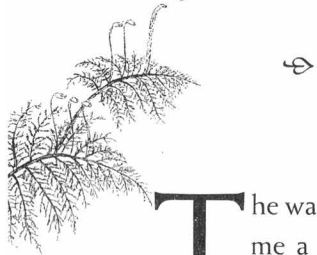


The Advantages of Being Small: Life in the Boundary Layer



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The wailing toddler attached to the end of my arm earns me a disapproving look from a sour-faced lady. My niece is inconsolable, because I made her hold my hand when we crossed the street. She is in full voice now, yelling, "I am not too little, I want to be big!" If she only knew how quickly her wish would come true. Back in the car, after she has whined through the ignominy of being buckled into her car seat, I try to have a reasonable talk with her, reminding her of the advantages of being small. She can fit in the secret fort under the lilac bush, and hide from her brother. What about stories in grandma's lap? But, she's not buying it. She falls asleep on the way home, clutching her new kite, a stubborn pout still on her face.

I brought a moss-covered rock to her pre-school for a science show and tell. I asked the kids at pre-school what a moss was. They skipped right over the question of animal, vegetable, or mineral and got directly to the most salient feature; mosses are small. Kids recognize that right away. This most obvious attribute has tremendous consequences for the way mosses inhabit the world.

Mosses are small because they lack any support system to hold them upright. Large mosses occur mostly in lakes and streams, where the water can support their weight. Trees stand tall and rigid because of their vascular tissue, the network of xylem, thick-walled tubular cells that conduct water within the plant like wooden plumbing. Mosses are the most primitive of plants and lack any such vascular tissue. Their slender stems couldn't support their weight if they were any taller. This same lack of xylem means that they can't conduct water from the soil to leaves at the top of the shoot. A plant more than a few centimeters high can't keep itself hydrated.

However, being small doesn't mean being unsuccessful. Mosses are successful by any biological measure—they inhabit nearly every ecosystem on earth and number as many as 22,000 species. Like my niece finding small places to hide, mosses can live in a great diversity of small microcommunities where being large would be a disadvantage. Between the cracks of the sidewalk, on the branches of an oak, on the back of a beetle, or on the ledge of a cliff, mosses can fill in the empty spaces left between the big plants. Beautifully adapted for life in miniature, mosses take full advantage of being small, and grow beyond their sphere at their peril.

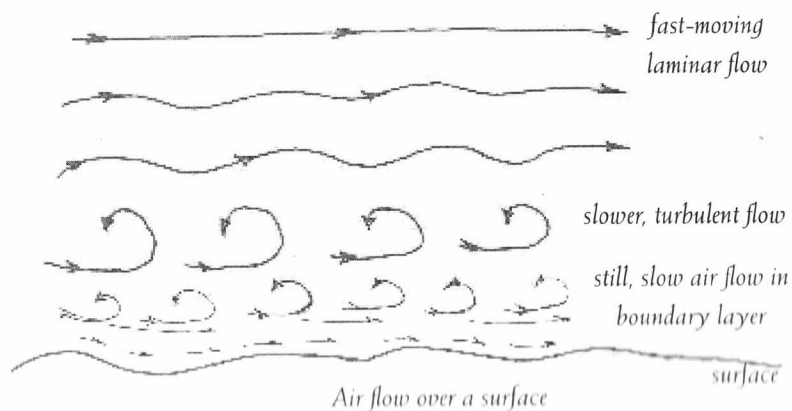
With extensive root systems and shading canopies, trees are the undisputed dominants of the forest. Their competitive superiority and heavy leaf fall are no match for mosses. One consequence of being small is that competing for sunlight is simply not possible—the trees will always win. So mosses are usually limited to life in the shade, and they flourish there. The type of chlorophyll in their leaves differs from their sun-loving counterparts, and is fine-tuned to absorb the wavelengths of light that filter through the forest canopy.

Mosses are prolific under the moist shaded canopy of evergreens, often creating a dense carpet of green. But in deciduous forests, autumn makes the forest floor virtually uninhabitable by mosses, smothering them under a dark wet blanket of falling leaves. Mosses find a refuge from the drifting leaves on logs and stumps which rise above the forest floor like buttes above the plain. Mosses succeed by inhabiting places that trees cannot, hard, impermeable substrates such as rocks and cliff faces and bark of trees. But with elegant adaptation, mosses don't suffer from this restriction; rather, they are the undisputed masters of their chosen environment.

Mosses inhabit surfaces: the surfaces of rocks, the bark of trees, the surface of a log, that small space where earth and atmosphere first make contact. This meeting ground between air and land is known as the boundary layer. Lying cheek to cheek with rocks and logs, mosses are intimate with the contours and textures of their substrate. Far from being a liability, the size of mosses allows them to take advantage of the unique microenvironment created within the boundary layer.

What is this interface between atmosphere and earth? Every surface, be it as small as a leaf or as large as a hill, possesses a boundary layer. We've all experienced it in very simple ways. When you lie on the ground on a sunny summer afternoon to look up and watch the clouds go by, you place yourself in the boundary layer of the Earth's surface. When you are flat on the ground, the wind speed is reduced; you can scarcely feel the breeze that would ruffle your hair if you were standing up. It's warm down there as well; the sun-warmed ground radiates heat back at you, and the lack of breeze at the surface lets the heat linger. The climate right next to the ground is different from the one six feet above. The effect that we feel lying on the ground is repeated over every surface, large and small.

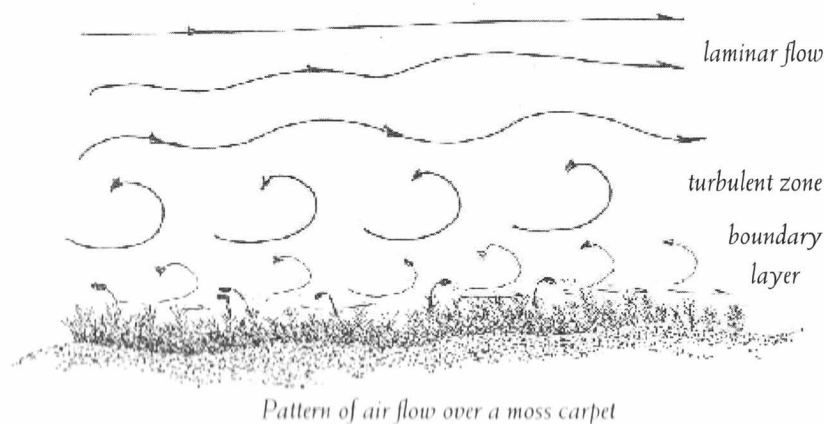
Air seems insubstantial, but it interacts in interesting ways with the things it touches, much as moving water interacts with the contours of the riverbed. As moving air passes over a surface like a rock, the surface changes the behavior of the air. Without obstacles, the air would tend to move smoothly in a linear path called *laminar flow*. If we could see it, it would look like water flowing freely in a smooth deep river. But as the air encounters a surface, friction tugs at the moving air and slows it down. You see this in the flow of water; when a river meets a rocky bottom or logs fallen in its path, the water slows. As the laminar flow is disrupted by the drag of the surface, the air stream becomes separated into layers of different speed. There is swiftly moving air aloft, flowing in a smooth sheet. Beneath it lies a zone of turbulence, where the air swirls and eddies as it encounters obstacles. Down toward the surface,



the air becomes progressively slower and slower until, immediately adjacent to the surface, the air is perfectly still, captured by the friction with the surface itself. It is this layer of still air that you experience while lying on the ground.

