffer exposure. Photo by Janice Glime.

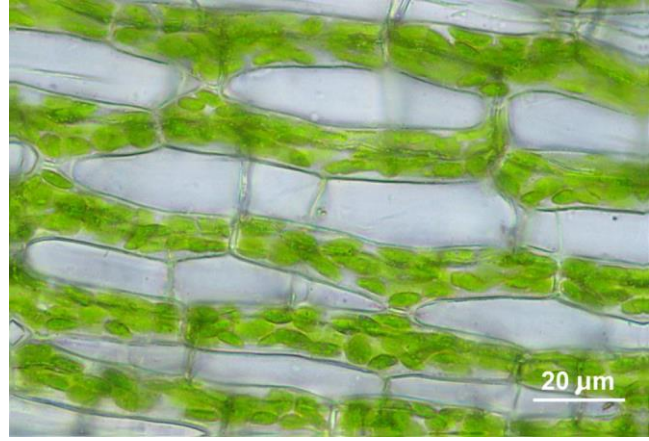


Figure 66. *Leucobryum glaucum* showing photosynthetic and hyaline leaf cells. Photo by David Wagner, with permission.



Figure 64. *Leucobryum glaucum*, one of the mosses that is ready to photosynthesize when the snow melts. Photo courtesy of Eileen Dumire.



Figure 67. *Leucobryum glaucum* leaf cross section showing photosynthetic and hyaline cells. Photo by Walter Obermayer, with permission.



Figure 65. *Leucobryum glaucum* showing the whitish color due to hyaline cells that help to keep the photosynthetic cells hydrated. Photo by Janice Glime.



Figure 68. *Bryoandersonia illecebra*, a moss that one can find when the snow melts in Ohio, USA. Photo by Bob Klips, with permission.



Figure 69. *Bryoandersonia illecebra* on tree, a species of vertical surfaces. Photo by Bob Klips, with permission.



Figure 70. *Dicranum scoparium* in early autumn, a moss that overwinters and looks bright when the snow melts. Photo by Janice Glime.



Figure 71. *Dicranum scoparium* with capsules. Photo by Michael Lüth, with permission.



Figure 72. *Plagiomnium ciliare* with antheridia, a moss that overwinters and is ready to grow when the snow leaves. Photo by Robert Klips, with permission.



Figure 73. *Rhizomnium punctatum* looking etiolated after its winter snow cover. Photo by Michael Lüth, with permission.



Figure 74. *Conocephalum conicum*, a liverwort that is active in early spring. Photo by Janice Glime.



Figure 75. *Marchantia polymorpha* with gemmae cups, a liverwort that is active when the snow melts. Photo by David T. Holyoak, with permission.



Figure 78. *Dicranella heteromalla*, a soil bank moss that is ready to grow when the snow melts. Photo by Michael Lüth, with permission.



Figure 76. *Pellia epiphylla* in the mountains of Wales. Photo by Janice Glime.



Figure 79. *Pohlia nutans* at snowmelt time in the Khibiny Mountains, Russia. Photo by Michael Lüth, with permission.



Figure 77. *Atrichum undulatum* in snow, a species that has a distinct increase in cold tolerance from summer to winter and is ready for photosynthesis when the snow melts. Photo by Michael Lüth, with permission.



Figure 80. *Pohlia nutans*, one of the first plants to be seen in spring. Photo by Michael Lüth, with permission.



Figure 81. *Bartramia pomiformis* in its typical cliff-hanger habitat. Photo by Janice Glime.



Figure 82. *Bartramia pomiformis*, a moss that is green in early spring. Photo by Michael Lüth, with permission.

Gaberščik and Martinčič (1987) demonstrated seasonal changes in growth of *Sphagnum papillosum* (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing season, a time when water is usually plentiful. During winter months, the photosynthetic activity declines and ceases completely in February.



Figure 83. *Sphagnum papillosum* on exposed rock where it can benefit from spring snowmelt runoff. Photo by Michael Lüth, with permission.



Figure 84. *Sphagnum papillosum* in a flush created by melting snow. This one is still wet in late July in the mountains of Wales. Photo by Janice Glime.



Figure 85. *Sphagnum papillosum*, shown here with sundews. This *Sphagnum* species has seasonal changes in growth, with photosynthetic activity declining in winter in Yugoslavia. Photo by Michael Lüth, with permission.

One restoration technique in peat-mined bogs in Canada has been an attempt to enhance the moisture content (Rocheffort *et al.* 2002). To do this, *Sphagnum* (Figure 83-Figure 85) is reintroduced in the restoration areas and may be covered by extended periods of flooding, especially following snowmelt or heavy rainfall. These flooding events can cause production of **innovations** in which the buds and shoots grow. Some species grow **capitula** (compact apical branches of *Sphagnum*) from fragments under a variety of conditions. The most species in their study grew from whole plants under long-term conditions of shallow flooding. However, many of the species under long-term flooding suffered from **etiolation** (condition of plants grown in partial or complete absence of light, characterized by long, weak stems and smaller, sparser leaves).

In the Niigata Prefecture of Japan, the floating liverwort *Ricciocarpos natans* (Figure 86) is common in cultivated rice fields (Shirasaki 1996). It grows best where there are warmer temperatures and a snow depth of 0.5-3.0 m.

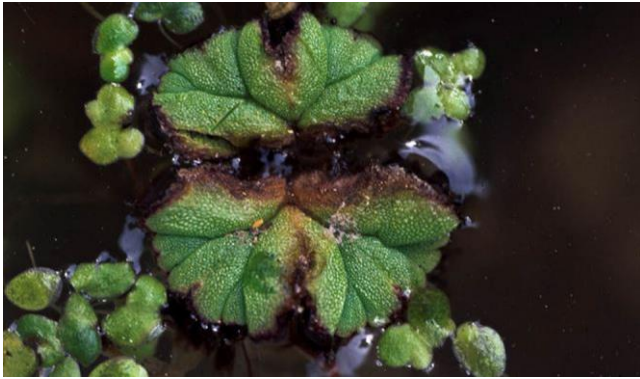


Figure 86. *Ricciocarpus natans* with duckweed. Photo by Martin Hutten, with permission.

