Glime, J. M. 2020. Stream Physical Factors Affecting Bryophyte Distribution. Chapt. 2-1. In: Glime, J. M. Bryophyte Ecology. Volume 4. Habitats and Roles. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 13 May 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

CHAPTER 2-1
STREAM PHYSICAL FACTORS AFFECTING BRYOPHYTE DISTRIBUTION

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Figure 1. Tolliver Falls 7 January 1961, Swallow Falls Park, Maryland, USA. The stream remains open even though the ground is buried in snow. The leafy liverwort ***Scapania undulata*** is common in the falls. Photo by Janice Glime.

In the early stages of my career, few purely ecological studies of aquatic bryophytes existed. At that time, an emphasis on pollution fawned studies on the uptake and binding of heavy metals and other pollutants. Since that time, many studies on the ecology and physiology of these aquatic species have emerged. These have helped us to understand the roles of various ecological factors that determine which bryophytes can occupy a particular location. This chapter will introduce those stream parameters that are able to affect the bryophyte populations.

Aquatic, and especially stream, bryophytes must be able to survive both complete submersion and periods of desiccation and even high light when their substrate becomes exposed. This exposure can often be coupled with high temperatures that are more conducive to respiration than to photosynthesis. Acrocarpous mosses tend to dominate in the frequently exposed situations, whereas pleurocarpous mosses have better survival where water is flowing most of the time, and especially during periods of rapid flow.

Aquatic habitats provide adaptive challenges that can be quite different from those of terrestrial habitats. These have been adequately described in several books and publications on limnology and flowing waters (*e.g.* Margalef 1960; Ruttner 1963; Hynes 1970; Allan 1995). Streams, because of their flowing water and sometimes intermittent flow, can be even more challenging. Hence, the number of truly aquatic bryophytes in streams is relatively small.

Factors Affecting Bryophyte Presence

In their study of 187 Portuguese water courses (mostly headwaters), Vieira *et al.* (2012a) assessed the effects of fluvial and geologic gradients among the streams, focussing on type of river segment, micro-habitat, immersion level, water velocity, depth range, shading, rock types, and altitude. They identified 140 taxa (102 mosses, 37 liverworts, and 1 hornwort). They furthermore noted that water velocity, local incident light, and hydrologic zone explained the taxonomic groups, life forms, and life strategies present (Vieira *et al*. 2012b). The most common taxa in these streams were ***Racomitrium aciculare*** (Figure 2), ***Platyhypnidium lusitanicum*** (Figure 3), ***Hyocomium armoricum*** (Figure 4), ***Scapania undulata*** (Figure 5), and ***Fissidens polyphyllus*** (Figure 6), with **Brachytheciaceae** (Figure 3), **Grimmiaceae** (Figure 2), and **Fissidentaceae** (Figure 6) being the most frequent families.

Figure 2. ***Racomitrium aciculare*** (**Grimmiaceae**), one of the common bryophytes in Portuguese streams. Photo by Michael Lüth, with permission.

Figure 3. ***Platyhypnidium lusitanicum*** (**Brachytheciaceae**), one of the common bryophytes in Portuguese streams. Photo by David T. Holyoak, with permission.

Figure 4. ***Hyocomium armoricum***, one of the common bryophytes in Portuguese streams. Photo by David T. Holyoak, with permission.

Figure 5. ***Scapania undulata***, one of the common bryophytes in Portuguese streams. Photo by Michael Lüth, with permission.

Figure 6. ***Fissidens polyphyllus***, one of the common bryophytes in Portuguese streams. Photo by David T. Holyoak, with permission.

Scarlett and O'Hare (2006) studied the community structure of stream bryophytes in rivers of England and Wales. They analyzed the 50 most common bryophytes, determining that ***Fontinalis antipyretica*** (Figure 7) and ***Platyhypnidium riparioides*** (Figure 8) were the dominant species. They found the strongest environmental gradient to be the transition from the lowland chalk geology to those of steeply sloping, high altitude systems with less erodable rocks. This trend relates to substrate size, altitude of source, distance to source, and site altitude as important predictors of species richness (stepwise regression analysis, $p < 0.0001$, adjusted $R^2 = 0.30$).

Figure 7. ***Fontinalis antipyretica***, a species that became less abundant when flow was reduced or when erosion covered it with inorganic siltation. Photo by Andrew Spink, with permission.

Figure 8. ***Platyhypnidium riparioides***, a dominant stream bryophyte. Photo by Hermann Schachner, through Creative Commons.

Heino and Virtanen (2006) found that mean local abundance and regional occurrence were strongly positively related in streams, but that for semi-aquatic species, this relationship was very weak. Their results suggest that obligatory stream bryophytes are limited by dispersal and metapopulation processes, whereas the semi-aquatic species are more likely to be limited by habitat availability. Life history strategies and growth forms differed greatly between those of dominants and those of the transients or subordinate species.

Suren (1996) did a massive study involving 118 streams on the South Island of New Zealand. He identified five types of streams, one of which has no bryophytes. They were absent in streams surrounded by development such as pastures and pine woodlands, where rocks were easily eroded. Furthermore, these streams were highly influenced by humans, having higher nutrient levels and more common low-flow events. They also lacked the bedrock and boulders that contribute to stability. Instead, streams with bryophytes were stable and experienced fewer low-flow events.

Using the parameters that were important in New Zealand, Suren and Ormerod (1998) conducted an extensive study in Himalayan streams and found many of the same factors were important as in the New Zealand streams. These included substrate stability, substrate size, flow, alkalinity, and human interference with the surrounding landscape.

Slack and Glime (1985) examined niche characteristics in Appalachian Mountain streams, USA. They found height on the rock and type of substrate, including rock size (an indicator of stability), were important niche parameters. Height above water level causes a zonation pattern that separates niches of closely related species (Figure 9). In these streams, it separates two species of ***Brachythecium*** (***B. rivulare*** close to water and ***B. plumosum*** above it; Figure 10-Figure 11) and two growth forms of ***Hygrohypnum ochraceum*** (Figure 12-Figure 13).

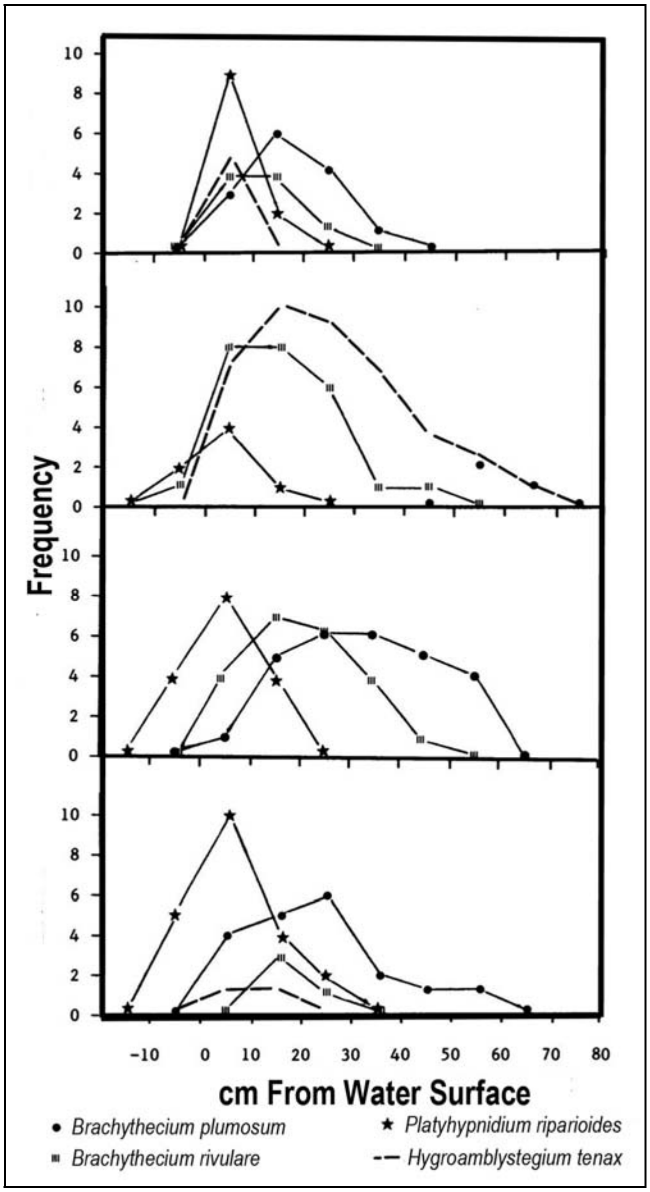

Figure 9. Distance of bryophytes from water surface at four locations in the White Mountains, New Hampshire, USA. From Slack & Glime 1985.

Figure 10. ***Brachythecium rivulare***, a species that tends to occur closer to the water than does ***B. plumosum***. Photo by Michael Lüth, with permission.

Figure 11. ***Brachythecium plumosum***, a species that tends to occur higher on rocks than does ***B. rivulare***. Photo by Michael Lüth, with permission.

Figure 12. ***Hygrohypnum ochraceum*** in water, exhibiting lack of leaf falcations. Photo by Andrew Simon, through Creative Commons.

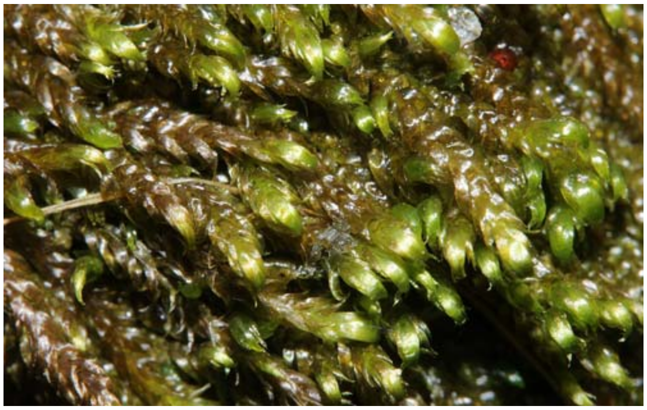

Figure 13. ***Hygrohypnum ochraceum***, showing the falcate leaves present when further from the water. Photo by Hermann Schachner, through Creative Commons.

Ceschin *et al*. (2012) determined that water velocity, water clarity, substrate size, and poor water quality were important determining factors at 99 stations in 18 streams in the Tiber River basin, Italy. Aquatic bryophytes preferred substrates with medium to large granulometry, fast-flowing, clear water with good oxygenation (mean 9.2 mg L^{-1}). They also preferred low nutrient levels of ammonia (mean 0.10 mg L^{-1}) and phosphates (mean 0.09 mg L^{-1}).

Stability and Stream Order

Bryophytes tend to inhabit stable substrates in higher flow velocities, whereas other **macrophytes** (generally aquatic plants large enough to be seen by the unaided eye) tend to inhabit less stable, finer substrates in environments with slower flow velocities (Gecheva *et al.* 2013; Manolaki & Papastergiadou 2013). Consequently, bryophytes tend to inhabit lower-order, higher-elevation stream reaches; other macrophytes (**tracheophytes**) tend to inhabit higher-order, lower elevation stream reaches. **Stream order** permits us to describe the tributary relationship of a stream or river. It is numbered from the initial tributary as 1, to the joint flow with another tributary as 2, and so forth. But there are several schemes in use (and not all use the numbering convention I describe), with two, the Shreve (1966) and Strahler (1957, 1964), being the most commonly used. In both of these, a 2 represents the merger of two 1's, but in the Shreve system the next number represents the sum of the two branches that merge (Figure 14), whereas in the Strahler system it requires two of the same number to increase the merged number (Figure 15) (Wikipedia 2018).

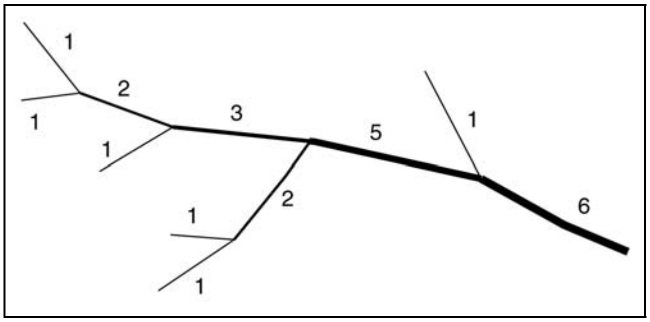

Figure 14. Shreve stream order. Drawing by Langläufer, through Creative Commons.

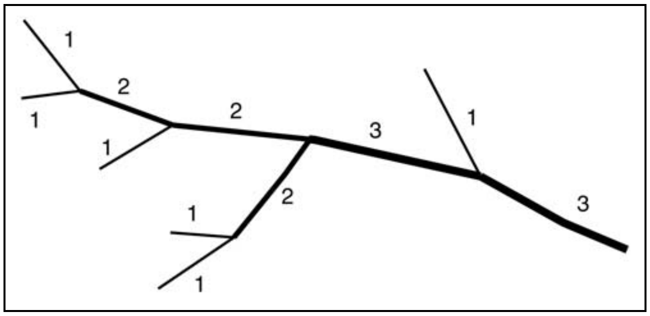

Figure 15. Strahler stream order. Drawing by Langläufer, through Creative Commons.

Substrate

Substrate Type

Substrate is important in fast-flowing water to give the bryophyte a place to attach. Silt and sand are too mobile and thus suitable only in slow flow, but then other plants can survive there as well, typically out-competing the slow-growing bryophytes. Tree roots and decorticated logs are suitable substrates for some species. Rocks are more stable, and are by far the dominant substrate for bryophytes in fast-flowing water. Suren (1996) demonstrated that streams with easily eroded rocks typically had no bryophytes.

I was surprised in my literature search to see that type of substrate, with the exception of acid vs alkaline, has received almost no attention by researchers studying stream bryophytes. The only experimental study I could find on relationship of attachment to rock types was my own. Most studies relate to alkaline vs acid, not to rock texture.

In their attachment study, Glime *et al.* (1979) tested attachment to four different rock types: basalt, sandstone, shale, and granite. All of these have rough (like fine sand paper) surfaces except the shale, which is very smooth. The mosses [***Fontinalis duriaei*** (Figure 16), ***Hygroamblystegium fluviatile*** (Figure 17) were both species of relatively rapid water, at least part of the time. After 15 weeks in artificial streams (both species) and in Cole's Creek near Houghton, Michigan, USA (only ***F. duriaei***), the species demonstrated attachment, but there were differences among rocks and between species.

Figure 16. ***Fontinalis duriaei***, a species of rapid water. Photo by Michael Lüth, with permission.

Figure 17. ***Hygroamblystegium fluviatile***, a species that of fast water that attached best to sandstone rock in an artificial stream. Photo by Michael Lüth, with permission.

Surprisingly, the basalt rock had the highest attachment in the artificial streams, but the lowest attachment in Cole's Creek where the mosses had been collected (Table 1) (Glime *et al.* 1979). Sandstone had the highest attachment for some species in Cole's Creek (***Fontinalis duriaei*** – Figure 16) and in the artificial stream (***Hygroamblystegium fluviatile*** – Figure 17). But this is only part of the picture. The bryophytes in this experiment were artificially held on the rocks with a nylon mesh, so dispersal and impingement were not part of the experiment. Only the ability to attach and the time required to do it were compared.

Table 1. Attachment percentage after 15 weeks. From Glime *et al.* 1979.

	Fontinalis duriaei		***Hygroamblystegium fluviatile***
	artificial stream	**Cole's**	
shale	17	58	
granite	42	20	
basalt	67	0	8
sandstone	75	80	75
felsite			25
gneiss			33

Although the nylon mesh created an advantage in the artificial streams, mosses and debris are often pinned on the upstream sides of rocks by the flowing water. The mosses can often stay there for weeks, giving them ample time to attach.

Steinman and Boston (1993) compared substrate preferences of bryophytes in Walker Branch, Tennessee, USA. These actually sorted out by size, with bedrock having the greatest cover, but most rock categories were preferred to wood (Figure 18). Sand was not colonized at all.

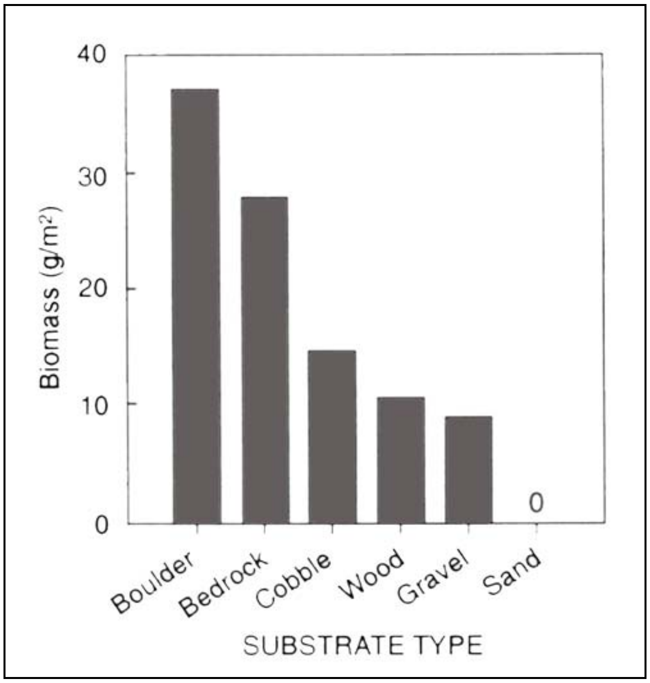

Figure 18. Substrate type preference by bryophytes in Walker Branch, Tennessee, USA. Modified from Steinman & Boston 1993.

Some aquatic bryophytes are able to live on both rock and wood surfaces. ***Cinclidotus fontinaloides*** (Figure 19) is typically a rock dweller, but in Burren, Co. Clare, Ireland, it occurs on the bases and trunks of ***Rhamnus*** trees (Figure 20), where it forms dense growth up to 2 m from the ground (Coker 1993). Likewise in southern Ireland, ***Porella pinnata*** (Figure 21-Figure 22, Figure 45) rarely grows submerged, but is able to grow on trees, shrubs, and stone walls, where it is often fertile (Figure 23) (Conard 1968). North of the 40th parallel ***Porella pinnata*** is mostly aquatic (Figure 24), but is rarely fertile. For example, Gilbert (1958) reported it from a stream in Iosco County, Michigan, USA. Nichols (1935, 1938) also reported it from the Huron Mountains in the Upper Peninsula of Michigan.

Figure 19. ***Cinclidotus fontinaloides***, a rock dweller that can also occur on *Rhamnus* tree bases. Photo by Hermann Schachner, through Creative Commons.

Figure 20. ***Rhamnus cathartica***; the genus ***Rhamnus*** can have ***Cinclidotus fontinaloides*** at its base. Photo by Ryan Hodnett, through Creative Commons.

Figure 21. ***Porella pinnata*** on ***Nyssa ogeche***, showing zonation in floodplain area. Photo by Christine Davis, with permission.

Figure 22. ***Porella pinnata*** on tree. Photo by Ken McFarland and Paul Davison, with permission.

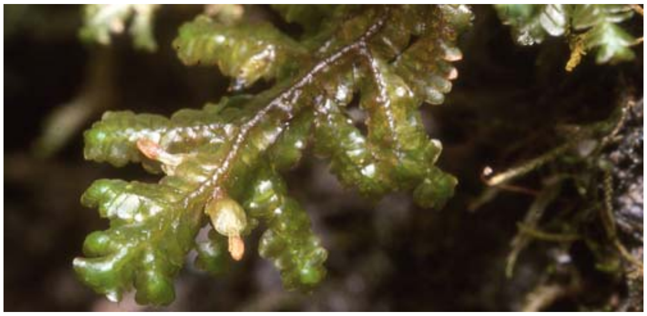

Figure 23. ***Porella pinnata*** with capsules, near Tallahassee, FL, USA. Photo by Janice Glime.

Figure 24. ***Porella pinnata*** habitat in water. Photo by Ken McFarland & Paul Davison, with permission.

Rock Size

Generalizations on the role of substrate size and stability in determining bryophyte communities do exist. The need for a stable substrate can account for the higher number of bryophyte taxa in streams with little flow variation and limited substrate movement (Ormerod *et al.* 1987; Nolte 1991; Bowden *et al.* 1999). For example, in their survey of 18 watercourses in the Tiber River basin of Italy, Ceschin *et al.* (2012) found that substrate size was an important parameter determining the presence of aquatic bryophytes.

The size of rock needed for bryophyte colonization is at least in part dependent on the rate of flow and frequency of flooding with high flow rates. For a bryophyte to become established, the rock must remain with the same side up to avoid burial. Hence, gravel and pebbles tend to have too much disturbance for the establishment of bryophytes. However, if these same rocks are only disturbed once per year, and bryophytes are deposited on them as waters recede, it is possible for the bryophyte plants to establish and provide the necessary stability. Steinman and Boston (1993) clearly showed a preference for larger, more stable rocks and bedrock (Figure 18), presumably because stable small rocks are seldom an option.

If disturbance is more frequent, larger rocks are necessary to accomplish bryophyte establishment (McAuliffe 1983; Slack & Glime 1985; Englund 1991; Suren 1991, 1996; Steinman & Boston 1993; Suren & Ormerod 1998; Suren & Duncan 1999; Bowden *et al.* 1999). One reason for this is that bryophytes are somewhat slow to attach new rhizoids to the rocks, a necessity for assuring themselves of remaining with that rock (Glime *et al.* 1979). At least for some species [*e.g.* ***Hygroamblystegium*** spp. (Figure 17, Figure 25), ***Fontinalis*** spp. (Figure 16)], this requires a minimum of about eight weeks (Glime *et al.* 1979; Englund 1991).

Figure 25. ***Hygroamblystegium tenax***, a species that requires about 8 weeks of contact before any attachment occurs. Photo by Hermann Schachner, through Creative Commons.

Slack and Glime (1985) found that rock size was an important parameter in determining bryophyte colonization in 10 New Hampshire, USA, streams, particularly for ***Hygrohypnum ochraceum*** (Figure 13) and several members of the **Brachytheciaceae** (Figure 3, Figure 10-Figure 11). Only ***Chiloscyphus polyanthos*** (probably ***C. rivularis***; Figure 26) was able to establish on small stones. Freeman-Tukey niche width for bryophytes based on rock size in these streams ranged from 0.20 to 0.97, indicating that some species such as ***Atrichum undulatum*** (Figure 27) are more sensitive, having a narrow niche width, whereas others such as ***Rhizomnium punctatum*** (Figure 28) have wide niche widths. But both of these species typically grow on wet, but not submersed substrates. For the truly submersed ***Fontinalis*** species, they ranged from 0.35 for ***F. antipyretica*** (Figure 7) to 0.73 for ***F. dalecarlica*** (Figure 29).

Figure 26. ***Chiloscyphus rivularis***, a leafy liverwort that is able to become established on small stones. Photo by Jan-Peter Frahm, with permission.

Figure 27. ***Atrichum undulatum***, a species with a narrow niche width for rock size. Photo by Michael Lüth, with permission.

Figure 28. ***Rhizomnium punctatum***, a species that dominates in streams with high stability and low conductivity. Photo by J. C. Schou, with permission.

Figure 29. ***Fontinalis dalecarlica*** habitat, Highlands, North Carolina, USA. This species becomes less abundant when flow is reduced. Photo by Janice Glime.

Based on their study of 33 Quebec streams, Cattaneo and Fortin (2000) determined that substratum size (>25 cm diameter – bucket size of Slack and Glime (1985) – accounted for 42% of the distribution variability of mosses within the streams and was the major factor in explaining among-stream bryophyte variation. But Suren and Ormerod (1998), while finding rock size to be important in New Zealand streams, found that rock size seemed unimportant in Nepal. Rather, stability was the most important parameter.

It appears, however, that rock size may in fact be a measure of stability (Downes *et al.* 2003). This has been demonstrated experimentally in geological studies (Chin 1998; Melo & Froehlich 2004). Chin indicated that it can require 5 to 100 years to restructure the stability of step pools in mountain streams. Downes *et al.* (1998) used 1200 marked rocks to determine effect of size on movement. They found that small rocks had the greatest movement and large ones the least. They also found that surface rocks left in place had less movement that surface rocks they had placed on the stream bed, suggesting that rocks in the stream may come to rest in positions that are not random, but rather locations where they experience less drag.

The niche width for rock size seems to be greatest in locations below -5 cm from the water surface (Figure 30) in mountain streams of the Canadian Rockies (Glime & Vitt 1987). Species in the range of 10-30 cm above the water surface have the most narrow niches. I would guess that this relates to suitable moisture gradient. Those under water all have the same moisture and are seldom out of the water. Furthermore, if the rock is large enough to be 30 cm above the water level, it is a large rock. The niche overlap also varies with ecology, and it is not surprising that the widespread taxa have the greatest niche overlap for rock size (Figure 31). The calciphilous emergent species have the least overlap.

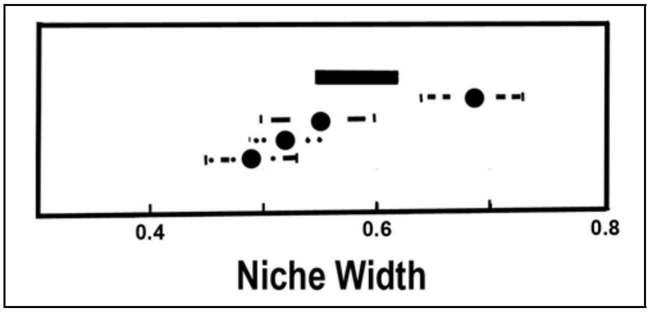

Figure 30. Niche width differences with substrate size as related to stream zone. ▬ overall mean; ● mean of zone range; -- all species in zone 1 (< -5 cm); – – species occurring in zone 2, but not zone 1 (-5 to 5 cm); • • species in zone 2 or 3, but not zone 1; • - • - species only in zone 3 (10-30 cm). Redrawn from Glime & Vitt 1987.

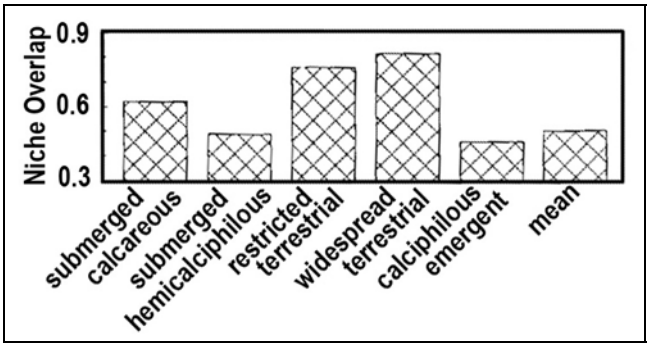

Figure 31. Niche overlap based on rock size among five ecological groupings. Redrawn from Glime & Vitt 1987.

Downes *et al*. (2003) found a positive correlation between bryophyte cover and rock size. A similar relationship exists on rocks of Costa Rican tropical rainforest streams (Martinez 2005). This relationship of species number to size of area compares well with the theory of island biogeography, whereby larger islands tend to have more species (MacArthur & Wilson 1967).

Those studying the effect of substrate size on macroinvertebrates in streams seem to have done the most of the experimental work on the effect of substrate size on the biological component of streams. Using fine gravel (~1 cm diameter), pebbles (~2.5 cm diameter), and large cobbles (~8.5 cm), Reice (1980) demonstrated that rock size was a "prime determinant" of the structure of macroinvertebrate communities. Bond and Downes (2000) found that the densities of **Hydropsychidae** (net-spinning caddisflies; Figure 32) related to rock size. The density of these caddisflies was an order of magnitude higher on large rocks compared to small ones. However, following a flood those densities were all similar. Fortunately, the caddisfly densities returned to pre-flood levels in four weeks.

Figure 32. ***Cheumatopsyche*** (**Hydropsychidae**) nets, with one large and a number of smaller nets. Photo by Justin, through Creative Commons.

How long does it require for bryophytes to recolonize? It is likely that in many cases the stolons and rhizoids and perhaps even stem bases will remain. These can survive as living tissue, and because of the ability of bryophyte tissue to grow from such small fragments, such species will return rather quickly. But it will still take years to reach the clump size and depth that was present before the disturbance.

Carrigan (2008) examined the effect of rock size on bryophyte frequency in Victorian rainforest streams of Australia. Pebbles (<10 cm) proved to be inhospitable habitats, due to their instability. Only two species occurred there: ***Fissidens serratus*** and ***Lophocolea semiteres*** (Figure 33) in the Otway Range and these were each found only once, none in the Central Highlands, and ***Fissidens taylorii*** (Figure 34) in East Gippsland. Small rocks (10-30 cm) likewise had species that occurred only once in more than half the cases. They were dominated by the thallose liverwort ***Aneura alterniloba*** (Figure 35) in the Otway Ranges and the Central Highlands and the **dendroid** (having tree-like shape) moss ***Hypnodendron spininervium*** (Figure 36) in the Otway Ranges. In Gippsland, small rocks were dominated by ***Thamnobryum pumilum*** (Figure 37) and ***Fissidens leptocladus*** (Figure 38). Medium rocks (31-60 cm) were likewise dominated by ***Hypnodendron spininervium***, and again, more than half the species occurred only once in the Otway Ranges. In East Gippsland, medium-sized rocks were more consistent, being dominated by ***Fissidens leptocladus*** and ***Thuidiopsis furfurosa*** (Figure 39), with ***Wijkia extenuata*** (Figure 40), ***Hypnodendron vitiense*** (Figure 41), and ***Chiloscyphus semiteres*** (Figure 42) also highly frequent. The extra large rocks (>91 cm), *i.e.* boulders, had low richness, with only five total species in the Otway Region. In the Central Highlands, it was ***Hypnodendron vitiense*** and ***Achrophyllum dentatum*** (Figure 43) that dominated the large rocks (61-90 cm) and boulders. In East Gippsland, no species dominated on large rocks, with the highest frequency being 2.

Figure 33. ***Lophocolea semiteres***, a species that is able to inhabit pebbles in Victorian rainforest streams. Photo by Brian Eversham, with permission.

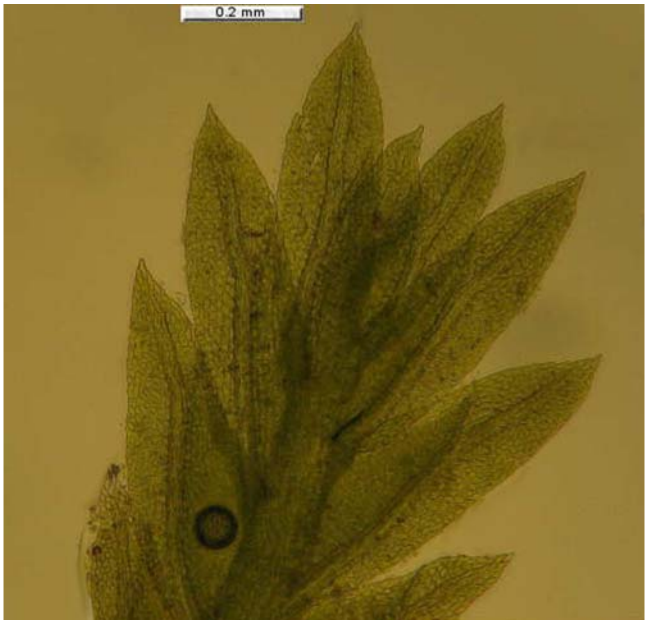

Figure 34. ***Fissidens taylorii***, a species found on small pebbles in East Gippsland of the Victorian Rainforest. Photo by Tom Thekathyil, with permission.

Figure 35. ***Aneura alterniloba***, a thallose liverwort that dominates on small rocks in the Otway Ranges and the Central Highlands of the Victorian rainforest. Photo by Tom Thekathyil, with permission.

Figure 36. ***Hypnodendron spininervium***, a dominant moss on the small rocks in the Otway Ranges in the Victorian rainforest. Photo by Colin Meurk, through Creative Commons.

Figure 37. ***Thamnobryum pumilum***, a dominant moss on small rocks in Gippsland in the Victorian rainforest. Photo by Niels Klazenga, with permission.

Figure 38. ***Fissidens leptocladus***, a dominant moss on small rocks in Gippsland in the Victorian rainforest. Photo by Peter de Lange, through Creative Commons.

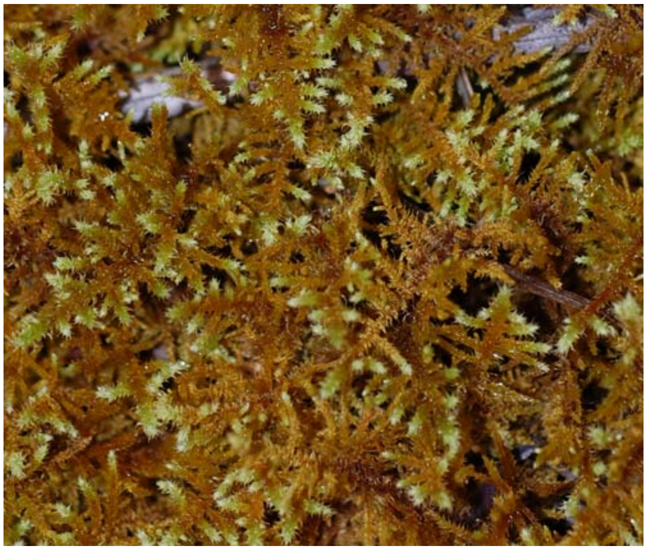

Figure 39. ***Thuidiopsis furfurosa***, a species common on medium-sized rocks in East Gippsland in the Victorian rainforest streams. Photo by David Tng, with permission.

Figure 40. ***Wijkia extenuata***, a frequent species on medium-sized rocks in East Gippsland in the Victorian rainforest streams. Photo by Budawang Coast, through Creative Commons.

Figure 41. ***Hypnodendron vitiense***, a frequent species on medium-sized rocks in East Gippsland in the Victorian rainforest streams. Photo by Marshall Simon, through Creative Commons.

Figure 42. ***Chiloscyphus semiteres***, a frequent species on medium-sized rocks in East Gippsland in the Victorian rainforest streams. Photo by John Steel, through Creative Commons.

Figure 43. ***Achrophyllum dentatum***, a species that dominates large rocks in the Central Highlands of the Victorian rainforest. Photo by Budawang Coast, through Creative Commons.

In seeming contradiction to many of these studies, Grinberga (2010) found in middle-sized streams in Latvia, both fast and slow streams with gravel substrates supported mostly bryophytes, with only sparse **helophyte** (sun-loving plant) stands. The narrow, fast-flowing streams limited aquatic vegetation according to velocity and shading from riverbank vegetation.

Substrate Stability

Heywood (1362) seems to be the origin of the statement "The rolling stone gathereth no moss" (cited in Stevenson 1947). Madsen *et al.* (1993) notes that bryophytes and other stream macrophytes are attached basally, preventing movement in the flowing water. But this means that when their rocks are overturned, they may be locked under the rocks.

Using this theme, Suren and Duncan (1999) investigated the stability of the substrate on bryophyte richness and community composition. It is interesting that they found richness to be low in both stable and highly unstable stream areas. They considered that competition might account for the low bryophyte diversity in stable sites, but attributed the low richness at unstable sites to the inability of the bryophytes to grow there. The abundance of these bryophytes was positively associated with stable types of substrate. As seen above, a number of researchers have demonstrated the importance of substrate stability on bryophyte distribution in streams by recording the rock sizes on which they found bryophytes.

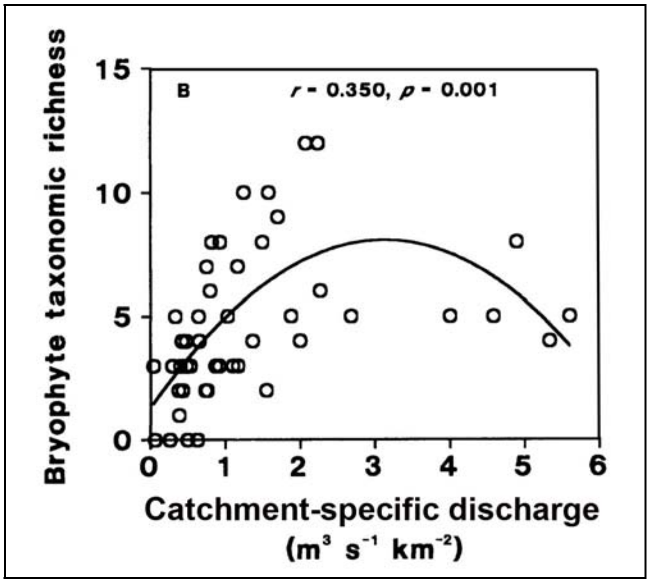

Figure 44. Relationship between bryophyte taxonomic richness along a 40-m transect at 48 study sites on South Island, New Zealand, and the catchment specific discharge ($SPECQ_{BF}$). Modified from Suren & Duncan 1999.

Englund (1991) showed the effect of rock size and stability in two North Swedish woodland streams. Duncan *et al.* (1999) showed that both biomass and taxon richness declined in response to increased instability. On the other hand, the bryophyte cover had a highly significant correlation with bankfull discharge. They were unable to find a significant relationship between cover and the **Newbury Instability Index** (indicates sensitivity of substrate particle to tractive force τ by dividing τ by median substrate size) (see Newbury 1984; Cobb & Flannagan 1990).

Lang and Murphy (2012) assessed the environmental variables influencing bryophyte communities in headwater streams at high elevations in Scotland. They found that streambed stability and water chemistry were the primary drivers of bryophyte communities. These were possible due to adaptations in bryophyte morphology and life cycle strategy.

Muotka and Virtanen (1995) related bryophytes to substrate heterogeneity. They used movement of the streambed in rivers to indicate disturbance frequency and water level fluctuation in small streams. In these streams potentially fast-colonizer bryophytes dominate at the disturbed end of a gradient, providing a community with low stature. At the stable end of the gradient, large perennial bryophyte species dominate. They found that ***Fontinalis*** spp. (Figure 16) and ***Platyhypnidium riparioides*** (Figure 8) dominated the most stable substrata in the spring.

As in many other studies noted here (McAuliffe 1983; Englund 1991; Steinman & Boston 1993; Muotka & Virtanen 1995), Vuori *et al*. (1999) found that in the Tolvajärvi region, Russian Karelia, abundance and species diversity of mosses decreases coincidentally with greater substrate mobility. Substrate heterogeneity increases the bryophyte diversity. McAuliffe (1983) noted that within the physical limitations of streams, organisms may be further limited by current velocities, substrate types, and disturbance regime. These factors limit both the bryophytes and their invertebrate inhabitants.

Steinman and Boston (1993) suggested that the abundance of bryophytes in Walker Branch, a woodland stream in Tennessee, USA, might be possible because of the stable substrata of bedrock and boulders in this habitat of high velocity. The most abundant of these bryophytes were the leafy liverwort ***Porella pinnata*** (Figure 45) and the mosses ***Brachythecium** cf. **campestre*** (Figure 46) and ***Amblystegium*** (***Hygroamblystegium***? – Figure 17, Figure 25) sp.

Figure 45. ***Porella pinnata***, a species of stable substrata in the southeastern USA. Photo by Alan Cressler, with permission.

Figure 46. ***Brachythecium campestre*** with capsules, a species of stable substrata in the southeastern USA. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Suren (1993) sampled bryophytes in 103 first-order alpine streams in Arthur's Pass, New Zealand. He found that only half the streams had bryophytes, and that bryophyte distributions were strongly determined by streambed stability. Shading seemed to have little influence. Suren (1996) later sampled bryophytes in 118 New Zealand South Island streams, with similar results. Of these, 95 had bryophytes. Mean cover, however, was only 17%, with a maximum cover of 86%. The streams that lacked bryophytes were typically in developed catchments of pastures and pine woodlands and had easily eroded rocks. Their streambed stability was low, with a lack of bedrock or boulders.

Suren and Ormerod (1998) examined the effect of a number of parameters on the distribution of bryophytes in 108 Himalayan streams. Both community composition and cover exhibited "highly significant" correlation with altitude, streambed stability, and alkalinity, with further influence from riparian land use. The cover was greatest in streams with high stability. Nevertheless, there was a weak but significant increase in richness at high altitudes and moderate stability. These streams were dominated by ***Rhynchostegium*** spp. (***Platyhypnidium*?** – Figure 8), ***Fissidens grandifrons*** (Figure 47), and ***Hygroamblystegium*** spp. (Figure 17, Figure 25). By contrast, the unstable streams at low altitudes had the lowest bryophyte species richness and cover. There was no taxon that was consistently the most abundant in these conditions. Suren and Ormerod considered that the importance of stability in the Himalayan streams may be related to the strong monsoonal floods and their effect of increasing stream bed movement. They considered that this habitat requires a large plant size and that vegetative reproduction may facilitate the widespread distribution of some of the species, even on the unstable substrata. In these Himalayan streams, the greatest cover occurred in streams of low to middle altitudes where the slopes were more than 15º, there was high stability, and conductivity was low (<60 µS cm^{-1}).

Figure 47. ***Fissidens grandifrons***, a dominant stream bryophyte. Photo by Scot Loring, through Creative Commons.

Duncan *et al.* (1999) assessed the streambed stability of steep, bouldery streams in New Zealand. Like other researchers, they found that both biomass and species richness decreased with the decline in stability of the substrate. In fact, they found that bryophytes were better indicators of stream stability than some of the standard indices. There was a weak correlation with the **Pfankuch score** (rating of capacity of a reach to resist detachment of bed and bank materials and to recover from their changes; Pfankuch 1975) and bryophyte cover ($p=0.023$), but no significant relationship between cover and the Instability Index. Rather, they presented a new index P(BF) what was highly significantly correlated ($p<0.001$) with bryophyte cover.

Downes *et al.* (2003) marked randomly selected rocks and recorded rates at which they disappeared from their original location. Like other researchers mentioned earlier, they found a strong positive association between bryophyte cover and rock size, indicating that substrate stability drives bryophyte abundance. In the unregulated streams, the highest cover occurred on emergent rocks, again supporting the importance of rock size and stability. Nevertheless, regulated streams did not have lower disturbance frequencies but the percent cover of bryophytes were lower, resulting from reduced cover on large rocks. Small (<10 cm) and medium (10–20 cm) rocks were not affected.

Erosion

Erosion of stream channels is a normal phenomenon. This occurs naturally, but the problem can be exacerbated by livestock. Myers and Swanson (1992) assessed the role of livestock in northern Nevada, USA, and found that ungulate bank damage varied among the stream types and different parts of their cross-sections. Vegetation is more important for some stream types than others. Sand and gravel banks are the most sensitive to livestock grazing. Cobb *et al.* (1992) found that substrate stability was important for stream insects. Bottom-dwelling insect densities decrease as discharge increases and particle movement increases. Substrate stability accounts for differences in insect density, with decreases up to 94% in areas with the most unstable substrata. These studies support the conclusion of Webster *et al.* (1983) that stream stability is a fundamental property. Such studies as these indicate the importance of considering stream stability when assessing the impact of logging and other disturbances. It should be no different for assessing bryophyte communities.

Stability, Bryophytes, and Macroinvertebrates

Bond and Downes (2000) examined the flow-related disturbances in streams on macroinvertebrate population densities. Using members of the caddisfly family **Hydropsychidae** (Figure 32), they found that flow events on large and small rocks (in this case, bricks) resulted in reduction of numbers, with the more abundant fauna of large rocks being reduced in numbers to the same as that remaining on smaller rocks. Hence, for these insects, it is not the stability of the substrate itself, but the force of flow on the insects that prevents these stable rocks from providing a refugium. However, both small and large bricks moved during the periods of high flow. Nevertheless, movements differed between the two sizes. When bryophytes grow on real rocks, the roundness of the rock can result in a tumbling motion, placing young plants and protonemata on the new bottom, under the rock. Once the bryophytes become established, particularly on somewhat larger rocks, they may interfere with that tumbling and help to hold the rock in place.

Englund (1991) likewise demonstrated that disturbance affected the structure of the macroinvertebrate community, but his study implicated loss of mosses as the reason. He overturned moss-covered rocks to simulate the effect of a strong flow, noting that 16.7% of the moss-covered rocks had been overturned naturally in the past few years. They also noted that mosses were rare on small stones except for those embedded in the substrate. But on stones >12 cm in diameter, the moss abundance and embedment had no effect on the moss distribution. When the rocks were overturned by the researchers, it reduced the ash-free dry weight and species diversity as well as total abundance of invertebrates. On the other hand, 3 of the 16 macroinvertebrates increased in density, but their peak densities were on the moss-covered undersides of overturned rocks. For all other macroinvertebrates, the highest densities were among the mosses of control rocks. Recovery was still weak for both mosses and macroinvertebrates after 14 months.

Not surprisingly, mosses were rare on small stones except for those embedded in the substrate (Englund 1991). Stones larger that 12 cm supported abundant moss growths, and embedment in the substrate made no difference because these rocks were generally stable. When Englund experimented with overturning rocks, the ash-free dry weight of mosses and bryophyte diversity decreased on those rocks that he overturned, whereas some of the invertebrate taxa increased, particularly among the mosses on the under sides of rocks. Many invertebrates apparently migrated to the control stones, where peak densities occurred on the upper side. Even after 14 months, the turned rocks had only weak recovery of both mosses and invertebrates. Shelley (1999) likewise concluded that streambed stability was an important factor in the spatial distribution of mosses in Massachusetts, USA. Thus, stable rocks can minimize the effects of disturbance.

What permits plants, in this case bryophytes, to survive the hydraulic effect of streams? Klinger (1996) found that resources (light, nutrients, temperature) are the predominant forces governing biomass gain. Biggs and Saltveit (1996; Klinger 1996) reported that it is hydraulic factors that cause stream biomass loss. They suggested that these factors determine the dominance of **periphyton** (associated algae and bacteria on rocks and plants), bryophytes, or other macrophytes (Figure 48) in periods greater than a year. For less than a year, flow velocity still dominates accrual of periphyton biomass. At high velocities, the accumulation of organic matter is curtailed. But bryophytes are often restricted to locations with high velocity on stable substrata, whereas other plants and periphyton are negatively correlated with velocity of flow (Biggs & Saltveit 1996; Klinger 1996; Baker *et al*. 1996).

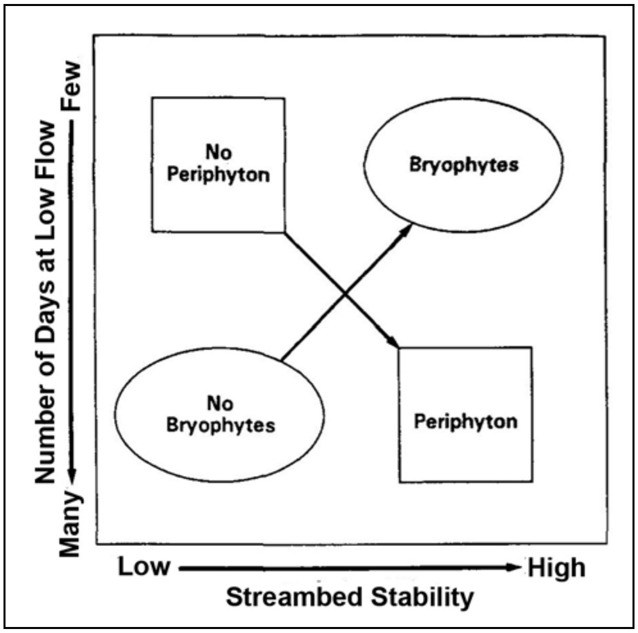

Figure 48. Conceptual model of the relationship between bryophytes and periphyton under conditions of flow and streambed stability. Modified from Suren 1996.

Step Pools

Step pools (Figure 49) tend to be stable bedforms, but stability depends on size, scale, and perspective. Chin (1998) reported that even these tend to be restructured within 5 to 100 years. Particle size determines the mobility. The steps dissipate stream energy and regulate the channel hydraulics, but stability decreases at larger scales where the step pools are dependent variables that respond to discharge and its sediment load. Thus at these larger scales they become one of channel adjustment.

Disturbance Factors

Lake (2000) warned that it is too easy to confuse the effects of a disturbance with the effects of the response by the biota. To fully understand disturbance effects, we need to understand these differences. Disturbances may occur as a pulse, a press, or a ramp. The consequent response may likewise be a pulse, a press, or a ramp.

Floods and droughts are the major forms of natural disturbance in streams and rivers (Lake 2000). Floods accentuate downstream and streamside connections. Droughts create patchiness. Levels of diversity tend to be negatively correlated with flooding levels at the regional scale, although they recover rather quickly at the local scale of individual patches. In fact, flooding may be one of the central factors regulating species diversity in streams and rivers. Understanding these factors is essential to understanding streams and rivers for purposes of management and expected results of climate change.

Figure 49. Tolliver Run, Swallow Falls Park, MD, showing step falls and pools. Photo by Janice Glime

Lack of substrate stability is one type of disturbance, sometimes placing the bryophytes under the rocks where they can't get the light needed to grow. But a number of disturbances are common to stream environments. Muotka and Virtanen (1995) considered movement of streambed as a measure of disturbance in rivers. In small streams, water level fluctuation is used as an indicator of the frequency of disturbance. They found that a change in species composition accompanied the disturbance gradient. As already noted, species with low stature and fast colonization rates dominated the disturbance end of the gradient, with large perennial species at the stable end. Just above the water line there was an abrupt increase in the species richness, with species of broad tolerance for both water and drying. Low and high standing crops were characterized by low species richness, whereas intermediate standing crops had the highest species richness. The most stable habitats were frequently dominated by single species of ***Fontinalis*** (Figure 16) or ***Platyhypnidium riparioides*** (Figure 8). At sites with low biomass, the species composition was more variable. When the biomass is intermediate, small-scale disturbances result in a more varied community. Muotka and Virtanen considered disturbance to be the filtering factor for eliminating traits that are unsuitable for a given stream environment.

Bryophytes contribute to the stability of the substrate, but they typically decline as a result of disturbance (Englund 1991; Suren 1991; Steinman & Boston 1993). In New Zealand Suren (1996) found that liverworts were more sensitive than mosses to modification of the catchment area and thus occurred mostly in undisturbed forests. But in Nepal, it is not apparent that disturbance to the catchment area has much effect on the stream bryophyte composition (Suren & Ormerod 1998).

Muotka and Virtanen (1995) quantified disturbance as movement of the streambed in rivers, but as water level fluctuation in small streams. They found that stable portions of streams and rivers were characterized by large, perennial bryophyte species, whereas the disturbance sites were characterized by low-statured, potentially fast colonizers. Perennial species such as ***Fontinalis*** spp. (Figure 16) and ***Platyhypnidium riparioides*** (Figure 8) are able to monopolize space, permitting them to dominate the most stable habitats. In sites with low biomass, the species composition is more variable, but the growth form is one of low stature with a high allocation to spore production. Where the biomass is intermediate, the bryophyte community exhibits ever greater variation in response to small-scale disturbances. Hence disturbance seems to be an important, if not the most important, factor in filtering which species are able to live there.

Suren and Ormerod (1998) likewise found that streambed stability was an important factor in bryophyte distribution. Richness had a moderate increase with moderate stability and the communities were dominated by ***Eurhynchium praelongum*** (Figure 50), ***Platyhypnidium*** spp. (Figure 8), ***Fissidens grandifrons*** (Figure 47), and ***Hygroamblystegium*** spp. (Figure 17, Figure 25). Unstable streams had the lowest richness and cover and no taxon was consistently abundant. In stream reaches with high stability (and low conductivity), communities were dominated by two species of ***Isopterygium*** (Figure 51), ***Philonotis*** spp. (Figure 52), ***Rhizomnium punctatum*** (Figure 28), and the leafy liverwort family **Lejeuneaceae** (Figure 53-Figure 54).

Figure 50. ***Eurhynchium praelongum***, a species that increases with an increase to moderate stability. Photo by Michael Lüth, with permission.

Figure 51. ***Isopterygium*** sp., a species that dominates in streams with high stability and low conductivity. Photo by Biopix, through Creative Commons.

Figure 52. ***Philonotis pyriformis***, a New Zealand species and probably one requiring streams with good stability. Photo by Mary Joyce, through Creative Commons.

Figure 53. ***Lejeunea lamacerina***, a species that dominates in streams with high stability and low conductivity. Photo by Jan-Peter Frahm, with permission.

Figure 54. ***Lejeunea lamacerina*** habitat. Photo by Michael Lüth, with permission.

Flow

Many researchers have concluded that flow rates are a strong filter for determining which bryophyte species occur (Muotka & Virtanen 1995). It seems that in most streams, a steady flow, even a fast flow, is advantageous to bryophytes (McAuliffe 1983; Englund 1991; Steinman & Boston 1993). It helps to keep periphyton growth to a minimum (Finlay & Bowden 1994), thus permitting maximum access of the bryophyte leaves to light, CO_2, and nutrients. And it seems that these fast-growing algal periphyton can at times cover the substrate and compete with the mosses (Figure 55; Suren 1996), but that scouring caused by fast flow permits the more firmly anchored and stronger bryophytes to survive and out-compete them. Nevertheless, even bryophytes can be excluded in water that is too fast, especially if it carries abrasives. Vegetation was absent from Canadian rivers when the mean water velocity exceeded 1 m sec^{-1} (Chambers *et al.* 1991). In New Zealand, Henriques (1987) found no vegetation in 22 streams with a mean velocity greater than 0.9 m sec^{-1}.

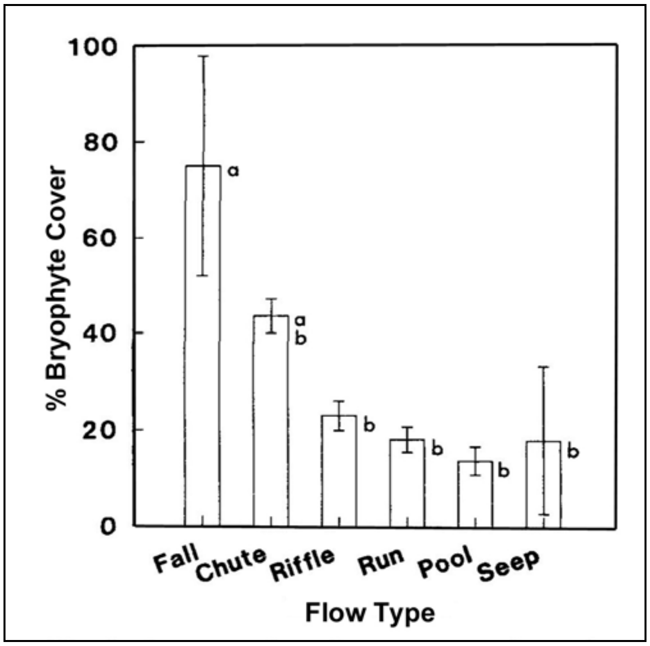

Figure 55. Percentage bryophyte cover relative to flow types in 118 New Zealand streams. Letters denote which conditions have similar bryophyte species groupings. Those with only different letters are significantly different (Tukey's test, $p<0.05$). Vertical lines represent 2 standard errors. Modified from Suren 1996.

Bryophytes seem to prefer sites with water movement and turbulence. In an Arctic tundra stream, ***Fontinalis neomexicana*** (Figure 56) and species of ***Hygrohypnum*** (Figure 13) occur in abundance in riffles (Finlay & Bowden 1994). When P was abundant, there was no growth difference for ***Hygrohypnum*** species in riffles vs pools. Periphyton mass, on the other hand, was 4-4.5 times as great on artificial mosses in slow-flowing pools compared to that in fast-flowing riffles. This resulted in epiphyte chlorophyll content reaching 4X as great a level on ***Hygrohypnum*** growing in pools compared to those in riffles. Finlay and Bowden suggested that the greater periphyton biomass in pools could result from a greater detrital deposition and by reduced grazing by invertebrates.

Figure 56. ***Fontinalis neomexicana***, an abundant species in riffles in the Arctic. Photo by Faerthen, through Creative Commons.

Similar to the findings of Suren (1996) in New Zealand, Baker *et al.* (1996) found that stability over periods greater than a year was an important factor in determining if the stream was dominated by periphyton, bryophytes, or macrophytes in northeastern Iowa, USA, streams (Figure 48). Contrasting with periphyton and macrophytes, bryophytes were frequently restricted to areas that had high velocity but stable substrata.

Martínez-Abaigar *et al.* (2002a) found that species richness, cover, and Shannon's diversity all had a negative correlation with the no-flow (dryness) period in irrigation channels in the River Iregua basin, northern Spain. On the other hand, they had a positive correlation with water flow and velocity. Higher water availability was important for the mosses ***Cratoneuron filicinum*** (Figure 57) and ***Platyhypnidium riparioides*** (Figure 8). ***Leptodictyum riparium*** (Figure 58), on the other hand, dominated where the current was slower and the water was rich in mineral nutrients (hard water).

Figure 57. ***Cratoneuron filicinum***, a species that requires higher water availability. Photo by David T. Holyoak, with permission.

Figure 58. ***Leptodictyum riparium***, a species of slow flow and higher nutrients. Photo by Scott Zona, through Creative Commons.

Steinman and Boston (1993) found that bryophyte abundance in Walker Branch, Tennessee, USA, peaked in late summer, then was reduced by a severe winter storm. Bryophyte abundance, mostly the leafy liverwort ***Porella pinnata*** (Figure 45), was positively associated with rapid velocity such as bedrock steps and riffles. This liverwort in these areas had greater area-specific rates of photosynthesis and phosphorus uptake than did the periphyton.

While Biggs and Saltveit (1996) considered light, nutrients, and temperature to be the main governing factors for biomass gain, they found hydraulic factors to govern the processes of biomass loss. For periods over one year, the hydraulic stability is the determining factor for dominance by periphyton, bryophytes, or aquatic tracheophytes. For less than a year, hydraulic stability governs periphyton biomass. Both periphyton and tracheophytes benefit from low velocities, although growth rate and organic matter accumulation increase at moderate velocities. On the other hand, high velocities retard periphyton colonization and organic matter accumulation, creating conditions that instead favor bryophytes if the substrate is stable.

Englund *et al.* (1997) used 52 rapids in regulated and unregulated rivers of northern Sweden to assess the impact of flow on bryophyte species richness and abundance. Species richness was 22% lower at sites with reduced flow and 26% lower at sites with regulated but unreduced flow. However, the overall abundance of bryophytes was not significantly affected. Reduced flow resulted in a reduction in the abundance of ***Fontinalis antipyretica*** (Figure 7) and ***F. dalecarlica*** (Figure 29). ***Blindia acuta*** (Figure 59) and ***Schistidium agassizii*** (Figure 60) had a greater abundance at sites that had regulated, but not reduced, flow.

Figure 59. ***Blindia acuta*** with capsules, a species that became less abundant when flow was reduced. Photo by Hermann Schachner, through Creative Commons.