At a larger scale, I encounter these layers of air every spring. On the first mild day in April, our beautiful kites that have been hanging draped with cobwebs on the porch all winter rustle in the breeze and remind us of blue sky. So, we take them out to play in the boundary layer. In our sheltered valley, the breezes are seldom strong enough to immediately catch the big dragon kites that the kids and I love. So we run crazily back and forth over the back pasture, dodging cow pies and trying to generate enough wind to carry the kite upward. Close to the surface of the earth, the winds are too slow to support the kites' weight. They are trapped, beyond the reach of the breeze. Only when our mad dashes loft one of the kites up to escape the layer of still air does it pull and dance on the string. Its wild pitches and threatened crashes show that it has ascended into the turbulent zone. And then at last, the kite's string pulls taut and the red and yellow dragon sails into the freely moving air above. Kites were made for the airy zone of laminar flow; mosses were made for the boundary layer.

Our pasture is littered with rocks left by the glacier, and I stop to sit on one and spool out the kite string, listening to meadowlarks. The rock is warm from the sun and softened by mosses. I can imagine the pattern of air, flowing smoothly around it until it encounters the surface, where the mosses live. The sun's warmth gets trapped in the tiny layer of



still air. Since the air is nearly motionless, it acts as an insulating layer, much like the dead space in a storm window, which forms a barrier to heat exchange. The spring breeze around me is chilly, but the air right at the surface of the rock is much warmer. Even on a day when the temperature is below freezing, the mosses on a sunlit rock may be bathed in liquid water. By being small, mosses can live in that boundary layer, like a floating greenhouse hovering just above the rock surface.

The boundary layer traps not only heat, but water vapor, as well. Moisture evaporating from the surface of a damp log is captured in the boundary layer, creating a humid zone in which the mosses flourish. Mosses can grow only when they are moist. As soon as they dry out, photosynthesis must cease, and growth is halted. The right conditions for growth can be infrequent, and so mosses grow very slowly. Living within the confines of the boundary layer prolongs the window of opportunity for growth, by keeping the wind from stealing the moisture. Being small enough to live within the boundary layer allows the mosses to experience a warm, moist habitat unknown by the larger plants.

The boundary layer can also hold gases other than water vapor. The chemical composition of the atmosphere in the slim boundary layer of a log differs considerably from that of the surrounding forest. The decaying log is inhabited by a myriad of microorganisms. Fungi and bacteria are constantly at work degrading the log, with an outcome as sure as that of a wrecking ball. The continual work of the decomposers slowly turns the solid log to crumbling humus and releases vapors rich in carbon dioxide, which is also trapped in the boundary layer. The ambient atmosphere has a carbon dioxide concentration of approximately 380 parts per million. But the boundary layer above a log may contain up to ten times that amount. Carbon dioxide is the raw material of photosynthesis, and is readily absorbed into the moist leaves of the mosses. Thus, the boundary layer can provide not only a favorable microclimate for moss growth, but also an enhanced supply of carbon dioxide, the raw material for photosynthesis. Why live anywhere else?

Being small enough to live in the boundary layer is a distinct advantage. Mosses have found the microhabitats where their size becomes an asset. The growth of a moss would be sharply curtailed if the shoots grew too tall and into the drying air of the turbulent

zone. We might predict therefore that all mosses are uniformly small, corresponding to the limits imposed by the boundary layer. However, mosses exhibit a tremendous range in height, equivalent to the height disparity between a blueberry bush and a redwood. They range from tiny crusts only a millimeter high to lush wefts that can be up to ten centimeters tall. These differences in stature can usually be traced to differences in the depth of the boundary layer in the particular habitat. The boundary layer on a rock face exposed to wind and full sun is quite thin. Hence, the mosses of such arid places must be very small in order to stay within the protective boundary layer. In contrast, mosses on a rock in a moist forest can grow much taller and still remain within a favorable microclimate, because the boundary layer of the rock is under the umbrella of the boundary layer of the forest itself. The trees slow the wind and their shade reduces evaporation, buffering the area against the drying atmosphere. In a humid rainforest, the mosses can be lush and tall. The larger the boundary layer, the larger the moss can be.

Mosses can also control the depth of their own boundary layers by changes in their shape. Any feature of a surface that increases friction with moving air can slow the air and create a thicker boundary layer. A roughened surface slows the passage of air more effectively than a smooth one. Imagine being caught in a fierce prairie blizzard with strong winds blasting sheets of snow against your face. To escape the force of the winds, you lie down, taking refuge in the shelter of the earth's boundary layer. Given a choice, would you be warmer lying in the open or in a field of tall grass? The projection of the tall grass into the moving air stream slows the air and makes a larger boundary layer, helping to conserve your body heat. Mosses utilize this same principle to enlarge the boundary layers above them. The surface textures of a moss itself can create resistance to airflow. The greater the resistance, the deeper the boundary layer. Like a tall grassy field in miniature, moss shoots exhibit adaptations that slow air movement. Many moss species have long narrow leaves held upright to slow the airflow around them. Moreover, the leaves of mosses in dry sites often possess dense hairs, long reflective leaf tips, or minuscule spines. These extensions from the leaf surface also slow the moving air and reduce evaporation of essential moisture by creating a thicker boundary layer.

In arid zones, mosses often rely on dew for their daily ration of water. The interplay of the atmosphere and the rock surface creates the conditions for dew formation. At night, when the sun's heat dissipates, the temperature differential between the rock surface (which has retained some warmth) and the air may provide a site for condensation of water. A thin film of dew is created right at the air-rock interface, where it can be readily absorbed by the mosses. Only a very small being can take advantage of such a thin and evanescent supply of moisture in the desert, living on dew.

The safe and balmy realm of the boundary layer provides a secure refuge for mosses. But the very same nurturing environment that sustains growth to maturity poses a problem for the next generation. Like my niece, mosses eventually need to escape from protection by their elders and find their own places. Mosses reproduce by the formation of spores, tiny powdery propagules that require wind to carry them far afield. Most spores can't germinate in the leafy carpet of their own parents, so getting away is imperative. Air currents in the still air of the boundary layer are not sufficient to disperse them. So, to catch a breeze and help them leave the home territory, mosses elevate their spores on long setae, stalks that poke up above the boundary layer. The rapidly maturing sporophytes are thrust up through the boundary layer and into the turbulent zone like a kite on the wind. Here vortices of air swirl around the capsules, pulling out the spores and carrying them off to new habitats. Like the young of every species they escape the restrictions of their elders and seek out the freedom of the wide-open spaces.

The length of the seta or stalk is strongly correlated with the depth of the boundary layer. The seta of a forest moss must be quite tall to escape the boundary layer and catch the light breeze that moves over the forest floor. In contrast, mosses of open sites where the boundary layer is thin typically have short setae.

