

# CHAPTER 7-5

## WATER RELATIONS: PHYSIOLOGICAL ADAPTATIONS

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Figure 1. *Riccia cavernosa*, a thallose liverwort that dries out during drought and recovers in the fall when rain returns. Photo by Jan-Peter Frahm, with permission.

### Water Relations on Land

Proctor (2014) points out that one of the basic needs of bryophytes is that of coping with the intermittent availability of water. To this end, poikilohydry is efficient at the small scale of a bryophyte, whereas endohydry is more beneficial for the large tracheophytes.

Physiological adaptations relate on one end to the morphology and on the other to the biochemistry. Although we have recognized morphological characters for a very long time, few have actually been tested experimentally on a large scale for their adaptive value in altering physiology. The biochemical adaptations, on the other hand, constitute a new and emerging field of bryology, one that coincides closely with physiology of tracheophytes. By using the more easily studied bryophytes, we have gained the possibility of better understanding of the physiology of tracheophytes. This unusual interest in bryophytes is largely because of the

relative ease with which genes can be moved into them or knocked out of them and their expressions be observed. And both bryophyte and fern gametophytes exhibit desiccation tolerance, whereas this ability is rare among sporophytic seed plants (Watkins *et al.* 2007). Long live the gametophytes! Even the lichens seem to have less desiccation tolerance than the bryophytes (Green *et al.* 2011).

Oliver *et al.* (2000) hypothesized that for photosynthetic plants to move onto land, desiccation tolerance was crucial. Using species of "resurrection plants" from both bryophytes and tracheophytes, Fisher (2008) concluded that desiccation tolerance arose among propagules as a means of survival. In bryophytes, nearly every part is a potential propagule in most species. For example, Maheu (1902) found that the moss *Tortula muralis* (Figure 2) would regenerate protonemata after

being stored dry for 14 years. Physiological adaptations may permit the bryophyte to retain water or to recover from loss of water, and to change its strategies with the seasons or the climate.



Figure 2. *Tortula muralis*, a moss species that can survive drought as protonemata. Photo by Christophe Quintin, through Creative Commons.

Alpert (2000) presented two main puzzles from the observed habitat patterns of desiccation-tolerant plants. "What are the mechanisms by which plants tolerate desiccation?" and "Why are desiccation-tolerant plants not more ecologically widespread?" There appear to be multiple mechanisms of tolerance, including protection from oxidants and loss of normal configuration of macromolecules during dehydration. Alpert suggests that their inability to occupy a wide ecological range is due to their inability to maintain a cumulative positive carbon balance during their repeated wet/dry cycles and the tradeoffs between desiccation tolerance and growth rate.

## Drought Tolerance vs Avoidance

As clear as the two words **tolerance** and **avoidance** may seem, they can lead to confusion because of differences in perspective. During (1979) tells us that **drought tolerance** is the ability to survive and maintain activity despite a lack of water in the environment. Proctor (2000) gives a more physiological definition that considers drought-tolerant plants to be those that are able to maintain a more or less normal metabolism at lowered cell volume and water potential, while tolerating elevated ionic concentrations in the cytoplasm and external environment. This physiological type of maintenance may be in evidence for the drought-tolerant *Hedwigia ciliata* (living on exposed boulders; Figure 82) and *Grimmia pulvinata* (often living on concrete; Figure 3). During a 5-day sequence of natural field drying, they showed no sign of plants drying and both maintained their photochemical efficiency, exhibiting normal day-night patterns (Schroeter *et al.* 1999).

Plants that show **tolerance** have vegetative parts that endure the stress period as best as possible (During 1979). But where is that lack of water, in the environment, or in the plant? I prefer to clarify this and say that **drought tolerance** is the ability of the plant to survive in a **habitat** that becomes dry. **Desiccation tolerance** is the ability of the **plant** to survive periods during which the **cells** are

water-stressed and the plant itself has become dry; it suffers dehydration of all its metabolic systems. Such vegetative desiccation tolerance is rare among tracheophytes, with few species withstanding vegetative desiccation: 60-70 species of fern and fern allies and 60 species of angiosperms (Oliver *et al.* 2000). Instead, most tracheophytes survive through reproductive structures. Bryophytes (and lichens), on the other hand, exhibit vegetative desiccation tolerance as well as through reproductive structures (Kappen & Valladares 1999; Proctor *et al.* 2007).



Figure 3. *Grimmia pulvinata*, a drought tolerator growing on concrete. Photo with permission from Botany Department website, University of British Columbia, Canada, with permission.

For sake of clarity, let us consider **drought** to be a condition of the environment and **desiccation** to be a condition of the plant, in this case the bryophyte. For tracheophytes, drought in the environment nearly always causes desiccation in the plant, but for bryophytes, this may not so often be the case.

Using that terminology, **drought tolerance** can be accomplished in two ways: **desiccation tolerance** and **desiccation avoidance**. **Desiccation avoidance** is the ability to prevent desiccation from occurring within the plant or the ability to go into a **dormant stage** during periods of low water availability; it is often characterized by plants that die and leave stress-tolerant **diaspores** (any structures that become detached from parent plant and gives rise to new individuals) that will grow the next season. Note the use of the word **stage** here, not **state**. For bryophytes, spores and gemmae provide dormant **stages**, although the entire **mature** sporophyte might be considered a stage that does not require water. On the other hand, a desiccation-tolerant vegetative plant can go into a dormant **state**, where metabolic activity slows to an imperceptible level, but where this same plant stage will regain its ability to gain carbon and grow.

Using these concepts, Smith (1986) considers that true desiccation tolerance among plants is rare or non-existent. The tracheophytes may in fact never be desiccation tolerators (Larcher 1983), generally relying on avoidance by storing water or by going into a dormant life cycle stage until the return of sufficient water (Smith 1986). Bryophytes, on the other hand, can be true desiccation tolerators, and suffer relatively little damage at relative humidity levels far below those tolerated by tracheophytes (Table 1). They do this in a vegetative stage through mechanisms that avoid desiccation damage.

**Desiccation resistance**, the ability to maintain an adequate water supply under drought conditions, is actually **drought avoidance**. Drought avoidance also includes the



ability to revert to a dormant stage that requires no water, such as spores and tubers. Water is essential to all life, and the ability to obtain it under limiting conditions or to store it until more is available permits some organisms to live in conditions that are intolerable for others. Most perennial bryophytes do not have the option of disappearing into the soil for the winter, and in fact the period of greatest drought for many of them is in the summer. However, bryophyte growth generally ceases during this hot and often dry time and metabolic activity is slowed considerably, if not completely.

Table 1. Comparison of desiccating percent relative humidity levels tolerated by various groups of plants. Table modified from Larcher (1983).

Plant	%RH Tolerated without injury	%RH Moderate injury
Marine algae		
Deep water algae	99-97	14-41
Algae of the ebb line	95-86	69-204
Intertidal algae	86-83	204-252
Liverworts		
Hygrophytes	usually 95-90	92-90
Mesophytes	usually 92-50	90-36
Xerophytes	usually (36)-0	0
Mosses		
Water mosses and hygrophytes	95-90	69-141
Mesophytes	usually 90-50 extreme 10	
Xerophytes	usually 5	0
Fern gametophytes		
Forest ferns	>90	50-90
Rock ferns	40-60	20-30
Tracheophytes (tissue sections)		
Leaf epidermis		96-92
Mesophyll	96	95-90
Root cortex		97-95

Both desiccation avoidance and desiccation tolerance strategies are available to bryophytes (Figure 4-Figure 5). You will soon see that whereas desiccation tolerance may be unavailable to tracheophytes, it is of considerable importance for bryophytes.

Desiccation Tolerance

In 1702 Anthony von Leeuwenhoek examined dry sediment from a gutter after hydrating it for an hour, and found tiny animals swimming about (Alpert 1982, 2000). These animals, rotifers, seemingly had arisen from the dead. Leeuwenhoek followed with experiments that showed these animals could remain in this dry state for months. But he did not imagine that they had lost all moisture because they retained their normal oval shape. During the next century, experiments demonstrated that rotifers, nematodes, and tardigrades all could undergo a dry, dormant state. In fact, some organisms can survive for over ten years without water, reaching immeasurably low water potentials (Alpert 2000). In this desiccated state they can endure temperature extremes from 0272 to 100°C.

But what was this dormant state? Words such as **anabiosis** (temporary state of suspended animation or

greatly reduced metabolism), **abiosis** (absence of life), **revivification** (restoring life), and **resuscitation** (action of making something active or vigorous again), arose to describe the dry state and ability to return from it (Alpert 1982). The term **cryptobiosis**, however, seems most appropriate, avoiding the question of whether or not the organism is still alive. Instead, it refers to the state of an organism when it shows no visible sign of life, when its metabolic activity is immeasurable (hidden life).

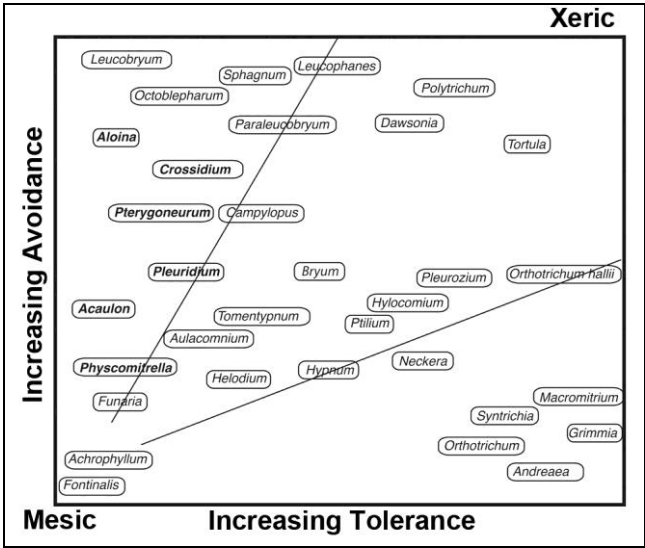


Figure 4. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

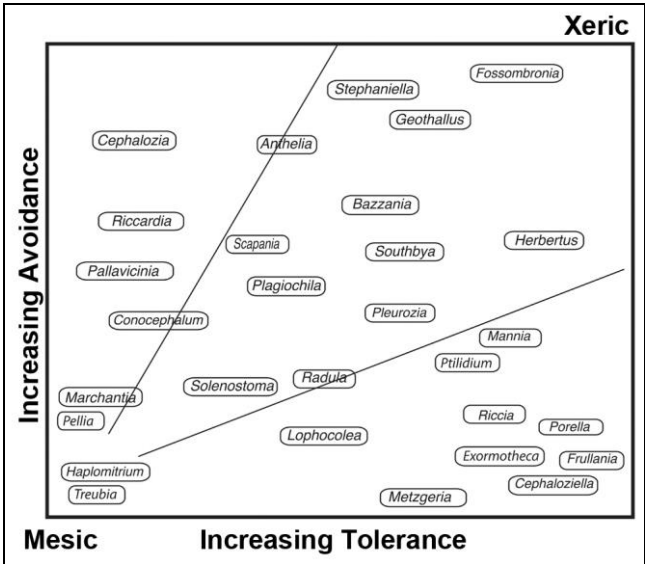


Figure 5. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

Low temperature physics helped to clarify the issue. Recognizing absolute zero as -273°C, the temperature at which everything freezes and all molecular movement stops, Becquerel (1950a, b, c, 1951) subjected tardigrades, rotifers, algae, seeds, bacterial and fungal spores, fragments of the lichen *Xanthoria parietina*, and leaves of the mosses *Grimmia* (Figure 79-Figure 80) and *Barbula* (Figure 6) to two-hour treatments at temperatures very close to 0.0°K



(0.05-0.008°K). These organisms returned to their active state and bacteria even reproduced. *Syntrichia ruralis* (Figure 77-Figure 93) survived after 24 hours at -198°C (Bewley 1973). Based on typical reduction in metabolism of ½ for every 10°C drop in temperature, Becquerel calculated that at absolute zero metabolism would be 7.13 trillion times as slow as the normal rate at 15°C (see Alpert 2000).



Figure 6. *Barbula convoluta* var. *commutata*, a species that survives at temperatures close to 0°K. Photo by Michael Lüth, with permission.

This did not support the hypothesis that life ceased and then was reactivated. In fact, three arguments can be made against that hypothesis, some of which have been demonstrated for desiccated mosses. First, Dilks and Proctor (1976b) have demonstrated that mosses recover more slowly as duration of desiccation increases, ultimately reaching a duration from which they are unable to recover. Second, for most organisms in this cryptobiotic state, there is still a minute uptake of oxygen (Pigón & Weglarska 1955a,b), indicating retention of metabolism. Third, there is a point at which all these organisms die.

Such desiccation tolerance, a common phenomenon among bryophytes, seems to have been lost in the evolution of tracheophytes. Rather, tracheophytes have experienced increased growth rates, more structural and morphological complexity, and mechanisms for conserving water rather than recovering from its loss (Oliver *et al.* 2000). Only in their reproductive structures, particularly seeds and underground storage organs, have tracheophytes retained and diversified the strategy of desiccation tolerance.

Norris (1990) contends that four dimensions of water relations must be understood to understand the problems of bryophytes compared to tracheophytes. To this I have added the fifth as a result of more recent experiments:

1. hydration/dehydration frequency
2. hydration duration
3. dehydration duration
4. degree of water loss
5. rate of water loss.

With the need for repair whenever moss cells become dry, it is not surprising that the frequency of the wet-dry cycle and the duration of the hydration period are important in determining survival. Even in such xerophytic bryophytes as *Grimmia pulvinata* (Figure 3), living on rock walls in Britain, the median length of wet and dry periods is generally between 5 and 15 hours (Proctor 2004). The longest dry periods in early summer are typically 15-

17 days, with the longest continuously wet period lasting nearly 28 days. The moss cushions typically remain wet about 1.7 times the duration of rain. It appears that dew fall is insufficient to cause hydration in this species, perhaps because water drops are trapped by the long hairs instead of reaching the leaf lamina. Such a mechanism could protect the species against frequent (daily) wet-dry cycles in which the nightly wet period is insufficient for damage repair before the moss becomes dry again. Growth occurred primarily in autumn when the moss was wet for long periods, despite relatively low levels of irradiation.