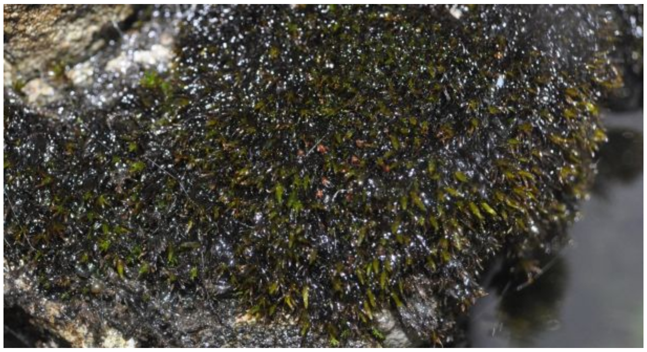

Figure 60. ***Schistidium agassizii***, a species that became less abundant when flow was reduced. Photo by Andrew Hodgson, with permission.

Regulated rivers have given us insights into the flow effects on bryophytes. Sometimes flushing flows are used to scour sediments and macrophytes to clear the river or stream, as practiced in some places in Norway (Rorslett & Johansen 1996). They found that sharply peaking flow is the most efficient method to control the excessive macrophyte growth – only the initial surge has much effect in scouring. When flushing mosses, there is a strong linear relationship to significant flow.

Holmes and Whitton (1981a) developed a standard method for describing the plant communities in fast-flowing water. Using permanent plots, they were able to assess the bryophyte cover at six sites in the River Tees. At the site below the Cow Green reservoir, where flow was regulated, bryophytes exhibited greater cover throughout the year than at other locations.

Flow rate can affect net photosynthesis. In tracheophytes, the net photosynthesis declined 34-61% as the flow velocity increased from 1 to 8.6 cm s^{-1} (Madsen *et al*. 1993). At the same time, dark respiration increased 2.4-fold over that flow range. But the moss ***Fontinalis antipyretica*** (Figure 7) was least susceptible to flow. It, like two of the tracheophyte species for which net photosynthesis was unaffected by flow, is unable to use dissolved bicarbonates as a carbon source in photosynthesis. But how does this affect the photosynthetic rate as a response to flow? We know that flow can affect growth rate, which implies an effect on photosynthetic rate, but I am unaware of any experiments directly testing effect on photosynthesis.

Conflicting effects of flow rate, based on changes in flow, suggest that the important factor may be the conditions of flow as the species grows. Tissue development is influenced by flow rate, so it seems logical that success when the flow is changed depends on the tissues built before the flow change. Reduction in flow can result in siltation that impedes photosynthesis by blocking light and encourages the growth of algae that further block the light and "steal" the CO_2.

Glime (1987a) experimented with flowing water vs pool conditions on six North American species of ***Fontinalis***, using artificial streams. In most cases, the growth was much greater in flowing water than in the nearly still water of the pool conditions (Figure 62). It is not surprising that ***F. gigantea*** (Figure 61) grew about equally well in both because its natural habitat is primarily in quiet water. Its large, folded leaves are subject to considerable damage from abrasion in rapid water. ***Fontinalis hypnoides*** (Figure 63) likewise exhibited nearly identical growth curves. This smaller species tends to occur in more gently flowing water than some of the other species. But why does flow make a difference in growth rate? I can only speculate that the greater flow brings greater renewal of nutrients and CO_2, and that it also helps to remove algae and detritus that collect on the moss. This study also indicated that the populations of ***F. novae-angliae*** (Figure 64) from New York and New Hampshire in northeastern USA behaved differently from the same species in Michigan.

Figure 61. ***Fontinalis gigantea***, a species that grew about equally well in flowing water and pool conditions in experimental streams. Photo by Paul Wilson, with permission.

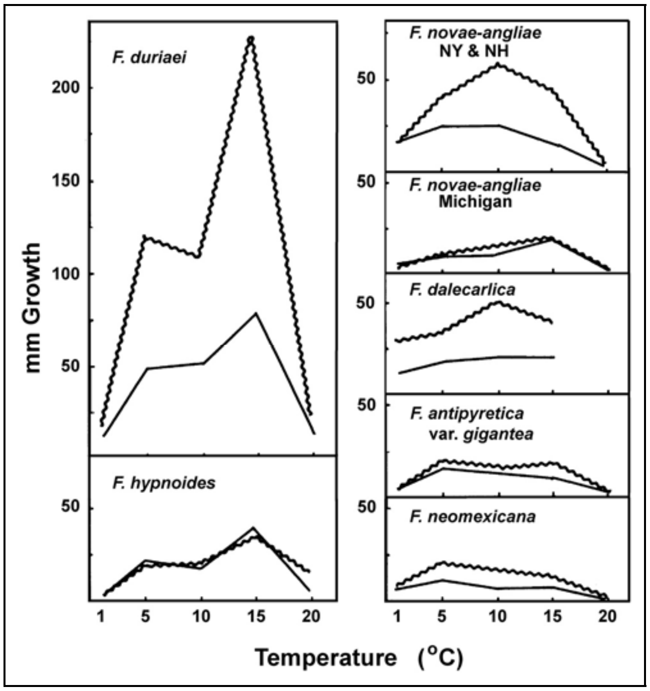

Figure 62. Comparison of growth of six species of ***Fontinalis*** grown at five temperatures in artificial streams under flowing water and pool conditions. Modified from Glime 1987a.

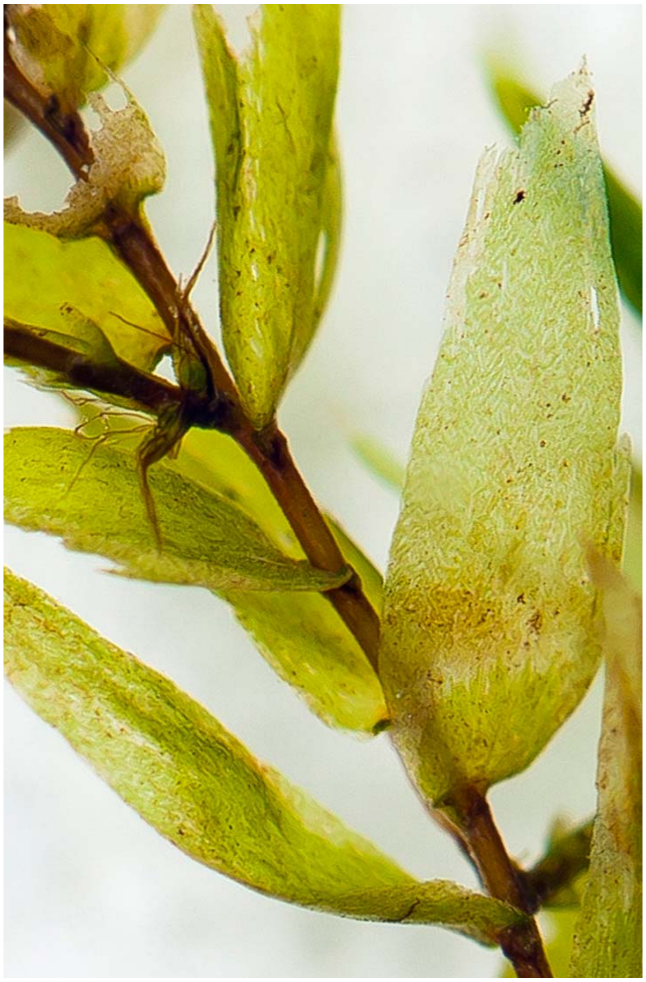

Figure 63. ***Fontinalis hypnoides***, a species of moderate flow. Photo by John Game, with permission.

Figure 64. ***Fontinalis novae-angliae*** capsules, a species with different growth rates from two widely separated geographic locations. Photo by Janice Glime.

Chambers *et al*. (1991) found that current velocity had a significant effect on both biomass and shoot density of the macrophytes in two slow-flowing Canadian rivers. Tracheophytes were greatly reduced by increasing flow rates.

Englund *et al*. (1997) found 22% lower species richness at sites with reduced flow and 26% lower at sites that were regulated but did not have reduced flow. However, the overall abundance was not significantly different from that predicted. On the other hand, abundance of ***Fontinalis dalecarlica*** (Figure 29) and ***F. antipyretica*** (Figure 7) was lower than predicted when the flow was reduced. Under regulated but unreduced flow, the abundance of ***Blindia acuta*** (Figure 59) and ***Schistidium agassizii*** (Figure 60) was higher than predicted.

Some mosses were able to colonize beds in the channelized and short-term regulated part of the Perhonjoki River, western Finland (Aronsuu *et al.* 1999). However, species of ***Fontinalis*** (Figure 7-Figure 29) were primarily restricted to sites above the power plant where there was little variation in flow. However, plants transplanted to constant flow did not grow, whereas those in the short-term regulated flow site survived winter and grew well during summer. At the controlled flow site, 10 of 30 substrates were lost during the winter, with more (67%) exhibiting severe damage in the mid-channel and 40% near the bank. ***Hygrohypnum*** (Figure 13) species attached to substrates during the summer.

Baker *et al*. (1996) examined the hydraulic role of stream macrophytes. Over periods of less than a year, the hydraulic stability controls the periphyton biomass. They, along with non-bryophyte macrophytes, colonize readily at low velocities, but moderate velocities increased accumulation of organic matter and growth rate. At high velocities, their colonization is retarded and less organic matter accrues. By contrast, the bryophytes are often restricted to areas with high velocity and stable substrates.

Dawson (1987) placed greater importance on flow, contending that it was the single physical factor dominating plant form. It thus controls the vegetation at high velocities. In lesser flows, vegetation may be forced to grow along the stream margins. Low flow areas, on the other hand, can develop plant communities that are similar to those of ponds and lakes. The species present are restricted by their availability and their ability to colonize.

Heino *et al*. (2015) provided somewhat contrasting results in their study of streams in Iijoki and Koutajoki basins, Finland. They found that bryophyte communities correlated with different chemical and physical parameters in different drainage basins. They furthermore found that different organism groups had different constraining factors in these environments. For bryophytes, stream width and velocity were most important factors in the Iijoki basin, but total phosphorus and conductivity were most important in the Koutajoki basin. These two basins had 21 and 40 species of bryophytes, respectively.

Desey (1981) also reported the importance of flow in determination of the community. Englund and Malmqvist (1996) likewise examined flow regulation on bryophytes in northern rivers in Sweden. Devantery (1987) assessed 24 variables and their effect on the moss ***Platyhypnidium riparioides*** (Figure 8). Devantery found that the current contributes food resources to the moss clumps and increases the spatial uniformity. Devantery (1995) then examined the sub-foliar retrocurrents among submerged bryophytes. Tracing water patterns with a colored dye in an artificial stream, he concluded that the mosses altered the current within the clumps of ***Platyhypnidium riparioides***. He found a symmetrical twirling of water behind the blade of a single leaf. Water crossing the leaf progressively slowed down as it turned toward the foliar insertion.

Abrasion and Scouring

Abrasion and scouring can occur during any period of heavy flow. These are most common during spring melt, but can also be effective when rains return after a summer drought. During the hot, dry periods, bryophytes may lose chlorophyll and vigor due to the high respiration to photosynthesis ratio when they are stranded out of water but still wet. That makes these leaves subject to greater effects of scouring by silt and small grains in early flow due to spates in the late summer and early autumn.

Muotka and Virtanen (1995) found that a parallel change in species composition occurred in bryophyte communities with low stature – typically fast colonizers in disturbed sites. In the more stable portions of a stream, the bryophytes were large perennials. This seems to be further evidence of the potential for scouring and abrasion as a contributing factor to the distribution of mosses in streams.

Like tracheophytes, bryophytes can be harmed by abrasion. Lewis (1973a, b) demonstrated the abrasive effects of coal particles on the moss ***Platyhypnidium riparioides*** (Figure 8). Not only does abrasion damage leaves and stems, but in her study, Lewis (1973a, b) found that it reduced the number of sexual organs, thus potentially affecting reproductive success.

Conboy and Glime (1971) measured the portion of the stem that had lost leaves to abrasion (Figure 65) and found that stream abrasion greatly reduced the photosynthetic portion of the moss ***Fontinalis novae-angliae*** (Figure 64) in a New Hampshire, USA, stream. Plants in slow water had a mean total stem length of 14.1 cm, with a mean leafy portion of 7.25 cm. Plants from fast water had a slightly greater mean stem length (16.7 cm), but the mean leafy potion was only 3.74 cm. This is a reduction from 50% of the plant being leafy to only 20% being leafy, and emphasizes the scouring nature of fast flow.

Figure 65. ***Fontinalis novae-angliae*** scoured; it was removed from the water for the picture. Photo by Janice Glime.

Drag Coefficients

Suren *et al*. (2000) found that there were significant increases in drag coefficient caused by three of the six stream bryophytes they studied. The cushion-shaped growth of ***Bryum blandum*** (Figure 66) increased the drag coefficient by ~10%. On the other hand, ***Blindia lewinskyae*** (Figure 67) and ***Syzygiella sonderi*** decrease the drag coefficient by 40 and 30% respectively. Hence, some bryophytes can make a more stream-lined surface than their substrate offers. These differences in streamlining ability may adapt the species to differences in flow rates and would also help to stabilize the rocks they colonize.

Figure 66. ***Bryum blandum***, a species that increases drag coefficient. Photo by David Tng, with permission.

Figure 67. ***Blindia lewinskyae***, a species common in streams with high catchment-specific discharge and low bankfull discharge. Photo by Melissa Hutchison, through Creative Commons.

Bryophytes themselves serve as safe havens for stream organisms because of their ability to divert flow and create safe sites within the matrix of leaves and branches. Not only is the flow reduced within the moss community, but Suren *et al*. (2000) found that ***Cryptochila grandiflora*** (Figure 68) and ***Blindia lewinskyae*** (Figure 67) can actually reduce the drag forces on the rocks. The moss ***Blindia lewinskyae*** (Figure 67) could reduce the drag force on rocks by up to 56%, hence reducing the likelihood that the rock would move during heavy flow.

Figure 68. ***Cryptochila grandiflora***, a species that can reduce the drag force on rocks. Photo by Juan Larrain, with permission.

Flooding

Comprehensive books on streams have recognized the role of flooding in the ecology of the stream inhabitants (Giller & Malmqvist 1993). Reid and Wood (1961) explain the substrate layering in the floodplain, noting that only the upper layers are penetrable by roots.

Disturbances such as flooding and drought have two phases (Lake 2000). First the disturbance removes or disturbs some of the biota, including bryophytes. Then there is a response to these changes caused by the disturbance. Lake suggested that the two should be considered separately. Flooding accentuates downstream, often damaging the stream or river habitat. Emergent rocks, especially with bryophytes, can serve as refugia for invertebrates, and the bryophytes themselves can serve in repopulating lost bryophytes in the excessive flow. Perhaps due to these refugia, flood recovery typically has returns to relatively constant diversity levels rather easily, even at the very local scale. On the other hand, Lake notes that on a regional scale many researchers have found that streams and their catchments can have negative correlations between diversity and levels of flood disturbance. But other researchers, working on intermediate-sized streams, found a unimodal relationship in diversity with disturbance. They suggested that at the regional scale, disturbance can play a central role in regulating diversity. This area of research is becoming more important as we face expected climate changes.

Suren (1996) found that low-flow events were common environmental factors among streams without bryophytes in New Zealand's South Island. In the streams with bryophytes, flooding had no significant impact once the bryophytes became established.

In his New Zealand study, Suren (1996) found separate groupings of moss-dominated and liverwort-dominated streams. Liverwort-dominated streams were most common in beech forests (Groups 3 and 4 in Figure 72). The liverworts had narrower niches than did mosses and were often absent in streams dominated by mosses. The hornwort ***Phaeoceros laevis*** (Figure 73) and liverwort ***Hepatostolonophora paucistipula*** (Figure 69) were the most common species in the liverwort streams. Dominating the moss streams were ***Fissidens rigidulus*** (Figure 70), ***Cratoneuropsis relaxa*** (Figure 71), and ***Bryum blandum*** (Figure 66). Liverworts seemed to be tolerant of more flood events than were mosses, but flood events had no significant effect once the bryophytes became established. However, the number of high-flow events differed between the streams, along with catchment geology, land use, and water quality, influencing the type of bryophyte community to develop. Elevation played no role in separating the moss and liverwort community groupings.

Figure 69. ***Hepatostolonophora paucistipula***, one of the two most common liverworts in the "liverwort" streams of New Zealand. Photo from Manaaki Whenua – Landcare Research, with online permission.

Figure 70. ***Fissidens rigidulus*** var. ***pseudostrictus***, one of the dominant mosses in the "moss" streams of New Zealand. Photo by Peter de Lange, through Creative Commons.

Figure 71. ***Cratoneuropsis relaxa***, one of the dominant mosses in the "moss" streams of New Zealand. Photo by Tom Thekathyil, with permission.

Learner *et al*. (1990) found that bank slopes, ranging 3-50º, were poor indicators of conservation status in river corridors, based on their assessment of taxon richness, density, and relative abundance of aquatic and terrestrial macro-invertebrates, tracheophytes, and bryophytes.

Bankfull Discharge

Suren and Duncan (1999) examined stability effects on the bryophyte communities in some North American streams. They found that bankfull discharge was among the parameters affecting the communities. The relationship between species richness and bankfull discharge was non-linear, with low richness occurring in both the stable and highly unstable ends of the spectrum. In some cases, this is due to intolerance to desiccation. In cases with high catchment specific discharge, low richness might be due to differences in resistance of the taxa to the high discharges. Low bankfull discharge and high catchment-specific discharge permitted growth of thalloid or weft liverworts (Figure 72).

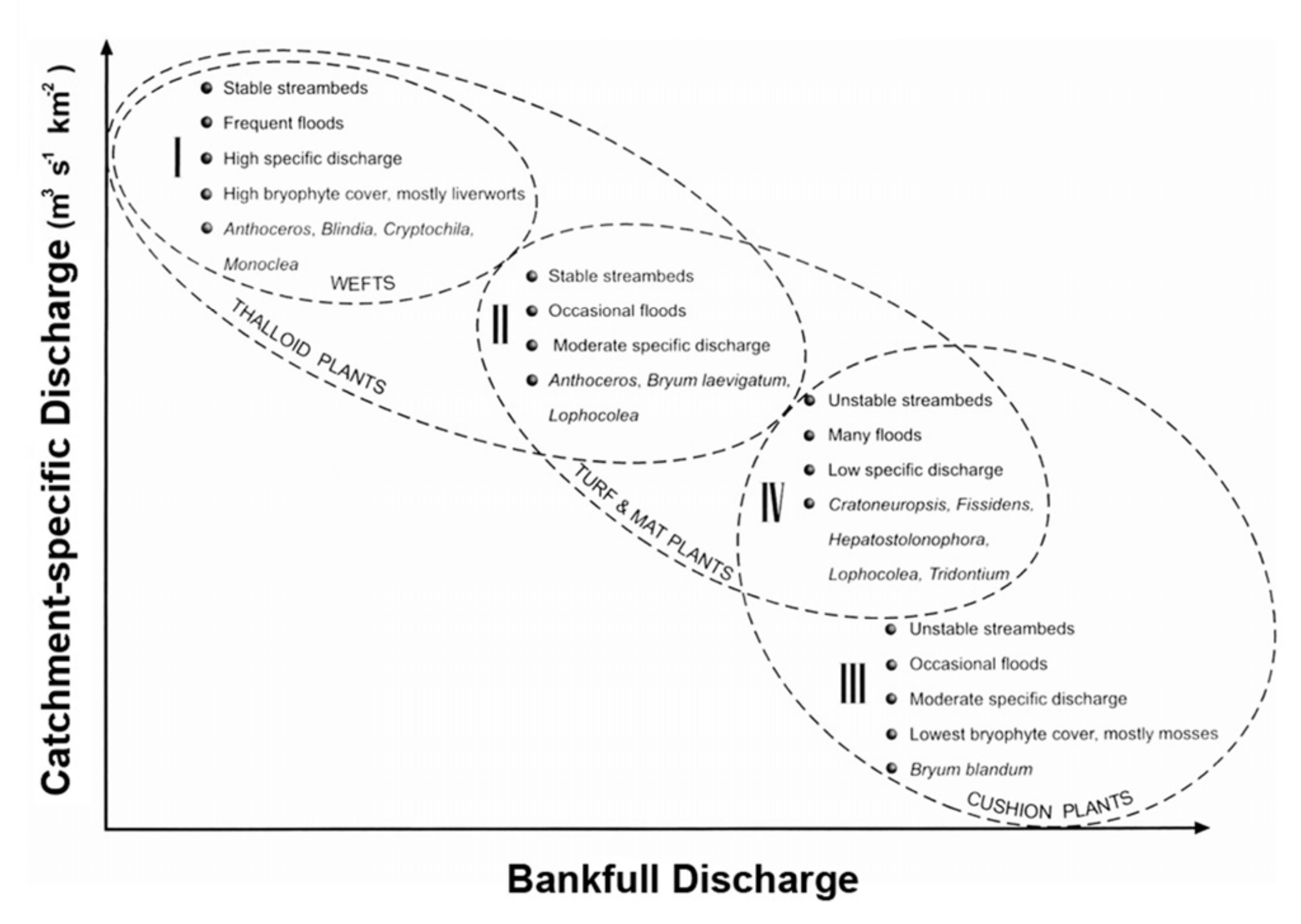

Figure 72. Stream groupings based on Twinspan analysis of 48 streams on New Zealand's South Island. Modified from Suren & Duncan 1999.

By contrast, streams with high bankfull discharge and low catchment-specific discharge were more suitable for cushion-forming mosses. Seven liverwort species, the hornwort ***Phaeoceros laevis*** (Figure 73), and the mosses ***Blindia lewinskyae*** (Figure 67) and ***Ditrichum punctulatum*** (Figure 74) were common in streams characterized by high catchment-specific discharge and low bankfull discharge. Changes in these regimes would affect that community structure.

Figure 73. ***Phaeoceros laevis***, a hornwort species common in streams with high catchment-specific discharge and low bankfull discharge. Photo by Oliver S., through Creative Commons.

Figure 74. ***Ditrichum punctulatum***, a species common in streams with high catchment-specific discharge and low bankfull discharge. Photo by L. Jensen, with permission.

Regulated Rivers

Regulated rivers provide unique challenges to bryophytes. Rivers do not normally remain constant. Regulated rivers deprive the river residents of the flooding, drought, and changes in flow rates to which they are adapted. This permits other species to establish and outcompete the original ones. Bryophytes are no exception to this problem.

Bryophyte sensitivity to water level regimes permits us to use them as high-water indicators (Rosentreter 1992). Loss of these changes in regulated rivers can alter the zonation pattern.

Papp and Rajczy (2009) documented the effects of changes in flow in the Danube. Due to a new hydropower plant, flow was diverted into a new riverbed. The bryophyte vegetation they found in their 2009 study differed from that present in 1991-1992 before the diversion. As the river became drier, the truly aquatic species decreased in both abundance and frequency. Instead, the mesophilous long-lived species and short-lived bryophytes increased.

In the study by Downes *et al.* (2003) the regulated streams did not have lower disturbance frequencies than unregulated systems. Percentage covers of plants, primarily bryophytes, were lower in regulated systems because of reduced cover on large substrata (>20 cm), but not small or medium ones. Downes and coworkers suggested that the rise and fall of the water level in the unregulated rivers provided wider zones subject to a variety of wetting conditions, favoring the bryophyte species that benefitted from alternating exposure rather than constant submergence. Submergence makes it more difficult to get the CO_2 needed for photosynthesis, but frequent submergence can provide the hydration state needed for photosynthesis when the bryophytes are above the water level. Competition did not appear to be a problem in this case.

Although regulated rivers are habitats with moving water, the lack of seasonal flow changes, or a change in those patterns, can be detrimental to stream bryophytes and their fauna. The regulation itself results in a reduction of flow niches, whereas the greater stability can permit some tracheophytes and bryophytes to become established where they could not under normal flow regimes. For example, in the River Rhine, ***Fissidens rufulus*** (Figure 70) and ***F. grandifrons*** (Figure 47) are becoming extinct, apparently due to the changes in flow regime (Vanderpoorten & Klein 1999, 2000). In Australia, Downes *et al.* (2003) reported the percent cover of bryophytes on large boulders decreased as a result of the lost natural flow pattern.

When regulation is the result of industry use, not only might the flow regime change, but water quality can be severely altered. Changes may include higher temperatures, more nutrients, and heavy metal and organic pollutant loading. Such changes normally disfavor the bryophytes, causing clean water species such as ***Platyhypnidium riparioides*** (Figure 8) to be replaced by more pollution-tolerant taxa such as ***Leptodictyum riparium*** (Figure 58) (Vanderpoorten & Klein 2000).

Biggs (1987) found that in outflow affected by hydroelectric power development in New Zealand, bryophytes and filamentous green algae benefitted most from inorganic N and P enrichment.

Lindmark Burck (2012) found that in human-manipulated streams, channelization and restoration both had a negative effect on bryophyte cover. But bryophytes in the channelized streams seemed to repopulate the stream bed. Unlike findings in a number of earlier studies, larger substrates did not seem to provide any benefit.

Hydropeaking, the frequent, rapid, short-term fluctuations in water flow and levels downstream and upstream of hydropower stations, can affect the vegetation, including bryophytes in those river flows (Bejarano *et al.* 2017). Like other regulated rivers, these unnatural occurrences do not provide the water level regime and timing to which the bryophytes and other macrophytes are adapted. The bryophytes and other plants are subjected to physiological and physical constraints that result from the shifts between submergence and drainage, as well as erosion of the substrates. They noted that hydropeaking can facilitate dispersal within a reservoir system, but not between them. On the other hand, this interrupted flow regime can reduce germination, establishment, growth, and reproduction. It favors species that are easily dispersed, flexible, flood-tolerant and amphibious – a limited number of species. These restrictions cause most of the riparian plant species to disappear or be restricted to the upper boundaries of these regulated rivers.

Drought and Desiccation

The opposite of flooding is drought, and bryophytes in many streams and rivers must be tolerant of both. As already noted by Lake (2000), whereas many studies have addressed flooding, few have addressed the effects of drought on stream biota. This is true for its effects on stream bryophytes. Suren (1996) noted that streams with no bryophytes were typically characterized by low-flow events, although this was not the only factor that seemed to contribute to the absence of bryophytes.

Bowden *et al.* (1999) divided streams into three levels of permanence based on hydrologic status during the spring wet season and late summer dry season. **Perennial** sites had flowing water during both seasons. **Intermittent** sites had flowing water in spring, but in the dry period of summer they were either dry or had water restricted to pools. **Ephemeral** sites had no water during the summer dry period. These three conditions had significantly different bryophyte assemblages, although overlap in species occurred. Liverworts were more frequent at the perennial sites, where **mats** and **weft** forms were most common. **Cushion** and **turf** growth forms were most common at the ephemeral sites, as were acrocarpous mosses. The ephemeral sites also tended to have higher species richness than did perennial sites, but there were a number of exceptions to this.

Some early studies noted effects of isolation from water on aquatic mosses. Both Henry (1929) and Davy de Virville (1927) reported that aquatic mosses grown out of water are pale-colored. They also found that these conditions caused the mosses to have more numerous chloroplasts, but less chlorophyll, than those grown in water.

Various studies have exposed a variety of species, including aquatic ones, to water loss in the laboratory, but laboratory conditions do not mimic the highly changeable conditions of the field. For example, I found that ***Fontinalis dalecarlica*** (Figure 29) and ***F. novae-angliae*** (Figure 64) died after 55 hours of laboratory desiccation, whereas the terrestrial ***Polytrichum*** (Figure 75) species survived as long as seven months under the same conditions (Glime 1971). I then attempted to determine the effects of isolation from submersion in ***Fontinalis dalecarlica*** and ***F. novae-angliae*** in a small stream in New Hampshire (Glime 1971). On 10 September 1969 I numbered 36 rocks with ***Fontinalis*** on them and placed them on the streambank. Thus they were not submersed during the 1-year period of study, but were covered with snow in winter. The rocks were returned to the stream as follows. Three rocks were returned on each of the following dates in 1969: 12, 15, 19, 23, 27 September; 4, 11, 25 October. In 1970, 11 rocks were returned to the stream on 23 April, and 5 on 19 September. Those mosses returned to the stream water in 1969 all regained a healthy color within several days or less following their return, despite many being chlorotic and yellow before their return.

Figure 75. ***Polytrichum commune***; some members of this genus can survive as long as 7 months of desiccation in the laboratory. Photo by Bob Klips, with permission.

But after one year, the remaining five rocks that I returned to the stream water on 19 September were not showing any signs of recovery after one week. The leaves remained yellow or brown and only a few branches displayed any green. Their recovery was, however, complicated by the season. The stream had reached a low point when only pools had water. Subsequently, on 24 October the water was swift and the plants had lost most of their leaves. But their stems had sprouted new green branches at the tips. Those plants that had been placed in pools in October had not lost their old leaves, but they too had new branches with green leaves.

Biggs and Saltveit (1996) considered seasonal temporal and spatial scales to govern the processes of biomass loss. Macrophytes and periphyton were more able to colonize at low velocities. Bryophytes, on the other hand, preferred areas of high velocity. This suggests that bryophytes grow in areas where low flow from drought are less common.

Arscott *et al.* (2000) demonstrated that desiccation affected net photosynthesis in ***Hygrohypnum ochraceum*** (Figure 13) and ***H. alpestre*** (Figure 76) more than it did ***Schistidium agassizii*** (Figure 60), an emergent rock species. Nevertheless, the latter species was inhibited by high temperatures, as were the ***Hygrohypnum*** species.

Figure 76. ***Hygrohypnum alpestre*** showing air bubbles that keep even submersed leaves in contact with the gases of air. Photo by Michael Lüth, with permission.

Depth

During a fish spawning survey, Mills (1981) measured depths at which ***Fontinalis antipyretica*** (Figure 7) was growing in the River Frome in southern England (Table 2). There was a significant negative correlation between the biomass of the moss and depth.

Table 2. Vertical distribution of ***Fontinalis antipyretica*** (Figure 7) in the River Frome, southern England. From Mills 1981.

cm depth	relative dry weight
0-10	14.9
10-20	5.6
20-30	6.2
30-40	9.0
40-50	5.5
50-60	5.3
60-70	1.8
70-80	1.2
80-90	0.6
90-100	0.0

Cattaneo and Fortin (2000) found that water depth was one of the factors that explained the distribution of mosses in the Quebec Laurentian Mountain streams they studied. Like the Mills (1981) study, the moss cover was negatively correlated with water depth, with an apparent competitive relationship with the **Cyanobacterium *Stigonema*** (Figure 77).

Figure 77. ***Stigonema ocellatum***, in a genus that is a competitor with stream mosses. Photo by Yuuki Tsukii, with permission.

On the other hand, in their attempts to determine if various groups of organisms responded in the same way to stream parameters, Paavola *et al.* (2003) found that macroinvertebrates and bryophytes were not correlated with stream depth, but that depth was important for fish.

Slack and Glime (1985) demonstrated that different bryophytes prefer different distances above and below the water surface (Figure 78). Furthermore, even the leaf form can change with distance above the water, as noted earlier for ***Hygrohypnum ochraceum*** (Figure 12-Figure 13) in Figure 78.

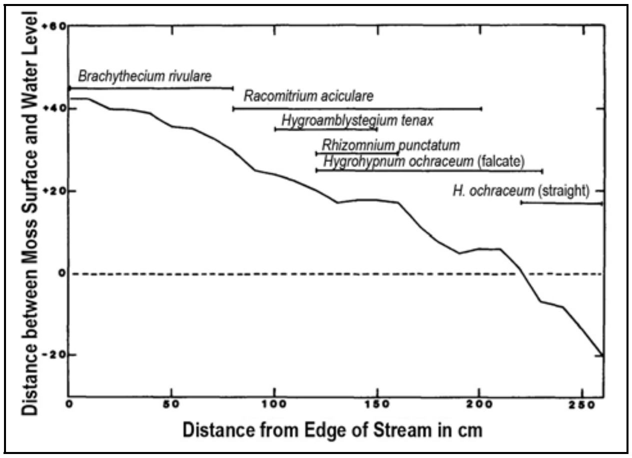

Figure 78. Stream cross section showing vertical and horizontal location of mosses in ten Adirondack stream locations. Modified from Slack & Glime 1985.

In my study of Appalachian streams, the lower, sunny, deeper section of larger streams lacked bryophytes (Glime 1968). ***Fontinalis dalecarlica*** (Figure 29) was the most ubiquitous of the submersed bryophytes, occurring at depths of 13 cm to ~80 cm, typically reaching lower depths than that of other stream bryophytes.

Sheath *et al.* (1986) examined Rhode Island, USA, streams. He found that mean stream depth increased by 3- to 8-fold from first order to fourth order streams. Interestingly, light penetration increased 11-fold from headwaters to the mouth in September when the canopy reached its maximum. ***Fontinalis antipyretica*** (Figure 7) was the most common species and occurred in all 4 stream orders and 51% of the samples.

Shevock *et al.* (2017) concluded that stream bryophytes that are exposed on rock surfaces in full sun during the hottest time of the year tend to be acrocarpous. Periods of submersion and emergence also affect when gametangia are produced, and especially when fertilization can be accomplished. Glime (1984b) suggested that sperm could be splashed as much as a meter to emergent branches of ***Fontinalis*** (Figure 7, Figure 16), accomplishing fertilization when the water level was low and sperm were above the water currents that could carry them away.

Shevock and coworkers (2017) considered the depth to width ratio to be the most critical factor in determining a suitable habitat for stream mosses. At a low ratio of depth to width, bryophytes have little opportunity to be submerged for extended periods of time. But in narrow, deep streams, there are bands of **rheophytes** [aquatic plants that live in fast-moving (1-2 m s^{-1}) and up to 1-2 m deep] dependent upon the varying water levels and duration of submersion.

Siltation

Slow-moving streams often do not provide suitable habitats for bryophytes due to siltation (Chutter 1969). The particulate load in slow stream water settles onto the mosses and "smothers" them, interfering with light, CO_2 exchange, and possibly even slowing nutrient uptake.

Melo and Froehlich (2004) noted that floods result in burial of streambed particles. However, frequency of burial was much lower than that of particle movement except in the smallest stream. Bryophytes can act as debris dams, accumulating 3-5 cm of silt in some locations.

Jones *et al.* (2012) also noted that macrophytes can increase the retention of fine sediment, but that the relationship is complex. The macrophytes not only trap the fine sediments, but they in turn are affected by such silt through such factors as light blockage and presentation of nutrients.

Agricultural input of fine sediment can easily become a stressor for stream bryophytes. Matthaei *et al.* (2006) found that sediment from various agricultural types increased sedimentation to the next higher category. In this case the sediments did not change the concentrations of phosphate, nitrate, and ammonium. Aquatic mosses were most common in the tussock streams and absent in dairy and deer streams. Sediment addition caused reductions in moss cover as well as richness of a number of insect groups.

Siltation can bring with it dissolved organic carbon. In five tributary streams of 1600-ha Trout Lake in northern Wisconsin, USA, Elder *et al.* (2000) found that the C loads bore little relationship to the surface-water catchment area. Instead, they were more closely related to the ground-water watershed area. Peatland porewater holds up to 40 mg L^{-1}, providing a significant potential carbon source. Nevertheless, the carbon yields were very low in the catchments. Elder and coworkers attributed these small yields to the low flow rates resulting from limited overland runoff and very limited stream channel coverage for the total catchment area.

Miliša *et al.* (2006) investigated the role of particulate organic matter (**POM**) related to bryophytes and flow rates on travertine barriers of the Plitvice Lake system in Croatia. Most of the organic matter was deposited in moss mats, but the amounts decreased exponentially with depth. More of the POM was deposited in the habitats with low flow velocity. Fine particulate matter seemed to be unaffected by depth. Coarse particulate matter had a positive correlation between the flow rate and deposition rate in the moss mats. The other size fractions experienced negative effects on deposition with increases in flow velocity.

Hynes (1966) describes the effects of flooding that introduces pollutants and deoxygenated water to the stream fauna, fungi, and algae. He also notes that ***Fontinalis antipyretica*** (Figure 7) is able to tolerate the sewage "fungus" ***Sphaerotilus*** (actually filamentous bacteria; Figure 79), but only where the current is sufficient to keep the stones free of silt. ***Platyhypnidium riparioides*** (Figure 8), on the other hand, grows below the lower limit of the fungus, but like ***F. antipyretica*** it grows where the stones are free of silt.

The effects of deposition on the growth of the mosses remains unclear. Dense coverage of silt can reduce or completely block light, but if the moss is able to maintain growing portions above the silt layer, growth can continue. Silt also brings nutrients, and these can favor development of periphyton that compete for light and CO_2. In areas of heavy deposition, the flow rate is typically lower, thus improving conditions for aquatic tracheophytes that can out-compete the bryophytes. Furthermore, the richer nutrients from these deposits would likewise be expected to favor tracheophytes. While these are expected outcomes, data are needed to support these hypotheses.

Figure 79. ***Sphaerotilus natans***, a bacterium that thrives on sewage water. Photo by Jürgen Mages, through Creative Commons.

Pasture and Plantations

On the South Island of New Zealand, mosses were relatively abundant in streams with some pine plantations and improved pasture, but bryophytes were absent in the heavily modified areas (Suren 1996). Suren found their absence to be concordant with high nutrient levels, unstable substrate, easily eroded rocks, and frequent low-flow events, all characteristics typical of pasture and plantation streams.

Agricultural runoff is often high in phosphorus due to fertilizer applications. In Bear Brook in the Hubbard Brook Experimental Forest, NH, USA, Meyer (1979) found that the leafy liverwort ***Scapania undulata*** (Figure 5) was important as a phosphorus sink. Both bryophytes and sediments remove P from the water. For the bryophytes, this is a function of both P concentration and flow rate, with higher flow rates resulting in lower P concentrations than lower flow rates. Nevertheless, the total P sorbed was greater at the higher flow rates.

In my own explorations, I soon learned to avoid open, level streams through pastures and plantations. These typically had no bryophytes, although the stream banks and springs often had their own unique flora.

Clear-cutting

Bormann *et al.* (1974) found that the clearcut forest at Hubbard Brook, New Hampshire, USA, could prevent erosion of the forest floor for the first two years because of remaining biomass, but that in the third year the flow of particulates lost to the stream due to erosion was much greater. But in those first two years, there was a highly significant increase in soluble nutrients lost to the stream. Thus the stream was first flooded with nutrients, then disturbed by non-soluble eroded particulates.

Sandberg (2015) monitored 10 tributaries of the Vindel River in northern Sweden to observe the effects of restoration on bryophyte communities. They found a lower abundance of bryophytes in the demonstration restored sites than in the unrestored or in the best-practice restored sites. There was no significant difference in bryophyte species richness, diversity, or species composition among these three comparison site types. Small sediment grain size had a negative effect on species richness. Other correlations of environmental variables with bryophyte abundance, richness, diversity, and composition were mostly related to the effects of restoration, but also to the disturbance associated with the restoration.

Forest Buffers

Gundersen *et al*. (2010) noted the importance of natural 10-m strips of riparian forests that occupy more than 2% of the forest area in Nordic countries. These natural buffer zones receive water and nutrients from the upslope areas and provide important and unique habitats. During forest clearing, these zones become important buffers against the upland changes that are occurring. In addition to protecting water quality and aquatic life, they increase the terrestrial biodiversity, especially when a strip greater than 40 m is maintained.

Using a before-and-after experiment of buffer strips along 15 small streams in northern Sweden, Hylander (2004) found that fewer bryophyte species disappeared in the 10-m buffer strips than in clear-cuts. Nevertheless, many bryophyte species, especially liverworts, decreased or disappeared in the buffer strips. These were mostly species that grew on elevated substrates. Endangered species were most affected. When bryophytes were transplanted, wet ground moisture helped to overcome the negative edge effects in these narrow buffer strips. In mesic sites, growth was almost as low as in the clear-cuts. North-facing slopes were less affected than were south-facing slopes. Bryophytes on concave substrates fared better than those on convex substrates. With such narrow buffer strips, the entire strip becomes an edge habitat.

Effects on Streams and Riparian Zones

Vuori and Joensuu (1996) reported that forest drainage, even with protective buffer zones, caused definite structural changes in the habitat structure. These were deposition of particles on the benthic habitats and particle movement along the surfaces. In the control riffle areas, the aquatic moss ***Fontinalis dalecarlica*** (Figure 29) was the dominant habitat. Where forest ditches impacted the stream, sand dominated the riffles. Those tufts of ***Fontinalis*** in the affected areas were covered with silt and contained significantly more inorganic matter than those mosses in control areas. Furthermore, the species richness of macroinvertebrates was significantly lower in the impacted sites than in the control sites. Stoneflies (shredders) dominated mosses in control riffle sites, whereas blackflies were dominant in the impacted riffle sites.

Clear-cutting can result in major changes in stream dynamics. Dynesius and Hylander (2007) examined the effects of buffer strips in mediating streamside bryophyte disturbances. Using paired before and after plots from clear-cut forests, they assessed the effects of these buffer strips. After 30-50 years, the bryophyte species richness showed little response to clear-cutting. Nevertheless, richness had changed in many subgroups by habitat or substrate affinity and the phylogenetic groups comprising the communities. Liverworts were reduced significantly by clear-cuts. Narrow buffer strips prevented most of the short-term species losses in the stream-side forests. This raises the question of their effect on the stream bryophyte flora.

Forests are important in ameliorating stream disturbances. Suurkuuka *et al*. (2014) included 50 headwater streams in their study of **riparian** (relating to or situated on banks of rivers or streams) forests in northern Finland. They found that all studied taxonomic groups except diatoms and chironomid larvae responded negatively to forest site modification. These included bryophytes and macroinvertebrates. They found that woodland habitats can be valuable for protecting stream biodiversity.

Buffer Size: Hylander *et al*. (2005) found that buffers along streams where logging occurs can be important in maintaining stability. They examined buffer strips of mosses and liverworts along 15 small streams in boreal forests, comparing before logging to 2.5 years after logging. Using 10-m wide buffers, they compared bryophytes with plots in clear-cut areas (no buffer). They found fewer than half as many bryophyte species disappeared in the buffer zones compared to the clear-cut streamside zones. The remaining species in the clear-cut zones were more affected than those in the buffer zone. Nevertheless, there was a significant species composition change in the buffer strips. Substrate form was important, with species on concave substrates experiencing little effect. Liverworts were somewhat more sensitive than mosses. **Red-listed** (protected based on rarity status) species were also the most likely to decline in the buffer strips. They suggested that increasing the width of buffer strips would provide more protection for bryophytes along streams by decreasing windthrow frequency and edge effects.

Castelle *et al*. (1994) considered vegetated buffers to be necessary to protect wetlands, streams, and aquatic resources. They found that a buffer of at least 15 m was usually necessary to protect wetlands and streams. They found that a range of 3-200 m may be needed, depending on the purpose and situation.

In the state of Washington, USA, Brosofske *et al*. (1997) determined that the stream microclimate was affected by buffer width and the microclimate created in the surrounding area. They concluded that this buffer should be at least 45 m on each side of the stream, but depending on the slope, the buffer may need to be up to 300 m. These 2-4 m wide streams had moderate to steep slopes, 70-80% overstory, and experienced hot, dry summers with mild, wet winters. These factors are all important in determining the size of buffer needed to protect the stream. The greater effects may be on the streambank and near-stream locations.

Gradients: The upland gradient is affected differentially. Dynesius *et al*. (2009) found that bryophyte species composition in old forests 30-50 after cutting was significantly less affected in the streamside forests than in the upland forest. They attributed this to lower survival and recolonization in the upland forests due to stronger associations with old stands in the upland. Furthermore, when a species occurred in both forest types, fewer appeared in the upland sites. Some of the streamside bryophyte species even increased in frequency. They also suggested that short-term recovery does not necessarily indicate higher long-term ability to recover the original communities.

Baldwin *et al*. (2012) used 15-m buffers on both sides of the stream in high-elevation streams of British Columbia, Canada. Using bryophyte functional group frequency, they found that both distance from the stream and canopy treatment were strongly associated with variation in bryophyte communities. The highest richness of functional groups occurred adjacent to the streams. As expected, richness of forest species and extent of cover was highest in the continuous forests, intermediate in buffers, and lowest in clear-cuts. In undisturbed forests, differences in bryophyte communities did not differ from those in buffers. But when buffers and clear-cuts were compared, the communities differed significantly at all distances.

Time Lags

Hylander and Weibull (2012) questioned the effectiveness of buffer strips due to the time-lagged extinctions. Their observations on species extinctions parallels the observations of Bormann *et al*. (1974) on the delay in erosion. In an inventory 10.5 years after logging, Hylander and Weibull found that both clear-cuts and buffer strips had greater differences from predisturbance than they did 2.5 years after the logging. Studies are need to observe the time effects on bryophyte communities.

Ice and Snow

Ice on streams can provide a surface where snow can accumulate (Figure 80). This not only reduces the light intensity, but also changes the light quality in the water below. Deep snow, like water, tends to absorb red light, thus reflecting the bluish colors we see (NSIDC 2020). And the scattering of the light by the ice grains also contributes to its bluish color.

Figure 80. Snow on top of ice in a New Hampshire, USA, stream. Photo by Janice Glime.

Ice breakup can rip bryophytes from their substrates. Sometimes these effects an be massive, but usually enough of the bryophyte remains to permit regrowth of the colony (Figure 81-Figure 82). Similarly, mosses can become imbedded in snow, especially at the margins of snowbanks on the sides or even within the streams. These can break loose and carry small or large fragments that become potential propagules (Figure 83).

Figure 81. ***Fontinalis*** frozen in ice at Fox Inlet, Plymouth, New Hampshire, USA. This demonstrates how the ice could remove the moss when the ice breaks loose. Photo by Janice Glime.

Figure 82. ***Fontinalis*** frozen in ice (see Figure 81), demonstrating how the ice could remove the moss when the ice breaks loose. Photo by Janice Glime.

Figure 83. ***Fontinalis*** frozen in snow, Fox Run, NH, USA, illustrating how small fragments can break loose and be dispersed downstream by the flow. Photo by Janice Glime.

Snow and ice play major roles as moisture sources in cold regions (Prowse 1994). When the flow reaches a channel system, floating ice can control the flow system. These are the most significant events causing floods as well as low flows. This spring **freshet**, when ice begins to melt, is often the largest hydrologic event in the year (Prowse & Carter 2002). Ice breakup creates unique in-channel and riparian habitats (Prowse 2001). The aquatic and floodplain vegetation can be modified, affecting our understanding of river ecology and flood-pulse theory. Prowse (1994) reported a 30-fold increase in suspended particles during ice breakup in the Liard River, Northwest Territories, Canada. Beltaos (1993) demonstrated that ice could cause sufficient shear stress to move rocks 20 cm in diameter. Ice can also cut away at the banks of streams and rivers (Scrimgeour *et al*. 1994). And the water temperature remains close to 0ºC until the ice is gone. It can then increase rapidly (Terraux *et al*. 1981; Parkinson 1982; Marsh & Prowse 1987; Marsh 1990). It has been observed to rise 9ºC in 13 hours in the lower Mackenzie River, Northwest Territories, Canada, when the ice yields to open water (Parkinson 1982).

Stream edges can form unique and interesting patterns as snow melts, then freezes as the air cools at night (Figure 84).

Figure 84. Ice stalactites under snow on stream. Photo by Allen Norcross, with permission.

Anchor Ice

I was first introduced to **anchor ice** (Figure 85) in a stream in lower Michigan, USA. My colleagues were excited to show me an abundant ***Fontinalis*** flora near a university where I was interviewing. But when we arrived at the stream, the bryophytes were totally gone! Instead, we found large clumps of ice on many of the rocks and evidence of scouring on others.

Anchor ice (Figure 85) is that ice that forms on rocks on the bottom of a stream or lake. It is most common in fast-flowing rivers during periods of extreme cold. It also occurs in various waterways as they enter cold ocean water.

Lind and Nilsson (2015) found that the number of winter floods was greater in reaches with anchor ice than in reaches without it. Lind and Nelson found that when a freezing period occurred early in winter, underwater ice could form and restructure the channel, obstruct flow, and cause flooding, causing more ice to form. By midwinter, slow-flowing water can freeze on the surface. Henceforth, snow accumulates on the ice, protecting the underwater habitat from ice formation. But this reduces light and hence reduces photosynthesis. During late winter or spring, ice breaks up. Ice floes can cause jams, floods, and major erosion events.

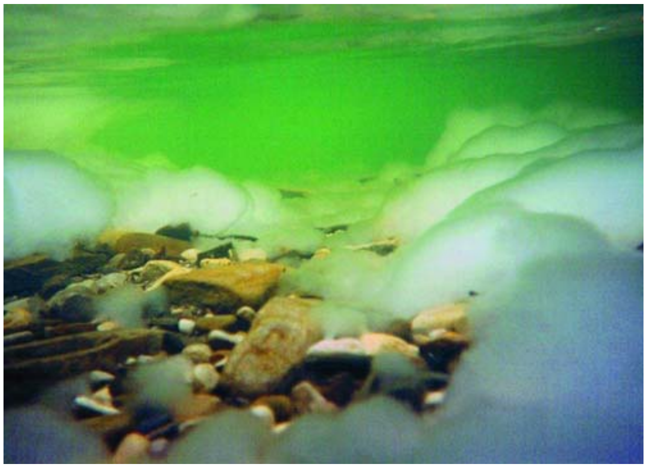

Figure 85. Anchor ice in a stream in Alberta, Canada. Photo from Pacific Northwest National Laboratory.

In the cases of both surface ice and anchor ice, cell damage can occur to plants frozen into the ice (Lind & Nilsson 2015). Large magnitudes of ice dynamics tend to favor species richness of the community, but individual plants can suffer great harm. For bryophytes, this can mean dispersal, probably with very little cell damage, but it can have a huge impact in some areas of the stream. Surprisingly, Lind and Nilsson found a lower cover of algae but a higher cover of bryophytes in anchor ice reaches. These anchor ice events seem to permit the less competitive species such as bryophytes to establish along small boreal streams. This relationship seems to be widespread in streams and rivers of high altitudes and high latitudes (Lind *et al*. 2014).

Its presence in streams can be devastating to the bryophytes there (Glime 1987a; Englund 1991; Muotka & Virtanen 1995). Bryophytes can totally disappear from a site, as I observed near Ypsilanti, Michigan, USA. Moving ice, whether from the surface or anchor ice, causes scouring and can move the substrate (Muotka & Virtanen 1995). These events can create gaps that provide openings for bryophyte colonization (Virtanen *et al*. 2001).

Finlay and Bowden (1994) found that anchor ice in the Kuparuk River, Alaska, USA, persists up to two weeks while the melt waters erode it away slowly. This ice cover protects the periphyton. The persistence of the ice negates the disturbance that might remove the bryophyte communities. And bryophytes frozen in dry or wet conditions seem to be resilient (Glime 1971). These bryophytes become photosynthetically active within hours of becoming hydrated with liquid water (Longton 1988).

In Alaskan streams with extensive freeze-up surrounding them, overland water diminishes and ice encroaches from the sides (Breck Bowden, pers. comm. 29 July 2019). In low-order streams, the stream may freeze to the bottom, although snow can insulate the stream and permit lenses of liquid water. In the spring, the meltwater is **over** the frozen anchor ice, thus the ice is protecting the benthic communities of bryophytes and other organisms. By the time the water has eroded the anchor ice and the stream has open flow, the spring melt water is mostly in the past. Such mosses as ***Hygrohypnum*** (Figure 13, Figure 76) species are thus protected in these streams against the abrasion of heavy flows.

Stickler and Alfredsen (2005) studied the effects of ice in two Norwegian rivers. They found that anchor ice dams formed in areas with large substrates and shallow water, with the reduced water velocity in steep sections triggering ice cover formation. The second river was a hydropower river, so its flow was regulated. It was also a larger river with a lower flow rate. This latter river has frequent anchor ice events. In both rivers, the anchor ice events were relatively frequent, and the ice was usually released the next afternoon. Through this regime, algae and plants frozen into the ice are removed.

Engström (2010) investigated the function of ice, wood, and rocks as regulating elements in riparian systems, considering their role in retention and dispersal. Retention of propagules was highest in low flows and sites where there were large boulders and large wood. But he found that propagules were unlikely to establish unless they were dispersed during the subsequent high flows of spring that could lodge them in higher riparian habitats that were suitable for establishment. Thus, the immigration process due to ice floes is a stepwise process. Like Lind and coworkers, Engström found that the overall species richness increased in the plots with ice events.

Lindmark Burck (2012) found no clear relationship between ice and substrate in boreal streams in Sweden. It is possible that restoration in the channels eliminated harmful ice formation. There was some evidence that the channelized streams have less cohesive surface ice but more anchor ice.

Summary

Truly aquatic bryophytes must be able to survive both complete submersion and shorter periods of desiccation and high light. Taxonomic groups, life forms, and life strategies are selection factors for tolerance of water velocity, local incident light, and hydrologic zone. Factors influencing suitability of a site for individual species and species richness include substrate size, substrate stability, type of substrate, altitude of source, site altitude, distance to source, flow rate ($\sim<0.9$ m s^{-1}), drag coefficients, depth, frequency of disturbance (especially flooding frequency and ice release), drought frequency, bankfull discharge, water clarity, water quality, alkalinity, light intensity, temperature, and human interference in the stream and surrounding landscape. Of these, substrate stability is perhaps the most important. Light, nutrients, siltation, and temperature govern biomass gain and the relative dominance of bryophytes vs periphyton biomass.

The most common genera in streams are ***Fontinalis*** and specialized members of ***Fissidens***, ***Hygroamblystegium***, ***Platyhypnidium***, ***Racomitrium***, and ***Scapania***. The most common families are **Brachytheciaceae, Fissidentaceae**, **Fontinalaceae**, and **Grimmiaceae**. Bryophyte richness tends to increase with stability, but decreases at high stability, seemingly due to competition from other macrophytes; the most unstable streams typically have the lowest richness. Bryophytes seem to benefit from relatively fast flow, perhaps because of cleaning of periphyton and detritus, as well as lack of tracheophyte competition.

Siltation impedes photosynthesis. Increased flow can bring more rapid nutrient replacement and trap CO$_2$. But rapid flow with a silt load can cause abrasion of the bryophyte leaves. Ice flows likewise can cause considerable abrasion and even remove entire clumps. Anchor ice can break lose, leaving a rock devoid of all bryophytes. Flooding seems to have less effect on well-established bryophytes. Frequent low-flow can promote the absence of bryophytes. Greater depth likewise supports fewer bryophytes. The depth to width ratio can be a critical factor, with a low ratio causing bryophytes to be submerged for shorter periods of time.

Increasing the available P and N can increase bryophyte biomass, but too much can lead to their being outcompeted by tracheophytes and periphyton. Forest buffers can ameliorate some of these nutrient changes following clear-cutting.

Many macroinvertebrates depend on the bryophytes in streams as safe sites and locations of food. The bryophytes can reduce drag forces and provide internal pools away from the flow. Some macroinvertebrates eat the bryophytes or build cases from them.

Vegetative reproduction is common among the stream bryophytes, with fragments being dispersed by the water.

Acknowledgments

For the entire stream section of this book, I have to thank my sister Eileen Dumire for her companionship in my field excursions and her help in sorting insects and maintaining my bibliography in index card form.

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CHAPTER 2-2
STREAM FACTORS AFFECTING BRYOPHYTE PHYSIOLOGY AND GROWTH

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STREAM FACTORS AFFECTING BRYOPHYTE PHYSIOLOGY AND GROWTH

Figure 1. Tolliver Run, Garrett Co., MD, USA, step falls showing ***Scapania undulata*** on the wet rocks of the falls. Photo by Janice Glime.

*p*H and Alkalinity

The *p*H is a measure of the H^+ concentration. It is expressed as the negative log, *i.e.*, it is the denominator of a fraction. Therefore, the lower the number, the higher the concentration of H^+. The lowest possible *p*H is 0, the highest is 14; 7 is neutral.

$$pH = -\log[H^+]$$

Thus, *p*H is the base-10 logarithm of the hydrogen ion concentration in moles per liter solution.

Alkalinity is the capacity of water to resist changes in *p*H that would make the water more acidic, *i.e.*, its buffering capacity. Alkalinity is the strength of a buffer solution composed of weak acids and their conjugate bases. This explains why juices like cranberry juice and orange juice can alkalinize your body. The juices are weak acids providing that buffering capacity.

Alkalinity and *p*H are products of the underlying substrate, but can be buffered by things dissolved in the water and affected by runoff and air pollution. Nitrates and CO_2 in the rain can alter the *p*H when they become dissolved in the water. The latter explains why the *p*H of distilled water drops when it is exposed to the air.

The *p*H varies throughout the year and throughout the day. Respiration at night can lower the *p*H, whereas photosynthesis during the day can raise it as the plants and algae absorb the CO_2 for photosynthesis. These same activities are dependent on temperature and thus can exhibit seasonal differences. Furthermore, since CO_2 is a gas, it remains in cold water longer than in warm water, a reason for keeping your soft drinks cold. This additional time for keeping CO_2 in the water seems to explain the presence of some mosses in really cold glacial melt streams traversing alkaline substrata (*e.g.* Glime & Vitt 1987).

Even snow contributes to changing the *p*H of a stream, creating another seasonal variation. For example, during the winter of 1977-78 the snow pack in central Ontario had a *p*H of 4.0-4.5 (Jeffries *et al*. 1979). The following spring, the runoff experienced a 2-13-fold increase in H^+ content, consequently experiencing a lower *p*H. Runoff from agriculture and changes in forest drainage patterns can also modify the *p*H (Ramberg 1981; Neal *et al*. 1992).

Substrate is the most important natural factor contributing to the acidity and alkalinity. For example, east of the Weichselian terminal moraine in Denmark, the streams are alkaline and resist acidification from various inputs (Rebsdorf *et al*. 1991). West of the moraine, the sandy soils are leached; alkalinity is lower, and the belief was that even these streams could not be acidified. Nevertheless, over a 12-year period the *p*H dropped each year, as did the alkalinity. These occurrences coincided with an increase in free CO_2 in the water – 7.9 times that found if the water is in equilibrium with the air. The researchers suggested that the acidification was from atmospheric deposition. CO_2 in water can form bicarbonates (HCO_3^-) with the water, releasing H^+ ions and lowering the *p*H. Dissolved CO_2 is important for aquatic photosynthesis, especially in bryophytes, as will be revealed in a later subchapter.

Acidification due to pollution has permitted before and after studies on a relatively large scale. In one of these in the Vosges Mountains of northeastern France, Thiebaut *et al*. (1998) compared six chemical variables and their effects on bryophyte communities. They found 19 species at 31 study sites. Ca^{2+} and Mg^{2+} had the most impact on the distribution, with a lesser effect from *p*H and Al. Both calcium and magnesium can form buffers in the water. The acidophilous leafy liverwort ***Marsupella emarginata*** (Figure 2) seems to be sensitive to high concentrations of **cations** (ions with positive charge) such as Ca^{2+} and Mg^{2+}. The neutrophilous ***Platyhypnidium riparioides*** (Figure 3) reacts little to acidity, but appears to be sensitive to protons or Al.

Figure 2. ***Marsupella emarginata***, a species sensitive to high concentrations of cations. Photo by Hermann Schachner, through Creative Commons.

Figure 3. ***Platyhypnidium riparioides***, a species that exhibits little reaction to acidity, but is sensitive to protons and Al. Photo by Michael Lüth, with permission.

