

CHAPTER 7-4

WATER RELATIONS: LEAF STRATEGIES



Figure 1. *Campylopus introflexus* demonstrating the ability of water to cling and collect on the thin, wiry leaves. Photo by Michael Lüth.

Overlapping Leaves

Most bryophytes have their leaves inserted at angles on the stem. In some cases, especially leafy liverworts (Figure 3), these are **incubous** in arrangement [leaves overlapping like shingles on a roof, with the part of the leaf closer to the stem base being nearer the substrate (ventral) and the more apical side emerging on the upper (dorsal) side of the stem], whereas others are **succubous** [basal edge dorsal, apical edge ventral]. Clee (1937) found that in the succubous *Plagiochila asplenioides* var. *major* (Figure 2), water could move up to 3.7 cm in one minute. However, with the incubous arrangement, water moved less than 1 cm per minute. On the other hand, Basile and Basile (1987) questioned the role of the incubous vs. succubous leaf orientation in water conduction. They found that conduction proceeds equally in both orientations and that there is no correlation between the direction of leaf overlap and the angle of the substrate slope where they commonly grow.



Figure 2. *Plagiochila asplenioides* with overlapping, succubous leaves. Photo by Michael Lüth.

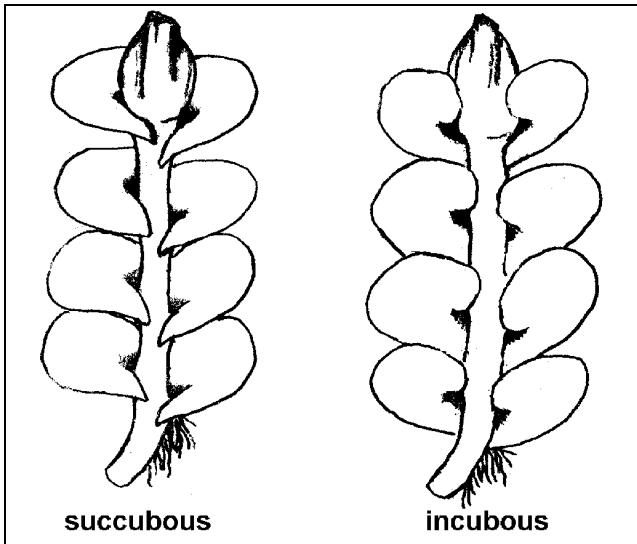


Figure 3. Succubous leaf arrangement of liverworts such as *Jungermannia* (left) and incubous arrangement of those such as *Calypogeja* (right). Note the decurrent leaf bases in the liverwort on the left. Redrawn by Margaret Minahan from Iwatsuki.

Bowen (1933) considered the erect habit of leaves to hold and conduct more water than spreading leaves. This effect was enhanced if the leaves had **decurrent** bases (extensions of the leaf base down the stem; Figure 3).

Bayfield (1973) found that as water content declined in *Polytrichum commune*, the leaf arrangement changed. As the moisture decreased, the leaves wrapped closer around the stem, seemingly increasing moisture retention, a phenomenon that makes *Hedwigia ciliata* almost unrecognizable when wet (Figure 4). Bayfield also found that external conduction is possible in the capillary spaces between the stem and the overlapping leaf bases. In this endohydric moss, the loss of water was controlled by a complex series of changes in the leaf arrangement, whereas in the ectohydric *Racomitrium lanuginosum*, little or no control was exercised over water loss. It is likely that all *Polytrichum* species benefit from this movement of the leaves upon drying (Figure 5).



Figure 4. *Hedwigia ciliata* showing wet leaves (upper left) and dry leaves (diagonally across lower right) as a result of drying from the edge of the mat inward. The plants were growing on exposed boulders at the base of a cliff. Photo by Janice Glime.



Figure 5. *Polytrichum juniperinum*. **Upper:** dry plants with leaves tight against stem. Photo by Janice Glime. **Lower:** Hydrated plants with leaves widespread. Photo by Michael Lüth.

Concave Leaves

Proctor (1979a) found that many taxa of ectohydric mosses have concave leaves (e.g. Figure 6). When examined in moist weather, the concavities will generally be full of water. This helps to solve the problem of gas exchange by exposing one surface to the atmosphere while keeping the other surface bathed in water. Gas diffusion in air is about 10^4 times faster than in water (Proctor 1982). Other mosses, like *Campylopus* and *Polytrichum*, are able to roll their leaves, like some grasses, when they are dry. In this mode, mosses like *Syntrichia ruralis* (Figure 7) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).



Figure 6. The moss *Scleropodium touretii* illustrating deeply concave leaves. Photo by Michael Lüth.



Figure 7. *Syntrichia ruralis* dry (**upper**) and wet (**lower**). Photos by Janice Glime.

Leaf spreading upon re-moistening is rapid in most bryophytes. Li (unpublished data) found that in *Sphagnum* sp., *Ptilium crista-castrensis*, *Pleurozium schreberi*, and *Dicranum polysetum* the first leaves spread within 1.5 to 2 seconds of receiving water (Table 1). To wet all the leaves in pieces 0.7 cm long required less than 2 minutes for most taxa, but required 24 minutes in *Rhodobryum ontariense* (Figure 8). Li found some indication that small leaves can spread more quickly than large ones, at least in *Fontinalis*. *Fontinalis duriaei* has smaller and thinner leaves than does *F. antipyretica* var. *gigantea*, and *F. duriaei* can spread its leaves in 1/3 the time required for *F. antipyretica* var. *gigantea*. However, the difference may be due to the stiffness of the **keel** (leaf fold) in *F. antipyretica* var. *gigantea*, whereas *F. duriaei* has flat leaves.



Figure 8. *Rhodobryum ontariense*, illustrating the dense cluster of leaves at the top of the stem. Photo by Janice Glime.

Table 1. Mean rate of leaf spreading and conduction after rewetting along 0.7 cm branches in 15 species of bryophytes (n = 30 & 10 respectively). Based on Li, unpublished data.