Like others, Stark *et al.* (2013) argued that desiccation tolerance is the most important evolutionary innovation permitting plants to colonize land. They used the desert moss *Pterygoneurum lamellatum* (Figure 7) and chlorophyll fluorescence to test recovery from drying of 30 minutes to 53 hours. As in other studies, rate of drying is a major factor in recovery, with only the shoot apex escaping the severe damage of very rapid drying. Rapidly desiccated shoots have slower growth rates, fewer regenerative shoots, and a compromised photosynthetic system. The responses to differences in rate of drying indicate that this xerophytic moss has inducible desiccation tolerance, in contrast to the assumption that xerophytic bryophytes have only constitutive desiccation tolerance.



Figure 7. *Pterygoneurum lamellatum*, a desert moss with inducible desiccation tolerance. Photo by Michael Lüth, with permission.

Although *Sphagnum* (Figure 63) may not be a good model for other kinds of bryophytes, it gives us an idea of the evaporative relationships of these non-tracheophytes. *Sphagnum* in a foggy coastal blanket bog in Newfoundland demonstrated that the bog surface loses little water during foggy periods, due, in part, to absence of a vapor pressure deficit. On the other hand, during dry, clear periods the surface of the bog dries, increasing the surface resistance to evaporation (Price 1991); at the same time, higher available energy from the sun causes the rate of evaporation to be higher than on foggy days. This results in a daily evaporation rate of 1.5 mm per day on clear days, contrasting to 0.7-1.1 mm per day for foggy or rainy days.

If we put the two strategies, avoidance and tolerance, into a different perspective, we find that some species tend to avoid drought by holding water more effectively while some survive better at a lower water content. Table 2 lists the survival time of a number of bryophytes. Mechanisms



to accomplish survival vary. As we have seen already (in Chapter 7-4a & b of this volume; Li *et al.* 1992) *Sphagnum magellanicum* (Figure 8) is superior to *S. papillosum* (Figure 9) at retaining water and transporting it from lower parts of its environment, but *S. papillosum* has a greater rate of survival (95%) after laboratory drying (80% for *S. magellanicum*). Thus, *S. magellanicum* is more of a drought avoider whereas *S. papillosum* is more of a short-term drought tolerator. On the other hand, *S. papillosum* death (65%) surpasses that of *S. magellanicum* (50%) when both are dried for 30 days.



Figure 8. *Sphagnum magellanicum*, a moss with good water retention and transport but inferior desiccation survival. Photo by Michael Lüth, with permission.



Figure 9. *Sphagnum papillosum*, a moss with poor transport and water holding ability, but good desiccation survival. Photo by Michael Lüth, with permission.

Table 2. Known durations of desiccation survival in bryophyte gametophyte plants.

<i>Sphagnum fuscum</i>	2-4 d	Schippenges & Rydin 1998
<i>Sphagnum papillosum</i>	2-4 d	Schippenges & Rydin 1998
<i>Sphagnum balticum</i>	2-4 d	Schippenges & Rydin 1998
<i>Sphagnum cuspidatum</i>	2-4 d	Schippenges & Rydin 1998
<i>Sphagnum magellanicum</i>	2-4 d	Schippenges & Rydin 1998
<i>Sphagnum magellanicum</i>	14 d	Sagot & Rochefort 1996
<i>Sphagnum fallax</i>	14 d	Sagot & Rochefort 1996
<i>Fontinalis flaccida</i>	3 mos	Glime unpubl
<i>Barbula torquata</i>	18 mos	Moore <i>et al.</i> 1982
<i>Oxymitra</i>	4 yrs	Volk 1984
<i>Riccia canescens</i>	7 yrs	Volk 1984
<i>Grimmia laevigata</i>	10 yrs	Breuil-Sée 1993
<i>Syntrichia ruralis</i>	14 yrs	Breuil-Sée 1993
<i>Tortula muralis</i> protonema	14 yrs	Maheu 1902
<i>Anoetangium compactum</i>	19 yrs	Malta 1921
<i>Riccia macrocarpa</i>	23 yrs	Breuil-Sée 1993

Lloyd Stark (pers. comm. 18 July 2015) found conflicting results among the publications on the duration of the dry period of *Sphagnum*. Desiccation tolerance alone did not explain the conflicting results. Sagot and Rochefort (1996) dried fragments three species of *Sphagnum* [*S. fallax* (Figure 14-Figure 16), *S. fuscum* (Figure 10), *S. magellanicum* (Figure 8)] and dried them at 60% relative humidity. These species were able to tolerate up to 14 days of desiccation under these conditions. On the other hand, when Schippenges and Rydin (1998) completely dried *S. fuscum* and *S. magellanicum*, and three other species, none of the five species survived. On the other hand, if the water content was maintained above 100% (normal hydration of *Sphagnum* is much greater than that), all the species survived 3-12 days in this "dry" condition. But with the standard water content considered to be near 10% dry weight (~equilibration with 50% relative humidity), This hardly qualifies as dry.

Hájek and Beckett (2008) likewise found that hummock species *Sphagnum magellanicum* (Figure 8) and *S. fuscum* (Figure 10) under desiccation conditions lose more water before turgor starts dropping than do other *Sphagna* from less exposed habitats (73% vs 56% on average). Nevertheless, the osmotic potentials [potentials of water molecules to move from hypotonic solution (more water, less dissolved solutes) to hypertonic solution (less water, more dissolved solutes)] across semi-permeable membrane at full turgor are similar in all species (-1.1 MPa). Unlike the desiccation-tolerant *Racomitrium lanuginosum* (Figure 78) and *Syntrichia ruralis* var. *arenicola* (Figure 77), the hummock *Sphagnum* species have more rigid cell walls than those of wet habitats. Thus, the leaves of hummock species lose turgor at higher relative water contents (0.61) than species lower in the hummock-hollow complex (0.46). Hummock species also begin a photosynthetic decline sooner during drying. On the other hand, the hummock species recover more completely after rehydration.

Hajek and Vicherova (2014) were able to harden 13 species of *Sphagnum* (Figure 8-Figure 9) to desiccation. Hardening agents included drought, slow drying, ABA application, and chilling or frost. They measured tolerance by recovery of chlorophyll fluorescence parameters after severe desiccation. The hardening was accomplished by subjecting the shoot apices to a very high relative humidity (98-99%) for seven days prior to exposing them to desiccating conditions. With that preparation, the bryophytes were able to tolerate 56% relative humidity. This indicates that in *Sphagnum* desiccation tolerance is inducible.

Despite its ability to induce desiccation tolerance, one important role of *Sphagnum* (Figure 8-Figure 9) as an ecosystem engineer is its ability to retain water (Hajek & Vicherova 2014). Its ability to survive desiccation is seasonal. Following initial dehardening in the lab, untreated shoots of *Sphagnum* lack desiccation tolerance. Nevertheless, desiccation tolerance was induced by all hardening treatments except chilling, and especially by slow drying, even in the aquatic section *Cuspidata*. Under field conditions, *Sphagnum* species in hollows and lawns developed desiccation tolerance several times during the growing season as the precipitation and lowered water table created changing conditions. On the other hand, hummock



and aquatic species responded only to frost in late autumn, becoming desiccation tolerant. The protonemata did not develop desiccation tolerance, suggesting that this may be a limiting stage in the life cycle. The desiccation avoiders do not develop desiccation tolerance and must live in compact hummocks or submerged. Thus, there seems to be a tradeoff between desiccation tolerance in species lower on the hummocks and submerged vs resources spent on water retention and desiccation avoidance at higher positions.



Figure 10. *Sphagnum fuscum*, a hummock species. Photo by Michael Lüth, with permission.

Hájek and Beckett (2008) suggest that the higher water-holding capacity of hummock *Sphagnum* (Figure 8-Figure 10) would allow them to continue their metabolism longer during desiccation, *i.e.*, they have greater desiccation avoidance. On the other hand, their faster recovery makes them desiccation tolerators. Species in lower positions suffer fewer wet-dry cycles but have more elastic cell walls, permitting them to maintain turgor through a wider range of conditions and thus continue metabolism.

Hájek and Beckett (2008) found that *Atrichum androgynum* (Figure 11), a moss of the New Zealand forest floor, behaved in a manner similar to hummock *Sphagnum* (Figure 8-Figure 10) species. Proctor (2000) suggests that it is the ability to use external water conduction that permits bryophyte leaf cells to maintain full turgor most of the time. Their carbohydrate content is similar to that of embryos in desiccation-tolerant seeds. They are furthermore able to recover rapidly without protein synthesis. As larger plants evolved, vegetative desiccation tolerance was lost; growth rates increased, structural and morphological complexity evolved (Oliver *et al.* 2000), and water conservation mechanisms were selected over rapid intake and recovery.

Oliver *et al.* (1993) noted that carbon balance, damage limitation, and cellular repair are necessary components of desiccation tolerance. Using desiccation tolerance of three desiccation-tolerant species of *Syntrichia* (Figure 12-Figure 13, Figure 77), they learned that electrolyte leakage is not an important measure of tolerance, but that differences in protein synthesis could be used to assess damage limitation. Using this assessment, they found the order of tolerance in descending order to be *Syntrichia caninervis* (Figure 12), *S. ruralis* (Figure 77), and *S. norvegica* (Figure 13). This basis of classification and

ranking correlates well with the water stress considered to be present in their natural habitat.



Figure 11. *Atrichum androgynum*, a species that retains turgor at lower water concentrations, much like a hummock *Sphagnum* species. Photo by Clive Shirley, Hidden Forest <[www.hiddenforest.co.nz](http://www.hiddenforest.co.nz)>, with permission.



Figure 12. *Syntrichia caninervis*, the most desiccation-tolerant of three *Syntrichia* species on the basis of protein synthesis. Photo by Michael Lüth, with permission.

Wagner and Titus (1984) compared two *Sphagnum* species – *S. fallax* (Figure 14-Figure 16), a hollow species that lives close to the water table, and *S. capillifolium* (Figure 17-Figure 18) (= *Sphagnum nemoreum*), a hummock species. Here, the relationship is somewhat surprising. The hollow species *S. fallax* is more desiccation tolerant than the hummock dweller *S. capillifolium*. *Sphagnum fallax* not only recovers a greater proportion of its predesiccation photosynthetic rate, but it also has a higher survival rate after 5-10 days of desiccation. This relationship can be explained by events in its habitat. *Sphagnum fallax* dries more frequently and for longer periods of time than does the hummock-dwelling *S. capillifolium*. *Sphagnum capillifolium* is able to retain moisture longer in the field. Growth habit may explain this ability, with *S. fallax* being larger and having a wide-spreading head, whereas *S. capillifolium* has a compact capitulum (head) (Figure 18) and lives in tightly packed clumps (Figure 17).





Figure 13. *Syntrichia norvegica*, the least desiccation-tolerant of three *Syntrichia* species on the basis of protein synthesis. Photo by Michael Lüth, with permission.



Figure 14. Habitat of *Sphagnum fallax* on hummocks in the pool where they undergo water level fluctuations. Photo by Michael Lüth, with permission.



Figure 15. *Sphagnum fallax* showing spreading branches in capitula and large spaces between plants. Photo by Michael Lüth, with permission.



Figure 16. Close-up view of a hummock of *Sphagnum fallax*. Photo by Michael Lüth, with permission.



Figure 17. *Sphagnum capillifolium capillifolium* hummock showing the tight relationship between plants. Photo by Barry Stewart, with permission.



Figure 18. *Sphagnum capillifolium* capitulum showing the tightness of the branches. Photo by Bernd Haynold through Creative Commons, with permission.

Bu *et al.* (2013) consider that peatlands have hummocks with drought-tolerant species and hollows with drought-intolerant species. They found that drought reduces the biomass production, height increment, and side shoot production of both hummock species [*Sphagnum palustre* (Figure 19) and *S. capillifolium* (Figure 17-Figure



18)] and hollow species [*S. fallax* (Figure 14-Figure 15). Bu and coworkers found that the leaf hyaline cell percentage increases in the hummock species but not in the hollow species. Furthermore, the nitrogen and carbon contents of the hummock species respond more to drought than they do in the hollow species. Instead, it is the presence of neighboring species of *Sphagnum* that causes the decrease in carbon in all three species. Despite this effect, there is no change in the competition under wet or dry treatment for any of the six species combinations. Contrary to expectations, *Sphagnum fallax* exhibits a change from facilitation in wet conditions to competition under dry conditions. This suggests that hummock species can facilitate the hollow species in wet environments but can outcompete them for water under drying conditions. The inability of hollow species to grow on hummocks could be the combination of superior competitors and the greater drought.



Figure 19. *Sphagnum palustre*, a drought-tolerant hummock species. Photo by Michael Lüth, with permission.

Wood (2007) summarized vegetative desiccation tolerance of bryophytes. Defining it as the "unique ability to revive from the air-dried state," he considered desiccation-tolerant species to be those that can survive equilibration with either modestly dry air (i.e., 70-80% RH) or extremely dry air (i.e., 0-30% RH). He considered these desiccation-tolerant species to comprise seven bryological classes: **Andreaeopsida**, **Bryopsida**, **Polytrichopsida**, and **Tetraphidopsida** (mosses), **Jungermanniopsida** and **Marchantiopsida** (liverworts), and the **Anthocerotopsida**. This omits the **Andreaobryopsida** and the **Sphagnopsida**. The **Andreaobryopsida** may be omitted simply due to lack of data. The **Sphagnopsida**, on the other hand, do indeed have desiccation tolerance in at least some species. In defense of the omissions, only 210 out of ~21,000 bryophyte species (ca. 1.0%) have been experimentally determined to possess vegetative desiccation tolerance – 158 species of mosses, 51 species of liverworts, and 1 species of hornwort.