Tremp and Kohler (1993) found that aquatic mosses were reliable indicators of the acidity of buffered waters in rivers. Through this and other studies we know that *p*H is an important factor in determining if a habitat is suitable for a particular bryophyte species. And conversely, bryophytes are good indicators of the acidity or alkalinity of a stream.

In comparing the effects of soil and water parameters (sand, clay, K, Fe, Mg, P, Ca, *p*H) on bryophyte species diversity in 11 Canadian Rocky Mountain steams, Glime and Vitt (1987) found that only *p*H had an effect, and that it was significantly evident (α=0.05) only for the stream bank. The vegetation in these streams is strikingly different from that found in Appalachian Mountain streams. This coincides with the basic Canadian Rocky Mountain streams vs the acidic Appalachian Mountain streams in the eastern US. Suren and Ormerod (1998), working in Himalayan streams, found that alkalinity was a statistically significant contributing factor in determining bryophyte community composition and cover.

Most streams in the Appalachian Mountain range, USA, are acidic, but pollution has increased that acidity. Stephenson *et al*. (1995) examined the effects of acidification on the bryophyte communities in West Virginia. They noted that bryophytes often respond sooner to changes in water chemistry compared to tracheophytes. Using line transects and stratified random sampling in six streams, they identified three groups of species: basic, moderately acidic, and very acidic. In sandstone beds, the diversity decreased with the acidity. At *p*H 3.15, no bryophytes were present. ***Scapania undulata*** (Figure 4) exhibited the highest tolerance to moderately and highly acidic streams, a tolerance also known from Europe and Japan. However, after three months, even these bryophytes exhibited ultrastructural damage when transplanted from a stream with *p*H 5.97 to one with 3.15. They cautioned that two of the streams with the most acidic conditions received acid mine drainage, resulting in very high levels of SO_4^{-2} and Al in addition to dissolved solids.

Figure 4. ***Scapania undulata***, a species that is highly tolerant of acidity. Photo by Hermann Schachner, through Creative Commons.

Tessler *et al*. (2013) found that narrow low *p*H niches were exhibited by the moss ***Andreaea rothii*** (Figure 5) and leafy liverwort ***Marsupella emarginata*** (Figure 2) or neutral mosses ***Hygrohypnum ochraceum*** (Figure 6) and ***Racomitrium aciculare*** (Figure 7). ***Hygrohypnum eugyrium*** (Figure 8), on the other hand, had relatively broad *p*H tolerance. In the streams studied, latitude, longitude, altitude, and dissolved Ca and Mg were important factors in the location of a species. The *p*H had a significant correlation with P. ***Fontinalis** cf.* ***dalecarlica*** (Figure 9-Figure 10) had the most pronounced *p*H preference, preferring a lower *p*H.

Figure 5. ***Andreaea rothii*** with capsules, a species with a narrow low *p*H niche. Photo by David T. Holyoak, with permission.

Figure 6. ***Hygrohypnum ochraceum***, a species with a narrow niche around a neutral *p*H. Photo by Paul Wilson, with permission.

Figure 7. ***Racomitrium aciculare***, a species with a narrow niche of a neutral *p*H. Photo by Michael Lüth, with permission.

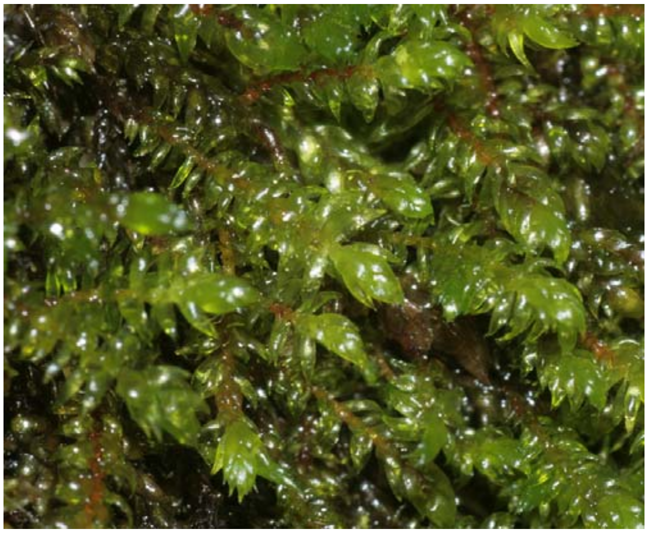

Figure 8. ***Hygrohypnum eugyrium***, a species with a relatively broad *p*H tolerance. Photo by Hermann Schachner, through Creative Commons.

Figure 9. ***Fontinalis dalecarlica*** habitat at Highlands, NC, USA, a species with a strong preference for lower *p*H levels. Photo by Janice Glime.

Figure 10. ***Fontinalis dalecarlica***, a species with a strong preference for a lower *p*H. Photo by Jean Faubert, with permission.

Glime and Vitt (1987) found distinctly different species in the 11 alkaline streams in the Canadian Rockies compared to those in the acidic Adirondack streams in eastern USA. The alkaline Canadian Rockies streams were dominated by the mosses ***Cratoneuron filicinum*** (Figure 11), ***Fissidens grandifrons*** (Figure 12), and/or ***Hygrohypnum bestii*** (Figure 13) (Glime & Vitt 1987). The acidic Adirondack streams were dominated by the mosses ***Fontinalis*** spp. (Figure 9-Figure 10), ***Hygrohypnum*** spp. (Figure 6), ***Brachythecium*** spp. (Figure 14), ***Platyhypnidium riparioides*** (Figure 3), and/or ***Hygroamblystegium tenax*** (Figure 15) (Slack & Glime 1985; Glime & Vitt 1987). In the mid Appalachian Mountains, USA, Glime (1968) grouped streams according to the dominant bryophyte(s). She found in the ***Fontinalis dalecarlica*** (Figure 9) streams (Figure 16): ***Fontinalis*** (especially ***F. dalecarlica***) and some occurrences of ***Scapania undulata*** (Figure 1, Figure 4); in the ***Hygroamblystegium fluviatile*** (Figure 17) streams (Figure 18): also ***Platyhypnidium riparioides*** (Figure 19, ***Hygroamblystegium tenax***, ***Amblystegium varium*** (Figure 20), ***Brachythecium plumosum*** (Figure 14), and ***Brachythecium rivulare*** (Figure 21); in the ***Hygrohypnum*** streams: ***Hygrohypnum*** spp. (Figure 6); and the leafy liverwort ***Scapania undulata*** (Figure 4) streams.

Figure 11. ***Cratoneuron filicinum***, a dominant species in alkaline streams of the Canadian Rockies. Photo by David T. Holyoak, with permission.

Figure 12. ***Fissidens grandifrons***, a dominant species in alkaline streams of the Canadian Rockies. Photo by Scot Loring, through Creative Commons.

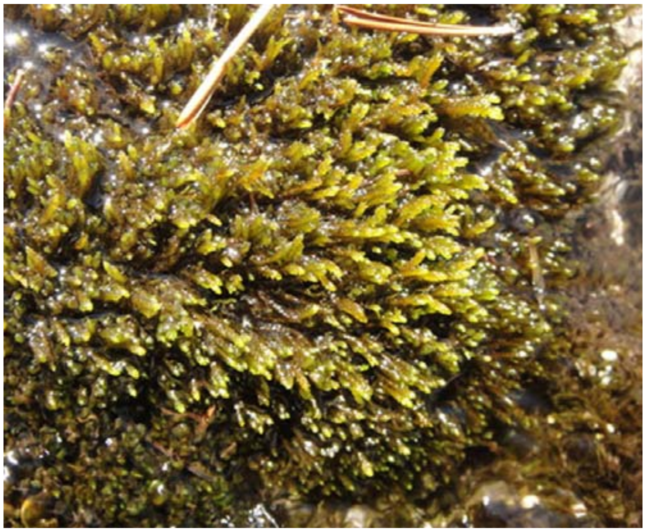

Figure 13. ***Hygrohypnum bestii***, a dominant species in alkaline streams of the Canadian Rockies. Photo by Luke Armstrong, through Creative Commons.

Figure 14. ***Brachythecium plumosum***, one of the dominant species in acidic Appalachian streams. Photo by Michael Lüth, with permission.

Figure 15. ***Hygroamblystegium tenax***, one of the dominant species in acidic Appalachian streams. Photo by Hermann Schachner, through Creative Commons.

Figure 16. A ***Fontinalis*** stream, Muddy Creek, Garrett Co., Maryland, USA. Photo by Janice Glime.

Figure 17. ***Hygroamblystegium fluviatile***, the dominant species in some acidic Appalachian Mountain streams. Photo by Michael Lüth, with permission.

Figure 18. Ginseng Run, Garrett CO, Maryland, USA, a ***Hygroamblystegium fluviatile*** stream. Photo by Janice Glime.

Figure 19. ***Platyhypnidium riparioides***, one of the more common species in some acidic Appalachian Mountain ***Hygroamblystegium fluviatile*** streams. Photo by Michael Lüth, with permission.

Figure 20. ***Amblystegium varium***, one of the common species in some acidic Appalachian Mountain ***Hygroamblystegium fluviatile*** streams. Photo by Bob Klips, with permission.

Figure 21. ***Brachythecium rivulare***, the common species in some acidic Appalachian Mountain streams. Photo by Michael Lüth, with permission.

Virtanen *et al.* (2009) found that bryophyte assemblages of boreal springs exhibited distinct differences based on temperatures and water chemistry, including *p*H. They compared these to the important variables for the chironomids (midge larvae) and found that these insects likewise were separated based on temperature, but that water chemistry had little importance. Instead, the physical parameters were more important. The bryophytes clearly did not serve as good surrogates for midge communities.

When Lang and Murphy (2012) identified four community drivers for bryophytes in high-latitude headwater streams in Scotland, they were able to identify two assemblages based on *p*H relations. The acid-sensitive, base-poor indicators are ***Scapania undulata*** (Figure 4) and ***Hygrohypnum ochraceum*** (Figure 6). Calcareous and mineral-rich indicators are ***Chiloscyphus polyanthus*** (Figure 22-Figure 23) and ***Hygrohypnum luridum*** (Figure 24).

Figure 22. ***Chiloscyphus polyanthos*** habitat in a mineral-rich stream. Photo by A. Neumann, through Creative Commons.

Figure 23. ***Chiloscyphus polyanthos***, a species that prefers mineral-rich streams. Photo by Barry Stewart, with permission.

Figure 24. ***Hygrohypnum luridum***, a mineral-rich indicator. Photo by Hermann Schachner, through Creative Commons.

In the Arctic stream, Imnavait Creek, there are pools up to 2 m deep, connected by narrow channels, known as a **beaded stream** (Oswood *et al.* 1989). Weathering is limited and the bedrock contributes little to the ionic composition of the stream water. The *p*H ranges 5.3 to 6.1 and alkalinity is low. The pools and channels are dominated by peat, with only occasional rock and moss substrates. When water flow is low in the summer, the pools become isolated. In this case, snowmelt is the major contributor to ions.

CO_2 Relationships

Whereas terrestrial bryophytes benefit from CO_2 emitted by soil organisms and ground-level decay, aquatic bryophytes are limited by the CO_2 that can dissolve in the water, a problem also for the algae (Bain & Proctor 1980; Gross 2000). This CO_2 availability is governed by the *p*H of the water. Hence, at a *p*H of less than 6.3, half or more of the CO_2 is available as carbonic acid, which can dissociate to form CO_2 and H_2O (Figure 25). Although a number of tracheophytic aquatic plants can use the bicarbonate form (HCO_3^-), it does not seem that bryophytes have that ability. Nevertheless, they are able to exist at *p*H levels at which carbonic acid and free CO_2 would not exist. But how?

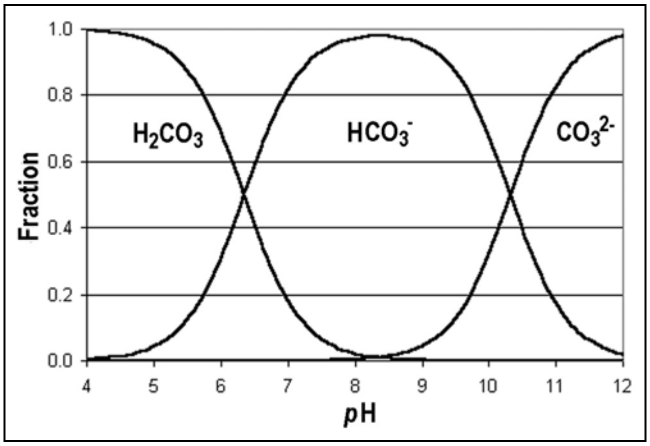

Figure 25. Bicarbonate equilibrium and potential sources of CO_2 through a *p*H range. Modified from <Ion.chem.usu.edu>.

One possible factor in the CO_2 availability in streams is turbulence. Splashing water running through rapids might temporarily trap atmospheric CO_2 (see Zappa *et al.* 2007; Alin *et al.* 2011). High flow rates help to maintain CO_2 levels among the aquatic plants (Sand-Jensen & Pedersen 1999). Yet the effect of these turbulent processes on CO_2 availability to bryophytes and other photosynthetic organisms remains unknown, with almost no data on the effect of turbulence on CO_2 content in stream water (Alin *et al.* 2011; Kokic *et al.* 2018), except to discuss its loss. I was surprised to find that streams generally have a net release of CO_2 into the atmosphere (Horgby *et al.* 2019), suggesting that in general CO_2 should not be limiting. In fact, mountain streams, a favorite habitat for aquatic bryophytes, appear to have a higher than average CO_2 emission rate than the much more studied streams at lower altitudes, due in part to the additional turbulence at higher elevations with steeper slopes, accounting for 10-30% of the CO_2 emissions from fluvial networks (Horgby *et al.* 2019). Oquist *et al.* (2009) demonstrated that in the headwater streams they studied, about 65% of the dissolved organic carbon in the groundwater was lost to the atmosphere within 200 m of the source. Van Geldern *et al.* (2015) similarly found a pCO_2 decline of 84% within 7 km downstream of a spring. The colder the water, the longer that CO_2 can remain in the water before it returns to the atmosphere (Marx *et al.* 2017).

Headwaters, in particular, emit high levels of CO_2 to the atmosphere (Duvert *et al.* 2018). Carbonate rocks are the primary sources of the CO_2 emissions from streams (Duvert *et al.* 2018; Horgby *et al.* 2019) and at the same time can provide CO_2 to the bryophytes living on them, ready to capture what is needed for photosynthesis before the gas escapes to the surface and the atmosphere. Turbulence greatly contributes to the escape of this CO_2 at the surface (Kokic *et al.* 2018). But to what extent can this turbulence capture CO_2 from the atmosphere and make it available to bryophytes in alkaline streams that lack the carbonate rock sources? This question still seems not to have been answered.

Another factor is that CO_2 reacts with the water to form carbonic acid (H_2CO_3). If the *p*H is appropriate (see Figure 25), the carbonic acid can subsequently lose protons to form bicarbonate (HCO_3^-). At still higher levels of *p*H, the equilibrium shifts to carbonate (CO_3^{2-}). This suggests that mosses in rapid, cold water might gain sufficient CO_2 to take it in and conduct photosynthesis, even when the water is in the higher *p*H range. But this is guesswork. Keeley *et al.* (1986) concluded that photosynthetic pathway did not cause differences in their Δ13C values. Although CAM plants (which are unknown among bryophytes) derive up to half their net carbon gain through dark fixation, their Δ13C is similar to that of associated non-CAM plants, apparently because the CAM carbon source for dark CO_2 uptake is CO_2 released from organic carbon by decomposition, or by respiration.

Sanford *et al.* (1974) found that ***Hygrohypnum ochraceum*** (Figure 6) was abundant in riffles in the Sacramento River. Its growth was related to water temperature, current velocity, and dissolved CO_2. These researchers found that as they increased CO_2 in experiments, the mean elongation increased. This was supported by observations that the moss was less abundant in areas of the river where there was a lower CO_2 concentration. They also concluded that bacterial flora produced CO_2 that could be used by the mosses.

Physical factors can alter the CO_2. Neel (1951) and Minckley (1963) demonstrated that in small Kentucky, USA, streams the CO_2 in the water increased and oxygen decreased in water as it passed through small pools. CO_2 can also be contributed by rainwater, soil runoff, $CaCO_3$ from limestone rocks.

*p*H

Since *p*H is so important in CO_2 availability, we should expect liming to have negative effects on the bryophytes. Brandrud (2002) investigated this relationship in lakes and rivers of Sweden and Norway. Brandrud found that liming favored acid-sensitive species such as some ***Fontinalis*** (Figure 9-Figure 10). The most sensitive bryophyte species exhibit a critical level at *p*H of about 5.5, a level that corresponds to a shift to bicarbonate (HCO_3^-). The more acidiphilous bryophytes such as the liverwort ***Nardia compressa*** (Figure 26-Figure 27) and peatmoss ***Sphagnum auriculatum*** (Figure 28) have declined with liming, and direct exposure to lime deposits usually kills them. However, submerged ***Sphagnum*** mats have, in some situations, temporarily increased in response to liming. Brandrud suggested that this temporary increase was due to the increased production of CO_2.

Figure 26. ***Nardia compressa*** habitat with an acidic *p*H. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Nardia compressa***, a species of acidic streams. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Sphagnum auriculatum***, a species of acidic habitats and that is intolerant of liming. Photo by Bernd Haynold, through Creative Commons.

Although substratum size and stability seem to be the most important factors in determining bryophyte abundance, Catteneo and Fortin (2000) found that *p*H accounted for 9% of the variation in stream bryophyte communities in the Quebec Laurentian Mountains, Canada. The bryophytes exhibited a negative correlation with the filamentous **Cyanobacterium** ***Stigonema*** (Figure 29), a relationship that may have reflected competition promoted by different *p*H optima.

Figure 29. ***Stigonema ocellatum***, in a genus that tends to have a negative correlation with bryophytes based on *p*H relationships. Photo by Yuuji Tsukii, with permission.

When sampling 108 streams in Nepal at over 3000 m, Suren and Ormerod (1998) found that bryophyte communities were highly correlated with altitude, streambed stability, and alkalinity.

Tessler *et al*. (2013) asked if *p*H matters for diversity and distribution of stream bryophytes. They found that in addition to latitude, longitude, and altitude, dissolved Ca and Mg were important factors, indicating that alkalinity was important. Furthermore, tissue P was correlated with *p*H. ***Fontinalis*** *cf.* ***dalecarlica*** (Figure 9-Figure 10) occurred in the lowest *p*H sites in some locations, but seemed to be indifferent to *p*H over the range of 4-7 in experiments. Similar differences between sites occurred in ***Scapania undulata*** (Figure 4). ***Hygrohypnum ochraceum*** (Figure 6) seemed indifferent to *p*H, with maximum PMEase activity at *p*H 5.0 regardless of collection location. Narrow *p*H optima were exhibited by a number of bryophytes. At low *p*H, one could find ***Andreaea rothii*** (Figure 30) and ***Marsupella emarginata*** (Figure 31). Neutral waters included species such as ***Hygrohypnum ochraceum*** (Figure 6) and ***Racomitrium aciculare*** (Figure 7). ***Hygrohypnum eugyrium*** (Figure 8), on the other hand, had a relatively broad *p*H tolerance.

Figure 30. ***Andreaea rothii*** with capsules, a species that does well at a low *p*H. Photo by David T. Holyoak, with permission.

Figure 31. ***Marsupella emarginata***, a species that does well at a low *p*H. Photo by Hermann Schachner, through Creative Commons.

Ormerod *et al.* (1987) found that in upland Welsh streams, ***Scapania undulata*** (Figure 4), ***Nardia compressa*** (Figure 26-Figure 27), and filamentous green algae were typical in streams with a mean *p*H of 5.2-5.8. ***Fontinalis squamosa*** (Figure 32) preferred somewhat higher levels of *p*H 5.6-6.2, with the red alga ***Lemanea*** (Figure 33) occurring at *p*H 5.8-7.0.

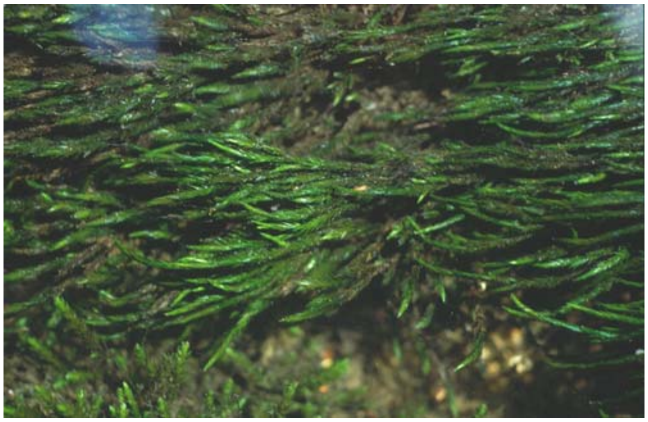

Figure 32. ***Fontinalis squamosa***, a species that prefers an acid *p*H range closer to neutral. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Lemanea fluviatilis***, a red alga; one species prefers an acid *p*H range close to neutral. Photo by J. C. Schou, with permission.

In Ontario, Canada, Yan *et al.* (1985) found no relationship between tracheophyte richness and *p*H in lakes, but a negative relationship of *p*H with bryophyte richness. This again suggests a CO_2 relationship.

Satake and Shibata (1986) took a different approach to the *p*H relationship of bryophytes. They showed that bacterial invasion of the cell wall of the leafy liverwort ***Scapania undulata*** (Figure 4) did not differ in acidic and near-neutral waters. Thus, it appears that decomposition would occur equally well in both acidic and near-neutral waters.

Satake *et al.* (1989) documented the change in *p*H resulting from inflow of neutral water from tributaries, thus raising the *p*H nearer to the mouth. In less acidic reaches, aluminum becomes less soluble. ***Solenostoma vulcanicola*** (Figure 34-Figure 35) is quite tolerant of the acidic water; ***Platyhypnidium riparioides*** (Figure 3, Figure 19) occurs in neutral water, but both disappear after acid and neutral waters meet. Only ***Scapania undulata*** (Figure 4) occurred in waters with >10% aluminum on a dry weight basis.

Figure 34. ***Solenostoma vulcanicola*** habitat, a very acid stream. Photo courtesy of Angela Ares.

Figure 35. ***Solenostoma vulcanicola*** removed from the clump under it. Photo by courtesy of Angela Ares.

CO_2 and Boundary Layer Resistance

Green and Lange (1995) note that bryophytes are considered **ectohydric** because of their uptake of water over the entire or nearly entire surface. They found that for ***Monoclea forsteri*** (Figure 36), the gas-phase CO_2 diffusion pathway is composed only of the boundary-layer resistance. Proctor (1981) determined that the boundary-layer resistance can be increased in leafy liverworts and mosses by growth forms in clumps or turfs.

Figure 36. ***Monoclea forsteri***, a species for which the gas-phase CO_2 diffusion pathway is composed only of the boundary-layer resistance. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Jenkins and Proctor (1985) used wind tunnel measurements to estimate the boundary-layer resistance of aquatic bryophytes for CO_2 diffusion. They found that at water velocities between 0.02 and 0.2 m s^{-1}, resistances were 35 to 5 S mm^{-1} and 70 to 9 S mm^{-1} (S = measure of conductance; Siemens; it is a measure of water's capability to pass electrical flow and is directly related to the concentration of ions in the water), respectively for the mat-forming leafy liverworts ***Nardia compressa*** (Figure 26-Figure 27) and ***Scapania undulata*** (Figure 1, Figure 4). In this same range of water velocities, the **streamer** moss ***Fontinalis antipyretica*** (Figure 37) has a CO_2 boundary-layer resistance of ~180 and 15 S mm^{-1}. In ***F. antipyretica***, boundary-layer resistance seems to limit photosynthesis at velocities below 0.01 m s^{-1}, whereas in mat-forming species it is limiting below 0.1 m s^{-1}. Jenkins and Proctor suggest that the high leaf-area index of the mat formers provides them a more effective exploitation of the low boundary-layer resistance at high velocities while providing them a growth form that is relatively invulnerable to drag. ***Fontinalis***, on the other hand, is able to maximize surface area with its **streamer** growth form in conditions where boundary-layer resistance is limiting.

Figure 37. ***Fontinalis antipyretica***, a species in which photosynthesis is limited by boundary-layer resistance. Photo by Andrew Spink, with permission.

Mägdefrau (1982) considered there to be two life forms in flowing water, "determined by the degree of adaptability to the stationary boundary layer (Prandtl layer) between rock and flowing water." Water flows over dense cushions where the surface of the moss cushion is in the zone of the stationary boundary layer. Loose moss assemblages such as ***Platyhypnidium riparioides*** (Figure 3, Figure 19) project over the boundary layer of the rock and into the rapidly flowing water.

Microbial CO_2

Where there is organic matter, there are microbes. These microbial communities contribute CO_2 to the stream environment through respiration. The rate of release of CO_2 from the microbes increases with temperatures within normal stream range (Vincent & Howard-Williams 1989). On the other hand, rate of release of CO_2 from the water to the air increases with temperature, resulting in a longer residence time in cold water. Vincent and Howard-Williams found that in the three communities they studied in Victoria Land, Antarctica, net loss of carbon from the streams either was induced or even worsened when the temperature was increased from 0 to 10ºC. Thus, in really cold alpine or glacial melt streams, CO_2 can remain in the water for a longer time, giving bryophytes a chance to capture it for photosynthesis.

I have to assume that microbes are important contributors to the CO_2 environment of the stream bryophytes. Bryophytes trap silt, with much contained organic matter and microbes, and they provide a substrate for periphyton, including algae, bacteria, and **Cyanobacteria**. Both of these are sources of CO_2. Our understanding of the relationship of any aquatic plants with periphyton has been limited by our inability to find suitable methods to measure their photosynthesis separately. Hence, to my knowledge, we are unable to give accurate measurements of the contributions of periphyton to the CO_2 used by the bryophytes.

As already noted, Sanford *et al*. (1974) suggested that microbial CO_2 contributed to the success of the moss ***Hygrohypnum ochraceum*** (Figure 6) in parts of the Sacramento River. But measured contributions of microbial CO_2 to stream bryophytes seems to have been neglected by researchers.

Even if we measure periphyton CO_2 intake and output on glass slides or other non-living substrates, it does not mean that the same would occur on the bryophytes. Bryophytes can rapidly take up the CO_2, altering the diffusion gradient at the surface. Bryophytes provide oxygen that can enhance the productivity of the bacteria. Other nutrient interactions may occur, such as the production of usable nitrogen compounds by the **Cyanobacteria** that can enhance productivity of both the bryophytes and the other periphyton.

Once again, we are left with a dilemma. Bryophytes in alkaline glacial meltwater streams have less opportunity to accumulate detritus and siltation, often living among rocks and boulders with little organic accumulation in the rapid flow. Once again we are left with no explanation of the source of CO_2 for photosynthesis for such bryophytes.

Diving Bell

One novel idea is that mosses may use their photosynthetic air bubbles like a diving bell. It is typical to find photosynthesizing aquatic mosses covered in tiny air bubbles, a phenomenon known as **pearling (**Figure 42**)**. If they are able to work like a diving bell, the bubble with a high concentration of photosynthetic O_2 would trade its O_2 for CO_2 that is dissolved in the water, thus creating a gaseous environment containing CO_2 at the leaf surface. Such mechanisms are used, in reverse, to keep diving insects and spiders alive under water, sometimes as long as an hour. But the insects carry their "bells" of oxygen-rich air under water, then breathe in O_2 and expel CO_2. As the O_2 concentration diminishes, more diffuses into the diving bell from the water, and the CO_2 from their respiration diffuses from the diving bell into the water. The same mechanism should work for bryophytes that produce their own bubble through photosynthesis, but this mechanism assumes that there is free gaseous CO_2 in the water column, not bicarbonate or carbonate. Thus, if it works at all, it presumably works only at lower *p*H levels where free CO_2 exists ... or perhaps where microbial contributions are available. We still have no explanation for CO_2 sources for bryophytes in alkaline water

Nutrient Availability

The nutrients available to the river mosses come from river substrate and human contributions (García-Alvaro *et al*. 2000). One potential source of nutrients in streams is from litter fall. However, Dawson (1976) found that passage from stream banks to the stream was insignificant because the bank vegetation was able to trap the litter. Nevertheless, leaves do enter the stream when the bank does not have suitable vegetation to trap it. It especially accumulates behind rocks (Figure 38.

Figure 38. Stream in central Canada showing leaf litter accumulating behind rocks. Photo by Robert Berdan, with permission.

In the Tyrolean Alps, Austria, Füreder *et al.* (2001) found that a spring-fed system and a glacial-fed stream differed in their seasonal peaks of nutrients. In the spring-fed stream, concentrations of suspended solids, nitrate, and particulate phosphorus occurred during maximum discharge during snowmelt in June. In the glacier-fed stream, the high discharge occurred in summer, creating strong **diel** (within 24 hours) fluctuations in flow and concentrations of suspended solids. This strong diel periodicity created harsh, unstable environmental conditions during summer. Winter in the glacial-fed stream, on the other hand, created relatively stable conditions.

García-Alvaro *et al*. (2000) found that there was a strong correlation between element concentrations in the water and that in the moss ***Platyhypnidium riparioides*** (Figure 3, Figure 19). This relationship is linear for N, P, and K, but is similar to Michaelis-Menten saturation-type curve for Ca and Mg. Furthermore, the enrichment ratios in the moss are much higher for N, P, and K than for Ca and Mg. In fact, when Ca and Mg are in high concentrations in the water, there is a negative correlation with the enrichment ratio in the moss. The researchers suggested that the uptake efficiency may be greater when the element concentrations are low, but decrease as the moss becomes saturated.

The nutrient needs of bryophytes are modest, permitting them to live in habitats that are not particularly inviting to algae. Often pollution that increases nutrients in a stream is detrimental to bryophytes because of the resulting increase in algal growth. In a New Zealand stream, addition of nutrients from sewage caused enhanced growth of the filamentous algae, with a concomitant reduction in the bryophytes. On the other hand, in the Kuparuk River, Alaska, Bowden *et al*. (1994) found that addition of phosphorus enhanced the growth of both the moss ***Fontinalis neomexicana*** (Figure 39) and several ***Hygrohypnum*** species (Figure 6). P enrichment did not seem to affect the distribution, abundance, or metabolism of the moss ***Schistidium agassizii*** (Figure 40-Figure 41), but ***Hygrohypnum alpestre*** (Figure 42) and ***H. ochraceum*** (Figure 6) went from being rare to producing extensive growths in these enriched reaches of the Kuparuk River (Arscott *et al*. 2000).

Figure 39. ***Fontinalis neomexicana***, a species that experiences enhanced growth with added phosphorus. Photo by Faerthen, through Creative Commons.

Figure 40. ***Schistidium agassizii***, a species that seems to be unaffected by addition of phosphorus. Photo by Andrew Hodgson, with permission.

Figure 41. ***Schistidium agassizii***, a species that did not respond to addition of phosphorus in an Alaskan stream. Photo by Michael Lüth, with permission.

Figure 42. ***Hygrohypnum alpestre***, shown here with air bubbles (**pearling)** that contribute to its gas exchange. This species benefits greatly by addition of phosphates in an Alaskan stream. Photo by Michael Lüth, with permission.

Nutrient concentrations may not be consistent within the regions of a single stream or stream system. García-Alvaro *et al*. (2000) demonstrated this when they examined element concentrations and enrichment in ***Platyhypnidium riparioides*** (Figure 3, Figure 19). They found that the lowest element concentrations were in the headwater populations, those in the middle course were Ca-enriched, and the lower course populations had the highest concentrations of N, P, K, and Na. These various concentrations in the moss tissues were significantly correlated with those in the water. When the concentrations in the water were high, the uptake was slower, permitting a kind of acclimation to changing water chemistry and avoiding deficiencies.

Meyer (1979 reported that the silty sediments had maximum buffering capacity, with a higher phosphorus buffering capacity in silty sediments than the in sandy sediments in Bear Brook, New Hampshire. The microbial community contributed little to the phosphorus-buffering capacity of sediments.

Many things can reduce the nutrients available in streams. Algae can be effective competitors for nutrients in streams. For example, Tate *et al*. (1995) found that approximately 90% of the phosphate injected into a stream was rapidly assimilated by the green alga *Ulothrix* sp. (Figure 43). Phosphates can be sorbed on iron oxides, thus being removed from the water column and unavailable.

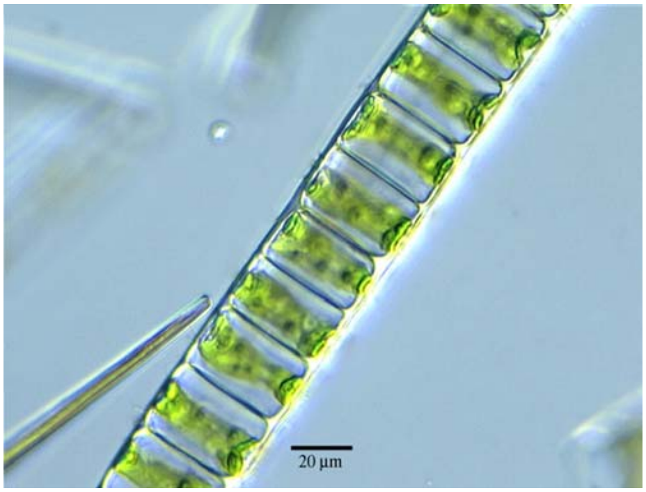

Figure 43. *Ulothrix* sp., a genus that rapidly assimilates phosphorus in Alaskan streams. Photo by Jason Oyadomari, with permission.

In Arctic Alaska, Finlay and Bowden (1994) found that the bryophytes ***Hygrohypnum*** spp. (Figure 6) and to a lesser extent ***Fontinalis neomexicana*** (Figure 39) were abundant in riffles that had been fertilized with phosphorus in the Kuparuk River. They were much less common in fertilized pools, and virtually absent in unfertilized reaches of the river. They discovered what I have long suspected, based on my observations, that in the presence of excess P, they were limited by epiphytes on their leaves. But P is typically low in streams, and in such cases P can be limiting for the bryophytes. The differences in response of ***Fontinalis neomexicana*** to P fertilization were more pronounced in flowing water than in pools.

Samecka-Cymerman (1988) found that nutrients separated the microhabitats of the mosses ***Fontinalis antipyretica*** (Figure 37) and ***Platyhypnidium riparioides*** (Figure 3, Figure 19). Gametophyte length of ***F. antipyretica*** correlated with potassium levels in the water, total nitrogen, nitrate content in water, and nitrogen content in plants. For ***P. riparioides***, length and number of lateral branches correlated with the potassium and phosphate levels in the water. Both have the ability to decompose phenol and ethylene glycol; high levels of nitrogen calcium, and magnesium give these two moss species greater resistance to these two toxic chemicals. This ability to decompose these two chemicals helps to purify the water.

Steinman (1994) found that P enrichment in Sludge Creek, Tennessee, USA, affected the N:P ratio in the leafy liverwort ***Porella pinnata*** (Figure 44-Figure 45***)***. With an original P:N ratio of 1, both the P:C ratio and P:N ratio of ***P. pinnata*** increased significantly when P was added to the stream. In this case, the epiphytes did not increase significantly, but Steinman suggested that snail grazing may have prevented that.

Figure 44. ***Porella pinnata*** on cypress knees, a typical habitat. Photo by Paul Davison, with permission.

Figure 45. ***Porella pinnata***, a species in which the P:N ratio increases significantly when P is added. Photo by Alan Cressler, with permission.

Schwoerbel and Tillmanns (1974) found that ***Fontinalis antipyretica*** (Figure 37) is able to assimilate both nitrate and ammonium. It is unable to take up nitrate in the dark, requiring energy, unlike the alga ***Chattonella antiqua*** (see Figure 46) that is able to take up nitrates in the dark, but at only 86% of the daytime rate (Nakamura & Watanabe 1983).

Figure 46. *Chattonella marina*, an alga that takes up nitrates in the dark. Photo from FWC, through Creative Commons.

Miyazaki and Satake (1985) concentrated their study on inorganic carbon and nitrogen uptake by the leafy liverworts ***Scapania undulata*** (Figure 1, Figure 4) and ***Solenostoma vulcanicola*** (Figure 34-Figure 35). ***Solenostoma vulcanicola*** may be the most acid-tolerant species among the bryophytes. They likewise found that these two species were able to use ammonium. Nitrate uptake was less than ammonium uptake. Their experiments, including light and dark, suggest that at least these liverworts use ammonium as their major N source, and that it is less dependent on light than is C uptake.

Li and Vitt (1994) demonstrated that different species have different responses to N and P gradients. Concentrations of these nutrients affected regeneration ability, establishment rates, and responses of establishment. Some species were able to benefit initially by enrichment, but then declined as other species increased.

Frahm (1975) found that ***Fontinalis antipyretica*** (Figure 37) was the least tolerant of toxic pollutants and ***Leptodictyum riparium*** (Figure 47-Figure 48) was the most tolerant among five aquatic species. Interestingly, these species were most tolerant of sodium and chlorine, but had low tolerances for NH_4^+, Fe^-, and PO_4^{3-}.

Figure 47. ***Leptodictyum riparium***, a species of shallow water and that can get stranded above water; it is more tolerant than most aquatic bryophytes of sodium and chlorine. Photo by Scott Zona, through Creative Commons.

Figure 48. ***Leptodictyum riparium***, a species that is more tolerant of sodium and chlorine than are most aquatic bryophytes. Photo by Hermann Schachner, through Creative Commons.

Vanderpoorten *et al*. (1999) found that ***Chiloscyphus pallescens*** (Figure 49), ***Apopellia endiviifolia*** (Figure 50), and ***Hygroamblystegium tenax*** (Figure 15) exhibited low-nutrient preference in comparison to ***Hygroamblystegium fluviatile*** (Figure 17), ***Cinclidotus danubicus*** (Figure 51), ***C. riparius*** (Figure 52), and ***Fissidens crassipes*** (Figure 53). ***Leptodictyum riparium*** (Figure 47-Figure 48), ***Fontinalis antipyretica*** (Figure 37), and ***Platyhypnidium riparioides*** (Figure 3, Figure 19) all had a broad trophic range, but they occurred more frequently in **eutrophic** (energy-rich) streams.

Figure 49. ***Chiloscyphus pallescens***, a species preferring low nutrient levels. Photo by Hermann Schachner through Creative Commons.

Figure 50. ***Apopellia endiviifolia***, a species preferring low nutrient levels. Photo by J. Claude, through Creative Commons.

Figure 51. ***Cinclidotus danubicus***, a species that does not prefer very low nutrient levels. Photo by Michael Lüth, with permission.

Figure 52. ***Cinclidotus riparius***, a species that does not prefer very low nutrient levels. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Fissidens crassipes***, a species that does not prefer very low nutrient levels. Photo by Michael Lüth, with permission.

Nutrient concentrations in streams change with the seasons. In summer and autumn, concentrations of K, Fe, P, and N increase, decreasing through winter and spring (Martínez-Abaigar *et al*. 2002). Ca and Mg, on the other hand, seemed to have random temporal patterns. The bryophyte stem tips (4.5 cm) had a uniform ion concentration response among the shoots, with the notable exception of Ca. However, some species were deviants.

Fontinalis antipyretica (Figure 37) had a higher N concentration and ***F. squamosa*** (Figure 32) had a greater accumulation of Fe. Both species had increasing concentrations of Ca, Mg, and Fe from the apex to base. N, P, and K had the reverse pattern. This is consistent with low solubility of Ca, Mg, and Fe, and their consequent non-transportability. On the other hand, N, P, and K are soluble, and their higher concentrations at the apex is consistent with their transport to growing regions.

During summer and winter low-flow conditions, Chapman *et al*. (1996) added potassium and nitrate to a small moorland stream in the headwaters of the River Wye, Wales. In the summer, ~18% of added nitrate and 58% of K was removed between the addition site and the catchment outlet. During winter, nitrate depletion did not seem to occur, and 93% of the K also passed through this stretch, but at a slower rate. In this case, ***Sphagnum*** (Figure 28) was considered a major contributor to the removal of the nutrients through biological activity.

Christmas and Whitton (1998) actually found that inorganic N and phosphate concentrations in the water increased downstream in the Swale-Ouse River system, north-east England. They investigated P and N relationships in ***Fontinalis antipyretica*** (Figure 37) and ***Platyhypnidium riparioides*** (Figure 3, Figure 19). They found that the variability in N and P concentrations were greatest in the headwaters, but like that in the stream water, inorganic N and phosphate concentrations in the mosses increased downstream. But the N:P ratio in the mosses changed, from 14.9 to 6.8 for ***F. antipyretica*** and from 12.5 to 5.5 for ***P. riparioides***, suggesting that P was increased proportionally more than N in these mosses.

Steinman and Boston (1993) found that ***Porella pinnata*** (Figure 44-Figure 45) in Walker Branch, Tennessee, USA had a significantly greater P uptake than did periphyton at all sites and seasons. The biomass-specific rates of ***P. pinnata*** were greater in fall, whereas the periphyton on the cobbles had their greatest biomass-specific photosynthesis and P uptake in winter and spring.

Núñez-Olivera *et al*. (2001) found relatively unpredictable correlations between the concentrations of the elements in the water and those in the bryophyte tissues [***Fontinalis antipyretica*** (Figure 37), ***F. squamosa*** (Figure 32), ***Jungermannia exsertifolia* subsp**. ***cordifolia*** (Figure 54-Figure 55), and ***Apopellia endiviifolia*** (Figure 50)]. Rather, the concentrations of N, P, K, Ca, Mg, Na, and Fe in the bryophytes reflected a complex interaction of internal and environmental factors, including the annual growth cycle of the bryophytes, changes in sclerophylly in ***Jungermannia exsertifolia*** subsp. ***cordifolia***, and temporal variation in the chemical features of the stream. For the elements N, P, Na, and Fe, the lowest concentrations typically occurred in spring and highest ones in autumn.

Figure 54. ***Jungermannia exertifolia*** ssp. ***cordifolia***, a species with unpredictable nutrient interactions. Photo by Michael Lüth, with permission.

Figure 55. ***Jungermannia exertifolia*** ssp ***cordifolia***, a species with complex nutrient interactions, with Diptera larva. Photo by Michael Lüth, with permission.

Suren (1996) examined 95 streams in South Island, New Zealand. He suggested that geology, land use, and water quality were among the factors influencing the type of bryophyte communities that developed.

Early investigations on mineral nutrition in aquatic bryophytes include those of Schwoerbel and Tillmanns (1968, 1974, 1977). They determined that ***Fontinalis antipyretica*** (Figure 37) assimilates both nitrate and ammonium, but that no uptake occurs in the dark. This uptake is facilitated by activity of nitrate reductase.

Temperature Effects

Although streams have much less temperature variation than terrestrial habitats, they do have seasonal differences. Stream bryophytes are protected by water that cannot go below 0ºC without becoming ice. The ice itself can serve as an insulator. We found that the water in our study stream near Plymouth, New Hampshire, USA, stayed at about 0.8ºC during the winter while snow was on the ground.

Summer temperatures can be a bit more problematic. Although our study stream rarely reached temperatures above 20ºC, streams in the open or at lower latitudes can exceed that temperature. Based on its distribution in both hemispheres, but not in tropical non-mountain sites, this seems to be a limiting factor for species of the largely aquatic moss ***Fontinalis*** (Figure 37) (Glime 1987a, b).

Biggs and Saltveit (1996) considered temperature, along with light and nutrients, to be one of main factors to govern biomass gain. As we might expect, temperature affects different species differently. For example, in the Kuparuk River, Alaska, USA, Arscott *et al*. (2000) found that species of ***Hygrohypnum*** (Figure 6) were more tolerant of temperatures above 20ºC than were the moss ***Schistidium agassizii*** (Figure 40). Somewhat reflecting their habitat differences, ***Hygrohypnum*** species had a strong response to temperature and increased light, but were susceptible to desiccation, whereas ***Schistidium agassizii*** had little response to increases in light, recovered rapidly from desiccation, but was inhibited by high temperatures.

Sanford *et al*. (1974) found that in experiments at temperatures above 26ºC some of the stem tips of ***Hygrohypnum ochraceum*** (Figure 6) died, with no survival after four weeks at 30ºC. On the other hand, growth occurred at temperatures as low as 4ºC. Optimal temperatures for growth ranged ~17-21ºC.

Fontinalis (Figure 37) species are among the more truly aquatic bryophytes. Nevertheless, while they do not thrive at high temperatures, they have a remarkable resilience. Glime and Carr (1974) experimented with maintaining ***Fontinalis novae-angliae*** (Figure 56) at a range of temperatures up to boiling. Plants treated at 1-35ºC wet had at least some survival and new growth, but most of those at the upper temperatures initially had brown leaves that were eroded away by heavy flows. Nevertheless, one clump of mosses that had been boiled 10 hours per day for 4 days produced a new green shoot that was located one year later. While these conditions do not exist in nature, they demonstrate the resilience of these stems.

Figure 56. ***Fontinalis novae-angliae*** with capsules from a stream in New Hampshire, USA. This species can survive up to boiling temperatures through its stem tissue, but the leaves quickly lose color above 20ºC. Photo by Janice Glime.

Alaskan streams seldom reach high temperatures. Irons and Oswood (1992) recorded temperatures of three streams in the Brooks range. The mean annual temperatures were 1.1, 2.3, and 2.9ºC, with maxima of 5.8, 13.0, and 21.4ºC. There were wide differences in the rates at which temperatures rose in the spring and dropped in the autumn. The maximum daily amplitude was 6.6, 4.1, and 11.6ºC. These patterns resulted in degree-days of 400, 950, and ~1000. The tundra stream, which is about 450 km farther north than the two subarctic streams, accumulated more degree-days, had higher maximum and mean temperatures, greater daily temperature amplitude, and steeper slopes of vernal temperature rise and autumnal temperature decline than the two subarctic streams. Irons and Oswood attributed the higher temperatures and greater variability in the tundra stream to the lack of a canopy.

Climate change can have a significant impact on the temperatures of stream waters. Leith and Whitfield (1998) compared historic records in south-central British Columbia, Canada. They found that spring runoff started earlier, late summer-early fall flows were lower, and early winter flows were higher when the climate was warmer. As we might expect, this pattern is similar to that of streams at a lower latitude.

One of the consequences of increased temperatures is the reduction of dissolved CO_2 in the water (Cappelletti & Bowden 2006). Soluble reactive phosphorus will also likely increase in the Arctic, since higher temperatures increase solubility.

Ceschin *et al*. (2012) determined that aquatic bryophytes in the Tiber River basin, Italy, preferred cool water with a mean of ~15ºC. But as expected, preferences differ by species. ***Palustriella commutata*** var. ***commutata*** (Figure 57), ***Cratoneuron filicinum*** (Figure 11), ***Fissidens bryoides*** (Figure 58), and ***Cinclidotus aquaticus*** (Figure 59) prefer temperatures below 12ºC. ***Fontinalis antipyretica*** (Figure 37) has a wide ecological niche. ***Leptodictyum riparium*** (Figure 47-Figure 48) and ***Riccia fluitans*** (Figure 60) prefer quiet water, and we can expect them to experience a rather wide temperature range.

Figure 57. ***Palustriella commutata*** var. ***commutata***, a species preferring temperatures below 12ºC. Photo by Malcolm Storey, with online permission.

Figure 58. ***Fissidens bryoides***, a species preferring temperatures below 12ºC. Photo by Bob Klips, with permission.

Figure 59. ***Cinclidotus aquaticus***, a species preferring temperatures below 12ºC. Photo by Hermann Schachner, through Creative Commons.

Figure 60. ***Riccia fluitans***, a species of quiet water that often has a wide temperature range. Photo by Christian Fischer, through Creative Commons.

Light

Abou-Handman *et al.* (2005) have demonstrated that light is an important factor in determining the composition and biomass of the stream macrophytes. Forest cover contributes to light reduction and alters light quality by absorbing proportionally more red light, leaving the transmitted light with more green proportionally. For example, Tiffett (1969) found that light reaching the stream bed through overhanging trees had only 20-30% of incident light intensity. When canopy cover was at its fullest in summer, only 4-6% of the light reached the stream bed.

Suren (1996) found that land use practices can alter light regimes. Typically, those in developed catchments receive more light that those in undeveloped catchments (Beschta & Taylor 1988; Collier *et al.* 1995). Bryophytes are typically shade plants with low light compensation points (Martin & Churchill 1982; Longton 1988), permitting the to survive in shaded forest streams (Suren 1992, 1993; Naiman 1983). But they can also acclimate to high light conditions by producing secondary pigments (Glime 1984; Glime & Vitt 1984; Núñez-Olivera *et al.* 2010). Suren (1993) documented this adaptability by observing similar bryophyte biomass in shaded and unshaded streams in the central southern Alps.

Light penetration is higher at 700 nm in laminar flow than at 470 nm (Swatland 2020). Turbulence changes the penetration, intensity, and quality of light in water. It causes more, shorter, and less intense peaks of light than that found with laminar flow. Bubbles make lenses that can create shadows, with smaller bubbles creating larger shadows than large bubbles.

Using shading cloth that reduced light by 75%, Ceneviva-Bastos and Casatti (2014) experimented with light effects on the food web structure of a deforested pasture stream in Brazil. They found that the shade favored the growth of bryophytes and pteridophytes, particularly at the land-water interface.

As already noted, Núñez-Olivera *et al.* (2010) found that UV radiation varied seasonally, and that several UV-protective compounds likewise varied with those seasons.

Seasonal Changes

The seasons change a number of stream parameters, as we have seen. Ice covered with snow can block the light in a pool area, whereas open flow may receive high light intensities due to loss of foliage on the trees and reflection from the surrounding snow. Anchor ice can remove huge areas of bryophytes, leaving the stream barren in some areas.

One of the changes that may have an impact on bryophytes is the winter blooms of diatoms in streams (Hynes 1970). The winter species are typically in the genera ***Achnanthes*** (Figure 61), ***Meridion*** (Figure 62), ***Gomphonema*** (Figure 63), ***Navicula*** (Figure 64), and ***Diatoma*** (Figure 65). In a northern Michigan, USA, stream, Vacco (1978) found the predominant taxa to be ***Cocconeis*** (Figure 66) and ***Meridion***. In another Upper Peninsula, Michigan, stream, ***Diatoma*** reached numbers that hid the mosses in early March (Glime unpublished). In a New Hampshire, USA, stream, my students and I found mostly ***Tabellaria*** (Figure 67) and ***Fragilaria*** (Figure 68) (unpublished), similarly blanketing and hiding the mosses.

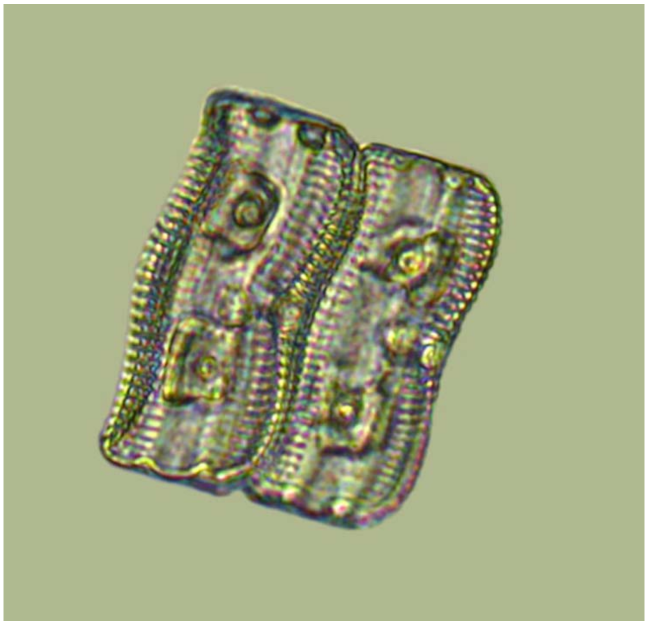

Figure 61. ***Achnanthes***, a typical winter stream diatom. Photo from Manaaki Whenua – Landcare Research, with online permission.

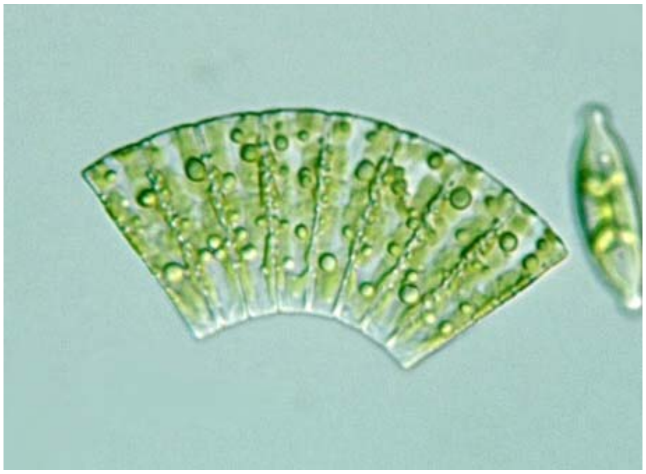

Figure 62. ***Meridion circulare***, a typical winter stream diatom. Photo by Yuuji Tsukii, with permission.

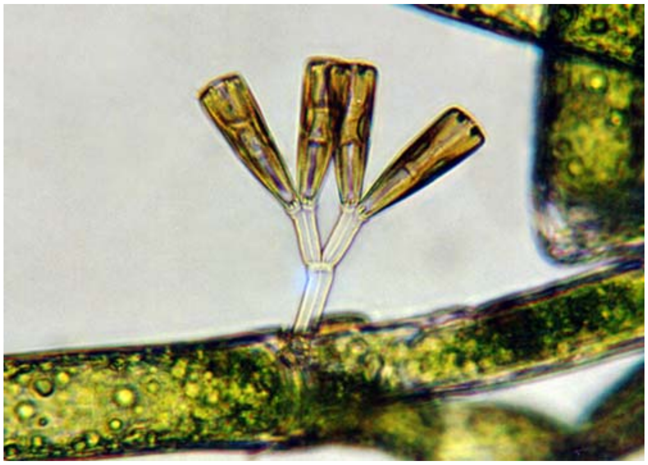

Figure 63. ***Gomphonema*** sp., a typical winter stream diatom. Photo from Manaaki Whenua – Landcare Research, with online permission.

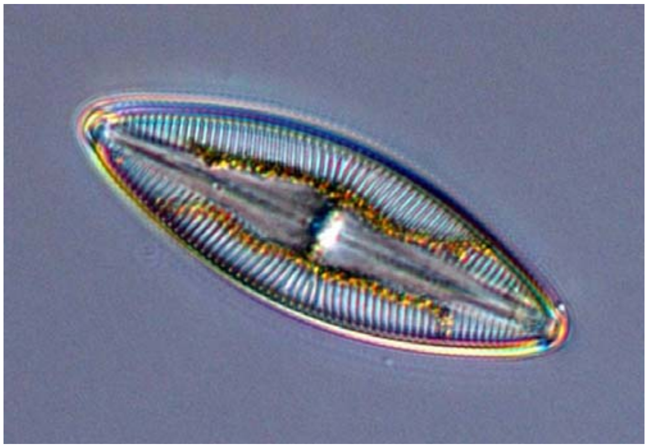

Figure 64. ***Navicula*** sp., a typical winter stream diatom. Photo from Phyto'pedia, through Creative Commons.

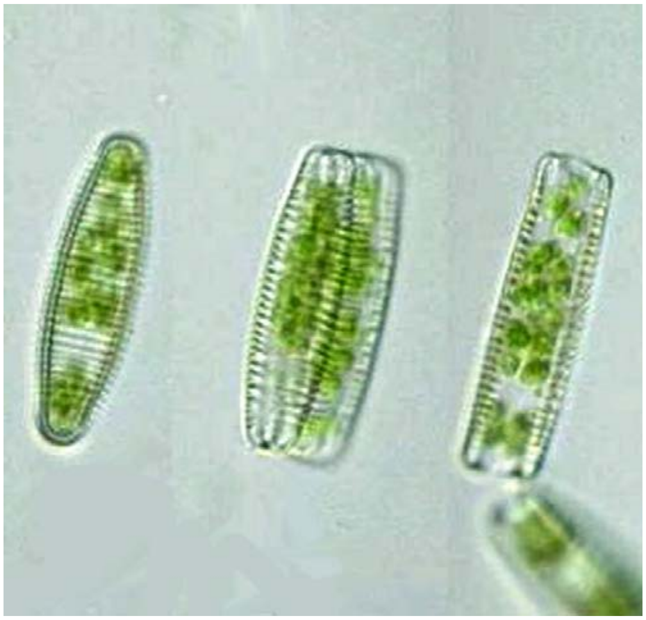

Figure 65. ***Diatoma vulgaris***, a typical winter stream diatom. Photo by Yuuji Tsukii, with permission.

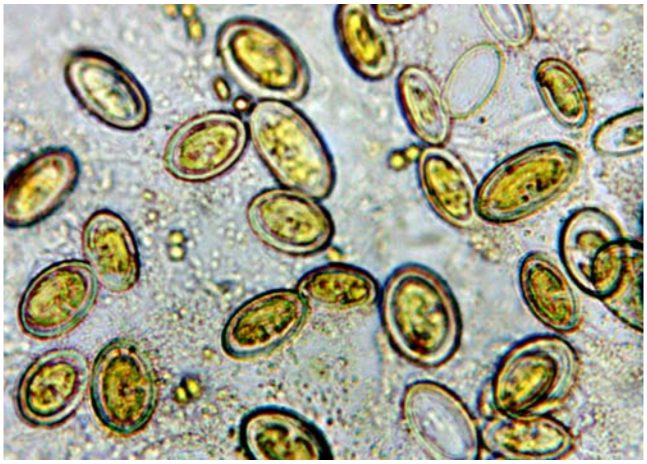

Figure 66. ***Cocconeis*** sp., a common winter and summer diatom on bryophytes in the Upper Peninsula of Michigan, USA. Photo by Manaaki Whenua – Landcare Research, with online permission.

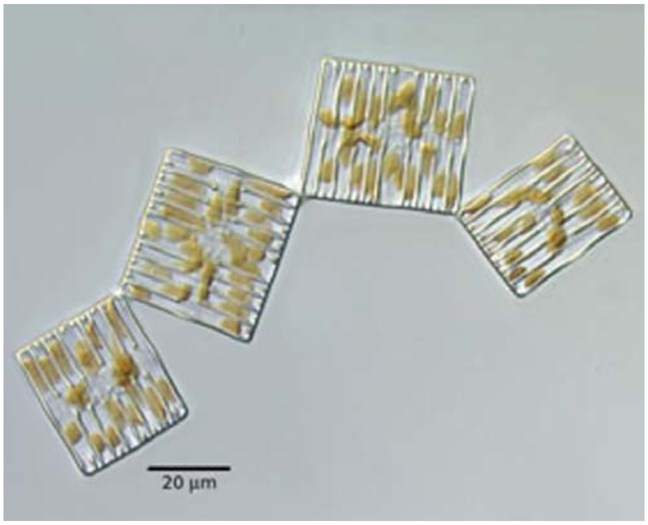

Figure 67. ***Tabellaria flocculosa***, a common winter and summer diatom on bryophytes in the Upper Peninsula of Michigan, USA. Photo by Jason Oyadomari, with permission.