Species	spreading conduction	
	sec	mm/min
<i>Ptilium crista-castrensis</i>	2	0.93
<i>Dicranum polysetum</i>	2	70.00
<i>Pleurozium schreberi</i>	5	140.00
<i>Hedwigia ciliata</i>	5	11.48
<i>Climacium dendroides</i>	8	21.00
<i>Fontinalis duriaei</i>	9	2.60
<i>Dicranella heteromalla</i>	10	11.48
<i>Lophozia barbata</i>	10	24.1
<i>Anomodon attenuatus</i>	14	0.06
<i>Fontinalis antipyretica</i> var. <i>gigantea</i>	26	27.5
<i>Porella platyphylla</i>	34	0.75
<i>Sphagnum</i> sp.	90	6.0
<i>Bryum pseudotriquetrum</i>	149	0.82
<i>Fissidens adianthoides</i>	284	0.08
<i>Rhodobryum ontariense</i>	1421	0.06

Among the slowest species to re-wet in Li's study were *Fissidens adianthoides* and *Rhodobryum ontariense* (Figure 8), both for rate of conduction and leaf wetting. *Fissidens adianthoides* has leaves that are large and partly two-layered. There is little overlap between the leaves except at the two-layered pocket (Figure 9), and Church and Nelson (unpubl data) noted that when these leaves are dry there is little or no overlap even at the pocket. Therefore, lack of capillary space may account for its slow response. The slowness of *Rhodobryum ontariense*, which has all its leaves crowded at the top of the stem like a palm tree (Figure 8), may likewise be explained by lack of capillary spaces. Below the crowded rosette of leaves at the apex are very reduced scale-like leaves along the stem, providing little capillary space and rendering it the slowest among the 15 species observed by Li. It required 123 minutes for the water to travel 0.7 cm up the stem! Although Li's data indicate a slight trend for rapid conduction to be coupled with rapid leaf spreading, there are enough exceptions to indicate that the relationship is not so simple.

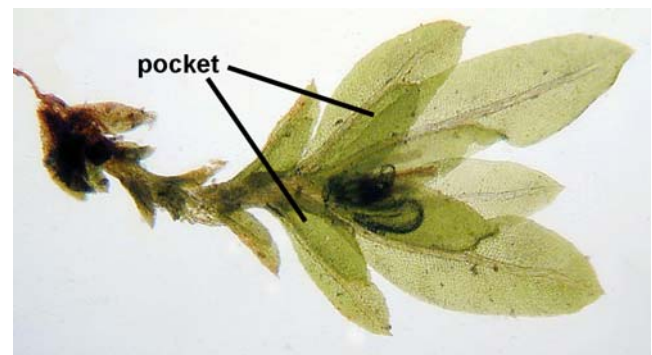


Figure 9. *Fissidens arnoldii* showing the overlap created by leaf pockets where the leaf blade has two, but separated, layers. Photo by Michael Lüth.

Lobules and Storage Organs

Daniels (1998) has compared leafy liverworts growing in a variety of habitats. **Xerophytic** (dry habitat adapted) taxa such as *Frullania* have helmet-shaped leaf **lobules** (Figure 10) and *Radula* has a saccate lobule, both

functioning for water storage. *Porella*, capable of both an **epiphytic** (living on plants) and a **saxicolous** (living on rock) habit, has leaf folds underneath and large underleaves. Liverwort plants in the humid rainforests have smaller lobules than those growing in drier, more exposed habitats (Cornelissen & ter Steege 1989; Gradstein 1995). Such structures help to hold water in capillary spaces in the absence of multiple rows of leaves. It is likely that the pockets of *Fissidens* (Figure 9) may have similar water-holding functions.

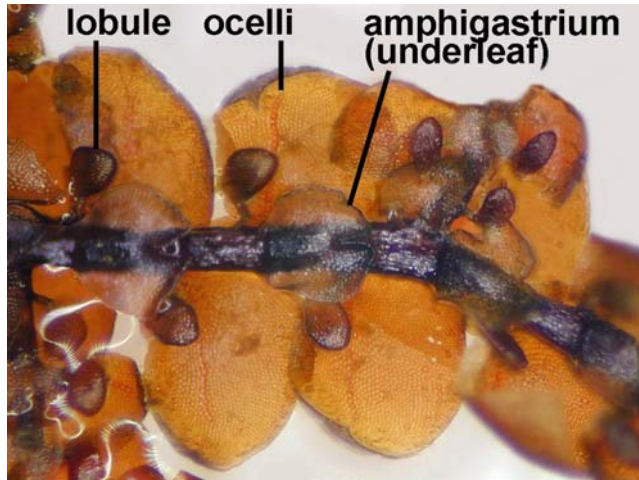


Figure 10. *Frullania tamarisci* showing lobules. Photo by Michael Lüth.

Alar Cells

Alar cells are enlarged cells, usually thin-walled, that occur at the base of many moss leaves (Figure 11). Those that are thin-walled shrink upon drying and readily gain water as it moves along external capillary spaces. Tucker and coworkers (1975) describe shrinkage of the basal cell cytoplasm during dehydration, creating gas pockets. Upon rehydration, the pockets of gas shrink and disappear within 10 - 30 seconds and the cytoplasm expands to fill the entire cell. This can explain the rapid unfolding of leaves upon rewetting in many taxa of bryophytes, with alar cells acting like the bulliform (expansion) cells of grasses.

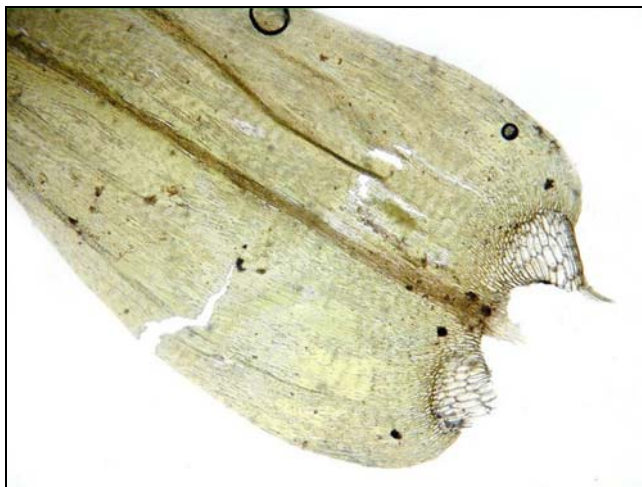


Figure 11. Leaf of *Calliergon giganteum* showing enlarged alar cells at leaf base and costa. Photo by Michael Lüth.