In western Norway, *Andreaea rupestris* (Figure 87-Figure 89) occurs along the flushing gradients created by snowmelt or is associated with snow cover (Hedger 2001). Species in the alpine areas of Norway are sensitive to the timing of snowmelt. In 43 sampled transects, 22 of the 41 taxa show a significant relationship to the time of snowmelt as the altitude increases. But these relationships are not necessarily direct responses to the temperature or water. Rather, at least some of them avoid locations of earlier snowmelt because of competition from other plants, especially tracheophytes.



Figure 87. *Andreaea rupestris* in the Khibiny Mountains of Russia in an area with snowmelt water and late snowbeds. Photo by Michael Lüth, with permission.



Figure 88. *Andreaea rupestris* with capsules, a species that grows in areas of late snowmelt. Photo by Des Callaghan, with permission.

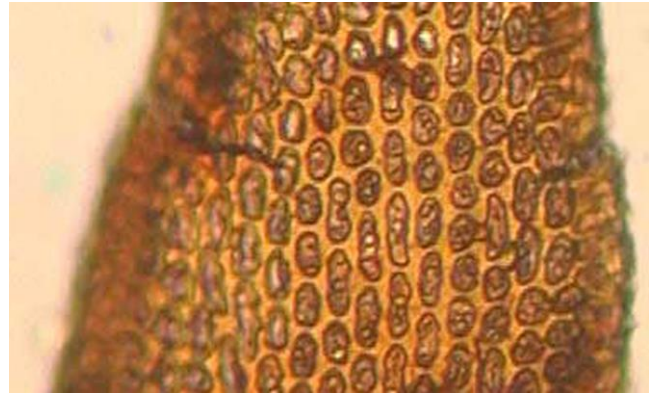


Figure 89. *Andreaea rupestris* leaf showing thick, pigmented cell walls that may help to protect the cell contents from cold temperatures and high UV light. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

Snowbed bryophytes must utilize low light and short growing seasons with low temperatures to attain sufficient photosynthesis for carbon gain. *Anthelia* (Figure 10) does especially well in the border zone of snowbeds because of its resistance to long-lasting cold, wet, and dark conditions (Lösch *et al.* 1983). *Polytrichastrum sexangulare* (Figure 18-Figure 20), on the other hand, is more productive and is therefore able to compete with the tracheophytes at less extreme sites.

Mechanical Effects

Snow has its down side for plants. The sheer weight can crush or break the plants. So how do tiny plants like bryophytes fare under this weight? Kennedy (1993) commented on how few studies have included the biomechanics of bryophytes, reminding us of their need for snow cover resistance.

Among the mosses receiving the greatest mechanical stress due to height is *Dendroligotrichum dendroides* s.l. This moss stands alone, supporting a height up to 40 cm where it lives in the forests of Chile and New Zealand. For this species, the dense hypodermal sterome provides considerable stiffness comparable to that of woody stems of tracheophytes. But for many smaller mosses, such support is usually not needed. Rather, the mosses of various habitats have a wide range of mechanical conformations. By contrast, size, development, and phylogenetic position seem to be less important than the habitat in determining growth form and mechanical adaptations.

Freeze-thaw Cycles

Free-thaw cycles can have some of the same damaging effects as dehydration-rehydration. And like many other epiphytes that tolerate the wet-dry cycles, the rock face and tree-trunk-dwelling *Leucodon sciurioides* (Figure 90) in the Mediterranean tolerates freezing and thawing with its photosynthetic apparatus fully operational after freezing (Deltoro *et al.* 1999). Both CO₂ fixation and chlorophyll fluorescence return to pre-freezing values during thawing. And like many desert mosses, it recovers its photosynthesis rapidly during thawing. Deltoro and coworkers suggest that this rapid recovery is possible through dissipative pathways that absorb excess light energy in frozen plants.



Figure 90. *Leucodon sciurioides* on tree bark, a species that tolerates freezing and is ready for photosynthesis as soon as it thaws. Photo by Michael Lüth, with permission.

Melick and Seppelt (1992) experimented with up to 16 freeze-thaw cycles in Antarctic bryophytes. After 16 days of immersion in water, there is a relatively low loss of glucose and fructose [10-29% of the total sugar pool in healthy mosses, but 69% from the dead *Schistidium chrysoneurum* (= *Grimmia antarctici*; Figure 91-Figure 92)]. Freeze-thaw cycles increase this leakage up to 2-3 times except in the dead mosses. *Bryum pseudotriquetrum* (Figure 49-Figure 50) lost 65% of its total sugar when subjected to 16 freeze-thaw cycles. The other species [*Ceratodon purpureus* (Figure 55-Figure 60, Figure 92), *Schistidium chrysoneurum*, *Cephaloziella exiliflora* (Figure 93)] lost less than 28%. This loss does not seem to be related to the freezing temperature.



Figure 91. *Schistidium chrysoneurum* in the Antarctic. Photo by Rod Seppelt, with permission.



Figure 92. *Schistidium chrysoneurum* hummock with *Ceratodon purpureus* in the hollows. Photo by Rod Seppelt, with permission.



Figure 93. *Cephaloziella* sp. *Cephaloziella exiliflora* loses some of its stored sugar during freeze-thaw cycles. Photo by Kristian Peters, with permission.

Schlensog *et al.* (2004) compared the recovery of lichens and mosses after winter in the continental Antarctic. Whereas the lichens recover **photosystem II** (PS II, first protein complex in light-dependent reactions of oxygenic photosynthesis; it captures photons of light to energize electrons) almost fully within a few minutes of hydration, the mosses take much longer to recover. The moss *Bryum subrotundifolium* (Figure 94-Figure 96) maintains highly elevated respiration rates for several days following activation. Like the response to desiccation, it appears that this moss must repair damages before it can make a positive photosynthetic gain.