Mosses take possession of spaces from which other plants are excluded by their size. Their ways of being are a celebration of smallness. They succeed by matching the unique properties of their form to the physical laws of interaction between air and earth. In being small, their limitation is their strength. Try telling that to my niece.

Back to the Pond



I shiver in the damp breeze, but I can't bring myself to close the window on this April night that is sliding off the cusp of winter into spring. The faint sound of the peepers flows in with the cold air, but it's not enough. I need more. So I go downstairs and slip my down jacket over my nightgown, slide bare feet into my Sorels and leave the woodstove's warmth behind in the kitchen. With bootlaces dragging through patches of remnant snow, I tromp up to the pond above the farmhouse, breathing in the scents of wet ground. I'm pulled by the sound. Coming closer feels like walking into a crescendo, rising with the chorus of voices. I shiver again. The air literally throbs with the massed calls of peepers, vibrating the nylon shell of my jacket. I wonder at the power of these calls, bringing me from sleep and bringing the peepers back to the pond. Do we share some common language that draws us both to this place? The peepers have their own plan. What is it that brings me here to stand like a rock in this river of sound?

Their ringing calls summon all the local peepers to this gathering place, for mass fertilization in the rites of spring. Females will squeeze their eggs out into the shallow water, where males cover them with milky drifts of sperm. Surrounded by a gelatinous mass, the eggs will mature to tadpoles and become adult frogs by summer's end, long after their parents have hopped back to the woods. Spring peepers spend most of their adult lives as solitary tree frogs, travelling the forest floor. As far afield as they may venture, they must all return to water to reproduce. All amphibians are tethered to the pond by their evolutionary history, the most primitive vertebrates to make the transition from the aquatic life of their ancestors to life on land.

Mosses are the amphibians of the plant world. They are the evolutionary first step toward a terrestrial existence, a halfway point between algae and higher land plants. They have evolved some

rudimentary adaptations to help them survive on land, and can survive even in deserts. But, like the peepers, they must return to water to breed. Without legs to carry them, mosses have to recreate the primordial ponds of their ancestors within their branches.

The next afternoon, I return to the now quiet pond, looking for some marsh marigolds to cook up for dinner. Bending to gather the leaves, I see the aftermath of last night, masses of eggs lying in the sunlit shallows. They're entangled with green algae whose surface is studded with tiny bubbles of oxygen. As I watch, a bubble shimmers toward the surface and breaks.

The traditional knowledge of the Zuni people tells that the world began as clouds and water until the marriage of earth and sun bought forth green algae. And from the algae there arose all the forms of life. Scientific knowledge tells us that, before the world was green, the only life was in the water. In shallow bays, waves broke on an empty shore. The sunbaked continent was without a single tree to make a pool of shade. The early atmosphere had no ozone, and the sun's full intensity beat down on the land, a deadly rain of ultraviolet radiation, damaging the DNA of any living thing that ventured up on the shore.

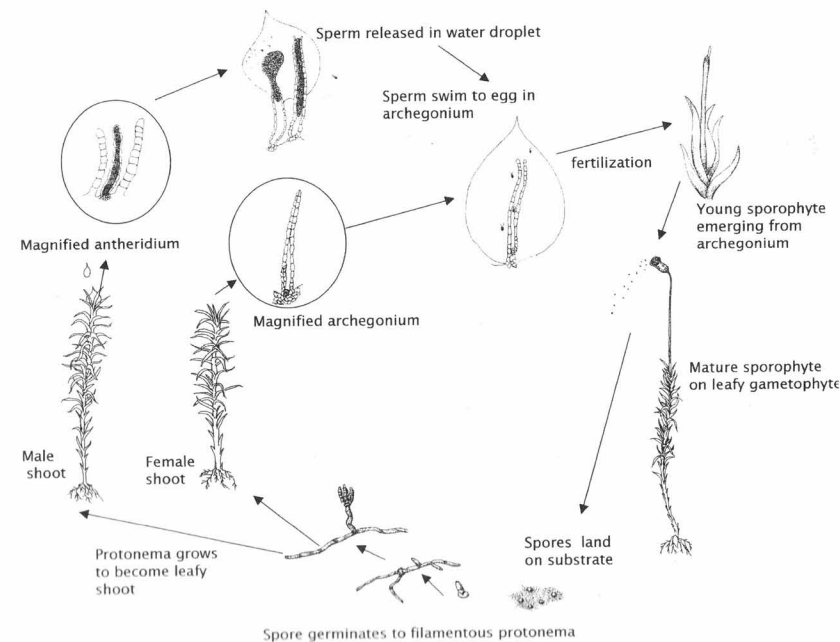
But, in the sea and inland ponds where water screened out the UV rays, algae were busily changing the course of evolutionary history, as the Zuni story explains. Oxygen bubbled from the algal strands, the exhaust fumes of photosynthesis accumulating molecule by molecule in the atmosphere. Oxygen, this new presence, reacted with strong sunlight in the stratosphere to produce the ozone layer that one day would shelter all terrestrial life under its umbrella. Only then did the surface of the land become safe for the emergence of life.

Freshwater ponds provided easy living for green algae. Supported by the water itself and constantly bathed in nutrients, the algae had no need for complex structure, no roots, no leaves, no flowers, simply a tangle of filaments to catch the sun. Sex in this warm bath was easy and uncomplicated. Eggs released from slippery strands floated aimlessly about, and sperm were released freely into the water. New algae would grow from that chance fusion of egg and sperm without need of a protective womb, the water providing everything.

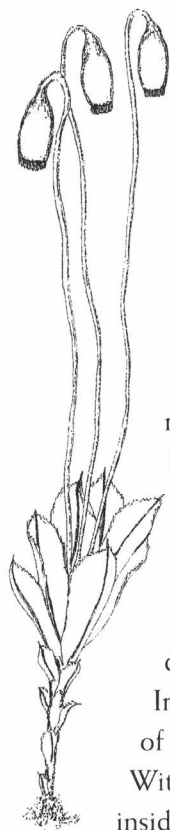
Who knows how it happened, the migration from the easy life in the water to the rigors of the land? Maybe the pools dried up, leaving algae stranded on the bottom like fish out of water. Maybe algae colonized the shady crevices of the rocky shore. Fossils record successful outcomes and rarely preserve the process. But we do know that during the Devonian era, 350 million years ago, the most primitive land plants ever seen emerged from the water to try and make a living on the land. These pioneers were the mosses.

To leave this easy aquatic life behind and venture out onto the land posed formidable challenges, chief among them the matter of sex. The algal ancestors handed down the legacy of floating eggs and swimming sperm, which was fine in the water, but a liability on dry land. A drying pond would be the end of peeper eggs. The drying air would doom an alga egg, as well. The life cycle of mosses evolved to meet these challenges.

Once my basket is full of greens, I take out an old canning jar and scoop it full of pond water and peeper eggs. I'll bring them back for my girls to watch as the eggs change into tadpoles. This fascinated me as



Life cycle of a typical moss



a kid, seeing the black speck in the middle of the egg sprout legs and a tail. The fat, rounded eggs remind me of being pregnant, the sensation of carrying around my own wiggling tadpole in the warm pond within. Each in our own way, we all go back to the pond to reproduce, connecting to our watery origins. The pond bank is tufted with mosses, so I take a clump of them, too. I can stick the moss under the microscope for the kids to look at.