Hair Points

Hair points are common on leaves of xerophytic mosses, including species of *Grimmia* (Figure 12), *Schistidium*, *Campylopus* (Figure 13), *Hedwigia* (Figure 16), and *Syntrichia*. As discussed earlier, Loeske, in 1930, demonstrated that in *Schistidium apocarpum* hair points are actually lost when the mosses are kept in damp air or deep shade. Proctor (1979a) considers these hairs to be organs that reflect some of the solar radiation, thus reducing energy absorption, temperature, and evaporation. But they reduce water loss more directly as well; hair points on *Syntrichia intermedia* and *Grimmia pulvinata* (Figure 12) reduced the boundary layer conductance by about 20-35% in his experiments (Proctor 1980). Not only does this thicker boundary layer trap stagnant air, thus reducing evaporation loss, but it increases the distance from the leaf surface to the surrounding air, thus decreasing the diffusion gradient (Proctor 1982).



Figure 12. *Grimmia pulvinata* showing the long hairs that reduce the boundary layer conductance. Photo by Michael Lüth.

It appears that hair points can help in collecting moisture from the air as well (Figure 13). Shaun Russell has described to me that in African highlands the mosses act as tiny collectors that trap moisture from the fog. This is often their only source of water for an entire year. Chang and coworkers (2002) have measured the water available to epiphytes in fog (Table 1) and in precipitation in a subtropical montane forest in Taiwan. In a one-year study, they found that the fog endured for a mean of 4.7 hours per day at its low in the summer to 11 hours per day the rest of the year, reaching nearly 15 hours per day in November. Furthermore, it contributed more than 50% of the nutrient ions.

Table 2. Absorption rate of fog in dominant epiphytes during a single dense fog event on 24 February 2001 at Yuanyang Lake, Taiwan. From Chang *et al.* (2002).

Species	absorption rate g H ₂ O gdw ⁻¹ h ⁻¹
<i>Bazzania fauriana</i>	1.28
<i>Bazzania</i> sp. 2	0.90
<i>Pleurozia acinosa</i>	0.67
<i>Mastigophora diclados</i>	0.59
<i>Schistochila acuminata</i>	0.58
<i>Dicranoloma blumii</i>	0.42
<i>Scapania</i> sp. 1	0.38
<i>Bazzania</i> sp. 1	0.23



Figure 13. *Campylopus introflexus* showing dry hair tips (**upper**) and hair tips that have collected moisture (**lower**). Photos by Michael Lüth.

Papillae

The role of papillae, those little bumps and extensions on cell walls (Figure 15), has been controversial for a long time, but their common appearance on bryophytes of dry habitats cannot be ignored. Nevertheless, Loeske (1926) points out that papillae are also found in a number of wetland and aquatic taxa, including *Dichodontium pellucidum*, *Philonotis* (actually **prorate** cells), *Aulacomnium palustre*, *Helodium blandowii*, and *Paludella* (Figure 14). Loeske observed that the papillae were maintained in a number of species through a wide range of wet to dry habitats, implying they are of genetic origin. On the other hand, these taxa are common in wet meadows, lake shores, and other wet habitats where they may periodically be dry while being exposed to high sunlight, suggesting that the papillae may be of value under those conditions.



Figure 14. *Paludella squarrosa*, emergent in full sun. Photo by Michael Lüth.

Proctor (1984) described the interstitial spaces between papillae as forming a capillary conducting system that is capable of rapid water movement, as we might expect in *Tortula muralis* (Figure 15). But papillae may be most important in altering the boundary layer and creating a dead space that reduces water loss. Both of these ideas, as well as their role in deflecting UV light, remain to be tested.

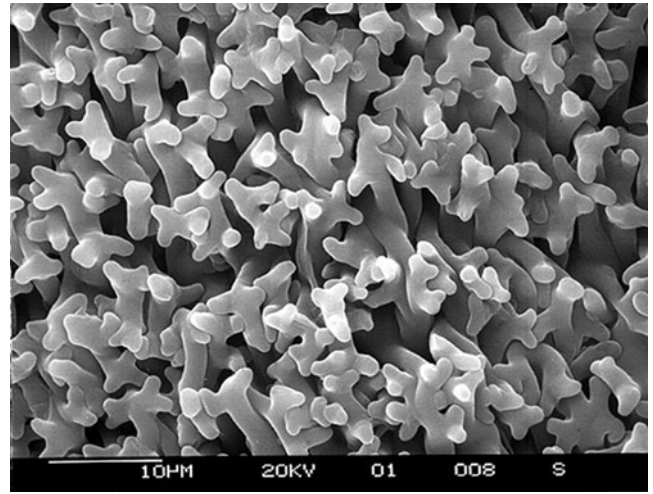


Figure 15. SEM of papillae on *Tortula muralis*, illustrating the type of channelling described by Proctor (1984). Photo with permission from Botany 321 website, www.botany.ubc.ca/bryophyte/LAB8.htm.

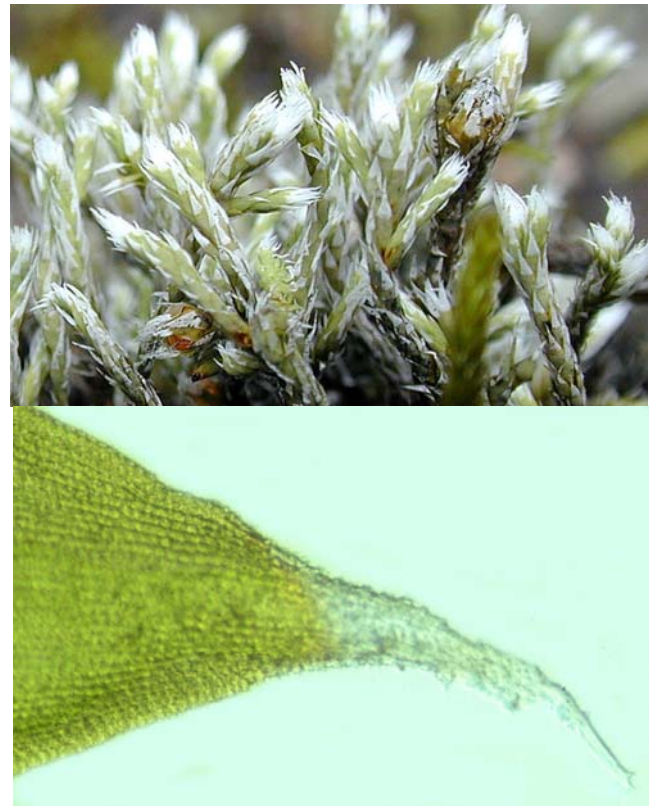


Figure 16. Hyaline hair tip on the leaf of *Hedwigia ciliata*. Note the numerous papillae on these awn (hair tip) cells as well as on the lamina cells in the lower picture. Photos by Michael Lüth (upper) and Janice Glime (lower).