Figure 94. Bed of *Bryum subrotundifolium* in meltwater on Antarctica. Photo by Rod Seppelt, with permission.



Figure 95. *Bryum subrotundifolium*, a moss that maintains high respiration rates for several days following rehydration. Photo by Rod Seppelt, with permission.



Figure 96. *Bryum subrotundifolium* in the Antarctic infected with a fungus that is taking advantage of suitable moisture conditions. Photo by Catherine Beard, with permission.

Freeze-thaw protection can be conferred on bryophytes by various compounds present prior to freezing (Rütten & Santarius 1993). In *Plagiomnium affine* (Figure 97) the uptake and release of sucrose does little to change the permeability of the leaf cell plasma membranes to sugars, **proline** (amino acid), or polyethylene glycols. However, pretreatment with these compounds sufficient to induce plasmolysis does protect the moss cell membranes from freeze-thaw damage. On the other hand, pretreatment with **glycerol** (compound that is soluble in water and is hygroscopic) causes **plasmolysis** (shrinking of cell membrane away from cell wall) without endowing the cells with protection against freeze-thaw damage.



Figure 97. *Plagiomnium affine*, a moss protected from freeze-thaw damage by various compounds and plasmolysis. Photo by Michael Lüth, with permission.

Winter Short-term Warming Events

Noting that climate change in northern high latitudes is likely to be greater in winter than in summer, Bjerke *et al.* (2011) examined the potential effects of more frequent short-term warming events. Whereas these warming event effects are known to be damaging to tracheophytes, their effect on bryophytes could be quite different. And the bryophytes and lichens are of major importance in these

high-latitude ecosystems. By simulating winter warming events with infrared lamps and soil warming cables in a sub-Arctic heath, Bjerke *et al.* were able to monitor the responses of the feather moss *Hylocomium splendens* (Figure 142). In the three winters of simulated warming events, this moss experienced significant reductions in net photosynthetic rates and growth rates (of up to 48% and 52%, respectively), starting in the first summer after these events began. In this species, growth begins early in the spring season, exposing young, vulnerable shoots to the effects of cold. The researchers suggest that the damage under winter warming events may be due to breaking dormancy and experiencing premature growth during the winter warming events that causes damage to those sensitive young shoot tissues. Subsequent drying following these events may cause desiccation damage to the tender shoots.

These winter warming events could change the distribution of acrocarpous vs pleurocarpous mosses in areas with winter snow cover. In the Front Range of the Rocky Mountains, USA, Flock (1978) found that acrocarpous mosses are more abundant in areas that are dry and maintain light snow cover. Pleurocarpous mosses, on the other hand, are more abundant in wet sites with deep snow cover.

As Longton (1988) has pointed out, bryophytes in general have phenotypic plasticity, opportunistic responses in CO₂ exchange, and a poikilohydrous water relationship that endows them with considerable tolerance for desiccation and frost. These make it possible for them to occupy snowbeds where few tracheophytes can succeed.

Protection from Light Damage

A potentially serious problem for desiccated mosses at low temperatures is that they are still able to absorb light energy. This can be a special problem for forest epiphyte species that experience more light exposure in winter, compared to summer, when the tree canopy has lost its leaves. Particularly on those cold days that lack snow cover, over excitation of chlorophyll electrons can be damaging. However, Heber *et al.* (2006) report that some mosses have seasonal differences in their ability to dissipate that excess light energy into heat.

Freezing and thawing can result in photoinhibition, as demonstrated by the endemic moss *Schistidium chrysoneurum* (Figure 91) from the Antarctic (Lovelock *et al.* 1995a). Jägerbrand (2011) considered the time immediately following snowmelt to be the most dangerous time for UV damage to bryophytes. Rehydration, lingering low temperatures, and rising UV levels coincide with a time when bryophytes must repair the damage due to absence of light and desiccation from winter. This is especially problematic in the Antarctic where the ozone layer is thinning. Fortunately, this highly variable photoinhibition is reversible during periods of warmer temperatures (Lovelock *et al.* 1995a). The inhibition that occurs between freezing and thawing events recovers best under low light conditions. After four cycles, recovery of hydrated mosses occurred within 12 hours of transfer to 5°C at 15 μmol quanta m⁻² s⁻¹.

During the dry summers, some desiccation-tolerant mosses are more protected against photo-oxidative damage when they are dry than they are in the humid winters (Heber *et al.* 2006). In mosses such as the **poikilohydric** *Rhytidiadelphus squarrosus* (Figure 98), desiccation reduction of chlorophyll fluorescence does not occur under even strong illumination in the desiccated state once the moss has achieved phototolerance. One protectant is **zeaxanthin** (one of the most common carotenoid alcohols and a powerful antioxidant), which requires drying in light. If the water is lost slowly, fluorescence is quenched. Quenchers accumulate during desiccation and remain stable until hydration occurs. Hydration results in their reversion to non-quenching molecules.



Figure 98. *Rhytidiadelphus squarrosus*, a moss that requires drying to induce protection (zeaxanthin) against photoquenching. Photo by Michael Lüth, with permission.

Lovelock and Robinson (2002) found that surface reflective properties of leaves also plays a role in dissipating the light, hence protecting the plants from light damage. They suggested that the water content, but not pigments, of the mosses are important in altering the red-edge and photochemical reflectance index. The water content may account for the differences in reflectance among the species. All the mosses maintain high levels of xanthophyll pigments that serve as photoprotectants. Interestingly, their abilities to reflect UV light differs little. *Bryum pseudotriquetrum* (Figure 49-Figure 50) has greater reflective values than the other mosses studied and also has higher levels of UV-absorbing pigments, but its carotenoid levels are lower than the other species tested. *Ceratodon purpureus* (Figure 55-Figure 60) has higher levels of anthocyanins but lower total chlorophyll concentrations. *Bryum pseudotriquetrum* has higher levels of the specific UV-screening pigments; *Ceratodon purpureus* and *Schistidium chrysoneurum* (Figure 91) have higher levels of pigments that protect against excess visible light.