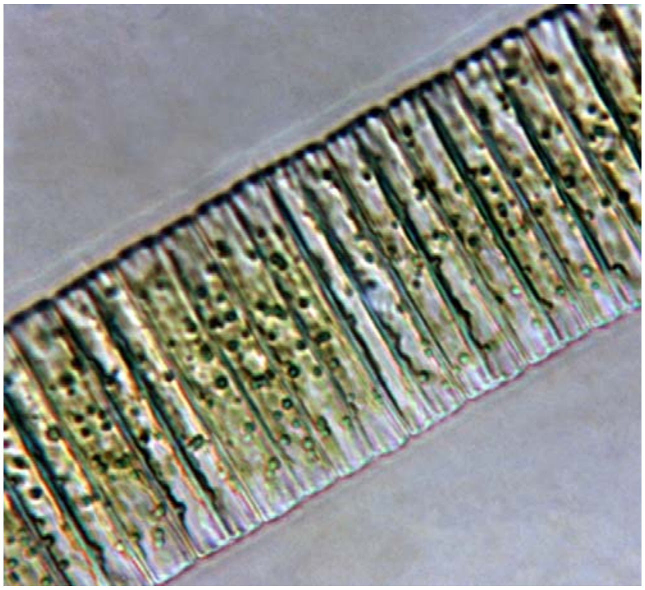

Figure 68. ***Fragilaria*** sp., a common winter and summer diatom on bryophytes in the Upper Peninsula of Michigan, USA. Photo from Manaaki Whenua – Landcare Research, with online permission.

In a Tennessee USA woodland brook, Steinman and Boston (1993) demonstrated that even the bryophytes have seasonal changes in biomass and percent cover (Figure 69). Biomass is often reduced by ice flow and silt in the water. The greatest biomass occurred in September and the least in January. Bryophyte abundance peaked late in the summer, then was reduced by a severe winter storm (Steinman & Boston 1993). Ice breakup and increased flow can greatly decrease bryophyte abundance and biomass. For ***Porella pinnata*** (Figure 44-Figure 45), the biomass-specific rates of photosynthesis and phosphorus uptake were greater than those of periphyton in autumn. But in winter and spring the biomass-specific rates of the periphyton on cobbles exceeded that of the bryophytes.

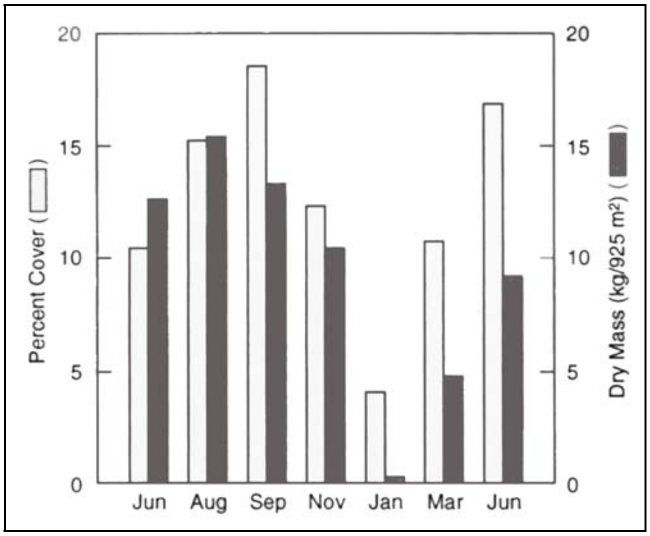

Figure 69. Bryophyte cover and dry mass by season in Walker Brook, Tennessee, USA. Modified from Steinman & Boston 1993.

In an unforested headwater stream, ***Bryum pseudotriquetrum*** (Figure 70) and ***Fontinalis antipyretica*** (Figure 37) showed seasonal variability of the photoprotection system (Núñez-Olivera *et al*. 2010). But the changes in environmental factors did not completely explain the photoprotection changes. Although variables including water temperature, stratospheric ozone (providing an atmospheric shield against UV), UV-A, and UV-B had distinct seasonal variation, only a few physiological variables were seasonal. Both species did exhibit seasonal variation in xanthophyll cycle activity and UV absorbance compounds. Physiological parameters such as the **sclerophylly index** [calculated as quotient between dry mass (dried at 80ºC for 24 h) and surface area of prostrate bryophyte apex onto the horizontal plane] and chlorophyll fluorescence parameters showed less relationship to seasons. For ***B. pseudotriquetrum***, UV-protective compounds were positively associated with radiation levels, but in ***F. antipyretica***, these photoprotective mechanisms did not correlate with any measured environmental variable. This suggests that the two species use different photoprotection mechanisms, with different environmental regulators.

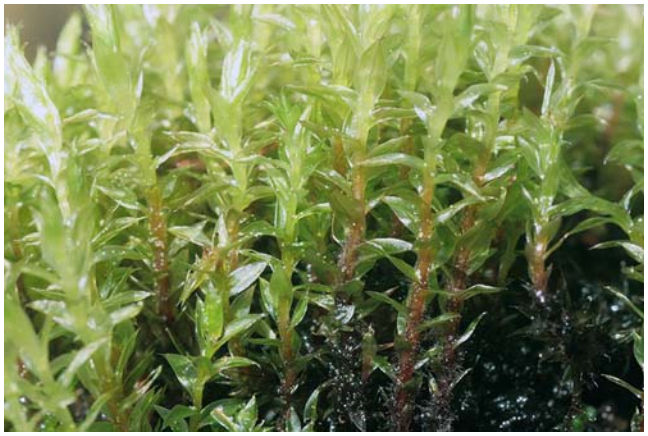

Figure 70. ***Bryum pseudotriquetrum***, a species with seasonal variation in its photoprotection system. Photo by Hermann Schachner, through Creative Commons.

Summary

The *p*H of water is mainly determined by the substrate, but pollution can contribute, especially to lowering it. The *p*H affects the response of bryophytes to dissolved ions, especially heavy metals, by affecting solubility and uptake. Ions like Ca^{2+} and Mg^{2+} can buffer the water and help to lessen *p*H fluctuations. The *p*H can be a major determinant of the bryophyte flora in the streams, with almost all disappearing at *p*H below 4.0. ***Solenostoma vulcanicola*** is a leafy liverwort tolerant of some of the lowest *p*H levels.

But perhaps the most important effect of *p*H is on the concentration of CO_2 in the water, with bicarbonates increasing above *p*H ~6 to the exclusion of free CO_2. The CO_2 also escapes from the water as a gas, but remains in the water longer in cold water. A further complication for the bryophytes is overcoming the boundary-layer resistance, a phenomenon that is affected by bryophyte growth form. In addition to contributions of CO_2 from acidic rocks, microbial CO_2 is an important contributor. The mosses might be able to use a **diving bell** to exchange photosynthetic O_2 for CO_2 that is dissolved in the water.

Nutrients enter the stream from bedrock, but mostly from runoff, and are carried downstream by flow. Some leaf litter may remain to provide nutrients through decomposition. Bryophytes are able to store some nutrients for later use, some metals are bound in the cell walls, and others remain in relative equilibrium. Bryophytes have low nutrient needs; high nutrients favor algae and tracheophytes that can out-compete the bryophytes for light and space. On the other hand, streams are often phosphorus-limited even for at least some bryophytes.

Temperatures above 15-20ºC are detrimental to many aquatic bryophytes. This is primarily due to the greater increase of respiration compared to that of photosynthesis. At higher temperatures, the CO_2 dissolved in the water diminishes, limiting photosynthesis.

Water absorbs red light rapidly, leaving deeper waters with a greater proportion of green and blue light. Since red light is important for photosynthesis, this presents another limiting factor. Bubbles and turbulence affect the water quality and intensity reaching the submersed bryophytes.

Bryophyte cover changes seasonally in response to light intensity, nutrient availability, scouring, and temperature.

Acknowledgments

For the entire stream section of this book, I have to thank my sister, Eileen Dumire, for her companionship in my field excursions and her help in sorting insects and maintaining my bibliography.

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CHAPTER 2-3
STREAMS: STRUCTURAL MODIFICATIONS – LEAVES AND STEMS

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CHAPTER 2-3
STREAMS: STRUCTURAL MODIFICATIONS – LEAVES AND STEMS

Figure 1. ***Fontinalis antipyretica***, demonstrating keeled leaves that might be advantageous in flowing water or in reducing water loss when water levels drop. Photo by Li Zhang, with permission.

Although bryophytes are considered by most textbooks to be abundant in moist habitats, few are strictly aquatic. Even fewer are able to live their entire lives submersed in water. However, bryophytes do seem to have a remarkable ability to survive and be productive in deeper water than do other plants and most algae.

The paucity of truly aquatic bryophytes seems to also result in fewer studies on their structural adaptations and life strategies. Nevertheless, several bryologists in the early 20th Century summarized some of the characteristics of aquatic bryophytes (Watson 1919; Gams & Bodensee 1927).

The diversity can be high when one includes the stream banks and emergent rocks. For example, in 165 stream locations in Portugal (Figure 2), Vieira *et al.* (2012) found more than 100 taxa that occurred in three or more of the sampled streams. Average richness was 4.2 species per 0.25 m^2 plot, ranging 1-18 taxa per plot.

In a comprehensive study in the Iberian Peninsula, Fernández-Martínez *et al.* (2019) suggested that the evolution of traits and species distribution in **hygrophytic** (plants living with abundant moisture) mosses are driven by climate and water chemistry. Both structural and physiological differences can result from genetically determined differences and environmental expressions.

Figure 2. Quarteria River, Portugal. Photo by Kolforn, through Creative Commons.

In streams, bryophytes may serve as reservoirs of heavy metals, which can subsequently be released by acid loadings (Caines *et al.* 1985). Bell and Lodge (1963) showed that the occurrence of certain aquatic mosses could be correlated with calcium or nutrient content in the water. Romanova (1965) and Jeglum (1971) found that bryophytes indicated the condition of *p*H and water level in peatland streams.

In the stream habitat, bryophytes must endure changing water levels, rapid flows, silt loads, loss of sperm to the flow, fragmentation and abrasion, being embedded in surface ice and anchor ice, low light in summer, and high light when leaves are off the trees. Light coming through the trees is heavy on green and the water further absorbs red light. Some bryophytes have adaptations to optimize their survival under these conditions. These adaptations include both structural and physiological modifications, as well as life cycle strategies that permit dispersal and colonization.

Vieira *et al.* (2005) considered the niche relationships of stream bryophytes to be specialized. These niches correlate with structural and physiological adaptations (Glime & Vitt 1984; Vitt & Glime 1984; Slack & Glime 1985).

Some stream bryophytes are able to exist in a wide variety of stream types and conditions, including adaptations to low light and temperature, rapid nutrient uptake, and resistance to scouring (Bowden *et al.* 1999). Their productivity can exceed that of the algae in the streams, but is much less known than that of the algae. But much remains unknown or poorly understood about stream bryophytes – rate of decomposition, dynamics of nutrient uptake, how they interact with microorganisms, and how much they are needed by fish for spawning and refuge.

Perhaps one reason some of the aquatic bryophytes have such wide niches is that many bryophyte taxa have invaded the water two or more times in their evolutionary history (Cook 1999). This back and forth evolutionary behavior has resulted in aquatic representatives in 440 genera and 103 families of embryo-bearing plants. Cook reminds us that bryophytes and other embryo-bearing plants are derived from aquatic ancestors. Thus, they have had the opportunity to accumulate genes suitable for both terrestrial and aquatic habitats. Cook suggests that invasion of water has taken place 10-19 times in the evolutionary history of the bryophytes, compared to 204-245 times in seed plants.

Adaptations to living in water can include modified structures, life and growth forms, life cycle strategies, physiological adaptations, phenological behavior, and herbivory protections.

Structural Modifications

Hedenäs (2001) used a monumental data set (439 pleurocarpous moss species, 86 characters) to compare taxa all over the world based on characters influenced by climatic zone, general habitat, and wetland vs. non-wetland. He identified two complex functions that explained differences in character state frequencies: water conduction and retention, and spore dispersal.

Even early researchers found the development of aquatic bryophytes to be interesting and instructive. Leitgeb (1868) provided a detailed description, with drawings, of the development of the stems of ***Fontinalis antipyretica***.

Evolutionary Drivers

Hedenäs (2001) found that climatic zone is the predominate force in determining moss characters (44%), followed by general habitat (35%), and last by wetland vs non-wetland (23%), although among stream mosses the rate of flow and water level fluctuation pose the most important gradients. Characters related to water conduction and retention included stem central strand (Figure 3), leaf orientation, leaf costa type (Figure 4), alar cells (Figure 5), paraphyllia (Figure 6), pseudoparaphyllia (Figure 7), inner perichaetial leaf plications, vaginular paraphyses (Figure 8), operculum type (Figure 9), stomatal pore (Figure 10), and possibly seta length. Characters related to spore dispersal included capsule shape and orientation, annulus (Figure 11), exostome (Figure 12) and endostome (Figure 12) appearance, spore size and maturation time, and possibly seta length. Water availability and exposure to wind were the most important habitat factors.

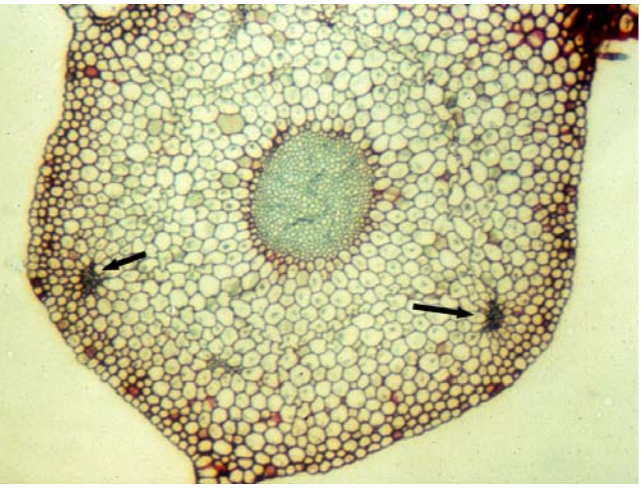

Figure 3. ***Mnium*** stem showing central strand (stained green). Arrows indicate leaf traces. Photo by Janice Glime.

Figure 4. ***Hygroamblystegium fluviatile*** leaves showing dark costa down the middle of the leaf. Photo by Hermann Schachner, through Creative Commons.

Figure 5. ***Calliergon giganteum*** leaf with inflated alar cells at leaf base. Photo by Michael Lüth, with permission.

Figure 6. ***Thuidium delicatulum*** showing paraphyllia. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

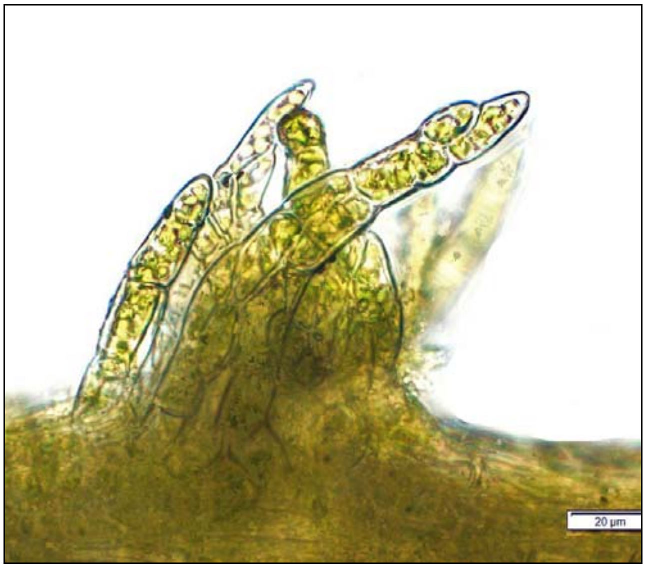

Figure 7. ***Homomallium mexicanum*** showing **pseudoparaphyllia** on the stem. Photo by Dale Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

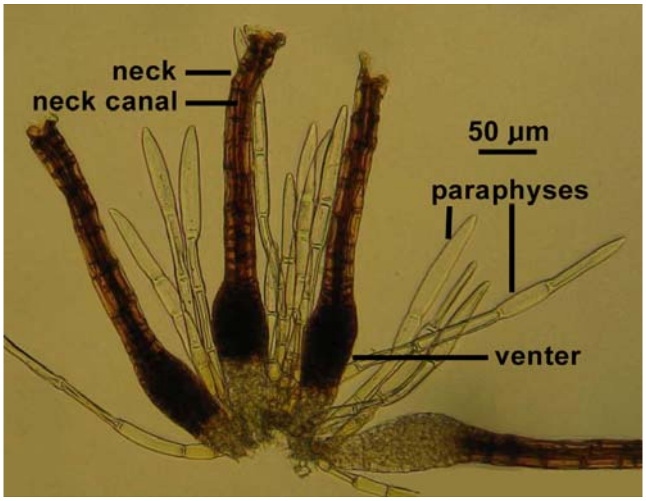

Figure 8. Moss paraphyses with archegonia. Photo by Tom Thekathyil, with permission.

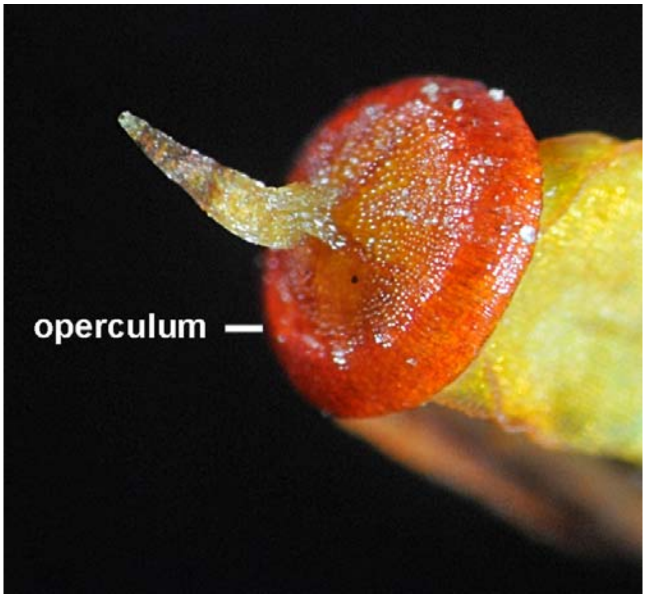

Figure 9. ***Polytrichum*** operculum. Photo by George Shepherd, through Creative Commons.

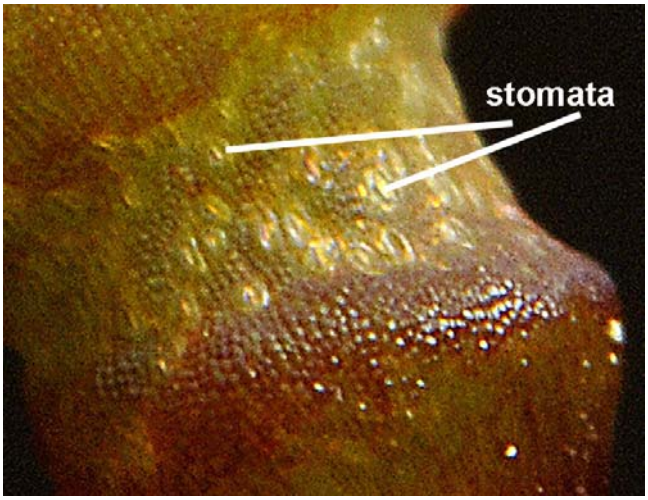

Figure 10. ***Polytrichum*** stomata on base of capsule. Photo by George J. Shepherd through Creative Commons.

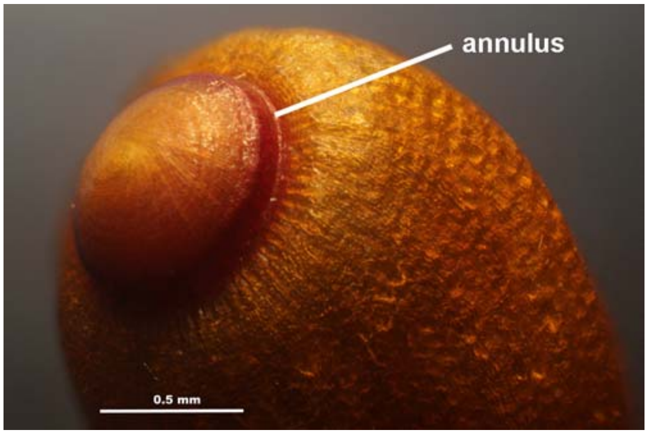

Figure 11. ***Funaria hygrometrica*** capsule showing annulus. Photo by Hermann Schachner, through Creative Commons.

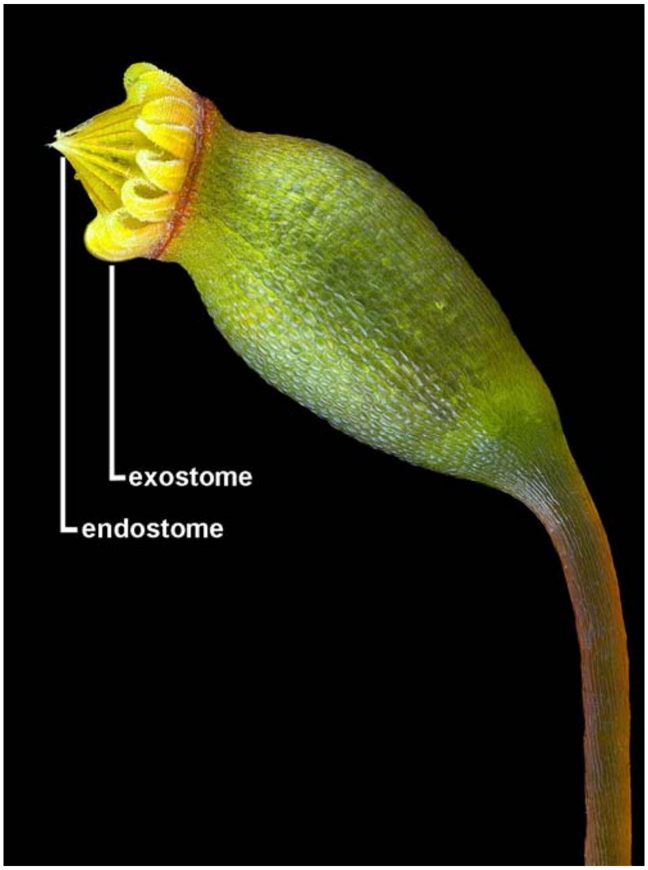

Figure 12. ***Sematophyllum demissum*** capsule showing two layers of peristome. Photo by Des Callaghan, through Creative Commons.

A recent study on **hygrophytic** (living in abundant moisture, here including aquatic and semi-aquatic) mosses from springs in the Iberian Peninsula indicates the role of water chemistry in **sclerophylly** (thickened, hardened foliage that resists loss of moisture) (Fernández-Martínez *et al.* 2019). Montefort *et al.* (2018) developed the **sclerophylly index** for bryophytes (ratio between dry mass and surface area of bryophyte shoot). Springs with a warm, dry climate and **hard water** (having high mineral content) have mosses that are dominated by those with denser, needle-like leaves and a lower water absorption capacity (Fernández-Martínez *et al.* 2019). In cold, humid, soft-water springs the hygrophytic mosses displayed the opposite traits.

Fernández-Martínez *et al.* (2019) identified three "distinguishable" groups of mosses based on their traits (Figure 13). Group 1 is predominantly monoicous, sexually reproducing, pleurocarpous, mat-forming, and having high water absorption capacity (WAC). Group 2 is predominantly dioicous, asexually reproducing with low sporophyte frequency, turf- or cushion-forming, and having needle-like leaves, high mass per area, and high moss density. Group 3 is predominantly acrocarpous, tall-turf-forming, and having large leaves and spores.

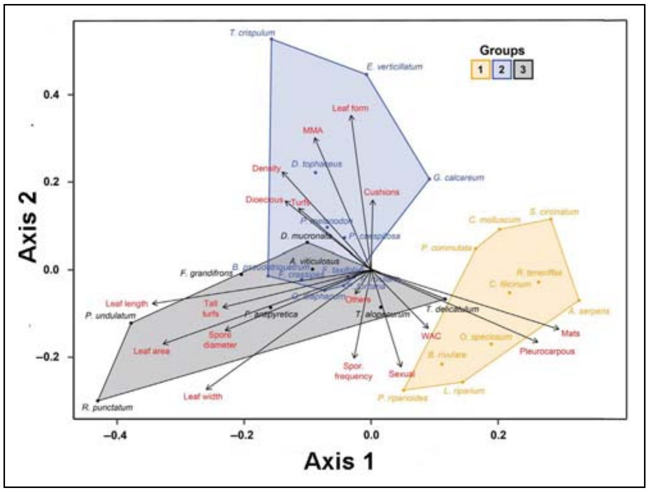

Figure 13. Hierarchical cluster analysis of traits that group bryophytes from springs in the Iberian Peninsula. Axis 1 is correlated with water conductivity, including ions such as Ca^{+2} and Mg^{+2}, high temperatures (lower altitudes), and drought. Axis 2 is mostly opposite of Axis 1, but has a stronger relationship to temperature seasonality and to Cd.

Bryophytes vs Tracheophytes

Akiyama (1992, 1995) considered there to be two main differences between adaptations of **tracheophytes** (plants with lignified vascular tissue) and those of bryophytes. Most moss **rheophytes** (plants living in rapid water) have **monopodial branching** (having a central axis that grows from a terminal bud, like a spruce tree or the moss ***Climacium***; *e.g.* Figure 14). [I have not found monopodial branching to be common – ***Fontinalis*** branches and rebranches from the axis (Figure 15) (Berthier 1965), although it does possess apical dominance (Berthier 1968), as do ***Hygroamblystegium*** (Figure 16) and ***Platyhypnidium*** (Figure 17).] He found that the rheophytic moss leaves are ovate with obtuse apices, causing a small leaf index. This is relatively true for mosses like ***Platyhypnidium riparioides*** (Figure 17), but I have seen many species that are more lanceolate, like most species of ***Fontinalis*** (Figure 18) or ***Hygroamblystegium*** (Figure 4). ***Fontinalis gigantea*** (Figure 19) has more ovate leaves with obtuse apices, but it is typical of stream pools and vernal pools, not fast water. Akiyama also noted that rheophytic mosses have a "special tolerance" to periodical drought, whereas the aquatic tracheophytes usually do not.

Figure 14. ***Polytrichum commune*** demonstrating monopodial branching. Photo by Bob Klips, with permission.

Figure 15. ***Fontinalis dalecarlica*** showing branching. Note the new shoots coming from this plat stranded above the water. Photo by Michael Lüth, with permission.

Figure 16. ***Hygroamblystegium tenax***, with branching from the main axis. Photo from Northern Forest Atlas, with permission from Jerry Jenkins.

Figure 17. ***Platyhypnidium riparioides***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 18. ***Fontinalis hypnoides*** leaf demonstrating lanceolate shape and absence of costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 19. ***Fontinalis gigantea***, a species that can be more than 70 cm long. Photo by Paul Wilson, with permission.

Vitt and Glime (1984) noted that a species may have aquatically adapted gametophytes, but have terrestrially adapted sporophytes (Figure 20). Other species, like those of ***Fontinalis***, have both generations adapted to submersion (Figure 21-Figure 22). The highly evolved structures of aquatic species suggest that these species are evolved from terrestrial ancestors. The large number of widely divergent families with aquatic members indicates that mosses have adapted to aquatic environments through numerous independent lineages. The large number of characters that these aquatic members have in common are a result of parallel evolution with adaptations to a highly specialized habitat.

Figure 20. ***Platyhypnidium riparioides*** with capsules that mature out of the water. Photo by Hermann Schachner, through Creative Commons.

Figure 21. ***Fontinalis dalecarlica*** with young capsules under water in New Hampshire, USA. Photo by Janice Glime.

Figure 22. ***Fontinalis dalecarlica*** with mature capsules under water in New Hampshire, USA. Photo by Janice Glime.

Modified Leaves

Higuchi and Iwatsuki (1986) experimented with the terrestrial mosses ***Hypnum plumiforme*** (syn. ***Hypnum plumaeforme***) (Figure 23) and ***Gollania japonica*** (Figure 24) by culturing them in water. New growth exhibited smaller and more scattered leaves with entire margins, thinner walls in the leaf lamina cells, and a more julaceous leaf arrangement. Cell size and shape did not appear to have any response to submersion in these two species.

Figure 23. ***Hypnum plumaeforme***, a species that develops smaller, more scattered leaves when grown submersed. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Gollania japonica***, a species that develops smaller, more scattered leaves when grown submersed. Photo from Taiwan Mosses, through Creative Commons.

Wehr and Whitton (1986) found similar variation in the aquatic moss ***Platyhypnidium riparioides*** (Figure 17) among the 71 streams they sampled. They scored these based on water chemistry, but other factors of the streams may also have contributed. The plants varied in size, robustness, dimensions and shape of leaves, degree of denticulation, and relative length of the costa. Less robust plants, smaller leaves, and weaker denticulations all correlated with nutrient-rich water.

There is no character that is found among all aquatic bryophytes, and those that seem to be adaptations may be present in one geographic region and not another. With that in mind, do not expect any of the following character observations to be universal.

Multistratose Leaves

It appears that having leaves with multiple layers of cells (**multistratose**) is common among some genera of aquatic or amphibious bryophytes. For example, the aquatic Neotropical species of ***Fissidens***, ***F. geijskesii*** (floating and aquatic), ***F. oediloma***, ***F. rigidulus*** (Figure 25), ***F. rochensis***, and ***F. hydropogon*** (Figure 26), all have multiple cell layers. Similarly, ***Fissidens grandifrons*** (Figure 27-Figure 29) grows in fast water, waterfalls, and other abrasive aquatic environments (Crum 1983) and like ***F. rigidulus*** has multilayered leaves (Iwatsuki & Suzuki 1982; Pursell & Allen 1994; Bruggeman-Nannenga 2013), a character these authors consider adaptive to the fast water. On the other hand, ***F. fontanus*** (Figure 30-Figure 31) lives in quiet water and has only one cell layer thickness (Pursell 1994; Pursell & Bruggeman-Nannenga 2004; Ron Pursell, pers. comm. 1 August 2011; Bruggeman-Nannenga 2013). ***Fissidens taxifolius*** (Figure 32-Figure 33) is a terrestrial species with only one layer of leaf cells.

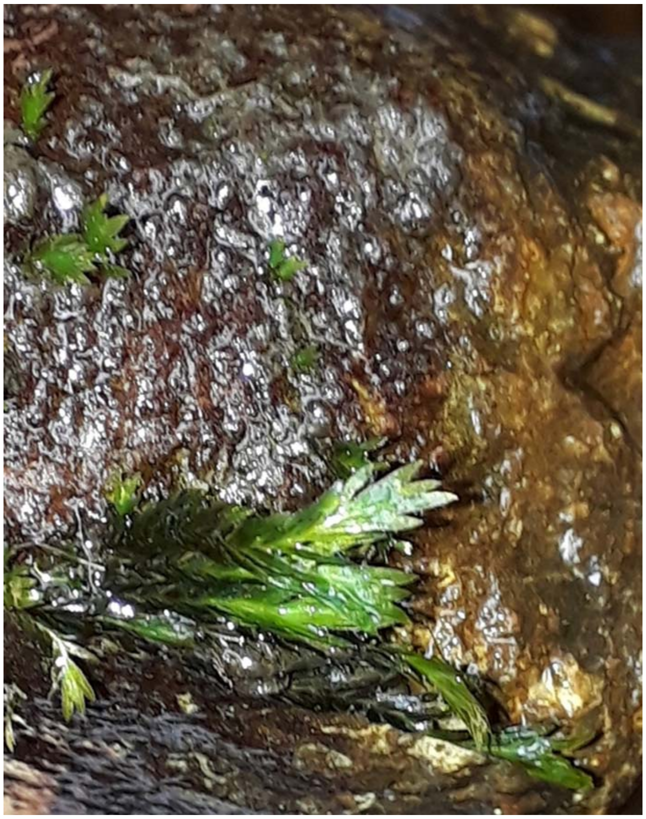

Figure 25. ***Fissidens rigidulus***, a tropical aquatic moss with leaves that have multiple cell layers. Photo by Leon Perrie, through Creative Commons.

Figure 26. ***Fissidens hydropogon***, a tropical species with multistratose leaves. Photo from Alchetron.com, through Creative Commons.

Figure 27. ***Fissidens grandifrons*** in its waterfall habitat in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

Figure 28. ***Fissidens grandifrons***, a moss of fast water with multiple layers of leaf cells. Photo by Michael Lüth, with permission.

Figure 29. ***Fissidens grandifrons*** leaf cs showing multiple layers of leaf cells. Photo by Li Zhang, with permission.

Figure 30. ***Fissidens fontanus*** in its quiet water habitat, showing lax stems. Photo by Matt Keevil, through Creative Commons.

Figure 31. ***Fissidens fontanus***, an aquatic species, showing one leaf cell layer. Photo by Dick Haaksma, with permission.

Figure 32. ***Fissidens taxifolius***, a terrestrial species with single-layered leaves. Photo by David T. Holyoak, with permission.

Figure 33. ***Fissidens taxifolius*** leaf cs showing single layer of cells. Photo by Ralf Wagner <www.drralf-wagner.de>.

To these species, Bruggeman-Nannenga (2013) added ***Fissidens bessouensis*** from Africa, with multistratose leaves along the costa and in scattered locations elsewhere in the leaf lamina. Likewise, the African ***F. harringtonii*** grows submerged and has partly bistratose leaves.

Beever (1995) compared two aquatic New Zealand species of ***Fissidens***. ***Fissidens strictus*** (Figure 34-Figure 35) is a typical rheophyte that has stiff, compact shoots. ***Fissidens berteroi*** (Figure 36) is a **limnophyte** (plant of marshy conditions or shallow water) and has a lax habit typical of that nearly flowless environment.

Figure 34. ***Fissidens strictus***, a species with stiff shoots. Photo by Bill Malcolm, with permission.

Figure 35. ***Fissidens strictus*** leaf. Photo by Bill Malcolm, with permission.

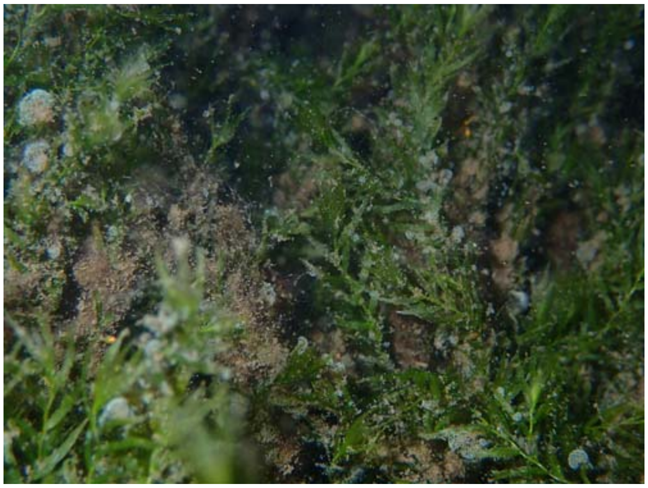

Figure 36. ***Fissidens berteroi***, a species with soft stems and leaves. Photo by Marley Ford, through Creative Commons.

Ryszard Ochyra described several moss genera from torrential waters as having multilayered leaf laminae (Tamás Pócs, Bryonet 24 July 2011). Pócs observed that many **rheophytic** (growing submerged for at least part of year) mosses with only single-layered leaves often lose all or part of the lamina and seem to survive with only the costa remaining. For example, the African ***Fissidens aegrotus*** and Asian ***Hydrocryphaea wardii*** do this. I have observed the same loss of lamina in ***Hygroamblystegium fluviatile*** (Figure 37).

Figure 37. ***Hygroamblystegium fluviatile*** showing leaf costae where laminae have been stripped. Photo modified from unknown photographer, Bryophytes of Hoxie Gorge website.

In the **Neckeraceae**, some of the rheophytic species have partly bi- or multistratose leaf laminae, including ***Neckeropsis*** *s.l.* (Johannes Enroth, Bryonet 1 August 2011). This is true for ***Neckeropsis touwii*** from Papua New Guinea (Ochyra & Enroth 1989). The Himalayan genus ***Handeliobryum*** (Figure 38-Figure 39) also has mostly bistratose leaves (Ochyra 1986). And also now included in **Neckeraceae**, ***Crassiphyllum fernandesii*** has 2-5 stratose stipe leaves and partly bistratose stem and branch leaves (Ochyra 1991) and ***Thamnobryum cataractarum*** (Figure 40-Figure 41) has multistratose stipe leaves and similarly multistratose basal parts of the stem and branch leaves, with mostly bistratose apical parts (Hodgetts & Blockeel 1992).

Figure 38. ***Handeliobryum sikkimense*** habitat. Photo by Jim Shevock, with permission.

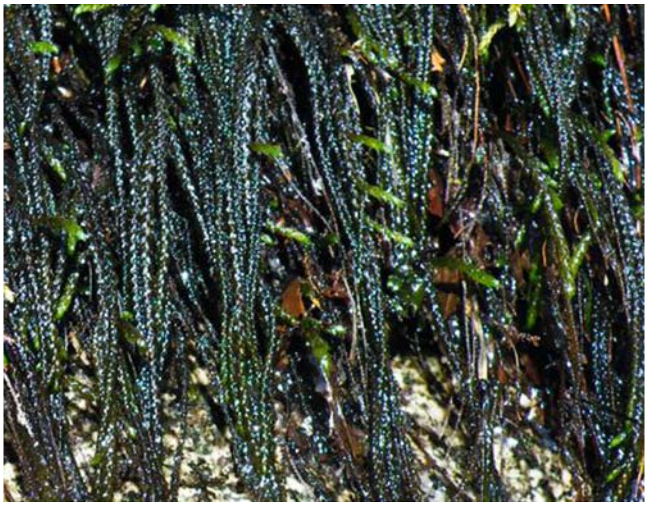

Figure 39. ***Handeliobryum sikkimense***, a rheophytic bryophyte with multistratose leaves. Photo from Earth.com, with permission.

Figure 40. ***Thamnobryum cataractarum*** habitat. Photo courtesy of Nick Hodgetts.

Figure 41. ***Thamnobryum cataractarum***, a species with multistratose stipe leaves, basal parts of the stem, and branch leaves. Photo courtesy of Michael Lüth.

Bernard Goffinet (pers. comm. 23 July 2011) added ***Vittia pachyloma*** (**Amblystegiaceae**; Figure 42-Figure 43) to the list of aquatic taxa with multistratose leaves. It also has a leaf border, short laminal cells, stiff stems, and a thick costa, all characters shared by ***Platylomella lescurii*** (Figure 44-Figure 45), an aquatic species of fast water and considered by some to be in the same family (Vanderpoorten *et al*. 2003). Other aquatic multistratose genera in **Amblystegiaceae** include ***Donrichardsia*** (Figure 46), ***Gradsteinia***, and the Pupu Springs version of ***Cratoneuropsis relaxa*** (syn. = *Hypnobartlettia fontana*; Figure 47). The latter species was so different at Pupu Springs that it was originally described as a different genus, *Hypnobartlettia* (Beever & Fife 2008). ***Platyhypnidium pringlei*** (Figure 48-Figure 50) in the **Brachytheciaceae** likewise has a strong costa that remains when the leaf is scoured away.

Figure 42. ***Vittia pachyloma*** habitat. Photo by Juan Larrain, through Creative Commons.

Figure 43. ***Vittia pachyloma***, a member of the **Amblystegiaceae** with multistratose leaves. Photo by Juan Larrain, through Creative Commons.

Figure 44. ***Platylomella lescurii***, a species of fast water Photo by Blanka Aguero, with permission.

Figure 45. ***Platylomella lescurii*** with leaf borders and strong costa. Note the torn away lamina on leaves. Photo from Northern Forest Atlas, with permission from Jerry Jenkins.

Figure 46. ***Donrichardsia bartramii***, ***Ectropothecium zollingeri***, ***Glossadelphus limnobioides***, and ***Papillidiopsis aquatica*** in a stream in China. Photo with permission from Jim Shevock.

Figure 47. ***Cratoneuropsis relaxa*** from Pupu Springs, with only the costa remaining for many of the leaves. Photo from the Museum of New Zealand, through Creative Commons.

Figure 48. ***Platyhypnidium pringlei*** habitat. Photo by Ken McFarland and Paul Davison, with permission.

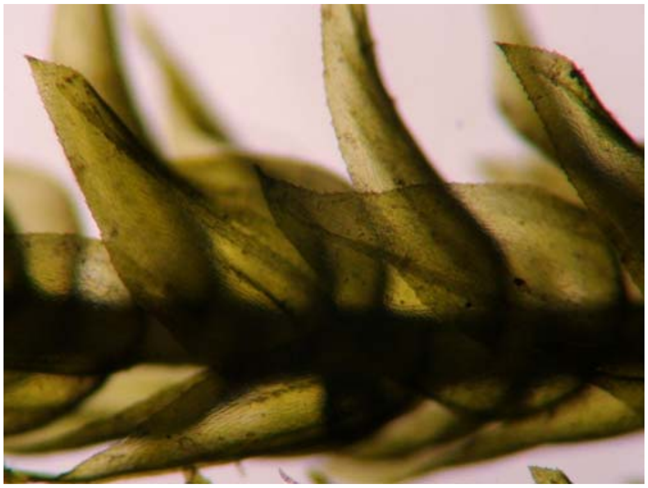

Figure 49. ***Platyhypnidium pringlei*** showing strong costa. Photo by Ken McFarland and Paul Davison, with permission.

Figure 50. ***Platyhypnidium pringlei*** showing costae remaining after the leaf lamina has been scoured away. Photo by Ken McFarland and Paul Davison, with permission.

The South African endemic ***Wardia hygrometrica*** (Figure 51) leaves are only one cell thick, but in addition to its occurrence in fast flow, this species also occupies splash zones of waterfalls and regions of slow flow (Jacques van Rooy, pers. comm. 2 August 2011). Instead of being multistratose, it has a strong, broad costa. There is considerable variation in both stem length and firmness, leaf shape, and leaf length (van Rooy 2014), a plasticity common to many aquatic bryophytes.

Figure 51. ***Wardia hygrometrica*** with capsules, a species of rapids and splash of waterfalls. Photo by Jonathan Sleath, Sanbi.

Spitale and Petraglia (2010) reminded us that the pluristratose leaf lamina is a recurring trait among unrelated lineages of aquatic pleurocarpous mosses, and that it has been considered an adaptation to the aquatic habitat. Using the aquatic moss ***Palustriella falcata*** (Figure 52) from springs in the Italian Alps as a study organism, they found varying numbers of leaf lamina cell layers among the specimens. They found that this character varied even among shoots from the same spring. The character correlated with the width of the costa, but had a negative correlation with cell length. The pluristratose character seemed most related to plants from constantly submerged locations. This character showed a continuum from single-layered ***P. falcata*** (Figure 53) to multiple-layered ***P. pluristratosa***. This suggests that the character may be a response to submersion, but not necessarily an adaptation to flowing water.

Figure 52. ***Palustriella falcata***, a species that seems to develop multistratose leaves when it is submersed. Photo by David T. Holyoak, with permission.

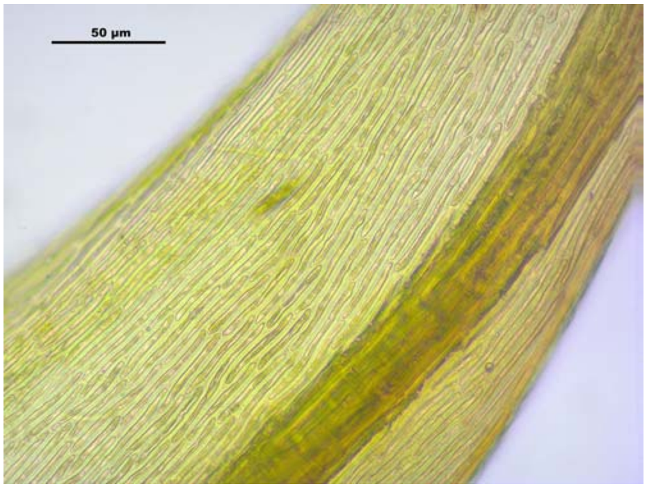

Figure 53. ***Palustriella falcata*** leaf cells of a unistratose leaf. Photo by Hermann Schachner, through Creative Commons.

Costa

The leaf costa can serve two functions: support and translocation of water and nutrients. But in the water, it appears that neither of these functions is important. ***Fontinalis*** lacks a costa (Figure 18), as do ***Wardia*** (Figure 51) and ***Rhabdodontium buftonii***. In other species, *e.g.* ***Warnstorfia exannulata*** (Figure 54-Figure 55) and ***Cinclidium stygium*** (Figure 56), the mesic form has a strong costa (Figure 57), but in water it becomes shorter, thinner, or disappears. On the other hand, many taxa have strong costae in the water (Vitt & Glime 1984; Ock 2014). These include ***Cinclidotus*** (Figure 86-Figure 87), ***Schistidium maritinum*** (Figure 58-Figure 59), ***Echinodium*** (Figure 60), and ***Scouleria*** (Figure 61-Figure 62). In some cases the costa occupies most of the leaf, as in ***Blindia*** (Figure 101-Figure 103), ***Theriotia*** (Figure 63), ***Dendrocryphaea tasmanica*** (Figure 64), and ***Tridontium tasmanicum*** (Figure 65-Figure 66). In the latter two, and in ***Hygroamblystegium fluviatile*** (Figure 4, Figure 37), the costa is often the only portion remaining except for a few new leaves. Hence, it appears that the costa is either strong, offering support, or absent.

Figure 54. ***Warnstorfia exannulata*** in a mesic habitat. Photo by David T. Holyoak, with permission.

Figure 55. ***Warnstorfia exannulata*** showing strong costa in leaves from mesic habitats. Photo by Štěpán Koval, with permission.

Figure 56. ***Cinclidium stygium*** in a mesic habitat. Photo by Michael Lüth, with permission.

Figure 57. ***Cinclidium stygium*** leaf showing strong costa that is typical of mesic habitats. Photo by Kristian Peters, through Creative Commons.

Figure 58. ***Schistidium maritimum*** in a typical seaside habitat. Photo by Michael Lüth, with permission.

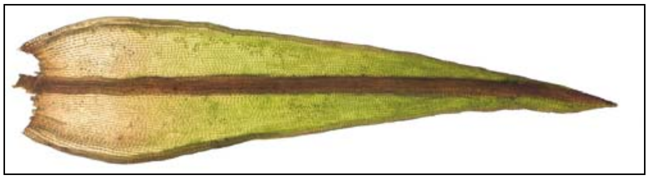

Figure 59. ***Schistidium maritimum*** leaf showing strong costa. Photo by Tomas Hallingbäck, with permission.

Figure 60. ***Echinodium renauldii***, in a genus that has a strong costa even in submerged habitats. Photo by Rosalina Gabriel, with permission.

Figure 61. ***Scouleria aquatica***, a streamside species, often occurring on wet canyon walls. Photo by Matt Goff, with permission.

Figure 62. ***Scouleria aquatica*** leaf showing strong costa. Photo by Matt Goff, with permission.

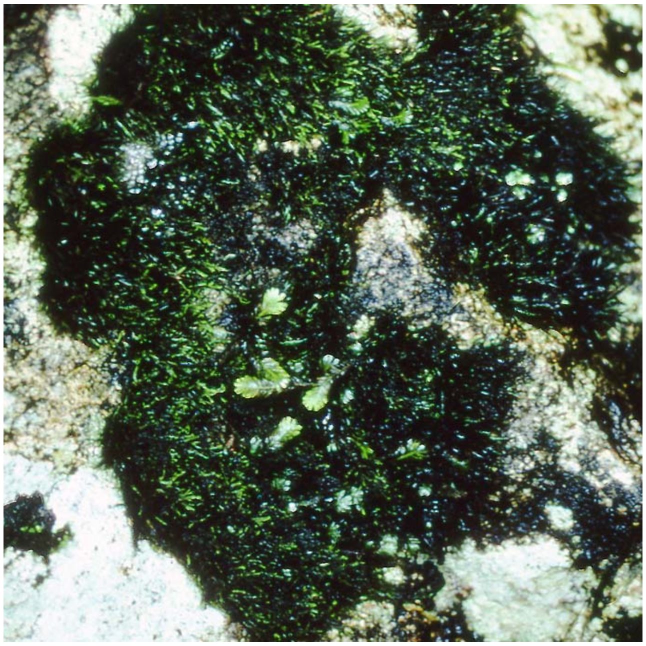

Figure 63. ***Theriotia lorifolia***, a genus in which the costa fills most of the leaf. Photo by Zen Iwatsuki, with permission.

Figure 64. ***Dendrocryphaea tasmanica***, a species with a thick costa that occupies the tip of the leaf. Photo by Tom Thekathyil, with permission.

Figure 65. ***Tridontium tasmanicum***, a species in which a strong costa fills most of the leaf. Photo by David Tng, with permission.

Figure 66. ***Tridontium tasmanicum*** leaf showing strong costa. Photo from Natural History Museum, London, through Creative Commons.

Borders

Ock (2014) considered multistratose leaf borders, along with thickened costae to help mosses tolerate white-water rapids that carry "sandblasting" sediments, and have prolonged desiccation with full sun. Although Ock considered rheophytes to be species living submerged for part of the year, but also emergent for part of the year, these traits apply more broadly to include those species that remain submersed. ***Platylomella lescuriii*** (Figure 44-Figure 45) is a good example of this. It is often present with only the costa and border remaining on many leaves after the rapid flow laden with particulate matter has destroyed the less resistant lamina cells (Figure 45, Figure 67).

Figure 67. ***Platylomella lescurii*** green leaf missing part of lamina. Photo courtesy of David Dumond.

Falcate Leaves

In the **Fontinalaceae**, ***Dichelyma*** (Figure 68), a flood zone species, has falcate leaves, but ***Fontinalis*** (Figure 15, Figure 18, Figure 21-Figure 22, Figure 88-Figure 89), an obligate aquatic does not. However, in my experiments it produced falcate leaves (Figure 69) when the shoots were exposed to air in artificial streams (Vitt & Glime 1984). ***Fontinalis*** leaves can also produce short costae (Allen 1983). Both of these traits suggest a plasticity of a suppressed gene. ***Hygrohypnum*** has an even more frequent expression of falcate leaves in exposed populations (***H. ochraceum*** (Figure 70-Figure 73), ***H. luridum*** (Figure 74-Figure 75) and straight leaves under water. Janssens (1981) has even used this behavior to analyze habitats from the Pleistocene, using microfossils. Such species as ***Pseudocalliergon lycopodioides*** (Figure 76), ***Warnstorfia exannulata*** (Figure 54-Figure 55), and ***Warnstorfia fluitans*** (Figure 77) are strongly falcate out of water, but lose the trait when submerged (Zastrow 1934; Lodge 1959).

Figure 68. ***Dichelyma falcatum*** with typical falcate leaves. Photo by Martin Hutten, with permission.

Figure 69. ***Fontinalis novae-angliae*** with falcate leaves when cultured in very shallow, flowing water in an artificial stream that exposed it to air. Photo by Janice Glime.

Figure 70. ***Hygrohypnum ochraceum*** habitat. Photo by Michael Lüth, with permission.

Figure 71. ***Hygrohypnum ochraceum*** with falcate leaves typical of the species when it is wet but not submersed. Photo by Michael Lüth, with permission.

Figure 72. ***Hygrohypnum ochraceum*** falcate leaf typical of wet but not submersed populations. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 73. ***Hygrohypnum ochraceum*** straight leaf, typical of submersed leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 74. ***Hygrohypnum luridum*** with falcate leaves, typical of wet populations growing out of water. Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Hygrohypnum luridum*** straight leaves, typical of submersed populations. Photo by Hermann Schachner, through Creative Commons.

Figure 76. ***Pseudocalliergon lycopodioides*** showing falcate leaves of emergent plants. Photo by David T. Holyoak, with permission.

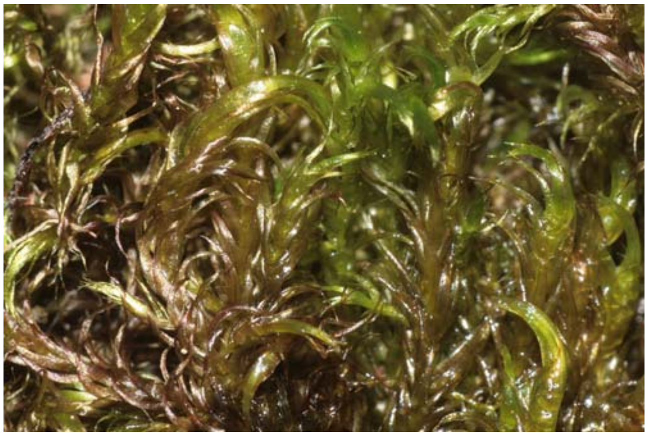

Figure 77. ***Warnstorfia fluitans*** with falcate leaves typical of emergent forms. Photo by Hermann Schachner, through Creative Commons.

Alar Cells

Alar cells (cells at margins of leaf base) are useful in swelling to make the leaves spread and appear to be helpful in absorbing water; thus, as we might expect, these seem to be absent in submerged species. Zastrow (1934) found that in submersed culture, ***Calliergon giganteum*** (Figure 78-Figure 79) and ***C. cordifolium*** (Figure 80-Figure 83) had indistinct alar cells, whereas in terrestrial habitats they have large alar cells. On the other hand, he was unable to induce any change in the alar cells of ***Warnstorfia exannulata*** (Figure 54-Figure 55) or ***Warnstorfia fluitans*** (Figure 77) when these were submersed, indicating that alar cells in these species were under genetic control. Vitt and Glime (1984) concluded that alar cells are common among species of mesic habitats or semi-aquatics, but not in the obligately submerged species.

Figure 78. ***Calliergon giganteum*** in shallow water. Photo by Michael Lüth, with permission.

Figure 79. ***Calliergon giganteum*** leaf showing enlarged alar cells at base, typical of emergent leaves. Photo by Michael Lüth, with permission.

Figure 80. ***Calliergon cordifolium*** in shallow water. Photo by Michael Lüth, with permission.

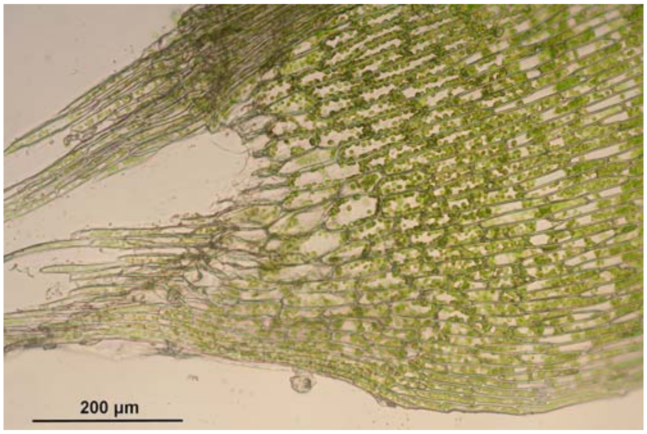

Figure 81. ***Calliergon cordifolium*** leaf base with little distinction in alar cells, typical of submersed leaves. Photo by Hermann Schachner, through Creative Commons.

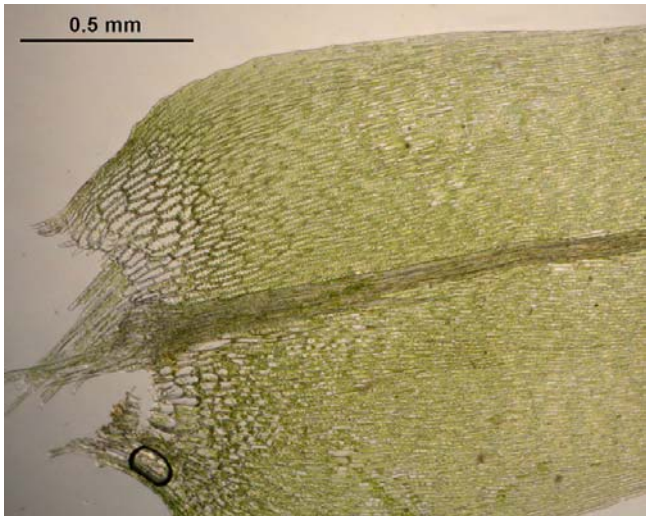

Figure 82. ***Calliergon cordifolium*** leaf base with slightly distinct alar cells, typical of some submersed leaves. Photo by Hermann Schachner, through Creative Commons.

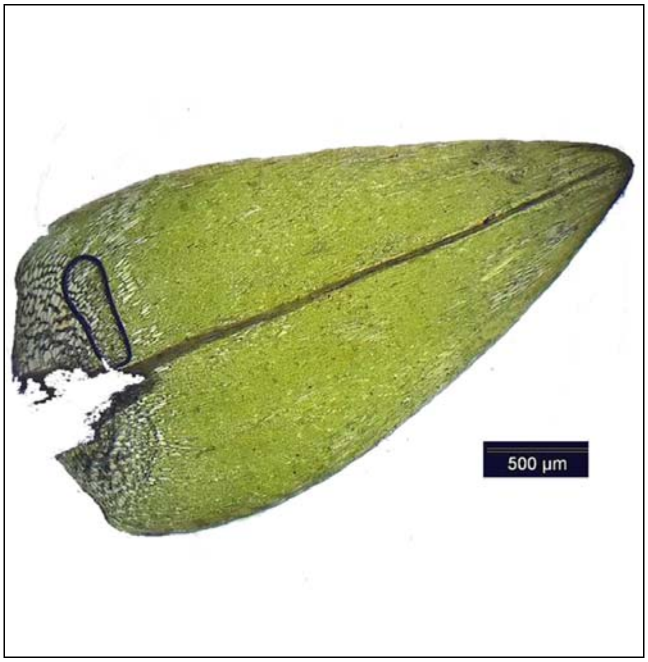

Figure 83. ***Calliergon cordifolium*** leaf with distinct alar cells, typical of emergent leaves and showing variation in alar cells compared to Figure 81 and Figure 82. Photo by Kristian Peters, through Creative Commons.

Higuchi and Iwatsuki (1986) experimented with two terrestrial moss species by submerging them in water. They found that this resulted in less differentiated alar cells, suggesting that this is an environmentally induced response.