At least some leaf papillae (*Andreaeobryum macrosporum*) are constructed in such a way that they provide a channel for the uptake of water (Crandall-Stotler & Bozzola 1990, 1991). This channel is within each papilla and is different from the channels formed between the papillae (cf. Proctor 1984). SEM observations indicate the channel within the papilla facilitates the rapid uptake of water during rehydration.

Costa

This is the supporting structure for many moss leaves, often also providing an avenue of water transport (Frahm 1985) (Figure 17). It resembles a midrib both in appearance and function (Figure 18). Habitat seems to play some role in its development, although its predisposition is usually genetically determined. The costa of some species may be shorter, thinner, and even disappear upon submersion in water (Zastrow 1934). For example, the submerged forms of *Drepanocladus exannulatus* have a costa that only reaches midleaf, whereas the terrestrial forms have a strong costa; similarly, *Cinclidium stygium* normally has a strong costa above water, but when grown submerged it becomes thin and small (Zastrow 1934). When cultured in artificial streams where the leaves were exposed to air, *Fontinalis novae-angliae* developed short costae, although these are normally absent when it grows submersed (Glime, unpubl.). Surprisingly, the broad costa in *Campylopus* (Figure 19) not only serves as the photosynthetic organ, but as a water reservoir as well.



Figure 17. Leaf of *Mnium spinosum* showing costa and border. Photo by Michael Lüth.



Figure 18. Cross section of *Trichodon cylindricus* showing costa. Photo by Janice Glime.



Figure 19. Leaf cross section of *Campylopus flexuosus* showing water-holding cells of broad leaf costa. Photo by Michael Lüth.

Plications

Plications, or Japanese fanfolds, in the leaf may reduce evaporation by reducing the exposed area and creating nearly dead space between the folds. On the other hand, it might simply be a means of neatly folding the leaf as it dries and loses the turgidity that kept it concave. These are present in *Brachythecium*, *Coscinodon* (Figure 20), and *Drepanocladus* (= *Hamatocaulis*) *vernicosus*, among others. Some taxa exhibit these only as they are drying or dry, so the system is responsive to water loss.

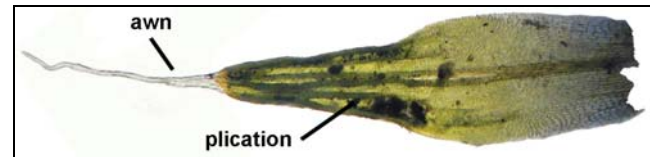


Figure 20. Leaf of *Coscinodon cribrosus* showing plications. Photo by Michael Lüth.

Lamellae

The term **lamella** shares the same root word as laminate and refers to layers, in this case vertical stacks of cells that form rows, often reaching the length of the leaf (Figure 22, Figure 23). They may cover the costa, the blade, or a liverwort thallus. These rows are arranged in such a way that they somewhat resemble a book that has just been opened and laid to rest, with its pages still parting from the middle. Some of the most xerophytic mosses, such as *Aloina* (Figure 21), have branched filaments over the costa, giving it a succulent appearance; *Crossidium* achieves a similar effect with dense filamentous outgrowths from the costa in the upper half of the leaf.

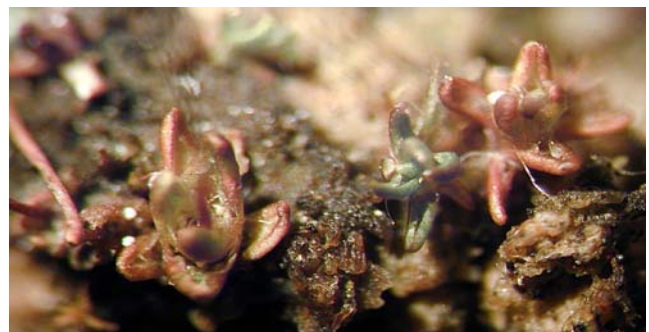


Figure 21. *Aloina brevirostris*, illustrating the succulent appearance caused by the numerous filaments on the costa. Photo by Michael Lüth.

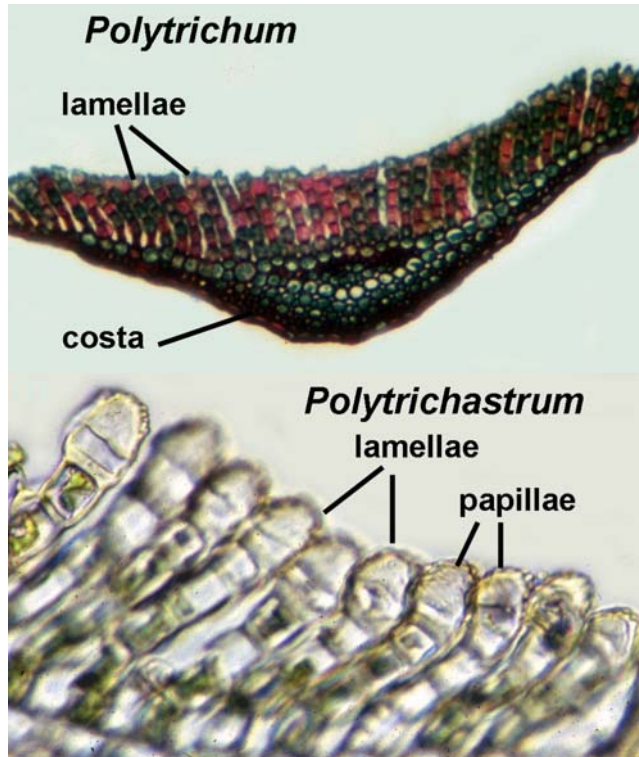


Figure 22. Cross section of lamellae of Polytrichaceae. **Top:** stained section of *Polytrichum*. **Bottom:** *Polytrichastrum alpinum*. Photos by Janice Glime.