For *Schistidium chrysoneurum* (Figure 91), freezing in darkness reduced the F_v/F_m ratio (ratio of variable:maximum fluorescence) and the initial fluorescence (Lovelock *et al.* 1995b). These were reversible when the mosses thawed. The reduction of

F_v/F_m may be the result of conformational changes in the pigment-protein complexes due to the desiccation that occurs during freezing. The photoinhibition during freezing is reversible and indicates that processes that protect the moss from photoinhibitory damage during freezing temperatures occur in consort with high solar radiation levels. These protections therefore limit the repair needed when favorable temperatures return.

Winter Growth

Proctor (2000) points out that bryophytes have a desiccation tolerance strategy that differs from that of tracheophytes. Bryophytes are able to survive because they can photosynthesize and grow when water is freely available, then suspend their metabolism when it is not. By being **ectohydric** (conducting water externally), many species can have wide variability in their external capillary water without affecting the water content of the cells. This external source permits the cells to function most of the time with full turgor. When they do desiccate, the period of water stress is brief. They have a carbohydrate content that is similar to that of the maturing embryos of desiccation-tolerant seeds. It is likely that these carbohydrates contribute to their rapid recovery upon rehydration. In short, they mimic temperate winter annuals or mesic desert ephemerals. For example, in the maritime climate of Britain, the wall top moss *Grimmia pulvinata* (Figure 99) takes advantage of the mild climate of autumn and early winter for most of its growth (Proctor 2004). During that period the moss is able to maintain hydration for long periods of time to carry out photosynthesis. Like many mosses, it is adapted to frequent and often short wet-dry cycles.



Figure 99. *Grimmia pulvinata* on rock where it grows mostly in autumn and early winter when it is well hydrated frequently. Photo by Michael Lüth, with permission.

Even growth rates seem to adjust to differences in temperature, perhaps because of differences in available moisture, perhaps just to acclimation (see Fornwall & Glime 1982). For example, *Brachythecium rutabulum* (Figure 100) has superior growth in winter compared to summer when grown at temperatures below 18°C (Furness & Grime 1982). Most species of temperate regions seem to have their optimum growth temperature at 15-25°C, but growth can be extensive at temperatures even below 10°C. Gaberšček and Martinčič (1987) demonstrated seasonal changes in growth of *Sphagnum papillosum* (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing

season, a time when water is usually plentiful. During winter months, the photosynthetic activity declined and ceased completely in February.



Figure 100. *Brachythecium rutabulum* on *Populus x canadensis* log, emerging from the snow. Photo by Pim Rijke, through Wikimedia Commons.

Asada *et al.* (2003) found that winter growth of a number of bryophyte species [*Racomitrium lanuginosum* (Figure 101-Figure 103), *Pleurozium schreberi* (Figure 104), *Sphagnum austinii* (Figure 105-Figure 106), *S. fuscum* (Figure 2), *S. rubellum* (Figure 107-Figure 108), *S. papillosum* (Figure 83-Figure 85), *S. lindbergii* (Figure 38-Figure 39), *S. tenellum* (Figure 109-Figure 110), *S. pacificum* (Figure 111)] in a coastal peatland in British Columbia, Canada, is an important contribution to the productivity of the system. But for this productivity to occur, water must be available during those times when the temperature permits photosynthesis to occur. Asada further supported the importance of water by demonstrating that productivity in these species correlated more strongly with precipitation than with temperature.

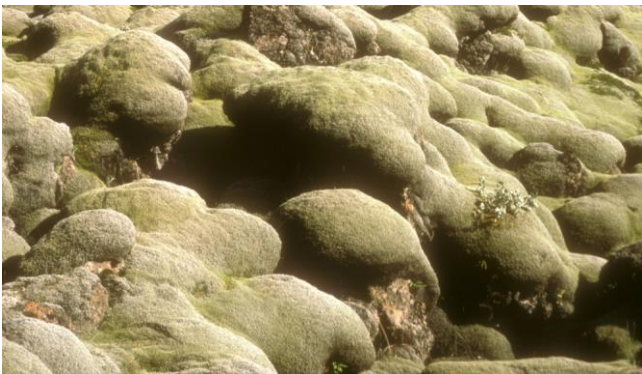


Figure 101. *Racomitrium lanuginosum* forming massive hummocks in Iceland. Photo by Janice Glime.



Figure 102. *Racomitrium lanuginosum* forming hummocks that benefit from late season snowmelt water. Photo by Michael Lüth, with permission.



Figure 103. *Racomitrium lanuginosum*, a species that has winter growth in coastal wetlands. Photo by Juan Larrain, with permission.



Figure 104. *Pleurozium schreberi*, a moss that can tolerate frequent wet-dry cycles and grows best in the seasons with the best hydration. Photo by Janice Glime.



Figure 105. *Sphagnum austinii* wetland habitat. Photo by Michael Lüth, with permission.



Figure 106. *Sphagnum austinii* with a sundew that shares its habitat. Photo by Michael Lüth, with permission.



Figure 107. *Sphagnum rubellum* wetland habitat. Photo by Michael Lüth, with permission.



Figure 108. *Sphagnum rubellum*, a species that benefits from winter growth in coastal peatlands. Photo by Michael Lüth, with permission.



Figure 109. *Sphagnum tenellum* showing its very wet habitat that permits it to take advantage of late season photosynthesis. Photo by Michael Lüth, with permission.



Figure 110. *Sphagnum tenellum*, a moss that can benefit from winter photosynthesis. Photo by Michael Lüth, with permission.



Figure 111. *Sphagnum pacificum*, a moss that takes advantage of late season photosynthesis. Photo by Vita Plasek, with permission.