Structural Protection from Desiccation

Watson (1919) summarized a number of leaf characters of freshwater bryophytes. He found that species of wet ground have larger leaf cells (*e.g.* ***Hookeria lucens*** – Figure 84-Figure 85) than do leaves from dry habitats, but in rapid streams, the cells can be smaller than those on wet ground or quiet water. Cell walls tend to be firmer or more thickened on plants of flowing water. Like other researchers, he found that leaves in rapid flow are often worn away on the lower parts of the stems. Some leaves have thickened borders [*e.g.* ***Cinclidotus*** (Figure 86-Figure 87), ***Platylomella*** (Figure 44-Figure 45)]. Others are keeled [***Fontinalis antipyretica*** (Figure 1, Figure 88), ***F. neomexicana*** (Figure 89)] or folded over (***Fissidens*** – Figure 90-Figure 91). In some of the shallow water and stream edge species, papillae are present (*e.g.* ***Dichodontium pellucidum*** – Figure 92-Figure 94), the leaf margin is recurved (*e.g.* ***Bryum pseudotriquetrum*** – Figure 95-Figure 96) or leaves are **falcate** (*e.g.* ***Palustriella commutata*** – Figure 97-Figure 98). Even ***Dicranella heteromalla*** (Figure 99), living near mountain streams, sometimes has very falcate leaves (Figure 100) with only the upper portions that are nearly all costa being exposed to the rapid waters of flooding.

Figure 84. ***Hookeria lucens***, a species of wet ground with large leaf cells. Photo by Matt Goff, with permission.

Figure 85. ***Hookeria lucens*** leaf showing large cells common on wet ground. Photo by Malcolm Storey, with online permission.

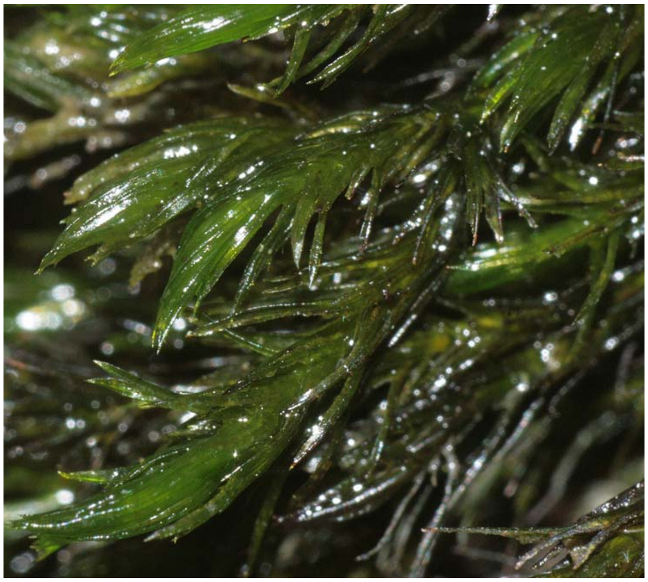

Figure 86. ***Cinclidotus aquaticus***, a plant with a strong border. Photo by Hermann Schachner, through Creative Commons.

Figure 87. ***Cinclidotus aquaticus*** leaf showing its strong border. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Fontinalis antipyretica*** var. ***antipyretica*** showing keeled leaves. Photo by David T. Holyoak, with permission.

Figure 89. ***Fontinalis neomexicana*** showing keeled leaves. Photo by Belinda Lo through Creative Commons.

Figure 90. ***Fissidens crispus***, a sometimes submersed species in a genus in which the leaf folds over to make a pocket. Photo by E. R. Gunnison, through Creative Commons.

Figure 91. ***Fissidens crispus*** leaves showing pockets due to leaf folding. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

Figure 92. ***Dichodontium pellucidum***, a shallow water and stream edge species. Photo by Hermann Schachner, through Creative Commons.

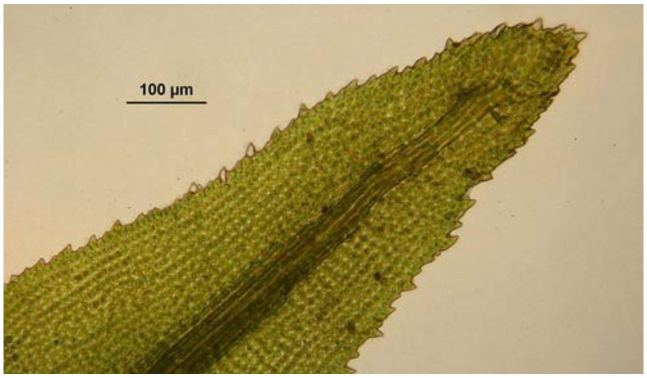

Figure 93. ***Dichodontium pellucidum*** leaf with papillose cells. Photo by Hermann Schachner, through Creative Commons.

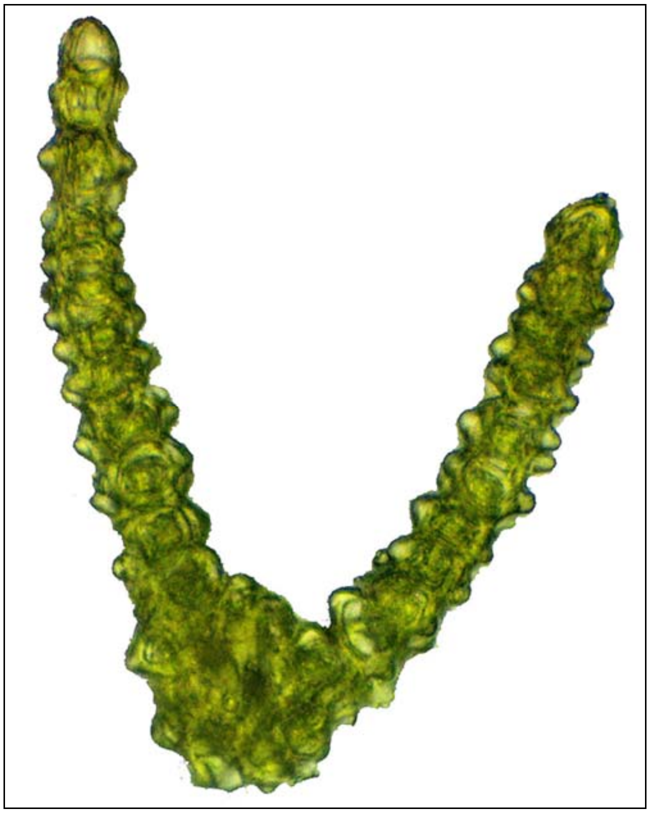

Figure 94. ***Dichodontium pellucidum*** leaf cs showing papillae on cells. Photo by Jean Faubert, with permission.

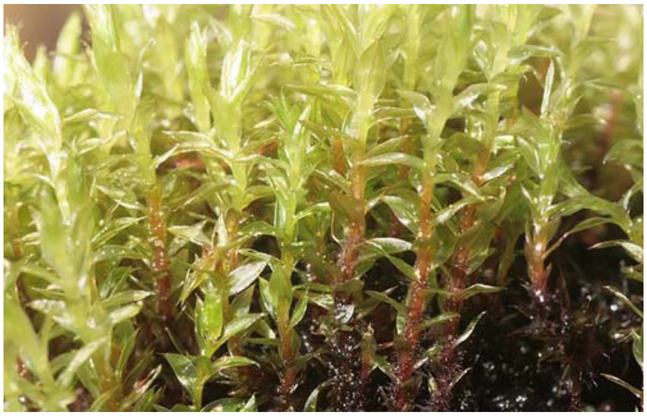

Figure 95. ***Bryum pseudotriquetrum*** emergent in its wet habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 96. ***Bryum pseudotriquetrum*** leaf with recurved margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman and Karen Blisard).

Figure 97. ***Palustriella commutata*** var. ***commutata***, a shallow water species. Photo by Malcolm Storey, with online permission.

Figure 98. ***Palustriella commutata*** showing falcate leaves. Photo by Malcolm Storey, with online permission.

Figure 99. ***Dicranella heteromalla*** with capsules. Photo from Botany Website, UBC, with permission.

Figure 100. ***Dicranella heteromalla*** with falcate leaves, a species that is sometimes flooded on stream banks. Photo by Bob Klips, with permission.

Blindia (Figure 101-Figure 103) is a genus with both terrestrial and aquatic species. The rheophytic species have really long **subulae** (long, slender points on leaves) and linear-elongate leaf cells (Bartlett & Vitt 1986). The terrestrial species, on the other hand, have short subulae and shorter leaf cells.

Figure 101. ***Blindia acuta***, a moss with a strong costa that fills the leaf tip. Photo with permission from Barry Stewart.

Figure 102. ***Blindia acuta*** leaf with strong costa filling the leaf tip. Photo by Hugues Tinguy, through Creative Commons.

Figure 103. ***Blindia acuta*** leaf cs showing strong costa typical of aquatic species in moving water. Photo by Hermann Schachner, through Creative Commons.

Leaf Arrangement

Ock (2014) described rheophytic mosses as **julaceous** (leaves crowded and overlapping, close to stem). This character aptly describes most species of ***Fontinalis*** (Figure 104-Figure 105). But the trait can also apply to species that extend above the water and may experience periods of drying, such as ***Philonotis fontana*** (Figure 106-Figure 107). These amphibious versions often spread when wet, taking advantage of more sunlight for photosynthesis and exposing more tissue for gas exchange.

Figure 104. ***Fontinalis antipyretica*** showing julaceous arrangement of leaves around the stem. Photo by Hermann Schachner, through Creative Commons.

Figure 105. ***Fontinalis duriaei*** showing julaceous habit that is common in several ***Fontinalis*** species. Photo by Michael Lüth, with permission.

Figure 106. ***Philonotis fontana*** at Haven Falls, Michigan, USA, where it can experience summer drying. It benefits from its julaceous habit that provides capillary spaces between the leaves. Photo by Janice Glime.

Biehle *et al*. (1998) found that in the low-flow/pool site the leaf angles of ***Fontinalis antipyretica*** (Figure 104) were 34º, whereas at the site with a higher velocity of flow the angles were only 25º (Figure 108), creating a more julaceous arrangement. Furthermore, the leaf area of plants from the higher flow site was significantly higher.

Figure 107. ***Philonotis fontana*** showing julaceous leaf arrangement that provides capillary spaces for emergent parts. Photo by Malcolm Storey, with online permission through Discoverlife.org.

Figure 108. Leaf angles of ***Fontinalis antipyretica*** from low (**left**) and high (**right**) flows. Modified from Biehle *et al*. 1998.

Devantery (1995) suggested that the leaves of bryophytes in streams modify the internal current of the mosses. Using ***Platyhypnidium riparioides*** (Figure 109) and a colored liquid, he was able to reveal the water movement patterns. A single leaf blade on a moss demonstrated symmetrical twirling behind it. Between leaves there is a retrocurrent in the direction of the leaf that progressively slows down as it turns toward the leaf insertion.

Figure 109. ***Platyhypnidium riparioides*** above and below fast water. Photo by Hermann Schachner, through Creative Commons.

Stem Characters

Bociag *et al*. (2009) surmised that individuals of submerged macrophytes are selected according to their ability to withstand the hydrodynamic forces. Using three aquatic flowering plants and the alga *Chara fragilis* (Figure 110), they compared those in water flowing at 0.1-0.6 m s^{-1} with those in stagnant water. *Batrachium fluitans* (Figure 111), *Chara fragilis*, and *Stuckenia pectinata* (Figure 112) are more resistant to stretching if they occur in a river current, whereas *Potamogeton natans* (Figure 113) is more resistant in stagnant lake water. The *P. natans* bending movement is much greater in lakes than those from flowing water. The resistance of these stems to breaking is directly proportional to the stem or thallus cross-sectional areas. The more resistant stems are thicker with a higher proportion of air spaces. If these differences span from algae to flowering plants, we should expect to see differences among bryophytes that enable them to live in various flow regimes.

Figure 110. *Chara fragilis*, a species more resistant to stretching when in flowing water. Photo by Alex Lomas, through Creative Commons.

Figure 111. *Batrachium fluitans*, a species more resistant to stretching when in flowing water. Photo through Creative Commons.

Figure 112. *Stuckenia pectinata*, a species more resistant to stretching when in flowing water. Photo by Christian Fischer, through Creative Commons.

Figure 113. *Potamogeton natans*, a species that is more resistant to stretching in stagnant water. Photo by Christian Fischer, through Creative Commons.

Based on these differences, we might expect that various adaptations might permit the various species of bryophytes to be differently adapted to flowing vs standing water. And we might also expect that the flow itself can cause structural changes that are adaptive.

Stem Length

Beals (1917) reported ***Fontinalis gigantea*** (Figure 19) that was 71 cm long. Species like ***Fontinalis antipyretica*** (Figure 1, Figure 88) and ***F. dalecarlica*** (Figure 15, Figure 21-Figure 22) can reach close to 2 m in length. I am holding ***Fontinalis duriaei*** in Japan with a length of 60-70 cm (Figure 114). Takaki (1985) reported ***Fontinalis dalecarlica*** from Amchitka Island in the Aleutians based on a picture from A. J. Sharp. This moss was 166 cm long. This creates a tremendous surface that is subject to drag in rapid-flow waters. Thus, we should expect modifications of the stem that permit these mosses to withstand the force of the flowing water.

Figure 114. Janice Glime holding ***Fontinalis duriaei*** in Japan. Photo courtesy of Zen Iwatsuki.

Stem Rigidity and Drag Force

Rheophytic mosses tend to have wiry, rigid stems, as seen in ***Scouleria*** (Figure 61-Figure 62), ***Cinclidotus*** (Figure 86-Figure 87), ***Andreaeobryum*** (Figure 115), and ***Fontinalis dalecarlica*** (Figure 15, Figure 21-Figure 22). Likewise, ***Hygrohypnum bestii*** (Figure 116) occurs in strongly flowing water and has very rigid, wiry stems. ***Hygrohypnum luridum*** (Figure 74), ***H. polare*** (Figure 117-Figure 118), and ***H. alpestre*** (Figure 119-Figure 120), on the other hand, occur in less rheophilous and sometimes streambank habitats and have less wiry stems. In her experiments, Jenkins (1982) found that the stems of ***Platyhypnidium riparioides*** (Figure 17, Figure 109, Figure 152) and ***Hygrohypnum luridum*** have stem strength that is three orders of magnitude higher than the typical drag force of their habitats.

Figure 115. ***Andreaeobryum macrosporum*** with capsules, a species with strong stems. Photo by Botany Website, UBC, with permission.

Figure 116. ***Hygrohypnum bestii***, a species of fast water and wiry stems. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 117. ***Hygrohypnum polare*** habitat on emergent rocks. Photo by Dale Vitt, with permission.

Figure 118. ***Hygrohypnum polare***, a species with less wiry stems than those of rheophilous ***Hygrohypnum*** species. Photo by Michael Lüth, with permission.

Figure 119. ***Hygrohypnum alpestre*** on an emergent rock. Photo by Jean Faubert, with permission.

Figure 120. ***Hygrohypnum alpestre***, a species with less wiry stems than those of rheophilous ***Hygrohypnum*** species. Photo by Michael Lüth, with permission.

Biehle *et al*. (1998) examined stems of ***Fontinalis antipyretica*** (Figure 88) from various flow rates in the field. They found significant differences in the strength of the stems to resist tension, depending on the velocity. They found that those specimens that typically grow in fast water, with greater drag, have more strengthening tissue and greater elasticity. Cross sections revealed that the proportion of strengthening tissue in the stem was greater in the higher flow rate (58.4%) compared to that in the pool-like conditions (49.2%).

Sée and Glime (1984) compared the structure of the stems of the submersed mosses ***Fontinalis dalecarlica*** (Figure 15, Figure 21-Figure 22, Figure 121), a fast-water species, and ***F. flaccida*** (Figure 122-Figure 123), a slow-water/pool species. ***Fontinalis*** has an outer ring of thick-walled cells surrounding a core of thin-walled cells. This provides the stems with the same kind of stress resistance as found in a hollow pole, and also as demonstrated by Bociag *et al*. (2009) for other macrophytes. When the stems are bent by flowing water, the stem interior is flexible and the stem does not break. To visualize this, think of a paper straw (hollow cylinder) vs a paper lollipop stick (solid cylinder). The lollipop stick will break (unless the paper is a set of twisted filaments), but the paper straw will bend without breaking.

Figure 121. ***Fontinalis dalecarlica*** in a stream in Finland, showing effect of drag that makes these mosses **streamers**. Photo by Michael Lüth, with permission.

Figure 122. ***Fontinalis flaccida***, a species of quiet water. Photo by Marsha L Kuzmina, through Creative Commons.

Figure 123. ***Fontinalis flaccida*** with perigonia, a species typical of slow water and lakes. Photo by Janice Glime.

Between these two species, the fast-water ***F. dalecarlica*** has a much larger ratio of cell diameter of epidermal cells to that of cortical cells (Figure 124) than does the slow-water ***F. flaccida*** (Figure 125) (Sée & Glime 1984). In both species, the central tissue has larger cells and thinner cell walls than does the cortex (Figure 124-Figure 125). This creates the same flexibility at the hollow straw.

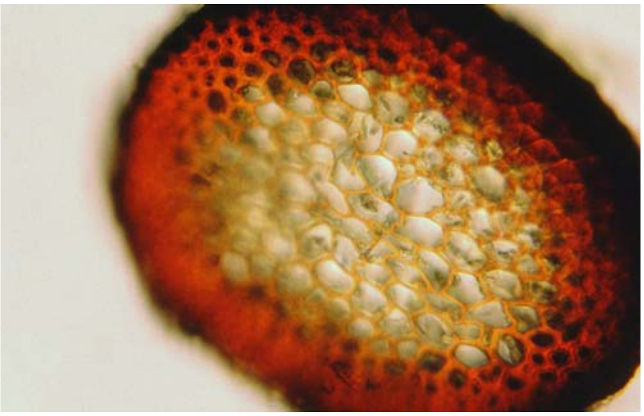

Figure 124. ***Fontinalis dalecarlica*** stem cs from common garden artificial streams, showing a much larger ratio of cell diameter of epidermal cells to that of cortical cells than is found in ***Fontinalis flaccida***. The central tissue has larger cells and thinner cell walls. Photo by Janice Glime.

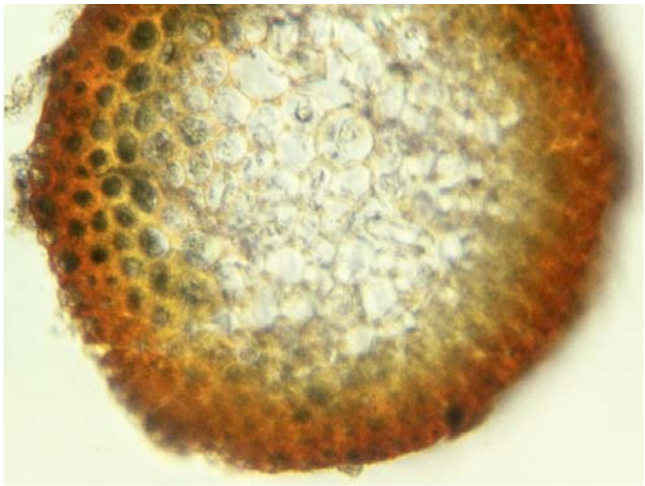

Figure 125. ***Fontinalis flaccida*** stem cs, a species of quiet water. The central tissue has larger cells and thinner cell walls than the outer cortex and epidermis. Photo by Janice Glime.

Sée and Glime (1984) could distinguish ***Fontinalis dalecarlica*** (Figure 121) from ***F. flaccida*** (Figure 122, Figure 123) based on stem cross sections (Figure 124-Figure 125) based on stems grown together in common garden experiments in artificial streams. The fast-water species ***F. dalecarlica*** has a significantly greater mean epidermal cell diameter (10.75 ± 0.75 µm) compared to those of ***F. flaccida*** (7.59 ± 0.58 µm), smaller mean cell diameter of the central tissue (15.77 ± 1.04 µm) compared to that ***F. flaccida*** (20.56 ± 1.59 µm), and a greater range of cortex cell layers (1-8) compared to those of ***F. flaccida*** (1-6). Thus, ***F. dalecarlica*** has a higher ratio of epidermal cell diameter to that of the cortex (1.4) compared to ***F. flaccida*** (1.0). Differences in stem anatomy are even more evident when you handle the two species. The stems of ***F. dalecarlica*** are wiry, strong, and coarse, whereas those of ***F. flaccida*** are softer, more flexible – flaccid. The thicker, colored cell walls in the central core suggest that phenolic compounds may add to the strength.

Other species of ***Fontinalis*** exhibit variations in these stem cell layers (Figure 126). Biehle *et al*. (1998) compared specimens of ***Fontinalis antipyretica*** (Figure 88) from natural habitats with different flow velocities. They found that velocity influences the biomechanical properties and anatomy of submerged ***Fontinalis antipyretica***. Flow velocity influenced both the growth form and biomechanical properties through changes in the anatomy of this species. The stems differ in the proportion of strengthening tissue and the branching angle of the stem. They noted that drag forces increase with the length of the plant, and the elasticity permits these stems to survive strains of extension "remarkably" well. They found that this species has a remarkably high ability to withstand critical strains. The stem tissue presents a viscoelastic behavior. These stems have outer cells with a small lumen surrounded by a thick wall, whereas the center of the stem is characterized by thin-walled cells with a large lumen (Figure 126).

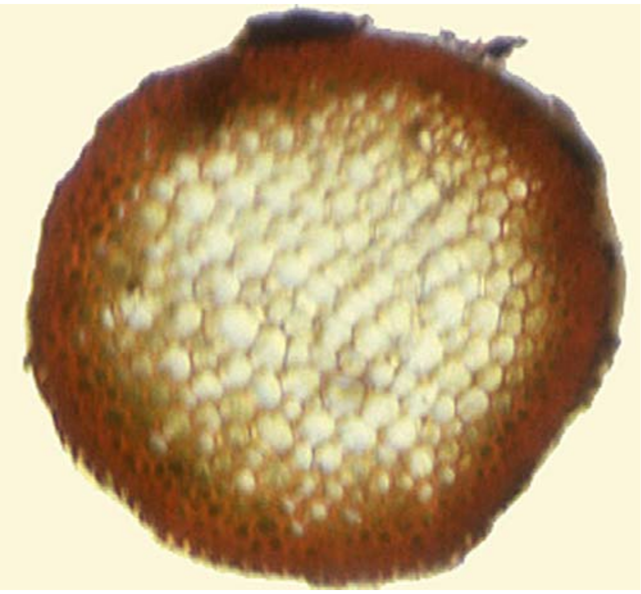

Figure 126. ***Fontinalis gigantea*** stem cs from common garden artificial streams, showing outer cells with thick walls and central core cells with thin walls. Photo by Janice Glime.

Thamnobryum cataractarum (Figure 127) is a species that can grow in very rapid water in streams and waterfalls (Figure 128). Thus, its strong stem is beneficial. But it seems to accomplish this somewhat differently. Instead of the outer tough layers of thick-walled cells seen in ***Fontinalis*** species, it has small cells in both inner and outer stem positions (Figure 129). The outer layer cells are, like those of ***Fontinalis***, colored and have thicker walls than those in the core. The surprise is the presence of a central strand (Figure 130), perhaps an adaptation to periods of low water.

Figure 127. ***Thamnobryum cataractarum*** removed from the water to show the long, strong stems. Photo courtesy of Michael Lüth, with permission.

Figure 128. ***Thamnobryum cataractarum*** habitat. Photo courtesy of Nick Hodgetts.

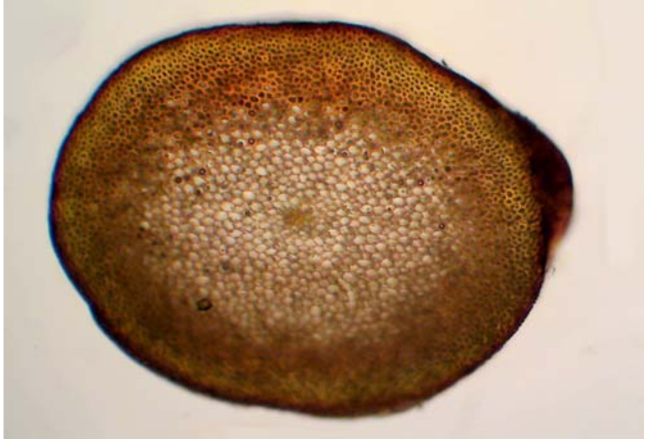

Figure 129. ***Thamnobryum cataractarum*** stem cs showing the numerous small cells that contrast with those of ***Fontinalis*** species. Photo courtesy of Nick Hodgetts.

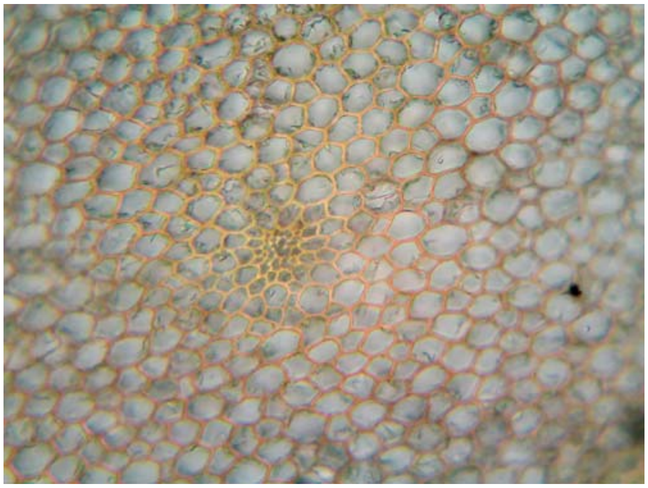

Figure 130. ***Thamnobryum cataractarum*** stem cs showing central strand. Photo courtesy of Nick Hodgetts.

The need for bending and reduction of drag forces is not unique to bryophytes in streams. Miler *et al*. (2010) examined the biomechanics in four aquatic plants, one of which was ***Fontinalis antipyretica*** (Figure 88). They noted that in order to reduce drag forces in water flow, the plants had to withstand bending and tension forces. They found that under high water velocities, all four of these plants [tracheophytes *Hydrochloa fluitans* (Figure 131), *Ranunculus penicillatus* (Figure 132), *Myriophyllum alterniflorum* (Figure 133), and moss ***Fontinalis antipyretica***] are flexible and able to bend, coupled with high 'tension' **Young's modulus** [breaking force and breaking stress; mechanical property that measures stiffness of solid material; defines relationship between stress (force per unit area) and strain (proportional deformation) in material in linear elasticity regime of a uniaxial deformation]. In lower flow rates, the stems are less flexible and display lower breaking stress levels and breaking force levels. The most rigid stems are those in slow-flow habitats. While this makes some sense for the three tracheophytes, it seems to be contradictory for the thin stems of the moss. For ***Fontinalis dalecarlica*** (Figure 15, Figure 21-Figure 22, Figure 124), the dense stem that is able to resist abrasion seems to be an adaptive character.

Figure 131. *Hydrochloa fluitans*, a flexible plant in high water velocities. Photo from <www.aphotofauna.com>, with permission.

Figure 132. *Ranunculus penicillatus*, a flexible plant in high water velocities. Photo by Jamie McMillan, through Creative Gardens.

Figure 133. *Myriophyllum alterniflorum*, a flexible plant in high water velocities. Photo <www.aphotofauna.com>, with permission.

In less abrasive, slower water, flaccid stems are beneficial. This is the case with ***Fissidens fontanus*** (Figure 134) (Ida Bruggeman-Nannenga, pers. comm. 10 April 2020). ***Fontinalis flaccida*** (Figure 135-Figure 136) likewise grows in pools and slow water and has flaccid stems and leaves.

Figure 134. ***Fissidens fontanus*** showing the flaccid leaves and stems. Photo by John Hilty, Illinois Wildflowers, with online permission.

Figure 135. ***Fontinalis flaccida***, a species of slow water and pools, with flaccid stems. Photo by Lance Biechele, Earth.com, with permission.

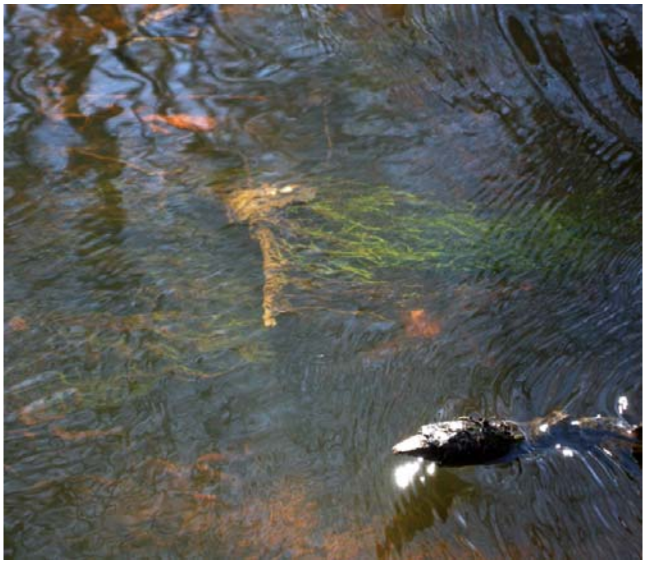

Figure 136. ***Fontinalis flaccida*** habitat in Wicomico Co., MD, USA. Photo by Lance Biechele, permission pending.

Drag Reduction

Suren *et al*. (2000) found that difference in drag coefficient between the bare rock and the moss on the rock varied significantly in three of the six stream bryophytes tested. For the **cushion** moss ***Bryum blandum*** (Figure 137), the drag coefficient increased about 10%. But for ***Blindia lewinskyae*** (**weft**; Figure 138) and the liverwort ***Syzygiella sonderi*** (**low turf**; see Figure 139), it decreased by 40% and 30%, respectively. Differences in drag for ***Phaeoceros laevis*** (**thallus**; Figure 140), ***Fissidens rigidulus*** (**turf**; Figure 141), and ***Lophocolea*** sp. (**mat**; Figure 142) were not significant. Suren and coworkers suggested that the streamlined growth habit of the latter two permitted them to reduce the drag. They suggested that drag characteristics may be important in determining where some bryophytes could succeed in streams. And some bryophytes, furthermore, can increase substrate stability by decreasing drag and reducing opportunity for substrate movement.

Figure 137. ***Bryum blandum***, a cushion form that increases the drag coefficient by 10%. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 138. ***Blindia lewinskyae***, a weft moss that decreases the drag coefficient by 40%. Photo by Melissa Hutchison, through Creative Commons.

Figure 139. ***Syzygiella autumnalis***; ***Syzygiella sonderi*** (**low turf**) decreased the drag coefficient by 30%. Photo by Hermann Schachner, through Creative Commons.

Figure 140. ***Phaeoceros laevis*** with sporophytes, a thallus species that has little effect on the drag coefficient, at least when there are no sporophytes. Photo by Bob Klips, with permission.

Figure 141. ***Fissidens rigidulus*** var. ***rigidulus***, a turf that has little effect on the drag coefficient. Photo by Peter de Lange, through Creative Commons.

Figure 142. ***Lophocolea heterophylla***, a mat that has little effect on the drag coefficient. Photo by Bob Klips, with permission.

Central Strand

The **central strand** (Figure 3) can provide support or a means of transporting solutions – or both. Water movement and conservation are important for terrestrial mosses, but these adaptations are typically lost in the aquatic environment. The **central strand**, useful in the terrestrial environment, is missing in most truly aquatic species (Buch 1947; Hébant 1970; Vitt & Glime 1984).

The large genus ***Fissidens*** provides a good comparison. Central strands (Figure 143) are lacking in the often aquatic ***Fissidens bessouensis*** (Figure 144) and ***Fissidens fontanus*** (Figure 145). In her description of the new aquatic species ***Fissidens bessouensis***, Bruggeman-Nannenga (2013) noted the absence of a central strand (Figure 144) as being an aquatic adaptation.

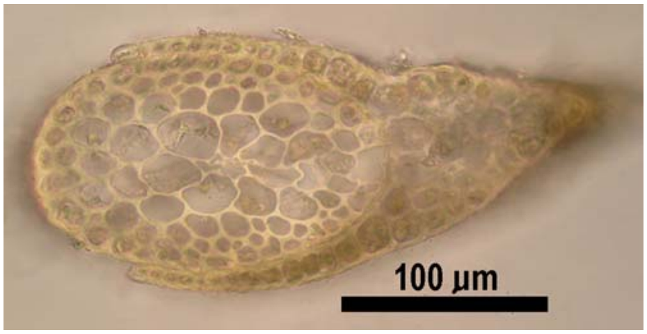

Figure 143. ***Fissidens leucocinctus*** stem cs showing central strand. Photo courtesy of Ida Bruggeman-Nannenga.

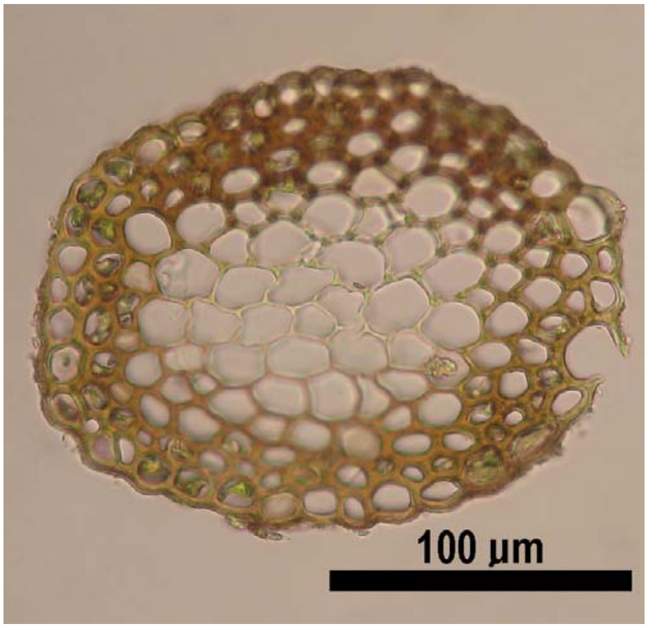

Figure 144. ***Fissidens bessouensis*** stem cs showing absence of a central strand in this tropical aquatic species. Photo courtesy of Ida Bruggeman-Nannenga.

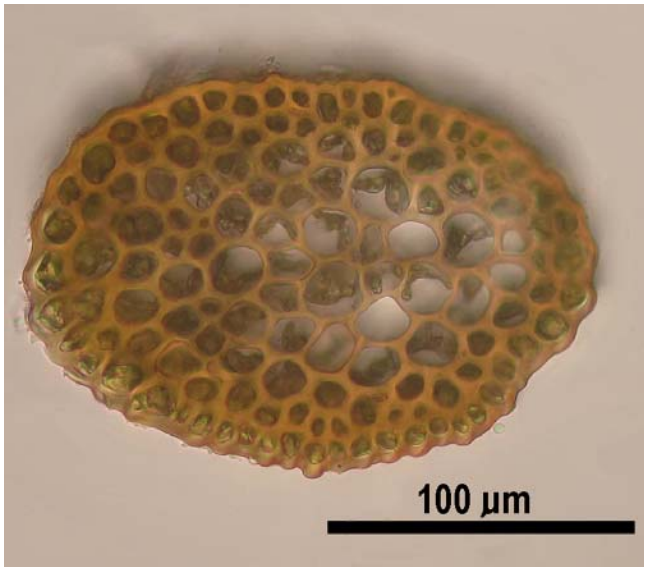

Figure 145. ***Fissidens fontanus*** stem cs showing absence of central strand. Photo courtesy of Ida Bruggeman-Nannenga.

Even terrestrial mosses that have a central strand may fail to develop one when grown in water. This can be seen in ***Paludella squarrosa*** (Figure 146-Figure 147), ***Aulacomnium palustre*** (Figure 148), ***Brachythecium rivulare*** (Figure 149), ***Fissidens adianthoides*** (Figure 150), and ***Tomentypnum nitens*** (Figure 151) (Zastrow 1934). On the other hand, Elssmann (1923-1925) found that ***Platyhypnidium riparioides*** (Figure 17, Figure 152) developed a structure with cells resembling those of a central strand only when grown in water. Could it be that it serves a strengthening function in species of flowing water? ***Philonotis fontana*** (Figure 153-Figure 155), a moss of wet but not fully submerged conditions, has only a poor conduction system and very slow rates of conduction (Bowen 1933). Bowen concluded that this moss required a saturated atmosphere. Zastrow (1934) did note that the central strand cells were larger in submersed forms, consequently resembling cortex cells, but with thinner walls. Vitt and Glime (1984) suggested that perhaps what Bowen observed was a response to the saturated environment rather than an adaptation to it.

Figure 146. ***Paludella squarrosa***, a wetland species that loses the central strand in plants grown under water. Photo by Hermann Schachner, through Creative Commons.

Figure 147. ***Paludella squarrosa***, branch with falcate leaves. Photo by Hermann Schachner, through Creative Commons.

Figure 148. ***Aulacomnium palustre***, a wetland species that loses the central strand in plants grown under water. Photo by Kristian Peters, through Creative Commons.

Figure 149. ***Brachythecium rivulare*** on wet soil where it is emergent. Photo by David T. Holyoak, with permission.

Figure 150. ***Fissidens adianthoides***, a wetland species that loses the central strand in plants grown under water. Photo by Paul Norwood, through Creative Commons.

Figure 151. ***Tomentypnum nitens***, a wetland species that loses the central strand in plants grown under water. Photo by Scot Loring, through Creative Commons.

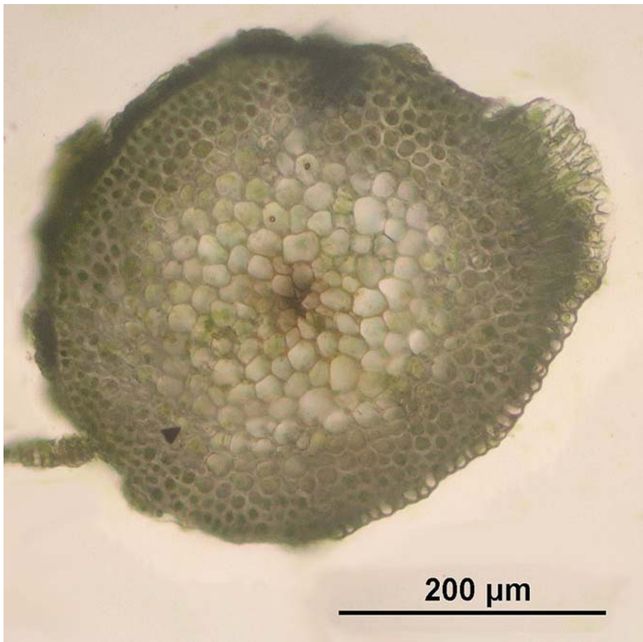

Figure 152. ***Platyhypnidium riparioides*** stem cs showing the central strand that develops in water. Photo by Hermann Schachner, through Creative Commons.

Figure 153. ***Philonotis fontana*** habitat at Haven Falls, MI, USA. Photo by Janice Glime.

Figure 154. ***Philonotis fontana*** at Pictured Rocks, MI, USA. Photo by Janice Glime.

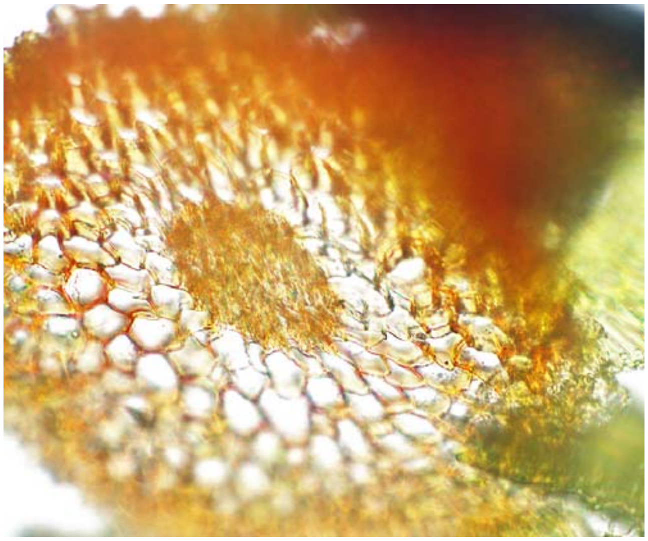

Figure 155. ***Philonotis fontana*** stem cs showing central strand. Even so, it has a poor conduction system. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Stolons

In addition to providing relatively rigid, yet somewhat flexible stems, ***Fontinalis dalecarlica*** (Figure 15, Figure 21-Figure 22, Figure 124) and ***F. novae-angliae*** (Figure 156) produce stolons (Figure 157). Welch (1948) noted the development of stolons in ***Fontinalis novae-angliae*** and considered these a means to extend onto nearby substrate surfaces. A number of aquatic species produce stolons, and some of these will be discussed under the individual species in a later subchapter.

Figure 156. ***Fontinalis novae-angliae*** habitat, Fox Run, NH, USA. Photo by Janice Glime.

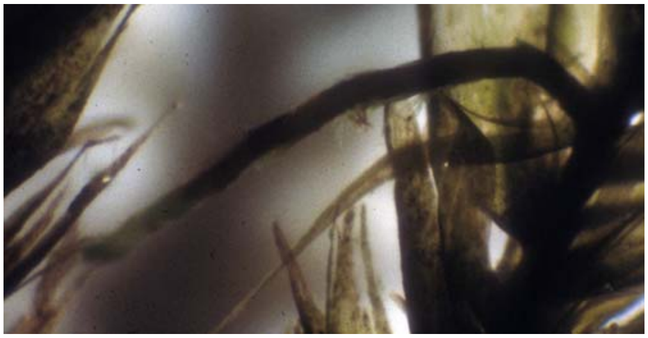

Figure 157. ***Fontinalis novae-angliae*** showing the leafless stolon. Photo by Janice Glime.

Ethylene Response?

We know that production of **ethylene**, a gaseous hormone, responds to stress, and ethylene can cause thicker cell walls to develop in plants (*e.g.* Goeschl *et al.* 1966). Included among these stress responses is a wound response by the ACC pathway (Hyodo 2018). There are few studies addressing ethylene in bryophytes, but we know that in two species of the aquatic moss ***Fontinalis*** (Figure 15, Figure 18, Figure 21-Figure 22, Figure 88-Figure 89) the precursor ACC can stimulate responses like those caused by ethylene (Glime & Rohwer 1983). Rowher and Bopp (1985) demonstrated the presence of ethylene in protonemata of the terrestrial moss ***Funaria hygrometrica*** (Figure 158-Figure 159). We further know that wind can cause an ethylene production that inhibits stem growth in tracheophytes (Emery *et al*. 1994). We can then infer that a similar stress caused by increased flow might cause a similar inhibition of stem growth in bryophytes. Thus, ethylene can provide plants with plasticity that could adapt them to the changing conditions of flow. To complete the story for potential adaptation in bryophytes, we find that ethylene responses to mechanical stress in plants can cause the stems to thicken (Anten *et al*. 2006). If such a response is available to aquatic bryophytes, it could explain why some species are able to withstand the physical stress of rapid flow. Nevertheless, in their experiments Niklas *et al.* (2006) found similar responses to mechanical stress in mutant control plants that lacked the ability to produce ethylene, suggesting that ethylene is not the only possibility in facilitating the response.

Figure 158. ***Funaria hygrometrica***, a moss species known to produce ethylene. Photo by James K. Lindsey, with permission.

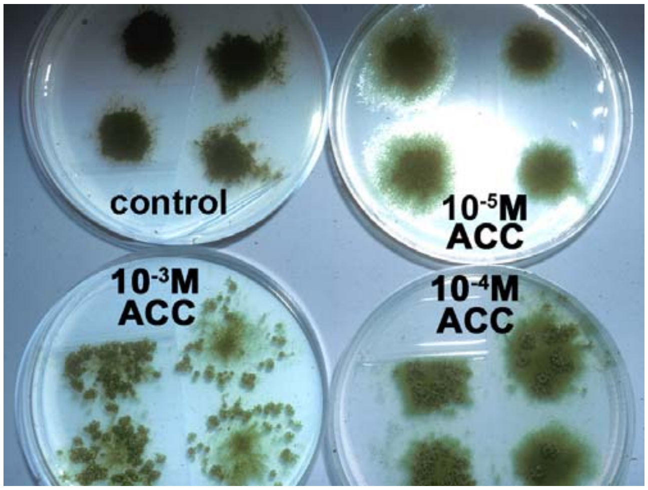

Figure 159. ***Funaria hygrometrica*** protonemata showing the effects of ACC, an ethylene precursor. Photo by Janice Glime.

In Bryophytes, we know almost nothing about ethylene production and plant responses. We know that application of ACC causes structural responses in two species of ***Fontinalis*** (Figure 88). We have evidence that bryophytes can produce ethylene (Rowher & Bopp 1985). We know that application of ethylene to the developing setae of one liverwort species inhibits the elongation of the setae (Thomas *et al*. 1983). And we know that ethylene responds to submergence in the terrestrial moss ***Physcomitrella patens*** (Figure 160), contributing to its plasticity when submerged (Yasumura *et al*. 2012). But we lack experiments to demonstrate ethylene responses to flow in bryophytes, and as nearly as I can determine, such studies are missing for tracheophytes as well. Nevertheless, we have physical responses, discussed below, that indicate the ability to respond. We just do not understand the physiology and biochemistry behind the response.

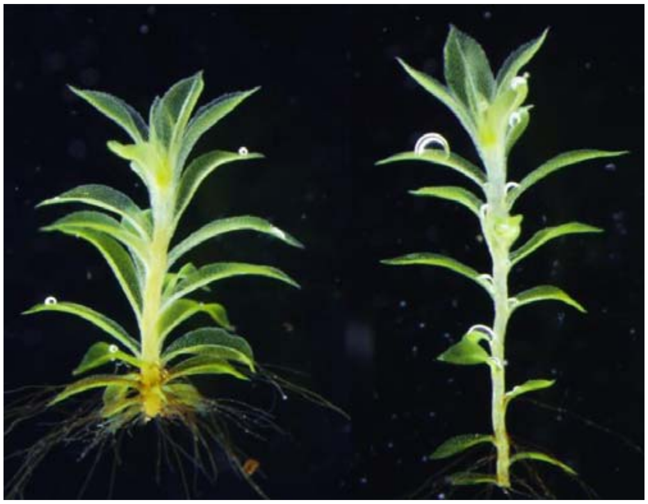

Figure 160. ***Physcomitrella patens*** with plant on right having 6 disrupted MADS box genes, causing a response like that in submersion. Photo by Koshimizu & Hasebe, with online permission.

Summary

Stream bryophytes are subject to changing water levels, rapid flows, silt loads, loss of sperm to the flow, fragmentation and abrasion, being embedded in surface ice and anchor ice, low light in summer, high light when leaves are off the trees, and reduction in red light. Their leaf adaptations include multistratose leaves, thickened costa, wider costa, leaf borders, loss of falcation, and reduction of alar cells. Stem adaptations include thickening of the stem, central parenchyma cells that provide flexibility, stem rigidity, growth and life forms that reduce drag, loss of central strand, and production of stolons. Some species also exhibit a proliferation rhizoids. These character modifications may be facilitated by changes in ethylene concentrations, but it appears that other substances are most likely involved as well.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. Jim Shevock alerted me to the story of *Cratoneuropsis relaxa*/*Hypnobartlettia fontana*. Ida Bruggeman-Nannenga has helped me with email discussions and made cross-sections of *Fissidens* species and photographed them for me. David Dumond provided me with images of eroded leaves of *Platylomella lescurii*.

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CHAPTER 2-4

STREAMS: STRUCTURAL MODIFICATIONS – RHIZOIDS, SPOROPHYTES, AND PLASTICITY

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CHAPTER 2-4
STREAMS: STRUCTURAL MODIFICATIONS – RHIZOIDS, SPOROPHYTES, AND PLASTICITY

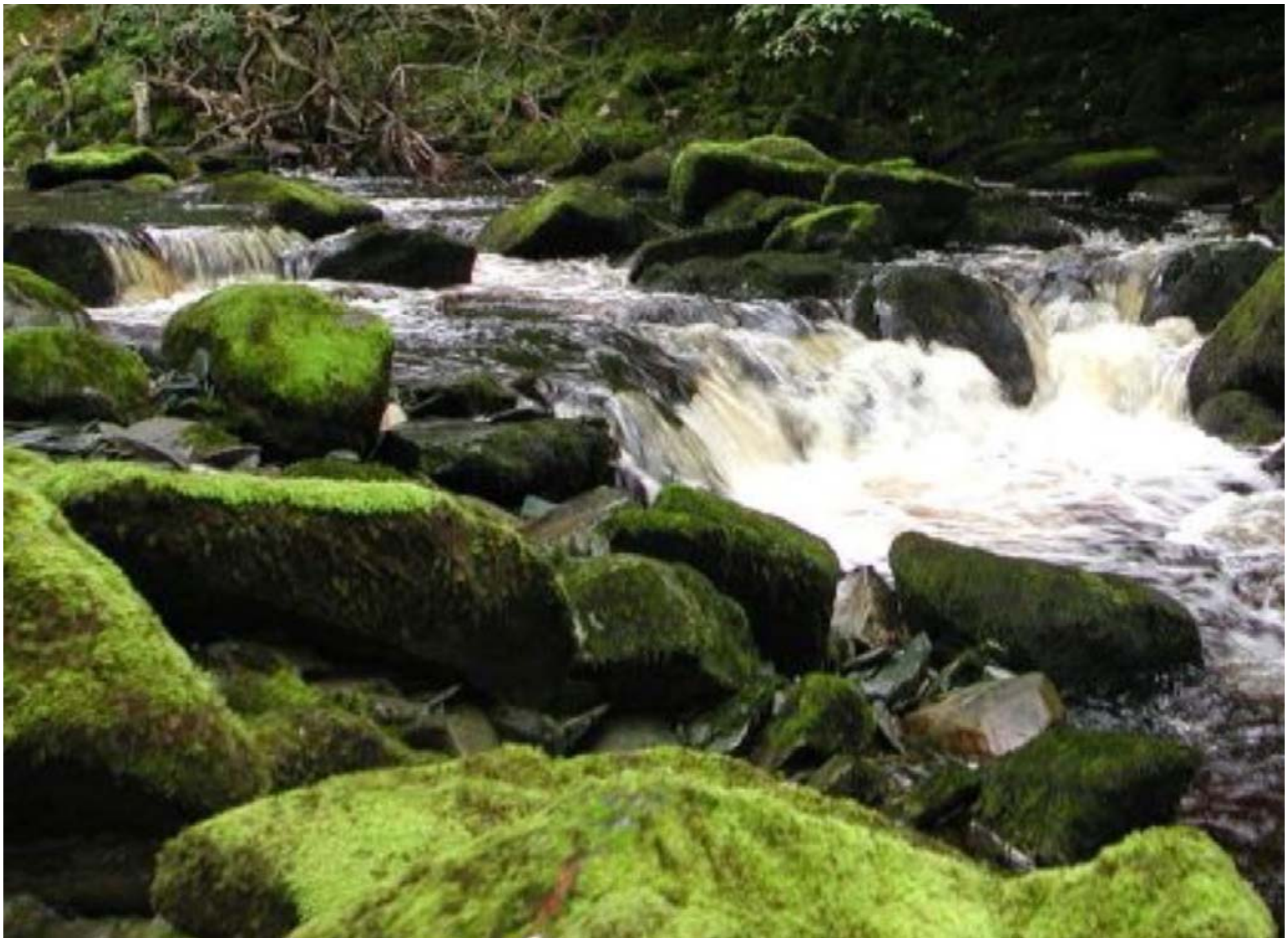

Figure 1. ***Thamnobryum cataractarum*** habitat at The Dales, UK. Photo by Nick Hodgetts, with permission.

Rhizoids and Attachment

Rhizoids on bryophytes are primarily used for attachment. In flowing water, this would seem to be the only function, whereas in terrestrial habitats they may help in forming capillary spaces and moving water from substrate to moss. Thus, in stream habitats the rhizoids are often a necessity for staying in place.

Effects of Submersion

Odu (1978) concluded that production of rhizoids is related to the habitat. Floating and submersed wetland plants often lack rhizoids (Watson 1919; Odu 1978). But when plants grow on the edges of lakes or in flowing streams, they require rhizoids for anchorage (Vitt & Glime 1984). Earlier, Watson (1919) concluded that for bryophytes to live in flowing water they need strong and numerous rhizoids to affix them firmly to the substrate.

Higuchi and Imura (1987) tested the effects of submersion on rhizoid characters, using ***Bryum*** (Figure 2-Figure 3), ***Pohlia*** (Figure 4-Figure 5), ***Macromitrium*** (Figure 6), and ***Trachycystis*** (Figure 7). He was unable to detect any difference between aerial and submersed rhizoids in the species tested, except that ***Macromitrium gymnostomum*** lost its mucilage in water culture.

Figure 2. ***Bryum pseudotriquetrum*** in a typical habitat. Photo by Michael Lüth, with permission.

Figure 3. ***Bryum pseudotriquetrum*** stem with rhizoids. Photo by Bob Klips, with permission.

Figure 4. ***Pohlia wahlenbergii*** habitat. Photo by J. C. Schou, with permission.

Figure 5. ***Pohlia wahlenbergii***, in a genus in which at least some species do not change rhizoid production depending on submersion. Photo by Betsy St. Pierre, with permission.

Figure 6. ***Macromitrium*** sp., typically a terrestrial moss. Tested species in this genus did not change rhizoid production depending on submersion. Photo by Niels Klazenga, with permission.

Figure 7. ***Trachycystis flagellaris***, in a genus in which at least some species do not change rhizoid production depending on submersion. Photo by Misha Ignatov, with permission.

But other researchers have found that rhizoid production can differ between terrestrial and aquatic habitats. Odu (1978) found that pleurocarpous mosses produce more rhizoids on hard substrates. Acrocarpous mosses have more attachment problems because all the rhizoids are at the base of the stem, contributing to their lack of success on steep slopes and tree trunks. Auxins are known to stimulate rhizoid formation in diverse mosses and liverworts; auxins produced by microbes in the soil or sediments may promote the growth of rhizoids, but that hypothesis needs experimental exploration.

Effects of Flow on Rhizoid Production

Plants in quiet water have fewer rhizoids than those in fast water. Thus, the floating ***Scorpidium*** (Figure 8) lacks rhizoids, but the anchored ***Fontinalis*** requires them (Figure 9-Figure 10) (Vitt & Glime 1984). ***Drepanocladus*** *s.l.* species (Figure 11) typically lack rhizoids, but when ***Warnstorfia fluitans*** (=*Drepanocladus fluitans*; Figure 12) is cultured on agar it produces them. In mountain streams, ***Fontinalis gigantea*** (Figure 13), a species of quiet water, rarely produces rhizoids, but ***Fontinalis hypnoides*** (Figure 14) from streams produces abundant rhizoids (Glime 1980). Bruggeman-Nannenga (2013) similarly reported masses of rhizoids on ***Fissidens bessouensis***, including those firmly attaching the stems, on axillary perigonia and perichaetia, and on infertile branches.

Figure 8. ***Scorpidium revolvens***, typically a floating species with no rhizoids. Photo by David T. Holyoak, with permission.

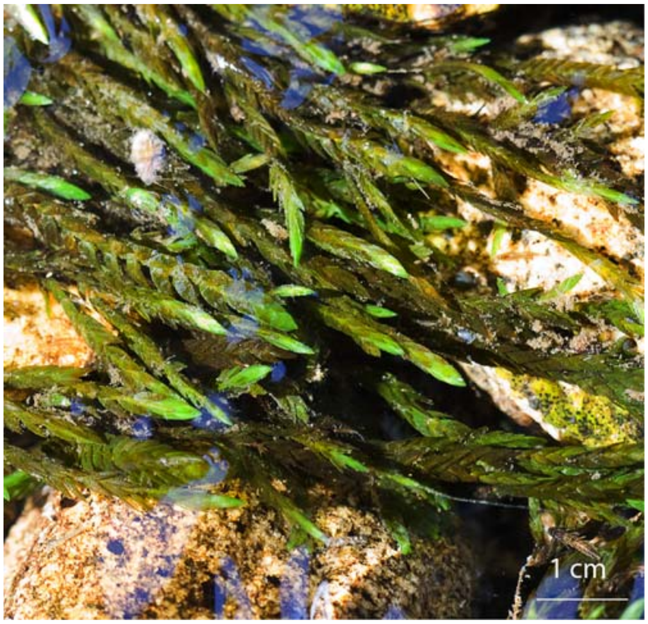

Figure 9. ***Fontinalis antipyretica*** attached to rock in flowing water. Photo from Projecto Musgo, through Creative Commons.

Figure 10. ***Fontinalis antipyretica*** wound rhizoids. Photo by Janice Glime.

Figure 11. ***Drepanocladus aduncus***, a species that typically lacks rhizoids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 12. ***Warnstorfia fluitans***, a species that produces rhizoids when cultured on agar, but not in water. Photo by Michael Lüth, with permission.

Figure 13. ***Fontinalis gigantea***, a species of quiet water that rarely produces rhizoids. Photo by Paul Wilson, with permission.

Figure 14. ***Fontinalis hypnoides*** with collected detritus in the Manganese River Gorge, MI, USA. Photo by Janice Glime.

Temperature and flow conditions are both important in the production of rhizoids in ***Fontinalis*** species, a pleurocarpous genus (Glime 1980). Both ***F. hypnoides*** (Figure 14) and ***F. novae-angliae*** (Figure 15-Figure 26) produced significantly more rhizoids in flowing water than in pool conditions in laboratory experiments, except for ***F. novae-angliae*** at 20ºC (Figure 17). ***Fontinalis hypnoides*** produced significantly more rhizoids than did ***F. novae-angliae*** at temperatures below 15ºC, both species increased their rhizoid production with increasing temperatures up to 20ºC (see Figure 16), and ***F. novae-angliae*** greatly exceeded rhizoid production of all other species at that temperature (Figure 17). This response should be adaptive in many streams where flow is low when the temperature is as high as 20ºC, permitting attachment while the flow is less able to detach them. Furthermore, the plant growth rate is very slow at this higher temperature (Figure 18). This combination of behaviors would permit the mosses to remain on a rock without high flows to wash them away while they grow their rhizoids and attach.

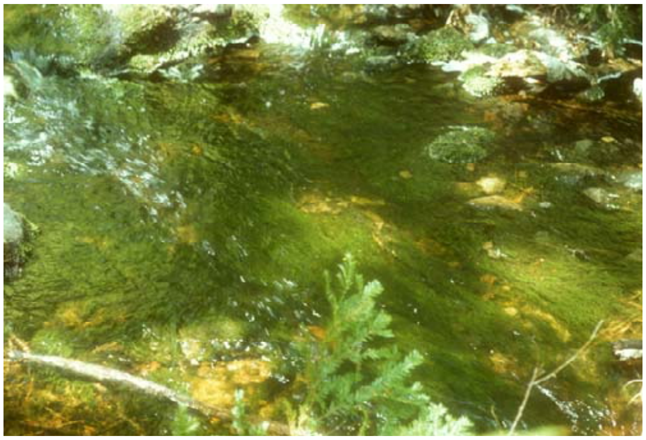

Figure 15. ***Fontinalis novae-angliae***, a species of rapid water. Photo by Janice Glime.

