The World of Mosses

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While the more charismatic trees and flashy flowers initially catch our attention, mosses have an enchanting, charming presence. What is it about these tiny plants that intrigue us? Perhaps we are aware that there is so much more to their story, but their secrets remain intangible, concealed by their diminutive size.

Mosses differ from other plants largely in their life cycle. Mosses and tracheophytes (traditionally known as vascular plants) both alternate between two conditions throughout their lives, the gametophyte and sporophyte. The gametophyte is haploid \((n)\), having 1 set of chromosomes, and the sporophyte, being the product of fertilization, is diploid \((2n)\) with 2 sets of chromosomes. Tracheophytes conceal their gametophytes in reproductive structures, like flowers, never to be seen while they develop into the gametes (sperm and egg). For tracheophytes, the dominant condition is the sporophyte—the woody or herbaceous plant itself. The sporophyte produces spores that remain hidden when they develop into the gametophytes which then develop into the gametes. In essence, the gametophytes are dependent on the sporophyte.

But in mosses, the sporophyte is dependent on the gametophyte. The dominant condition is reversed; the conspicuous green leafy plant is the gametophyte, and the sporophyte is an ephemeral structure produced seasonally. The roles are the same, though—gametophytes produce gametes and the sporophyte produces spores. The spores, however, are released into the air before they develop into the gametophyte, rather than remaining hidden in reproductive structures.
SEXUAL REPRODUCTION IN MOSSES

1. A leafy female gametophyte (n) with attached terminal sporophyte (2n).
2. A papery protective covering, the calyptra (n), sheds off when the capsule (2n) fully develops; a remnant of the interior archegonial wall. Spores develop by meiosis inside the capsule.
3. A cap, the operculum (2n), pops off the capsule when spores are mature.
4. A row of tiny teeth, the peristome (2n), aids in spore dispersal.
5. A spore (n) settles on a place to germinate.
6. The protonema (n) emerges from the spore, reminiscent of filamentous algae, and develops into mature male and/or female plants depending on the species.
7. A cluster of antheridia (n) develop on the male.
8. A cluster of archegonia (n) develop on the female.
9. In the presence of water, flagellate sperm (n) are released from the antheridium and swim to the egg (n) in the archegonium to fertilize it.
10. The fertilized egg (2n, zygote) develops inside the archegonium and emerges as the sporophyte.
When conditions do not favor sexual reproduction, mosses can always reproduce vegetatively from broken fragments of the plant. Moss cells are totipotent, which means that a single, differentiated cell has the ability to develop into an entire, fully functional plant. Some species produce propagules specifically designed to break off with the help of a passing animal or a raindrop. Above are two examples of these asexual structures.

A couple of studies were recently published which introduced the idea that mosses are not exempt from the animal pollinator association. The flagellate sperm were thought to require a film of water to swim to an egg. But this study has shown water is not necessarily a limiting factor in fertilization (Cronburg 2006). Apparently springtails and mites can play a significant role in moss fertilization, independent of sufficient water availability. A second study found that mosses produce pheromone-like chemicals that actively entice these tiny invertebrates to carry the sperm to an egg (Rosensteil 2012). This profound discovery gives credence to the theory that mosses may have instigated the plant-pollinator relationship so prevalent in...
higher plants today. This model may also bridge the gap between their aquatic algal ancestors and the terrestrial tracheophytes.

MOSSES UP CLOSE

When you first take a look at a moss plant, with your naked eye or under a hand lens, often the first thing you notice are striking similarities to other plants. Mosses have stems, tiny leaves, and little rootlike structures. With the aid of a microscope you may see more parallels: a midrib, a serrated margin, conductive tissues, even tomentum. These structural analogs have similar purposes in both mosses and tracheophytes.

Mosses come in an enormous array of shapes, sizes, forms, colors, and textures, but most are made up of the same components. Members of the genus *Polytrichum* are commonly used to represent a typical moss species because of their relatively large size and distinct features. The gametophyte consists of parts similar to most other tracheophytes. The leaves of mosses are called phyllids to distinguish them from the true leaves of tracheophytes, which have lignified vascular tissues, but bryologists will call them leaves regardless, understanding their technical differences. These simple leaves are arranged spirally along the stem. This is a good distinguishing characteristic from liverworts, whose leaves are distichous (arranged in a two-ranked fashion on opposite sides of the stem). Instead of roots, mosses have similar structures called rhizoids. They do not make up an extensive subterranean network; rather, they are superficial and act more as a holdfast to anchor the moss to its substrate. The sporophyte consists of a stalk called a seta and the capsule, whose main parts are shown in the lifecycle image.