In order to survive on land, mosses evolved a whole new architecture that surpassed the simpler algae. The floating ribbons of algae were replaced by stems that can hold themselves upright. Under the microscope you can see the whorls of perfect little leaves and tiny root-like rhizoids, a tuft of brown fuzz that anchors them to the soil. At the tip of the shoot, the leaves look different and are all clustered together in a tight circle.

Invisible, concealed among bunched-up leaves at the tip of the moss, lies the female structure, the archegonium. With gentle probing I can part the leaves to see what is inside. Nestled among them are three or four structures, chestnut brown and shaped like long-necked wine bottles.

On another stem, in the axil of a leaf, is another tuft of hair-like leaves. Pushing them aside, I find a cluster of sausage-shaped sacs, each one green and bulging. These are the antheridia, the male structures turgid with sperm ready to be released.

Mosses made a huge innovation to cope with the difficulties of reproduction on dry land. The egg is protected inside the female, rather than cast out on the water. All contemporary plants, from ferns to fir trees, use this same strategy that first arose in the mosses. Like a protective womb, the swollen base of the archegonium holds the egg. The clustered leaves trap water, keeping the egg from drying out and creating a pool through which the sperm can swim. The unfertilized egg sits safely in the archegonium and waits.

But getting sperm to egg is an exceedingly difficult task. The first obstacle is simply the necessity for water, which is unreliable in the terrestrial world. In order to get to the egg, swimming sperm must

have a continuous film of water. Rain and dew are captured between the densely packed leaves. The capillary spaces between leaves channel the water among plants, forming a transparent aqueduct between male and female. But any break in the water film poses an uncrossable barrier that prevents the sperm from reaching the egg. It's a race between the sperm and evaporation, which will steal away the temporary bridges of water. Unless the moss is soaked with rain, dew, or the spray of a waterfall to carry the sperm, the eggs will remain unfertilized. In a dry year, reproduction will likely fail.

Moss sperm are produced in great numbers, but each tiny cell has a vanishingly small chance of ever finding an egg. Unlike the peepers who call so strenuously to their mates, moss sperm have no signal to guide them to their destination and so swim at random in the water film. Most are simply lost in the labyrinth of leaves. The small sperm are weak swimmers and carry limited energy for their travels. Once released from the antheridium, the clock begins to count down their survival probability. Within an hour, all will be dead, having exhausted their resources. The eggs continue to wait.

The third challenge lies in the nature of water itself. From the vantage point of a human, water seems so fluid as we dive easily into its depths. But, at the scale of microscopic moss sperm, getting through water is like a person trying to swim through a pool filled with Jell-O. The surface tension of a water droplet presents an elastic barrier for moss sperm; despite wiggling and pressing against it, they can't break through. However, they have devised a number of ingenious means of escaping the grip of water. When the sperm are ready to be released, the antheridium absorbs excess water, swelling until it bursts. The sperm are pushed out under hydraulic pressure, given a head start on their journey.

Another way the moss overcomes the surface tension of water is by packaging a surfactant along with the sperm. When the antheridium ruptures, the chemical surfactant acts like soap, making water less viscous. As soon as the surfactant meets a taut droplet of water, the surface tension breaks and the dome of the drop suddenly flattens to a moving sheet of water, carrying the sperm along like surfers on a wave.

The sperm need all the help they can get in moving toward the egg, seldom travelling more than four inches from the antheridium that produced them. Some species have devised other means to increase

the distance, harnessing the power of a splash to spread the sperm. In species like *Polytrichum*, the antheridia are surrounded by a flat disk made of leaves, radiating around them like the petals of a sunflower. A raindrop plummeting onto this disk can splash the sperm as far as ten inches, more than doubling the distance they can travel.

If all the conditions are right, the sperm will be able to swim to the female and down the long neck of the archegonium to the waiting egg. Fertilization yields the first cell of the next generation, the sporophyte. In the life of spring peepers, the fertilized eggs are at the mercy of the environment, floating in the pond protected only by a gelatinous coating. But the moss mothers don't abandon their young. They nurture the next generation right inside the archegonium. Special transfer cells, akin to those in a placenta, allow nutrients to flow from the parent moss to the developing offspring. How amazing to have such kinship with these plants, who nourish their children with cells so like the ones that helped bring my daughters into the world.

The fertilized peeper eggs transform first to tadpoles and then to copies of their parents. Young mosses don't grow directly into adults, leafy copies of their parents. Instead, the fertilized egg develops into an intervening generation, the sporophyte. Still attached to the parent, and nourished by it, the sporophyte will create and disperse the next generation.

Back at the pond, the summer has warmed the water and my daughters and I are tempted by a swim. But the water is murky with algae and none too inviting, even on this hot day. So we stretch out on our bellies on the bank and soak up the sun instead, our books open on the ground. I like having the ground at eye level. I idly run my fingertip over the sporophytes that have formed on the mosses along the shore. Resilient, they spring back from my touch with a little puff of spores released on the breeze. Each one arises from the stem tip, where the archegonium had sheltered the egg in the spring. The sporophyte is now a plump, barrel-shaped capsule at the end of an inch-long stalk, the seta. Inside are masses of powdery spores to be sent off to seek their fortune wherever the wind may carry them.

Finding a home is an improbable business; most spores will haphazardly land in unsuitable places. But should a spore drift to the

ground at the moist edge of another pond or in another suitable, moist place, another transformation will take place. The round amber spore will swell with moisture and send out a green thread, the protonema. The threads will branch and spread over the moist ground, establishing a web of green. At this point in its life, the moss most resembles its distant relative: it is nearly indistinguishable from filamentous green algae. Like a newborn bearing the face of great-grandma, the protonema has all the attributes of its algal ancestor, an evolutionary echo contained in its genes. But the resemblance soon passes and leafy shoots rise up from buds along the protonema and form a new thick moss turf.

Most moss stories don't have such a happy ending. Mosses are amateurs in the business of reproduction on land, and it shows. Their adaptations allow them to reproduce, but with very low efficiency. Few sperm ever make it to the vicinity of the archegonium, and many eggs are left waiting like disappointed brides at the altar, an enormous waste of energy. So many factors conspire against successful sexual reproduction, is it any wonder that many species of mosses have given up on sex altogether? Production of sporophytes is rare for many species and totally unknown for others.

Without sexual reproduction, there would be no more peepers, no ringing chorus in the spring. But unlike peepers, mosses can still spread and multiply, even when sperm never meets egg. Sex is not the only opportunity for propagating themselves. Long before the advent of biotechnology, mosses have been making clones, saturating the environment with genetically identical copies of themselves. In fact, most species of moss can regenerate themselves entirely from just a small fragment. A single leaf, broken off by accident and lying on moist soil, can produce an entire new plant. Asexual propagation can also be an alternative reproductive plan. Gemmae, bulbils, brood bodies, branchlets—mosses produce a whole menu of specialized asexual propagules, which are simply detachable appendages on various parts of the moss plant. They break off and disperse to new habitats, where they can form new colonies without the costs and inefficiency of sex. Cloning eliminates the need for getting egg and sperm together, and spending time and energy to produce a sporophyte. All these ways of going on in the world, sexual and asexual, are a complex dance of genes

and environment, evolutionary variations on the theme of continuity, of perpetuation.

