

# CHAPTER 7-8

## WATER RELATIONS: HABITATS

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# CHAPTER 7-8

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Figure 1. *Bryum caespitium* at a high elevation where winds and ice crystals contribute to desiccation, but where at other times fog can maintain moisture without rain. Photo by Michael Lüth, with permission.

### Habitat Relations

Proctor (2014) summarized the importance of water relations for bryophytes in their invasion of land. He pointed out that the poikilohydric strategy is optimal at smaller scales, *i.e.*, bryophytes. Microhabitat and habitat structure are important in conferring the hydration state of bryophytes, and drought sensitivity varies according to species (Irmscher 1912). Norris (1990) found that *Braunfelsia* disappeared from some areas of tropical rain forests in Papua New Guinea following disturbance to the forest because of the increased dehydration frequency and the admission of greater wind movement. In the Mediterranean area in the southern and southeastern Iberian Peninsula, Varo and coworkers (1992) found that as the climate has become drier and warmer the bryophyte taxa have changed, with leafy liverworts and pleurocarpous mosses diminishing and *Sphaerocarpos* (Figure 2) and acrocarpous mosses becoming more prominent. In central Sweden, greater numbers of bryophytes occur in spruce forests on more moist north-facing slopes, whereas

vascular plants are more abundant on the exposed south-facing slopes (Söderström 1981).



Figure 2. *Sphaerocarpos michelii*, member of a genus that becomes more prominent as the climate dries. Photo by Michael Lüth, with permission.



Bryologists learn inductively through field experience that certain bryophytes are characteristic of dry habitats and others of wet habitats. Actual studies that correlate these conditions with species are less common than descriptive observations, with a number of these being relative to water level in peatlands. Bates *et al.* (2004) used canonical correspondence analysis (CCA) to develop a more rigorous approach to these relationships by sampling epiphytes along a transect across southern Britain from southwest to northeast. With climate, presence of water courses, and forest cover contributing to the analysis, they determined that *Frullania tamarisci* (Figure 3), *Metzgeria temperata* (Figure 4), *Microlejeunea ulicina* (Figure 5), *Neckera pumila* (Figure 6), and *Hypnum andoi* (Figure 7) were restricted to habitats with high moisture availability. On the other hand, *Syntrichia ruralis* (Figure 39), *Grimmia pulvinata* (Figure 8), *Tortula muralis* (Figure 9), and *Aulacomnium androgynum* (Figure 10) only occurred as epiphytes in locations with low moisture. They did not sample these species in other habitats.



Figure 5. *Microlejeunea ulicina*, a leafy liverwort that is restricted to areas with high moisture levels. Photo by Michael Lüth, with permission.



Figure 3. *Frullania tamarisci*, a leafy liverwort that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.



Figure 6. *Neckera pumila*, a moss that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.



Figure 4. *Metzgeria temperata*, a leafy liverwort that is restricted to areas of high moisture levels. Photo by Michael Lüth, with permission.



Figure 7. *Hypnum andoi* near Swallow Falls in Wales, a moss that is restricted to areas with high moisture content. Photo by Janice Glime.





Figure 8. *Grimmia pulvinata*, a cushion moss that can only survive as an epiphyte in areas that have high moisture. Photo by Barry Stewart, with permission.



Figure 9. *Tortula muralis* habitat on a wall. This moss is unable to live as an epiphyte unless the habitat has low moisture levels. Photo by Janice Glime.



Figure 10. *Aulacomnium androgynum*, a moss that can only survive as an epiphyte in areas that have high moisture. Photo by Jan-Peter Frahm, with permission.

In mature black spruce forests of central Alaska, the endohydric *Polytrichum commune* (Figure 11) is able to avoid moisture stress more so than such ectohydric taxa as *Hylocomium splendens* (Figure 12; Skré *et al.* 1983). The latter species remains below its compensation point for water for nearly 50% of the July growing season.



Figure 11. *Polytrichum commune*, an endohydric moss that is able to avoid moisture stress in black spruce forests more readily than ectohydric taxa. Photo by Michael Lüth, with permission.



Figure 12. *Hylocomium splendens*, an ectohydric moss. Photo by Janice Glime.

Open expanses of urban areas are notoriously devoid of extensive bryophyte cover, even on trees where taxa are already xerophytically adapted. Hébrard and Rolando (1985) found that when comparing four holm-oak thickets in France, species composition correlated more with plot exposure than with thicket age, suggesting that desiccation, light, and temperature may be most influential. Sheard (1968) likewise found a correlation between the prevailing north wind and the pattern of moss-lichen heath on Jan Mayen Island.

Among the most significant climatic stress inducers for mosses are high temperatures, frost, and drought (Longton 1979). Dry mosses are typically much more heat resistant than wet mosses. For example, Nörr (1974) found that eight European mosses reach lethal limits at 42-51°C when turgid, but survive to 85-110°C when dry. Lange (1955) found similar dry survival of mosses from 70-110°C. Temperature relationships will be discussed more thoroughly in the chapter on temperature.

These relationships also exemplify that, although bryophytes are able to survive on rocky and shallow substrates with little water, they are unable to compete with the tracheophytes in areas where there is sufficient soil, light, and moisture for the tracheophytes to root. But at the extremes, bryophytes may have an advantage. Therefore, it is fitting to conclude our attempt to understand the water stresses of bryophytes by comparing them at the two extremes, the aquatic and the arid habitats.



Using electrolyte leakage as an indication of desiccation stress, Šinžar-Sekulić *et al.* (2005) compared the desiccation tolerance of three mosses from different moisture regimes. *Thamnobryum alopecurum* (Figure 13), a moss of open, vertical limestone cliffs, has the highest degree of desiccation tolerance among these three. *Anomodon viticulosus* (Figure 14), a moss of limestone rocks in the forest, releases electrolytes under desiccation, causing pronounced changes in the cells. The aquatic moss *Platyhypnidium riparioides* (Figure 15) suffers irreversible change following desiccation. It is likely that speed of drying plays a role for the latter species because its frequency on emergent rock habitats suggests that it should be adapted to slow drying. Nevertheless, it seems to live where it stays moist even during periods of low water levels.



Figure 13. *Thamnobryum alopecurum*, a moss that has high desiccation tolerance on limestone cliffs. Photo by Michael Lüth, with permission.



Figure 14. *Anomodon viticulosus*, a moss of limestone rocks that releases electrolytes when desiccated. Photo by Michael Lüth, with permission.

Among the hornworts (**Anthocerotophyta**) little information exists on desiccation tolerance. Some are drought avoiders, producing special structures that survive periods of desiccation (Vitt *et al.* 2014). These, occurring on hornworts of seasonally dry localities, include abundant swollen, marginal or apical tubers on the thalli (*Phaeoceros* spp.; Figure 16-Figure 17) or long-stalked, subterranean ventral tubers (*Phymatoceros*; Figure 18). Both of these

special tubers form as the sporophytes mature and persist in the soil crust or soil bank after the vegetative thallus has deteriorated. Rainfall causes these tubers to germinate and form new plants (Crandall-Stotler *et al.* 2006). Hartung *et al.* (1994) found that these tubers contain large amounts of ABA, a hormone known to induce desiccation tolerance in bryophytes (Pence *et al.* 2005). These tubers can survive at least nine months of dryness and still germinate (Vitt *et al.* 2014).



Figure 15. *Platyhypnidium riparioides*, an aquatic moss that can suffer irreversible damage from desiccation. Photo by Des Callaghan, with permission.



Figure 16. *Phaeoceros* sp. showing abundance of light green tubers in the center of the thallus. Photo by Juan Larrain, with permission.



Figure 17. *Phaeoceros pearsonii* with thickened tubers. Photo by Li Zhang, with permission.





Figure 18. *Phymatoceros bulbosus* ventral side with tubers. Photo by David Wagner, with permission.

Other hornworts take advantage of short life cycles. For example, rapid spore release in *Notothylas* (Figure 19), coupled with the ability to survive many years dry (Renzaglia *et al.* 2009) permit this genus to avoid drought conditions.



Figure 19. *Notothylas orbicularis* showing numerous young horizontal sporophytes. Photo by Michael Lüth, with permission.

Liverworts are known for loving damp habitats, but they contain their xerophytic members as well. Seppelt (pers. comm. 1999) relayed to me that these include species surviving in as little as 150 mm of rainfall per year [*Fossombronia* (Figure 20), *Asterella* (Figure 21), *Plagiochasma* (Figure 22)]. At somewhat higher levels (200 mm), such taxa as *Lethocolea* (Figure 23), *Cephaloziella* (Figure 24), *Riella* (Figure 66), *Enigmella*, and *Gongylanthus* (Figure 25) appear. *Enigmella* is ephemeral in its vegetative phase, but its reproductive structures are well suited to their environment. Some taxa survive drought by having a shortened life cycle, *e.g.* *Riccia cavernosa* in the Arctic (Seppelt & Laursen 1999).



Figure 20. *Fossombronia angulosa* with capsule, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Des Callaghan, with permission.



Figure 21. *Asterella lindenberiana* with archegoniophores, a member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Martin Hutten, with permission.



Figure 22. *Plagiochasma appendiculatum*, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Michael Lüth, with permission.





Figure 23. *Lethocolea glossophylla*, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Cephaloziella* cf. *hampeana*, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Barry Stewart, with permission.



Figure 25. *Gongylanthus ericetorum*, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Michael Lüth, with permission.

## Peatlands

Peatlands provide a good ecosystem for comparing adaptations for differences in moisture regimes by habitat. But the dominant moss, *Sphagnum*, has unusual structural adaptations that can complicate this analysis.