### Desiccation Avoidance

Many options of desiccation avoidance are available to tracheophytes that are not available to bryophytes. Bryophytes cannot make use of deep roots or increase the length of their roots (or in bryophytes - rhizoids), as do

many tracheophytes, because this would have little effect at the scale of a bryophyte. Nor do they have large underground storage organs to permit dormancy. But many do have underground **tubers** (see Chapter 4-10 of this volume) that store significant quantities of lipids or starches (Duckett & Pressel 2003) and that seem to be an adaptation to drought avoidance (El-Saadawi & Zanaty 1990).

Bryophytes cannot conserve water by using an alternate photosynthetic pathway to store CO<sub>2</sub> (Rundel *et al.* 1979, James 1981) because it would provide no water conservation advantage due to their lack of leaf stomata. Their developmental structure does not permit the loss of leaves because no buds occur at the base of each leaf, and one must wonder if such a small stem could store sufficient energy to support the growth of new leaves prior to any new input from photosynthesis.

The plants protect each other from desiccation and may hide buds of younger shoots within the clump. In *Bazzania trilobata* (Figure 20), field plants are able to tolerate drying, whereas lab drying is lethal (Sollows *et al.* 2001). Field conditions do not provide the desiccation level one might suppose by measuring air moisture. But it is also likely that the drying rate is different, and the integrity of the clump may have been altered in the lab.



Figure 20. *Bazzania trilobata* illustrating overlapping leaves and layering of branches. Photo by Janice Glime.

Many bryophytes can roll their leaves, as do some vascular plants, and they have several other related options to reduce the exposed surface area. These include curling and contorting the leaves (see Chapter 7-4 in this volume), a mechanism that creates small air spaces and presumably decreases air movement across the leaf surface. Others appress their leaves closely to the stem, protecting the upper surface from exposure and overlapping leaves sufficiently to protect even portions of the back surface of the leaf from exposure. And, despite their lack of specialized energy-storing organs (with some exceptions), they do have life cycle options. Perhaps the most important of these adaptations is the ability to withdraw water from the cell and form extracellular ice, with desiccation tolerance being an important adaptation (Dilks & Proctor 1975). (See Chapter 7-9 and 7-10 for further information on effects of freezing.)

### Life Cycle and Life Strategy Adaptations

Hedderson and Longton (1996) evaluated the relationship between life history traits and taxonomic group, relating these to water relationships. They found



that 40-50% of the life history variation was related to water relations. The capacity for water uptake and retention arranges species from short-lived **monoicous** (having both sexes on same plant) taxa that produce few, large spores to those **dioicous** (having separate sexes) taxa with the opposite traits. The **endo-ectohydric** (internal vs external water control) gradient similarly relates to the investment in spores as a function of life expectancy.

One way to survive dry periods is to avoid them by leaving your spores behind to carry on the species. In the Murray River Valley, Australia, where flooding occurs every spring, long dry periods ensue and many taxa such as the ephemeral mosses persist there as spores (Peintinger 1988). In such genera as *Riccia* (Figure 1), which typically inhabit seasonally dry areas, dispersal of spores by animals, aided by the ornamentation of the spore, is important (Volk 1984; see Chapter 4-8 in this volume). Survival is facilitated by the ability to endure temperatures as high as 80°C when dry, whereas temperatures higher than 50°C when wet will injure them.

Alternatively, ephemeral bryophytes such as *Riccia cavernosa* (Figure 1), *Physcomitrella patens* (Figure 21), and *Physcomitrium eurystomum* (Figure 22) are able to grow on the muddy floodplain soil (Peintinger 1988), then become dormant in the fall until water returns again.



Figure 21. *Physcomitrella patens* on wet soil after flooding recedes. Photo by Michael Lüth, with permission.



Figure 22. *Physcomitrium eurystomum*, an ephemeral bryophyte that grows on floodplains. Photo by Michael Lüth, with permission.

For some bryophytes, altering their phenology according to available water is an adaptive strategy to take advantage of water when it is available. *Octoblepharum albidum* (Figure 23) in Nigeria produces antheridia and archegonia two months earlier when watered regularly (Egunyomi 1979). In nature, they produce archegonia during the rainy season, then produce capsules and take advantage of the dry season for dispersal of spores. This moss furthermore has leaves that can regenerate after as much as 29 weeks of dry storage, permitting an alternate means of propagation in those years when weather is not favorable for sexual fertilization.

In the very hot and dry summers of Kuwait, El-Saadawi and Zanaty (1990) found that a different avoidance strategy can be used. *Bryum bicolor* (Figure 24) forms subterranean rhizoidal **tubers** (see Figure 25) (Risse 1993) and stem tubers that permit it to be dormant as an avoidance mechanism, but it also exhibits tolerance in its protonemata, main stems, and stem apices (El-Saadawi & Zanaty 1990). *Funaria hygrometrica* (Figure 26) survives only by avoidance in the same conditions, using subterranean corm-like or bulbiform bases and bulbils to span the drought period.



Figure 23. *Octoblepharum albidum* growing epiphytically in India. This moss modifies its **phenology** (timing of life cycle events) when more water becomes available. Photo by Michael Lüth, with permission.



Figure 24. *Bryum bicolor*, a moss that survives drought through stem apices and rhizoidal tubers. Photo by Michael Lüth, with permission.





Figure 25. *Bryum sauteri* rhizoidal tubers, a means of surviving drought. Photo by David T. Holyoak, with permission.



Figure 26. *Funaria hygrometrica* with young sporophytes, growing abundantly on charcoal, where it will continue growth for several years until competition moves in. Note the bulbiform basal leaves that can protect the plant and young sporophyte during drought. Photo by Janice Glime.

Even in less xeric conditions, drought-resistant **tubers** (Figure 25) are present in such taxa as *Atrichum tenellum* (Figure 27), *A. crispum* (Figure 28) (Arts 1987), and *Fissidens cristatus* (Figure 29) (Arts 1986). In *Haplodontium notarisii* (Figure 31), tubers are viable for up to 10 years (Arts 1988).



Figure 27. *Atrichum tenellum*, a moss that can survive drought as tubers. Photo by Michael Lüth, with permission.



Figure 28. *Atrichum crispum*, a moss that can survive drought as tubers. Photo by Jan-Peter Frahm, with permission.



Figure 29. *Fissidens cristatus*, a moss that is able to survive drought and freezing as tubers. Photo by Jan-Peter Frahm, with permission.

Some bryophytes actually require a dry season. In *Orthotrichum anomalum* (Figure 30), this dry period is necessary for the **operculum** (capsule lid) to dehisce (Johnsen 1969). The leafy gametophyte grows only when it is cool and moist, but watering during the dry period is detrimental.



Figure 30. *Orthotrichum anomalum* with dehiscent capsules. Photo by Michael Lüth, with permission.

## Seasonal Changes

As we have just seen, the physiological state of the bryophyte, and hence **desiccation tolerance**, varies with the **season**. Many bryophytes [e.g., *Plagiochila spinulosa*



(Figure 32), *Hylocomium splendens* (Figure 61-Figure 62), *Scorpiurium circinatum* (Figure 33), *Syntrichia ruralis* (Figure 93), *Racomitrium aquaticum* (Figure 34)] seem to be most sensitive during autumn and early winter, the times when most bryophytes resume growth after a hot summer (Dilks & Proctor 1976a). Desiccation tolerance increases from spring to a maximum in early summer, the season when many species become dormant. Some degree of acclimation may be occurring, resulting in increased tolerance as summer approaches (Richardson 1981).



Figure 31. *Haplodontium notarisii* with capsules, a moss that can survive for ten years as tubers. Photo by Jan-Peter Frahm, with permission.



Figure 32. *Plagiochila spinulosa*, a leafy liverwort species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.



Figure 33. *Scorpiurium circinatum*, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.



Figure 34. *Racomitrium aquaticum*, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Bryophytes apparently adjust their desiccation tolerance and resistance according to their experiences with the environment (Dilks & Proctor 1976a), as will be discussed in greater detail later with regard to rehydration. That is at least part of the reason for different studies showing different results, even from the same researchers. It is interesting that not all bryophytes adjust in the same way, with one group of bryophytes having their least desiccation tolerance time in autumn and winter and others in late summer in Britain (Figure 35), in this case coinciding with differences among their habitats. *Andreaea rothii* (Figure 36) seems to have no response to season.

Ochi (1952) examined the effects of season on drought tolerance and concluded that mosses with active buds at the beginning of the growing season are generally more drought resistant than in other seasons. Seemingly in contrast to this statement, Ochi showed that in Japan *Dicranum japonicum* (Figure 37) survives drought longer (28 weeks) if the plant has active buds in early January rather than in early September or April (~4 weeks),



whereas *Polytrichastrum formosum* (= *Polytrichum attenuatum*; Figure 38), when dried on the same dates, survives longest when buds become active in September (>56 weeks compared to 28 in January and 11 in April). He concluded that these seasonal strategies represent three types of seasonal fluctuations in osmotic value: higher values in summer (dry season), lower in winter (wet season); higher in winter, lower in summer; no seasonal fluctuations (those from wet habitats).

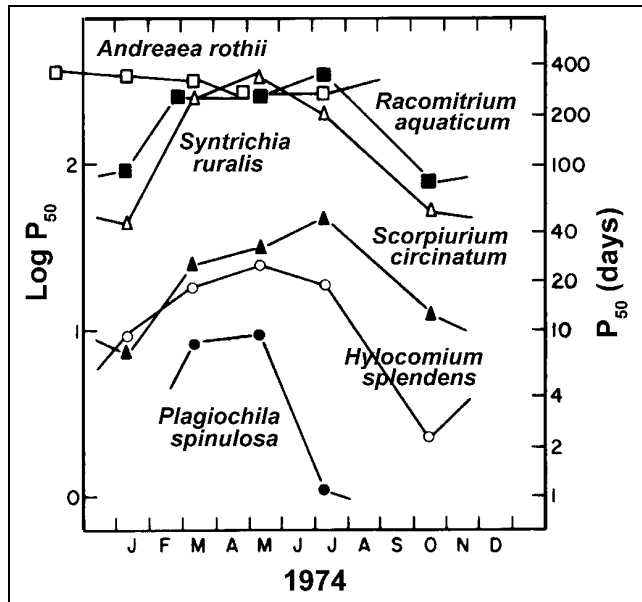


Figure 35. Relationship between season and maintenance of photosynthesis during desiccation of British bryophytes.  $P_{50}$  is the number of days (in this case) of desiccation at which photosynthesis upon rehydration is reduced to 50% its initial value. Redrawn from Dilks and Proctor (1976a).



Figure 36. *Andreaea rothii*, a season-neutral moss with respect to its desiccation tolerance. Photo by Michael Lüth, with permission.

Davey (1997) found that in Antarctic bryophytes, the photosynthetic rate following a desiccation/rehydration cycle decreased from spring to summer to autumn. The pattern was clearest in the hydric taxa, with less effect in the xeric species.



Figure 37. *Dicranum japonicum*, a moss where early January buds result in ability to survive drought longer. Photo by Li Zhang, with permission.



Figure 38. *Polytrichastrum formosum*, a moss that survived longest when buds became active in September. Photo by David T. Holyoak, with permission.

Akande (1984, 1985) likewise attributed seasonal differences in desiccation tolerance of four **epiphytic** (growing on other plants, especially trees) bryophytes to changes in osmotic values, with osmotic values increasing from wet to dry season. He found that the mosses *Entodontopsis nitens* (= *Stereophyllum nitens*) and *Calymperes palisotii* (Figure 39) had a greater osmotic potential and greater desiccation tolerance than the leafy liverworts *Mastigolejeunea florea* and *Frullania spongiosa*.





Figure 39. *Calymperes palisotii*, a moss in which good osmotic potential increases desiccation tolerance. Photo by Scott Zona, with permission.



Figure 40. *Cratoneuron filicinum*, a moss species intolerant of rapid drying. Photo by Ivanov, with permission.

## Physiological Adaptations

All of us have observed that bryophyte assemblages differ with habitats (e.g. Šinžar-Sekulić *et al.* 2005). Oliver *et al.* (2000) note that most of the desiccation-tolerant plants are bryophytes, in addition to algae and lichens. They agree that desiccation tolerance was an important step in the evolution of land plants. They suggested that such tolerance requires constitutive cellular protection coupled with active cellular repair. But as evolution progressed, plants gained structural and morphological complexity. Plants developed mechanisms that conserve water within the plant, and vegetative desiccation like that seen in bryophytes was no longer necessary.

But Alpert and Oechel (1985) contend that desiccation-tolerant plants are rarely present in the most xeric microhabitats, suggesting that in these locations they are unable to maintain a positive cumulative carbon balance. They demonstrated this in *Grimmia laevigata* (Figure 83), the dominant green plant on exposed granitic boulders in the California, USA, chaparral by measuring the response of net CO<sub>2</sub> flux to light, temperature, plant water content, and previous desiccation.

Among desiccation-tolerant bryophytes, rehydration is rapid, with leaves returning to normal form in as little as 2 minutes and chloroplasts returning to normal conformation in 2-5 minutes in such desiccation-tolerant mosses as *Syntrichia ruralis* (Figure 77) (Tucker *et al.* 1975; Oliver & Bewley 1984). On the other hand, following rapid drying such intolerant species as *Cratoneuron filicinum* (Figure 40) still have misshapen organelles after 24 hours, and about half the cells of slow-dried plants still contain misshapen organelles (Oliver & Bewley 1984). In slow-dried plants respiration recovers, but it does not in rapid drying of desiccation-intolerant plants.

Charron and Quatrano (2009) considered two general mechanisms for survival in the xeric aerial environment. The descendants of the early land plants evolved specialized transport tissues while the bryophytes retained and perfected their co-equilibrium of their water content with that of their surroundings, relying on cellular processes to recover from damages due to water stress.