Every spring, my daughters and I say that the peepers are "calling up the daffodils" with their song. The green shoots push up after the first peepers are heard and come to full flowering before they are finished. My Potawatomi ancestors had a word for this mystery: *pubpowee*, the power that causes a mushroom to rise up from the earth overnight. I think it is this that draws me to the pond on a night in April, bearing witness to *pubpowee*. Tadpoles and spores, egg and sperm, mine and yours, mosses and peepers—we are all connected by our common understanding of the calls filling the night at the start of spring. It is the wordless voice of longing that resonates within us, the longing to continue, to participate in the sacred life of the world.

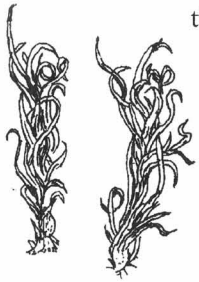
Sexual Asymmetry and the Satellite Sisters



Our local NPR station has a show in the Saturday morning lineup that usually accompanies my Saturday errands or a drive to the mountains. Sandwiched in between "Car Talk" and "What Do You Know?" is "The Satellite Sisters." "We're five sisters on two continents, with the same parents and living very different lives. Let's talk." The sisters check in by telephone from all over the world, but the show has the feel of a kitchen table, half-filled coffee cups, and a plate of sticky buns. The talk wanders from career strategies to kids, women as environmental activists, and the ethical dilemma posed by sampling grapes in the grocery store. And of course, relationships.

My husband is home puttering in the barn, my daughters are at a birthday party, and I'm feeling as contented and lazy as the Sisters' conversation this morning. Too wet to walk, too muddy to garden, the morning is mine, all mine, and I've been wanting to take a look at all these unidentified *Dicranums*. What luxury, to come to work in order to play. The rain streams down the windows of the lab and the voices of the Sisters are my only company. I can laugh out loud with them, and who will notice? There are no students, no phone calls, just some handfuls of moss and a few hours stolen from the normal hubbub of a weekend.

Dicranum is a genus of moss with many species, sisters in the same family. I think of them as only females, since the menfolk have met an unusual, and perhaps fitting, fate which strong women will understand immediately. We'll get to that later. While the Sisters trade stories of the vulnerability that comes with a new hairstyle, the exposure of a tentative self, I'm laughing at how I'd never noticed before that the *Dicranums*, more than any other moss, look like hair, combed hair, neatly parted and swept to one side. Other mosses bring to mind carpets or miniature forests, but *Dicranum* evokes hairstyles: ducktails, waves, corkscrew curls, and buzzcuts. If you lined them up for a family photograph, from

*Dicranum montanum*

the smallest, *D. montanum*, to the largest, *D. undulatum*, you'd definitely see the family resemblance. They all have the same hair-like leaves, long and fine with a curl at the end, brushed in one direction for that windswept look.

Like the Satellite Sisters phoning in from Thailand and Portland, Oregon, the *Dicranums* are widely distributed in forests all over the world. *Dicranum fuscensens* lives in the far north, while *D. albidum* goes all the way to the tropics. Perhaps the distance between them helps for peaceful coexistence between siblings. The genus *Dicranum* has undergone considerable adaptive radiation, that is, the evolution of many new species from a common ancestor. Adaptive radiation, whether in Darwin's finches or in *Dicranum*, creates new species that are well adapted for specific ecological niches. Darwin's finches evolved from a single ancestral species lost at sea and swept out to the barren Galapagos Islands, where the birds evolved into new species. Each island in the archipelago supports a unique species, with a unique diet. Likewise, the original *Dicranum* diverged into many different species, each with a distinctive appearance and habitat, lifestyle variations on the ancestral theme.

The force behind this divergence into new species is related to the inevitable competition between siblings. Remember wanting what your brother had, just because he had it? At the family dinner table, if everyone wants a drumstick from the Sunday chicken someone will be disappointed. When two closely related species put the same demands on their environment, with not quite enough to go around, both will end up with less than they need to survive. So, in families, siblings can coexist by developing their own preferences, and if you specialize in white meat or the mashed potatoes, you can avoid competition for the drumsticks. The same specialization has taken place in *Dicranum*. By sidestepping competition, numerous species can coexist, each in a habitat that they don't have to share with a sibling species, the mosses' equivalent of "A Room of One's Own."

In the *Dicranum* clan, there are family roles that could easily apply to sisters in any big family. You'll recognize them right away. *D. montanum* is

*Dicranum scoparium*

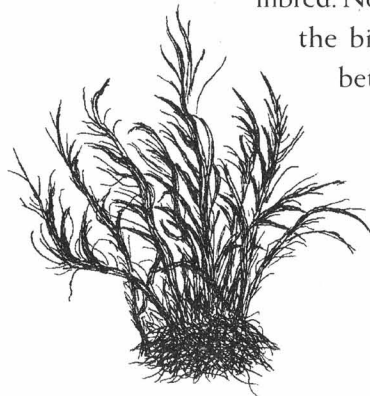
the unassuming one; you know the type—nondescript, overlooked, with her short curls always in disarray. She's the one who gets the leftover habitats, the chicken wings of the Sunday feast, the occasional exposed root of a tree or bare rock. Moist shady rocks are also the habitat of the glamorous *D. scoparium*, the one who draws the looks with long, shiny leaves, tossed to one side. This is the plush *Dicranum*, the one that makes you want to run your hand over its silkiness and pillow your head in its deep cushions. When these sister species live together on a boulder, the showy *D. scoparium* takes all the best places, the moist sunlit tops, the fertile soil, while *D. montanum* fills in the gaps. No one is surprised when *D. scoparium* crowds out the little sister, invading her space and driving her to the edges.

The other *Dicranums* tend to avoid the conflicts that arise from sharing the same space, where strong identities can clash. *D. flagellare*, with leaves trim and straight, like a military buzzcut, remains aloof from the others, choosing to live only on logs in an advanced state of decay. She's the conservative one, celibate for the most part, foregoing family in favor of her own personal advancement by cloning. Solitary and intensely green, *D. viride* has a hidden fragile side, with leaf tips always broken off like bitten fingernails. *Dicranum polysetum*, on the other hand, is the most prolific mother of the family, an inevitable outcome of her multiple sporophytes. Then there's the long, wavy-leafed *D. undulatum*, capping the tops of boggy hummocks, and *D. fulvum*, the black sheep of the family; more than a dozen species of powerful females.

I'm filling a second cup of coffee and patiently cataloging the moss samples, when the Saturday conversation of the Satellite Sisters wanders to men. Some of the sisters are happily married and others are sharing last weekend's episode of looking for Mr. Right, pondering commitment and probable fatherhood personalities. Finding the right mate, a universal female concern, is also an issue for *Dicranum*. Sexual reproduction in mosses is an iffy business, as we have seen, given the limited abilities of the weak, short-lived males. Thwarted by a lack of swimmable water between them and the egg, their success depends on

well-timed rainfalls. The sperm must swim to the egg, facing barriers that isolate them even though they are only a few inches apart. So near and yet so far, most eggs sit and wait in the archegonium for a sperm that never comes.