Wagner and Titus (1984) compared desiccation tolerance of the hummock species *Sphagnum nemoreum* (Figure 26) to that of the hollow species *S. fallax* (Figure 27). The hollow species is more desiccation tolerant than the hummock species. It has both a higher number of plants surviving and a better recovery of its photosynthetic rate. However, its ability to recover decreases as the desiccation periods are lengthened or the water content is decreased. Despite being close to the water, *S. fallax* apparently dries more frequently and for longer periods of time than does *S. nemoreum*. The latter species, instead, is able to remain moist in the field by holding more water when the habitat dries.



Figure 26. *Sphagnum nemoreum*, a compact hummock moss. Photo by Michael Lüth, with permission.



Figure 27. *Sphagnum fallax*, a loose moss of hollows. Photo by David Holyoak, with permission.

Schipperges and Rydin (1998) compared the responses of photosynthetic CO<sub>2</sub> exchange in five species of *Sphagnum* in response to tissue water content. These species ranged in microhabitat from hummock top (*S. fuscum*; Figure 28), hummock mid to top [*S. papillosum* (Figure 29) & *S. magellanicum* (Figure 30)], wet areas of ombrotrophic bogs and ditches (*S. balticum*; Figure 31), to submerged (*S. cuspidatum*; Figure 32). Laboratory experiments using infrared gas analysis (IRGA) measured recovery of net photosynthesis after several long-lasting desiccation/rehydration events. One important structural adaptation that emerged is the importance of contact between capitula and basal parts of the mosses; if the



capitula were isolated from the water table, they were unable to recover from complete desiccation (<10-20% of compensation point water content; 15°C for 2-4 days). It is interesting that they found no relationship between recovery of net photosynthesis and wetness of the natural habitat. Rather, those species that live under regularly drying conditions are able to avoid death by themselves avoiding drying out, using high capillarity or a dense growth form such as that of *S. fuscum* (Figure 28).



Figure 28. *Sphagnum fuscum*, a hummock top species. Photo by Michael Lüth, with permission.



Figure 29. *Sphagnum papillosum*, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.



Figure 30. *Sphagnum magellanicum*, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.



Figure 31. *Sphagnum balticum*, a species of wet areas of bogs and ditches. Photo by Michael Lüth, with permission.



Figure 32. *Sphagnum cuspidatum*, a submerged species. Photo by Jan-Peter Frahm, with permission.

Hájek and Vicharová (2013) concluded that *Sphagnum* species have inducible desiccation tolerance. These species are generally desiccation intolerant, instead using mechanisms to avoid internal desiccation, as noted by Schipperges and Rydin (1998). Hájek and Vicharová tested the inducible nature of their tolerance by using various bryophyte species, including *Sphagnum*. They hardened the bryophytes by slow drying, ABA application, and chilling or frost. Both chilling and frost can create desiccating conditions by drawing water from the cells through the hygroscopic nature of ice crystals, much like the effects of freezer burn in your freezer. Presuming that the tolerance was inducible, they monitored the seasonal changes in desiccation tolerance of bog bryophytes. Among these, *Sphagnum* species in hollows and lawns developed desiccation tolerance several times during the year as a response to reduced precipitation and lowered water table. The hummock and aquatic species developed this tolerance only in the autumn, possibly responding to frost. Following initial de-hardening in the lab, untreated *Sphagnum* shoots lacked desiccation tolerance. On the other hand, all hardening treatments except chilling induced desiccation tolerance in all groups except those in section *Cuspidata* (Figure 32), a submersed species. They suggest that lack of adequate desiccation tolerance may prevent *Sphagnum* establishment in the drier habitats that are otherwise suitable. Those species that avoid desiccation typically do so by forming compact hummocks – or living submersed. Thus, hummock species invest their



resources in water retention, avoiding desiccation, but have a lower ability to develop desiccation tolerance.

Peatlands typically have moisture gradients, and Hettenbergerova *et al.* (2013) took advantage of this gradient to compare species richness relative to water availability. They were fortunate to have a system that graded from a spring fen to a semi-dry grassland in the Czech and Slovak Republics. They found that the number of species of tracheophytes tended to increase toward the lower moisture values. The species richness had a negative correlation with the N:P biomass ratio, whereas the percentage of endangered species had a positive correlation. These relationships for bryophytes differed markedly from those of the tracheophytes. Instead, bryophyte species richness decreased linearly toward the dry end of the transects, and there was no correlation with any of the nutrient measurements (N, P, K, C, Ca). Furthermore, the bryophytes exhibited a very high percentage of specialists in fen plots.

Sagot and Rochefort (1996) were concerned about the effects of desiccation on regeneration. They found that fragments of *Sphagnum fallax* (Figure 27), *S. fuscum* (Figure 28), and *S. magellanicum* (Figure 30) could survive 14 days without water when air dried at 20°C, relative humidity ~60%, but regeneration was delayed. *Sphagnum fallax* and *S. magellanicum* survived better than did *S. fuscum*.

## Aquatic Habitats

The aquatic bryophytes are distributed worldwide, but they seem to be more common in temperate than in tropical areas. Aquatic species are classified as **obligate aquatics**, having little or no tolerance to drought conditions, **facultative aquatics**, having some degree of tolerance to desiccation and xerophytic conditions, and **semi-aquatic emergents** (Vitt & Glime 1984), being in locations where they are partly in the water and partly out of it, but usually moist (Figure 33).



Figure 33. *Fontinalis novae-angliae* submerged and *Plagiochila porelloides* on the rock above the water in a New Hampshire stream. The *P. porelloides* is subject to intermittent flooding but can become dry when the stream level is low in mid and late summer. Photo by Janice Glime.

Rehydration in aquatic mosses is much like that of tracheophytes. Whereas many mosses are able to protect their ribosomes during dehydration (Bewley 1974), permitting rapid recovery of protein synthesis and respiration upon rehydration, aquatic bryophytes are not. Instead, irreversible ribosome damage occurs (Krupa

1977). For example, *Cratoneuron* (Figure 34), a semi-aquatic moss, loses ATP during rapid drying, and with its damaged ribosomes it is unable to replace it upon rehydration (Bewley & Gwozdz 1975). Aquatic mosses typically suffer membrane damage during desiccation, but **xeric** (dry habitat) mosses often do not (Brown & Buck 1979). Thus, in aquatic mosses, rehydration results in loss of nutrients.



Figure 34. *Cratoneuron filicinum*, a moss known to lose ATP during rapid drying. Photo by Ivanov, with permission.

Even such obligate aquatic mosses as *Fontinalis* are subject to periods low water when they are exposed above water. Carvalho *et al.* (2011) found that the aquatic moss *Fontinalis antipyretica* (Figure 65) demonstrates desiccation tolerance. Laboratory experiments can be misleading because this species requires slow drying in order to survive, supporting the hypothesis of induced desiccation tolerance. In fact, Cruz de Carvalho *et al.* (2011) concluded that the protein profiles following rehydration were similar to those of the terrestrial mosses *Physcomitrella patens* and *Syntrichia ruralis* (Figure 39). They concluded that desiccation tolerance mechanisms were similar regardless of habitat.

## Arid Habitats

Contrary to the popular concept that mosses must grow in wet places, a number of species are **xerophytic**, that is, adapted to places like the dry, hot desert. In such habitats, some mosses are able to absorb water from dew and night air, permitting brief photosynthesis during the early hours of morning. They dry again each day, cycling on a 24-hour wet-dry cycle (Kappen *et al.* 1979). Where the sun reaches the mosses directly, as on the south-facing slopes in North American deserts, the temperature can increase by as much as 20°C in the first 30 minutes of daylight, thus providing too short a period for the moss to gain photosynthetic energy before drying out (Nash *et al.* 1977). In such locations the mosses are restricted to the north-facing slopes. The biomass is quite small, less than 2 g m<sup>-2</sup>, but at least 18 different species are able to survive, the most common being tuft-forming taxa such as *Syntrichia ruralis* (Figure 39), *Grimmia laevigata* (Figure 36), and *Bryum caespitium* (Figure 1).

One advantage of having sufficient moisture in the desert habitat is that it can provide evaporative cooling. But that does not seem to be the case in all situations. In the Mojave Desert, Nevada, USA, *Crossidium*



**crossinervium** (Figure 62) experienced temperatures above ambient, independent of the state of hydration (Stark 2005). During cooler months, the moss patch exhibited a temperature lower than ambient, again with state of hydration failing to play a role. The periods of hydration were essentially restricted to the cooler months of October to April with hydration lasting 3.7-4.9 days. The longest dry period was 191 days during the measurement period. In late winter, drying was slow, lasting several days, but in the summer the mosses were dry in as little as three hours.

Peatland bryophytes are not the only ones that practice avoidance and tolerance. These practices are also common among bryophytes that live in some of the most harsh moisture conditions on the planet. One mechanism is to go dormant during the dry periods, surviving as spores, gemmae, and probably in some cases protonemata (Vitt *et al.* 2014). Such an **escape strategy** is advantageous to bryophytes that lack a physiological tolerance to desiccation in the leafy gametophore (Figure 35). Liverworts have fewer genera with an escape strategy, but many thallose liverworts have tubers or other means, especially *Riccia*, to survive (see Figure 69); many leafy liverworts have gemmae.