Bates (1997) examined the effects of wet/dry cycles on the nutrient economy of two pleurocarpous mosses of different habitats – *Brachythecium rutabulum* (Figure 56-Figure 57; wet ground, among grasses, logs; shade or open) and *Pseudoscleropodium purum* (Figure 41; grasslands and heaths). When provided with weekly drying periods of 24 hours every week, these plants had noticeably less biomass production than those plants that were continuously hydrated. *Brachythecium rutabulum* experienced bleaching of green tissues, unlike *Pseudoscleropodium purum*. When NPK (mix of nitrogen, phosphorus, and potassium salts) was added to the growing solutions once a week, *Pseudoscleropodium purum* exhibited growth stimulation even among the weekly desiccated plants. Uptake of N was similar in both hydrated and desiccated plants of both species. P and K<sup>+</sup> were considerable in *B. rutabulum*, but in desiccated plants they were greatly reduced. As with phosphorus, uptake of P and K<sup>+</sup> differed little between hydrated and intermittently desiccated *Pseudoscleropodium purum*. In both species, P and K<sup>+</sup> were leaked from cells during desiccation, were retained on the cells by cation exchange, and taken up again during rehydration. But even this maintenance has a cost. K<sup>+</sup> and Mg<sup>+2</sup> intracellular levels in new growth are maintained at the expense of exchangeable cations. Uptake is greatest during the early stages of recovery, most likely due to damaged membranes, and that is when the NPK application has the greatest effect on growth. These experiments suggest that *P. purum* has a lower nutrient requirement than *B. rutabulum* and they explain why *B. rutabulum* requires a more continuous hydration to maintain its greater production. An interesting revelation is the ability of these species to initiate new growth without additional nutrient absorption.

Bohnert (2000) asked what makes desiccation tolerable. He considered that bryophytes tolerated rapid desiccation, using protective mechanisms. Most research has focussed on repair mechanisms. The photosynthetic apparatus and cell integrity are maintained during desiccation, but rehydration leads to cellular damage. Despite this damage, recovery is rapid. mRNA (messenger RNA, the molecule that carries information from DNA to the ribosome) exists in RNPs (nucleoproteins that contain RNA) before the stress conditions arise. During recovery,



non-reducing sugars, **dehydrins** (group of proteins produced in response to cold and drought stress), and **rehydrins** (transcripts used during rehydration) appear. Hoekstra (2005) reported on the importance of fatty acid saturation in membranes in imparting survival of desiccation.



Figure 41. *Pseudoscleropodium purum*, a species in which intermittent desiccation seems to have little effect on K and P uptake. Photo from Proyecto Musgo, through Creative Commons.

Yang *et al.* (2012) sought the genetic determinant(s) for stress tolerance. Using *Syntrichia caninervis* (Figure 12) they identified ScALDH21, a gene that responds to **ABA** (abscisic acid, a stress hormone; see Chapter 7-7 Water Relations – Biochemistry) and desiccation and that plays an important role in response to desiccation and salinity stresses.

When the desiccation-tolerant *Syntrichia ruralis* (Figure 77) is desiccated, it retains all its pigments, chlorophyll included, and is able to recover physiological function rapidly upon rehydration (Hamerlynck *et al.* 2002). But all is not equal among these plants of both sun and shade habitats. *Syntrichia ruralis* has lower plant mass, as well as lower tissue N, C, total photosynthetic pigment concentrations, and carbon isotope discrimination ( $\Delta$ ) values compared to shade plants. The ratio of carotenoid to chlorophyll in sun plants is typical of high light plants, but the ratio of chlorophyll *a* to chlorophyll *b* in these plants is lower than expected, resembling those of plants adapted to shade. As a consequence, the levels of optimal quantum efficiency of **PS II** ( $F_v/F_m$ ) (= variable fluorescence / maximum fluorescence; PS II is photosystem II of photosynthesis, where oxygen is liberated from water) are lower in the sun plants. Reciprocal transplants reveal that *Syntrichia ruralis* is able to adjust to altered light levels. This is evidenced by increases in  $F_v/F_m$ , **NPQ** (non-photochemical quenching), light-adapted PSII yield ( $\phi$ PS II) in transplanted sun plants, and concurrent decreases in sun-transplanted shade plants. Nevertheless, the transplanted sun plants did not adjust sufficiently to reach performance levels exhibited by the undisturbed shade plants. These plants demonstrate at least some ability to adjust to the loss of shade canopy or other disturbance in the light regime.

*Sphagnum* (Figure 8, Figure 9, Figure 14-Figure 18) has a unique cell structure (Figure 42) providing a water reservoir. We might expect that this reservoir increases the

drying time, sparing the moss from the detrimental effects of rapid drying. But differences do exist among *Sphagnum* species.

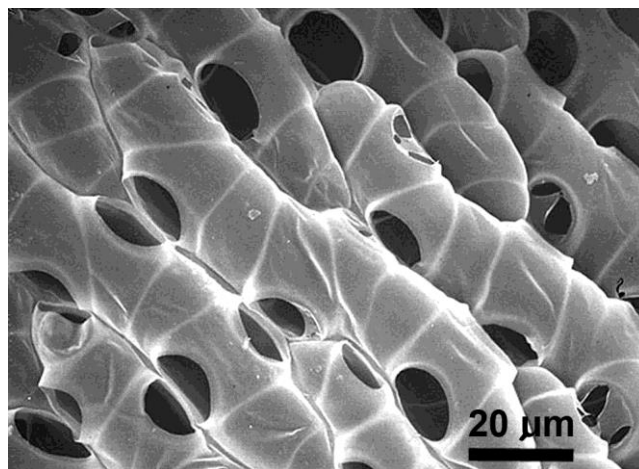


Figure 42. *Sphagnum hyaline* leaf cells and pores. Photo from Botany Department website, University of British Columbia, Canada, with permission.

In the hummock-forming *Sphagnum fuscum* (Figure 10) and *S. magellanicum* (Figure 8), desiccation results in a greater water loss before turgor sets in, compared to other non-hummock species (mean of 73% water loss vs 56%, respectively) (Hájek & Beckett 2008). The hummock species have more rigid cell walls than those of wet habitat species ( $\epsilon$  = 3.55 vs 1.93 MPa, respectively). This rigidity results in loss of turgor in chlorophyllous cells at a higher relative water content in hummock species compared with species of wet habitats (0.61 vs 0.46) and at less negative osmotic potentials (-2.28 vs -3.00 MPa, respectively). Compared with other species, hummock *Sphagnum* (Figure 8, Figure 9) species that have been desiccated to -20 or -40 MPa recover more completely after rehydration. The **mesophytic** (intermediate habitat based on moisture) *Atrichum androgynum* (Figure 43) responds similarly to the hummock *Sphagnum* species.



Figure 43. *Atrichum androgynum*, a moss that behaves similarly to hummock *Sphagnum* species when it loses water. Photo by Jan-Peter Frahm, with permission.



Under a given rate of desiccation, the hummock species of *Sphagnum* (Figure 8-Figure 10), with their higher water content, continue their metabolism longer than species with lower water-holding capacities (Hájek & Beckett 2008). And these species recover faster, indicating a higher drought tolerance. These behaviors permit them to survive in the drought-exposed hummocks. The species growing in wet habitats have smaller water-holding capacities but are able to maintain turgor and have more elastic cell walls that permit them to metabolize longer during drying.

Most *Sphagnum* (Figure 8-Figure 10) species live where intermittent desiccation is inevitable. Hence, this genus appears to have inducible desiccation tolerance (Hájek & Vicharová 2013). In experiments to **harden** (process by which a plant becomes tolerant to the effects of such stresses as frost and drought) the species, Hájek and Vicharová subjected them to slow drying, ABA application, and chilling or frost. In the laboratory, *Sphagnum* species that were de-hardened and remained untreated lacked desiccation tolerance. Slow drying, ABA application, and frost induced hardening and desiccation tolerance. The section *Cuspidata* (Figure 44) – aquatic species – did not exhibit hardening. Similar hardening occurs multiple times each year among hollow and lawn species in the field. Hummock and aquatic species, on the other hand, develop their tolerance only in late autumn, a phenomenon that Hájek and Vicharová attributed to frost. Protonemata, however, did not develop desiccation tolerance under any of the hardening treatments. The hummock species exhibit a tradeoff, having greater water-holding capacity to the detriment of their physiological desiccation tolerance.



Figure 44. *Sphagnum cuspidatum*, an aquatic species that does not seem to experience hardening. Photo by Bernd Haynold, through Creative Commons.

*Cratoneuron filicinum* (Figure 40) demonstrates the effects of slow vs rapid drying on a semi-aquatic species (Krochko *et al.* 1978). In rapid drying, the cell contents are very disrupted and become increasingly disorganized over the next 24 hours. In slow drying, only some cells have

this appearance while others maintain their cellular integrity. The greater the rate of drying, the more protein synthesis is reduced on rehydration, but it will resume following rapid water loss down to 50% of the fresh weight. On the other hand, respiration does not resume following rapid drying and rewetting.

## Mode of Conduction

Can the mode of conduction provide a beneficial edge that permits success when faced with limited water? Raven (1999) claims there is a "mechanistically mysterious size limit" for poikilohydric, desiccation-tolerant plants, suggesting an upper limit of 1 m. Anderson and Bourdeau (1955) demonstrated that external water can travel only to a "certain level." Bowen (1933c) and Mankiewicz (1983, 1984a,b, 1987a,b) remind us that this upper limit is imposed by the height to which water can rise by capillarity alone, a distance Héban (1977) considers to be only a few centimeters without the addition of other forces. As stated by Mankiewicz, "geometry of bryophytes may be constrained by the cohesive and adhesive forces of water," a statement he was able to confirm by empirical measures of flow rates through bryophyte colonies. However, we are reminded that most bryophytes receive their water from above, hence that capillary limit is of little importance for most of them. Therefore, we might ask, is the endohydric system important for the slow-growing, short bryophyte?

Bowen (1933a,b,c) compared conduction of bryophytes in wet, moist, and dry habitats. External water movement was faster than internal movement in all but two cases [*Thamnobryum alopecurum* (Figure 50) and *Plagiomnium undulatum* (Figure 52)]. *Plagiomnium undulatum* has a well-developed internal conducting system and lacks significant capillary channels externally. *Thamnobryum alopecurum*, on the other hand, typically lives where it is constantly wet from splashing or dripping water and seems to lack external conduction, perhaps due to external saturation. However, as the moisture of the habitat increases, the ability of the bryophyte plant to conduct decreases both externally and internally.

All of the taxa Bowen (1933a,b,c) studied had a **central strand** (Figure 45), varying considerably in relative size. But just how important is that strand in moving water from substrate to plant tissues? If the central strand is important in water movement, should we expect it to be most important in those mosses that suffer frequent drought conditions? In the epiphytic (but pleurocarpous) *Hypnum cupressiforme* var. *filiforme* (Figure 46-Figure 47), the central strand appears only occasionally and is absent in branches. In the boreal forest floor *Rhytidiadelphus triquetrus* (Figure 48), the cells are short with numerous transverse walls, suggesting inefficient water movement through walls. Nevertheless, in *Aulacomnium palustre* (Figure 49), internal conduction seems not to exist, despite a "relatively large central strand;" external conduction is rapid, suggesting that other factors, not the central strand, are more important in determining importance of internal versus external conduction.



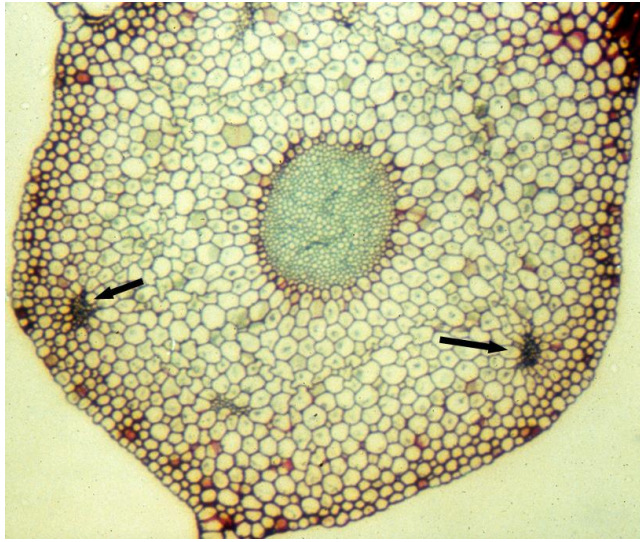


Figure 45. *Mnium* stem cross section showing central strand. Arrows indicate leaf traces. Photo by Janice Glime.



Figure 48. *Rhytidiadelphus triquetrus* on the forest floor. This moss has short stem cells with numerous transverse walls, making internal transport slow. Photo by Michael Lüth, with permission.



Figure 46. *Hypnum cupressiforme* in its epiphytic habitat. This moss usually lacks a central strand. Photo by Dick Haaksma, with permission.

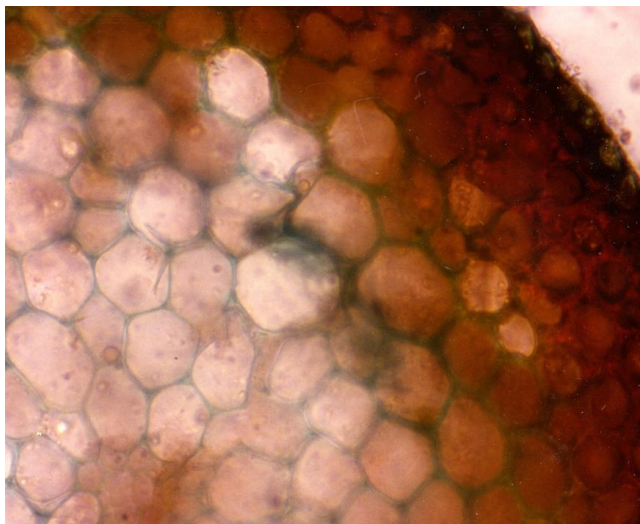


Figure 47. Cross section of stem of *Hypnum* sp. showing indistinct central strand. Photo by Isawo Kawai, with permission.