Some species have evolved a means to increase their chances of finding a mate. They become bisexual. After all, fertilization is virtually guaranteed when egg and sperm are produced by the same plant. The good news is that there will be offspring; the bad news, they are all inbred. None of the *Dicranum* species have evolved the bisexual lifestyle, keeping distinctions between the genders very clear indeed.



Dicranum fulvum

Given the difficulties in getting males and females together, it's surprising how common it is to see a colony of *Dicranum* bristling with sporophytes, the outcome of numerous sexual encounters. I have a clump of *D. scoparium* here, which must have fifty sporophytes on it, representing potentially fifty million spores. How do they do it? You might

guess that the key to their reproductive success was a very favorable sex ratio, with numerous males hovering around every female. Some mosses have adopted this strategy, but not *Dicranum*.

While the radio Sisters compare their rules for first dates, I take this clump of *Dicranum* apart, looking for the macho males who are responsible for all these babies. The first shoot I pull out is a female. So is the second. And the third. Every single shoot in the colony is a female, and yet every single shoot has been fertilized. Pregnant females without a male in sight? Immaculate conception has not yet been documented in mosses, but it makes you wonder.

I slide one of the female shoots under my microscope for a closer look, and see just what I'd expect: the female anatomy, fertilized eggs swelling with the next generation. The stem is covered by a sheaf of long leaves, swept gracefully to the side with that unmistakable *Dicranum* flair. I follow one of the curving leaves along its arc, its smooth cells

and shining midrib. And then I notice a whiskery little outgrowth, something I've seen only once before. Dialing up the magnification of my microscope, I can see that it's a tiny little cluster of hair-like leaves, a miniature plant growing from the massive *Dicranum* leaf like a clump of ferns growing on a tree branch. At even higher power, sausage-shaped sacs come into focus, unmistakably antheridia, swollen with sperm. Here are the missing fathers: microscopic males reduced to hiding out among the leaves of their would-be mates. They have entered female territory with a single purpose, a kind of stealthy intimacy, putting themselves so close to the females that the impotent sperm easily swim the distance to the egg.

Females dominate all aspects of *Dicranum* life, in numbers, in size, in energy. Whether or not males even exist lies in the power of the females. When a fertilized female produces spores, those spores are without gender. Each one is capable of becoming a male or a female, depending on where it lands. If a spore drifts to a new rock or log that is unoccupied, it will germinate and grow up to be a new full-size female. But should that spore fall onto a patch of *Dicranum* of the same species, it will sift down among the leaves of the existing females and become trapped there, where the female will control its fate. The female emits a flow of hormones which cause that undecided spore to develop into a dwarf male, a captive mate that will become the father of the next generation in the matriarchy.

The Sisters are interviewing someone on the effects of the two-career family. I want to call in to the show to see what they'd say about *Dicranum*'s domestic arrangement. Five sisters, five perspectives on dwarf males: a clear case of female tyranny, surrender of masculinity to strong women, turnabout is fair play ... hey, give them the benefit of the doubt, it's possible that they are sensitive '90s kinds of guys, giving the females their space. Will they still think that size matters?



Dicranum polysetum


In this time and place, men and women have the luxury of creating our relationships quite independently of their survival value to our species. Heaven knows there are plenty of us already. The ways we negotiate the balance of power and domestic harmony are unlikely to change the trajectory of our population.

But from the evolutionary perspective of *Dicranum*, the asymmetry of the sexual relationship matters a great deal. Dwarf males are an efficient solution to the problem of getting fertilized. The entire species, both sexes, benefits from this arrangement. A full-size male actually stands in the way of his own genetic success, his leaves and branches increasing the distance between sperm and egg. A dwarf male will produce many more offspring than will a full-size male. He can best contribute to the next generation by delivering sperm and then getting out of the way.

The very same impulse that propels sister species to diverge from one another creates the sharp difference between *Dicranum* males and females. Competition in a family decreases everyone's potential success. So evolution favors specialization, avoiding competition, and thus increasing the survival of the species. A large female and a dwarf male cannot compete with each other. The male is small, to better deliver sperm. The female is large to nurture the resulting sporophyte, their future, their offspring. Without competition from their mates, females get all of the good habitat, the light and water and space and nutrients, all for the benefit of the offspring.

The hour with the Satellite Sisters is winding down, with a recipe for lemon mousse. It sounds great. The rain has stopped and my mosses are done, so I turn off the radio with a smile. It's time to go home for lunch, lovingly prepared by my full-size male.

An Affinity for Water

On the hilltops of my home in upstate New York, the bare gray branches of the maples seem to be traced with a newly sharpened pencil against the winter sky. But in the Willamette Valley the Oregon oaks are drawn in thick green crayon. The steady winter rains keep the tree trunks lush and green with moss, while their leaves lie dormant. This mossy sponge drips a constant flow of water to the tree roots, saturating the ground below and filling the soil reservoir for the summer ahead.

By August, the winter rains have long been consumed, and the land is thirsty again. The oak leaves hang in the hot air and the buzzing cicadas broadcast the weather forecast: the 65th day without rain. The wildflowers have retreated underground to avoid the drought, leaving a landscape of parched brown grasses. The moss carpets now lie desiccated on the bark of the summer oaks, their shriveled, wiry skeletons barely recognizable. In the summer drought, the oak grove is hushed and waiting. All growth and activity is suspended in drought-sleep.

Linden's plane is late, so I amble down to the AeroJava stand, joining the line, killing time. There is a jar on the counter, half full of dimes and pennies, with a hand-lettered sign: "If you fear change, leave it here." Unaccountably, I find my eyes filling for a moment, wishing I could empty my pockets, casting off my load of change, bringing my daughter back, the little one, standing on a chair with my apron tied three times around her, cutting out Valentine cookies and splattering the kitchen with pink frosting.

The mosses begin their time of waiting. It may be only a matter of days before the dew returns, or it may be months of patient desiccation. Acceptance is their way of being. They earn their freedom from the pain of change by total surrender to the ways of rain.

I've lost a lot of days to waiting, holding my breath until circumstances have changed, straining toward the scent of rain. I remember waiting for what seemed like forever to be big enough to ride the school bus, which gave way to waiting for that same bus, stomping my feet against the biting cold. Waiting nine sweetly rounded months for the arrival of my babies was followed too soon by waiting for them outside the high school basketball game, fingers tapping impatiently on the steering wheel. And now I wait for the touchdown of Linden's plane, bringing her back from college, waiting to slip my arm through hers, while we wait together at my grandfather's bedside.

What art of waiting is practiced by the mosses, crisped and baking on the summer oak? They curl inward upon themselves, as if suspended in daydreams. And if mosses dream, I suspect they dream of rain.