Growth can actually occur at sub-zero temperatures. *Brachythecium geheebii* (Figure 112) and *Homalothecium philippeanum* (Figure 113-Figure 114) in Romania montane areas are able to assimilate CO₂ down to -9°C (Atanasiu 1971). *Isoetecium alopecuroides* (Figure 115-Figure 116) had net gain down to about -8°C. Both of these temperatures are lower than those for evergreen trees tested in winter. But not all bryophytes are created equal. Davey and Rothery (1996) found that in *Brachythecium austrosalebrosum* from the Antarctic, respiration rates were highest in summer and lowest in winter regardless of temperature within the natural range, but that in *Chorisodontium aciphyllum* (Figure 117-Figure 118) and *Andreaea depressinervis* (Figure 119), there was little change with season.



Figure 112. *Brachythecium geheebii*, a species that can have net photosynthetic gain down to -9°C. Photo by Michael Lüth, with permission.



Figure 113. *Homalothecium philippeanum* in a habitat where it can be exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.



Figure 116. *Isoetecium alopecuroides*, a species that has photosynthesis down to -8°C . Photo by David Holyoak, with permission.



Figure 114. *Homalothecium philippeanum* on a boulder where it can photosynthesize when the air temperature is as low as -9°C . Photo by Michael Lüth, with permission.



Figure 117. *Chorisodontium aciphyllum* in Antarctica where its respiration differs little with seasons. Photo from Polar Institute, through Creative Commons.



Figure 115. *Isoetecium alopecuroides* growing epiphytically where it is exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.



Figure 118. *Chorisodontium aciphyllum*, a moss whose respiration differs little with season. Photo by Juan Larrain, with permission.



Figure 119. *Andreaea depressinervis*, an Antarctic species whose respiration differs little with season. Photo from Wikimedia Commons.

A recent addition to the known flora of the British Isles, the thallose liverwort *Athalamia hyalina* (Figure 120) is a Northern Hemisphere montane species (Long *et al.* 2003). In Scotland it has its active growth in the winter and produces its spores in spring. This permits it to live on the thin soil of eroding limestone ledges where it can take advantage of the moisture in fog of winter and intermittent thaws.



Figure 120. *Athalamia hyalina*, a liverwort that grows in winter in Scotland. Photo by Michael Lüth, with permission.

Winter warming (and possibly summer drought?) in the UK seems to account for the increases in *Campyliadelphus chrysophyllus* (Figure 121) and *Fissidens dubius* (Figure 122) in a limestone grassland, as demonstrated with experiments in winter warming and increased supplemental rainfall in summer (Bates 2006). Spread of the epiphytes *Cololejeunea minutissima* (Figure 123) and *Colura calyptrifolia* (Figure 124) seems likewise to be the result of rising temperatures in winter, and possibly a change in the summer moisture. On the other hand, winter warming coincides with decreases in *Rhytidiadelphus squarrosus* (Figure 98) and *Lophocolea bidentata* (Figure 125).



Figure 121. *Campyliadelphus chrysophyllus*, a species that is increasing in abundance in the UK as a result of winter warming. Photo by David Holyoak, with permission.

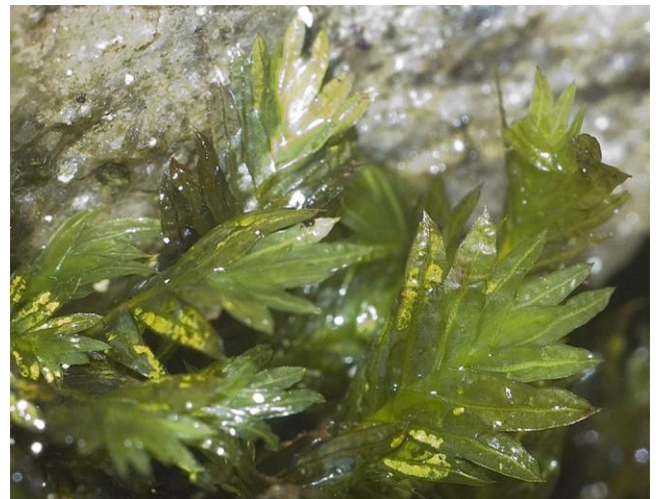


Figure 122. *Fissidens dubius*, a species that is increasing in abundance in the UK as a result of winter warming. Photo by Aimon Niklasson, with permission.



Figure 123. *Cololejeunea minutissima* on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by David T. Holyoak, with permission.

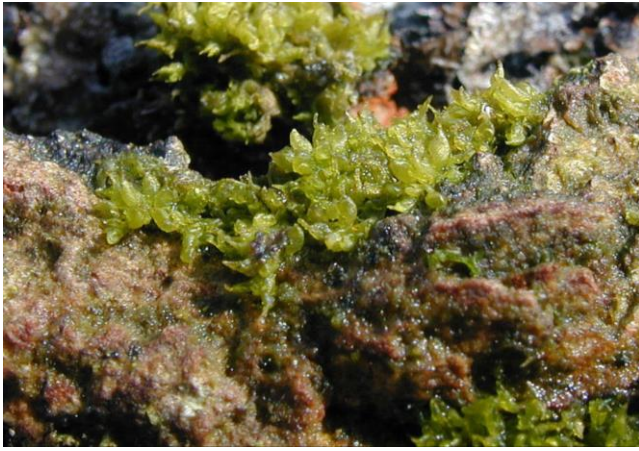


Figure 124. *Colura calyptrifolia* on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by Michael Lüth, with permission.



Figure 125. *Lophocolea bidentata*, a species that seems to be disappearing from the UK due to winter warming. Photo by Michael Lüth, with permission.

Winter and Reproduction

Since winter is often the season with moisture in some habitats like deserts, we can expect this to be the season of gamete transfer and fertilization. In the Negev Desert of southern Israel, Herrnstadt and Kidron (2005) found that *Bryum dunense* initiates its reproductive organs prior to the first winter rain, using atmospheric humidity from dew and fog as the source of water. The most sporophytes form in the partially shaded microhabitats following winter rains, interestingly exceeding those in the shaded microhabitats. When the first rain arrives, *B. dunense* is ready to disperse its bulbils and to complete fertilization. The shrubs seem to be essential to provide the partial shade in which this species is most successful at reproducing.