My undergraduate professor, Dr. Robin Kimmerer, described mosses as “time made visible,” and mosses undoubtedly do lend a certain timeless aesthetic to the landscape. Intuitively we relate the amount of mosses in an area to the length of time it has remained undisturbed. What perpetuates their reputation for being slow growing? Mosses, unlike most life forms on this planet, are poikilohydric. This means that they cannot internally regulate water, so are subject to moisture fluctuations in their

The acrocarpous *Ulota hutchinsiae* has sporophytes that emerge terminally from the gametophyte.

The mat-forming pleurocarp *Hypnum imponens* sends out sporophytes laterally.
immediate environment; when it is wet, they are wet, when it is dry, they are dry. Like other plants, mosses need to have access to water and light simultaneously to photosynthesize—only then can they actively grow. They are adept at capturing light at very low levels, but not at holding water, so their window of opportunity to grow is limited in many natural systems.

Moss leaves are usually only one cell layer thick. They lack an epidermis and mesophyll layer, and rarely have a waxy cuticle as found in true leaves. This is what makes mosses poikilo-hydric, but it also gives them great flexibility in where they can live. Water and nutrients are acquired primarily through the surface of their leaves. This also makes them especially sensitive to toxins and other pollutants, making them ideal environmental indicators. They do not necessarily depend on their substrate for their nutritional needs; their rhizoids provide minimal water and nutrient uptake. The combination of their rhizoids and their thin leaves allow them to grow superficially on impermeable surfaces like rocks and tree trunks.

With little to guard them against their environment, mosses are quite vulnerable. They are always open and receptive to what is offered to them, to their benefit or detriment. Amazingly, they can lose up to 98 percent of their water content and cease their metabolic functions for a time. Any other organism in this state would be considered dead, but mosses will revive once water returns.

Mosses can be divided into two growth forms—acrocarpous or pleurocarpous—based on the location of their sporophyte. Acrocarps bear theirs terminally, while pleurocarps bear theirs laterally. This is often the initial distinction used when identifying mosses. Typically the gametophytes of either form are distinctive enough, which helps in year-round identification if the sporophyte is not present. Acrocarps are generally upright, rarely branched, and form turfs and cushions, whereas pleurocarps are generally prostrate with pinnate, ferny forms.

**FORM FOLLOWS FUNCTION**

Within these two growth forms, mosses are segregated into many different life forms; six of the most common are shown here. One thing about these life forms that is especially fascinating is the link between morphology and habitat. In the diagram above, the forms are arranged along a water availability gradient ranging from aquatic to xeric habitats. Clearly morphology is a function of water availability. Those species that grow in fresh water are not limited by extended dry periods, so their gametophytes are
filamentous and essentially formless, offering much of their surface area to the open environment. As you move through mesic to drier habitats, the forms become more complex. The dendroid forms are still loose, but have rigid stems to support upright growth on saturated land. The pinnate forms with more intricate and rigid designs increase the amount of capillary spaces, helping to conserve water in mesic areas. Habitats with limited water tend to support turf and cushion forms best. Their tight, dense forms and specialized cellular structures and appendages facilitate water retention in drier environments.

Their desiccation tolerance is also directly related to their morphology; those species that live in wet areas will have less tolerance to desiccation than those species that are subjected to intermittent water availability. Because of their poikilohydric nature, mosses have had to develop ways to survive those dry periods in order to continue colonizing land further away from a water source.

The length of time that some mosses can survive without water is remarkable. Aquatic mosses can remain desiccated for a few months to as much as a year, mesophytic species can wait several years without water, and xerophytic species are known to survive decades or centuries without water. Once water returns, they will begin repairing the cellular damage incurred by the desiccation process and then begin photosynthesizing once more. Of course, this is observed along a spectrum. The trend between form and desiccation tolerance, though positive, is dependent on the rate of the desiccation process; the slower the drying rate, the longer it can survive in that state.
Mosses are able to tolerate colder temperatures than tracheophytes. Some species that live in harsh winter climates are nearly black when dry, allowing them to absorb as much light energy as possible to increase warmth. When the snow arrives, they lie protected underneath the icy blanket until it begins to melt. As water becomes available and even slight amounts of sunlight penetrate through the snow, the moss will begin photosynthesizing. Even the minor amount of nutrients dissolved in melted snow is enough to sustain them. Their incredible temperature tolerance and low-light-capturing ability gives them the upper hand at colonizing the harshest of climates. They are unique among plants in that they are found on all seven continents and every ecosystem except the ocean.

THE WIND IN THE MOSSES

The boundary layer exists as the interface between any surface and the surrounding air. At the surface, air is slowed by friction, while higher up the air is unimpeded. In between is turbulence. Mosses thrive close to their substrates, where, in the stillness, they can capture and retain heat, water, nutrients, and gases in their capillary spaces.