Figure 49. *Aulacomnium palustre*, a moss with predominately external conduction despite its central strand. Photo by Janice Glime.

When Bowen (1933b) compared nine species of moist habitat bryophytes (Figure 53), she found that external conduction likewise predominated in all but *Rhizomnium magnifolium* (Figure 52; as *Mnium punctatum*, but based on her description most likely what is now called *Rhizomnium magnifolium*). *Thamnobryum alopecurum* (Figure 50), apparently erroneously reported in cm instead of mm in her table, has almost no water movement internally or externally (Mägdefrau 1935), but relies instead on the constant humidity of waterfalls and streamsides. Among the dry habitat mosses in the study, only *Plagiomnium undulatum* (Figure 52) exhibits more rapid internal conduction than external conduction.





Figure 50. *Thamnobryum alopecurum*, a moss of dripping habitats that seems to have little water movement internally or externally. Photo by Michael Lüth, with permission.

Based on Bowen's (1931, 1933a,b,c) comparisons, we can derive little satisfaction about the relationship between the central strand and habitat. None of the species lacking a central strand were examined, nor were any extremely xerophytic or aquatic mosses or any liverworts examined. However, external adaptations to movement of water do seem to correlate with habitat, with those mosses from wet habitats having poor conduction capability both internally and externally, relative to taxa from drier habitats (Figure 53). The central strand appears to have only a minor role in conduction, being most useful in those taxa with a well-developed central strand, such as the **Mniaceae** (Bowen 1933c), and providing almost no value in those taxa with a small strand (Mägdefrau 1935; Zacherl 1956).

Despite Bowen's (1931, 1933a,b,c) small sample size and the presentation of "representative" data rather than means, one can still infer several patterns that indicate water pathway adaptations. The **Mniaceae** are a good example (Figure 52). There is good external conduction in *Mnium hornum* (Figure 52), where the leaf insertion is relatively small, but the leaves are strongly overlapping, as are the plants. In the very tomentose *Rhizomnium magnifolium* (Figure 52), with somewhat overlapping and encircling leaves, external conduction is relatively good, but internal conduction is much better than in *Mnium hornum*. However, in *Plagiomnium undulatum* (Figure 52), where the leaves are non-overlapping and the leaf tapers to the equivalent of a petiole at insertion, external conduction is almost non-existent. It is noteworthy that members of this family are particularly difficult to rehydrate for slide preparation, presumably due to thickened cell walls and cuticular substances on the leaves. It is reasonable to expect rapid internal conduction in the

**Mniaceae** because these mosses have well developed central strands of conducting tissue. In *Plagiomnium undulatum* the central strand occupies up to 2/3 of the stem diameter. Members of the family **Mniaceae** and *Polytrichum commune* (Figure 54-Figure 55) are also the only ones examined that have hydroids in the leaves (Bowen 1931, 1933a,b,c). As noted in *Aulacomnium palustre* (Figure 49), factors other than the size and construction of the central strand are important in determining relative conductance.

In *Brachythecium rutabulum* (or *B. rivulare*?) (Figure 56-Figure 57), the slightly decurrent leaf bases form channels that retain capillary films of water. In *Entodon rubicundus* and *Calliergonella cuspidata* (Figure 58), internal conduction is appreciable in young tissues, becoming negligible in older stems (Mizushima 1980). Bowen (1933b) attributes this to the changes in **hypodermal tissues**, which are thin-walled in young stems, becoming thick-walled in older ones. Rather, the epidermis absorbs water and sends it cell-to-cell to the tip of the plant where the young hypodermal cells permit the water to penetrate to the center of the plant where a very thin central strand occupying about 10% of the stem exists. Entry of water into the apex is rapid, as is the external movement to the tip. *Campylopus brevipilus* (Figure 59) has a central strand of 5-15 cells in diameter. As might be expected in a genus so well adapted to dry habitats, even this more wetland species has little absorption through its stem epidermis and movement of water through the hypodermis is slow, entering primarily at the stem apex. Likewise, little conduction occurs from the base through the central strand.



Figure 51. *Entodon rubicundus* with capsules & dew drops, a species with internal conduction in young tissues. Photo by Shu Suehiro, permission pending.



Figure 52. Comparison of external morphology of three members of the Mniaceae. **Left:** *Rhizomnium magnifolium*. **Middle:** *Mnium hornum*. **Right:** *Plagiomnium undulatum*. Photos by Michael Lüth, with permission.



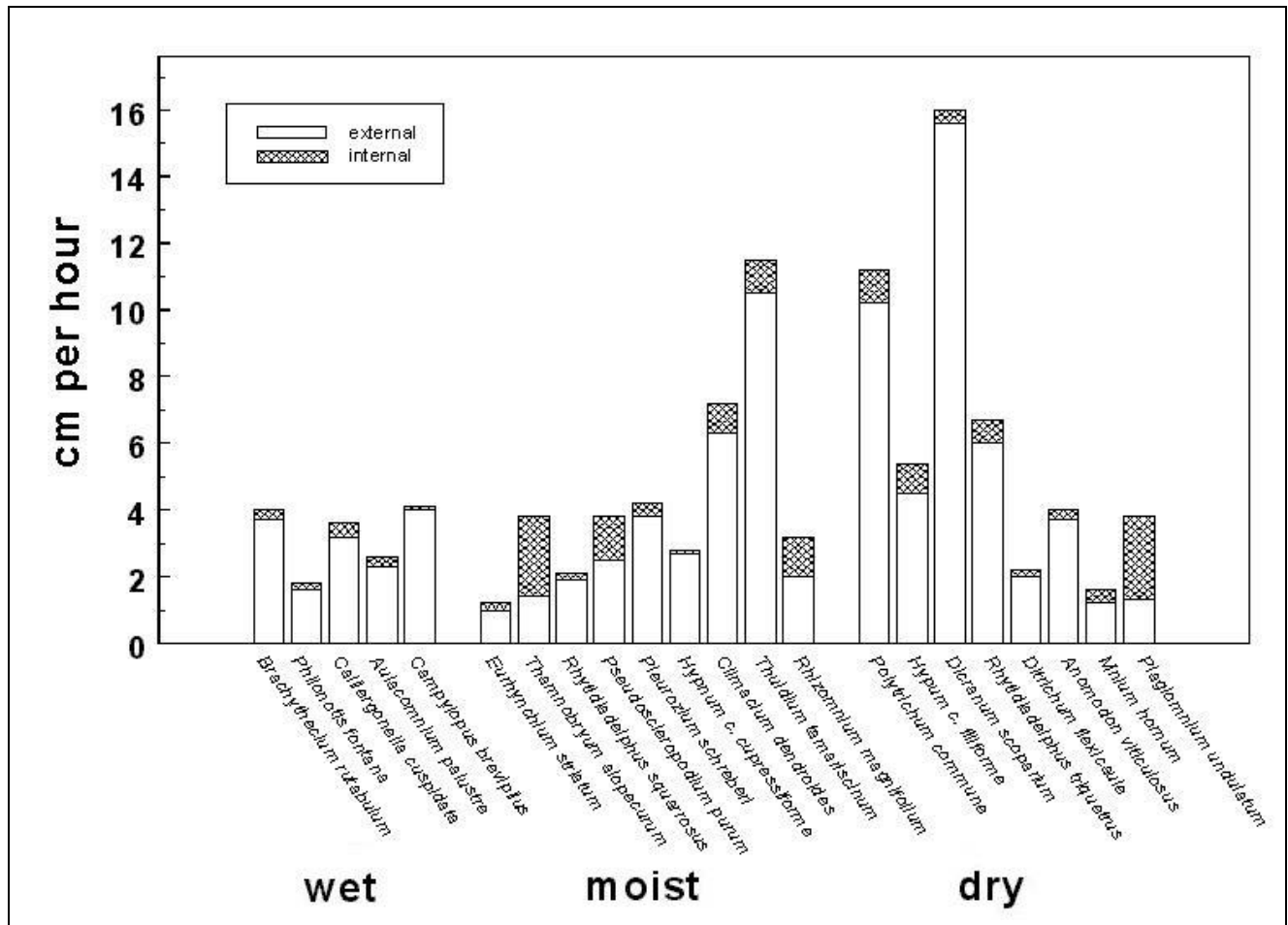


Figure 53. Comparison of movement of water up the stems in wet, moist, and dry habitat mosses. Note that for *Brachythecium rutabulum*, *Hypnum cupressiforme* var. *filiforme*, and *Rhytidiadelphus triquetrus* the internal movement is for 18 hours. (Based on the description of decurrent leaf bases and habitat, *Brachythecium rutabulum* may actually have been *B. rivulare*.) For *Thuidium tamariscinum*, *Hypnum cupressiforme* var. *filiforme*, and *Dicranum scoparium*, the external water reached the tip before one hour. In *Ditrichum flexicaule* and *Anomodon viticulosus* the water reached the tip in 15 minutes. Based on Bowen (1931, 1933a,b,c).



Figure 54. *Polytrichum commune*, a moss with good internal conduction in stem and leaves. Photo by Michael Lüth, with permission.

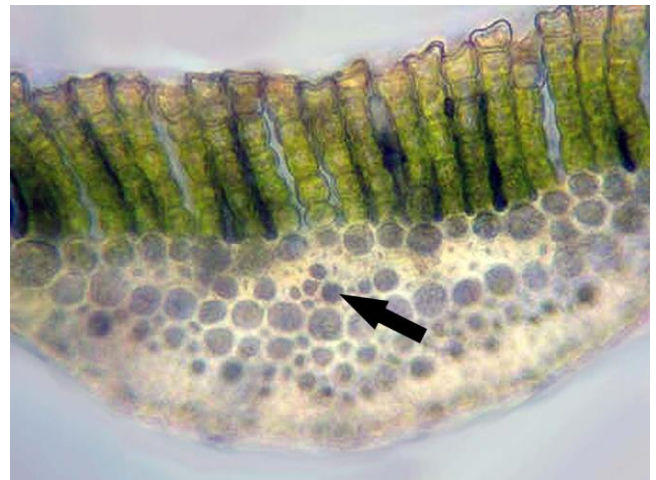


Figure 55. *Polytrichum commune* leaf cross section showing hydroids (arrow). Photo from Botany website, University of British Columbia, with permission.





Figure 56. *Brachythecium rutabulum*, a moss whose leaf bases create capillary channels. Photo by Janice Glime.



Figure 57. *Brachythecium rutabulum* leaf showing slight decurrency that aids in holding capillary water. Photo by Tom Thekathyl, with permission.



Figure 58. *Calliergonella cuspidata* has mostly internal conduction in young stems but lose it in older stems. Photo by Des Callaghan, with permission.



Figure 59. *Campylopus brevipilus*, a moss in which water enters through the stem apex. Photo by Michael Lüth, with permission.

Could it be that the central strand serves a different function? In an Alaskan black spruce forest, Skré *et al.* (1983) found that endohydric *Polytrichum commune* (Figure 54-Figure 55), which has a well-developed central strand (Figure 60) and considerable internal conduction, suffers less moisture stress than the three ectohydric mosses studied [*Hylocomium splendens* (Figure 61-Figure 62), *Pleurozium schreberi* (Figure 64), and *Sphagnum subsecundum* (Figure 63)] during the summer dry period. *Hylocomium splendens* remained below its water compensation point for nearly 50% of the July measurement period. The rates of water loss and moisture level required to reach field capacity correlate well with the moisture status observed for mosses in the field. This water retention in the endohydric *Polytrichum* supports the suggestion of Skré and coworkers that a major function of the central strand may be water storage.

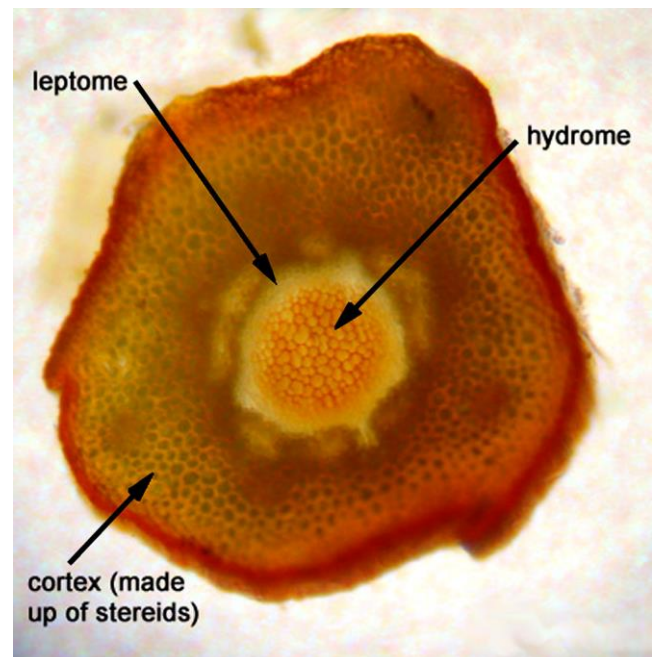


Figure 60. *Polytrichum commune* stem cross section showing hydrome. Photo from Botany website, University of British Columbia, Canada, with permission.





Figure 61. *Hylocomium splendens*, an ectohydric, on black spruce forest floor. Photo by Janice Glime.



Figure 62. *Hylocomium splendens* stem cross section showing absence of central strand. Conduction is external. Photo from Botany website, University of British Columbia, Canada, with permission.



Figure 63. *Sphagnum subsecundum*, an ectohydric moss. Photo by Michael Lüth, with permission.