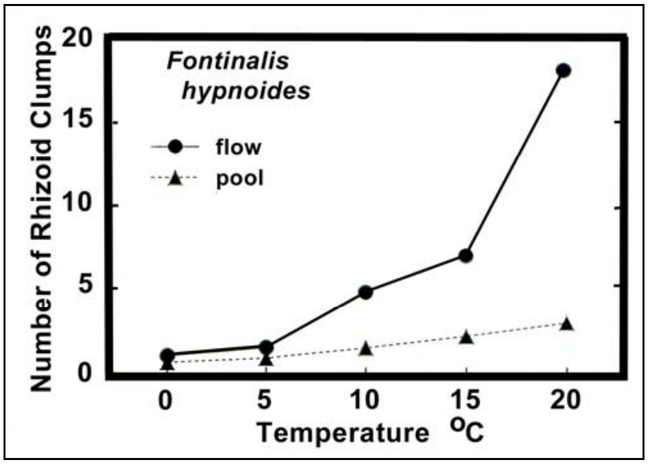

Figure 16. Comparison of rhizoid clumps per moss stem (5 cm starting length) produced by ***Fontinalis hypnoides*** after 15 weeks of growth in artificial streams with flowing water and pool conditions. Modified from Glime and Raeymaekers 1987.

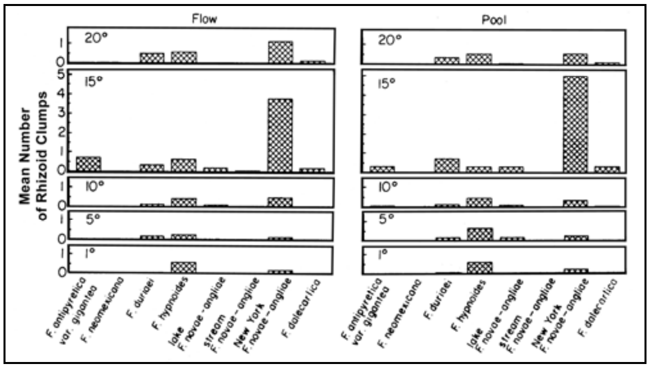

Figure 17. Comparison of ***Fontinalis*** species and their production of rhizoids at temperatures of 1-20ºC in flow and pool conditions.

Since rhizoids are very important in anchoring ***Fontinalis*** and other mosses to the rocks and wood in streams, it is predictable that species living in faster water would have higher rhizoid production. Glime (1980) showed that ***Fontinalis hypnoides*** (Figure 14) produced significantly more rhizoid clumps than did ***F. novae-angliae*** (Figure 15). Glime and Raeymaekers (1987) also found that the most rhizoids in ***Fontinalis hypnoides*** were produced at 20ºC compared to plants at lower temperatures, contrasting with the best growth at 15ºC, and those plants in flowing water conditions produced considerably more rhizoid clumps than did plants in pool conditions.

The pleurocarpous stream moss ***Fontinalis dalecarlica*** (Figure 19) in axenic culture produced rhizoids on all sides of the stem (Figure 20) (Glime 1980), a trait mostly restricted to acrocarpous mosses (Odu 1979). Such a growth pattern would facilitate attachment wherever the stem made contact with a substrate. More rhizoids were produced at 15-20ºC (Figure 17), depending on the species, than at lower temperatures (Glime 1980, 2015; Glime & Raeymaekers 1987). This would encourage rhizoid growth when stream water was low during the summer, making it easier for attachment to occur without the danger of being dislodged by heavy flows. When heavier rains return in the autumn, the mosses would already be well attached.

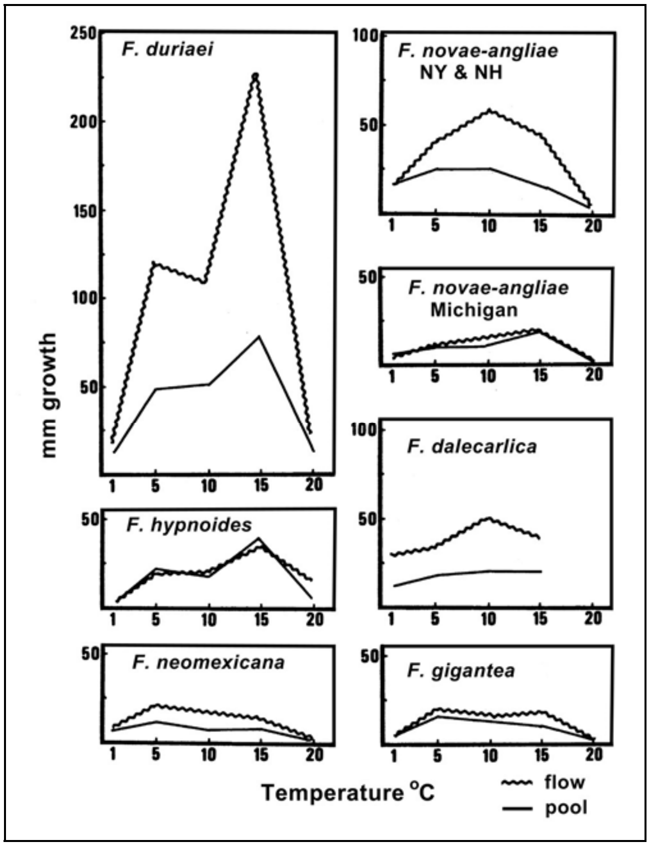

Figure 18. Growth rates of six ***Fontinalis*** species at five temperatures in flowing water and pool conditions in artificial streams. From Glime 1987b.

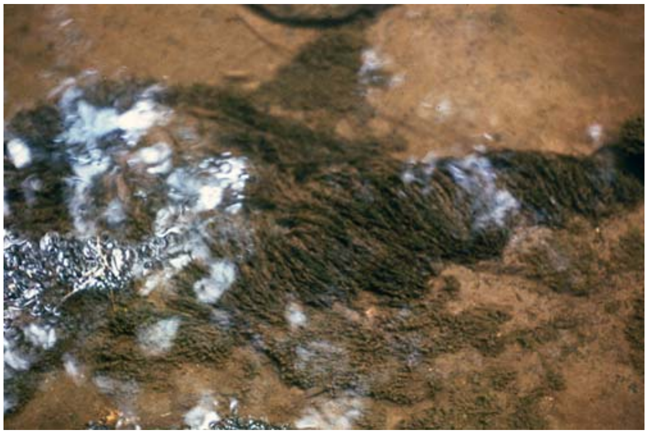

Figure 19. ***Fontinalis dalecarlica*** habitat in Tolliver Run, Garrett County, MD, USA. Photo by Janice Glime.

Finding and Recognizing the Substrate

In flowing water, rapid flow and ice flows can easily dislodge fragile bryophytes. I found two strategies of attachment in members of ***Fontinalis*** that grow in rapid water. In ***F. dalecarlica*** (Figure 19) rhizoids appear along the stem at points of contact. These can arise on any side of the stem (Figure 20) (Glime 1980). When fragments of the plant are developing new rhizoids, these rhizoids spiral (Figure 21) in growth until they make contact with a substrate (Figure 22) (Glime 1987a). Schuepp (1928) noted the frequent presence of spirals in nature, including

Fontinalis. Once the rhizoids contact a substrate, they branch at the tips and attach to the substrate with an adhesive (Glime 1987a).

Figure 20. ***Fontinalis dalecarlica*** rhizoidal branch in liquid culture. Culture courtesy of Dominic Basile; photo by Janice Glime.

Figure 21. ***Fontinalis squamosa*** rhizoid spirals from a broken stem. Photo by Janice Glime.

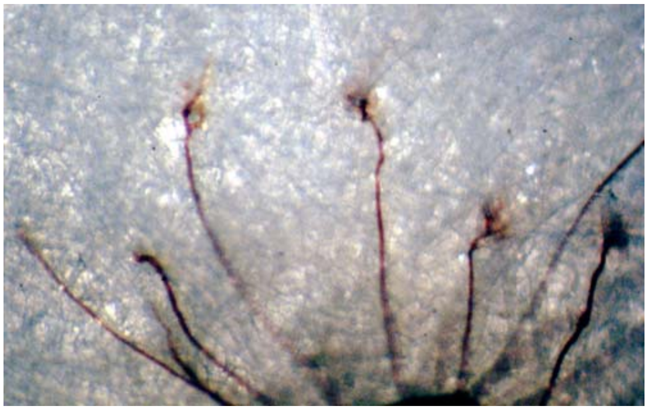

Figure 22. ***Fontinalis squamosa*** rhizoid tips branching where they contact the filter paper. Photo by Janice Glime.

Using the bryophytes ***Hypnum*** (Figure 23), ***Rhynchostegium*** (***Platyhypnidium***? – Figure 24), and ***Lophocolea*** (Figure 25), Odu (1989) demonstrated that their rhizoids produce extra-wall materials when they contact a solid object. These are sulfated mucopolysaccharides that are highly viscous and sticky. These compounds are also involved in adhesion of microorganisms and algae. Odu also noted that pleurocarpous mosses, such as those typical of rapid water, have flattened parts toward the rhizoid tips, but in acrocarpous mosses the flattenings extended far behind the tips.

Figure 23. ***Hypnum sauteri*** with rhizoid attachments to its substrate; rhizoids in tested members of this genus produce extra-wall materials when they contact a solid object. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Platyhypnidium riparioides***, a common species on emergent rocks in rapid streams. Photo by Michael Lüth, with permission.

Figure 25. ***Lophocolea heterophylla***, in a genus that produces extra-wall materials when the rhizoids contact a substrate. Photo by Janice Glime.

In ***Fontinalis dalecarlica*** (Figure 19) and ***F. novae-angliae*** (Figure 15, Figure 26), both species of relatively rapid water, the moss spreads by producing **stolons** (horizontal stem that typically lacks leaves or has reduced leaves; Figure 26), and rhizoids are restricted to these stolons in the latter species (Glime 1980). This may actually be a better strategy than normal branching because the stolon grows along the substrate and its leaf reduction would save energy over producing a leafy branch. Experiments are needed to determine if the stolon truly has a faster growth rate than a normal branch. This would appear to be beneficial for a species that branches and rebranches while dangling in rapidly flowing water.

Figure 26. ***Fontinalis novae-angliae*** stolon, where rhizoids are produced. Photo by Janice Glime.

Growing the Right Direction

Fontinalis also uses **tropisms** (turning responses to a stimulus) to orient the rhizoids. The rhizoids are **negatively phototropic**, *i.e.*, they grow away from light, but seem to lack **gravitropism** (growth toward the Earth's gravity), or it is not as strong as the **phototropism** (Figure 27) (Glime 1987a). In ***Fontinalis squamosa*** (Figure 27), once the substrate is located, the moss expands the tips of the rhizoids by their branching, and attaches. The negative phototropism can prevent the rhizoids from "exploring" locations closer to the water surface and may be adaptive in helping them find suitable locations on the rocks. It would be interesting to track where the moss first attaches and follow its development on the rock.

Figure 27. ***Fontinalis squamosa*** rhizoid negative phototropism. Based on Glime 1987a.

Rate of Attachment

Rhizoids serve primarily for attachment, and the ability of ***Fontinalis*** fragments to attach to rocks takes advantage of the ability to produce rhizoids on all sides of the stem and all along the stem. This is necessary for even small fragments to stay in place (Figure 28). Glime *et al*. (1979) attached ***Fontinalis duriaei*** (Figure 29-Figure 30) and ***Hygroamblystegium fluviatile*** (Figure 31) to rocks in artificial streams to follow the rate of attachment. It required at least 9 weeks for the mosses to attach (Figure 32). But these mosses were held in place artificially, whereas mosses in nature must remain in place by natural mean for this attachment to occur. Following that initial attachment, the rhizoid proliferates rapidly, resulting in a network of rhizoids. This rapid rhizoid growth diminishes after 12-13 weeks from the initial introduction of the moss stem to the rock.

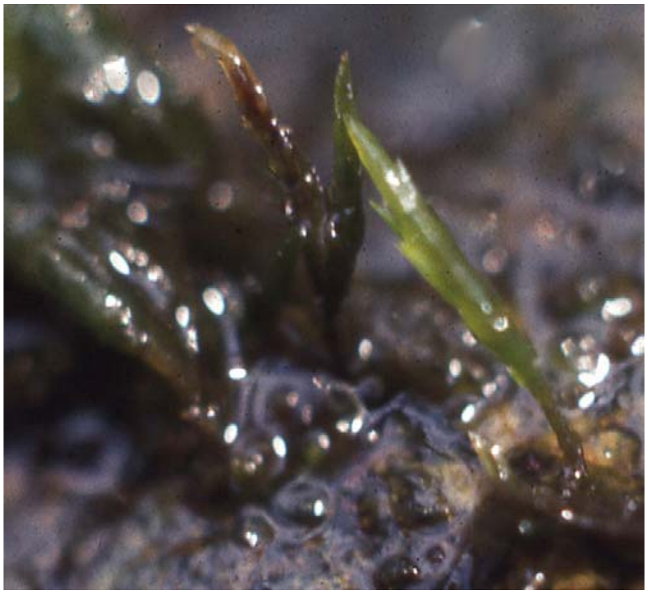

Figure 28. Young shoots of ***Fontinalis novae-angliae*** in Fox Run, Grafton Co., New Hampshire, USA, showing that even these young shoots are attached. Photo by Janice Glime.

Figure 29. ***Fontinalis duriaei***, a species of streams with moderate flow. Photo by Jan-Peter Frahm, with permission.

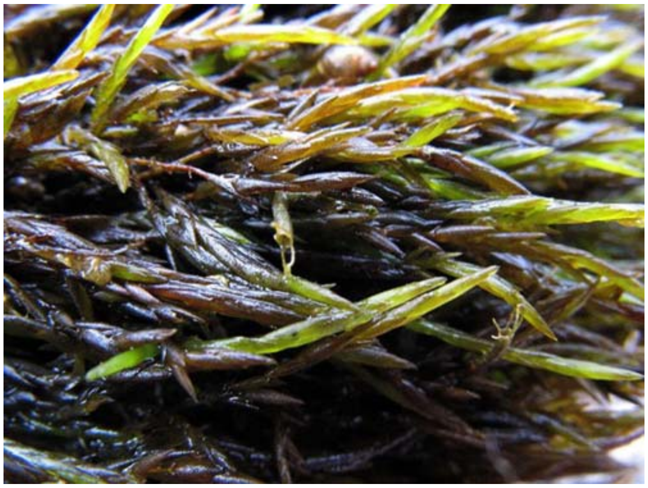

Figure 30. ***Fontinalis duriaei***, a species that attaches to rocks in ~9 weeks after establishing contact. Photo by Michael Lüth, with permission.

Figure 31. ***Hygroamblystegium fluviatile***, a species that can begin attachment in 9 weeks when in contact with a substrate. Photo by Hermann Schachner, through Creative Commons.

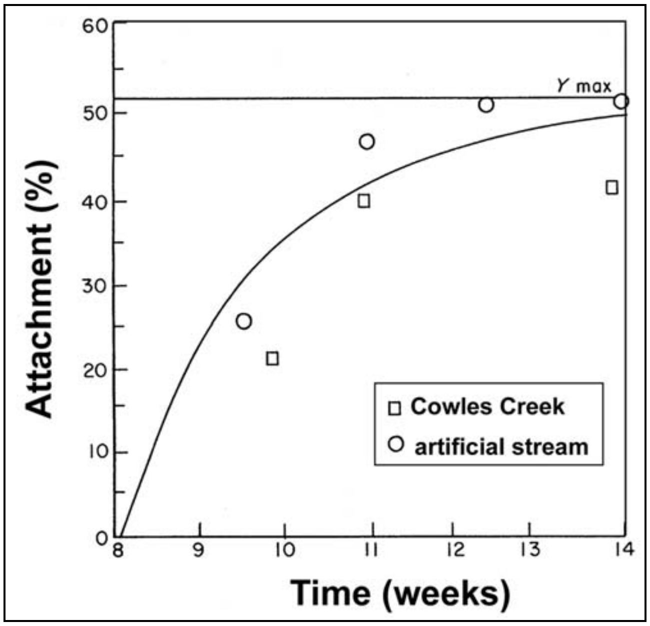

Figure 32. Attachment time for ***Fontinalis duriaei*** and ***Hygroamblystegium fluviatile*** in artificial streams. From Glime *et al*. 1979.

If you examine a stream during autumn leaf fall, you would notice that a collection of leaves is impinged against the rocks on the upstream side of the rock. For mosses like ***Fontinalis***, one might imagine that the drifting moss fragments can be trapped behind rocks (Figure 33) and debris when the higher temperatures of summer cause the water levels to drop. With little or no rapid flow during summer, the moss could remain in place. At the same time, the higher temperatures of summer would stimulate rhizoid growth (Glime 1980; Figure 17). This combination of events could permit the mosses to attach to the rocks by time the heavier rainfall occurs in autumn.

Figure 33. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales. At this time, rhizoids can grow more prolifically in the warmer temperatures. Photo by Janice Glime.

Reductions and Other Modifications

Reduction is helpful to some species in water (Watson 1919). ***Marchantia*** (Figure 34) species have fewer pores (Figure 35); ***Dumortiera*** (Figure 36-Figure 37) has fewer ventral scales or none; ***Sphagnum*** (Figure 38-Figure 39) has fewer hyaline cells. ***Sphagnum*** in pools may have fewer strengthening fibers in the hyaline cells, but those living in rapid streams display no such reduction. ***Atrichum crispum*** (Figure 40) has fewer and lower leaf lamellae than other members of the genus that occur on drier ground, with similar differences also in ***Polytrichum*** *s.l.* (Figure 41-Figure 42). Species in streams are often robust and very elongated, *e.g.* the leafy liverwort ***Nardia compressa*** (Figure 43. Species with pinnate branches often lose that character and the branches become long (*e.g.* ***Platyhypnidium alopecuroides*** – Figure 44). In other species, the leaves are large and may be lengthened. In the thallose liverwort ***Pellia epiphylla*** (Figure 45) the number of strengthening bands is typically more pronounced in rapid streams than in moist habitats along streams.

Figure 34. ***Marchantia polymorpha***, a species that survives a wide range of habitats. Photo from Botany Website, UBC, with permission.

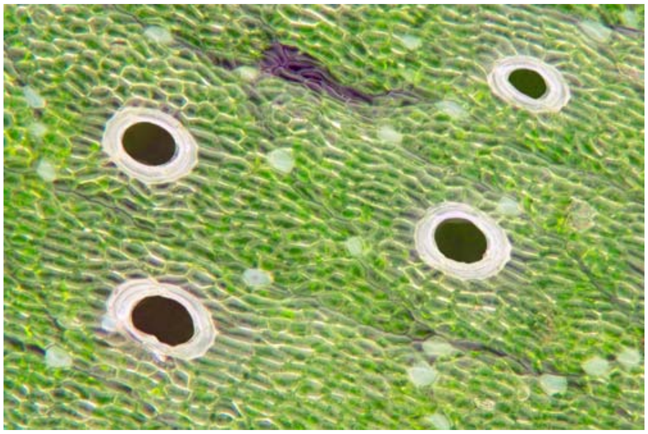

Figure 35. ***Marchantia polymorpha*** air pores that become less dense under water. Photo by Des Callaghan, through Creative Commons.

Figure 36. ***Dumortiera hirsuta*** in a typical habitat in the splash. Photo by Michael Lüth, with permission.

Figure 37. ***Dumortiera hirsuta*** has fewer ventral scales or none in water. Photo by Li Zhang, with permission.

Figure 38. ***Sphagnum cuspidatum***, a species that can be submersed or emergent from water. Photo by Michael Lüth, with permission.

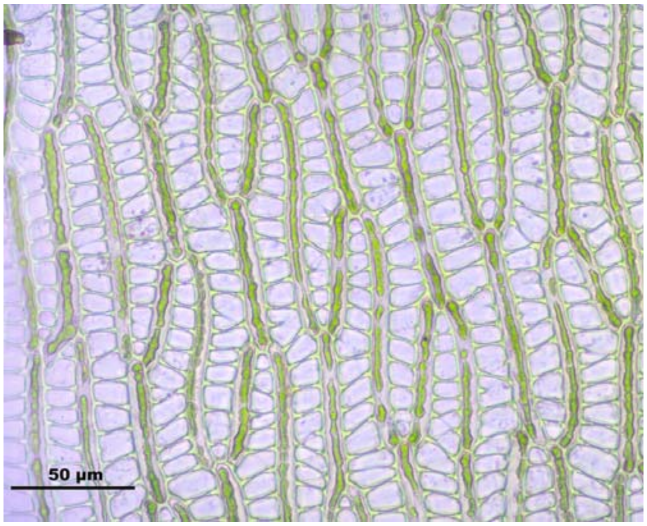

Figure 39. ***Sphagnum cuspidatum*** leaf cells showing fibrils; these become fewer in submersed ***Sphagnum***. Photo by Hermann Schachner, through Creative Commons.

Figure 40. ***Atrichum crispum*** showing leaf lamellae; these are lower and have fewer cells when grown in water. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Figure 41. ***Polytrichum commune***, a wetland and bog species. Photo by Alan J. Silverside, with permission.

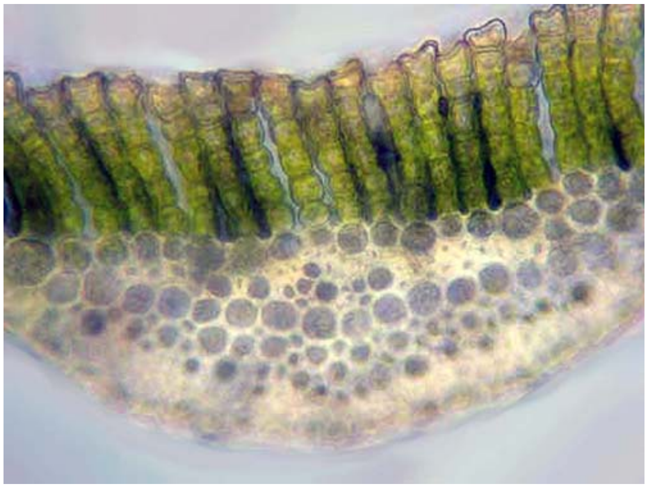

Figure 42. ***Polytrichum commune*** leaf lamellae; these are shorter when the moss is grown in water. Photo from Botany Website, UBC, with permission.

Figure 43. ***Nardia compressa*** representing a leafy liverwort species that is robust and very elongated. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Platyhypnidium alopecuroides***, a species that loses its pinnate branching in water. Photo by David T. Holyoak, with permission.

Figure 45. ***Pellia epiphylla***, a common streamside species that develops more strengthening in fast water. Photo by Kristian Peters, through Creative Commons.

Duckett (1994) described yet another modification that would be helpful in some aquatic environments. In ***Straminergon stramineum*** (Figure 46-Figure 47) rhizoids develop below the apex of each leaf (Figure 48). Damaged apices regrow, providing a means of reproduction. These rhizoids are more frequent further down the stem. They become highly branched on peaty substrata or on dead *Molinia* leaves. He found that rhizoid branches would coil around other rhizoids of both ***S. stramineum*** and ***Aulacomnium palustre*** (Figure 49), whereas others were unbranched and wove their way through ***Sphagnum*** hyaline cell pores (Figure 50). When the rhizoids occur in water cultures, the new parts branch and adhere upon contact. When new leaves form in culture, they produce numerous rhizoids upon contact; those that grow unobstructed do not. This is similar to the behavior of ***Fontinalis*** rhizoids (Figure 22) described above.

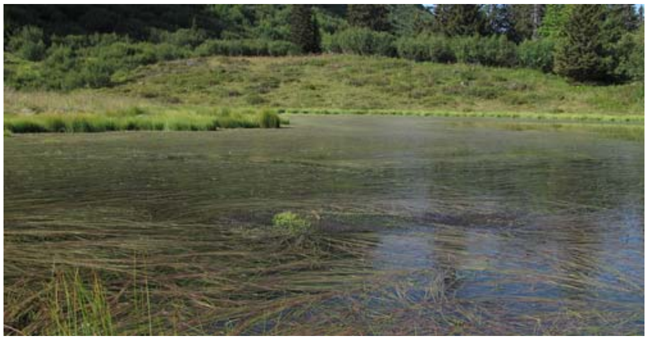

Figure 46. ***Straminergon stramineum*** habitat. Photo by Michael Lüth, with permission.

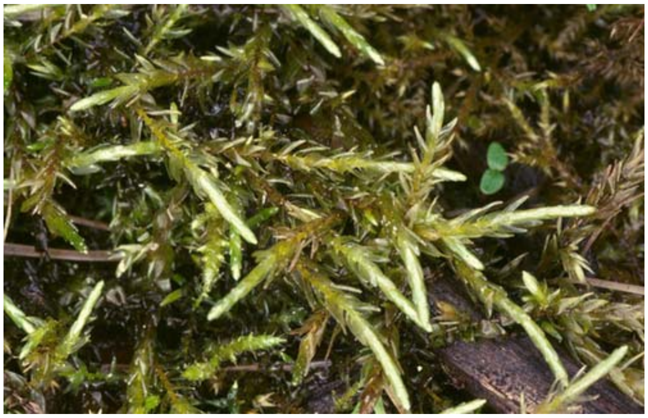

Figure 47. ***Straminergon stramineum***, a species that produces rhizoids on the leaf tips. Photo by Malcolm Storey, with online permission.

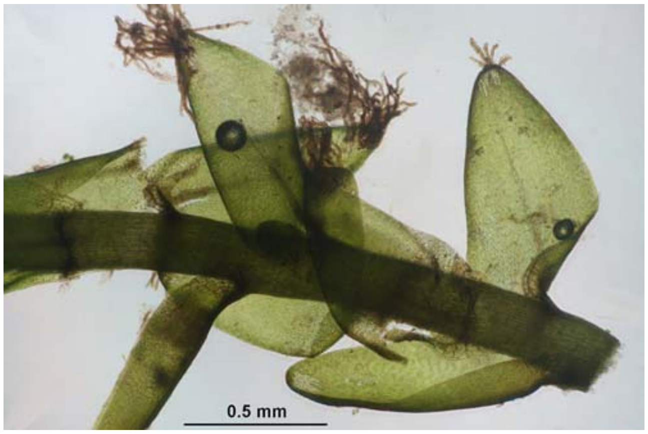

Figure 48. ***Straminergon stramineum*** showing rhizoids at leaf tips. Photo by Hermann Schachner, through Creative Commons.

Figure 49. ***Aulacomnium palustre*** showing rhizoidal tomentum. Photo by J. C. Schou, through Creative Commons.

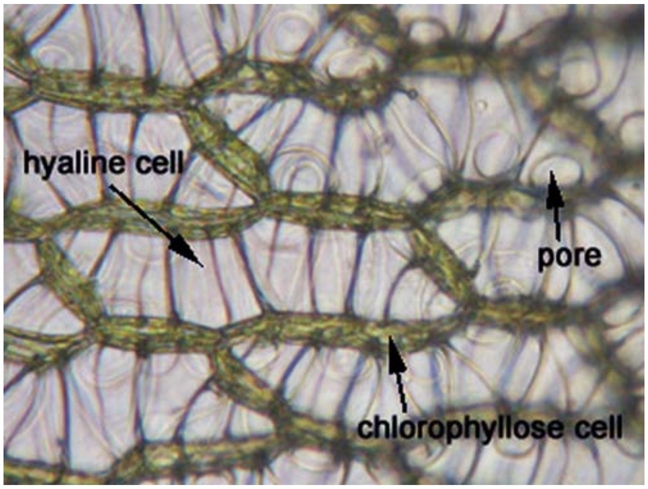

Figure 50. ***Sphagnum*** leaf hyaline cell with pore. Photo from Botany website, UBC, with permission.

When these ***Straminergon stramineum*** leaves (Figure 48) are detached, they produce numerous branched chloronemal filaments not only at their apices, but also at the margins and bases (Duckett 1994). At the bases of these filaments, gametophores develop, making these leaves highly likely propagules.

Sporophyte Characters

Most of the stream mosses produce their capsules above the water and therefore these capsules resemble terrestrial capsules (Vitt 1981; Vitt & Glime 1984). But several produce capsules under water. These include ***Blindia*** (Figure 51), ***Cinclidotus*** (Figure 52), ***Fontinalis*** (Figure 53), ***Hydropogon***, ***Hydropogonella*** (Figure 54), ***Rhabdodontium***, and ***Wardia*** (Figure 55). These underwater capsules are characterized by immersed, smooth, ovate-oblong capsules, short, thick setae (Figure 53), somewhat reduced peristome, and capsule surrounded by enlarged, sheathing perichaetial leaves.

Figure 51. ***Blindia acuta*** with capsules that can be produced under water. Photo by Hermann Schachner, through Creative Commons.

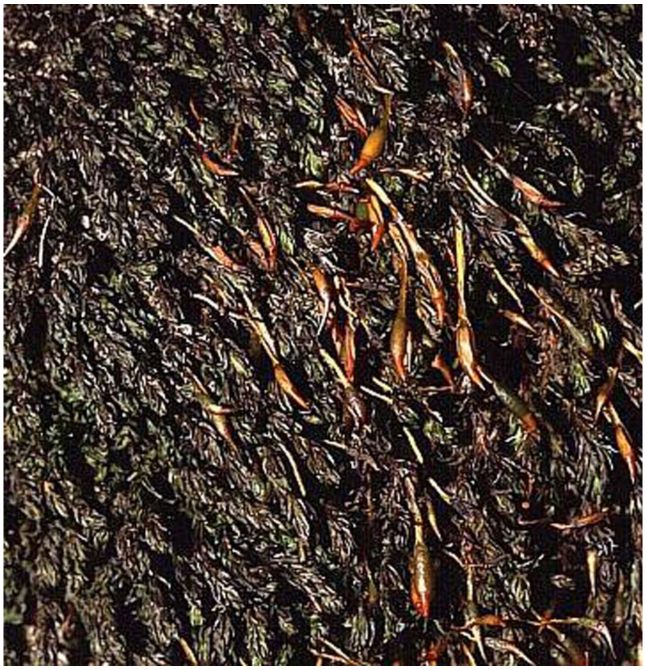

Figure 52. ***Cinclidotus confertus*** with capsules that can be produced under water. Photo by Michael Lüth, with permission.

Figure 53. ***Fontinalis dalecarlica*** capsules that are produced under water. Although it has a well-developed peristome, that peristome is quickly damaged and broken off in the water, as in the lower capsule. Photo by Janice Glime.

Figure 54. ***Hydropogonella gymnostoma***, a species that produces capsules under water. Photo from <aqvium.ru> through public access.

Figure 55. ***Wardia hygrometrica*** with capsules that can be produced under water. Photo by Jonathan Sleath, Sanbi.

Fissidens fontanus likewise has a reduced peristome (Figure 56) (Bruggeman-Nannenga 2013) and ***F. bessouensis*** has a very short seta (Figure 57), the latter also seen above in ***Fontinalis*** (Figure 53). To these sporophyte characters, Ida Bruggeman-Nannenga (Bruggeman-Nannenga 2013; pers. comm. 10 April 2020) adds loss of stomata in the capsule, a character often omitted in moss species descriptions.

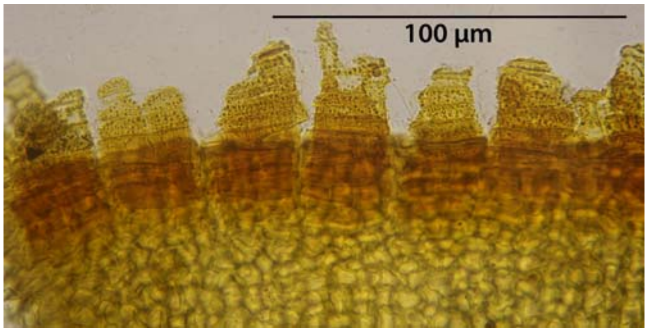

Figure 56. ***Fissidens fontanus*** with reduced peristome, a common character of submersed species. Photo by courtesy of Ida Bruggeman-Nannenga.

Figure 57. ***Fissidens bessouensis*** sporophyte showing short seta. Photo courtesy of Ida Bruggeman-Nannenga.

Pursell (1987) noted that in the ***Octodiceras*** subgenus of ***Fissidens*** the capsules tend to break off in the herbarium. Kortselius *et al.* (2018) reported that the calyptrae of ***Fissidens*** (***Octodiceras***) ***fontanus*** (Figure 58) frequently develops new plants from the calyptra (Figure 59). If the breakage also occurs in the field, it would provide these species with an additional dispersal mechanism in the water.

Figure 58. ***Fissidens fontanus***, a species that can grow new plants from the calyptra. Photo by Matt Keevil, through Creative Commons.

Figure 59. ***Fissidens fontanus*** calyptrae with germination. Photo courtesy of Hans Kruijer.

The recently described ***Ochyraea tatrensis*** (Váňa 1986) was collected from granite rocks in a stream in Nízké Tatry in Slovakia. It has since then been found with sporophytes (Bednarek-Ochyra & Váňa 2014). These sporophytes showed no morphological differences from their more familiar terrestrial relatives.

Spores

Some of the aquatic species have multicellular spores (Bruggeman-Nannenga 2013). One such species with multicellular spores is ***Fissidens bessouensis***, a potential advantage in permitting the protonema to develop quickly before it can be washed away.

Character Plasticity

Berthier (1965) concluded that the environment intervenes in the development of ***Fontinalis antipyretica*** (Figure 9-Figure 10). In support of Berthier's conclusion, Frahm (2006) concluded that ***Fontinalis antipyretica*** var. ***gracilis*** (Figure 60) was only a modification of ***Fontinalis antipyretica***. On the other hand, he (Frahm 2013) concluded that ***F. antipyretica*** var. ***rotundifolia*** (Figure 61) is a valid separate species (***F. rotundifolia***). These forms can be modified by flow rate, submersion vs emergent, nutrient levels, light penetration, and probably other factors.

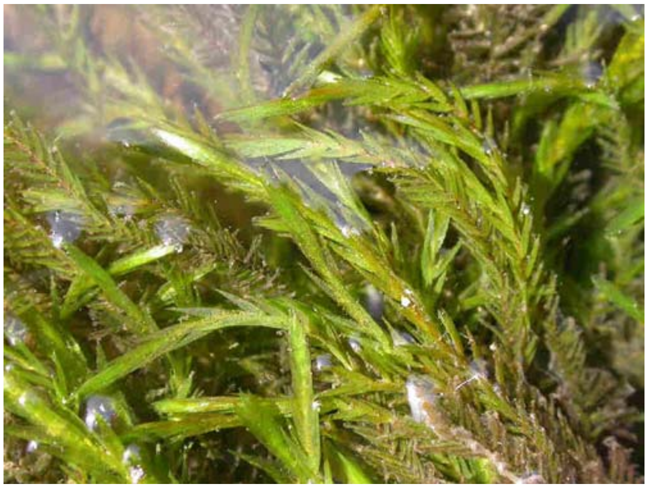

Figure 60. ***Fontinalis antipyretica*** var. ***gracilis***, a more conservative classification of ***Fontinalis gracilis***. Photo by David T. Holyoak, with permission.

Figure 61. ***Fontinalis antipyretica*** var. ***rotundifolia*** holotype, a distinct variety. Photo by Jan-Peter Frahm, with permission.

Vanderpoorten and Jacquemart (2004) demonstrated, using culture experiments, that most of the morphological variation exhibited by the aquatic moss genus ***Amblystegium*** (***Hygroamblystegium***?; Figure 31) occurred as a result of plasticity. Furthermore, those genetic characters that resulted in morphological evolution tended to occur in consort; constraining the characters to be independent from each other produced less likely results than in models that permitted them to evolve as correlated traits. This has made it difficult to describe distinguishing characters for separating species.

Philonotis fontana (Figure 62), sometimes a stream edge species in quiet, shallow water, exhibits phenotypic plasticity (Buryová & Shaw 2005). When grown under two light and two water regimes, both habitat characters affected growth. Light treatments had greater effects and affected more characters. Several traits indicated genetic variation, with the plasticity varying among plants from six populations in the common garden experiments. Leaf dimensions seemed to have a strong genetic component, but the cell dimensions showed little genetic variation.

Figure 62. ***Philonotis fontana*** from a stream edge habitat. Photo by J. C. Schou, with permission.

Resultant Identification Problems

Morphological plasticity complicates identification of aquatic bryophytes, but permits the species to live in a greater range of habitats. We have demonstrations that some of these differences result from the environmental factors, but others are apparently genetic. For example, Huttunen and Ignatov (2010) considered the genetics of the genus ***Rhynchostegium*** *s.l.* (Figure 63). ***Platyhypnidium*** (Figure 24), an aquatic member of the ***Rhynchostegium*** complex, proved to be polyphyletic (having more than one ancestor for the genus). Huttunen and Ignatov found that phylogeny of ***Rhynchostegium*** and ***Platyhypnidium*** indicates there have been numerous habitat shifts between terrestrial and aquatic habitats, as well as between different terrestrial (epiphytic and epigeic) habitats, which may have affected taxonomic complexity in ***Rhynchostegium***.

Figure 63. ***Rhynchostegium confertum***, member of a genus that has had many shifts between terrestrial and aquatic habitats. Photo by Michael Lüth, with permission.

Species can even mimic other species. De Mey and During (1972) found that ***Fontinalis squamosa*** (Figure 21-Figure 22, Figure 27, Figure 33) in the Netherlands sometimes had keeled leaves like those of ***F. antipyretica***. I have seen a similar keeling occasionally in ***F. duriaei*** (Figure 64), a trait also observed by Zastrow (1934), but only among some of the leaves of the plant. But any adaptive value for keeled leaves is elusive. Glime and Trynoski (1977) suggested that in ***Fontinalis neomexicana*** (Figure 65) the trait might provide rigidity and keep the leaves tightly together, providing a smooth surface in deep water. ***Fontinalis antipyretica*** (Figure 9-Figure 10), on the other hand, often has its leaves torn along the keel (Figure 66), suggesting that it is not really adaptive against abrasion. ***Fontinalis gigantea*** (Figure 13) occurs in quiet water, and thus its keeled leaves do not suffer the tearing of abrasion and rapid flow. One explanation for the presence of keeled leaves has been revealed by experiments conducted on ***Fontinalis antipyretica*** (Zastrow 1934). Zastrow found that in acid waters, the leaves were strongly keeled, in neutral water they were less keeled, and in alkaline water they were the least keeled and most narrow. It seems to be a consequence, but not necessarily an adaptation.

Figure 64. ***Fontinalis duriaei***, a species that can have some keeled leaves among the typically concave ones. Photo by Michael Lüth, with permission.

Figure 65. ***Fontinalis neomexicana***, a species with keeled leaves that might provide a smooth surface. Photo by Amy Gibson, through Creative Commons.

Figure 66. ***Fontinalis antipyretica*** split leaf, a common occurrence when the plant is in rapid flow. Photo by Malcolm Storey, with online permission.

Differences are often so great between terrestrial and aquatic habitats that the plants are described as different species. For example, Beever and Fife (2008) determined that the aquatic moss ***Hypnobartlettia fontana*** (Figure 67) from Te Waikoropupuu (Pupu Springs), New Zealand, is but an environmental expression of ***Cratoneuropsis relaxa*** (Figure 68). ***Hypnobartlettia fontana*** had been placed not only in a different species, but in a different family. ***Cratoneuropsis relaxa*** varies widely throughout its wide range of habitats in New Zealand. Among these are waterfalls, irrigated and shaded rocks, stream beds, and seepages. It likewise occupies a wide range of substrates. The Pupu Springs version differs in having bistratose laminae, a very stout, excurrent costa, and linear-flexuose lamina cells that are 40-100 µm long, all features that are common among submersed species. It also has paraphyllia on its stems (Ochyra 1985), a feature not usually seen in submersed taxa. Beever and Fife concluded that the environmental form erroneously named as ***H. fontana*** is a form induced by the unusual conditions at Te Waikoropupuu. It is known only from this type locality, where the water is nearly perfectly clear, high in calcium, and cold (11.7ºC).

Figure 67. ***Cratoneuropsis relaxa***, previously treated as ***Hypnobartlettia fontana***, from Pupu Springs, TePapa. Photo by John Bartlett, through Creative Commons.

Figure 68. ***Cratoneuropsis relaxa***; one form is so different it was named to a different family and genus as ***Hypnobartlettia fontana***. Photo by Tom Thekathyil, with permission.

Further evidence of the variability of ***Cratoneuropsis relaxa*** (Figure 68) is that ***Sciaromium bellii*** (Figure 69) likewise is now considered to be a variant of this variable species (Sainsbury 1948, 1955; Beever & Fife 2008). It differs in having laminal cells that are unistratose except occasionally a few bistratose marginal cells. They also have only a weak laminal border of thicker-walled cells in the lower part of the leaf. This form is widespread on both of the main islands of New Zealand. In Pupu Springs, the leaves have bistratose margins and nearly equal areas of unistratose and bistratose mid-leaf laminal cells.

Figure 69. ***Cratoneuropsis relaxa***, previously treated as ***Sciuromium bellii*** from Te Papa. Photo from TePapa, through Creative Commons.

Plastic Characters

Flow rate is one cause of polymorphisms in ***Fontinalis antipyretica*** (Figure 9-Figure 10). These differences include stem thickening and branching angle of the leaves, as already noted in subchapter 2-3 of this volume.

Plications (folds like a Japanese fan; Figure 71, Figure 73) also seem to have no value in the water. ***Tomentypnum nitens*** (Figure 70-Figure 71) and ***Climacium dendroides*** (Figure 72-Figure 73) both lose their plications when grown submersed (Zastrow 1934).

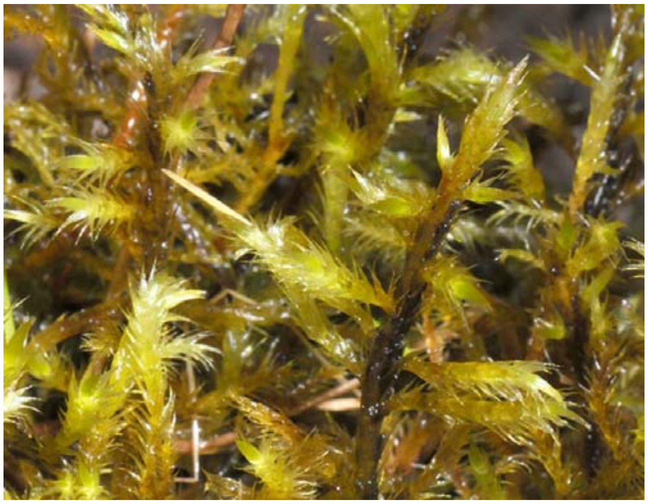

Figure 70. ***Tomentypnum nitens***, a species that loses its plication when grown in water. Photo by J. C. Schou, with permission.

Figure 71. ***Tomentypnum nitens*** plicate leaf. Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Climacium dendroides***, a moss often found on stream banks and other moist habitats. Photo by Jeremy Baker, through Creative Commons.

Figure 73. ***Climacium dendroides*** plicate leaves; plications are lost when the species grows under water. Photo by Matt Keevil, through Creative Commons.

Warnstorfia exannulata (Figure 74), when grown submersed, has stems four times as long as those grown out of water (Zastrow 1934). This results from longer internodes (Lodge 1959). Lodge suggested that the elongation may result from the lower light levels, *i.e.* an **etiolation** (characterized by long, weak stems; smaller leaves; longer internodes; and pale yellow color) response, a response I have seen by terrestrial bryophytes in a terrarium.

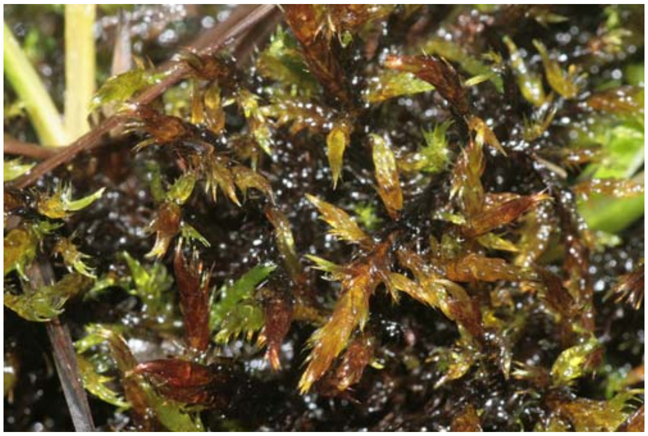

Figure 74. ***Warnstorfia exannulata***, a species that can grow four times as long in the water. Photo by Hermann Schachner, through Creative Commons.

Falcations are typically lost in the water. This is clearly visible in ***Warnstorfia exannulata*** (Figure 74). It can be very falcate when it is emergent (Figure 75), but have completely straight leaves (Figure 76) when it grows submerged. Likewise, ***Fontinalis novae-angliae*** has straight leaves (Figure 77) in nature when it grows in water but when I grew it in an artificial stream where it was exposed to air, but constantly wet, it grew falcate leaves! (Figure 78). This is interesting because the mostly terrestrial genus ***Dichelyma*** in the same family typically has falcate leaves. The monotypic ***Brachelyma*** in that family is often inundated but has straight leaves, but they are keeled, like some species of ***Fontinalis***.

Figure 75. ***Warnstorfia exannulata*** emergent, showing falcate leaves. Photo courtesy of Michael Lüth.

Figure 76. ***Warnstorfia exannulata*** submersed, showing straight leaves. Photo courtesy of Michael Lüth.

Figure 77. ***Fontinalis novae-angliae*** growing submersed, showing straight leaves. Photo by Matt Keevil, through Creative Commons.

Figure 78. ***Fontinalis novae-angliae*** growing in artificial stream where its leaves are exposed to air but constantly wet, showing the resulting falcate leaves. Photo by Janice Glime.

Even thallose liverworts have thallus plasticity. The best known of these examples is ***Riccia fluitans***. In water, the thallus is composed of narrow, ribbon-like branches (Figure 79), whereas on soil the thallus is broader (Figure 80), more similar to other ***Riccia*** species.

Figure 79. ***Riccia fluitans*** aquatic form showing narrow thalli. Photo courtesy of Michael Lüth.

Figure 80. ***Riccia fluitans*** terrestrial form showing broader thallus. Photo courtesy of Michael Lüth.

Zastrow (1934) also found that *p*H affects height growth in aquatic and semi-aquatic species. ***Aulacomnium palustre*** (Figure 81), ***Bryum pseudotriquetrum*** (Figure 2-Figure 3), ***Fissidens adianthoides*** (Figure 82), and ***Fontinalis antipyretica*** (Figure 9-Figure 10), all grow taller when in alkaline water than when in neutral or acid water.

Figure 81. ***Aulacomnium palustre***, a species known to grow taller in alkaline water. Photo by Michael Lüth, with permission.

Figure 82. ***Fissidens adianthoides***, a species known to grow taller in alkaline water. Photo by Janice Glime.

Platyhypnidium riparioides (Figure 24), a species that frequently grows intermixed with ***Hygroamblystegium fluviatile*** (Figure 31), varies among populations (Wehr & Whitton 1986). In 105 sites in 71 streams and rivers, there was variation in size and robustness of the plants, dimensions and shape of leaves, degree of leaf denticulation, and relative length of the costa. The characters of less robustness, smaller leaves, and weaker denticulation correlated with the nutrient richness of the water.

Alterations of Terrestrial and Wetland Species in Water

Water culture can alter the anatomy and morphology of wet habitat species. For example, ***Aulacomnium palustre*** (Figure 81), ***Brachythecium rivulare*** (Figure 83), ***Fissidens adianthoides*** (Figure 82), and ***Tomentypnum nitens*** (Figure 84) exhibit loss of central strand, loss of papillae, loss of border, reduction of costa, and loss of alar cells when grown submersed (Zastrow 1934). Furthermore, chlorophyll is often reduced, although that is more likely a response to reduced red light than it is an adaptation.

Figure 83. ***Brachythecium rivulare***, a species that loses its central strand in water. Photo by Snappy Goat, through public domain.

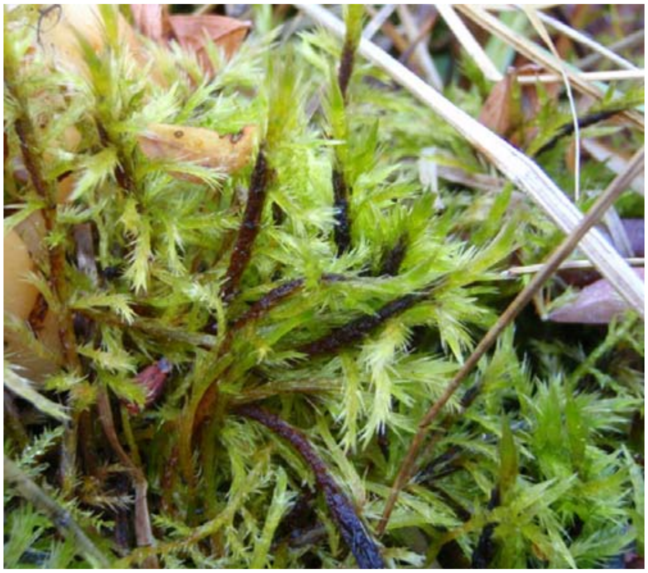

Figure 84. ***Tomentypnum nitens***, a species that exhibits character plasticity when submerged. Photo by Scot Loring, through Creative Commons.

It appears that even mosses that do not ever grow aquatically have the potential to change their morphology when grown submersed. Higuchi and Iwatsuki (1986) submersed two terrestrial mosses to discover what characters were plastic under these conditions. They found that ***Hypnum plumiforme*** (Figure 85) and ***Gollania japonica*** (Figure 86) produced smaller leaves that were scattered, *i.e.* longer internodes. The leaves had a more or less entire margin with thinner-walled lamina cells and less defined alar cells. The new shoots were more julaceous. Leaf shape and cell size showed little change.

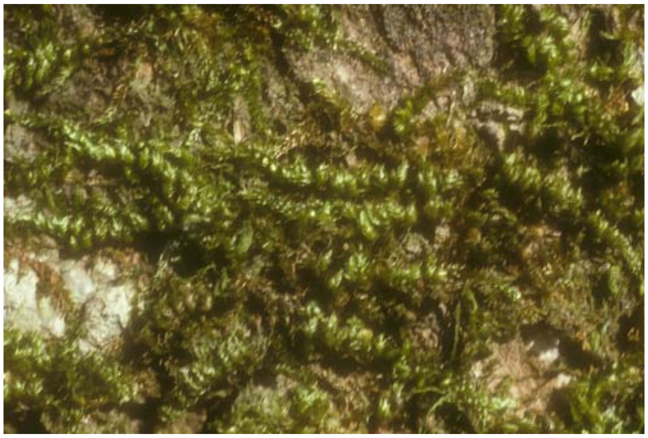

Figure 85. ***Hypnum plumaeforme***, a terrestrial moss that produces smaller leaves with longer internodes if cultured under water. Photo by Janice Glime.

Figure 86. ***Gollania japonica***, a terrestrial moss that produces smaller leaves with longer internodes if cultured under water. Photo from Taiwan Mosses, through Creative Commons.

Genetic Variation

In ***Hygroamblystegium tenax*** (Figure 87) the genetic variation within a species can be higher than that between this species and ***H. fluviatile*** (Figure 31) (Vanderpoorten & Tignon 2000). Such variability can explain the many forms found among some aquatic species, but it does not explain the variability expressed by one plant under different growing conditions.

Figure 87. ***Hygroamblystegium tenax***, a species with high genetic variation. Photo by Štěpán Koval, with permission.

The Central American ***Platyhypnidium pringlei*** (Figure 88) is an aquatic montane species of Central Mexico and Guatemala (Wynns *et al.* 2009). But this species seems to be somewhat widespread, albeit uncommon. A morphologically different form occurs in sheltered coves of the Blue Ridge Mountains in SE USA. In both locations, the plants are sterile. A more robust form occurs in Arizona and California, USA, where all plants are females. In the Himalayas of India, the populations are fertile. Here there are several forms that intergrade, whereas those in North America appear to be geographically isolated. Genetically, this species seems to belong to ***Oxyrrhynchium*** (Figure 89). The aquatic species in that genus are characterized by their dark green color, frequent branching, loose leaf arrangement, short leaf laminal cells, and long costae, characters that seem to differ from those of ***Platyhypnidium riparioides*** (Figure 24).

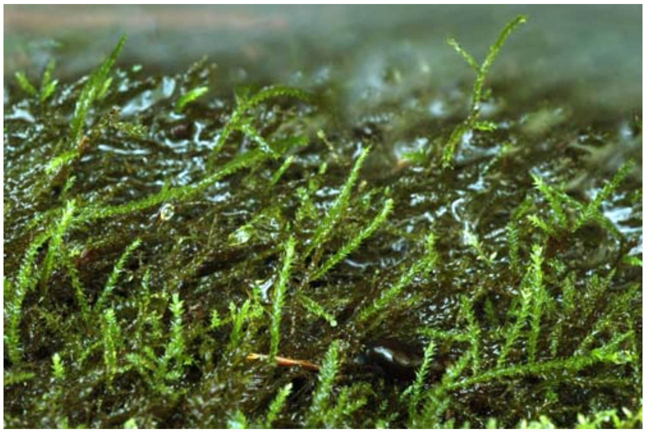

Figure 88. ***Platyhypnidium pringlei***, a widespread species with many known forms. Photo by Ken McFarland and Paul Davison, with permission.

Figure 89. ***Oxyrrhynchium hians***; genetically, ***Platyhypnidium pringlei*** seems to be in the genus ***Oxyrrhynchium***. Photo by Hermann Schachner, through Creative Commons.

Zhu *et al.* (2007) found 67.2% of the ***Brachythecium rivulare*** (Figure 83) populations were polymorphic. Genetic variation reached 91.2% within populations, but only 8.8% among different populations. Genetic distance did not correlate with elevation gradient.

Mechanisms Facilitating Morphological Changes

Changes in light quality and intensity can account for such differences as stem elongation and greater internode differences. Rapid flow carrying siltation can cause abrasion, a possible selection pressure to cause genetic and morphological differences between pools and flowing water. But even with these physical factors as causes, there must be a physiological response. Few studies address these physiological responses and the biochemical differences that might facilitate them.

Ethylene may play a role in the morphological plasticity of ***Fontinalis*** (Glime & Rowher 1983). Ethylene is a stress hormone. In ***Fontinalis squamosa*** (Figure 21-Figure 22, Figure 27, Figure 33) and ***F. antipyretica*** (Figure 9-Figure 10) it causes color changes (Figure 90), leaf undulations (Figure 91), inhibition of rhizoid production, and crumpled branches and leaves (Figure 92). The stress of flow and contact with a substrate could alter the morphology by both affecting production of ethylene and by slowing its rate of dissipation. In these experiments, the two species responded somewhat differently. Changes in stem characters were not assessed.

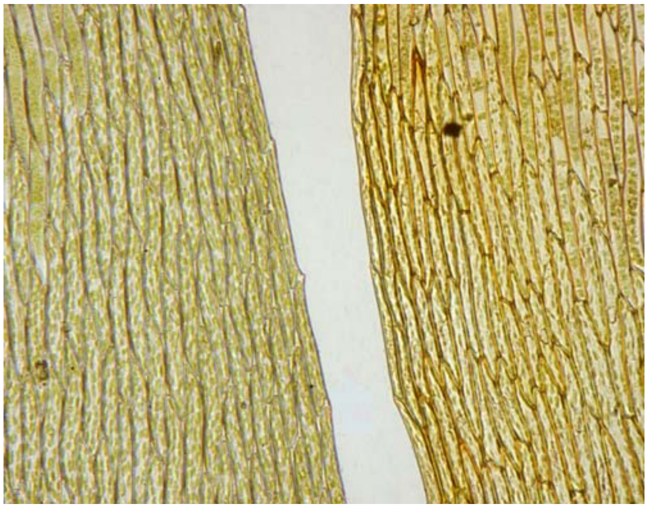

Figure 90. ***Fontinalis antipyretica*** leaf cells of control (**left**) and with ACC10^{-4} (**right**), showing color changes in presence of ACC, an ethylene precursor. Photo by Janice Glime.

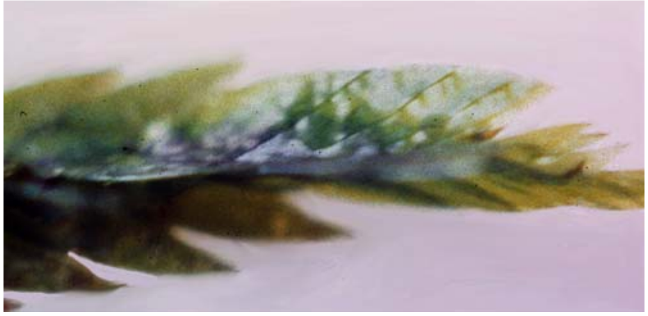

Figure 91. ***Fontinalis antipyretica*** showing undulate leaf modifications due to ACC, an ethylene precursor. Photo by Janice Glime.

Figure 92. ***Fontinalis squamosa*** showing crumpled-leaf modifications due to ACC, an ethylene precursor. Photo by Janice Glime.

We also cannot ignore the potential role of **ABA** (hormone – abscisic acid) in the morphological differences within aquatic bryophyte species. Takezawa *et al.* (2011) noted the presence of ABA in all the living kingdoms and specifically demonstrated its role in drought tolerance in the terrestrial moss ***Physcomitrella patens*** (Figure 93). Wanke (2011) noted that ABA is a "key factor" in the expression of heterophylly in aquatic plants, making it possible for them to switch from submersed leaf forms to emergent ones. He surmised that such heterophylly is present in ferns and flowering plants, but that it is absent in aquatic bryophytes, citing studies by Hsu *et al.* (2001), Lin (2002), Villani and Etnier 2008), and Takezawa *et al.* (2011). But is this heterophylly really totally absent in bryophytes?

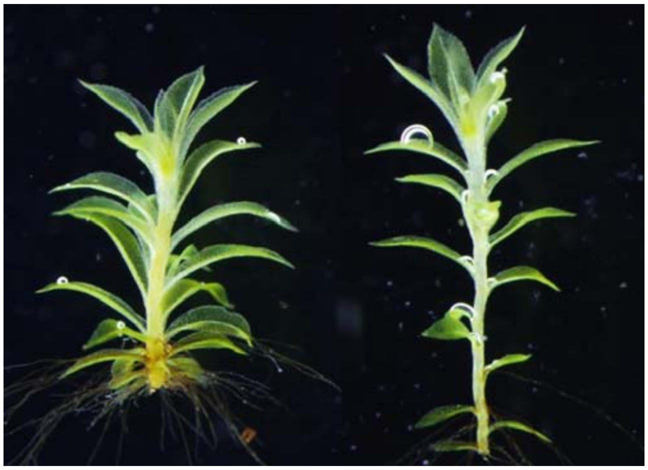

Figure 93. ***Physcomitrella patens*** with plant on right having 6 disrupted MADSbox genes (Koshimizu *et al.* 2018). The elongated internodes are similar to that seen if the species is grown in water and prevent the typical capillary movement of water upward. Photo by Koshimizu & Hasebe, with online permission.

Koshimizu *et al.* (2018) learned that the MADSbox genes regulate cell division and growth in the stems of ***Physcomitrella patens*** (Figure 93), thus controlling the appropriate internode distance for the water availability through external conduction. Could this control be important in the larger internode distance in aquatic populations? Does water block these genes? How does the water interact with light intensity? Are the longer internodes adaptive in making the species more flexible?