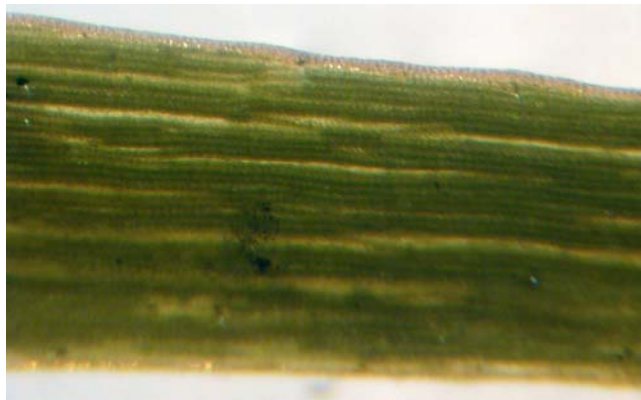


Figure 23. Lamellae on leaf of *Polytrichum ohioense*, viewed down onto leaf surface at 100X. Photo by John Hribljan.

Members of the Polytrichaceae, such as *Polytrichum* and *Dawsonia*, which are all endohydric, have vertical lamellae on their leaves that provide capillary spaces and create dead air spaces that can reduce water loss across the broad surface of these atypically large moss leaves (Figure 22). In addition, some species (*Polytrichum hyperboreum*, *P. piliferum*, *P. juniperinum*) have the edge of the leaf lamina (flattened part of leaf not including costa or border) rolled over the lamellae (Figure 24), creating an internal structure somewhat like the **palisade mesophyll** (columnar cells of inner leaf tissue) of a higher plant, with the lamina behaving in some ways like an epidermis. The leaves have the additional ability to flex like a hinge (van Zanten 1975), causing them to be spread lengthwise away from the stem under moist conditions but be straight or curved slightly around the stem when dry. Such behavior retards water loss and protects the chlorophyll during dry periods, while permitting maximum use of light during wet periods.

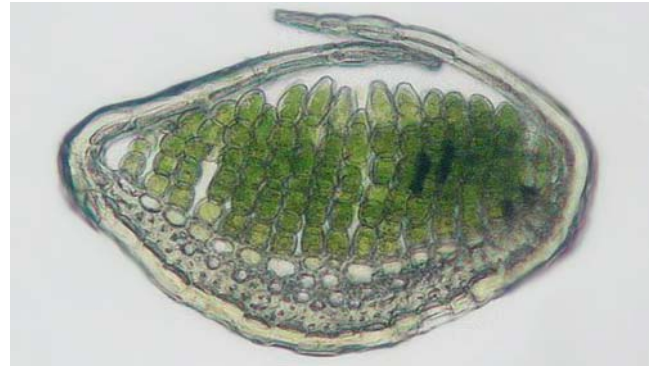


Figure 24. *Polytrichum hyperboreum* leaf cross section showing lamina folded over lamellae. Photo by Michael Lüth.

In *Pilopogon laevis* the costa is ribbed; in *P. peruvianus* it has 3-4-cell-high lamellae, adapting this species to its dry coastal desert habitat. Likewise, *Campylopus pilifer* has similar lamellae and prefers such dry habitats as rocks, soil-covered boulders, and gravel. On the other hand, *C. introflexus* has only 1-2-cell-high lamellae and lives on humus, wet sand, and peat. Although Frey and Kürschner (1991) found a correlation between costal lamellae and increasing aridity, the lamellae of *Polytrichum* seem not to be so much an adaptation to prevent water loss as to provide for additional surface area (2.4-fold in *Polytrichum commune*) and gas exchange during photosynthesis (Thomas *et al.* 1996). Proctor (1979a, b) and Thomas *et al.* (1996) described wax on the terminal cells of the lamellae of *Polytrichum* and attributed to this wax the repulsion of water that prevented it from entering between the lamellae. Perhaps lamellae are adapted to increasing gas exchange and are more important in water retention or repulsion than in absorption.

Thickened Leaf

Many leaves partially protect themselves from water loss by having all or part of the leaf more than one cell thick. This is a common character for the borders and costa, where it most likely serves for support and possibly water movement, but in the leaf **lamina**, this reduces the exposed surface area (Figure 25).

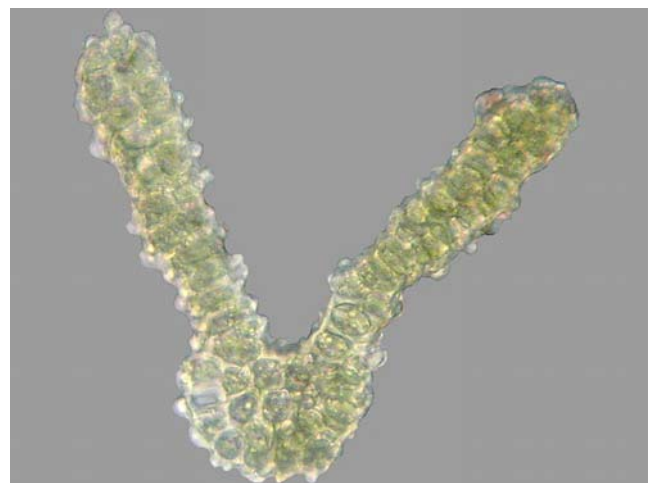


Figure 25. *Grimmia anomala* leaf section showing double layer of cells and papillae. Photo by Michael Lüth.

Stereids

In the stem, **stereids** are thick-walled cells that contain living protoplasm and have been compared to xylem parenchyma cells (Héban 1970). In leaves, they form ribs on one or both sides of the costa (Figure 26) and seem to function as protection against desiccation (Frahm 1985). Those *Campylopus* taxa surviving habitats with changeable conditions have well-developed costal stereids (Frahm 1985). Frahm found that dorsal costal lamellae aid in water uptake, whereas the ventral costal stereids common among *Campylopus* species help to reduce desiccation. *Campylopus savannarum* survives its savannah habitat with the aid of such stereids, whereas *Campylopus* taxa occurring on wet cliffs, dripping rocks, and swamps lack stereids.

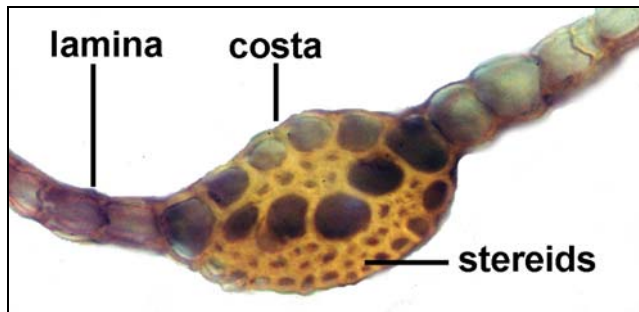


Figure 26. *Trichostomum tenuirostre* (moss) leaf cross section showing stereids. Photo by Janice Glime.