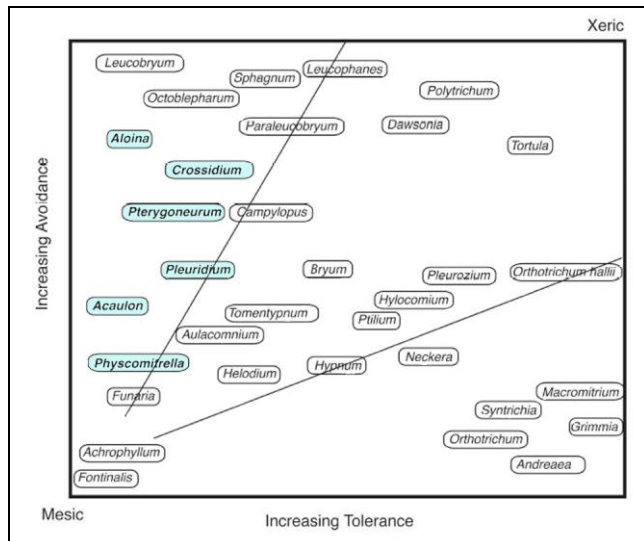


Figure 35. Comparison of representative moss genera that are able to use desiccation avoidance compared to desiccation tolerance. Those genera in blue frames are able to use escape strategies. Modified from Vitt *et al.* 2014.



Figure 36. *Grimmia laevigata*, a desert survivor. Photo by Michael Lüth, with permission.

In the Sonoran Desert of North America, Alpert (1979) found that an overnight storm provided 85% of the saturated water contents, available at 6 a.m., for *Bryum capillare* (Figure 37), *Grimmia* spp. (Figure 36), *Syntrichia* spp. (Figure 39), and *Weissia controversa* (Figure 38). By 9 a.m., eleven of the twelve species investigated had only 2 g water per g of plant dry mass, and by 3 p.m., only 0.5 g remained. By 5 p.m., less than 0.1 g per gram of plant remained, resulting in only about 9 hours of water available from that rare storm. Richardson (1981) points out that it is not damage by drought that eliminates many species from the desert, but the very short time available for photosynthesis.



Figure 37. *Bryum capillare* on a tombstone, a moss that benefits from short moisture episodes, but that holds water for only about 9 hours after a desert storm. Photo by Andrew Fogg, through Creative Commons.



Figure 38. *Weissia controversa* dry, a moss that may have only 9 hours of hydration following a desert storm. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

One adaptation that permits some mosses to tolerate frequent dehydration/rehydration cycles is that those xeric mosses with undamaged membranes are able to retain ions by binding them to the cell wall (Brown & Buck 1979). Another adaptation in the desert moss is that rapid water loss, typical of the desert, can result in a retention of 50% of the polysomes, whereas slow drying can completely deplete them. Fortunately, in drought-tolerant mosses like *Syntrichia ruralis* (Figure 39), the polysomes can be strongly rebuilt after two hours of rehydration (Oliver & Bewley 1984b), but the process continues for a longer



period of time in those that were dried rapidly. RNA synthesis likewise requires six hours after rapid drying and only two hours after slow drying to reach the level of that in non-dried control mosses (Oliver & Bewley 1984a).



Figure 39. *Syntrichia ruralis*, a drought-tolerant moss. Photo by Michael Lüth, with permission.

One unclear factor in this story is the role of nitrite. Nitrite accumulates during slow dehydration of *Syntrichia ruralis* (Figure 39), but not when desiccation is rapid (Mahan *et al.* 1998). Upon rehydration, the nitrite in the slowly-dried moss declines and reaches normal levels within one hour. Mahan and coworkers considered that the nitrite might provide a nitrogen source for the nitrogen metabolism needed during rehydration. On the other hand, Brown and Mahmood (1996) determined that nitrite apparently causes considerable membrane damage in the mesophytic *Mnium hornum* (Figure 40); thus we need further research to understand the conditions under which it is detrimental vs adaptive.



Figure 40. *Mnium hornum*, a moss in which cell membranes suffer damage from elevated nitrite concentrations during dehydration. Photo by David T. Holyoak, with permission.

Marschall (1998) examined the activity of nitrate reductase during desiccation and rehydration of nine bryophytes and concluded that there was no difference in the proportional decrease in nitrogen reductase activity between desiccation-tolerant and non-tolerant bryophyte taxa. Eight of these bryophytes did exhibit detectable nitrate reductase (NR) activity. Pretreatment with  $\text{KNO}_3$  did affect the increase in NR activity between these two

types, with the desiccation-tolerant *Syntrichia ruralis* var. *arenicola* (Figure 39) increasing activity by a factor of 3 while the desiccation-intolerant *Dicranum majus* (Figure 41) and *Hookeria lucens* (Figure 42) had a 6-fold increase in nitrate reductase activity. Following rehydration, *Syntrichia ruralis* (Figure 39) exhibited a marked decline in NR activity during the first hour, whereas the epiphytic/saxicolous *Porella platyphylla* (Figure 43) maintained a relatively constant low level in the light but increasing NR activity in the dark. While we might assume that these physiological differences relate to survival, it is too early to explain just how this is accomplished.

Proctor (1982) considers such structures as papillae to be adaptive in ensuring that the moss does not spend a long period of time in a semi-dry state, during which it is likely to lose more carbon by respiration than it gains by photosynthesis. He notes that the papilla systems, so common on xerophytic leaves, are often separated by regions where the capillary continuity is broken at high water potentials, causing the leaf to have either an abundant water supply, or none. Such discontinuities could be amplified if the leaf rolls as it dries and bends away from the discontinuity. Vanderpoorten and Engels (2002) considered papillae so important as to be one of only four life history traits contributing to predictability of species occurrence in a particular environment on a regional scale. Nevertheless, experiments on the role of papillae in conserving water have mostly failed (Frey & Kürschner 1991).



Figure 41. *Dicranum majus* near Swallow Falls, Wales, a moss that is desiccation-intolerant. Photo by Janice Glime.



Figure 42. *Hookeria lucens*, a desiccation-intolerant species. Photo by David T. Holyoak, with permission.





Figure 43. *Porella platyphylla*, an epiphytic/saxicolous liverwort. Photo by Michael Lüth, with permission.

Few bryophytes approach the succulent or sclerophyll strategies known in tracheophytes (Grime 1977), although one might argue for succulence in the Marchantiales. Plants with numerous or large papillae take on the appearance of sclerophylls, and for many years we assumed that papillae functioned to prevent the loss of water. However, as Frey and Kürschner (1991) pointed out, tests to validate that theory have failed. Nevertheless, while it appears that the papillose mosses do not slow down water loss, the papillae may have a function in water uptake (Crandall-Stotler & Bozzola 1991). As discussed earlier with leaf strategies (see Chapter 7-4a of this volume), papillae in *Andreaeobryum macrosporum* (Figure 44) are constructed in such a way that they provide a channel for the uptake of water.



Figure 44. *Andreaeobryum macrosporum*, a moss with papillae that provide a pathway for uptake of water. Botany website, University of British Columbia, Canada, with permission.

I have suggested that papillae on some mosses might also function to scatter light during dry periods, thus aiding in the protection of the chlorophyll from the UV light during the lengthy time the leaf is exposed, with no chance for repair between rainfall events.

Alpert (1979, 1982, 1985, 1988) investigated five species of **poikilohydric** mosses (those that depend on external conditions to regulate their water content): *Schistidium apocarpum* (Figure 45), *Grimmia laevigata* (Figure 36), *Hedwigia ciliata* (Figure 46), *Orthotrichum rupestre* (Figure 47), and *Syntrichia ruralis* var. *crinata* (see Figure 39). These bryophytes are characterized by short cushions of tufted growth, except for *Hedwigia ciliata*. The latter moss has a whitened appearance due to numerous papillae, and its leaves are closely appressed to the stem when dry. When wet, the leaves spread broadly, causing it to look sufficiently different from its dry state that it causes many bryologists to stop and puzzle over its identity.

Alpert (1979, 1982, 1985, 1988) found that these five mosses were able to colonize unoccupied, stressful boulder habitats, but that they were intolerant of competition or of disturbance beyond their normal desiccation regime. They grew in particular microclimatic niches on the rock substrata and were unable to occupy the most xeric conditions within the same macroclimate, although laboratory studies indicated that they can tolerate both temperatures and droughts that exceed those of the habitats they occupy. Alpert showed through transplant experiments that they could indeed occupy additional locations, suggesting that dispersal and establishment impose limits on their distribution.



Figure 45. *Schistidium apocarpum* with capsules, an ectohydric moss. Photo by Michael Lüth, with permission.



Figure 46. *Hedwigia ciliata*, an ectohydric moss shown here on rock. Photo by Janice Glime.





Figure 47. *Orthotrichum rupestre*, a xerophytic moss on rock. Photo by Michael Lüth, with permission.

The aspect and angle of slope had strong influences on the evaporation stress experienced by these mosses (Alpert 1979, 1982, 1985, 1988). Mosses growing under rock overhangs should experience the least water stress by late day, but do not regain as much moisture as those at 15° and 75° slopes (Figure 48). As expected, mosses at the tops of boulders had the greatest peaks of evaporation stress. Alpert's work illustrates the importance of 24-hour measurements in comparing potential evaporative stresses of different microsites.