## Osmotic Potential and Turgor

Unlike tracheophytes, whose net photosynthesis decreases when the water potential drops below -1 to -3 bars (Busby & Whitfield 1978), drought-tolerant mosses can resume normal photosynthesis after a drop in water potential to about -1000 bars, a condition found during the dry, hot days of summer in the open (Dilks & Proctor 1979). Even in the shaded forest, the water potential of a moss can drop to -200 to -400 bars. While flowering plants and ferns may have negative photosynthesis at water potentials of -12 to -15 bars, mosses such as the woodland to semi-shaded species *Hylocomium splendens* (Figure 61-Figure 62), *Pleurozium schreberi* (Figure 64), and *Tomentypnum nitens* (Figure 65) can continue net photosynthesis until the water potential falls below -55 to -100 bars (Busby & Whitfield 1978), and *Camptothecium lutescens* (Figure 66) from the United Kingdom can maintain a net positive photosynthesis down to -150 bars (Dilks & Proctor 1979). The drought-intolerant moss *Hookeria lucens* (Figure 67), on the other hand, must maintain 100% humidity and cannot maintain positive photosynthetic gain when the water potential drops below 80 bars (Dilks & Proctor 1979). Yet this highly drought-intolerant moss, relatively speaking, has primary cell walls with **pit fields** in its stem parenchyma, structures common to tracheids and vessels and permitting lateral transport, suggesting that *Hookeria lucens* may use these cells in internal conduction (Cortella *et al.* 1994).



Figure 64. *Pleurozium schreberi*, an ectohydric moss with leaves completely covering the stem. Photo by Janice Glime.



Figure 65. *Tomentypnum nitens*, an ectohydric moss. Note dense tomentum covering stems. Photo by Michael Lüth, with permission.



One adaptation to maintaining water is to increase the osmotic value of the cells. Ochi (1952) compared a number mosses and showed that the highest osmotic values were generally in mosses adapted to xeric conditions. He obtained high values (0.90-0.62) in such tree-trunk and sunny rock dwellers as *Hedwigia ciliata* (Figure 82), *Thamnobryum subseriatum* (= *Thamnobryum sandei* var. *cymbifolium*?) (Figure 68), *Myuroclada maximoviczii* (Figure 69), *Thuidium cymbifolium* (Figure 70), *Neckera yezoana*, and *Anomodon giraldii* (Figure 71). Intermediate values characterized those on soil (0.70-0.30), including *Dicranum japonicum* (Figure 37), *Pogonatum inflexum* (Figure 72), *Plagiomnium maximoviczii* (Figure 73), and *Plagiomnium cuspidatum* var. *trichomanes* (Figure 74). In shady, wet, forested areas, Ochi obtained the lowest value (0.26), exemplified by *Plagiomnium vesicatum* (Figure 75) and *Hookeria acutifolia* (Figure 76). Surprisingly, values were highest in older plants and mature portions, not the vital young buds.



Figure 66. *Camptothecium lutescens*, a moss that can maintain photosynthesis at very low water potential. Photo by Michael Lüth, with permission.



Figure 67. *Hookeria lucens*, showing thin leaves that are very drought-intolerant. Photo by Michael Lüth, with permission.



Figure 68. *Thamnobryum subseriatum*, a moss from emergent rocks of streams. Photo by Michael Lüth, with permission.



Figure 69. *Myuroclada maximoviczii*, a rock dweller with high osmotic values. Photo by Janice Glime.



Figure 70. *Thuidium cymbifolium*, a sunny rock dweller with high osmotic values, with capsules. Photo by Li Zhang, with permission.





Figure 71. *Anomodon giraldii*, a xerophyte. Photo by Misha Ignatov, with permission.



Figure 72. *Pogonatum inflexum*, an endohydric soil moss. Photo from Digital Museum, Hiroshima University, with permission.



Figure 73. *Plagiomnium maximoviczii*, an endohydric species. Photo from Hiroshima University Digital Museum of Natural History, with permission.



Figure 74. *Plagiomnium cuspidatum*, a soil moss with endohydric water transport. Photo by Hermann Schachner, through Creative Commons.



Figure 75. *Plagiomnium vesicatum*, an endohydric moist forest soil moss. Note the wide spacing of the leaves – a morphology that is unsuitable for good ectohydric transport. Photo from Digital Museum, Hiroshima University, with permission.



Figure 76. *Hookeria acutifolia*, a moist forest species with poor desiccation tolerance. Photo by Steve Joya, permission pending.

Proctor (1999) likewise examined a number of bryophytes to determine their osmotic potential. He found that the leafy ones (mosses and leafy liverworts) have a full turgor osmotic potential of -1.0 to -1.5 MPa, whereas the multistratose thallose liverworts have -0.5 to -1.0 MPa.



The full turgor content of water varies with season, ranging 100-300% in bryophytes from well-drained habitats. But Proctor found that the highest turgor occurs in the new growth. The cell walls are highly extensible in most of the thallose liverworts and such drought-tolerant mosses as *Syntrichia ruralis* var. *arenicola* (Figure 77) and *Racomitrium lanuginosum* (Figure 78), but it is quite low in certain leafy liverworts with very rigid cell walls. Unlike Ochi (1952), Proctor found that variations in water relation parameters seem to bear little relationship to habitat for most bryophytes. He attributed this lack of relationship to the consideration that they are usually only metabolically active when they are fully hydrated.

Some bryophytes can tolerate turgor up to 1400% of their dry mass [*Dumortiera hirsuta* (Figure 79) & *Conocephalum conicum* (Figure 80)] (Proctor *et al.* 1998). On the other hand, xerophytic mosses such as *Syntrichia ruralis* (Figure 77) and *Andreaea alpina* (Figure 81) reach full turgor at only 110%.



Figure 77. *Syntrichia ruralis* var. *arenicola*, a drought-resistant moss with very extensible cell walls. Photo by Michael Lüth, with permission.



Figure 78. *Racomitrium lanuginosum*, a drought-resistant moss with very extensible cell walls. Photo by Janice Glime.

### Water Content

Given sufficient water, water content is related to the cell's osmotic potential. Low water content seems to be related to a xeric habitat (Hernández-García *et al.* 1999), suggesting tolerance rather than the avoidance that might be obtained by maintaining high osmotic potential. In the xeric and mesic pine forests of Tenerife, water content of all mosses tested was <140% of dry mass. *Hedwigia ciliata* (Figure 82), *Grimmia laevigata* (Figure 83), *G. trichophylla* (Figure 84), and *Pterogonium gracile* (Figure

85), the rock dwellers, have the lowest field water content and fastest absorption and water loss rates among the species. *Polytrichum juniperinum* (Figure 86), *Bartramia stricta* (Figure 87), and *Anacolia webbii* (Figure 88) have the highest field water content and slowest water absorption and loss rates. The highest drought tolerance occurs in *H. ciliata*, *B. stricta*, *G. laevigata*, and *G. trichophylla*.



Figure 79. *Dumortiera hirsuta* showing hairs on edges of thalli and a turgid condition. Photo by Li Zhang, with permission.



Figure 80. *Conocephalum conicum*, a liverwort that can tolerate turgor up to 1400% of its dry mass. Photo by Dick Haaksma, with permission.



Figure 81. *Andreaea alpina*, a xerophytic moss that can only tolerate turgor up to 110% of dry weight. Photo by Andrew Hodgson, with permission.





Figure 82. *Hedwigia ciliata*, a very drought-tolerant species. Photo by Michael Lüth, with permission.



Figure 85. *Pterogonium gracile*, a rock-dweller with low water content and rapid water uptake. Photo by David Holyoak, with permission.



Figure 83. *Grimmia laevigata*, a rock-dweller with low water content and rapid water uptake. Photo by Jonathan Sleath, with permission.



Figure 86. *Polytrichum juniperinum*, an endohydric moss with high water content and slow water absorption. Photo by Keith Bowman, with permission.



Figure 84. *Grimmia trichophylla*, a rock-dweller with low water content and rapid water uptake. Photo by Michael Lüth, with permission.



Figure 87. *Bartramia stricta*, a moss with high water content and slow water absorption. Photo by Michael Lüth, with permission.





Figure 88. *Anacolia webbii*, a rock-dweller with low water content and rapid water uptake. Photo by Jan-Peter Frahm, with permission.

Nevertheless, most bryophytes apparently do not exhibit the low **water capacity** (50-250%) that permits some seed plants and lichens to survive areas with very low rainfall (During 1992). Known **water capacities** (percent of wet mass relative to dry mass) in bryophytes mostly fall into the high water capacity range of 650-1700% (During 1992), except for endohydric taxa, ranging 190-577% (Coufalová 1951). For example, the damp forest leafy liverwort *Bazzania trilobata* (Figure 89) at saturation had a moisture content of 1300% of its dry mass (Sollows *et al.* 2001).



Figure 89. *Bazzania trilobata*, a damp forest species with a saturation moisture content of ~1300% dry weight. Photo by Jan-Peter Frahm, with permission.

Nichols (1918) reported that *Sphagnum* (Figure 63) pads, used for bandages in World War I, could absorb up to 22 times their mass (water capacity = 2200%), making them 5-6 times as absorptive as cotton pads. Other bryophytes, as in some South African montane areas, survive on the water they collect from early morning mist in low-lying clouds (Russell 1982), suggesting that these bryophytes may indeed have low water capacities. Furthermore, many bryophyte taxa are tolerant of very low water contents (5-10% of dry mass), resuming photosynthesis upon remoistening (Proctor 1990).

It appears that at least for some bryophytes, it is best to be wet or be very dry. Water pressure in the range of -100 to -200 MPa is best for survival in a dry state (Proctor 2001). Akande (1984, 1985) has examined the effects of the degree of dehydration on Nigerian bryophytes and found that those maintained at 0% humidity for one week and for one month both resumed respiration more quickly than those maintained for the same time period at 32% and 54% (Akande 1984). He found that the leafy liverwort *Mastigolejeunea florea* is less desiccation-tolerant than the two mosses studied, but all three taxa did have individuals that survived at 0%, 32%, and 54% relative humidity at ambient temperature (Akande 1985).

### Water-logging

Despite their needs for high water content, bryophytes cannot afford to be too wet or they are unable to carry out photosynthesis. Acquiring CO<sub>2</sub> must occur through the leaf surface, and a continuous layer of water interferes with that transfer. Silvola (1991) found that in all the boreal forest mosses he tested except *Polytrichum commune* (Figure 54-Figure 55), photosynthesis decreased when the water content exceeded a certain optimal level (see also Williams & Flanagan 1991). It is likely that the leaf lamellae provided air spaces for CO<sub>2</sub> transfer in *P. commune*. Many *Sphagnum* species suffer similarly from water-logging.

### Inducible vs Constitutive Desiccation Tolerance

As recently as 2011, Green *et al.* reviewed the literature and reported that bryophytes appear to all be constitutive. To support this they cite that no protein synthesis is required upon rehydration before metabolism can commence. Bryophytes furthermore appear to always be protected from desiccation mortality. Further support is the constant presence of high sucrose levels. And the cellular structure is usually maintained during desiccation.

Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] **desiccation tolerance** exist among bryophytes (Stark *et al.* 2013). Those with **constitutive desiccation tolerance (CDT)** are not dependent on the rate of drying to determine their recovery, whereas those that depend on **inducible desiccation tolerance (IDT)** are. Reduced or no desiccation tolerance following rapid drying is generally an indicator that the plants are IDT plants. Tracheophytes, with the exception of some ferns (Watkins *et al.* 2007), are IDT plants (Oliver *et al.* 1998, 2000), whereas bryophytes are mostly CDT plants (Toldi *et al.* 2009), hence their high ability to survive drying.



Those bryophytes with **constitutive desiccation tolerance (CDT)** are not dependent on the rate of drying, whereas those with only **inducible desiccation tolerance (IDT)** are. Therefore, the IDT plants, including IDT bryophytes, are likely to die when exposed to rapid drying.

But bryophytes can use both strategies. Stark and coworkers have investigated the inducible protections that permit bryophytes to survive desiccation. Those bryophytes that survive slow drying but not rapid drying provide us with evidence that something happens during that slow drying process, and that happening provides the inducible desiccation tolerance (Stark *et al.* 2013). Bryophytes also possess constitutive desiccation tolerance, a tolerance that is common among terrestrial bryophytes. For example, the desert moss *Pterygoneurum lamellatum* (**Pottiaceae**; Figure 7) exhibits both a constitutive and an inducible response. The bryophyte tolerance strategy couples **constitutive** cellular protection during dehydration with the **induction** of a recovery/repair mechanism upon rewetting (Oliver *et al.* 2005; Toldi *et al.* 2009; Stark & Brinda 2015).

More recently, Stark and Brinda (2015) have found that not only can a desert moss have both inducible and constitutive desiccation tolerance, but it can have each in different parts of the same shoot at the same time or in different stages in the life cycle. Stark and Brinda propose that as the sporophyte grows older, the presence of sugars in the sporophyte facilitates desiccation tolerance. This would help to explain the greater danger of death by desiccation in the early embryonic stage before significant sugar accumulation occurs. At the same time, the early embryo exhibits inducible desiccation tolerance (IDT) and requires slow desiccation, usually not a problem within the protection of the apical gametophyte leaves. As the embryo develops and the seta emerges from these protective leaves, the sporophyte changes from IDT to partially CDT. Stark and Brinda suggest that this evolutionary change resulted from selection pressures of intermittent drying in this exposed sporophyte. This exposed sporophyte tissue is most likely subject to faster rates of desiccation, making an inducible system inadequate to meet the time demands and selecting for the constitutive desiccation tolerance. The presence of a waxy cuticle in the capsules of *Funaria hygrometrica* (Figure 26) provide an example of this CDT (Budke *et al.* 2011, 2012, 2013).

Stark and Brinda (2015) concluded that once the seta elongation phase reaches the stage of capsule expansion, sucrose imported from the gametophyte (Renault *et al.* 1992) should be present in the sporophyte, endowing the sporophyte with the raw materials needed to tolerate rapid drying (Stark & Brinda 2015). In *Acaulon muticum* (Figure 92), small vacuoles are present in the placental region of the sporophyte-gametophyte junction (Rushing & Anderson 1996). These abundant vacuoles may be present in the embryonic sporophyte as well, where they could provide protection from water stress in the rapidly growing sporophyte.