Cuticle

Although waxy cuticles seem to be rare in moss gametophytes, various mosses have some sort of cuticular covering. In some mosses, this is expressed as granules, platelets, or ribbons that are soluble in chloroform (Proctor 1982), satisfying the test for cuticular wax in tracheophytes. This type of cuticle endows *Pohlia cruda*, *P. albicans*, *Saelania glaucescens* (Figure 27), *Schistostega pennata*, *Pogonatum urnigerum*, and many Bartramiaceae with their **glaucous** (whitish) appearance (Proctor 1982).



Figure 27. *Saelania glaucescens* showing waxy appearance. Photo by Michael Lüth.

Proctor contends that the ability to shed surface water is important to these plants in their low-light habitats of crevices and caves or in waterside habitats of waterfalls. He cites the waxy surfaces of the tops of photosynthetic lamellae of the Polytrichaceae as support for this contention. In *Marchantia*, as in the stomata of tracheophytes, the pores have strongly water-repellent ledges (Schönherr & Ziegler 1975, in Smith 1982), like the

waxy ridges of tracheophytes, preventing water from entering and interfering with the photosynthetic interior.

But these cuticular surfaces may have a more important function. Gas exchange works poorly through a wet surface. Waxy or oily surfaces help to repel the water, yet allow a higher rate of gas exchange than does water. Hence it is not uncommon to find such surfaces among aquatic taxa (Proctor 1984).

Cell Structure

Proctor (1979a) contends that coarse leaf cell walls (Figure 28) seem to aid water movement, possibly creating more internal capillary spaces among the fibrils of the cell wall (Proctor 1982). On the other hand, Frey and Kürschner (1991) could find no correlation between thickened cell walls and increasing aridity. Later, Proctor (1982) pointed out that such xerophytic mosses as *Syntrichia*, *Encalypta*, and *Anomodon viticulosus* have quite thin walls and external conduction, suggesting that the thick walls are associated with species having internal conduction. It is interesting that many acrocarpous mosses have short leaf cells and tend to be more endohydric, whereas the pleurocarpous mosses, largely lacking a central strand and endohydric conduction, have mostly elongate leaf cells. These elongate cells would seemingly facilitate conduction between cells and from the leaf surface to the stem, but we lack experimental evidence to support this. In leafy liverworts, slime papillae on marginal leaf cells can help to absorb and hold water, as in the leaf margins of *Porella* and *Heteroscyphus* (Daniels 1998).

Cell wall structure – Mosses of dry habitats tend to have thick cell walls that can occupy more than half the cross section of the leaf (Proctor 1984). The moss *Rhacocarpus purpurascens* appears to have a unique means of facilitating rapid absorption of fog, dew, and rain (Barthlott & Schultze-Motel 1981; Edelmann *et al.* 1998). It has four layers of cell wall with a "peculiar architecture," forming cavities within the wall.

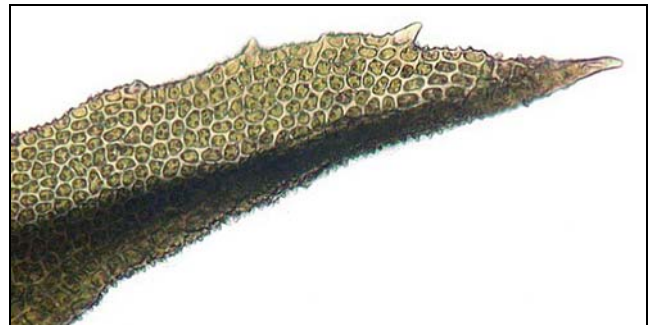


Figure 28. Leaf of *Zygodon dentatus* showing thick cell walls and papillae. Photo by Michael Lüth.

Flexibility of the cell wall is undoubtedly an aid to cell survival. This permits the cells to shrink upon dehydration, up to 50-70% in *Syntrichia ruralis*, without allowing for air to enter the drying cells (Moore *et al.* 1982).

Popper and Fry (2003) suggest that the addition of xyloglucans to the cell wall components may have been an important contribution to the ability of bryophytes to invade land. The presence of high concentrations of uronic acids would have permitted these plants to hold nutrient ions until such time as water was available for transport.

Borders

It appears that long border cells (Figure 29) are able to move water and facilitate uptake. But they may provide an additional role in the wet to dry state transition of the leaf in at least some taxa (Lowell 1998). When the leaf of *Atrichum undulatum* is wet, the elongate cells of the border are turgid and extend the leaf lamina out into a nearly straight surface. But as the leaf dries, the opposing forces of the drying leaf cells and the border result in the contorted leaf shape that is exhibited by the dry *Atrichum undulatum* leaf (Figure 30). The margins roll toward each other and the tip rolls toward the base, creating a "boat" shape. The border acts much like a wire sewn into the edges of a cloth ribbon, but somewhat more flexible.

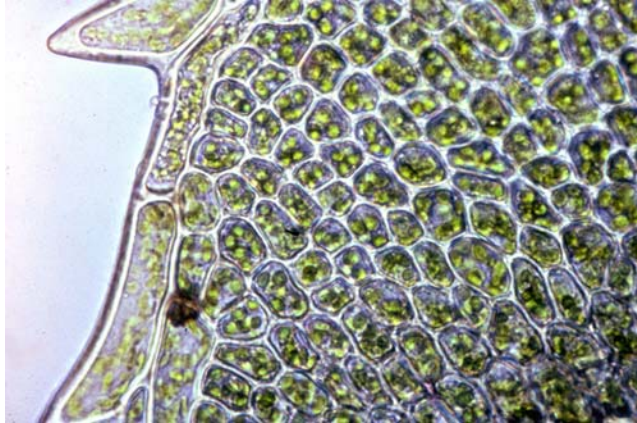


Figure 29. *Plagiomnium* border cells. Photo by Zen Iwatsuki.



Figure 30. *Atrichum undulatum* in its dry condition with contorted leaves. Photo by Janice Glime.

In *Atrichum* the leaf is prestressed; that is, it has a natural dry state that is highly convoluted, but when wet the turgor forces it to become straight (Lowell 1998). Thus, when the leaf dries, the leaf itself contorts into a form that is able to trap and hold water next to the leaf and stem surface. As Lowell describes it, the border is like the party toy that you blow into and it extends straight out, but when it is relaxed, it forms a coil. Species of Mniaceae with borders seem to have similar responses, with the borders causing the leaf margins to curl toward each other, the leaf to become somewhat concave, and the leaf to become contorted.