Mosses must be awash in moisture in order for the alchemy of photosynthesis to occur. A thin film of water over the moss leaf is the gateway for carbon dioxide to dissolve and enter the leaf, beginning the transformation of light and air into sugar. Without water a dry moss is incapable of growth. Lacking roots, mosses can't replenish their supply of water from the soil, and survive only at the mercy of rainfall. Mosses are therefore most abundant in consistently moist places, such as the spray zone of waterfalls and cliffs seeping with spring water.

But mosses also inhabit places that dry out, such as rocks exposed to the noonday sun, xeric sand dunes, and even deserts. The branches of a tree can be a desert in the summer and a river in the spring. Only plants that can tolerate this polarity can survive here. The bark of these Oregon oaks is shaggy with *Dendroalsia abietinum* all year round. The name *Dendroalsia* translates from scientific Latin to something like "Companion of Trees." Like others of its kind, beautiful *Dendroalsia* tolerates these wide swings in moisture, with a suite of evolved adaptations known as *poikilohydry*. Its life is tied to the comings and goings of water. Poikilohydric plants are remarkable in that the water content of the plant changes with the water content of the environment. When moisture is plentiful, the moss soaks up the water and grows prolifically. But when the air dries, the moss dries with it, eventually becoming completely desiccated.



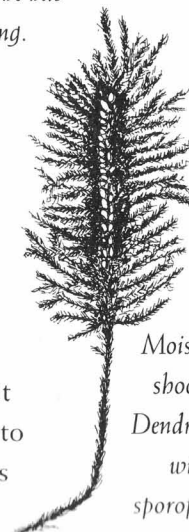
Dry curled shoot of
Dendroalsia

Such dramatic drying would be fatal to higher plants, which must maintain a fairly constant water content. Their roots, vascular systems, and sophisticated water-conservation mechanisms allow them to resist drying and stay active. Higher plants devote much of their effort to resisting water loss. But when water depletion becomes severe, even these mechanisms are overcome, and the plants wilt and die, like the herbs on my windowsill when I left for vacation. But most mosses are immune to death by drying. For them, desiccation is simply a temporary interruption in life. Mosses may lose up

to 98 percent of their moisture, and still survive to restore themselves when water is replenished. Even after forty years of dehydration in a musty specimen cabinet, mosses have been fully revived after a dunk in a Petri dish. Mosses have a covenant with change; their destiny is linked to the vagaries of rain. They shrink and shrivel while carefully laying the groundwork of their own renewal. They give me faith.

Linden steps off the plane so glad to be home, beaming a girl's smile, but her woman's eyes scan my face for signs of concern. I grin back reassuringly and hug her tight. Walking along beside her I see right away that she has not been wasting her days in waiting; she has been becoming. I know now there's nothing in the world that would have me trade this lovely young woman, radiant, with her arm linked through mine, for the toddler who slept in my arms.

Poikilohydry enables mosses to persist in water-stressed habitats which more advanced plants cannot endure. But this tolerance comes at a serious cost. Whenever the moss is dry, it cannot photosynthesize, so growth is limited to brief windows of opportunity when the moss is both wet and illuminated. Evolution has favored those mosses that can prolong this window



Moistened
shoot of
Dendroalsia
with
sporophytes

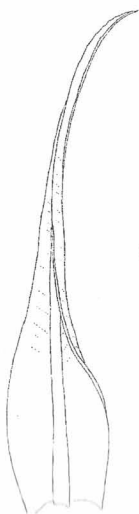
of opportunity. They have elegantly simple means of holding on to precious moisture. And yet, when the inevitable drought arrives, their acceptance is total and they are beautifully equipped for endurance, waiting until the rains return.

The atmosphere is possessive of its water. While the clouds are generous with their rain, the sky always calls it back again with the inexorable pull of evaporation. The moss isn't helpless; it exerts its own pull to counter the powerful draw of the sun. Like a jealous lover, the moss has ways to heighten the attachments of water to itself and invites it to linger, just a little longer. Every element of a moss is designed for its affinity for water. From the shape of the moss clump to the spacing of leaves along a branch, down to the microscopic surface of the smallest leaf, all have been shaped by the evolutionary imperative to hold water. Moss plants almost never occur singly, but in colonies packed as dense as an August cornfield. The nearness of others with shoots and leaves intertwined creates a porous network of leaf and space which holds water like a sponge. The more tightly packed the shoots, the greater the water-holding capacity. A dense turf of a drought-tolerant moss may exceed three hundred stems per square inch. Separated from the rest of a clump, an individual moss shoot dries immediately.

I feel myself expand in her presence. Her stories make me laugh and waken

my own stories to intertwine with hers. With her next to me in the car, fiddling with the radio to find her favorite station, I somehow know myself again, and know that the ache her absence brings is not only about losing her, but about losing it all, my grandfather, my parents, myself. How fearfully we fight the losses that Dendroalsia so gracefully embraces. Straining against the inevitable, we spend ourselves on futile resistance, as if we could somehow outrun the drying of a dewy cheek.

Water has a strong attraction for the small spaces in a clump of moss. The water molecules attach themselves readily to leaf surfaces, due to the adhesive properties of water. One end of the water molecule is positively charged, the other is negative. This allows water to adhere



to any charged surface, positive or negative, and the moss cell wall has both. The bipolar nature of water also makes it cohesive, sticking to itself, with the positive end of one molecule linking up head to tail with the negative end of another. As a result of this strong cohesion and adhesion, water can form a transparent bridge between two plant surfaces. The tensile strength of this bridge is sufficient to span small spaces, but collapses if the gulf is too broad. The delicate leaves and small stature of mosses provide spaces of just the right size for these bridges to form by the capillary forces of water. Moss shoots, branches, and leaves are arranged in such a way as to prolong the residence time of water and to counter the forces of evaporation, with the pull of capillarity. Mosses without such favorable design dried out too quickly and were eliminated by natural selection.

Watch a drop of rainwater fall on a broad, flat oak leaf. It beads up for a minute, reflecting the sky like a crystal ball, and then slides off to the ground. Most tree leaves are designed to shed water, leaving the task of water absorption to the roots. Tree leaves are covered with a thin layer of wax, a barrier to water entering by absorption or leaving via evaporation. But moss leaves have no barrier at all, and are only one cell thick. Every cell of every leaf is in intimate contact with the atmosphere, so that a raindrop soaks immediately into the cell.

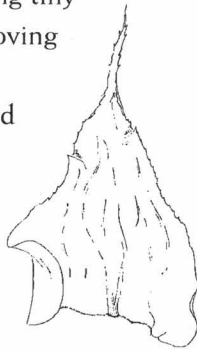
On the way to the hospital, we talk and talk, sometimes about her great-grandpa, but mostly about an amazing slice of time, her freshman year in progress. She tells me about her classes, people I've never met, a backpacking trip—I hear passions she never guessed at, courageous ventures into unknown territory. Listening, I realize I'm a little envious of her openness to the world, where change is only the lure of imagined possibilities, not the agent of impending losses. But I know there is no barrier I can construct which will hold those losses back, that won't also shut me out, alone, and disconnected from the world.