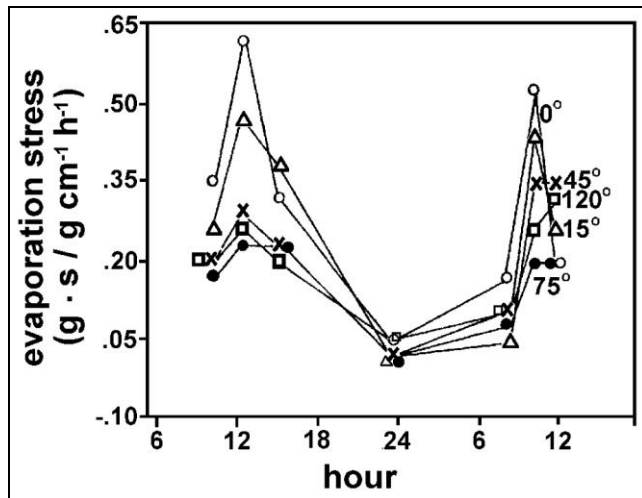


Figure 48. Effects of degree of slope on potential evaporation on 21-22 February 1980 for mosses (based on uniform paper samples) on arid north sides of rocks in five slope microsites. (n=4) Modified from Alpert (1982).

Aspect separated the evaporation stresses even more clearly (Figure 49), with evaporation stress on the east side peaking at about 10:00 hours and at most other aspects peaking at about 12:00 hours (Alpert 1982). Stress on the west side peaked last, at 14:00 hours, but with a lower peak than at the other aspects. The north, as might be expected, had the least daily variation. Although daily evaporation potential was high, a brief nighttime rainfall of no more than 5 mm was sufficient to rewet the moss for several days (Figure 50, Alpert 1982).

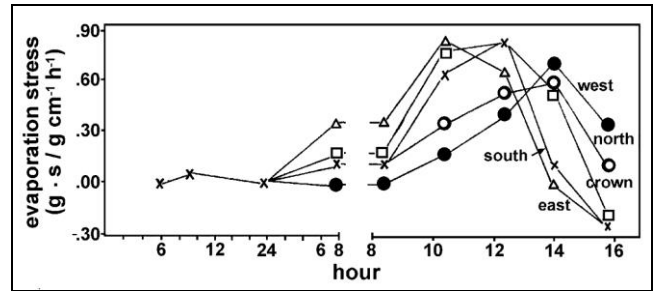


Figure 49. Effect of aspect on potential evaporation on 7-8 March 1980 for mosses (based on uniform paper samples) on arid 45° slope in five aspect microsites. (n=4) Modified from Alpert (1982).

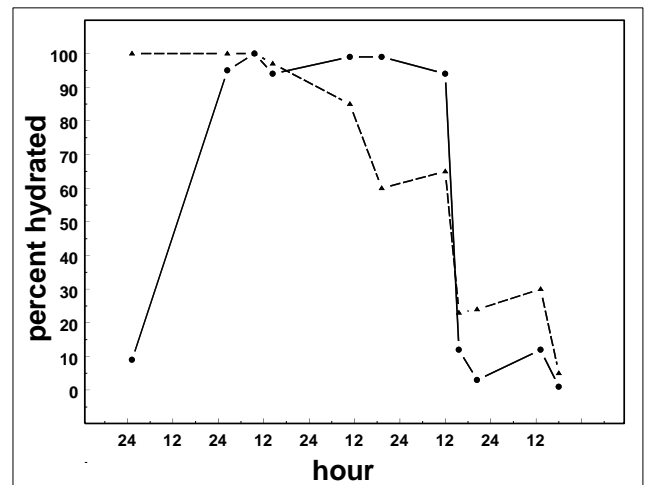


Figure 50. Percent hydration of natural moss cover on boulders following nighttime rainfalls of ~5 mm in spring and winter. Redrawn from Alpert (1982).

Open, exposed soils in temperate climates are arid for bryophytes because of their insignificant soil penetration by which to obtain water. In these habitats, the mosses *Barbula* (Figure 51), *Syntrichia* (Figure 39), and the thallose liverwort *Riccia* (Figure 52) are able to survive (Schofield 1985). The two mosses are both papillose and able to roll their leaves and contort them as they dry. The *Riccia* thallus usually has inrolled margins and a thick cuticle; Frey and Kürschner (1991) have demonstrated that thallus and leaf inrolling correlate with increasing aridity, suggesting a protective role. *Ceratodon* (Figure 53), *Funaria* (Figure 54), and *Cephaloziella* (Figure 55) seem to lack any structural adaptations to their sometimes dry habitats, although *Ceratodon* does have crispate leaves and rolled margins.

In cryptogamic crusts of arid regions, bryophytes are important in holding water, retaining several times their volume after rainfall (Mücher *et al.* 1988; Rivera-Aquilar *et al.* 2005). This leads to higher germination rates of seed plants compared to areas with no crust (Mücher *et al.* 1988; Rivera-Aquilar *et al.* 2005; Serpe *et al.* 2006)





Figure 51. *Barbula convoluta* var. *commutata*, an ectohydric moss growing on rock over little or no soil. Michael Lüth, with permission.



Figure 52. *Riccia nigrella*, a thallose liverwort surviving on dry soil. Photo by Michael Lüth, with permission.



Figure 53. *Ceratodon purpureus* on rocky soil, a moss that has few structural adaptations to such a dry habitat. Photo by Janice Glime.

A comparison of mosses from a variety of habitats in Israel revealed varying degrees of drought tolerance that related well to their habitats (Di Nola *et al.* 1983). The desert mosses *Tortula brevissima* (Figure 56) and *Trichostomopsis aaronis* exhibited rapid return of metabolic activity after prolonged drying and were able to resume photosynthesis without new chlorophyll synthesis. The Mediterranean moss *Barbula fallax* (Figure 57) behaved similarly to the desert mosses, but

*Homalothecium aureum* (Figure 58) and *Didymodon tophaceus* (Figure 59), more mesic mosses, had slow recovery after desiccation. *Mniobryum* sp. (Figure 60) had almost no drought tolerance and was killed by the prolonged drying.



Figure 54. *Funaria hygrometrica*, a moss with no noticeable xerophytic adaptations, living on sand and rocks. Photo by Michael Lüth, with permission.



Figure 55. *Cephaloziella stellulifera*, a leafy liverwort that seems to lack structural adaptations to this rock habitat. Photo by David T. Holyoak, with permission.



Figure 56. *Tortula brevissima*, a desert moss that rapidly returns its metabolic activity upon rehydration. Photo by Michael Lüth, with permission.



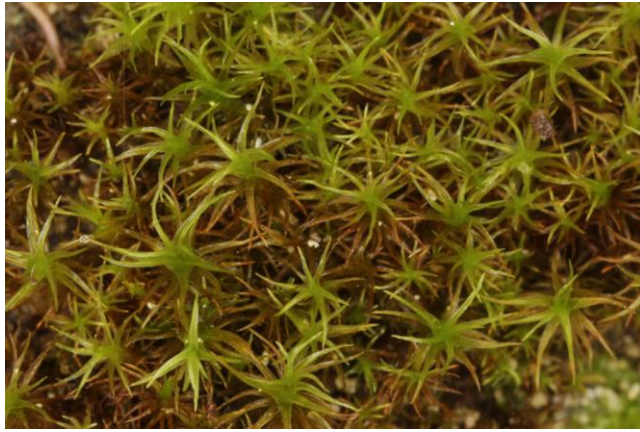


Figure 57. *Barbula fallax*, a Mediterranean moss that resumes metabolic activity rapidly upon rehydration. Photo by Jan-Peter Frahm, with permission.



Figure 58. *Homalothecium aureum*, a mesic moss. Photo by Michael Lüth, with permission.



Figure 59. *Didymodon tophaceus*, a mesic moss. Photo by Michael Lüth, with permission.

Longton (1988b) pointed out the importance of dispersal among desert bryophytes, since many of them are drought avoiders. Since sexual reproduction will occur infrequently, he contends that desert mosses should be acrocarpous **perennial stayers** with long-lived, desiccation-tolerant gametophytes, small spores, and long setae. The **annual** taxa are **ephemeral** (short-lived) mosses and liverworts that can develop rapidly after a rain because their dormancy is accomplished by large spores; their capsules are often immersed, presumably shortening the time required to mature and preserving moisture. The **perennial shuttle** species are mostly thallose liverworts that have both desiccation-tolerant gametophytes and large

spores. **Fugitives** generally stay only one to two years while the habitat remains suitable at a site and produce small spores that permit them to be dispersed easily.



Figure 60. *Mniobryum wahlenbergii*, a moss that has little or no drought tolerance. Photo by Jan-Peter Frahm, with permission.

The short duration of the life cycle is one of the advantages provided to many desert bryophytes. In the southwestern desert habitat (USA), the desiccation-tolerant *Syntrichia ruralis* (Figure 39) requires a year to reach maturity, producing new innovations in midwinter and growing slowly through spring (Mishler & Oliver 1991). In late summer, it lengthens rapidly, completing its growth by midwinter. Female gametangia are initiated in midwinter and terminate the growth of these innovations. However, the female gametangia are present during the next 6 to 9 months on these innovations, ultimately disappearing some time between June and August. In the New Mexico populations observed by Mishler and Oliver, there were no male gametangia, and thus no sporophytes produced. Consequently, this plant must propagate entirely by vegetative means.

In the Negev Desert, southern Israel, the dioicous moss *Bryum dunense* takes advantage of fog and dew prior to the first winter rain to initiate its reproductive organs (Herrnstadt & Kidron 2005). The sporophytes are most common in partially shaded habitats and appear following the winter rains. This reproduction is supplemented by the typically more reliable reproduction through bulbils in the partially shaded and exposed habitats, whereas secondary protonemata are most abundant in the shaded habitats.

Alpert and Oechel (1985) hypothesized that even the xerophytic mosses cannot live in the most xeric habitats due to their inability to maintain a positive carbon balance. *Grimmia laevigata* lives under the xeric conditions of rocks and boulders. When subjected to such extreme conditions of long, severe drought and extreme temperatures, this moss supported the hypothesis.