A similar adaptation appears in Lejeuneaceae and *Porella*, where a hyaline row of marginal leaf cells function in water storage (Daniels 1998). Perhaps the same function occurs in some of the mosses such as some *Fissidens* or *Plagiomnium* with well-developed borders. Because of their elongate structure, water can be expected

to move more quickly along the border because of fewer end walls to traverse. Yet there seem to be no experiments to demonstrate that these cells are of any advantage in gaining, moving water to vital parts, or holding water.

Teniolae

The **teniola** is a border-like row of differentiated cells (Figure 31), differing from a true border by being intramarginal (*i.e.* not at the margin). They are more than one cell thick and this condition may extend also throughout the blade portion. These are found in *Calymperes* and function for support, but may also provide water transport (Reese 1993).

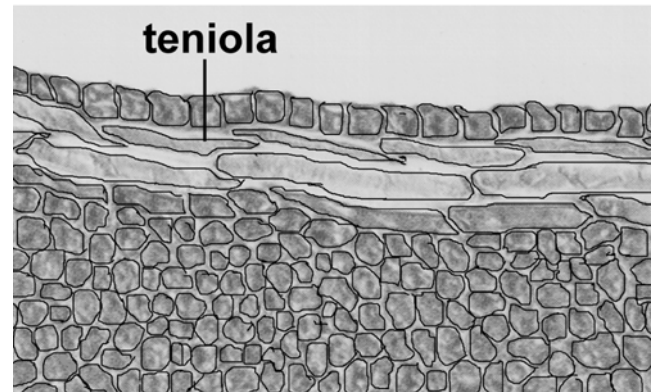


Figure 31. Portion of leaf showing the intramarginal border, the **teniola**. Drawing by Janice Glime.

Revolute and Involute Margins

Just as elongate cells of the border permit leaves to become contorted as they dry, the involute and revolute margins add structural support to the margin that causes contortions when the leaf dries (Figure 32). This contorted condition is known as **crispate**.



Figure 32. *Bryoerythrophyllum recurvirostrum* leaf showing strong costa and revolute leaf margin. Photo by Michael Lüth.

Hyalocysts and Cancellinae

These colorless or **hyaline** cells (Figure 33) are typical of leaves of *Sphagnum* and *Hedwigia*, and the awns of numerous xerophytes. Frahm (1985) examined the correlation between **hyalocysts** and habitat in *Campylopus*. *Campylopus shawii* occurs in wet swamps where it can obtain and store water easily; it has large ventral hyalocysts. *Campylopus setifolius*, on the other hand, grows on wet, dripping rocks that dry out occasionally; it has smaller hyalocysts, presumably to reduce the water loss to evaporation from these cells. The presence of ventral hyalocysts in *C. flagelliferus* seem to adapt it to its life restricted to the bark of living trees where it needs a means of rapid water uptake.

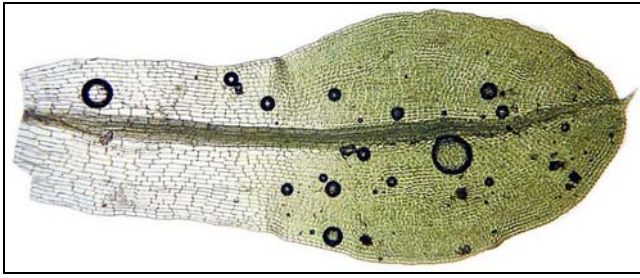


Figure 33. Leaf of *Tortula vahliana* showing hyalocysts. Photo by Michael Lüth.

Species of the cushion moss, *Leucobryum* (Figure 34), appear very succulent because of the hyalocysts among the photosynthetic cells. In this case, the leaf is several cells thick and the hyalocysts give them a whitish appearance.



Figure 34. *Leucobryum juniperoides*, showing the thick, whitish leaves. Photo by Michael Lüth.

Sphagnum species are considered xerophytic hydrophytes with many adaptations to deal with periodic drought (Andrus 1986). Living in a watery mire for most of the year, this genus has no internal conducting system and must face a severe threat of drying in the full sun of the summer when the water table is low. The ectohydric *Sphagnum* is a poor drought tolerator, but a relatively good drought avoider (Li *et al.* 1992). It has two types of leaf cells, small photosynthetic cells and large hyaline cells (Figure 35).

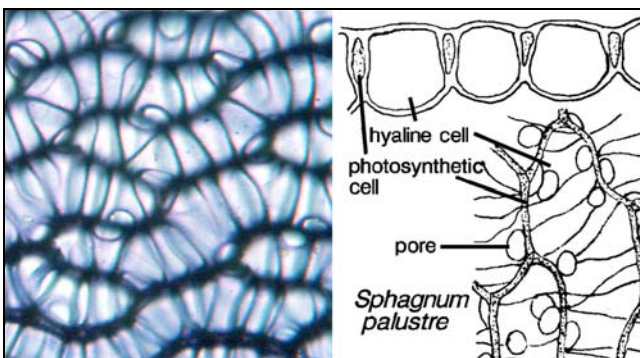


Figure 35. *Sphagnum* leaf cell types and pores. **Left:** *Sphagnum* leaf cells stained with crystal violet. Photo by Janice Glime. **Right:** *Sphagnum palustre* photosynthetic and hyaline cells as seen in cross section (**upper**) and flat (**lower**). Drawings by Margaret Minahan.

Hyaline cells bathe the photosynthetic cells in water by providing a reservoir. Since the hyaline cell is a dead cell, its sole purpose seems to be to supply water to the

photosynthetic portion of the leaf. These cells give some species of *Sphagnum* the ability to hold up to 25 times their own mass in water (Andrus 1986).

Transplant studies indicate that species of *Sphagnum* differ in abilities to inhabit different heights above the water level, and these differences seem to correlate with the positions they occupy in the field (See Li *et al.* 1992, Rydin 1993, and discussion in competition chapter). Studies by Hintikka (1972) hint that the mechanism for some of these adaptive differences may not relate to water, but to other factors associated with submersion. When grown in sterile culture, *S. fallax* produced no hyaline cells in the presence of high ammonium, high organic nitrogen, or low carbohydrates. In nature, ammonia from decomposing plant matter would be greater under water than around emergent plants, quickly diffusing away in the atmosphere. Likewise, amino acids from organic decomposition would be present only in water. Response to low carbohydrates may be a limit in carbon available for making additional cell wall tissue, or it could likewise relate to decomposing plant material in interstitial bog or fen waters.

