

CHAPTER 7-8

WATER RELATIONS: HABITATS



Figure 1. *Bryum caespiticium* 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.

Habitat Relations

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* 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).

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*, *Metzgeria temperata*, *Microlejeunea ulicina*, *Neckera pumila*, and *Hypnum andoi* were restricted to habitats with high moisture availability. *Syntrichia ruralis*, *Grimmia pulvinata*, *Tortula muralis*, and *Aulacomnium androgynum* only occurred as epiphytes in locations with low moisture. They did not sample these species in other habitats.

In mature black spruce forests of central Alaska, the endohydric *Polytrichum commune* is able to avoid moisture stress more so than such ectohydric taxa as *Hylocomium*

splendens (Figure 2; Skré *et al.* 1983). The latter species remains below its compensation point for water for nearly 50% of the July growing season.



Figure 2. *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, Norr (1974b) 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 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.

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 3).

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*, 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 3. *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 quite dry when the stream level is low in mid and late summer. Photo by Janice Glime.

Arid Habitats

Contrary to the popular concept that mosses must grow in wet places, a number of species are **xerophytic**, that is, adapted to 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⁻², but at least 18 different species are able to survive, the most common being tuft-forming taxa such as *Syntrichia ruralis*, *Grimmia laevigata* (Figure 4), and *Bryum caespiticium* (Figure 1).

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*, *Grimmia* spp., *Syntrichia* spp., and *Weissia controversa*. 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 4. *Grimmia laevigata*, a desert survivor. Photo by Michael Lüth.

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 5), 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 5. *Syntrichia ruralis*, a drought-tolerant moss. Photo by Michael Lüth.

One factor in this story is the role of nitrite. Nitrite accumulates during slow dehydration of *Syntrichia ruralis*, but not when desiccation is rapid (Mahan *et al.* 1998). Upon rehydration, the nitrite in the slowly-dried moss declined and reached 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 *Mnium hornum*; thus we need further research to understand the conditions under which it is detrimental vs adaptive.

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 KNO_3 did affect the increase in NR activity between these two types, with the desiccation-tolerant *Syntrichia ruralis* var. *arenicola* increasing activity by a factor of 3 while the desiccation-intolerant *Dicranum majus* and *Hookeria lucens* had a 6-fold increase in activity. Following rehydration, *Syntrichia ruralis* exhibited a marked decline in NR activity during the first hour, whereas the epiphytic/saxicolous *Porella platyphylla* (Figure 6) maintained a relatively constant low level in the light while increasing it 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.



Figure 6. *Porella platyphylla*, an epiphytic/saxicolous liverwort. Photo by Michael Lüth.

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 failed (Frey & Kürschner 1991).

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 these 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, papillae in *Andreaeobryum macrosporum* are constructed in such a way that they provide a channel for the uptake of water.

I have suggested that papillae 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 it 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 apocarpa*, *Grimmia laevigata*, *Hedwigia ciliata*, *Orthotrichum rupestre*, and *Syntrichia ruralis* var. *crinata*. 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 most 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.

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 7). 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.

Aspect separated the evaporation stresses even more clearly (Figure 8), 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 9, 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*, *Syntrichia*, and the thallose liverwort *Riccia* 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*, *Funaria*, and *Cephaloziella* seem to lack any structural

adaptations to their usually xeric habitat, although *Ceratodon* does have crispate leaves and rolled margins.

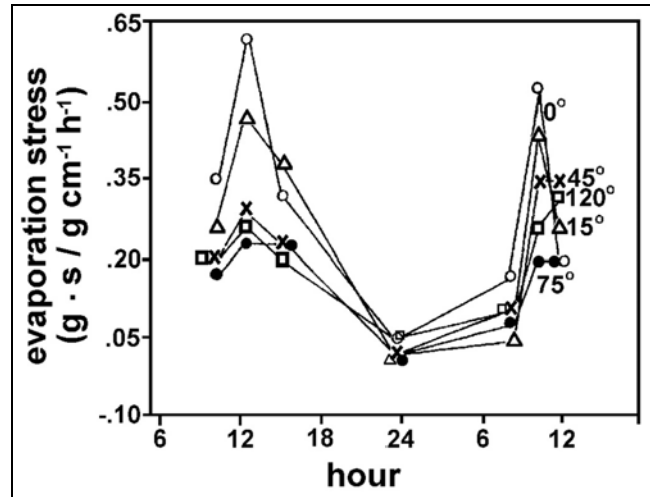


Figure 7. Effects of degree of slope on potential evaporation on 21-22 February 1980 for mosses (based on uniform paper samples) on arid north sides of rocks in five slope microsites. (n=4) Modified from Alpert (1982).

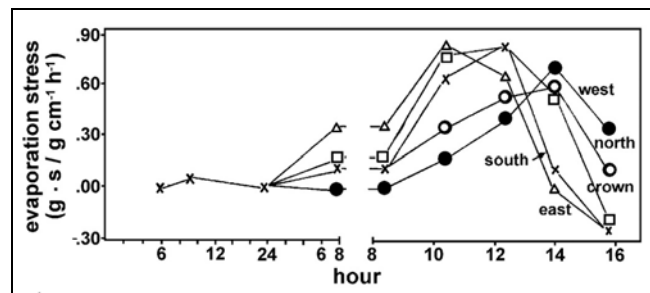


Figure 8. Effect of aspect on potential evaporation on 7-8 March 1980 for mosses (based on uniform paper samples) on arid 45° slope in five aspect microsites. (n=4) Modified from Alpert (1982).