### Sporophyte Damage

The leafy gametophyte is not the only generation affected by desiccation. For desert mosses, too little rainfall in early sporophyte development can also be a problem. In the Mojave Desert, Nevada, USA, the moss *Syntrichia inermis* (Figure 61) experienced 66% abortion of sporophytes due to a reduced winter-spring rainfall



(Stark 2002). But unusually heavy rains in the summer likewise resulted in an increase in sporophyte abortion from 9 to 43%. Stark suggested that the summer abortions may have been the result of membrane damage resulting from rapid drying as well as from high temperatures while hydrated. *Crossidium crassinervium* (Figure 62) experienced similar sporophyte abortions in the same desert (Stark 2005).



Figure 61. *Syntrichia inermis* dry, a moss whose sporophytes experience considerable abortion due to desiccation. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 62. *Crossidium crassinervium* with one young sporophyte, a moss whose sporophytes experience considerable abortion due to desiccation. Photo by Michael Lüth, with permission.

*Grimmia orbicularis* (Figure 63) can suffer sporophyte abortion as a result of poor timing. It was summer rainstorms in the Mojave Desert that led to the demise of ~50% of the sporophytes, mostly in the seta elongation phase (Stark 2001). As in *Syntrichia inermis* (Figure 61), Stark suggests that the abortion resulted from stresses caused by wet-dry cycles during summer heat, a time when the moss would normally be dry and have arrested metabolism. This may have been complicated by the premature seta elongation that resulted in more exposure during the remainder of the summer or that set in motion the physiology for capsule maturation at a time when insufficient nutrients were available.

The arid and semi-arid lands occupy approximately 40% of the land on planet Earth (Reed *et al.* 2012). Climate change that changes annual rainfall could result in profound mortality of bryophytes growing there. An increase of rainfall frequency, resulting in only a 1.2 mm increase in summer rainfall, reduced the moss cover of

*Syntrichia caninervis* (Figure 64) from approximately 25% cover to less than 2% in just one growing season. The addition of small precipitation events resulted in a negative carbon balance; larger events are able to maintain carbon balance. The loss of moss cover changed the nitrogen cycling, reducing soil fertility. On the other hand, increased temperature had no effect.



Figure 63. *Grimmia orbicularis*, a moss that suffers sporophyte abortion if the wet/dry cycles have the wrong timing during sporophyte development. Photo by Michael Lüth, with permission.



Figure 64. *Syntrichia caninervis*, a desert moss. Photo by Michael Lüth, with permission.

*Syntrichia caninervis* has served as a model for successful desert living by bryophytes. Wu *et al.* (2015) demonstrated that when only 2 mm of precipitation wets the leaves of *Syntrichia caninervis* (Figure 64), the moss loses carbon. It requires 5 mm of precipitation for a carbon gain. Hence, short storms can be detrimental to the moss, explaining the loss of moss cover with the increase in frequency of rainfall and gain of 1.2 mm rain in the Colorado Plateau, USA (Reed *et al.* 2012).

This loss of carbon is despite the rapid recovery of *Syntrichia caninervis* (Figure 64). Within only one minute, it recovers 90% of its photosynthetic yield (Zhang *et al.* 2011). In fact, this species can use moisture from dew and fog, collected and directed into the leaf by its hair points (Tao & Zhang 2012). In addition to the collection effect of the hair tips, mosses from dry habitats have high osmotic values that enable them to absorb water vapor from the air. These attributes seem almost contradictory to the



loss of cover due to a minor increase in rainfall events in the desert, but a short daytime rainfall is quite different from the prolonged moisture available from fog or dew at night. Daytime moisture from a short rainfall lasts for a very short time, apparently insufficient to recover the lost energy before high temperatures and evaporation shut it down. Yet this leaves the question of rebuilding energy at night. It suggests that it is the cellular changes that use up one readily available form of energy but do not permit rebuilding it, whereas the hydrated cells from dew are fully functional and ready for photosynthesis with the first light of day – there should be no delay at all. At this time the moss is still cool from the night and evaporation should be slower.

### Desiccation from Salt

Salt pans and regions of salt spray, when not under water, can be the most arid conditions of all. Few bryophytes are adapted to this regime, although some species of *Fontinalis* (Figure 65) can tolerate **brackish** (somewhat salty, often from a mix of fresh and salt water) waters. The liverworts *Riella helicophylla* (Figure 66), *R. numidica*, and *Carrpos* (?) are among the few (Schofield 1985).



Figure 65. *Fontinalis antipyretica*, member of a genus where some species tolerate brackish water. Photo by Bernd Haynold, through Wikimedia Commons.

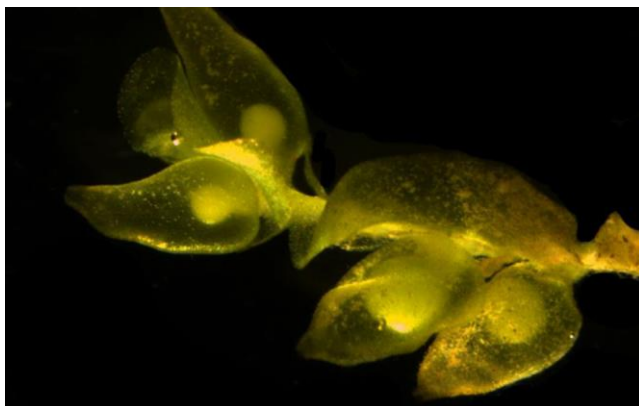


Figure 66. *Riella helicophylla*, a thallose liverwort that is able to tolerate brackish water. Photo by NACICCA, through Creative Commons.

### Flood Plains

The flood plain habitat is one of extremes. For part of the year the inhabitants are under water, but once the water recedes the habitat can become extremely dry. This regime requires different adaptations from other kinds of dry habitats.

A number of thallose liverworts exhibit drought or desiccation tolerance (Figure 69) and are able to live in these alternating habitats (Bischler 1998; Wood 2007). Such genera include fairly small liverworts with thick thalli and short life cycles: *Corsinia* (Figure 67), *Cronisia*, *Exormotheca* (Figure 68), *Monocarpus*, *Riccia* (Figure 52), and *Targionia* (Figure 70). But larger thalli in the *Aytoniaceae* [*Asterella* (Figure 71), *Mannia* (Figure 72), *Reboulia* (Figure 73)] also exhibit desiccation tolerance (Vitt *et al.* 2014). Much of this tolerance may be structural. For example, these genera typically roll their edges to avoid desiccation. Their pegged rhizoids serve as water conduits and help them to resist desiccation in periodically dry habitats by providing capillary spaces [e.g. *Mannia*, *Plagiochasma* (Figure 74), *Targionia*] (Duckett *et al.* 2014). On the other hand, liverworts from moist habitats tend to be drought intolerant (Figure 69). These include genera with thin thalli such as *Pellia* (Figure 75), *Fossombronia* (Figure 76), *Moerckia* (Figure 77), *Pallavicinia* (Figure 78), and *Symphyogyna* (Figure 79). Likewise, the primitive genera of *Haplomitrium* (*Haplomitriidae*; Figure 80), *Treubia* (*Treubiidae*; Figure 81), and *Apotreubia* (*Treubiidae*) all grow on constantly moist soil and are drought intolerant (Wood 2007).



Figure 67. *Corsinia coriandrina*, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.



Figure 68. *Exormotheca pustulosa*, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.



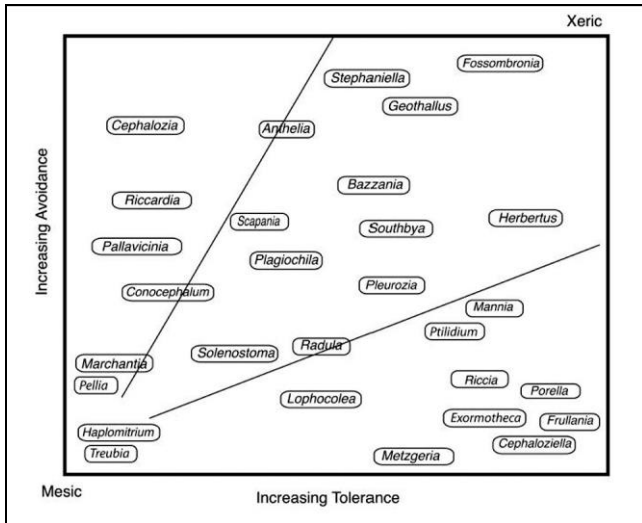


Figure 69. Comparison of liverwort genera with desiccation tolerance vs those with avoidance. Many species of *Riccia* are able to use the escape strategy by going dormant to avoid desiccation. From Vitt *et al.* 2014.



Figure 72. *Mannia fragrans*, a large thallus with desiccation tolerance. Note how it rolls as it dries. Photo by Michael Lüth, with permission.



Figure 70. *Targionia lorbeeriana*, member of a genus with thick thalli and short life cycles. Note the black marsupia visible from the ventral side of the thalli. Photo by Michael Lüth, with permission.



Figure 73. *Reboulia hemisphaerica*, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.



Figure 71. *Asterella saccata*, a large thallus with desiccation tolerance. Photo by Jan-Peter Frahm, with permission.



Figure 74. *Plagiochasma appendiculatum*, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.





Figure 75. *Pellia epiphylla*, member of a genus with thin thalli that are desiccation intolerant. Photo by David T. Holyoak, with permission.



Figure 76. *Fossombronia caespitiformis*, member of a genus with thin thalli that are desiccation intolerant. Photo by Des Callaghan, with permission.