Wolkers *et al.* (2001) had already suggested that a slower rate of drying may permit the proteins and sucrose to interact in a more protective manner. For example, in *Physcomitrella patens* (Figure 21, Figure 90) and

*Syntrichia ruralis* (Figure 93), a slow drying treatment induces the production of either ABA (see below) or dehydrin, or both (Werner *et al.* 1991; Hellwege *et al.* 1994; Cuming *et al.* 2007). When ABA is applied to the outside of *Exormothes holstii* (Hellwege *et al.* 1994), it elevates sucrose levels and increases protection against rapid drying (see also Pence 1998; Oldenhof *et al.* 2006). Koster *et al.* (2010) demonstrated the genetic connection between ABA and the expression of several homologs to stress proteins, including two dehydrin-like proteins. The only problem with this logic is that the natural presence of ABA is still unknown in *Physcomitrella patens* and *Syntrichia ruralis* (Stark & Brinda 2015).



Figure 90. *Physcomitrella patens* sporophyte, a species in which a slow drying treatment induces the production of either ABA or dehydrin. Photo from Ralf Reski Lab, through Wikipedia Commons.

In *Aloina ambigua* (Figure 91), Stark and Brinda (2015) considered that the seta may elongate too fast for the inducible desiccation tolerance system to respond. This exposed tissue may therefore rely on the constitutive system to provide desiccation tolerance for the developing capsules.



Figure 91. *Aloina ambigua* with capsules. The seta may grow too rapidly in this species for inducible desiccation tolerance to protect it. Photo by Michael Lüth, with permission.



## Hardening

**Hardening** is a phenomenon known for flowering plants, but the concept is usually associated with preparation for winter. Beckett *et al.* (2005) induced desiccation hardening in the moss *Atrichum androgynum* (Figure 11) by reducing the relative water content of apical portions for 1/2 to 3 days, followed by storage fully hydrated for another day. Plants were then desiccated for 16 hours over silica gel, and the recovery of PSII during rehydration was monitored. Hardening affected photosystem II (PSII) before desiccation, decreasing its efficiency, especially at saturating light intensities. Upon rehydration, however, hardened plants recovered their PSII activity more quickly and greatly increased the non-photochemical quenching in the first few hours compared to those plants not subjected to hardening. Beckett *et al.* concluded that hardening shifts the photosynthetic apparatus from a state of high efficiency to one of less efficiency but having a photoprotected state.

Hardening can confound physiological experiments when comparing desiccation tolerance. Once hardened, the plant is likely to receive the benefits in desiccation resistance for a prolonged period of time, such that a rehydration period of 24-72 hours may not remove that benefit (Bopp & Werner 1993; Stark *et al.* 2014). Instead, regenerates from fragments (regenerated more than once to eliminate prior hardening) or plants grown from spores may be necessary to create plants that have no prior desiccation experience, hence no hardening (Stark & Brinda 2015).



Figure 92. *Acaulon muticum*, a species with small vacuoles in the placental region that may protect the sporophyte from water stress. Photo by Michael Lüth, with permission.

## Desiccation-induced Changes

Iljin (1953, 1957) considered that mechanical injury to the protoplast membranes during the drying and rewetting processes is the primary cause of desiccation sensitivity. He considered the tensions that develop in cells during dehydration, pulling protoplasm inward as the vacuoles shrink and cell walls pulling membranes outward, are the primary causes of lethal injuries in drought-sensitive species. Drought-tolerant plants mitigate these tensions by

such cellular aspects as reduced cell size, small or absent vacuoles, lack of plasmodesmata, easily deformed cell walls, and reduced osmotic pressure. For example, small cytoplasmic vesicles (vacuoles) are present in such desiccation-tolerant species as *Syntrichia ruralis* (Figure 93), *Neckera crispa* (Figure 94), *Pleurozium schreberi* (Figure 64), and *Triquetrella papillata* (Figure 95) (Oliver & Bewley 1984). But this does not hold true for all species – in the desiccation-tolerant *Ceratodon purpureus* (Figure 96-Figure 98) and *Didymodon vinealis* (Figure 99), the vacuoles are quite large. And the desiccation-intolerant *Cratoneuron filicinum* (Figure 40) does not have large vacuoles. **Plasmodesmata** (microscopic channels that traverse cell walls of plant and some algal cells, enabling transport and communication between them) likewise do not seem to be related to desiccation-tolerance, but these are difficult to see and often require electron microscopy for viewing.



Figure 93. *Syntrichia ruralis*, a species in which slow drying induces the production of ABA. Photo by John Game, with permission.



Figure 94. *Neckera crispa*, a species with small cytoplasmic vesicles (vacuoles). Photo by David Holyoak, with permission.





Figure 95. *Triquetrella papillata* from New Zealand, a species with small cytoplasmic vesicles (vacuoles). Photo by Jan-Peter Frahm, with permission.



Figure 96. *Ceratodon purpureus*, a desiccation-tolerant species dry on a rock. Photo by Michael Lüth, with permission.



Figure 97. *Ceratodon purpureus* hydrated on a rock. Photo by Michael Lüth, with permission.

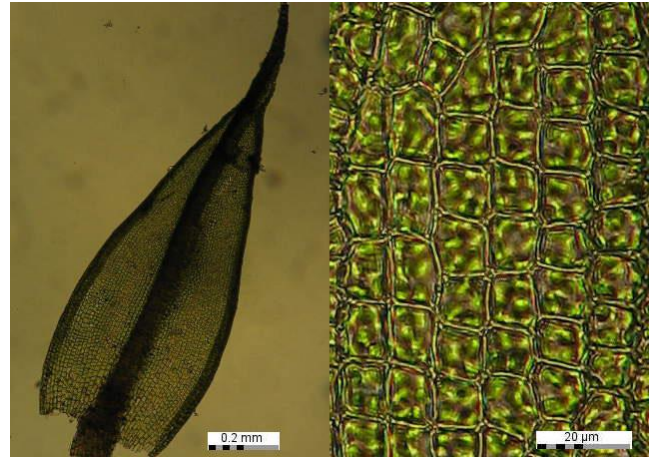


Figure 98. *Ceratodon purpureus* leaf and leaf cells, a desiccation-tolerant species with large vacuoles. Photo by Tom Thekathyl, with permission.

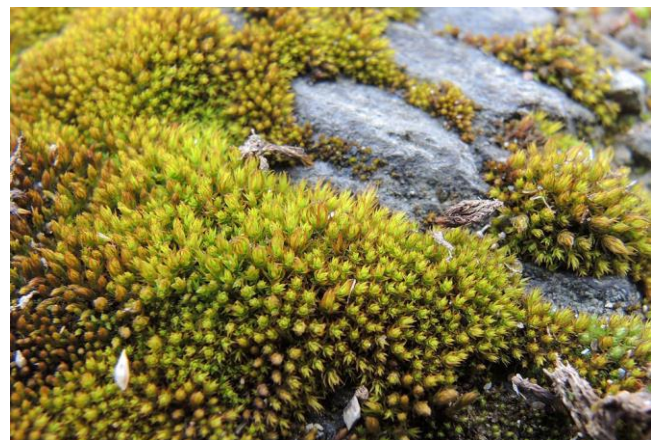


Figure 99. *Didymodon vinealis*, a desiccation-tolerant species with large vacuoles. Photo by Michael Lüth, with permission.

Henckel and Pronina (1968, 1969, 1973) suggest that those plants that are drought-tolerant are continuously prepared for desiccation, *i.e.*, have constitutive desiccation tolerance. However, this theory likewise did not fit the evidence presented by slow vs rapid drying in bryophytes. Bewley (1979) suggested that instead, three factors are critical to desiccation tolerance:

1. limiting damage during desiccation to a repairable level
2. maintaining physiological integrity in the dry state so that metabolism can be reactivated quickly upon rehydration
3. putting repair mechanisms into effect upon rehydration, in particular to retain or regain integrity of membrane and membrane-bound organelles.

As bryophytes desiccate, a series of changes occurs. In *Physcomitrella patens* (Figure 21, Figure 90), these changes include plasmolysis, chloroplast remodelling, and microtubule depolymerization, as demonstrated by desiccation for more than one month to 10% of fresh weight (Wang *et al.* 2009). Nevertheless, Wang and coworkers found that the membranes retain their integrity. These changes involved 71 responsive proteins. Most of these were involved in metabolism, cytoskeleton, defense, and signaling. But not all changes seem to be that of repair



or stability. Cytoskeletal protein degradation might cause cytoskeletal disassembly and resulting changes in cell structure. **Late embryogenesis abundant proteins (LEA proteins)** and reactive oxygen species-scavenging enzymes are among those prominently induced, possibly helping to reduce the damage caused by desiccation. Oliver *et al.* (2004) likewise found that the LEA proteins were the most abundant transcripts associated with drying tissues. They suggest that the LEA proteins might play a role in recovery from desiccation.

Oliver *et al.* (2004) took a genetic approach to understanding desiccation tolerance, using the desiccation-tolerant *Syntrichia ruralis* (Figure 93). They found that the **transcriptome** (set of all RNA molecules, including mRNA, rRNA, tRNA, and other non-coding RNA transcribed in a cell) has a diverse population of transcripts that reflects a period of metabolic upheaval in the gametophyte cells. Much of the emphasis in this transcriptome is on the protein synthesis machinery, ion and metabolite transport, and the biosynthesis and repair of membranes. When gametophytes are rehydrated, there is a large number of transcripts that code for enzymes involved in oxidative stress metabolism and phosphorylating activities.

When *Pterygoneurum lamellatum* (Figure 7) is subjected to very rapid drying, it is severely damaged throughout the entire shoot except the shoot apex (Stark *et al.* 2013). This damage results in slower growth rates, fewer regenerative shoots, and a damaged photosynthetic system as demonstrated by alterations in fluorescence.

### Cell Contents

As one might expect, cell contents respond to desiccation stress. In the mosses *Bryum argenteum* (Figure 100) and *Didymodon vinealis* (Figure 101) from cryptogamic crusts, the free proline content was significantly greater than in those from a typical (wetter) grassland (Xu *et al.* 2005).



Figure 100. *Bryum argenteum* in crack in parking lot, a species that manufactures proline in dry habitats. Photo by Paul Davison, with permission.

In the moss *Plagiomnium acutum* (Figure 103), concentrations of proline, soluble sugar, and reducing sugar all increase noticeably during dehydration, reaching maximum concentration after 12 hours (Li *et al.* 2009). As the membrane permeability increases, activities of protective enzymes likewise increase, including SOD,

CAT, and POD. DNA degrades gradually, with only some of the low molecular weight fragments remaining. Upon rehydration, all of these changes reverse. *Physcomitrella patens*, like *Plagiomnium acutum*, accumulates the osmoprotectants altrose, malitol, ascorbic acid, and proline when subjected to drought stress (Erxleben *et al.* 2012).



Figure 101. *Didymodon vinealis*, a cryptogamic crust species that maintains high concentrations of proline in dry conditions. Photo by Michael Lüth, with permission.



Figure 102. *Physcomitrella patens*, a species that accumulates altrose, malitol, ascorbic acid, and proline in response to drought stress. Photo by Michael Lüth, with permission.



Figure 103. *Plagiomnium acutum*, a moss that demonstrates increases in proline, soluble sugar, and reducing sugar during desiccation. Photo by Liu; permission pending.



Cruz de Carvalho *et al.* (2015) found that the low water potentials in dehydrating cells of the aquatic moss *Fontinalis antipyretica* (Figure 104) is coupled with osmoregulation due to increase of such soluble materials as soluble sugars and compatible inorganic ions. These increase turgor pressure. In addition to its role as an osmolyte, sucrose stabilizes membranes and proteins through **vitrification**, *i.e.*, by creating glasslike substances. When the moss was dehydrated slowly, the cell walls became more elastic, permitting cell shrinkage that maintained turgor and helped to preserve metabolic functions. However, in rapid drying, there was a loss of turgor and osmotic potential. Although the sucrose content increased, rehydration of the fast-dried samples resulted in 50% loss of sucrose through cell leakage as a result of cell membrane rupture. Slowly dehydrated leaves, on the other hand maintained their sucrose content upon rehydration. The thick mats of long dangling *Fontinalis antipyretica* facilitates slow drying of this species in nature.

Sucrose acts as an osmotic "spacer" in membranes (Werner *et al.* 1991; Oldenhof *et al.* 2006; Cruz de Carvalho *et al.* 2014). This is accompanied by ABA mediation of protein synthesis, strengthening the cellular glasses typical of inducible desiccation tolerance in mosses, as shown in *Physcomitrella patens* (Oldenhof *et al.* 2006).

### Chloroplast Responses

Bryophyte chloroplasts undergo ultrastructural changes when undergoing desiccation. Chloroplasts become smaller and more spherical with a less-well defined internal structure (Noailles 1978). The general lamellar structure collapses, with the **thylakoids** (chlorophyll vesicles) becoming dispersed; starch granules are lost. This response is similar to that induced by ABA in experiments related to freezing tolerance (Nagao *et al.* 2005).

Bryophyte chloroplasts contain **plastoglobuli** (Tucker *et al.* 1975; Oliver & Bewley 1984) in groups within the stroma. These increase in size and number during dehydration in *Syntrichia ruralis* (Figure 93) (Tucker *et al.* 1975).

It appears that the chloroplasts may be altered by desiccation in other ways we do not fully understand. I found that I could not extract chlorophyll effectively from dry *Fontinalis* spp. (Figure 104) using acetone unless I rewet them for about 15 seconds first. Tuba (1984) reported a possible decoupling of the chlorophyll from its protein, but later (Tuba 1985) attributed that apparent phenomenon to the separation of upper and lower shoots and the extraction process. In fact, he stated that the chlorophyll *a* and *b* remained unchanged during daily desiccation and early rehydration of *Syntrichia ruralis* (Figure 93). He concluded that the **neoxanthin** (a carotenoid pigment), due to its hydrophilous nature, may be adaptive in binding the **LHCP** (light-harvesting chlorophyll protein) to the **PS II** chlorophyll core, thus stabilizing the LHCP.