Too little rainfall in winter can be detrimental to desert mosses. *Syntrichia inermis* (Figure 126) in the Mojave Desert, Nevada, USA, failed to initiate sporophytes in 1996 and 1997 when the winter-spring rainfall was reduced (Stark 2001). In *Crossidium crassinerve* (Figure 127), the appropriate hydration periods occurred in the cooler months of October to April (Stark 2005). Hydration in the summer was detrimental because the patches dried too quickly (as few as 3 hours) following the rainfall, prohibiting sufficient repair and carbon gain. During the

four years of the study, the five patches monitored initiated 248 sporophytes; only 9 survived. Embryonic abortion (69%) and capsule herbivory (30%) accounted for most of the deaths.

Acaulon triquetrum (Figure 128) in southwest Germany initiates most of its gametangia in October to December (Ahrens 2003). These develop rapidly, permitting fertilization to occur during the same time period. Sporophytes grow in October-November to January-February, with dispersal in April or May. The **chloronemal** (branches of protonemata that give rise to gametophore buds) filaments are persistent through summer but die off during winter (December – February). The rhizoid system, however, persists throughout the winter, once again giving rise to new chloronemata and gametophores in the spring. Having rhizoids that persist through the winter permits this moss to rapidly occupy bare surfaces, especially the loess created by small, burrowing mammals.



Figure 126. *Syntrichia inermis* dry, a species that frequently fails to produce sporophytes due to insufficient rainfall in winter and spring in the Mojave Desert, USA. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 127. *Crossidium crassinerve*, a species that is hydrated mostly in winter and early spring in the Mojave Desert. Photo by Michael Lüth, with permission.



Figure 128. *Acaulon triquetrum*, a species that initiates its gametangia October-December in Germany. Photo by Michael Lüth, with permission.

Laaka-Lindberg and Heino (2001) found that the leafy liverwort *Lophozia ventricosa* (var. *silvicola*; Figure 129) in southern Finland has two types of gemmae. One of these becomes dormant and the other is non-dormant. Only the dormant gemmae are able to survive the winter. She provided the evolutionary argument that if the winter mortality (of non-dormant gemmae) increases compared to the mortality during the growing season, then evolution would favor an increase in the percentage of dormant gemmae, especially among those produced at the end of the growing season.



Figure 129. *Lophozia ventricosa* with gemmae. This species produces two types of gemmae, one of which survives winter. Photo by Jan-Peter Frahm, with permission.

Spore dormancy is also subject to temperature. Spores require water to germinate, but dormancy loss also occurs in response to temperature. For *Sphaerocarpos texanus* (Figure 130) at 35/20°C, loss of spore dormancy increases faster than that in even modestly lower temperatures of 30/15°C or 25/15°C (McLetchie 1999). The best spore germination occurs at 16/10°C and spores fail to germinate at 35/20 or 30/15°C. But low temperatures induce the spores to return to dormancy. McLetchie considered this behavior to be similar to that of seeds of obligate winter annuals.



Figure 130. *Sphaerocarpos texanus*, a species that loses its spore dormancy at higher temperatures. Photo by Martin Hutten, with permission.

Longton and Greene (1969) demonstrated that in Britain the boreal forest moss *Pleurozium schreberi* (Figure 104) sustains survival of its antheridia through winter. The antheridia begin development in August but remain immature through winter. The archegonia likewise overwinter in an immature stage. When spring arrives, both undergo rapid development, preparing them for fertilization in April and May. The sporophyte matures in autumn and spores are dispersed between January and April.

It is likely that the moss *Dichelyma japonicum* is excluded from high altitudes and latitudes because its sporophytes have a late sporophyte maturation (Shirasaki 1997). This species grows on the woody plants beside ponds and streams and is covered by deep snow in winter. In the aquatic family **Fontinalaceae**, this species requires deep snow in winter and high precipitation in summer.

Riccia cavernosa (Figure 131) avoids most of the problems of cold, dark, dry winters by having an extremely short life cycle on the banks and sandy flats of the Kobuk River in Alaska (Seppelt & Laursen 1999). Its spore to spore cycle is only three to four weeks of late summer and autumn! Hence, it is able to overwinter as spores and avoid all the problems. On the other hand, this same species (perhaps a different race?) has a life cycle of two - three months of winter and early spring in Australia.



Figure 131. *Riccia cavernosa*, a species with a 3-4-week life cycle in Alaska and one of 2-3 months in Australia. Photo from <www.aphotofauna.com>, with permission.

Hennediella heimii (Figure 132) holds the record for the most polar sporophytes. Seppelt *et al.* (1992) reported this species with young sporophytes from the Lower Taylor Valley, Victoria Land, Antarctica (77°55'S).



Figure 132. *Hennediella heimii* with capsules; this species has the record for capsules at the highest latitude in the Antarctic. Photo by Michael Lüth, with permission.

Asexual Survival

We have learned much about preparation for winter conditions through studies in cryopreservation. The pioneer moss *Ditrichum plumbicola* (Figure 133) survives winters and desiccation in the field, but has poor survival of cryopreservation, even with pretreatment (Rowntree *et al.* 2007). Using a series of treatments and observations, Rowntree and co-workers attempted to determine the effects of ABA, sucrose, and desiccation on various stages of the protonemata. What they found was that most of the protonemal cells pretreated with ABA and sucrose died, but the ones that survived had thick cell walls with deep pigmentation, numerous small vacuoles, and cytoplasmic lipid droplets. Those with only desiccation and cryopreservation exhibited little cytological change. Removal of the ABA-sucrose pretreatment permitted normal development and activity of the protonemata, whereas the pretreatment induced propagules from the protonemata, and these propagules were highly desiccation tolerant and easily survived the cryopreservation. In nature, this species forms highly desiccation-tolerant rhizoids that serve the same perennating function.