Sphagnum seems to require a tremendous water content to achieve its maximal net photosynthesis, probably supplied by the large reservoir of water in its non-photosynthetic hyaline cells. In *S. fuscum*, a hummock top species, 600-1000% saturation was optimal, whereas in *S. angustifolium*, which tends to occur somewhat lower as well, 900-1300% was optimal (Silvola & Aaltonen 1984), indicating the greater need for water in species that live closer to the water level. The photosynthetic decrease with water reduction was steeper for *S. fuscum*, and plants in the field generally occurred where their water content was within this 600-1000% range. In *S. angustifolium*, however, plants often occurred where their water content was outside their optimum range, thus defining narrow and broad relative niches.

Sphagnum is well known for its morphological plasticity in response to water availability (Miller 1991). An adaptive response of *Sphagnum magellanicum* and *S. papillosum* is that dry conditions result in leaves that are longer (Figure 36) with more pores per cell (Figure 37). Li and coworkers (1992) suggest that these modifications may promote water-holding and absorbing properties.

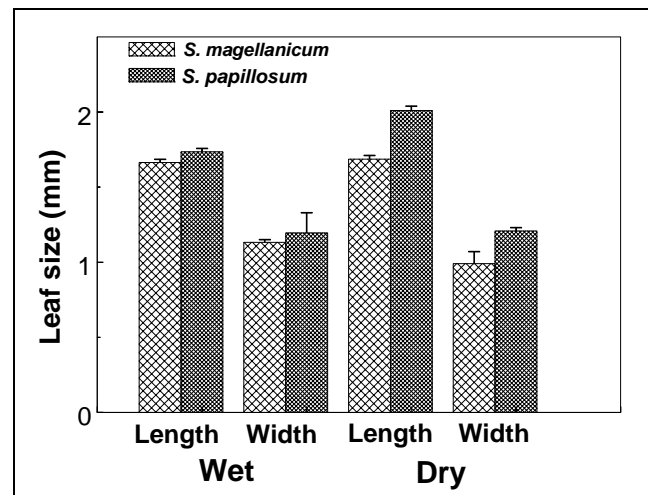


Figure 36. Comparison of leaf dimensions in *Sphagnum magellanicum*, a drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al.* (1992).

Yet, these two species also differ in their water relations. *Sphagnum magellanicum* seems to be a better competitor for water than is *S. papillosum* under dry conditions. This is exhibited by its better water transport ability and greater water content under the same atmospheric moisture conditions. This greater ability may

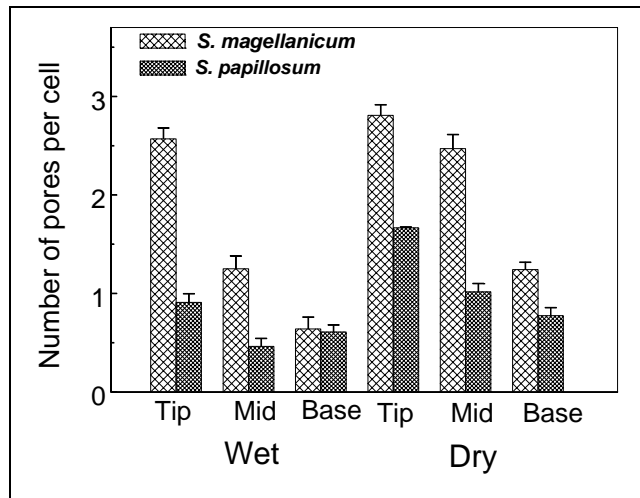


Figure 37. Comparison of number of pores per leaf cell in *Sphagnum magellanicum*, a more drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al.* (1992).

Superiority in water transport permits *S. magellanicum* to occupy a higher position in the hummock than that of *S. papillosum*. Li and coworkers (1992) found that when the two species grow intermixed in the higher hummock positions, both species grow better than if either is alone, provided at least half of the plants are *S. magellanicum*. They suggest that lateral transport among stems may occur to facilitate this, with *S. magellanicum* providing water for both species. If *S. papillosum* is dominant, even at somewhat lower positions in the hummock, both species can dry out more quickly.

The **cancellinae** (sing. cancellina) occur in few bryophytes, but especially in the Calymperaceae, Pottiaceae, *Encalypta*, and some species of *Leptodontium*. They are large, empty basal leaf cells, usually hyaline, that form a lattice. In the Calymperaceae, these are porate (having pores), and may serve as water storage cells.

Vacuoles

Mosses, for some reason, were long thought to lack vacuoles. However this is not the case, as demonstrated in the liverwort *Lunularia cruciata* (Carginale *et al.* 2004), the mosses *Physcomitrella patens* (Nagao *et al.* 2005), *Ephemerum cohaerens* (Kwok & Rushing 1999), and *Fontinalis antipyretica* (Bruns 1998). In fact, the vacuoles can be quite large, as witnessed by the chloroplasts crowded around the periphery of the cell in many species. But there has been no systematic study to indicate which bryophytes have vacuoles and which do not. We might ask if there is some correlation between the ability to withstand drought or to take up water, or even to hold on to cellular water as the environment dries and the presence of one or more vacuoles.

be facilitated by its greater stem diameter due to larger hyaline cells, greater pore number, and smaller leaf size. On the other hand, *S. papillosum* seems to be a better drought tolerator, having a higher survivorship following severe drought conditions.

Vacuoles are known in plants to contain solutes that control the water uptake by the vacuole (Taiz & Zeiger 1991). In bryophytes, Nagao *et al.* (2005) have demonstrated that ABA affected the appearance of vacuoles during treatment with freezing. Since ABA is also involved in drought tolerance and has resulted in the increased osmotic concentration of protonemal cells, this mechanism of vacuolar preparation should be explored for possible relationships to drought tolerance in various bryophytes. Could presence of a vacuole help the cell take in water more quickly by storing solutes that create an osmotic gradient, yet are safely out of the way of cellular metabolism? Could it also have a role in the ability of the cells to shrink as they dry and expand when wet?

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves, concave leaves, multi-layered leaves, crispate leaves, hair points, papillae, alar cells, costae, revolute or involute margins, plications, lamellae, stereids, cuticles, borders, hyaline cells, pores, cancellinae, teniolae, vacuoles, and lobules** aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Acknowledgments

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