One factor in the protection of chlorophyll against light damage during desiccation is that the pigment **zeaxanthin** can bind to the chlorophyll-containing thylakoid protein (Deltoro *et al.* 1998; Heber *et al.* 2001). On the other hand, loss of chlorophyll fluorescence during drying of pre-darkened mosses suggests that energy dissipation in the desiccated mosses is unrelated to zeaxanthin availability.

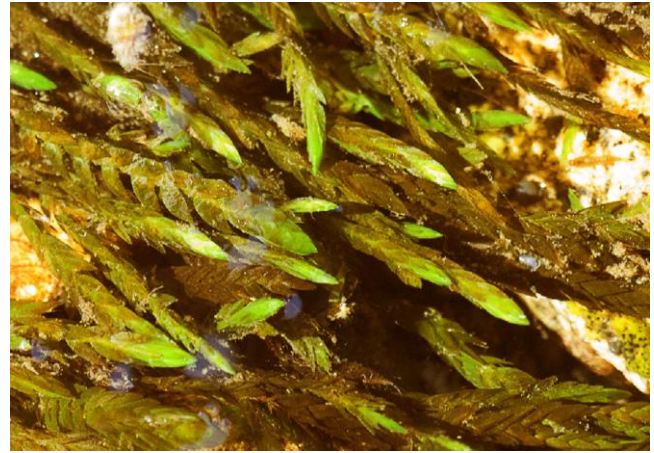


Figure 104. *Fontinalis antipyretica*, a moss that, when dry, has a delay before its chlorophyll dissolves in alcohol, suggesting that the chlorophyll may be complexed during dehydration. Projecto Musgo, through Creative Commons.

Even among the desiccation-tolerant bryophytes, the rate of recovery of chlorophyll fluorescence varies widely upon rehydration (Proctor 2010). For example, some species have high values of  $F_v/F_m$  in the early minutes of recovery, accompanied by low absolute values of  $F_m$ . But most recovery curves are logistic (S-shaped curve that starts slow, goes up exponentially, then approaches horizontal) for photosynthetic  $\text{CO}_2$  fixation in the light.

### Photosynthesis

Lee and Stewart (1971), using *Calliergonella cuspidata* (Figure 58), *Climacium dendroides* (Figure 105), and *Hypnum cupressiforme* (Figure 46-Figure 47), found that the degree of desiccation tolerance correlates with the degree of moisture stress experienced in the habitat. This tolerance is expressed as a rapid recovery of photosynthetic rate in taxa from habitats with severe moisture deficits, whereas those from habitats with no appreciable moisture deficits lose photosynthetic capability more quickly and are slower to recover.

Seel *et al.* (1992) made similar comparisons using *Syntrichia ruralis* (Figure 93), *Bryum pseudotriquetrum* (Figure 106), and *Dicranella palustris* (Figure 107) from a range of habitats with different water availabilities. All three species become photosynthetically inactive when dried to a water content of 100-200%. But recovery differs. The xeric *Syntrichia ruralis* from sand dunes recovers to its pre-desiccation photosynthetic rates, but its rate of recovery is affected by irradiance during its desiccation. Those mosses from hydric habitats, when rehydrated, have partial resumption of their photosynthetic electron transport if they are dried in the dark, but if they are dried in even low light they did not resume their photosynthetic activity. Their symptoms indicate a lasting photoinhibition of photosynthesis following rehydration. On the other hand, the desiccation-tolerant *Syntrichia ruralis* (Figure 93) experiences significant photoinhibition only when receiving continuous high irradiance ( $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) while hydrated. But if it is dehydrated while receiving high irradiance it shows less evidence of photoinhibition after rehydrations. Desiccation at low irradiance has no effect following rehydration. Leaf curling reduces photon flux absorption by 50-60% in dry mosses compared to hydrated mosses, although it is



possible that changes in optical properties of papillae may contribute to that reduction.



Figure 105. *Climacium dendroides*, a species that shows acclimation to its habitat adjusting its tolerance to the moisture stress experienced in the habitat. Photo by Michael Lüth, with permission.



Figure 106. *Bryum pseudotriquetrum*, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.



Figure 107. *Dicranella palustris*, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.

Both thylakoid lipids and chlorophyll reduction coincide with the loss of photosynthesis in dehydrating *Atrichum androgynum* (Figure 11) (Guschina *et al.* 2002).

The desert moss *Syntrichia caninervis* (Figure 12) recovers quickly when shoots are remoistened in the dark (Zhang *et al.* 2011). This is an advantage for this moss that receives much of its moisture from dew, a night-time phenomenon. Its leaf hairs are able to trap the dew (and also fog and raindrops) and direct them to the base of the leaf where it rapidly is absorbed. The chlorophyll fluorescence has a narrow optimum range. The moss seems to experience no damage to its membranes or organelles and reaches 90% of its 30-minute photosynthetic yield within the first minute of rehydration. This permits it to take rapid advantage of small amounts of moisture from fog, dew, snow, and short rainfall events.

### Mitochondria

The mitochondria [cell organelle that generates most of the cell's supply of **ATP** (adenosine triphosphate), used as a source of chemical energy] become deformed as they dehydrate, becoming small and rounded (Noailles 1978). Internal cristae may be greatly reduced in size or lost completely.

### Nuclei

The nuclei seem to suffer little from the effects of desiccation, retaining their normal size (Noailles 1978).

### Vacuoles and Vesicles

Normal bryophyte cells have one to several large vacuoles (Noailles 1978). During dehydration, these break down to form numerous small vesicles (Oliver & Bewley 1984). It appears that ABA may be involved in this transformation, since the response is similar to that induced by ABA during freezing (Nagao *et al.* 2005). ABA-treated cells have slender chloroplasts, and the quantity of starch grains is reduced in comparison with those of non-treated cells.

### Membranes

Membranes in general suffer from dehydration, including thylakoids, cristae, and cytoplasmic membranes like endoplasmic reticulum and dictyosomes, resulting in the shrinkage of organelles (Noailles 1978). The chloroplast membrane itself may exhibit clefts (Tucker *et al.* 1975). It is the ability to repair this damage that makes many bryophytes desiccation tolerant (Li *et al.* 2009).

Both desiccation-tolerant and intolerant bryophytes leak electrolytes when rehydrated (Gupta 1976, 1977, 1979), as do dry viable seeds, lichens, pollen grains, fungi, and their spores (Simon 1974, 1978). This leakage lasts only a few minutes except in cases of permanent damage (Oliver & Bewley 1984). Oliver and Bewley (1984) listed amino acids, mono-, di-, and tri-saccharides, sugar alcohols, organic acids, hormones, phenolics, phosphates, and various electrolytes as leaked substances during rehydration, although the leakage often lasts only minutes.

The desert moss *Syntrichia caninervis* (Figure 12) is the dominant species in the Gurbantunggut Desert, a cold desert in Central Asia. Wu *et al.* (2012) investigated the



membrane changes during desiccation of this species. There are no significant changes in electrical conductivity of the rehydration water during dehydration or rehydration. There also appears to be no ultrastructural damage to the membrane during dehydration or rehydration, but there are major changes in cellular ultrastructure. Wu and coworkers suggest three possible explanations for the apparent disruption of the membranes in desiccated state:

1. Adaptive morphological features of the leaf that remain intact permit the leaves to regain membrane integrity rapidly upon rehydration.
2. The moss becomes dormant rapidly, maintaining some level of membrane integrity.
3. Soluble sugars and free **proline** (constitutive substances) increase rapidly during desiccation, contributing to membrane stabilization.

### Plasmolysis

One of the consequences of desiccation can be **plasmolysis** of the cells (shrinkage of protoplast away from cell wall) (Oliver & Bewley 1984). In some cases, very narrow elongate cells seem to resist plasmolysis, perhaps due to the small cell volume and strong adhesion to the cell walls. But plasmolysis can occur in bryophytes and can result in cell damage to both the plasma membrane and the cell wall.

In *Didymodon vinealis* (Figure 99) and *Triquetrella papillata* (Figure 95), the dehydrated cells contract to 50-70% of the original volume (Moore *et al.* 1982). The cell walls contract, permitting the protoplasm to fill the cell and preventing entry of air into the drying cells.

It appears that at least the liverwort *Sphaerocarpos donnellii* (Figure 108) is able to partially compensate for this plasmolysis damage (Grusak *et al.* 1980), where both normal and plasmolyzed tissues are composed primarily of hemicellulose and cellulose. But in plasmolyzed cells, labelled C<sup>14</sup> is considerably lower than in normal cells. Rather, these cells have higher radioactivity in pectin and hemicellulose and less in cellulose, suggesting a possible mechanism for enhancing wall stability. This transformation would provide numerous sites for cross-linkage between the cellulose microfibrils as walls regenerate.



Figure 108. *Sphaerocarpos donnellii*, a species that has the ability to partially compensate for plasmolyzed cells. Photo by Belinda Lo, through Creative Commons.

### Liverworts

Liverworts have received surprisingly little attention relative to their drought tolerance strategies. Granted, these plants seem to require higher moisture conditions in general, but their presence as epiphytes in many areas attests to the ability of at least some liverworts to survive long periods of drought, and certainly the thallose liverworts of flood plains and other seasonal habitats provide another set of highly desiccation tolerant or desiccation avoider species.

Pressel *et al.* (2009) found that liverworts undergo "profound" cytological changes during dehydration. As in tracheophytes and mosses, these include fragmentation of the vacuole, rounding of chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged. Furthermore, chlorophyll fluorescence returns to normal within 24-48 hours during rehydration. And like the mosses, their dehydration and rehydration are associated with the depolymerization and repolymerization of the cortical microtubule cytoskeleton. But unique among the bryophytes is the presence of **oil bodies** in liverworts, membrane-bound organelles that take on many shapes among the species (Kozłowski 1921; Kis & Pócs 1997). And these cellular inclusions, long considered only for their taxonomic value, seem to have an important role in liverwort recovery from dehydration (Pressel *et al.* 2009).

Taxonomists have been aware that these oil bodies usually disappear in herbarium specimens, and that they do not reappear upon re-wetting and microscopic observation. But it appears that to see these in herbarium specimens, one must treat the liverworts as nature does – dry them slowly and give them time to recover upon rehydration. It turns out that they remain largely unchanged while they are dry (Pressel *et al.* 2009), but who observes dry specimens under the microscope? Rather, they become flattened when rehydrated and in the six liverworts tested, they require 48 hours to regain their normal shapes, long after the taxonomist has cleaned the microscope slide. Fast drying causes them to disintegrate upon redrying, along with other liverwort organelles. Pressel *et al.* interpreted this initial loss of shape upon rewetting to indicate a shift in soluble carbohydrates or other components into the cytosol, suggesting that these may be crucial energy reserves needed for recovery and desiccation tolerance.

Kronstedt (1983) found that there was seasonal variability in the oil bodies of the floating liverwort *Ricciocarpos natans* (Figure 109). But as He *et al.* (2013) made clear, the function of oil bodies in most liverworts still remains unclear.



Figure 109. *Ricciocarpos natans*, a species with seasonal variability of oil bodies. Photo by Norbert Stapper, with permission.



## Habitat Relations

In their review of lichen and bryophyte desiccation and rehydration, Green *et al.* (2011) considered that the rate of recovery may relate to the length of the hydrated activity period. They reported that species that hydrate and then dry rapidly (e.g. rock surfaces) recover rapidly. By contrast, those species from habitats that remain wet for a long time recover from dryness more slowly when rehydrated.

Cruz de Carvalho *et al.* (2014) found that even the aquatic moss *Fontinalis antipyretica* (Figure 104) can survive slow dehydration, during which both dehydration and rehydration proteins are induced. These protein profiles are similar to those of the terrestrial moss *Physcomitrella patens* and *Syntrichia ruralis*. The proteins associated with photosynthesis and the cytoskeleton were reduced during dehydration. In their place, the cells accumulated proteins involved in sugar metabolism and plant defenses. Upon rehydration the protein accumulation patterns for photosynthesis and the cytoskeleton return to normal levels. However those for sugar accumulation and defense remain high. During fast dehydration, on the other hand, this moss exhibited little change in proteins. Upon rehydration, proteins were leaked. The researchers suggested that bryophytes from contrasting habitats may share common desiccation tolerance mechanisms.

### Summary

Bryophytes may be **desiccation tolerant**, surviving dry tissues and beginning photosynthesis upon rehydration, or they may be **drought avoiders**, using structural adaptations and life cycle stages to escape having a dry vegetative plant. The presence of a **central strand** does not seem to correlate with the degree of internal conduction, but habitat does.

Life cycles are a major protector against dry seasons, permitting bryophytes to survive as tubers, gemmae, spores, fragments, and buds. These stages are typically timed to coincide with drought seasons. They are likely to be combined with physiological changes, including dormancy, in the plants as they respond to changes in the environment.

Xeric bryophytes are more likely to have greater internal conduction and faster external conduction than mesic and hydric taxa. It is possible that the central strand may serve as a water reservoir in some taxa. Physiologically, some bryophytes can increase the osmotic value of the cells, and they typically have a high water capacity compared to drought-tolerant seed plants. Desiccation tolerance permits some bryophytes to remain dormant in a vegetative state for as many as 23 years.

During drying, chloroplasts undergo ultrastructural changes, **mitochondria** become **deformed**, and **vacuoles break down** to form smaller vesicles. Nuclei seem to remain intact. At least some taxa apparently protect their cell membranes from oxidative destruction. **ABA** seems to induce the production of  $H_2O_2$  in light, reduce the loss of  $K^+$ , and may facilitate the reduction

of oxygen release from photosystem II. Despite these adaptations, plasmolysis can occur and membranes can become damaged, requiring repair upon rehydration.

Liverworts may have one more trick in their cells – **oil bodies** that disappear rapidly upon rehydration, apparently converting oils into more usable forms of stored energy that could contribute to repair.

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