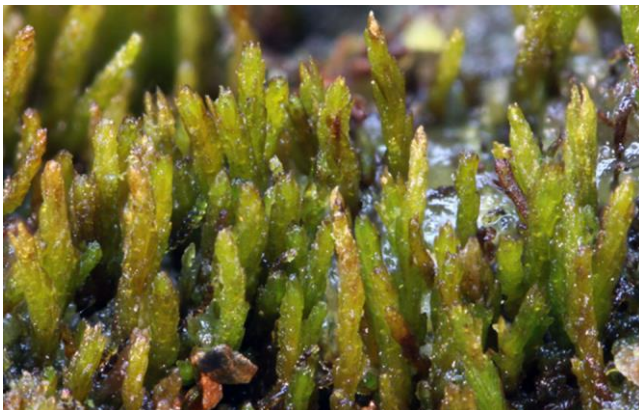


Figure 133. *Ditrichum plumbicola*, a species that survives winter and desiccation in the field, but it has little ability to survive cryopreservation except as propagules. Photo by Des Callaghan, with permission.

Sympatric Differences

Seasonal differences in reproduction often separate **sympatric** (existing in same or overlapping geographic area) species and keep them separated reproductively. Such is the case for three species of *Dicranoloma* in Australia (Milne 2001). In *D. menziesii* (Figure 134) and *D. platycaulon* (Figure 135), the antheridia are initiated during winter and archegonia in the following spring, whereas in *D. billardierei* (Figure 136) the antheridia initiate during late spring to summer whereas archegonia originate in autumn. Differences in development time place the times of fertilization in three different time periods, late summer for *D. menziesii*, mid autumn for *D. platycaulon*, and early winter for *D. billardierei*. For all three species, the winter season is an important period for this process, providing sufficient moisture and avoiding these activities during the high summer temperatures that can cause excessive respiration.



Figure 134. *Dicranoloma menziesii*, a species separated from its congeners by its reproductive times. Photo by Andrew Hodgson, with permission.



Figure 135. *Dicranoloma platycaulon*, a species separated from its congeners by its reproductive time. Photo by David Tng, with permission.



Figure 136. *Dicranoloma billardieri*, a species separated from its congeners by its reproductive times. Photo by Michael Lüth, with permission.

In Japan, *Trachycystis flagellaris* (Figure 137) has developing sporophytes that do well in the lower temperatures and deep snow at higher altitudes (Shirasaki 1998). *Trachycystis microphylla* (Figure 138), on the other hand, has its sporophyte maturation in early spring; it seems to be restricted to coastal areas with only thin snow cover in winter.



Figure 137. *Trachycystis flagellaris*, a species whose developing sporophytes survive well under deep snow. Photo by Ivanov, with permission.



Figure 138. *Trachycystis microphylla*, a species that can survive only a thin snow cover. Photo by Li Zhang, with permission.

Effects of Bryophytes on their Communities in Winter

We cannot ignore the importance of the perennial nature of most bryophytes. Many remain active in winter, but even more importantly they are present and active within hours of snowmelt on their leaves.

The ability of the mosses to remain green and moist throughout winter in some areas is important for their invertebrate inhabitants. For example, in the Black Forest of Germany, *Rhytidiadelphus squarrosus* (Figure 98) is home to several species of tardigrades (water bears) (Schuster & Greven 2007). These tiny animals are well attuned to the seasonal changes in moss habitats. Their diversity is greatest in winter, although numbers decline then. (See Volume 2, Chapter 5).

Mosses are able to modify the effects of frost on the soil community. In a feather moss community in northwestern Alberta, Canada, dominated by *Pleurozium schreberi* (Figure 104), removal of the moss layer increased soil temperatures in summer and lengthened the frost-free period (Startsev *et al.* 2007). But rather than causing the soil to be warmer, the bare soil had temperatures as low as -13°C during the frost-free times.

In China, mosses are a critical part of the gall nut industry, a valuable source of medicines and chemicals. The gall aphid, *Kaburagia rhusicola* spends its winters on mosses, including *Brachythecium* spp., *Entodon*, and *Oxyrrhynchium* (Lai & Zhang 1994). The mosses are able to provide both cover and a moist location. The gall aphid *Kaburagia ovogallis* uses eight species of the *Brachytheciaceae* for its winter hosts (Li 1990). In fact, as of 1990, 24 species of mosses were identified as winter hosts of various species of gall aphids. By providing more of these mosses, those in the gall nut industry were able to sustain higher yields.

Lichens (especially reindeer "moss") are well known as food for caribou and other large herbivores in winter. But bryophytes are less well known for this role. Oloffson *et al.* (2002) demonstrated the importance of bryophytes and other food sources by using exclosures around parts of snowbeds in Arctic-alpine tundra communities. Following eleven years of exclosure, the snowbed developed significant increase in both tracheophytes and bryophytes. The same response did not occur in the tall herb meadow. The primary herbivores in the study were rodents – grey-sided voles (*Clethrionomys rufocanus*), red voles (*C. rutilus*), field voles (*Microtus agrestis*), root voles (*M. oeconomus*), and lemmings (*Lemmus lemmus*). Bryophytes accounted for most of the cryptogamic changes in biomass. Predominant among those increasing in biomass were *Sanionia uncinata* (Figure 46-Figure 48) (584% increase) and *Polytrichum juniperinum* (Figure 139) (113,584% increase). *Pleurozium schreberi* (Figure 104) was absent in the controls and increased by 2.7g m^{-2} in the exclosures. The researchers concluded that the low competition of the unproductive snowbeds was caused by these mammalian herbivores that depressed the plant biomass. The presence of food under the snow, including the bryophytes, permits these animals to remain hidden from aerial predators.



Figure 140. *Polytrichum juniperinum*, a species that increases in biomass following grazing by rodents in the Arctic. Photo by Michael Lüth, with permission.

Prins (1982) asked why mosses are eaten in cold climates only. Could it be that they like the sweet taste of sucrose that is stored in some species in preparation for winter?