Figure 77. *Moerckia blyttii*, member of a genus with thin thalli that are desiccation intolerant. Photo by Michael Lüth, with permission.



Figure 78. *Pallavicinia lyellii*, member of a genus with thin thalli that are desiccation intolerant. Photo by Jan-Peter Frahm, with permission.



Figure 79. *Symphyogyna brasiliensis* female plant, member of a genus with thin thalli that are desiccation intolerant. Photo by George J. Shepherd, through Creative Commons.



Figure 80. *Haplomitrium hookeri*, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Janice Glime.





Figure 81. *Treubia* sp, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Jan-Peter Frahm, with permission.

Volk (1984) elucidated the behavior of the genus *Riccia* in these flood plain circumstances in Namibia. These are seasonally very dry habitats and members of the genus *Riccia* are very common. In this genus, the dorsal (upper) surface is unable to take in water. The ventral surface can absorb water through capillary action among rhizoids and scales, and in some cases hairs. During the dry period, they roll their thalli, exposing these rhizoids and scales from the ventral surface. This rolling thus facilitates the uptake of water from rainfall when it first occurs. These perennial species are very drought resistant and can survive up to seven years with no new water input. They are able to endure heat to greater than 80°C when dry, whereas temperatures above 50°C injure wet plants. They are unable to compete with other plants, but annual species survive by producing large numbers of spores. Perennial species produce fewer spores and survive primarily by going dormant.

## Arctic and Antarctic

Kennedy (1993) asked "What limits the presence, distribution, and abundance of life in Antarctica?" To this question he answered that isolation restricts arrival and the paradigm has been that the extreme cold limits survival. But he challenges the latter tenet, suggesting that instead it is moisture that limits the organisms on vertical, horizontal, and temporal scales. Gradients in meltwater, seepage, and upwelling create moisture differences on a continental scale.

Antarctic communities, in particular, experience physiological extremes in water availability and bryophytes must survive both desiccation and submergence (Wasley *et al.* 2006). Growth rate is slow (mean for 17 yrs was 3.7 g dw m<sup>-2</sup> y<sup>-1</sup>) (Kanda 1986), providing limited opportunity to compensate for losses during drying. Exposure accounts for the loss of bryophyte flora in many circumstances. This can be particularly true in Arctic climates. Flock (1978) found that acrocarpous mosses dominated in areas with only light snow cover, but in areas with deep snow the pleurocarpous mosses were more abundant. The reason for this is unclear, but one might hypothesize that pleurocarpous mosses are less likely to suffer apical damage from the heavy snow, and even if they do, they usually have numerous growing points to permit their

continuation. In this seasonally arid climate, primarily soil moisture and slope account for the distribution of moss communities (LaFarge-England 1989).

At Wilkes Land, Antarctica, colonies of *Bryum algens* with a dense tomentum of rhizoids held significantly more water than those with sparse rhizoids (Lewis Smith 1988). In *Schistidium antarcticum*, the dense shoot arrangement facilitates its high water-holding capacity in the turf form, whereas when this species has less densely packed shoots and thicker cell walls in xeric cushions it maintains a lower water content. On the other hand, the loss of water was much faster in the turf form and the tomentose form of *Bryum algens*, but this relationship was reversed when it was expressed as a percentage of the initial water content. The mosses take several times longer to reach minimal water conditions when compared to the lichens.

Some mosses form large mounds on the Antarctic terrain. Robinson *et al.* (2000) were able to demonstrate the relationship of desiccation tolerance to habitat in three of these moss species. *Schistidium antarcticum* (Figure 82), limited to relatively wet sites, had the least ability to sustain photosynthesis during desiccation. The worldwide *Ceratodon purpureus* (Figure 83) had the most and inhabited the driest sites. Intermediate in tolerance was *Bryum pseudotriquetrum* (Figure 84), which occupied intermediate habitats and exhibited the greatest plasticity of the three. These responses fit their typical habitat distribution, with *Ceratodon purpureus* being common in the driest sites and *Schistidium antarcticum* living in relatively wet sites. Following desiccation, *Bryum pseudotriquetrum* contains **stachyose**, a soluble carbohydrate known to provide desiccation tolerance to seeds.

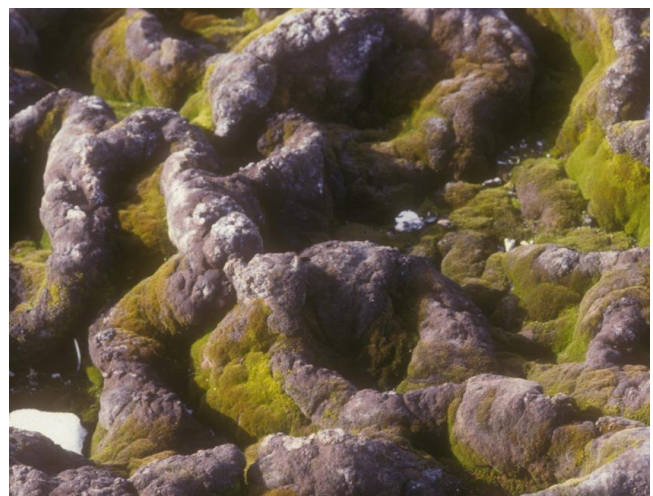


Figure 82. *Schistidium antarcticum*, a moss limited to relatively wet sites. Photo by Rod Seppelt, with permission.

By contrast, *Ceratodon purpureus* has poor survival when it is submerged (Wasley *et al.* 2006). The wet habitat *Schistidium antarcticum*, on the other hand, has high submersion tolerance. *Bryum pseudotriquetrum* (Figure 84) is an intermediate species that is able to co-exist with both of these species and has flexible responses.

Davey (1999) summed up the Antarctic situation by stating that mosses from hydric habitats had lower carbohydrate and higher protein, nitrogen, and phosphorus content than species from drier habitats, suggesting that the



constant flushing provided nutrients. This emphasizes another aspect of the importance of both water and physical factors in the success of Antarctic mosses.



Figure 83. *Ceratodon purpureus*, the moss with the greatest ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al.* (2000). Photo Rod Seppelt, with permission.



Figure 84. *Bryum pseudotriquetrum*, the moss with intermediate ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al.* (2000). Photo by Rod Seppelt, with permission.

Are the responses of Antarctic species different from those of other habitats? Apparently not very. Davey (1997) examined effects of various desiccation regimes on photosynthesis of 14 bryophyte species. Using testing intervals of 6 months and 12 months of desiccation, Davey found that the photosynthetic rate decreased as the length of dehydration period increased in all these species. The xeric species had greater retention of photosynthetic rate than did the hydric species, but even the hydric species retained some photosynthesis. Repeated cycles of wet/dry do more harm than continuous dehydration to the hydrophytic species, but the mesophytic and xerophytic species show the opposite response, suggesting that the mesophytic and xerophytic species were able to recover better during short periods of hydration. As the season progresses from spring to autumn, the percentage loss of photosynthetic rate following dehydration/rehydration increases, and this change is most evident in the hydrophytic species. At the same time, it appears that the long winters with concomitant water stress have driven

these species to similar adaptations to those of some desert species.

Longton (1988a) concluded that phenotypic plasticity, opportunistic responses in CO<sub>2</sub> exchange, and a poikilohydric water strategy endowed the polar bryophytes with their considerable frost and desiccation tolerance. But he was quick to point out that this plasticity was not unique to polar bryophytes, but rather was common among bryophytes in general. To really understand polar adaptations we need to do physiological studies on the **endemic** (restricted to a certain area) species.

Bryophytes and water level are intimately related in the Arctic. Where the water table is maintained above the bryophyte surface, marshes develop. Where the water table is high above the permafrost, but remains below the bryophyte surface, fens develop. These moss tundras normally have no standing water and water courses are able to move through them from below the surface, maintaining the fen status. The standing water level is thus the primary factor determining the species alliances in that area. Some species complexes, such as that of the *Catoscopium nigratum* community (Figure 85), require a temporary period of desiccation to subsist (Vanderpuye *et al.* 2002).



Figure 85. *Catoscopium nigratum* exhibiting its fen community where temporary desiccation is required. Photo by Michael Lüth, with permission.

The role of bryophytes in mediating water in the sub-Arctic is crucial for making climate models that adequately predict the effects of climate change. Using *Sphagnum fuscum* and *Polytrichum piliferum*, Street *et al.* (2012) demonstrated that the model does not adequately predict the effect of turf water content on their primary productivity fluxes.

In subarctic mires, water balance often determines which species will dominate (Sonesson *et al.* 2002). When the codominant mosses *Sphagnum fuscum* and *Dicranum elongatum* were subjected to increased precipitation, both species increased their growth rate, up to 5 mm per day. *Sphagnum fuscum* had a 50% higher response in growth compared to *Dicranum elongatum*, a species of drier habitats than those of *S. fuscum*. In winter, the responses were affected by the neighboring plants. *Sphagnum fuscum* grew better when it was next to *Dicranum elongatum*, but *D. elongatum* also did better when next more *D. elongatum*.

In the Arctic tundra, Rixen and Mulder (2005) found that high moss species diversity increased productivity, especially in low-density plots, when the plots were



watered regularly. Furthermore, moisture retention was greater in plots with high species richness. Furthermore, plant height was greater in mixed cultures than in single-species cultures. Likewise, 10 out of 12 species grew better in mixture than in monoculture when the density was high and droughts were short. It is interesting that this is the opposite of the relationships found in temperate moss communities.