The leaves of trees are uniformly flat, to intercept as much light as possible, and spaced far from one another to prevent shading. But light is of less concern to mosses than is water. Therefore, the nature of moss leaves is entirely different from trees'. Each leaf is shaped to make a home for water. Lacking roots or an internal transport system

of any kind, mosses rely entirely on the shape of their outer surfaces to move water. In some species, the flow of water is accelerated by the wicking action of minute threads, or *paraphyllia*, that densely cover the moss stem, like a blanket of coarse wool. The shape and arrangement of some moss leaves collect and retain water, a concave leaf holding a single raindrop in its upside-down bowl. Others have long leaf tips, rolled into tiny tubes that fill with water and channel the droplets to the leaf surface. Leaf overlaps leaf, closely spaced, creating tiny concave pockets, a continuous conduit for water moving among them.

Even the microscopic surface of the leaf is sculpted to attract and hold a thin film of water. The leaves may be pleated into minute accordion folds that trap water in the crevices, undulations in the leaf creating a microtopography of rolling hills and water-filled valleys. Species of arid habitats often have leaf cells that are studded with tiny bumps called *papillae*, forming a roughened surface you can feel if you rub the leaf gently between your fingertips. A film of water stretches between the papillae, which rise like little hills above a lake, allowing the leaf to hold water and photosynthesize just a little longer, even while the sun beats down.

The top shelves of my office are stacked with cartons of dry mosses, packed away as references to one research project or another. Each time I take out a specimen it must be wetted so that I can see its fine-scale features on which identification depends. I suppose I could just soak it in a Petri dish for a few minutes. But even after all these years, I still delight in the ritual of adding the water, drop by drop, and watching with the microscope as the shoots revive. I think of it as a small act of homage to a remarkable marriage between moss and water. The moss and the water seem to have a magnetic attraction for each other. I add a drop of water to the tip of the dry shoot, and it rushes among the moss leaves like a flash flood down a narrow canyon. Dry contorted leaves unfurl, all is light and movement as the drops follow every passageway and penetrate every little space, swelling beneath the convex leaves and bowing them outward.



Just where the leaf attaches to the stem are specialized groups of alar cells. To the naked eye, they appear as shiny crescents at the corners of the leaves. Under the microscope, alar cells are much larger than a typical leaf cell and often are thin walled.



The large empty space of the alar cell absorbs water rapidly and can inflate like a transparent water balloon. This swelling causes the leaf to bend out and away from the stem, to a more favorable position to capture light. Without nerve or muscle, the moss can sense the water that makes growth possible, and adjust the leaf angle to the optimal plane for photosynthesis. Leaf bases fill and overflow, with the excess drawn to the leaf below, creating an interconnected string of pools beneath each overlapping leaf. Within minutes the shoot is saturated and the water comes to rest, leaving the shoot plump and shining. And then it's over. The shape of the water is changed by the moss and the moss is shaped by the water.

The mutuality of moss and water. Isn't this the way we love, the way love propels our own unfolding? We are shaped by our affinity for love, expanded by its presence and shrunken by its lack.

Plants and animals of all kinds have sophisticated means of maintaining water balance, using pumps and vessels, sweat glands and kidneys. Considerable energy is devoted to water regulation in these organisms. But mosses engineer the movement of water simply by harnessing the attraction of water for surfaces. Their forms take advantage of the adhesive and cohesive forces of water, to move the water at will over their surfaces, without expending any energy of their own. This elegant design is a paragon of minimalism, enlisting the fundamental forces of nature, rather than trying to overcome them.

My grandfather would have appreciated the elegant design of a moss, if he'd ever had the chance to see it. He was a carpenter. His shop was a warren of tools, precision lathes and hand drills, antique planes and sculpting chisels, each tool to its own purpose. No material was wasted, there were baby-food jars of carefully sorted

screws, a walnut board, a salvaged oak newel post waiting to be transformed into a bowl for my grandmother's kitchen. His designs were clean and simple, to match the potential of the wood to the task at hand.

Despite all these remarkable tactics for water retention, they are only a temporary respite from evaporation. The sun always wins the battle and the moss begins to dry. Profound changes in the shape of the mosses occur as water is pulled back to the atmosphere. Some mosses begin to fold their leaves, or roll them inward. This reduces the exposed surface area of the leaf and helps the plant cling to the last bits of surface water. Nearly all mosses change their shape and color when they dry out, making identification of species doubly difficult. Some leaves wrinkle, some spiral and twist their leaves around the stem, a sheltering cloak against the dry wind. The plumes of *Dendroalsia* darken and coil inward looking like the black tail of a mummified monkey. Crisp, dry, and contorted, the mosses are transformed from soft fronds to brittle, blackish tufts.

My grandfather looks too tall for his hospital bed, surrounded by the thicket of equipment that is keeping him alive. His softness seems like an alien presence in this realm of hard surfaces, sharp angles, and the confident hum of electronics. An IV tube runs into his arm, battling dehydration. It's calibrated to maintain the 87% of his body that is water, while the other 13% begins the march of surrender.

At the same time that drought begins to shrink the moist leaves, preparations for drying are also going on in the biochemistry of the moss cell. Like a ship being readied for dry dock, the essential functions are carefully shut down and packed away. The cell membrane undergoes a change that allows it to shrink and collapse without sustaining irreparable damage. Most importantly, the enzymes of cell repair are synthesized and stored for future access. Held in the shrunken membrane, these lifeboat enzymes can restore the cell to full vigor when the rain returns. The internal machinery of the cell can turn on and quickly repair the desiccation damage. Only twenty minutes after wetting, the moss can go from dehydration to full vigor.

We stand together in the cemetery with all the paraphernalia of resistance now set aside. With her hand in mine, my grandmother's face is brittle and ready to break. My mother's gaze moves among us, gathering each of us in. My pink-cheeked child shifts from foot to foot, not knowing where to stand. She stands in a circle of daughters, with hands joined, where one day she will be the one to let go. When the roses slip from her hands, we hold each other's tighter.

Holding water against the pull of the sun, and welcoming it back again is a communal activity. No moss can do it alone. It requires the interweaving of shoots and branches, standing together to create a place for water.

The soft fall clouds finally darken the hard summer sky and a wet wind stirs the dry oak leaves scattered on the ground. The air is charged with energy, as if the mosses are poised and alert, tasting the wind for the scent of rain. Like captives of the drought, their senses are tuned to the approach of their rescuers.

When the first drops begin to fall, and shower turns to downpour, it is an exuberant reunion. The water courses through the old paths constructed especially to welcome its arrival. Flooding down the canals of tiny leaves, the water finds its way through the capillary spaces and soaks deeply into every cell. Within seconds the eager cells grow turgid and contorted stems spread toward the sky, leaves outstretched to meet the rain. I run out to the grove when the rains arrive, I want to be there when the unfolding begins. I, too, can have a covenant with change, a pledge to let go, laying aside resistance for the promise of becoming.

Animated, released from stillness by the rain, *Dendroalsia* begins to move, branch by delicate branch unfolding to recreate the symmetry of overlapping fronds. As each stem uncurls, its tender center is exposed and all along the midline are tiny capsules, bursting with spores. Ready for rain, they release their daughters upon the updrafts of rising mist. The oaks once more are lush and green and the air smells rich with the breath of mosses.