Winter Dispersal

Winter can be a time for dispersal. Dry, brittle mosses easily break, presenting fragments that can travel long distances across the smooth snow or caught up in winds unimpeded by canopy leaves. McDaniel and Miller (2000) demonstrated this by collecting bryophyte fragments from late-spring snowbeds in the Adirondack Mountains, New York, USA. The diversity of fragments from the higher elevations of alpine and krummholz vegetation was much greater than that in the forested site. (The diversity also surpassed that of the tracheophytes.)

Miller and Howe Ambrose (1976) were able to collect bryophyte fragments from late snowbeds on Bathurst Island in the Canadian high Arctic. These collections contained large numbers of both mosses and liverworts. Most of the species represented those on the nearby ridges and slopes and Miller and Howe Ambrose presumed that these had been dispersed during the previous winter, resulting from surface winds. In lab cultures, 12% of these fragments exhibited viability, producing protonemata, new shoots, rhizoids, or renewed growth. But parts were not equally viable. Detached moss leaves did not grow and only one leafy liverwort fragment was viable. Rather, the leafy gametophore tips were the most successful. Nevertheless, the researchers estimated that a cubic meter of granular snow contained more than 4000 viable propagules!

Pollution Effects – Vital Water or Deadly Poisons?

Kennedy (1993) reminded us that traditional wisdom tells us that life in the Antarctic is restricted by the arrival of new species and the extreme cold. But recently biogeographical evidence indicates that water may be the primary limiting factor. But it can also bring danger.

Winter can be a particularly dangerous time for bryophytes that are subject to air pollution. The snow collects the pollutants over the extended period of snow cover (Thomas 1981). When melting occurs, the bryophytes are subjected to that long-term collection of

pollutants, *i.e.*, concentrated pollutants, in what is known as **acid flush** (Woolgrove & Woodin 1996). Woolgrove and Woodin documented that these concentrated pollutants in the snowbed moss *Kiaeria starkei* are causing damage to the underlying bryophytes. This damage is greatest when the snow cover is gone and meltwater is delivered to the active plants. This exposure can last for a sufficient period of time that no recovery is measured after 4 weeks. This, combined with the short growing season of these mosses in snowbeds, can have serious impacts on their survival.

Markert and Weckert (1993) found that plants of *Polytrichastrum formosum* (Figure 141) had the maximum concentrations of pollutants in winter and the lowest in summer, attributing this to the higher biomass productivity of this species in the spring. But I suspect that part of this effect was due to the accumulation effect by the snow. Hynninen (1986) attributed the greater winter accumulation of heavy metals by *Sphagnum* (Figure 83-Figure 85) in moss bags in Finland to the summer holiday breaks. Could these winter highs be due to the absence of rain to wash the pollutants away and the long time for continuous collection?

In the boreal forest *Hylocomium splendens* (Figure 142) uses both organic and inorganic nitrogen deposited in the snow (Forsum *et al.* 2008). Snowmelt N is dominated by nitrates (86%), followed by ammonia (11%) and amino acids (3%). The *H. splendens* is able to take up 24% of the nitrogen from the snow nitrogen. On the other hand, Björk (2007) showed that 1.0 g m⁻² yr⁻¹ N added to the snow water had little effect on the bryophyte community over a three-year period. Other nutrients become available in the snowmelt water as well (Björk & Molau 2007; Jägerbrand 2011).



Figure 141. *Polytrichastrum formosum* with capsules, a species that accumulates the most pollutants in winter. Photo by David T. Holyoak, with permission.

Like growth, uptake of pollutants depends on the availability of water, and it may or may not be significantly affected by temperature. As concluded by Hébrard *et al.* (1974) for *Grimmia orbicularis* (Figure 143), the activities of ⁹⁰Sr transfer to the mosses coincide with those times of maximum rainfall in autumn, winter, and spring. The accumulations of the pollutant in dust on the moss is unavailable to the moss until water enters the cells.



Figure 142. *Hylocomium splendens*, a species that takes a great deal of its nitrogen from snowmelt. Photo by Chmee, through Creative Commons.



Figure 143. *Grimmia orbicularis*, a species that collects pollutants that are detrimental to it when it rains. Photo by Michael Lüth, with permission.

Summary

Late snowbeds provide a refuge for bryophytes where there is sufficient water in "spring" and reduced competition from tracheophytes. Species living there have life cycles that take advantage of snowmelt water and that have life cycle stages that can live through winter. The growth forms may be altered and duration of the snow is a determining factor in species composition. Prominent among the snowbed bryophytes are species of *Anthelia* and *Kiaeria*. Snowmelt waters create flushes that have their own species, including several *Sphagnum* species.

Freeze-thaw cycles can be beneficial to some and detrimental to other bryophytes. Short thaw periods may be insufficient to repair damage from desiccation and freezing. These can become lethal for some bryophytes that are unable to realize any carbon gain. In some locations, especially the Antarctic, exposure in winter subjects the bryophytes to higher UV light intensities, coupled with low temperatures. Some live in exposed sites where wind clears the snow or on vertical surfaces that do not hold the snow, exposing the bryophytes to drying, intense light, and extreme low temperatures.

On the other hand, some bryophytes grow best in winter when more moisture is available. Others survive winter through asexual propagules. The life cycle adaptations to winter microclimate are effective means for maintaining species differences among sympatric members of the same genus.

Bryophytes occupy habitats where tracheophytes cannot complete their life cycles in the short growing seasons. These bryophytes provide a refuge and food for invertebrates, rodents, and even some large free-range mammals. They modulate the ground temperature, preventing extremes, hold water longer than bare ground, and prevent destructive runoff during spring flushes.

The dry air of winter facilitates breakage of bryophyte fragments. These easily blow across the snow, taking advantage of the absence of leaves on the trees in deciduous forests, making winter dispersal significant.

Pollutants accumulate in the snow and rapid melt may expose the bryophytes to heavy concentrations in a short time frame. In some cases, the bryophytes gain important nutrients from the collected pollutants, but some are detrimental.

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