As suggested by the Antarctic species discussed above, growth form is important in these cold environments that are frequently subjected to water stress. In the subalpine habitat, Nakatsubo (1994) found that large cushions and compact mats were the most common among the xerophytic species. The mesophytic species of the coniferous forest, by contrast, were smooth mats, wefts, and tall turfs. The relation between evaporation rate per basal area of the moss and dry weight per basal area of the colony correlated closely with the growth form. Nakatsubo concluded that the difference in the evaporation rate per weight between the xerophytic and mesophytic species was largely due to the difference in dry weight per basal area of the colony, and that the growth forms of the xerophytic species were suitable for increasing dry weight per basal area of the colony without increasing surface roughness. Increasing surface roughness would lead to an increase in evaporation rate due to increased exposed surface area and increased air turbulence.

## Forest Floor

The forest floor would seem to be the most straightforward and familiar habitat for most of us who have lived our lives in the temperate zone and who hunt mosses. But water relations in this habitat are not so simple. Bryophytes may actually deprive the trees of water in several ways.

In her collections of water samples under moss mats and without moss mats in a Jack pine forest (*Pinus banksiana*), Scafone (unpublished data) found that there were many occasions when 1-2 cm of water accumulated in the collectors with no moss, but the collectors under the moss mats were dry. This means the soil does not receive any of the throughfall during short or light rainfall events where there is a substantial moss mat on the surface. Such a cover is common in boreal and pine forests, depriving upper fine roots of much needed moisture.

But it appears that mosses can even derive their moisture at night from the soil. Carleton and Dunham (2003) accounted for moisture available to mosses during dry summer weather by explaining nocturnal cooling on the forest floor. Cooling of the soil surface at night was sufficient to bring the moss to dew point, reversing the daytime temperature gradient in the forest floor organic profile. By using a vapor barrier for comparison, they determined that the soil provides an upward movement of water at night that permits moss shoots to survive summer "dry-downs." This happens most noticeably in late summer when organic layers have accumulated the most warmth.

## Temperate Epiphytes

Epiphytes are subjected to feast or famine for their water needs. In the growing season, they can get flooded by stem flow and may grow best on the side of the tree that

gets better stem flow. In the winter they often remain exposed, unprotected by snow, and subject to the harsh, dry winds.

Trynoski and Glime (1982) demonstrated the apparent role of winter when they mapped the locations of epiphytic bryophytes in a northern deciduous forest in the Keweenaw Peninsula of Michigan, USA. The highest cover at the base was on the north side of the tree, but contrary to popular belief, midway between the base and breast height it was greatest on the south side. They attributed this southern location to the drying winds from the north and a safe haven in the space between the tree trunk and the snow that provided a moist microcosm where sufficient sun could penetrate through the snow to permit photosynthesis in winter.

Where winters are not in a constant state of snow cover, they may afford a better growing season for epiphytes due to cooler temperatures and fewer dry days. In British woods, Pitkin (1975) found that most of the growth of the epiphytes *Hypnum cupressiforme* (Figure 86) and *Platygyrium repens* (Figure 87) occurred in autumn and winter. A similar pattern of growth was found for epiphytes at a second location, and growth periods in both locations corresponded with greater moisture. When summers were wet, the winter growth did not increase proportionally to the summer increase. In wetter climates, temperature and day length have greater importance in determining growth rates.



Figure 86. *Hypnum cupressiforme*, a species that grows mostly in winter in British woods. Photo by Michael Lüth, with permission.



Figure 87. *Platygyrium repens* with bulbils, a species that grows most in autumn and winter in British woods. Photo by Michael Lüth, with permission.



Wu *et al.* (1987) found that epiphyllous liverworts in southeast China required about two hours of direct light and ten hours of diffuse light in winter, with light, temperature, and humidity being the primary factors to control their distribution.

## Tropics, Rainforests, and Cloud Forests

Cloud forest (Figure 88) and rainforest bryophytes can experience a wide range of water status in a single 24-hour period (Zotz *et al.* 1997). In a submontane tropical rain forest in Panama, both low and high water content limited carbon gain significantly on a daily basis for bryophytes exhibiting a variety of life forms. More than half of the daily carbon gain (mean 2.9 mg C per g plant) is lost through respiration at night.



Figure 88. *Macromitrium* habitat on a tree in a New Zealand cloud forest. Photo by Vita Plasek, with permission.

Although we are beginning to understand the broad aspects of tropical bryophyte ecology, understanding of their physiology has been hampered by taxonomic difficulties and remoteness of the study site from most of the research labs. Hence, only a few studies exist on their desiccation tolerance (*e.g.* Renner 1933; Biebl 1964a, b).

Johnson and Kokila (1970) reviewed desiccation responses in primitive photosynthetic organisms and surmised that in the algae, accumulation of fat in cells, thickening of the cell walls, and accumulation of mucilage can facilitate desiccation resistance. Other characters that correlate with resistance in some algae include resistance to plasmolysis in a hypertonic solution, rigid and viscous protoplasm, and more abundant granules. But in the mosses *Bryum* (Figure 1) and *Mnium* (Figure 40) the viscosity decreased during drying. Hence, Johnson and Kokila considered how applicable these attributes might be

to the desiccation tolerance of tropical bryophytes. They examined ten species that represented a wide range of habitats and exhibited a number of structural adaptations that might contribute to survival of drought.

Some species exhibit damage near the tips, with damage spreading slowly to the lower leaves, and others experience more apparent damage near the base (Johnson & Kokila 1970). The species they studied fell into two groups that mostly coincided with this pattern of damage progression:

Low resistance to desiccation:

(those with \* have damage near the tips):

*Calymperes moluccense*\*

*Fissidens crassinervis*

*Leucobryum sanctum*\*

*Semibarbula orientalis*\*

*Syrrhopodon loreus*\*

High resistance to desiccation:

*Bryum coronatum* (Figure 89)

*Leucophanes octoblepharioides* (Figure 93)

*Neckeropsis lepneana* (Figure 94)

*Paraleucobryum longifolium* (Figure 95)

*Pelekium velatum*



Figure 89. *Bryum coronatum* surviving on an exposed rock. Photo by Michael Lüth, with permission.

In the tropics, epiphytes can experience long periods of drought during the dry season. Salazar Allen (1985) found that the genus *Leucophanes* (Figure 90) survives the drought by an unusual life form strategy. *Leucophanes* is an acrocarpous moss that may be branched or unbranched and that forms turfs. The unusual feature is that leaf-tip gemmae germinate on the parent plant to form a new layer of gametophores (Figure 91). In many bryophytes, there seems to be an inhibitory substance that prevents such occurrences (see interaction chapter). However, in *Leucophanes*, this seems to be an important adaptation for water retention. Lacking subterminal innovations, *Leucophanes* benefits from the thicker turf where the numerous stems can protect each other from drying out. It is my guess that if the tips were to become so dry that they would die in an unusually dry year, there would be at least some lower (older) stems with enough life remaining to re-establish the colony. If not, surely some of the gemmae would survive. In any event, this habit of germination of gemmae within the parent colony provides *Leucophanes* with a dense turf that could resist drying.



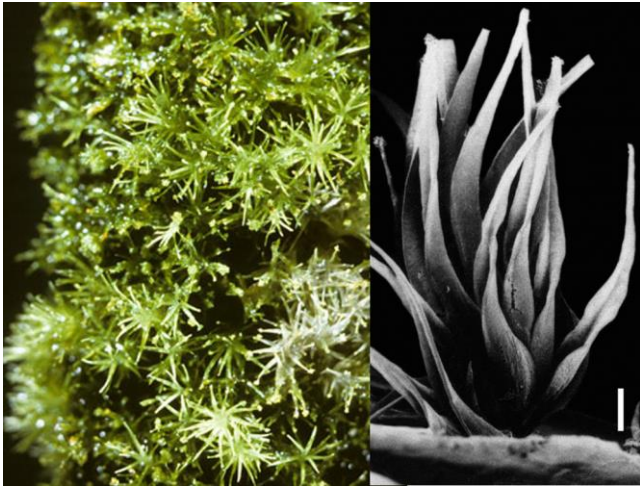


Figure 90. *Leucophanes molleri* on tree bark. **Left:** showing plants with leaves tipped with gemmae and **Right:** gemmae on leaf tip. Bar = 20  $\mu$ m. Photos courtesy of Noris Salazar Allen.



Figure 92. *Pelekium velatum*, a species with very small leaves and papillae. Photo © <www.NatureLoveYou.sg>, with online permission.



Figure 91. Protonemata forming at the tip of a gemma of *Leucophanes molleri* while the gemma is still attached to the parent leaf. Photo courtesy of Noris Salazar Allen.

Among those adapted for drying, with little damage down to 10% humidity, *Leucophanes octoblepharioides* (Figure 93) has abundant leucocysts that serve as a water reservoir (Johnson & Kokila 1970). The costa is thickened and prevents the leaf from collapsing. *Paraleucobryum longifolium* (Figure 95), a species of exposed situations in the hill forest, has a thickened costa and thick-walled lamina cells. *Pelekium velatum* (Figure 92) uses a different strategy with very small leaves pressed against the stem and with papillose cells. *Neckeropsis lepineana* (Figure 94) holds its secondary branches at an angle to the tree trunk in a way that subjects it to drying.

Those species with low desiccation resistance are damaged at humidity of 63% and are likely to die at 10% (71-94% of cells damaged) (Johnson & Kokila 1970). These species live in habitats that have near saturation humidity levels. Three of these species live on the ground where the humidity is constantly and exceedingly high. Two are **corticolous** (growing on bark) species [*Calymperes moluccense* (Figure 96) and *Syrrhopodon loreus*) that live on the wettest side of the tree in areas that are constantly wet due to runoff.