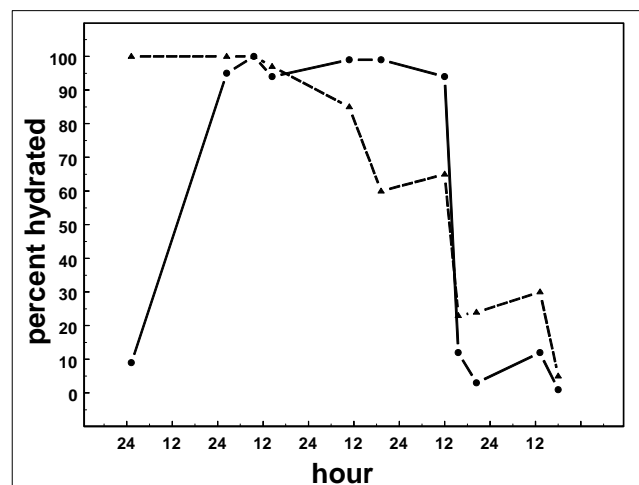


Figure 9. Percent hydration of natural moss cover on boulders following nighttime rainfalls of ~5 mm in spring and winter. Redrawn from Alpert (1982).

A comparison of mosses from a variety of habitats in Israel revealed varying degrees of drought tolerance that

related well to their habitats (DiNola *et al.* 1983). The desert mosses *Tortula brevissima* 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* behaved similarly to the desert mosses, but *Homalothecium aureum* (Figure 10) and *Didymodon tophaceus* (Figure 11), more mesic mosses, had slow recovery after desiccation. *Mniobryum* sp. had almost no drought tolerance and was killed by the prolonged drying.



Figure 10. *Homalothecium aureum*, a mesic moss. Photo by Michael Lüth.



Figure 11. *Didymodon tophaceus*, a mesic moss. Photo by Michael Lüth.

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* can tolerate brackish waters. The liverworts *Riella helicophylla*, *R. numidica*, and *Carrpos* are among the few (Schofield 1985).

Longton (1988) 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 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 at a site and produce small spores that permit them to be dispersed easily.

In the southwestern desert habitat (USA), the desiccation-tolerant *Syntrichia ruralis* (Figure 5) 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 tropics, epiphytes can experience long periods of drought during the dry season. Salazar Allen (1985) found that the genus *Leucophanes* (Figure 12) 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 13). 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. In any event, this habit of germination of gemmae within the parent colony provides *Leucophanes* with a dense turf that could resist drying.

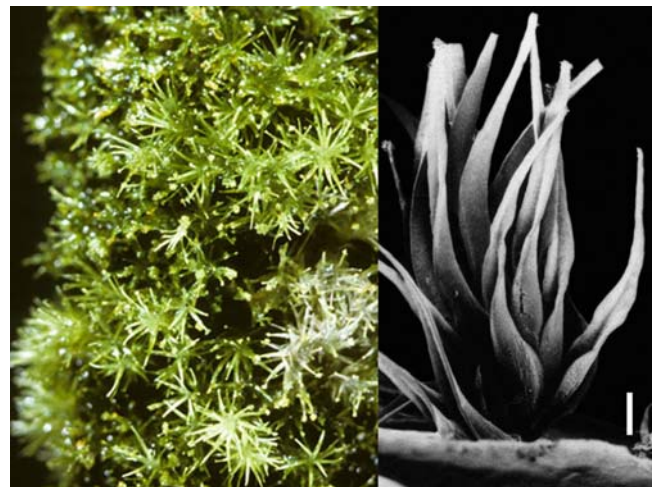


Figure 12. *Leucophanes molleri* on tree bark. **Left:** showing plants with leaves tipped with gemmae and **Right:** gemmae on leaf tip. Bar = 20 μ m. Photos by Noris Salazar Allen.



Figure 13. Protonemata forming at the tip of a gemma of *Leucophanes molleri* while the gemma is still attached to the parent leaf. Photo by Noris Salazar Allen.

The leafy gametophyte is not the only generation affected by desiccation. *Grimmia orbicularis* 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). 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.

Pendant mosses (those that hang down; Figure 14) often suffer desiccation, with little surrounding them to help hold in the water. *Floribundaria floribunda* and *Pilotrichella ampullacea* 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 do so, with *F. floribunda* recovering more slowly and less completely. Following only 20 hours of air drying, *P. ampullacea* achieved a positive carbon balance within 30-60 minutes.



Figure 14. Pendant mosses in a forest in Kyushu, Japan. Photo by Janice Glime.

Arctic

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).

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 15), require a temporary period of desiccation to subsist.



Figure 15. *Catoscopium nigratum* exhibiting its fen community where temporary desiccation is required. Photo by Michael Lüth.

In the Antarctic, Robinson *et al.* (2000) were able to demonstrate the relationship of desiccation tolerance to habitat in three moss species. *Schistidium antarcticum* (Figure 16), limited to relatively wet sites, had the least ability to sustain photosynthesis during desiccation. *Ceratodon purpureus* (Figure 17) had the most and inhabited the driest sites. Intermediate in tolerance was *Bryum pseudotriquetrum* (Figure 18), which occupied intermediate habitats and exhibited the greatest plasticity of the three.



Figure 16. *Schistidium antarcticum*, a moss limited to relatively wet sites. Photo by Rod Seppelt.



Figure 17. *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.



Figure 18. *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.

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*), Scafione (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.

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.

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.

In some arid habitats, nighttime dew is the only source of water for bryophytes. In others, cooling of soil can bring bryophytes to dewpoint 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.

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