Dimorphic Forms?

Welch (1948) reported that the leaves of ***Fontinalis sphagnifolia*** (Figure 94) exhibited dimorphism (Figure 95). Similarly, I have seen ***Fontinalis duriaei*** with both keeled leaves and rounded leaves on the same plant. Could it be that at different times they grew under different conditions? Are there other examples?

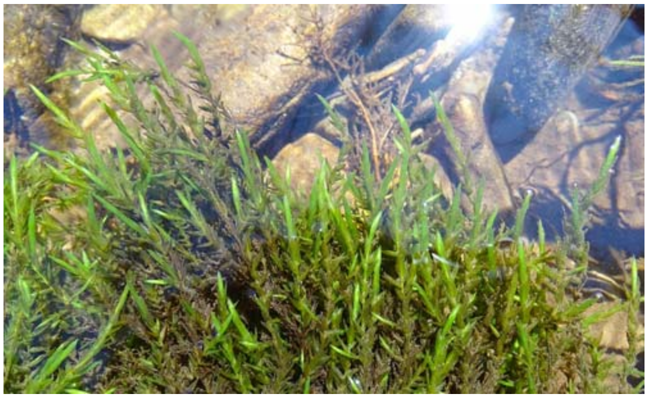

Figure 94. ***Fontinalis sphagnifolia***, a species known for dimorphic leaves. Photo by Will Van Hemessen, through Creative Commons.

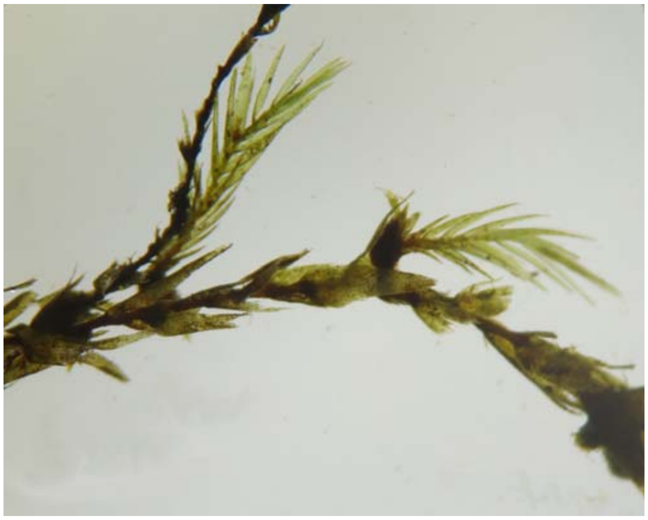

Figure 95. ***Fontinalis sphagnifolia*** leaf dimorphism between stem and branch leaves, Hudson Bay. Photo courtesy of Eric Snyder.

Among the liverworts, the semi-aquatic ***Colura irrorata*** (Figure 96) (= *Myriocolea irrorata*) from Ecuador has lobulate leaves on prostrate shoots and very different, elobulate leaves on erect (or pendent) shoots (pers. comm. S. Robbert Gradstein, 9 April 2020). These do not seem to relate to an aquatic environment, but perhaps to contact with a surface. Basile (1967, 1969) demonstrated that hydroxyproline could be responsible for controlling the size of underleaves in leafy liverworts, so it could play a role here. Differences in ethylene concentration might also provide an explanation.

Figure 96. ***Colura calyptrifolia*** on willow, showing lobules. Photo by Stan Phillips, through public domain.

Summary

Stream bryophytes tend to have more rhizoids than in other wetland types, and increased flow can cause that number to increase. The rhizoids of ***Fontinalis*** are negatively phototropic, thus growing toward the substrate. In ***Fontinalis*** and other species they produce an adhesive and branching at the rhizoid tips when they make contact.

In some groups, the standing water species are characterized by reductions, including of ventral scales or none, fewer hyaline cells, fewer strengthening fibers in the hyaline cells, and fewer and lower leaf lamellae, but those living in rapid streams display no such reduction. Submersed species can exhibit loss of central strand, loss of papillae, loss of leaf border, reduction of costa, and loss of alar cells.

Sporophytes are produced above water in many species, often taking advantage of low water levels. Submersed capsules are frequently characterized by being smooth and ovate-oblong, and having short setae, reduced peristome, and no stomata. Spores can be enlarged and may be multicellular.

Character plasticity is common, including stem elongation, modified leaf size and shape. Keels may disappear in alkaline water. Stems in fast water may thicken, plications and falcations disappear, branching angles may change. The thallus of thallose liverworts may be narrower in water, as in ***Riccia fluitans***. Nutrients may also affect elongation and leaf size. Species with dimorphic leaf expressions on the same plant are rare.

Among the physiological responses, it is possible that ABA and ethylene may play a role in morphological differences. MADSbox genes may regulate cell elongation based on moisture conditions. Some species have more genetic variability than terrestrial species.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. Jim Shevock alerted me to the story of ***Hypnobartlettia***. Ida Bruggeman-Nannenga has been very helpful in sharing her experience with ***Fissidens*** and providing images and references and even taking photographs I needed.

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CHAPTER 2-5
STREAMS: LIFE AND GROWTH FORMS AND LIFE STRATEGIES

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Figure 1. ***Fontinalis novae-angliae*** with capsules, exemplifying the **streamer** life form in a mountain stream. Photo by Janice Glime.

Life and Growth Forms

Definitions and Habitats

In bryophytes, **growth forms** are genetically determined forms of adult individual gametophyte plants (Meusel 1935; Mägdefrau 1982). **Life forms** are the environmental expressions of those plants and refer to the growth pattern of the colony. But for many species, perhaps most, a single protonema, developing from a single spore, develops multiple buds that develop into stems and thus form a colony from the onset, giving rise to a **life form** as that colony develops.

A number of bryologists have stressed the importance of life forms as adaptations to habitat conditions. Bryophyte growth forms and life forms can be used to indicate conditions of hydrologic permanence in non-polluted mountain streams (Fritz *et al.* 2009; Vieira *et al.* 2012a). In 165 locations in Portuguese water courses, Vieira *et al.* (2012a) found 11 life forms, with a mean of 2.7 per sample. There was a clear dominance of **smooth mats** (Figure 2; 37%), **tall turfs** (Figure 3; 25%), **fans** (Figure 4; 10%), and **short turfs** (Figure 5; 10%). As habitat zones were less frequently submersed, the number of life forms increased. The deepest or most permanently submersed regions had **mats** and **streamers** [Figure 1; long, dangling stems (Glime 1968)].

Figure 2. ***Frullania tamarisci*** **smooth mat**, a common species near water on canyon walls. Photo by Hermann Schachner, through Creative Commons.

Figure 3. ***Drepanocladus aduncus***, a **tall turf**; this species produces sporophytes when out of water. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Figure 4. ***Neckera crispa*** **fans**, in this case growing terrestrially. Photo by Malcolm Storey, with online permission.

Figure 5. ***Marsupella emarginata***, an aquatic liverwort that forms a **short turf**. Photo by Hermann Schachner, through Creative Commons.

When Vieira *et al.* (2012b) assessed life forms in mountain streams of Portugal, they found that **thallose liverworts** (Figure 6) typically avoided the flowing water, occurring in shaded locations where they were only seasonally submersed or splashed. These forms were easily damaged by submersion and drag forces. On the other hand, some leafy liverworts that formed **smooth mats** (Figure 2) occurred submersed. Those permanently submersed bryophytes tended to be **streamers** (Figure 1) and **smooth mats**, found up to 30 cm of depth in streams. The **streamers** tended to occur mostly in slower currents of the streambed in full sunlight, whereas **smooth mats** seemed to prefer the torrential water zones in deep shade. Bryophytes subject to frequent water level fluctuations, *i.e.* close to the water, were characterized by a more 3-dimensional life form, but one that was resistant to desiccation and drag forces. These included well anchored **fans** (Figure 4), **dendroids** (Figure 7), and **short turfs** (Figure 5), often occupying vertical surfaces of rocks short distances from the water, but able to benefit from the splash.

Figure 6. ***Pellia epiphylla***, a thallose liverwort that is common on stream banks. Photo by David Holyoak, with permission.

Figure 7. ***Climacium dendroides*** exhibiting the **dendroid** life form. This species can occupy stream banks that get submersed during snowmelt flooding. Photo by Stan Phillips, through public domain.

In the seasonally flooded habitats Vieira *et al*. (2012b) found **tall** and **open turfs** (Figure 8) that have stiff texture, multi-layered tissues, and thick cell walls (Figure 9). These permit them to resist both desiccation and water abrasion. On the upper zones of stones where strong currents are less frequent and in exposed streambeds, bryophytes are represented by **smooth densely-packed cushions** (Figure 10) and **short turfs** (Figure 5) that can resist drought stress (Gimingham & Birse 1957; Muotka & Virtanen 1995; Barrat-Segretain 1996; Vieira *et al*. 2012b). Here and at higher zones on boulders, but in the shade, smooth **mats** (Figure 2) and **fans** (Figure 4) develop (Vieira *et al*. 2012b). Above the level of maximum flooding annuals join the bryophytes, displaying **loose rough mats** (Figure 11) or **wefts** (Figure 12).

Figure 8. ***Tomentypnum nitens***, a wetland **tall turf** species that occurs in fens. Photo by Michael Lüth, with permission.

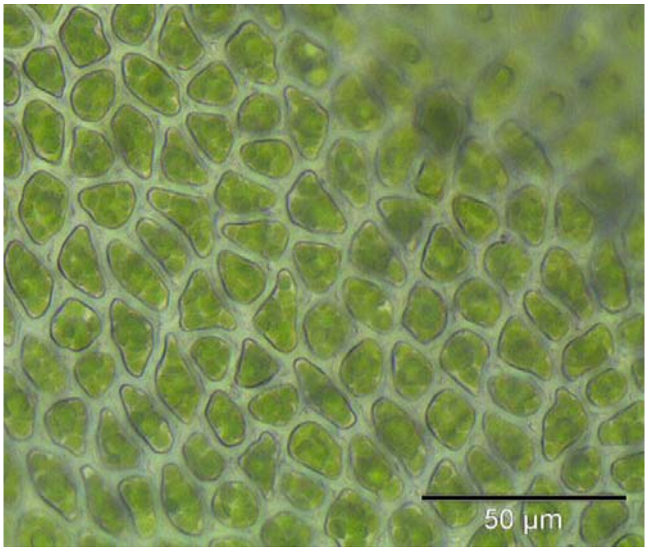

Figure 9. ***Aulacomnium palustre*** leaf lamina showing thick-walled cells. Photo by Kristian Peters through Creative Commons.

Figure 10. ***Andreaea alpina* cushion**, a species that can be found on rocks that are occasionally inundated on crags near lakes and streams. Photo by Michael Lüth, with permission.

Figure 11. ***Brachythecium rivulare* rough mat**, a species that occurs on stream margins, and in springs and marshes. Photo by Hugues Tinguy, with permission.

Figure 12. ***Trichocolea tomentella*** **wefts**, a species of fens and low areas that can become submersed. Photo by Li Zhang, with permission.

In this same top or higher zones of the boulders, if shaded conditions prevailed for most of the year, **smooth mats** (Figure 2) along with **fans** (Figure 4) developed. Additionally, microhabitats higher than the normal level of maximum floods could be recognized by the co-existence of **annuals** (must grow new plants every year), loose **rough mats** (Figure 11) or **wefts** (Figure 12) that developed mostly associated with deposited sediments.

Birse (1958) related life form to habitat. She found that **wefts** (Figure 12) were typical in freely drained habitats and conditions of intermediate moisture. **Tall turfs** (Figure 3) were more common when water was close to the soil surface. **Wefts** (Figure 12) and **dendroid** (Figure 7) life forms occupied habitats with moisture available from the water table in summer. The semi-aquatic emergents are more likely to be **tall turfs**. Truly aquatic mosses are rarely **tall turfs**, but may be **streamers** (Figure 1, Figure 15), a term introduced by Glime (1968).

Jenkins and Proctor (1985) considered aquatic bryophytes to have two main life forms: **turfs** of densely-set shoots such as those of ***Scapania undulata*** (Figure 13) and ***Hygrohypnum luridum*** (Figure 14) that cling to boulders experiencing turbulent, fast-flowing water; **streamers** (Figure 1, Figure 15) such as ***Fontinalis*** more typical of slower, more streamlined flow. On the other hand, ***F. dalecarlica*** (Figure 15) can occur on boulders in rapids, defending itself with numerous rhizoids and wire-like strong stems.

Thalloid liverworts (Figure 6) grow in zones that are rarely submersed. These liverworts are intolerant of the physiologic stress of continuous submersion or drought and the mechanical stress of mechanical scouring (Gimingham & Birse 1957; Kimmerer & Allen 1982; Martinez-Abaigar & Núñez-Olivera 1991). Rather, they develop in abundance in a more humid and shaded environment above the upper limit of flood-water impact.

Vieira *et al.* (2012b) found that **colonial** growth often occurred through shoot innovations that were firmly attached to the substrate (Figure 16), permitting them to remain in place during heavy flow (During 1990; Grime *et al.* 1990; Muotka & Virtanen 1995). **Ephemeral colonists**, on the other hand, indicate stream zones that are submerged by shifting currents that create abrasive events (Vieira *et al.* 2012b). They survive in tiny rock crevices where they are protected from the torrential currents (Muotka & Virtanen 1995). **Colonists** and **pioneer colonists** are positively correlated with a moderate distance to water and its impact, *i.e.*, in zones that are seasonally flooded with strong discharges (During 1979; Kimmerer & Allen 1982; Vieira *et al.* 2012b). Some **fugitives**, **annual shuttles**, and **stress-tolerant perennials** are able to tolerate slight and infrequent submergence.

Figure 13. ***Scapania undulata***, a **mat**-forming liverwort that can reduce drag in fast water. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Hygrohypnum luridum*** with capsule. Photo by Michael Lüth, with permission.

Figure 15. ***Fontinalis dalecarlica***, a **streamer** species that uses numerous rhizoids to maintain its position in rapid water. Photo by Jean Faubert, with permission.

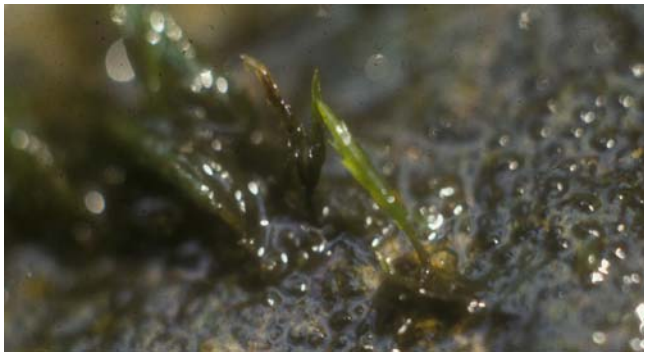

Figure 16. ***Fontinalis novae-angliae*** with new shoots beginning where a stem has been scoured and broken, forming a new colony. Photo by Janice Glime.

Although mountain streams are very different habitats from slow-moving lowland streams, it appears that the life forms defined by Gimingham and Robertson (1950) for English mountain streams can be broadly applied. They identified **large cushions**, **small cushions** (Figure 10), **large turfs** (Figure 3, Figure 8), **small turfs** (Figure 5), **dendroids** (Figure 7), **compact mats** (Figure 2), **thalloid mats** (Figure 6), and **wefts** (Figure 12). As noted, Glime (1968) added **streamers** (Figure 1).

In terrestrial situations, unstable environments are often characterized by acrocarpous mosses such as ***Bryum*** (Figure 17), ***Pottia*** (mostly now in ***Tortula***; Figure 18), and ***Gigaspermum*** (Figure 19) (Ramsay 2006). Pleurocarpous taxa such as ***Hypnum*** (Figure 20) and ***Thuidiopsis*** (Figure 21) seem to require more stable environments. Similar relationships hold in streams, where small, acrocarpous mosses such as ***Blindia acuta*** (Figure 22) live in disturbed areas with movable substrata, whereas the large, pleurocarpous moss ***Fontinalis*** spp. (Figure 23) is characteristic of stable boulders (Muotka & Virtanen 1995). Furthermore, the large **streamers** (***Fontinalis***; Figure 1) occur on the lower parts of stream rocks where they are continuously submersed, whereas the tops of the boulders support growths of low, but not mat-forming, mosses (Virtanen *et al*. 2001).

Figure 17. ***Bryum ruderale***, an **acrocarpous** moss of unstable habitats. Photo by Štěpán Koval, with permission.

Figure 18. ***Tortula lanceolata*** with capsules, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by Michael Lüth, with permission.

Figure 19. ***Gigaspermum repens***, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by David Tng, with permission.

Figure 20. ***Hypnum chrysogaster***, a **pleurocarpous** moss requiring a stable environment. Photo by Larry Jensen, with permission.

Figure 21. ***Thuidiopsis furfurosa***, a **pleurocarpous** moss requiring a stable environment. Photo by David Tng, with permission.

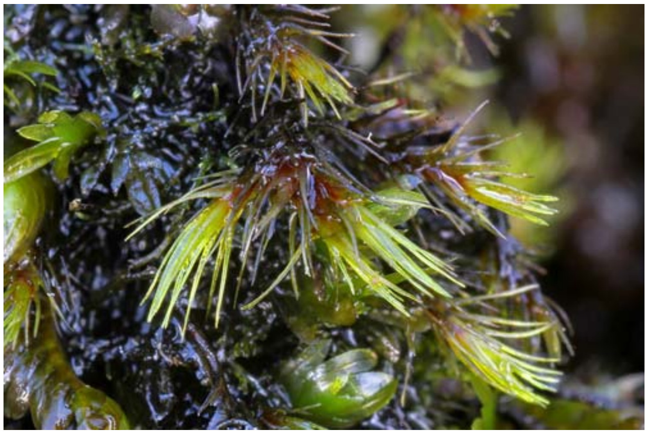

Figure 22. ***Blindia acuta***, an **acrocarpous** species that can live in small crevices in streams. Photo by Barry Stewart, with permission.

Figure 23. ***Fontinalis novae-angliae*** below the water surface and the leafy liverwort ***Plagiochila porelloides*** above. Photo by Janice Glime.

In the Victorian temperate rainforest streams of Australia, all seven of the Gimingham and Robertson (1950) life forms were represented, but not **streamers** (Carrigan 2008), **pendants**, or **tails** (Mägdefrau 1982). However, only two species were of the **cushion** (Figure 10) life form. **Mats** (Figure 2, Figure 11) and **turfs** (Figure 8) were the most represented, with 36 and 32 species, respectively. Wood and sediment had approximately the same distribution of life forms. No life forms stand out on the various sizes of rocks, with approximately the same distribution of life forms on each as for the total set. **Turf** was the only life form that appeared to have significant differences among the rock sizes, with the greatest representation on the medium-sized rocks.

Functional Groups

Monteiro *et al.* (2019) determined the functional structure of bryophytes in headwater streams in Portugal, as represented by life forms. The rock dwellers are typically **rough mats** (Figure 11). Truly aquatic species are mostly perennial, pleurocarpous mosses in **smooth mats** (Figure 24); they rarely produce capsules, and those are typically submerged. The very dynamic mountain flushes, springs, and ephemeral streams support pioneer colonists and **turfs**. Streamsides support **dendroid** (Figure 7) mosses and **thalloid liverwort mats** (Figure 6). At high altitudes, leafy liverworts and competitive perennials predominate. Basic substrates typically have **tufts** and **colonists** of **basophilous** (living or thriving in alkaline habitats) species.

Figure 24. ***Hypnum cupressiforme***, **pleurocarpous** moss forming a **smooth mat**. Photo by Michael Lüth, with permission.

Factors Influencing Life Forms

Life forms are important in determining the drag coefficient and in attenuating the flow velocity, especially within the clump. Dodds and Biggs (2002) showed that even **periphyton** (freshwater organisms attached or clinging to plants and other objects) attenuated the flow velocity with depth. In fact, dense colonies of diatoms (primarily ***Cymbella***; Figure 25) had more effect than did filamentous green algae or red algae. Macrophytes also attenuated the flow rates, but less than the periphyton, and their attenuation was more variable.

Figure 25. ***Cymbella***, a member of the periphyton that can attenuate the flow velocity. Photo by Janice Glime.

One of the factors that influences successful life forms is the **diffusion resistance** to CO_2 uptake. Jenkins and Proctor (1985) measured this resistance in the mat-forming leafy liverworts ***Nardia compressa*** (Figure 26) and ***Scapania undulata*** (Figure 13), both species typical of headwaters. The researchers suggested that the high leaf-area index compensates for the diffusion resistance and permits these mats to effectively exploit low boundary-layer resistance at high velocities while at the same time protecting the liverworts from drag. In the **mats**, boundary-layer resistance limits photosynthesis at flow rates less than ~0.1 m s^{-1}. ***Fontinalis antipyretica*** (Figure 27), on the other hand, is not limited until rates slow to 0.01 m s^{-1}. They attribute this to the **streamer** (Figure 1, Figure 15) life form of ***Fontinalis***.

Figure 26. ***Nardia compressa***, a mat-forming liverwort that can reduce drag. Photo by Barry Stewart, with permission.

Figure 27. ***Fontinalis antipyretica***, having a **streamer** life form that permits it to live in both relatively fast and almost still water. Photo by Hermann Schachner, through Creative Commons.

Proctor (1984) summarized both physiological and structural adaptations of bryophytes for the aquatic habitat. Priddle (1979) reported that bryophytes of still or slow-flowing water had open, slender, elongated life forms. Fast-flowing streams favor tight **mats** (Figure 13) or **cushions** (Figure 10) that mimic or even reduce the drag coefficient of the rocks (Jenkins 1982; Proctor 1984; Jenkins & Proctor 1985). ***Nardia compressa*** (Figure 28) and ***Scapania undulata*** (Figure 29) provide such **compact mats** (Proctor 1984). These two species show reductions in photosynthesis in flow rates below 10 cm s^{-1}; this is most likely due to the need for turbulence to penetrate the spaces between the leaves. But by contrast, as will be seen below, ***Fontinalis*** species typically have trailing shoots (**streamers**; Figure 1, Figure 15) that are able to move easily with the water flow, permitting water to enter the clump. ***Fontinalis antipyretica*** (Figure 30) shows little change in the rate of photosynthesis with flow reduction down to 1 cm s^{-1}.

Figure 28. ***Nardia compressa*** showing **compact mat**. Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Scapania undulata*** showing **compact mat**. Photo by Michael Kesl, through Creative Commons.

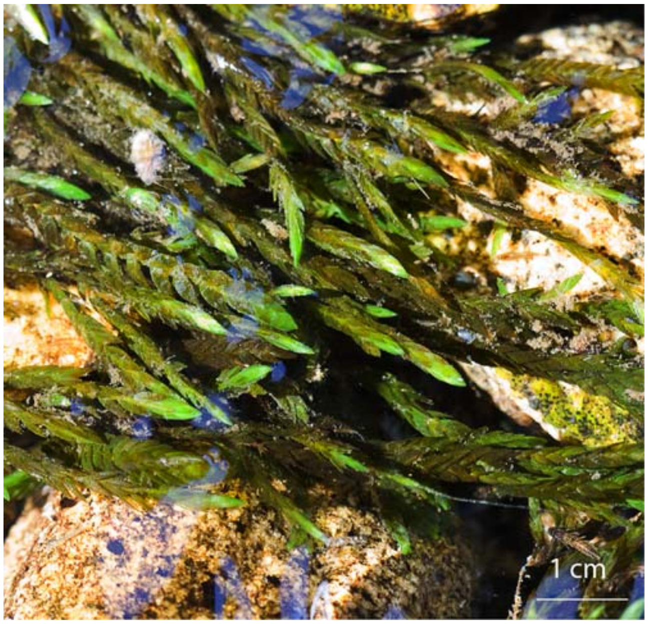

Figure 30. ***Fontinalis antipyretica*** showing a **streamer** life form. Photo from Projecto Musgo, through Creative Commons.

Morphological Plasticity of Life Form

Life forms can differ for a species when its habitats vary. ***Climacium dendroides*** (Figure 31) changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. The Southern Hemisphere species of ***Hypnodendron*** (Figure 32) and ***Hypopterygium*** (Figure 33) behave similarly.

Figure 31. ***Climacium dendroides***, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Li Zhang, with permission.

Bates (1998) reminded us that life forms "minimize evaporative water loss and maximize primary production." Many species show plasticity of life form according to environmental conditions. One of the common characteristics of aquatic bryophytes is the ability to express different life forms when being grown in different conditions. This can be sufficient to cause erroneous descriptions of new species.

Figure 32. ***Hypnodendron menziesii*** from New Zealand, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Hypopterygium novae-seelandiae***, Saddle Mtn. Rd., NZ, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Janice Glime.

Scapania undulata (Figure 13) occupies a range of habitats from full submersion to rocky ledges in streams of Poland (Samecka-Cymerman 1990). The ledge populations typically are 2-3 cm long, whereas the stream populations are usually 5-10 cm, up to 20 cm. Samecka-Cymerman suggested that low nitrogen might account for the smaller plants on the ledges, a phenomenon known from tracheophytes (Czerwiński (1976; Gumiński 1976). It exhibits a range of morphology that has caused at least one of its forms to be described as separate species (*e.g.* ***Scapania dentata***) (Hiesey 1940), now considered a synonym (Hiesey 1940).

Higuchi *et al.* (2003) reported **mat**-forming green plants from acidic rivers in Japan. When cultured, these produced bryophyte gametophyte buds, indicating that the filaments were protonemata (Figure 34). The large subunit of ribulose-1, 5- bisphosphate carboxylase/oxygenase indicated the moss was 98% similar to ***Dicranella heteromalla*** (Figure 35). This species is common in acidic habitats, including woodland banks, tree stumps, tree roots, hedge banks, dry peaty banks, and sheltered soil of crevices on crags and gullies in the mountains (Royal Botanic Garden, Edinburgh 2019). In Illinois, it occurs also on sandstone walls along streams (Hilty 2017). Its protonemal growth in the water may be a habitat response that inhibits gametophore development.

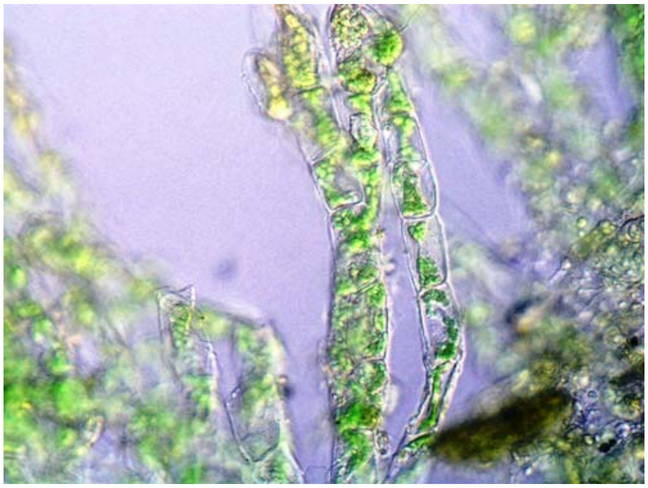

Figure 34. ***Dicranella heteromalla*** protonema, a stage that seems to stop development in very acidic rivers. Photo by Jiri Váňa, permission pending.

Figure 35. ***Dicranella heteromalla*** with capsules, a species with attenuated development in very acid water. Photo from Botany Website, UBC, with permission.

Life Strategies and Reproduction

I was surprised at how few studies appeared when I searched Google for aquatic bryophyte reproduction. But at least some studies exist. Field observations have suggested that production of capsules in submersed bryophytes is relatively rare (Carrigan & Gibson 2004; Ares *et al.* 2014). Instead, fragmentation has seemed to be a major strategy.

Like the life forms, the number of life strategies increases as the frequency of submergence decreases for bryophytes associated with Portuguese streams (Vieira *et al.* 2012a, b). Water velocity and hydrologic zone are the primary influences on the life strategies present (During 1979; Lloret 1986; Vieira *et al.* 2012b). The communities that were mostly submersed were characterized by **perennials** and **ephemeral colonists** (Vieira *et al.* 2012b). Those communities that were more frequently emergent had more diversity of life strategies. At higher altitudes, **perennials** seemed to be favored. Hence, **perennials** are more likely in permanent fast-flowing currents, whereas **pioneer colonists** and **colonists** are more common in the lower currents or emergent positions. In those habitats emerged for brief periods each season, **fugitives**, **annual shuttle species**, and **stress-tolerant perennials** were able to colonize deposited sediments.

In their study of environmental drivers for stream bryophytes, Lang and Murphy (2012) concluded that bryophyte abundance in high-latitude streams was typically a function of predominant growth morphology and life strategy. Ock (2014) included life cycle strategies among the adaptations to rheophytic conditions in bryophytes. He described them as mostly **dioicous** (having separate male and female plants) with rare or uncommon sporophytes. This results from the difficulty of travel for the sperm from the **antheridium** (Figure 36) as it attempts to overcome water flow on its way to the **archegonium** (Figure 37-Figure 38) that is located on a different plant.

Figure 36. ***Fontinalis duriaei*** antheridia on 13 September 1979 in Coles Creek, Houghton County, Michigan, USA, cultured at 20ºC in artificial stream. Photo by Janice Glime.

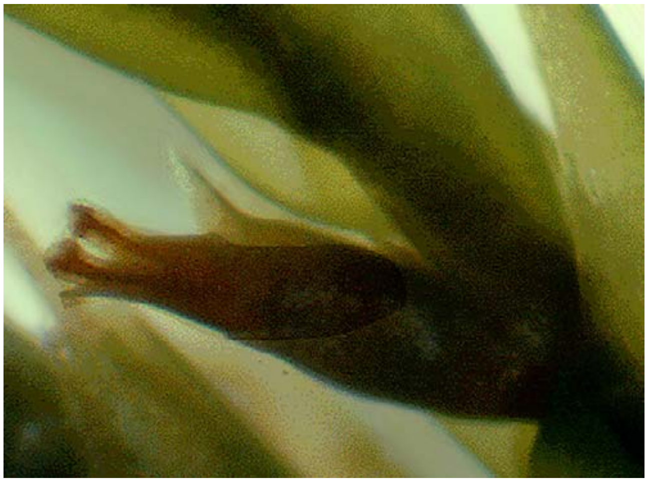

Figure 37. Archegonia of ***Fontinalis*** sp. showing red neck canal cells. Photo by Janice Glime.

Figure 38. ***Fontinalis*** archegonia, with the enlarged one indicating it has been fertilized. Photo by Janice Glime.

Thamnobryum alopecurum (Figure 39) is **dioicous**. During (1978b) found the largest numbers of inflorescences in places with constantly high air humidity. These places also tend to have greater mixing of male and female plants. In drier air, the plants remain mostly sterile. Instead, they develop into large sprouting systems that have little contact between each other. Some even form moss balls in these conditions.

Figure 39. ***Thamnobryum alopecurum*** with capsules, a **dioicous** species with more reproductive inflorescences in places with constantly high humidity. Photo by Snappy Goat, through public domain.

Sexual Strategies and Gametangia

Leitgeb (1868) found antheridia on ***Fontinalis antipyretica*** (Figure 27) from spring until fall, a pattern similar to that which I found in several ***Fontinalis*** species in the Keweenaw Peninsula of Michigan, USA and the long period of development for antheridia is typical of antheridia (see Volume 1, Chapter 5-8). Degree of **apical dominance** (physiological behavior in which the main axis grows more strongly than side branches) is important in determining the location of antheridia and archegonia in ***Fontinalis*** (Berthier 1968). With weak apical dominance, the sexual shoots occur at the axils of the first leaves on side branches. By contrast, when there is strong apical dominance, the main stem forms narrow leaves and these have densely branched first-order sexual shoots in their axils. These first-order shoots occur naturally when the free CO_2 decreases rapidly in the water of late spring, a phenomenon repeated at 8ºC in the laboratory. Apical dominance of the vegetative stem can be increased by cutting off some of the leaves or by using weak illumination.

Carrigan and Gibson (2003) compared the sexuality of species that occurred both streamside and on stream rocks at Cement Creek in the Yarra Ranges National Park, Victoria, Australia. They found that streamside populations had higher numbers of stems, inflorescences, and **gametangia** [archegonia (Figure 37-Figure 38) and antheridia (Figure 36)] than did the same species on stream rocks. The streamside populations of species tested produced more sporophytes than those species on stream rocks. ***Cyathophorum bulbosum*** (Figure 40), however, produced more sporophytes on the stream rocks than did its populations on streamside locations. The gender was generally female-biased for stem numbers and numbers of inflorescences.

Figure 40. ***Cyathophorum bulbosum***, a species that can produce more sporophytes on the stream rocks than do its populations on streamside locations. Photo by John Braggins, with permission.

Berthier (1966) explored the role of light in initiation and development of the sexual organs in ***Fontinalis*** (Figure 27). He found that light influenced both the density and development of buds, with antheridia forming on branches. A low growth rate enabled formation of these antheridial branches. Increased light intensity increased both the density and initiation of these antheridial branch buds.

Fertilization

Goebel (1913, 1915-1918) illustrated development in some of the water mosses, including ***Fissidens*** (Figure 41), ***Fontinalis*** (Figure 27), ***Hygroamblystegium*** (Figure 42), and ***Thamnobryum*** (Figure 39). His drawings included details of archegonia and antheridia. I translated one of his statements to mean that fertilization in ***Fontinalis*** took place in a "glass" of water. A better translation is that the gametangia are suppressed but can be richly formed. The sperm are easily swept away in flowing water. If both archegonia and antheridia are in small water volumes, the ***Fontinalis*** fruits richly. If the sporophytes are not under water, the spores perish. These observations of Goebel emphasize the importance of timing as part of the life strategies. For example, fertilization is likely to be more successful when the water level is low and they can swim without being washed away. In other cases, fast water might be required to splash sperm from males to females. This might mean that only emergent females get fertilized, but at least some should receive sperm.

Figure 41. ***Fissidens fontanus***, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by Matt Keevil, through Creative Commons.

Figure 42. ***Hygroamblystegium fluviatile***, in one of the genera for which fertilization was described by Goebel. Photo by Hermann Schachner, through Creative Commons.

Scapania undulata (Figure 13) is among the widely distributed species of aquatic bryophytes. It grows in shallow streams from boreal regions to subtropical zones (Holá *et al.* 2014). It is dioicous, making fertilization difficult, particularly in its typical submersion in rapid water. But Holá *et al.* (2014) found that it had an "overproduction" of males in 10 streams in southern Finland (100 plots) and suggested that this might be a strategy to overcome sperm dilution in the flowing water, "ensuring" fertilization over longer distances in the water. This male bias contrasts with most dioicous species and seems to relate to its flowing-water habitat. The males and females differ in branching pattern, but no size difference exists. They found few females sex-expressing in the female-only plots and female plants had only one sexual branch per female shoot. The low number of sex-expressing shoots in female-only plots, no co-occurrence of gemmae and female sex organs on a single branch, large number of male plants, and only one sexual branch per female shoot suggest a trade-off between sexual and asexual reproduction and a higher cost for female reproduction.

Belkengren (1962) further learned that sexual reproduction in ***Leptodictyum riparium*** (Figure 43) was induced by a CO_2-free period, followed by addition of CO_2 or sugar. It is a little more difficult to suggest how this might apply in nature, but it could be a change from high temperatures, hence low CO_2, followed by cooler temperatures in which more CO_2 can dissolve in water. Subsequently, it appears that senescence of the plants may induce the formation of sporophytes, perhaps by stopping the production of some inhibitory substance or reduction of photosynthesis.

Figure 43. ***Leptodictyum riparium*** with capsules, a species in which yeast inhibits development from protonemata to the next stage. Photo by Michael Lüth, with permission.

Sporophytes

Aquatic moss sporophytes can be divided into two groups (Vitt 1981). In one group, the gametophytes are aquatic, but the sporophytes are not, often being produced during periods of low water. This includes such taxa as ***Scorpidium*** (Figure 44), ***Hygrohypnum*** (Figure 14), ***Platylomella*** (Figure 45), ***Platyhypnidium riparioides*** (Figure 46), and ***Drepanocladus*** *s.l.* (Figure 3). The other group produces sporophytes that are adapted to the aquatic habitat. This group of species includes ***Blindia*** (Figure 47), ***Fontinalis*** (Figure 27, Figure 50), ***Scouleria*** (Figure 48), ***Wardia*** (Figure 49), and others with reduced or absence of peristomes, ovate or oblong, smooth, immersed capsules, enlarged perichaetial leaves, and pachydermal exothecial cells.

Figure 44. ***Scorpidium scorpioides*** with capsules, a species that produces these sporophytes while the plant is above water. Photo by Michael Lüth, with permission.

Figure 45. ***Platylomella lescurii***, a species that produces sporophytes while the plant is above water. Photo by Northern Forest Atlas, with permission from Jerry Jenkins.

Figure 46. ***Platyhypnidium riparioides*** with capsules, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by J. C. Schou, with permission.

Figure 47. ***Blindia acuta***, a species that produces sporophytes while the plant is below water. Photo by Barry Stewart, with permission.

Figure 48. ***Scouleria aquatica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Matt Goff, with permission.

Figure 49. ***Wardia hygrometrica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Sanbi, with online permission.

Carrigan and Gibson (2004) followed 9 mosses and 7 liverworts, representing 8 and 6 families respectively. They found sexual reproduction, but not in all species. As in the 2003 study, they found that sexual reproduction was lower on stream rocks than in more terrestrial habitats. Asexual reproduction was most important in maintaining colonies compared to sexual reproduction, with all species exhibiting asexual reproduction. There was a female sex bias in all but 2 species. There seemed to be no synchrony of phenological stages.

Landry (1973) collected field-grown capsules of ***Fontinalis dalecarlica*** (Figure 15) in June, 1973, in Plymouth, New Hampshire, USA. These immature capsules were permitted to develop in culture until 27 July 1973, but they remained green and did not appear to be completely mature. Capsules were sterilized, opened, and spores spread on a Chlorophyta medium with 3 ppm tannic acid added. There was still no germination on 10 August when it became necessary to terminate the experiment. This was an unusually late date for capsule maturation compared to what had been observed in prior years, and the sterilization process with 0.1N potassium permanganate may have damaged the spores. The other problem is that the capsules had been transported from New Hampshire to Houghton, Michigan and may have experienced excessive temperatures during the trip.

Kortselius (2003) found that ***Fontinalis antipyretica*** (Figure 27) produces capsules when it is submerged (Figure 50), but he considered dry conditions to be necessary for dehiscence (Figure 51). When desiccation occurs, the operculum is torn loose and lifted off by the hygroscopic movements of the exostome teeth (Figure 52). Spores are released during reversible shape changes in the capsule (Figure 53). It seems that this would require careful timing so that capsules were still pliable when they were desiccated. old capsules have thick walls and are quite hard, seemingly unable to change shape significantly.

Figure 50. ***Fontinalis dalecarlica*** submersed capsules on 26 November 1979 in Fox Run, Plymouth, New Hampshire, USA. Note that the operculum is still intact in the upper mature capsule, but missing in th lower one. Photo by Janice Glime.

Figure 51. ***Fontinalis*** capsule that is shedding its operculum out of water. Photo by Janice Glime.

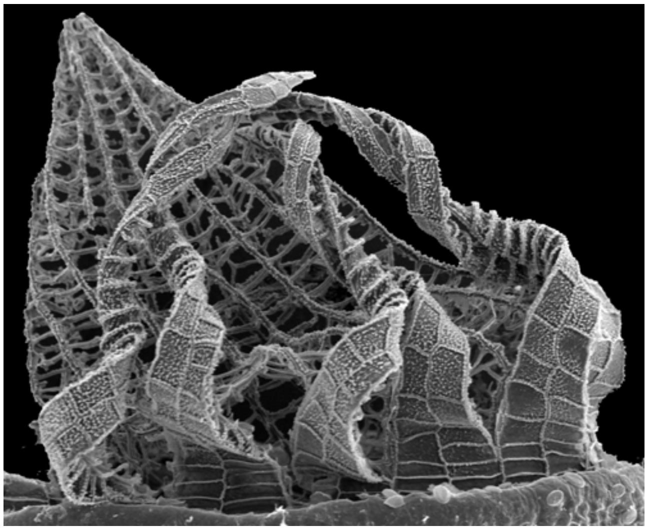

Figure 52. SEM of ***Fontinalis*** peristome showing inner trellis endostome and outer twisted teeth of exostome. Photo by Misha Ignatov, with permission.

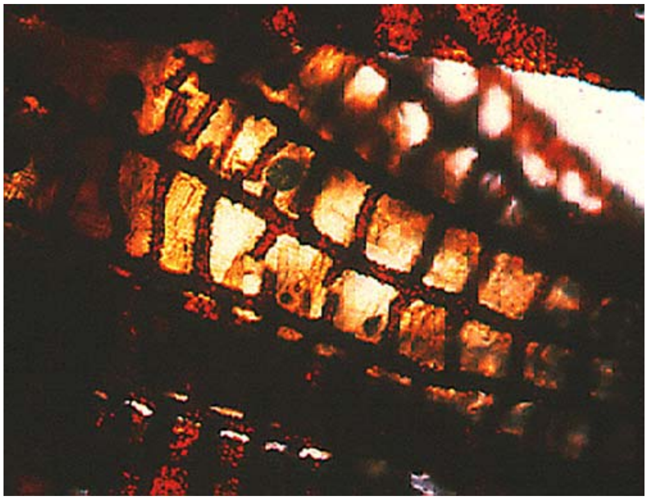

Figure 53. Trellis peristome of ***Fontinalis*** showing green spores among the teeth. Photo by Janice Glime.

During (1978a) found capsules on ***Fontinalis antipyretica*** (Figure 27) 30 April-2 May, but his short note did not indicate the degree of maturity. In my own studies I did not find this species with capsules, but this species was not nearly as common as other ***Fontinalis*** species in the areas that I studied.

Although ***Fissidens fontanus*** (Figure 41) produces capsules in the USA and Europe, capsules were unknown in Mexico. Pursell (1992) reported these in Mexico for the first time. However, no data were available on timing of capsule production. The capsules were illustrated, demonstrating the short seta compared to some species of ***Fissidens***. The capsule likewise was quite small, with an urn only about 0.2-0.3 mm long in the one illustrated.

Lawton (1966) reported capsule production in ***Hygrohypnum bestii*** (Figure 54). This was the first time that the sex organs and capsule had been described in this dioicous species. The species occurs in montane streams, typically at 1500-3000 m elevation, on wet rocks that are often covered with silt.

Figure 54. ***Hygrohypnum bestii***, a **dioicous** species that rarely produces capsules. Photo by Robin Bovey, with permission through Dale Vitt.

One of the reasons for the lack of capsule observations may be the timing of their presence (Glime 2014). In a stream in New Hampshire, USA, both ***Fontinalis dalecarlica*** (Figure 15) and ***F. novae-angliae*** (Figure 23) produce their capsules in the freezing waters of winter. The capsules are badly eroded by the spring runoff, and it seems likely that this is a major vehicle for spore dispersal. By the time the snow is gone, most of the capsules have disappeared, and only a few damaged capsules remain. Their appearance at that time suggests that it is abrasion, not loss of operculum, that permits spore dispersal.

The timing in Finland does not seem to fit this pattern. Kotilainen (1927) found capsules on ***Fontinalis dalecarlica*** (Figure 15) on 6 July 1925 in Finland.

Dispersal

Few studies have addressed dispersal in aquatic bryophytes. Miller (1985) examined subfossils of a number of bryophyte fragments in late Pleistocene deposits buried in sediments in the northeastern United States. These suggested that the fragments had served as propagules dispersed by wind and melting glaciers. Many of the fragments had shoots extending from them, supporting the notion that these were serving as propagules.

Elssmann (1923-1925) commented on the fact that capsules of ***Fontinalis antipyretica*** (Figure 27) retained their lids (Figure 51). He noted that Grimme had mentioned that the shedding of the operculum may be delayed until April of the next year, attributing this to the fact that the plants remain submersed. Rather, at least in culture, the capsules themselves were eventually shed several months after maturity, falling to the bottom of the culture dish. There they gradually died, as did the spores inside. Grimme had reported capsule ripening in August, so Elssmann harvested capsules from his cultures at the beginning of July and found them to contain spores with abundant chlorophyll. When the spores were then cultured, nearly all had germinated within 18 days. Elssmann also cultured capsules on moist sand starting in April. These drier capsules likewise failed to lose the operculum. But the spores developed as they had in the submersed capsules. The same behavior occurred in ***Cinclidotus fontanus*** (***C. fontinaloides***?; Figure 55), ***Fissidens fontanus*** (Figure 41), and ***Platyhypnidium riparioides*** (Figure 46). This begs the question, then, how do the spores escape the capsule? The image in suggests that they do indeed dehisce in nature.

Figure 55. ***Cinclidotus fontinaloides*** with capsules that have lost their opercula. Photo by Hermann Schachner, through Creative Commons.

Hydrochory

Hutsemekers *et al.* (2013) addressed the question of dispersal somewhat indirectly by examining gene flow in ***Platyhypnidium riparioides*** (Figure 46). They summarized the assumed effects of **hydrochory** (dispersal by water): decreases or erases patterns of isolation by distance, increases outbreeding, and results in downstream increase in genetic diversity. They found that the geographical partitioning of genetic variation was "substantial" in the river basin. Using this as indirect measurement of dispersal, they found that the overall dispersal ability of moss diaspores, including fragments, was weaker than that of pollen or windborne seeds. Thus, these spore-producing plants suffer from the severe limitations of clonal dispersal and establishment. Hydrochory does not enhance dispersal and fertilization, at least in ***P. riparioides***. Instead, the genetic structure suggests clonality and discrete events of spore migration, with the **unidirectional diversity/dispersal hypothesis** (downstream hydrochoric spread of propagules of aquatic and riparian plant species, without upstream compensation, can be expected to result in downstream accumulation of population genetic diversity) being unsupported by this species. Rather, **metapopulation** (group of populations separated by space but are same species) processes apply to this aquatic moss. As the concept of metapopulation implies, such spatially separated populations interact as individual members move from one population to another. This can occur through spores, fragments, or specialized vegetative propagules.

Certainly ***Fontinalis*** species benefit from downstream dispersal in flow. This is possible because vegetative propagation is usually successful in these species (Welch 1948). In fact, biologists with the Burley Irrigation District in Cassin County, Idaho, USA, complained that it (***Fontinalis duriaei*** – Figure 56-Figure 57) "catches on almost anything and holds silt, forming mounds in the canals. It is hard to kill, and costs considerable to keep it out." When wounded, stems of ***Fontinalis*** will produce protonemata at the site of a broken stem (Figure 58). Removal of the stem tip can result in new branches below the apex in several ***Fontinalis*** species (Figure 59-Figure 61).

Figure 56. ***Fontinalis duriaei***, a species that is rejected by Rainbow Trout, but that passes through the digestive tract mostly without physical damage. Photo by Michael Lüth, with permission.

Figure 57. Detached ***Fontinalis duriaei*** caught on wood in Gardner's Creek, Michigan, USA. Photo by Janice Glime.

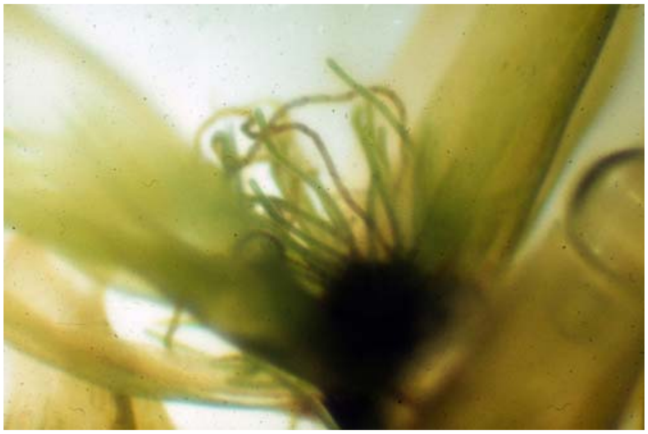

Figure 58. Protonemata growing from broken tip of ***Fontinalis hypnoides***. Photo by Janice Glime.

Figure 59. ***Fontinalis antipyretica*** wound rhizoids and a new branch just below the broken tip. Photo by Janice Glime.

Figure 60. ***Fontinalis squamosa*** branch below broken tip, exhibiting phototropism to a light source at the left. Photo by Janice Glime.

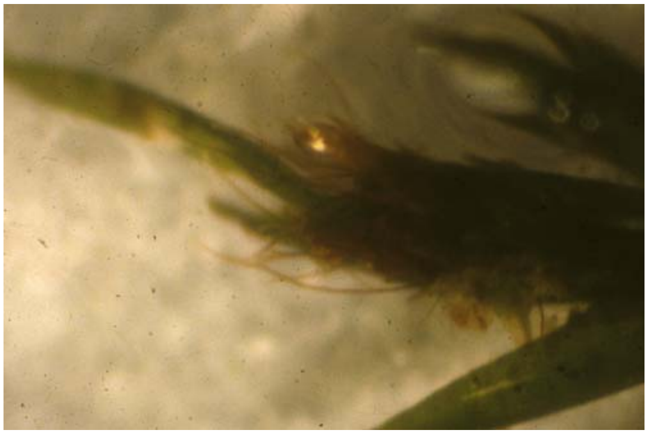

Figure 61. ***Fontinalis squamosa*** with broken tip and a new branch initiating just below that break. Photo by Janice Glime.

Welch (1948) noted that ***Fontinalis sphagnifolia*** (Figure 62) produces "rhizomes" with numerous rhizoids. This permits it to spread, but also provides a base ready for establishment in a new site when it gets carried downstream by water flow. The effectiveness of flow dispersal is suggested by observations of ***Fontinalis*** in a series of connected moraine ponds (Sayre 1945).

Figure 62. ***Fontinalis sphagnifolia***, a species that produces rhizomes with numerous rhizoids. Photo by Will Van Hemessen, through Creative Commons.

Korpelainen *et al*. (2013) used genetic markers in three clonal aquatic moss species in a connected lake system. They found a mean genetic diversity per population of 0.138 for ***Calliergon megalophyllum*** (a quiet water species; Figure 63), of 0.247 for ***Fontinalis antipyretica*** (slow to moderately rapid water; Figure 27, Figure 30), and of 0.271 for ***Fontinalis hypnoides*** (moderately rapid water; Figure 64). The total diversity of their populations in the connected lake system was 0.223, 0.385, and 0.421, respectively. Although the differences were significant, there was evidence of a moderate amount of gene flow within this system. The researchers suggested that both water flow and animal vectors, including water flow, dispersed these three bryophytes. Furthermore, the genetic structure suggests that fragments are the major contributors to this dispersal.

Figure 63. ***Calliergon megalophyllum***, a species that might be dispersed by both water flow and animal vectors. Photo from Earth.com, with permission.

Figure 64. ***Fontinalis hypnoides***, a species that can regenerate from broken stem tips. Photo by Ivanov, with permission.

Dispersal Vectors

One of the problems of dispersal in aquatic habitats is isolation (Figuerola & Green 2002). While streams can carry propagules downstream, they cannot carry them to a different stream or disconnected lake. Many rarely produce spores that could be transported by wind to a different water body. But recent studies have indicated that waterbirds can facilitate dispersal. Fortunately, even small fragments of leaves can develop new plants, and these can easily be transported by feathers and feet. And some may survive gut transport.

Lazarenko (1958) considered long-distance dispersal of moss spores unlikely, considering their dispersal to follow patterns like those of tracheophytes. Rather, he considered there to be polytopic origins to account for disjunctive species. While the dispersal of spores in ***Fontinalis*** (Figure 56-Figure 62) seems to be facilitated by abrasion and flowing water (Glime *et al*. 1979), the lack of dehiscence in most capsules would seem to support Lazarenko's suggestion. On the other hand, fragments can travel relatively long distances in the flow, and water birds might carry the moss fragments in their feathers. It is likely that bears and other mammals can carry the fragments in their fur and claws.

Proctor (1961) demonstrated that the liverwort ***Riella*** (Figure 65-Figure 66) spores can be dispersed by waterfowl. Mallard ducks were placed in a pen with ***Riella*** having mature spores. The ducks consumed the liverworts immediately. Feces were collected 50 minutes later and examined. Many individual spores were present, but there were no intact sporophytes and all the fragments were dead. Spores subsequently stored in water at 24ºC germinated after 60 days.

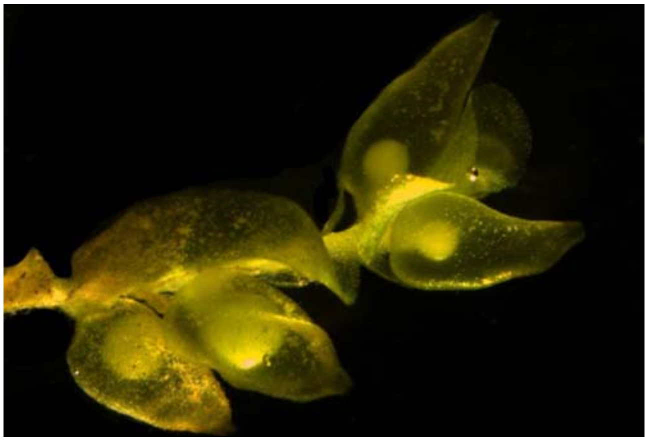

Figure 65. ***Riella helicophylla*** showing capsules. Photo by NACICCA through Creative Commons.

Figure 66. ***Riella cossoniana*** showing spores that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.

Laaka-Lindberg *et al*. (2003) reviewed dispersal of asexual propagules in bryophytes. They also noted that migrating birds, especially waterfowl, can carry vegetative attached to the mud on their feet (see also Davison 1976). Such a possibility for the floating liverworts ***Ricciocarpos natans*** (Figure 67) and ***Riccia fluitans*** (Figure 68) was suggested by Buch (1954). It would be interesting to see if these two species are eaten by waterfowl, especially as they accompany duckweed, and if they can germinate from the feces. Frahm (2007) also assumed that the worldwide distribution of ***Ricciocarpos natans*** had been facilitated by waterfowl.

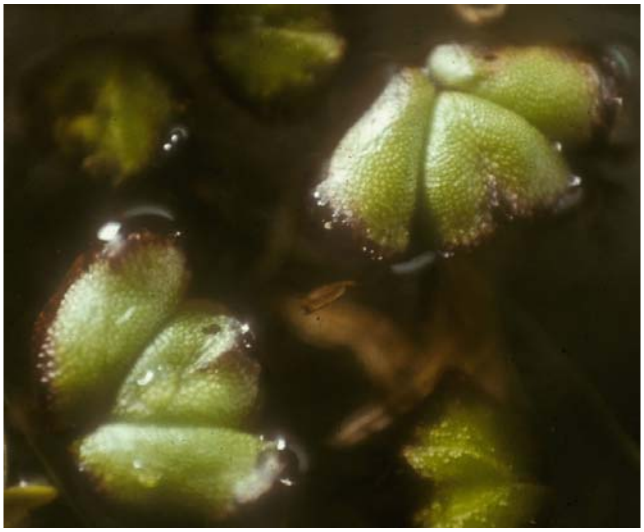

Figure 67. ***Ricciocarpos natans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Janice Glime.

Figure 68. ***Riccia fluitans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Štěpán Koval, with permission.

Lewis *et al*. (2014) brought further credence to these suggestions by showing correlations between transhemispherical migratory routes of shorebirds and the bipolar disjunctions in bryophytes. They then examined a number of birds in their Arctic breeding grounds, finding bryophyte propagules, among other propagules, clinging to the feathers. Eight species of these migrant waders had bryophyte diaspores among their feathers. The propagules were so common among the feathers that they suggested the entire population could potentially carry viable plant parts during migration.

It is possible that fish aid in the dispersal of aquatic mosses. Since the mosses provide cover for a number of aquatic insect species (Glime 1994; see Volume 2), they are a good site for foraging by fish. It is likely that at least occasionally the fish may ingest bits of mosses. Paulson (1980) collected a "packet" of feces (Figure 69) from Rainbow Trout (*Oncorhynchus mykiss*) that was comprised mostly of ***Fontinalis duriaei*** (Figure 56). The moss was bright green when it was expelled. It was placed in a baby food jar in the artificial stream, but by the second day it had lost its green color. If it had been deposited in a stream instead of such a confined space, the associated gut contents would have been diluted and might not have the same effect on the moss, perhaps permitting its survival. If so, this would be a potential mechanism for moving the mosses upstream as well as downstream for dispersal. However, I must point out that the moss had to be force-fed to the fish, so I suspect this mode of dispersal is rare.

Figure 69. ***Fontinalis duriaei*** in feces from force-fed Rainbow Trout. Photo by Janice Glime.

Boch *et al*. (2013) reasoned that slugs might be good dispersal agents for bryophyte spores since they often eat spores (Figure 70). But could the spores survive the digestive tract? They fed capsules of several bryophyte species to three species of slugs. They found an overall germination rate of 51.3% of bryophyte spores from the 117 samples. Among these was the streambank species ***Apopellia endiviifolia*** (Figure 71). There was little difference evident among the bryophyte species, but there was strong variation among the spores from the three slug species (Figure 72): ***Arion vulgaris*** (Figure 73), ***Arion rufus*** (Figure 74), ***Limax cinereoniger*** (Figure 75).

Figure 70. ***Ariolimax*** *cf.* ***californicus*** feeding on ***Asterella*** archegonial head and possibly the spores. Photo by Tom Voltz, with permission.

Figure 71. ***Apopellia endiviifolia*** with capsules. The spores can survive slug guts, a possible dispersal means. Photo by Janice Glime.

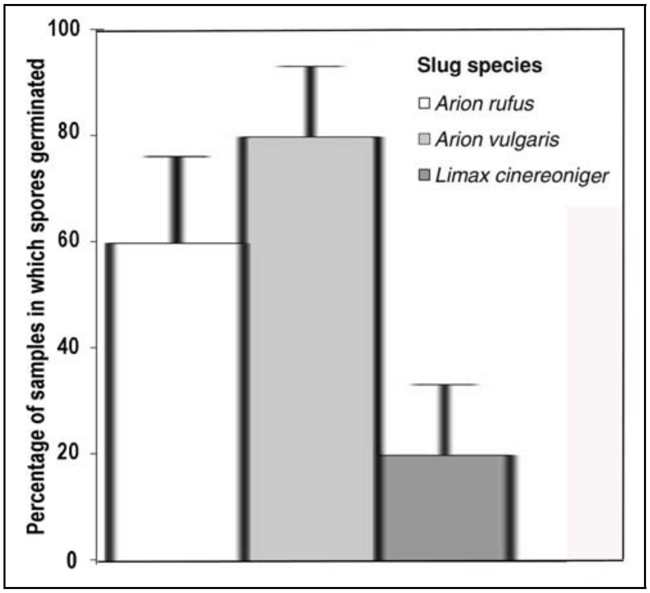

Figure 72. Slug gut dispersal of ***Apopellia endiviifolia*** spores. Modified from Boch *et al*. 2013.