While moss gametophytes are content to grow within the boundary layer, the sporophytes depend on air movement for spore dispersal. Most sporophytes are designed to extend beyond the boundary layer into the turbulent zone, elevating the capsules with the seta so that spores can be released into the wind. The peristome that surrounds the opening of the capsule ensures that the spores are released at optimal times and in an effective way. Spores travel farther in dry conditions, so the peristome teeth reflex outward when it is dry, allowing spores to escape, and retract inward when it is wet. These teeth also act as a “salt shaker” by making sure the spores do not clump together as they are released.

The effects of the boundary layer benefit not only the moss itself, but the whole ecosystem. In many respects mosses act like mulch by absorbing and releasing water slowly and maintaining humidity in the atmosphere and below ground. They also help reduce water runoff and control erosion. As water moves through a carpet of moss, most of the particulates and sediment is left behind, leaving clean, filtered water and keeping the top soil intact (Thieret 1956). Like all plants, mosses sequester carbon and other nutrients until they are released back into the environment from leaching or decay. Interestingly, this sediment retention is what gives some mosses the ability to literally build stone. Beds of moss can form the calcareous limestone known as travertine by providing a site that accelerates the evaporation of calcareous water, leaving the minerals underneath behind. The dissolution of this stone with acid can reveal tiny moss fragments as evidence (Thieret 1956).

The complex morphology of xerophytic mosses clearly illustrates the clever ways mosses have arranged themselves to conserve water. Many of these species can tolerate a good amount of sun exposure, so to counteract the subsequent water loss these species often possess filamentous apical structures called awns. The
The awns of *Tortula ruralis*. Polytrichum piliferum gives off a silvery cast with its very long clear awns and thin waxy cuticle that covers the leaves. Awns are often white or greyish, which is thought to aid in light reflection, thus cooling the plant and protecting it from damaging ultraviolet light. These awns extend beyond the leaf margins, increasing the boundary layer blocking desiccating air flow.

Some species have found ways to thicken their leaves to help retain water longer. Some can have short protrusions on the cell surface called papillae. Papillose species have a dull, matte appearance from a distance because of their roughly shaped cells, as opposed to the shiny appearance of species with smooth cells. Members of the Polytrichaceae have lamellae—multistratose plates of cells aligned perpendicularly over the leaf surface, effectively thickening the

The awn of *Tortula ruralis*. 

*Polytrichum piliferum* gives off a silvery cast with its very long clear awns and thin waxy cuticle that covers the leaves.
leaf. Those extra cells and the capillary spaces between the lamellae hold water as well as add more surface area for photosynthesis and gas exchange. Some species will even fold their leaf margins over the lamellae for added protection as seen in the image above.

Another way mosses counteract water loss is by altering their form as they dry out. For many species, their leaves begin to fold and curl when cells lose water. This reaction helps trap and hold any remaining water by creating more capillary spaces for water to adhere. The uneven surface created by the contorted leaves also increases the boundary layer. It is this action that makes some species look very different in a hydrated versus desiccated state. The rehydration process can take less than a minute and is amazing to watch. The thin leaves will readily absorb water, and as the cells expand, the tiny leaves unfurl gracefully.

**MOSSES: A WORLDVIEW**

A couple of years ago I took a trip to Denver. I have flown countless times, and I always enjoy viewing our planet from that altitude. It seemed during that trip, however, that my perception of plant life had crossed a new threshold. Over the years I had trained my eyes to focus on the patterns of mosses growing in their natural setting. So, at 32,000 feet, I could not help but draw the comparison between moss growth patterns and the patches of forest below. From that perspective I noted how trees formed turfs and tufts across the land, concentrating along waterways and protected areas. This is not unlike what we observe of mosses on the forest floor from our human perspective. The same natural, microclimatic forces apply in the colonization of a forest along land as it does for mosses along its substrate. I was reminded of the ancient hermetic axiom “As above, so below,” which points to the irrelevance of scale; the same ecological patterns are apparent throughout all level of natural systems.

On your next encounter, I invite you to stop and pet the mosses (by doing so you will be breaking off tiny pieces, helping it grow vegetatively) and reflect on their significance, similarities, and strength. They hold a necessary place in the ecological function of their environments and, while tiny, they still share many traits with their tracheophyte relatives. They model themselves in patterns congruent with much larger plants to perform the same processes optimally—that is the reason why some mosses resemble little conifer seedlings! Mosses reflect that which we already see and know of our natural world and while they can help us reflect on the importance of being open and accepting and having patience and faith, they will continue to enrich us with their concealed secrets and attractive aesthetic.

**Citations**


**References**

A moss microcosm composed of star-shaped *Polytrichum commune*, windswept *Dicranum scoparium*, and short, pale *Leucobryum glaucum*.