Figure 93. *Leucophanes* sp. *Leucophanes octoblepharioides* has low resistance to plasmolysis and is shown here surviving on bark. Photo by Niels Klazenga, with permission.



Figure 94. *Neckeropsis lepineana* surviving on bark with its branches extended – a common growth form in the tropics. Photo by Li Zhang, with permission.





Figure 95. *Paraleucobryum longifolium* on rock, a species adapted for drying by a thickened costa and thick-walled lamina cells. Photo by Janice Glime.



Figure 96. Saturated *Calymperes* sp. *Calymperes moluccense* lives on the wettest sides of trees in humid areas and is desiccation intolerant. Photo by Niels Klazenga, with permission.

Pardow and Lakatos (2013) explored the desiccation tolerance of epiphytic bryophytes from contrasting microsites in tropical lowland forests of French Guiana. Canopy species are well adapted, as indicated by the recovery of chlorophyll fluorescence, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after 9 days at 43% relative humidity. On the other hand, understory species were sensitive to desiccation and were only able to withstand a reduction to 75% relative humidity. The bryophytes were able to reactivate by reaching equilibration with water vapor as their only moisture source.

Pardow *et al.* (2012) noted the importance of lowland cloud forests in the Guianas as a site for high epiphytic bryophyte diversity. This area is subject to frequent early morning fog events that provide moisture for the bryophytes. The growth forms were those that could take greatest advantage of this cloud moisture: tail, weft, and pendent (Figure 97).



Figure 97. *Papillaria*, a pendent moss in the cloud forest at Mt. Budawang, Australia. Photo by Peter Woodard, through Public Domain

Romanski *et al.* (2011) likewise studied epiphytes, in this case in the lower montane (2400 m) rainforest of Peru. A single tree of *Weinmannia* supported 110 bryophyte species (77 hepatics, 1 hornwort, 32 mosses). They divided the tree into **Johansson zones** (lower trunk, upper trunk, mid-crown, mid-outer crown, outer crown) and found the greatest species richness and abundance on the upper trunk and large branches of the mid-crown. Exposure to light and desiccation appeared to account for the bryophyte distribution, but more research is necessary to tease out these relationships.

Atala *et al.* (2013) expressed concern that dendroid mosses with conducting tissues likewise lacked study. They examined desiccation tolerance in the *Dendroligotrichum dendroides* (Figure 98) from Chile, where it grows in the understory of temperate forests. They tested plants from two contrasting moisture conditions and found that both populations exhibited desiccation tolerance. But the responses were not equal. Those from the northern population lost water more slowly and recovered the PSII Fv/Fm to higher values when compared to the southern population. They suggested that exposure to summer droughts in the northern population could contribute to differences in their response.



Figure 98. *Dendroligotrichum dendroides*, a Chilean species with desiccation tolerance. Photo by Felipe Osorio-Zúñiga, with permission.



## Epiphytes

Epiphytes in most habitats have sharply contrasting moisture conditions. When it rains, they can be in a river of water rolling down the tree trunks. But when the rain stops, they are elevated where there is more access to wind and drying can be rapid.

These conditions are not so severe in a cloud forest due to the moisture in the clouds. Bryophytes are able to use such moisture and some are even adapted to collect it by providing fine wirelike structures, expressed as such structures as thin awns or pendent growth forms.

In two Venezuelan cloud forests, León-Vargas *et al.* (2006) the rainfall averages only 20 mm or less in January and February, 200 mm or more in August to October, and variable year-round. Continuous 100% relative humidity occurred 8.5% to 52.2% of the time. Humidity increased at night. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All of the six pendent bryophyte species survived at least a few days of desiccation.

### Pendent Mosses

**Pendent mosses** (those that hang down; Figure 99-Figure 100) often suffer desiccation, with little surrounding them to help hold in the water. *Floribundaria floribunda* (Figure 99) and *Pilotrichella ampullacea* (Figure 100) from Uganda humid tropical forests survive partly by avoidance, holding large quantities of external capillary water, with *Pilotrichella ampullacea* holding approximately twice as much as *Floribundaria floribunda* (Proctor 2002). Both species were able to recover from 11 months of dry storage at 5°C, although they required several days to recover, with *F. floribunda* recovering more slowly and less completely. Following 20 hours of air drying, *P. ampullacea* achieved a positive carbon balance within 30-60 minutes after rewetting.



Figure 99. *Floribundaria floribunda*, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.

León-Vargas *et al.* (2006) studied the epiphytes in the Venezuelan cloud forests. The rainfall there drops to an average of 20 mm or less in January and February and increases to 200 mm or more from August to October. Nevertheless, the longest recorded dry period was only 143 hours. Nighttime humidities of 90% relative humidity were common, with 100% for significant periods, creating cloud water deposition in about 50% of the nights. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All six species of pendent bryophytes survived for at least a few days of desiccation; these recovered better from high than from low humidities.

### Altitude Differences in the Tropics

In the tropics, altitude can have a strong effect on both biomass and diversity among bryophytes (Bader *et al.* 2013). The lowlands are characterized by low abundance and low species richness. These could be a consequence of short daily periods of suitable light, temperature, and moisture and nighttime high respiration due to high temperatures. Moisture regimes are quite different, with lowland forests having more concentrated but less frequent precipitation than montane cloud forests. They furthermore have sunny mornings that cause rapid drying. The high levels of moisture in high altitude cloud forests is manifest in a high diversity and cover by bryophytes (Figure 101). But both lowland and montane species are able to survive more than 80 days of dry periods, far exceeding the duration of lowland tropical dry periods.



Figure 100. *Pilotrichella ampullacea*, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.





Figure 101. Elfin cloud forest in the Luquillo Mountains of Puerto Rico. Photo by Janice Glime.

## Summary

Because of their small size, bryophytes are able to occupy microsites in otherwise unfavorable habitats. Their ability to recover from dehydration typically correlates with habitat, with aquatic bryophytes having little ability to tolerate dehydration and resume photosynthesis, whereas dry habitat bryophytes can withstand extended periods of desiccation. In aquatic bryophytes, ribosomes can be damaged irreversibly and membranes are more likely to be damaged than in dry habitat taxa. On the other hand, there is no difference in nitrogen reductase activity between dry and wet habitat bryophytes.

Peatland bryophytes (*Sphagnum*) of lawns and hollows are typically desiccation tolerant, benefitting from inducible tolerance. Those of hummocks generally are intolerant but are desiccation resistant. Submersed species rely on the water of their habitat and have little tolerance for desiccation.

Aquatic bryophytes have poor desiccation tolerance, especially with rapid drying, but usually benefit from slow drying and sometimes can survive considerable dry periods.

A number of bryophytes are xerophytic. Their life cycle is typically short and the strategy is adapted to the short periods of rainfall. But in some arid habitats, nighttime dew is the only source of water for bryophytes. Hair points gather the dew and facilitate its uptake. In others, cooling of soil can bring bryophytes to dew point and draw water upward from the soil. The real limiting factor is carbon balance. If the bryophyte loses too much carbon by respiration and experiences a hydrated state for which the duration is too short to recover it, the bryophyte will perish. Rapid repair and recovery of photosynthesis permit these bryophytes to take advantage of short periods of hydration. The rapid daytime drying makes constitutive desiccation tolerance essential for survival where short daytime storms are common. But at least some of these bryophytes also have inducible desiccation tolerance. Some use an **escape strategy** of desiccation-tolerant gemmae, spores, and protonemata that help these bryophytes succeed in habitats with extensive dry periods. Nitrite and nitrate reductase both seem to be involved in

recovery, but more research is needed to determine the mechanisms involved. Leaf rolling and papillae seem to provide a protective role, perhaps by reducing light damage of dry cells and facilitating water uptake, but their role in water retention remains to be demonstrated. Compact growth form is also important.

Flood plains have extremes of habitat and require special strategies to weather these. Many of the bryophytes adapted to these extremes are species of the thallose liverwort *Riccia*. This genus is able to go dormant when it is dry with a variety of strategies, including rolling the thallus, surviving as tubers, having hairs on the surface. Some have small thalli with short life cycles; others have thick thalli that survive the desiccation.

In the Arctic and Antarctic, frost can be a desiccant. Water height above permafrost determines existence of fens, where bryophytes are emergent, and marshes exist where the water table is high above the bryophyte surface. Arctic bryophytes suffer from exposure that creates desiccating conditions. Aspect and angle of slope play important roles in speed and frequency of drying. Acrocarpous mosses do better in areas of light snow cover, whereas pleurocarpous mosses suffer less apical damage from heavy snow. In the Antarctic, the longer the dry period, the lower the subsequent photosynthetic rate, especially among hydrophytic species.

On the forest floor, bryophytes may sequester all the water from a brief rainfall (1-2 cm). In the dry summer, bryophytes may derive moisture from the soil during the cooling temperatures.

Temperate epiphytes may take advantage of cooler temperatures of winter for maximum growth.

In the tropics, carbon balance can, as in the desert, be a problem. When the mosses are hydrated at higher temperatures, respiration loss exceeds photosynthetic gain. This is generally not a problem at higher altitudes in the cloud forests; bryophytes are abundant on nearly every substrate there. Physiology is poorly known for tropical bryophytes, but it appears that they have similar adaptations to those of other locales with similar moisture conditions such as thick costa and thick cell walls. Some (*Leucophanes*) have leaf-tip gemmae that germinate and layer the colony, making a thick turf.

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