Figure 73. ***Arion vulgaris*** on bryophytes, a slug that can potentially disperse spores of streamside bryophytes. Photo by F. Welter-Schultes, animalbase.uni-goettingen.de, through public domain.

Figure 74. ***Arion rufus*** on ***Sphagnum***, a potential endochorous bryophyte spore disperser. Photo by Walter Siegmund, through Creative Commons.

Figure 75. ***Limax cinereoniger*** feeding on lichen, a potential endochorous bryophyte spore disperser. Photo by H. Krisp, through Creative Commons.

Not only do bryophyte fragments get dispersed by wind and water, but so do their inhabitants. Bitušík *et al.* (2017) demonstrated that larvae of the chironomid (midge) ***Micropsectra uliginosa*** (Figure 76) travel in fragments of aquatic mosses, including ***Hygrohypnum*** sp. (*e.g.* Figure 14, Figure 54). This facilitates short-distance dispersal of the species, including the flightless males, albeit in their larval stage. They found detached moss tufts with chironomid larvae in their pan traps and assumed that these mosses had been flushed first by water, then trapped behind rocks or other obstructions in shallow water. Subsequently strong winds and gusts could lift the mosses and their inhabitants to mossy habitats above water nearby.

Figure 76. ***Micropsectra*** sp. larva; ***Microspectra uliginosa*** can be dispersed by blowing moss fragments. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Changes in Distribution

Frahm and Abts (1993) demonstrated the rapidity of dispersal of a number of aquatic species in the lower Rhine, Germany. From 1972 until 1992, the initial eight species were joined by ten more. The greater number of species in 1992 was attributed to improvement in water quality.

Frahm (1997) documented the distributional increase of aquatic mosses in the Rhein, Germany. ***Cinclidotus danubicus*** (Figure 77) has spread from its 1911 location to the Upper Rhine and Netherlands in 1997. ***Cinclidotus riparius*** (Figure 78) has spread northward. ***Fissidens arnoldii*** (Figure 79) spread from the Upper Rhine to the Lower Rhine in 70 years. ***Fissidens fontanus*** (Figure 41) was first recorded in the Upper Rhine in 1968 and by 1997 it had spread extensively along rivers in Central Europe. ***Hyophila involuta*** (Figure 80) spread 100 km northward along the Upper Rhine from 1927 to 1964. ***Fissidens rivularis*** (Figure 81) and ***Orthotrichum sprucei*** (Figure 82), both previously known only from British Isles, Belgium, and The Netherlands, have spread to the Rhine and its tributaries.

Figure 77. ***Cinclidotus danubicus***, a species that has spread in the Rhein (Rhine) since 1911. Photo by Michael Lüth, with permission.

Figure 78. ***Cinclidotus riparius***, a species that has spread northward in Germany. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Fissidens arnoldii***, a species that spread from the upper to the lower Rhein (Rhine) within 70 years. Photo by Michael Lüth, with permission.

Figure 80. ***Hyophila involuta***, a species that has spread rapidly among rivers in Central Europe. Photo by Bob Klips, with permission.

Figure 81. ***Fissidens rivularis***, a species that has spread rapidly and recently in Europe. Photo by David T. Holyoak, with permission.

Figure 82. ***Orthotrichum sprucei***, a species that has spread rapidly and recently in Europe. Photo by Michael Lüth, with permission.

Small Dispersal Units and Long-distance Dispersal

Heino *et al.* (2012) concluded that organisms with small propagules such as ferns and bryophytes may have weak geographical variation over broad areas due to unlimited dispersal. They found that environmental factors were most important in boreal headwater streams. The bryophyte data seemed to be better explained by environmental variables than by spatial characters.

Finlay (2002) contended that organisms less than 1 mm in size generally occur worldwide (the "everything is everywhere" hypothesis; see Vol. 1, Chapt. 4-8), whereas larger organisms are more restricted. He supported this with data on 1278 species of freshwater pond eukaryotic organisms showing that they were cosmopolitan. It follows that if the propagules are less than 1 mm, like bryophyte spores, they should follow the same principle. Kyrkjeeide *et al*. (2014) demonstrated a negative correlation of range with spore size of bryophytes in Europe based on spores up to 40 µm in diameter. In this case, those bryophytes reproducing (producing spores) less frequently had greater genetic differentiation than did bryophytes with frequent reproduction (p=0.04). Van Zanten (1978a, b) supported the possibility of long-distance travel of at least some species by placing the spores on airplane wings for trans-oceanic travel. Among these were the aquatic ***Warnstorfia fluitans*** (Figure 83) and ***Leptodictyum riparium*** (Figure 43), which could survive desiccation up to 13 months.

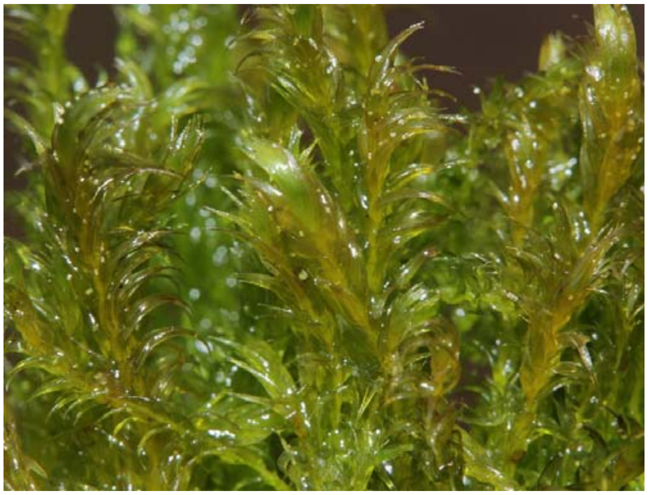

Figure 83. ***Warnstorfia fluitans***, a species in which spores can survive conditions necessary for long distance travel. Photo by Hermann Schachner, with permission.

Santos *et al*. (1996) collected airborne spores and other propagules on agar in Petri dishes. Once germinated, the collections revealed the presence of the bryophytes ***Fossombronia angulosa*** (Figure 84), ***Pellia epiphylla*** (Figure 6), ***Leptodictyum riparium*** (Figure 43), ***Bryum dunense*** (Figure 85), ***Ditrichum*** sp. (Figure 86), ***Gymnostomum calcareum*** (Figure 87), ***Pottia*** sp. (probably now in ***Tortula***; Figure 18), and ***Trichostomum brachydontium*** (Figure 88). Of these, ***Pellia epiphylla*** is a common streambank species and ***Leptodictyum riparium*** lives submersed in quiet water. It is also notable that a number of **Cyanobacteria** (Figure 89) arrived, providing potential nitrogen-fixers to associate with the bryophytes. Of the taxa collected, 75% were spores <25 µm. These successful spores suggest that diaspore banks can be important sources to recolonize a stream when it is disturbed or changes channel location.

Figure 84. ***Fossombronia angulosa***, a species that grew from collected spores. Photo by Jan-Peter Frahm, with permission.

Figure 85. ***Bryum dunense***, a species that grew from collected spores. Photo by Michael Lüth, with permission.

Figure 86. ***Ditrichum gracile***; ***Ditrichum*** sp. grew from collected spores. Photo from Snappy Goat, through public domain.

Figure 87. ***Gymnostomum calcareum***, a species that grew from collected airborne spores. Photo by Larry Jensen, with permission.

Figure 88. ***Trichostomum brachydontium***, a species that grew from collected airborne spores. Photo by David T. Holyoak, with permission.

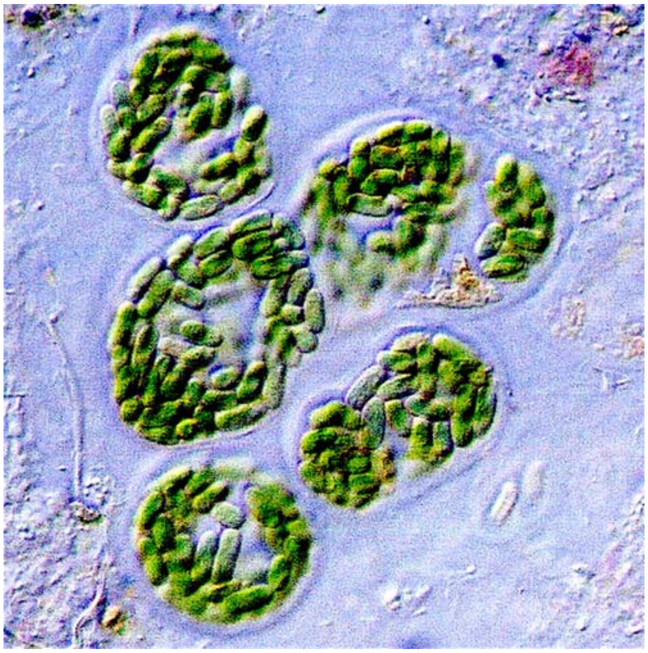

Figure 89. Cyanobacterial mat. **Cyanobacteria** germinated from airborne collections. Photo from NASA, through public domain.

Spore Germination and Protonema Development

Spore germination and protonema development have been studied in a number of bryophytes, including aquatic species (Kanda & Nehira 1976). These are illustrated and early stages following germination are described for the aquatic mosses ***Leptodictyum riparium*** (Figure 43) and ***Cratoneuron filicinum*** (Figure 90).

Figure 90. ***Cratoneuron filicinum***, one of the aquatic species for which protonema development was described by Kanda and Nehira (1976). Photo by J. C. Schou, with permission.

Glime and Knoop (1986; Glime 2014) concluded that ***Fontinalis squamosa*** (Figure 91) is an opportunist that releases spores (Figure 92) from multiple capsules over a relatively long period. This extended period of spore release may be the result of having fertilization over an extended time. Glime (1984) demonstrated that ***F. dalecarlica*** (Figure 15) produces mature archegonia over several months. A single collection of ***F. squamosa*** likewise provided both antheridia (Figure 36) and archegonia (Figure 37-Figure 38) in various stages of development. Capsules were also present in this single collection and similarly were in various stages of development. This spread of maturation could provide spores at different conditions of flow, and increase opportunities for at least some spores to meet favorable conditions. Elssmann (1923-1925) found that spores in capsules exposed to air ripened several weeks earlier than those that were submersed, providing further variability in response to changing water levels.

Figure 91. ***Fontinalis squamosa***, a species that produces both chloronemata and caulonemata. Photo from <www.aphotofauna.com>, with permission.

Figure 92. Longitudinal section of ***Fontinalis squamosa*** capsule showing green spores. Photo by Janice Glime.

Fontinalis squamosa (Figure 91) exhibits another potentially adaptive trait. Its spores within a single capsule (Figure 92) do not all mature at the same time. As the spores develop, some abort (Figure 93) (Glime 1983; Glime & Knoop 1986; Glime 2014). Others enlarge and are bright green, while some remain smaller and may be only partially green. Both can germinate, but the larger ones germinate more quickly (5 days) and have a higher germination success than the small ones (18 days). The protonemata in this species are also negatively **phototropic** (Figure 94) (Glime 2014). This habit of growing away from the light source may be adaptive in keeping them under water. It would be interesting to see if there is a threshold light level that elicits this phototropic response.

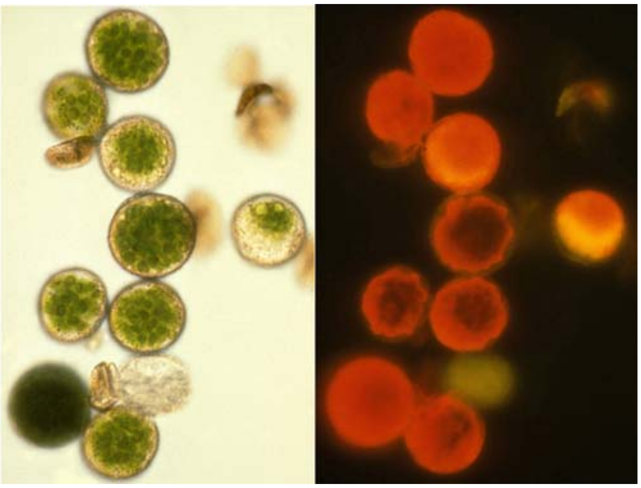

Figure 93. ***Fontinalis squamosa*** spores; those with clear areas on the left and yellow areas on the right are abortive. Those on the right are indicating chlorophyll fluorescence, showing red. Photos by Janice Glime.

Figure 94. ***Fontinalis squamosa*** protonemata singles typical of those grown at 3ºC. Light is coming from the lower right corner, indicating these protonemata are negatively phototropic. Photo by Janice Glime.

Glime and Knoop (1986) described the spore germination and development of ***Fontinalis squamosa*** (Figure 91). This moss develops both **chloronemata** (Figure 95) (protonemal filaments with many well developed chloroplasts and perpendicular cross walls) and **caulonemata** (protonemal filaments with fewer, less well developed chloroplasts and oblique crosswalls; portion of protonema that generates buds when both protonemal types are present). They can grow straight with no branches or have multiple branches, depending on lighting conditions. But buds failed to develop in the laboratory cultures until some of the abandoned plates became contaminated with fungi, suggesting that some developmental hormone might be supplied by the fungi.

Figure 95. ***Fontinalis squamosa*** branched protonema, with **caulonemata** forming at the tips of the branches, exhibiting lighter coloring due to fewer chloroplasts. This growth form was typical of cultures at 20ºC. Photo by Janice Glime.

Physiological conditions and environmental signals that are important to the developmental stages of aquatic bryophytes are poorly known. Belkengren (1962) experimented with ***Leptodictyum riparium*** (Figure 43) under a variety of conditions. Yeast inhibits its shoot growth in culture. But protonemal growth is not affected. Yeast causes death to shoot buds. As a result, the moss grows in the presence of yeast and never reaches another stage. Could this be the sort of interaction that maintains ***Dicranella heteromalla*** (Figure 35) in a protonema stage in the water (Higuchi *et al.* 2003)? The acid environment would be favorable to growth of fungi. Or is it some nutrient level?

Temperature can play a role in both germination success and form of the protonemata (Glime & Knoop 1986). At 3ºC, no spores germinated in culture, although distention occurred. At 20ºC, the protonemata grew aerially away from the agar and toward the light source, subsequently forming balls of irregular filaments with rounded cells.. The best growth was exhibited by cultures at 14ºC, with greater growth on the unshaded side of the plate. Growth forms differed with temperature (Figure 94-Figure 96). Nishida and Iwatsuki (1982) considered the protonema type to be adaptive, reflecting habitat more than its taxonomic affinity. Bud development did not occur until 3 months after the cultures were started, and the presence of buds was restricted to contaminated cultures, suggesting that the fungus might provide a needed stimulant to the bud development (Glime & Knoop 1986). Rhizoids formed before leaves at about an 8-cell stage.

Figure 96. ***Fontinalis squamosa*** protonemata with mostly 2 branches from the spore, typical of protonemata grown at 14ºC. Photo by Janice Glime.

Asexual Reproduction

Carrigan and Gibson (2003) concluded that reproduction of stream bryophytes is primarily asexual. This is supported by evidence that most fragments of these bryophytes seem able to develop new plants in nature. For example, Glime (1970) found a fragment of ***Scapania undulata*** (Figure 13, Figure 97) leaf with a new plant growing from the center of the leaf, even though this species is also able to produce gemmae. I don't know if it was able to develop rhizoids to attach, but as the new shoot got larger, I would expect it to be able to develop rhizoids at the leaf nodes.

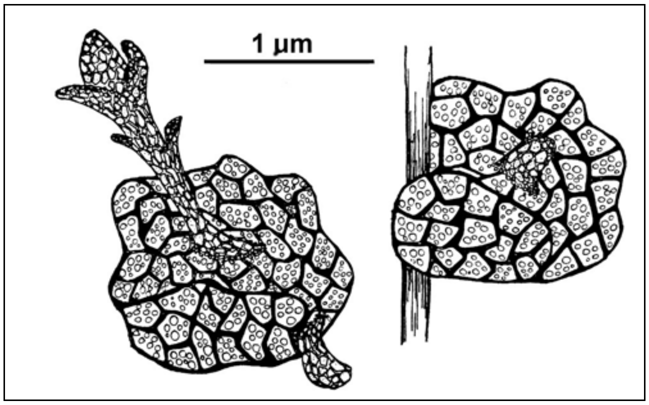

Figure 97. ***Scapania undulata*** plantlets from detached leaves of ***S. undulata*** in March 1969 in a stream near Plymouth, NH, USA. Drawings by Flora Mace.

It is likely that aquatic species are more successful at making new colonies from fragments because of their aquatic habitat. If a fragment arrives in a new location, it most likely arrived with flowing water and lodged somewhere that was wet. This would permit it to develop a new plant while it remains wet, whereas in the terrestrial environment new arrivals have a much greater chance of drying out and losing vigor before a new plant can begin growth or become established.

Regeneration

With the difficulty of accomplishing sexual reproduction and spore dispersal, fragmentation becomes more important. For this to succeed, these fragments must be able to dedifferentiate and regenerate new branches and whole colonies.

Regeneration is common among bryophytes. Giles 1971) describes the dedifferentiation and regeneration. Kreh (1909 in Giles 1971) demonstrated that every part of a liverwort except the antheridia could be induced to regenerate. Even diploid gametophytes can develop from pieces of a seta. In ***Plagiomnium affine*** (Figure 98), if a leaf remains on the stem it does not dedifferentiate. However, if it is removed from the stem in appropriate light, the leaf will dedifferentiate and redifferentiate to form **secondary protonemata**.

Figure 98. ***Plagiomnium affine***, a species that can regenerate from a detached leaf. Photo by Hermann Schachner, through Creative Commons.

Gimeno and Puche (1998) followed the responses of ***Platyhypnidium riparioides*** (Figure 99) in a polluted stream to assess damage to the moss and regeneration. They found that it produces caulonemata at the leaf bases of apical branches. Buds form while these filaments are still attached. When these sets of leaves become detached following **necrosis** (cell death), they can disperse. Rhizoids eventually develop, permitting these fragments to attach in a new location. In the lab, newly cut fragments developed the caulonema in only 5 days and buds arose in 11 days. Rhizoids developed in 21 days. Fragments and damaged leaves were common in the stream and the researchers suggested that in the apparent absence of sporophytes this was the major means of reproduction.

Figure 99. ***Platyhypnidium riparioides***, a species that can form new buds and rhizoids on detached pieces. Photo by Hermann Schachner, through Creative Commons.

Heald (1898) was unsuccessful in his attempts to regenerate ***Fontinalis antipyretica*** (Figure 27). He cultured leaves and stems in water, on earth, and with varying amounts of moisture with no success. On the other hand, I have successfully cultured broken stems of ***Fontinalis squamosa*** (Figure 60), ***F. hypnoides*** (Figure 64), and observed protonemata growing at the broken tips (Figure 58) of the latter. ***Fontinalis dalecarlica*** instead produced rhizoids from detached terminal buds (Figure 100) and leaves (Figure 101). I was also able to grow 2-cm pieces of ***F. antipyretica*** in artificial streams.

Figure 100. Unattached tip of ***Fontinalis dalecarlica*** developing rhizoids, hence serving as a propagule. Photo by Janice Glime.

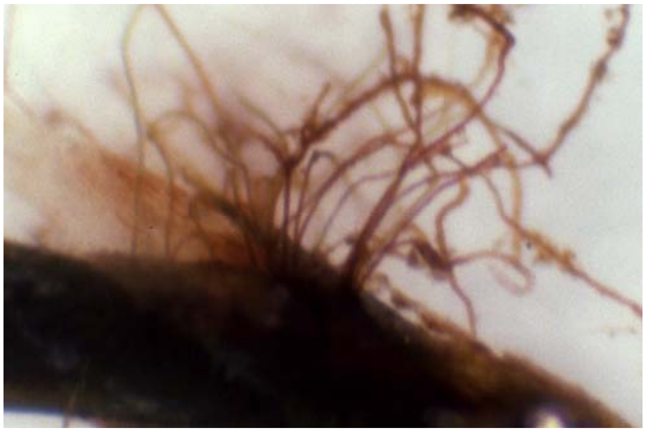

Figure 101. Rhizoids on detached leaf of ***Fontinalis dalecarlica***. Photo by Janice Glime.

The aquatic moss ***Fontinalis antipyretica*** (Figure 27) is capable of regeneration from nearly every part of the gametophyte (Ares *et al*. 2014). She was able to regenerate plants from cortical cells in the bases of detached shoots, margins and abaxial surfaces of leaves, stems with leaves removed, and laminae of detached leaves. These plant parts produce a variety of filament systems, including protonemata with short rectangular cells with transverse crosswalls, and unbranched rhizoids.

Fissidens fontanus (Figure 41) can regenerate even from its calyptra (Figure 102, Britton 1902). The capsules fall from the plants before they mature and the calyptra is still retained. Both the capsule and calyptra can float, so both can act as dispersal units. Goebel (1915-1918) also reported such a capsule of ***Fissidens fontanus*** with a young shoot emerging from beneath the calyptra (Figure 102); it even is producing an archegonium.

Figure 102. ***Fissidens fontanus*** calyptra exhibiting germination of a new shoot. Photo courtesy of Hans Kruijer.

Gemmae and Bulbils

Little has been written about gemmae and bulbils in truly aquatic bryophytes, especially in mosses. One study of interest is the induction of vegetative propagules in ***Porella pinnata*** (Figure 103). The leafy liverwort ***Porella pinnata*** did not fare well when cultured in moist chambers, with fungi and algae developing (Fulford 1944). However, when two cultures were transferred to nutrient media and given regular nutrient treatments and dim light, they developed vegetative propagules, ranging from bulging leaf cells to leafy shoots.

Figure 103. ***Porella pinnata***, a floodplain species that develops growths of fungi and algae when cultured in moist chambers. Photo by Alan Cressler, with permission.

Ares *et al.* (2014) discovered that the aquatic moss ***Fontinalis antipyretica*** produces gemmae. Filamentous gemmae are freed by **schizolysis** (splitting and breaking apart). Spherical brood cells are produced in ageing and desiccating cultures. Ares and coworkers suggested that these asexual propagules may occur in response to falling water levels in nature. These previously unknown means of reproduction may be important in spread and spatial genetic structure. These researchers also suggested that differences between axenic and contaminated cultures may be due to positive associations between the moss and bacterial or fungal contaminants.

Could there be other protonematal gemmae from other aquatic species hiding in the ecosystem, undiscovered because the protonemata are so difficult to find in nature?

Longevity

For many bryophytes that are not securely attached to the substrate, the living portion may only reflect a few years, whereas older basal portions are senescing or dying at the same rate. However, for a stream bryophyte, attachment makes decomposition of the basal portions a bigger problem. It is not unusual, however, to find basal portions that have lost their leaves, but the apical portions are vibrant, living plants. Therefore, **longevity** of the whole plant is an important part of a successful strategy, especially for **streamer** life forms.

Estimating the age of aquatic bryophytes can be challenging. Frye (1928) estimated the ages of a number of bryophytes based on apical regions that survived the winters, but none of these was submersed. These terrestrial bryophytes, including several streambank species, ranged up to 6 years of age present. I would estimate that ***Fontinalis*** (Figure 27) lives considerably longer than that, although the basal portions may be devoid of leaves. I grew a number of species in the lab and found that they could rebranch 1-2 times in just 15 weeks, so it does not appear that counting branches would be a useful indicator.

Life Cycle Strategy

All of these life cycle strategies work together to make a successful life cycle (Figure 104). Spore germination in the field is unknown for most aquatic species, but for ***Fontinalis novae-angliae*** and ***F. dalecarlica*** the capsules are produced in the winter and can release spores during early spring runoff. At the same time, the plants experience scouring and dispersal of fragments. In the later spring, when there is good sunlight and the trees do not yet form a canopy, growth and branching are at their best. In the summer, when temperatures rise and water levels drop, the rhizoids have their greatest growth. By fall, water levels rise again, temperatures cool, and days are shorter. Archegonia mature, reaching maturity as the longer-developing antheridia also mature. If the water level permits some branches to be wet, but above water, sperm can be splashed to new plants and accomplish fertilization.

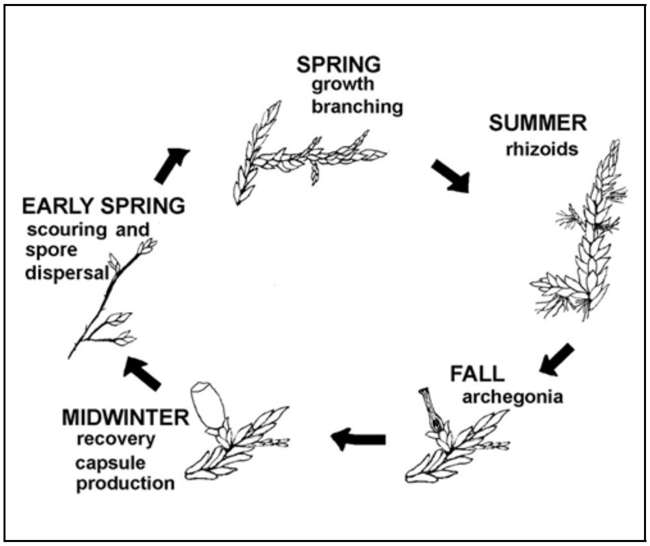

Figure 104. ***Fontinalis novae-angliae*** (Figure 23) and ***F. dalecarlica*** (Figure 15) seasonal life cycle. Diagram by Janice Glime.

Heino and Virtanen (2006) provide a good summary of the interrelationship of life strategies and stream bryophyte success. They considered that bryophytes could be divided into dominants and transients/subordinates. These two groups had sharp differences in life-history strategies and growth/life forms. They concluded that the abundance-occupancy relationships suggest that dispersal limitation and metapopulation processes may be the governing factors for the dynamics of the aquatic bryophytes, whereas in the semi-aquatic habitat, habitat availability may be more important in contributing to regional species occupancy.

The next subchapter will further discuss the physiological factors relating to the reproductive cycle. These will include temperature and light effects on the induction of reproductive structures.

Summary

Life forms are environmental expressions, whereas **growth forms** are genetically controlled. Both help to determine the suitability of the species for survival in streams. In fast water, these life forms include **streamers**, especially in permanently submersed sites. Other dominant forms include **smooth mats**, **tall turfs**, **fans,** and **short turfs**. Plasticity of life forms permits a species to occupy a wider range of moisture habitats, with stem elongation typically occurring in submersed conditions.

Asexual reproduction predominates; fertilization is difficult under water, particularly for dioicous species. Sporophytes are often emergent, even if the leafy portion is under water. For those submersed capsules, there is evidence that dehiscence might only occur when the capsule becomes emergent, or not at all. Fragments are particularly common as propagules. These can be dispersed by flowing water and animals, and once on land some might be dispersed by wind. Waterfowl might be especially important vectors for long-distance dispersal. The life cycle strategy seems to optimize energy and take advantages of the changing conditions with seasons. For example, in several ***Fontinalis*** species, spring is important for growth, summer for rhizoids, fall for sexual reproduction, early spring for scouring and dispersal, and capsule production depending on whether it can take advantage of emergence or must disperse under water.

Acknowledgments

Many bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. My permission for the ***Agriolimax*** feeding on ***Asterella*** required finding the email address for Tom Voltz. I started with Brent Mishler, who sent it to Amanda Heinrich, who sent it to Ken Kellman, who sent it to someone with the initials JJ, who sent it to Tom Voltz. And I got permission the same day this chain of emails started! Thank you to all of these people for their help!

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CHAPTER 2-6
STREAMS: PHYSIOLOGICAL ADAPTATIONS – WATER, LIGHT, AND TEMPERATURE

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STREAMS: PHYSIOLOGICAL ADAPTATIONS – WATER, LIGHT, AND TEMPERATURE

Figure 1. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales, demonstrating that the emerged moss is still wet, thus drying slowly. Photo by Janice Glime.

In 1996, I (Glime 1996) revelled in the realization that a number of scientists were applying aquatic bryophytes in the solution of environmental problems. These included monitoring, cleanup, culturing for restoration, and even prospecting. But to take full advantage of these possibilities, we need to understand the physiology of these bryophytes that constrains their habitats and permits them to do what they do.

Loss of bryophytes due to draining waterways also impacts the fauna of the waterway. McCarthy (1977) noted that the flora and fauna of the Trimblestown River in Ireland were seriously affected by drainage. They found that the submerged ***Fontinalis*** (Figure 1) and flowering plant *Rorippa* (Figure 2) had been replaced by emergent vegetation, filamentous algae, and *Chara* (Figure 3), changing the habitats available to the fauna. Although the numbers and biomass recovered rapidly one year after the drainage disturbance, the bryophyte beds did not. Thus, for many reasons we need to understand the biology and ecology of the bryophytes that occupy streams.

Figure 2. *Rorippa* sp., member of a genus that was replaced by emergent vegetation following drainage of the waterway. Photo by Gerrit Davidse, through Creative Commons.

Figure 3. *Chara* sp., member of a genus that replaced ***Fontinalis*** following drainage of the waterway. Photo from Carolina Biological Supply Company, with online permission.

Moisture Relations

The effects of flooding disturbance in streams and rivers has been relatively well studied (Lake 2000). The effects of drought have not. Both of these conditions destroy habitat and create new habitat, creating patchiness. Biota may survive by finding refugia in some of these patches.

The presence of nearly constant water as a medium will necessarily present physiological problems for aquatic bryophytes. Although the bryophytes were derived from algae, which originated in water, the bryophytes have since that time become highly adapted to survive severe desiccation for prolonged periods of time. The freshwater bryophytes appear to have returned to the water environment from largely terrestrial lineages. Nevertheless, that history of aquatic habitats could provide conserved genes that help to preadapt these bryophytes to water. On the other hand, streams in particular can present some real challenges.

A major water problem for aquatic bryophytes arises because of seasonal and short-term changes in water level. In the summer, bryophytes can be stranded out of water for weeks at a time. When water does come, it is likely to bring abrasion and siltation. Thus, the stream bryophytes must be prepared for desiccation as well as submersion. For a long time, aquatic bryophytes were considered to be intolerant of desiccation, but later experiments proved this assumption to be wrong (Carvalho *et al*. 2011).

One can observe aquatic bryophytes such as ***Fontinalis*** species in dry stream beds in late summer (Figure 4). Glime (1971) tested this drying effect on two species of ***Fontinalis*** [***F. dalecarlica*** (Figure 5), ***F. novae-angliae*** (Figure 6)] by removing their rocks with mosses intact to the stream bank where they were not submersed for one year. Many of these mosses survived this isolation, developing new growth from stem tissue, despite the apparent death of the leaves that had been exposed to the treatment.

Figure 4. ***Fontinalis antipyretica*** in dry stream in Michigan's Upper Peninsula, USA. Photo by Janice Glime.

Figure 5. ***Fontinalis dalecarlica***, a species that can survive for one year above water if the desiccation is slow. Photo by Jean Faubert, with permission.

Figure 6. ***Fontinalis novae-angliae*** with underwater capsules, a species that can survive for one year above water if the desiccation is slow. Photo by Janice Glime.

Gupta (1977a) compared photosynthesis in the drought-resistant ***Porella platyphylla*** (a terrestrial epiphytic leafy liverwort; Figure 7) with the non-resistant ***Scapania undulata*** (a usually submersed stream liverwort; Figure 8). Using a relative humidity of 96.5% for various periods, he found the same pattern of variation in the relative water content during the water stress, dropping steadily for up to 50 hours, then remaining unchanged, presumably having reached an equilibrium with the atmosphere. Both species exhibited peak photosynthesis during the initial phase of water loss, then experienced a steady decrease as more water was lost. But it was the drought-resistant ***P. platyphylla*** that reached its photosynthetic peak sooner (2 hours) compared to ***S. undulata*** after 6 hours. **Desiccation avoidance** (the ability to conserve water and prevent desiccation) is not the same as **desiccation tolerance** (the ability to survive despite being desiccated). The reason for this difference is not clear. Could it be the ability to gain more CO_2 as it dries but still has enough water?

Figure 7. ***Porella platyphylla***, an epiphytic leafy liverwort that is drought resistant. Photo by Evan Raskin, through Creative Commons.

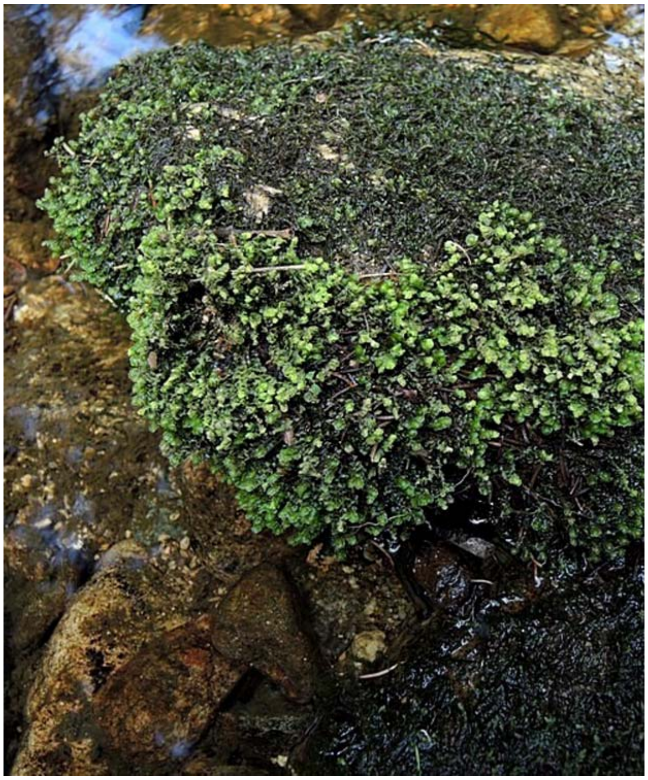

Figure 8. ***Scapania undulata***, an aquatic leafy liverwort that is non-resistant to the effects of desiccation. Photo by Michael Kesl, through Creative Commons.

Drying Effects

Tolerance of drying air differs by habitat (Johnson & Kokila 1970). For ten species of tropical mosses, two groups of resistance were evident. One group had high resistance to desiccation, and the other had low resistance. The high-resistance species occurred in niches with low humidity in the tropical forest. These mosses had high osmotic value and were able to absorb water vapor from the air. We should expect most aquatic bryophytes to fall into the second group.

Aquatic mosses grown out of water become pale in color (Davy de Virville 1927a, b; Henry 1929). These water-stressed mosses possess more numerous chloroplasts, but less chlorophyll, than those remaining submersed. These two researchers also report that some aquatic mosses, particularly ***Warnstorfia fluitans*** (often emergent; Figure 9), develop denser tissues when grown out of water (apparently meaning more, but smaller, cells). And the leaves also develop more denticulations in this species, but no denticulations were formed in ***Fontinalis novae-angliae*** (Figure 6) or ***F. dalecarlica*** (Figure 5), nor did the cells become more dense. It appears that species such as ***Warnstorfia fluitans*** that live partly in and partly out of the water may have more or different mechanisms for coping with lack of water.

Figure 9. ***Warnstorfia fluitans*** growing emergent. Photo by Norbert Schnyder, with permission.

A further mechanism to survive desiccation is the ability of leaf fragments or torn leaves to produce protonemata. This is known in ***Platyhypnidium riparioides*** (Figure 10 (Elssmann 1923). As noted in subchapter 2-5, when Glime (1971) removed ***Fontinalis dalecarlica*** (Figure 5) and ***F. novae-angliae*** (Figure 6) from a New Hampshire, USA, stream and placed them on the stream bank, the stems, but not the leaves, survived for one year. These stems were able to subsequently grow new leaves when they were returned to the water of the streams. ***Fontinalis*** stems are more resistant than the leaves, and at least some members of this genus are able to produce protonemata from broken stems (Figure 11), further helping isolated plants to survive when returned to water (Glime 2014).

Figure 10. ***Platyhypnidium riparioides***, a species of submerged and emergent rocks. Photo by J. C. Schou, through Creative Commons.

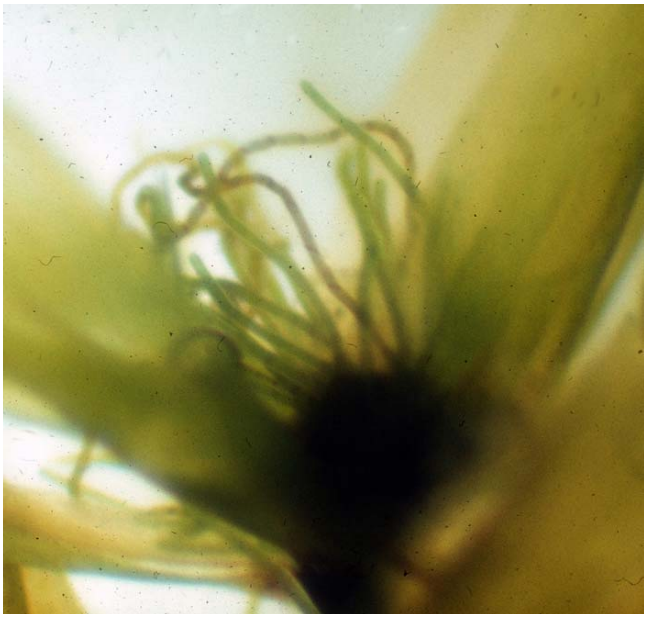

Figure 11. ***Fontinalis hypnoides*** regeneration, showing protonemata at broken stem tip. Photo by Janice Glime.

An early researcher, Schröder (1886), demonstrated the ability of bryophyte stems to be highly resistant to desiccation. Irmscher (1912) reported that leaves of air-dried ***Fontinalis antipyretica*** (Figure 4, Figure 12) and ***F. squamosa*** (Figure 1) died in only 7 days. Those in a desiccator died in 5 days. But he observed that both species produced numerous new sprouts when rewet. Irmscher demonstrated survival of ***Fontinalis*** stems after three weeks of desiccation (see for example Figure 13); these plants also produced new growth from the highly protected apical bud. On the other hand, leaves of ***Philonotis fontana*** (Figure 14), an emergent moss, remained healthy for 20 weeks when air-dried and 18 weeks in a desiccator.

Figure 12. ***Fontinalis antipyretica***, a species that dies after one week of lab drying with no preconditioning. Photo by Matt Goff at www.sitkanature.com, with permission.

Figure 13. ***Fontinalis antipyretica*** out of water, a common occurrence in small streams in summer. Photo by Andreas Rockstein, through Creative Commons.

Figure 14. ***Philonotis fontana*** at the edge of a stream where it is occasionally inundated. Photo by Janice Glime.

But since Irmscher (1912) made his observations, we have learned that rapid drying in the laboratory prevents bryophytes from preparing for desiccation (Gupta 1978b; Stark *et al*. 2013). On the other hand, in nature stream bryophytes typically remain moist for days following low water that leaves them stranded out of water (Figure 1).

Peñuelas (1984b) found that it took 1-4 weeks for bryophytes removed from stream water to the stream bank to show cellular damage. In similar experiments Glime (1971) found that when ***Fontinalis dalecarlica*** (Figure 5) and ***F. novae-angliae*** (Figure 6) were removed from the water to the stream bank in September and returned to the water from the same September to April, they restored their bright green leaf color within a few days. It is likely that they remained hydrated most of this time, either from autumn rain or snow cover.

Gupta (1978b) tested the effect of pretreatment by subjecting the mosses ***Calliergonella cuspidata*** (Figure 15), ***Fissidens adianthoides*** (Figure 16), and ***Fontinalis antipyretica*** (Figure 12), and the leafy liverwort ***Scapania undulata*** (Figure 8) to 98% humidity for 24 hours prior to reduction to 50% relative humidity. When this pretreatment occurred the plants lost much less water initially. He tested ***F. antipyretica*** for changes in water soluble proteins and found no increase. From this he concluded that the increase in resistance to desiccation was due to the change in rate of water loss rather than an effect on a physiological process. In these experiments, ***F. antipyretica*** had a much greater increase in desiccation resistance than did ***Scapania undulata***. The former is a fully submersed species that can be stranded above water at times of low flow. ***Scapania undulata*** often grows where it is subjected to water level fluctuations in step falls and on emergent but wet rocks, as well in locations with shallow submersion. It is possible that it was already naturally "pretreated."

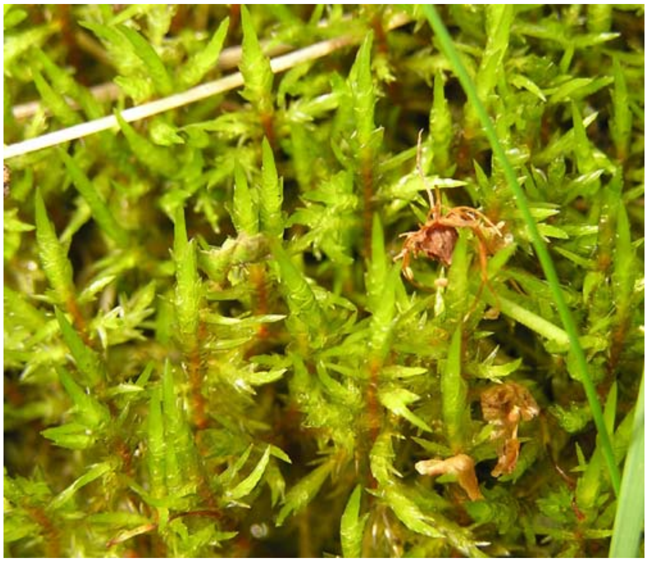

Figure 15. ***Calliergonella cuspidata***, an emergent species that survives desiccation when dried slowly, *i.e.* with pretreatment. Photo by Michael Becker, through Creative Commons.

Figure 16. ***Fissidens adianthoides*** with capsules. Photo by Bob Klips, with permission.

Even using the severe conditions of a lab, some emergent mosses [***Warnstorfia exannulata*** (Figure 17), ***Warnstorfia fluitans*** (Figure 18), ***Drepanocladus aduncus*** (Figure 19), and ***Philonotis fontana*** (Figure 14)] survived 15-20 weeks before dying (Irmscher 1912).

Figure 17. ***Warnstorfia exannulata***, an emergent species that can survive up to 15-20 weeks of drying. Photo by David T. Holyoak, with permission.

Figure 18. ***Warnstorfia fluitans***, an emergent species that can survive up to 15-20 weeks of drying. Photo by Michael Lüth, with permission.

Figure 19. ***Drepanocladus aduncus***, an emergent species that can survive up to 15-20 of drying. Photo by Bob Klips, with permission.

Fontinalis flaccida (Figure 20) from a lake bottom (about 1 m depth) survived drying as a herbarium specimen for three months, then resumed growth in an artificial stream (Glime & Vitt 1984). ***Fontinalis antipyretica*** (Figure 12) exhibited a desiccation threshold at 90% relative humidity, whereas ***F. squamosa*** (Figure 1) did not reach its threshold until 10% (Abel 1956). Abel suggested that hygrophytes have a primary desiccation threshold of 82% relative humidity, but habitats can be a major influence on that level.

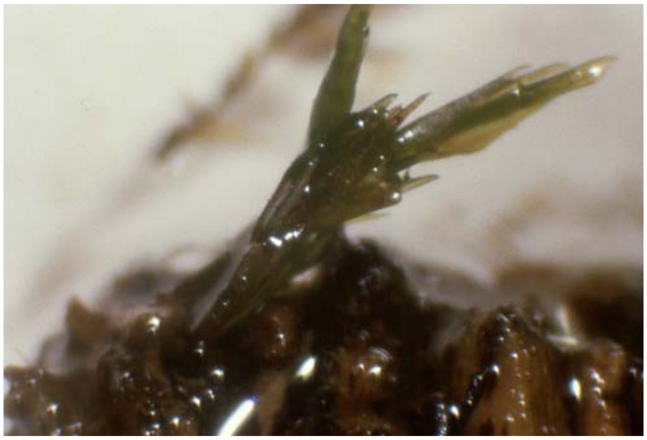

Figure 20. ***Fontinalis flaccida*** growing on limnephilid case at Tepee Lake, Michigan, USA. photo by Janice Glime.

Measurements of photosynthetic efficiency can help us understand some aspects of desiccation tolerance. Arscott *et al.* (2000) found that photosynthetic efficiency helped to explain the ability of ***Schistidium agassizii*** (=*S. alpicola*; Figure 21) to live in the river under cold, low-nutrient conditions, but ***Hygrohypnum alpestre*** (Figure 22) and ***H. ochraceum*** (Figure 23) could not. In the two ***Hygrohypnum*** species, respiration after 10 and 37 hours of rehydration were significantly lower than rates for those plants that had not been dehydrated. Desiccation effects on net photosynthesis in ***Schistidium agassizii*** were less dramatic and differed little from reference populations after 37 hours. On the other hand, ***Hygrohypnum*** species had greater tolerance of temperatures above 20ºC and significantly greater net photosynthetic rates at light saturation than did ***S. agassizii***.

Figure 21. ***Schistidium agassizii***, a wet rock species that has greater tolerance of desiccation than submersed species. Photo from Proyecto Musgo, with permission.

Figure 22. ***Hygrohypnum alpestre***, a species that is sensitive to desiccation. It is shown here with **pearling**, air bubbles produced by photosynthesis trapped among the leaves. Photo by Michael Lüth, with permission.

Figure 23. ***Hygrohypnum ochraceum***, a species that is sensitive to desiccation. Photo by S. H. Studdard, through Creative Commons.

Gupta (1978a) tested five bryophyte species for their desiccation tolerance. Of these, the aquatic liverwort ***Scapania undulata*** (Figure 8) had the least desiccation tolerance compared to the more terrestrial species. It lost water the fastest and had the greatest total loss after 8 hours compared to ***Syntrichia ruralis*** (Figure 24), ***Porella platyphylla*** (Figure 7), ***Mnium hornum*** (Figure 25), and ***Rhizomnium punctatum*** (Figure 26), all more terrestrial species. Both chlorophyll *a* and *b* were damaged by desiccation, with more damage to *a* than *b*.

Figure 24. ***Syntrichia ruralis***, a drought-tolerant species. Photo by Darkone, through Creative Commons.

Figure 25. ***Mnium hornum***, a forest floor drought-tolerant species. Photo by Bob Klips, with permission.

Figure 26. ***Rhizomnium punctatum***, a relatively drought-tolerant species often found on rocks in canyons. Photo by Hermann Schachner, through Creative Commons.

At least some aquatic moss cell walls appear to be adapted for the alternating wet and dry conditions (Roberts & Haring 1937). ***Fontinalis gigantea*** (Figure 27) has large quantities of pectic substances in its cell walls. These allow for rapid water intake. Cutin mixed with pectinaceous substances in the epidermis of the stems could account for water retention.

Figure 27. ***Fontinalis gigantea*** dry in a vernal pool. Photo by Janice Glime.

Cruz *et al.* (2008) used chlorophyll fluorescence as a measure of desiccation effects on the aquatic moss

Fontinalis antipyretica (Figure 4). These measurements were accompanied by O_2 evolution and ion leakage. There was considerable increase of O_2 consumption in the dark that was not inhibited by mitochondrial inhibitors. Photosynthetic activity suffered severe decreases under extreme desiccation and was unable to recover to its normal metabolic activity. Leakage of electrolytes indicated cellular membrane damage.

Membrane Leakage

One of the problems caused by desiccation is membrane leakage. This is most pronounced for soluble substances such as potassium (K). Deltoro *et al*. (1998) compared several bryophytes representing xeric [***Hedwigia ciliata*** (Figure 28), ***Hypnum cupressiforme*** (Figure 29), ***Leucodon sciuroides*** (Figure 30), ***Orthotrichum cupulatum*** (Figure 31), ***Pleurochaete squarrosa*** (Figure 32), ***Porella platyphylla*** (Figure 7), and ***Syntrichia ruralis*** (Figure 24)] as well as mesic, and hydric environments [***Barbula ehrenbergii*** (Figure 33), ***Cinclidotus aquaticus*** (Figure 34), ***Conocephalum conicum*** (Figure 35), ***Lunularia cruciata*** (Figure 36), ***Palustriella commutata*** (Figure 37), ***Philonotis calcarea*** (Figure 38), and ***Platyhypnidium riparioides*** (Figure 10)]. Deltoro and coworkers suggested that this lack of return to normal photosynthesis might be caused by **photoinhibition** (light-induced reduction in the photosynthetic capacity) or membrane damage. There was an accompanying large leakage of K. The leakage may have been exacerbated by more rapid than normal drying.

Figure 28. ***Hedwigia ciliata***, a xeric, rock-dwelling moss. Photo by Štěpán Koval, with permission.

Figure 29. ***Hypnum cupressiforme***, a relatively xeric moss. Photo by Kurt Stüber, through Creative Commons.

Figure 30. ***Leucodon sciuroides*** with capsules, a xeric moss. Photo by Hughes Tinguy, with permission.

Figure 31. ***Orthotrichum cupulatum*** with capsules, a xeric moss. Photo by Hermann Schachner, through Creative Commons.

Figure 32. ***Pleurochaete squarrosa*** dry, a xeric moss. Photo by David T. Holyoak, with permission.

Figure 33. ***Barbula ehrenbergii***, a species of hydric environments. Photo by Michael Lüth, with permission.

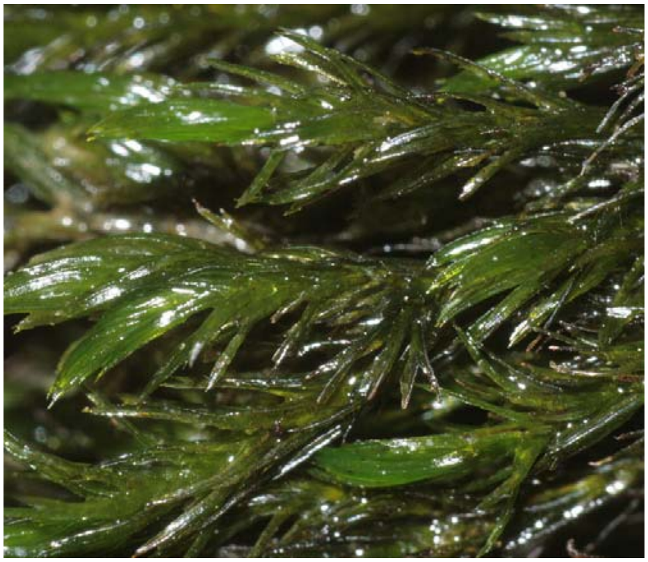

Figure 34. ***Cinclidotus aquaticus***, a species of hydric environments on emergent rocks. Photo by Hermann Schachner, with permission.

Figure 35. ***Conocephalum conicum***, a species of mesic to hydric environments. Photo by Hermann Schachner, through Creative Commons.

Figure 36. ***Lunularia cruciata***, a species of mesic environments. Photo from Botany Website, UBC, with permission.

Figure 37. ***Palustriella commutata***, a species of wet environments. Photo by Hermann Schachner, through Creative Commons.

Figure 38. ***Philonotis calcarea***, a species of wet environments. Photo by Hermann Schachner, through Creative Commons.

Gupta (1977b) found that maximum leakage occurred within the first two minutes of rewetting in the terrestrial ***Porella platyphylla*** (Figure 7), emergent ***Plagiochila asplenioides*** (Figure 39), terrestrial ***Plagiothecium undulatum*** (Figure 40), and aquatic ***Scapania undulata*** (Figure 8). After that, the leakage rate slowed down. Gupta suggested that this slowing is due to the reassemblage of the membrane structures or to the rapid decrease of solutes within the injured and dead tissues. All of these species occur in habitats with a wide range of moisture stress. If the solutes are not washed away, they can be reabsorbed by living cells.

Figure 39. ***Plagiochila asplenioides***, a species that exhibits one of the high levels of solute leakage in the first two minutes of rehydration. Photo by Hermann Schachner, through Creative Commons.

Gupta (1979) used tracers to determine the loss of leachates from the aquatic leafy liverwort ***Scapania undulata*** (Figure 8) during desiccation after pretreatment at 96% relative humidity for 48 hours. In this species 7 carbohydrates, 13 amino acids, and 3 organic acids were identified in the leachates. There appeared to be little selectivity in what was lost, and the leakage appeared to be simple diffusion. Nevertheless, the amino acids threonine, methionine, and valine were not detected in the leachate.

Figure 40. ***Plagiothecium undulatum***, a species that exhibits the most solute leakage among four species tested in the first two minutes of rehydration. Photo by David T. Holyoak, with permission.

Rate of Drying

But in many early studies, the question of rate of drying had not been considered. As early as 1990, Proctor recognized the importance of drought-hardening as the bryophyte dries. Growth form is a strong influence on both rate of drying and the ability to rehydrate when water becomes available. The growth form contributes to the boundary-layer resistance, a factor that is critically important in determining water loss.

Carvalho (2009) noted that whereas many studies exist on desiccation effects on terrestrial bryophytes, few exist for aquatic species. To help us understand some of the differences between terrestrial and aquatic bryophyte strategies, Carvalho desiccated ***Fontinalis antipyretica*** (Figure 12) at different relative humidities, then rapidly rehydrated them. The desiccation stress caused membrane damage. This, in turn, resulted in decreases in gross photosynthesis and the maximum photochemical efficiency of PSII (Fv/Fm). Rehydration resulted in a strong respiratory burst (ca 1200 µmol O_2 g^{-1} DW h^{-1}).

Krochko *et al.* (1979) noted that oxygen consumption increased considerably during the latter stages of desiccation in both the desiccation-tolerant ***Syntrichia ruralis*** (Figure 24) and the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 41). The ATP content was influenced not by the O_2 consumption, but by the rate of drying. The more rapidly the mosses dried, the more ATP was present in the dry mosses. When the mosses were rehydrated, the rate of O_2 consumption in ***S. ruralis*** was considerably elevated for up to 24 hours after rapid desiccation, but the elevation was small and endured for only a brief time after slow desiccation. In ***C. filicinum***, normal O_2 consumption did not return following rapid dehydration, but returned within a few hours following slow desiccation. In ***S. ruralis***, normal ATP levels returned within 5-10 minutes of rehydration. In ***C. filicinum***, the increases in ATP closely followed the O_2 consumption. The researchers suggested that the differences between the species might relate to the ability to repair cellular damage after rapid desiccation.

Figure 41. ***Cratoneuron filicinum***, a desiccation-intolerant species of wet areas. Photo by David T. Holyoak, with permission.

Recovery

I once dried ***Fontinalis flaccida*** (Figure 20) on index cards in the lab where air can be quite dry. After it stayed more than a month in that state, I put it in an experiment to determine the effects of flowing water on the stem structure, and hoped. Fortunately, it grew in the experiment!

One important difference is in recovery rate between terrestrial and aquatic species (Carvalho 2009). In the widespread aquatic moss ***Fontinalis antipyretica*** (Figure 12), H_2O_2 production increased immediately in the tips upon rehydration. This production increased when the relative water content was decreased, and production slowly decreased during the next 25 minutes of rehydration. Recovery of photosynthesis and respiration was slow over a five-day period and was even slower at lower relative water contents or when the desiccation rate was faster. Full photosynthesis and respiration had not yet returned after five days. It is interesting that the amount of water lost has a greater effect on membrane integrity and photosynthesis than does the rate of water loss. Nevertheless, a greater rate of water loss can exacerbate the stress effects of water loss. This suggested that rapid water loss did not allow sufficient time for activation of protective mechanisms against desiccation.

In their desiccation experiments with ***Fontinalis antipyretica*** (Figure 12), Carvalho *et al.* (2011) found that slow drying is necessary for the moss to recover fully. On the other hand, the extent of dehydration influences metabolism. In 2013, Carvalho followed up on these observations, concluding that desiccation tolerance in ***Fontinalis antipyretica*** (Figure 12) is determined by the extent of dehydration, the rate at which it occurs, or by both. The rehydration behavior of this species indicates that it is desiccation tolerant, a property that permits it to survive in waterways that dry up for part of the year. Oxidative stress is associated with survival of desiccation; this species experiences an increase in reactive oxygen species production due to metabolic impairment resulting from dehydration. The reactive oxygen species production was very high under rapid dehydration, but almost nonexistent under slow dehydration. This highly reactive oxygen reacts with such cellular constituents as proteins and lipids, causing damage to the cell.

Photoinhibition

Deltoro *et al.* (1998) found that at low water content, fluorescence characters indicated low efficiency of photosynthetic quantum conversion, closed PS II reaction centers, and strong nonphotochemical quenching only in those species known to be desiccation tolerant. Upon rehydration, return of fluorescence indicated that the photosynthetic apparatus had returned to full function. However, for those species from hydric and mesic habitats, photochemical activity did not return to normal. The researchers suggested that an increase in dissipation of thermal energy during dehydration might adapt xeric mosses to their erratic water supplies by lowering the potential for photodamage during water loss and early hydration, permitting the photosynthetic apparatus to recover quickly.

Supporting the suggestions of Deltoro *et al.* (1998), Carvalho *et al.* (2011, 2012) found that in ***Fontinalis antipyretica*** (Figure 12) PS II (PSII) regulation and structural maintenance are an important part of this induced desiccation tolerance mechanism that permits this moss to recover when it is dried slowly, as it would be in a drying stream bed. A decrease in the photochemical quenching coefficient (qP) immediately following rehydration may be important in alleviating the effects of excess energy on PS I (PSI) before the cells are fully functional, while low-level nonphotochemical quenching (NPQ) would allow an energy shift that enables recovery following extended periods of desiccation.

Sucrose Accumulation

During dehydration, sucrose can accumulate, changing the osmotic relationships (Carvalho 2013; Carvalho *et al.* 2014). Sucrose is important in desiccation tolerance through the prevention of macromolecule denaturation and the slowing of damaging reactions with the reactive oxygen species. Under fast dehydration, the characteristics of the cell walls change, permitting greater elasticity of the cytoskeleton. Hence, the bryophytes use a constitutive protection that permits tolerance of desiccation by protecting structural integrity. There is a reduction of proteins involved in photosynthesis and cytoskeleton structure, whereas those associated with sugar metabolism and plant defense increase. Then they use a repair-based mechanism upon rehydration to repair the damage of dehydration. This involves an accumulation of normal protein values for both photosynthesis and cytoskeleton while those proteins involved in sugar metabolism and defense remain light. This repair mechanism is activated by the accumulation of mRNA during rehydration. When the plants are dried rapidly, they lose nearly all proteins; this is not the case under slow drying. This supports the hypothesis that slow-drying is necessary to manufacture protective proteins. In short, desiccation-tolerance responses of aquatic bryophytes like ***Fontinalis antipyretica*** (Figure 12) appear to be the same as those of desiccation tolerant terrestrial bryophytes.

More Leakage Problems

Despite the protections of slow drying, dry membranes leak electrolytes (Carvalho *et al.* 2015). In terrestrial mosses, rehydration is typically slow, permitting the cells to reabsorb lost minerals and nutrients in the first few minutes of rainfall before they can be washed away. This may not be the case in aquatic systems where water can return suddenly from an upstream source. Slow dehydration permits the cell wall to gain elasticity, but rapid dehydration results in a higher sucrose accumulation. Sugar acts as an osmolyte in bryophytes, while stabilizing membranes and proteins through vitrification. But after rapid dehydration, leaves lose 50% of their accumulated sucrose through leakage. The result is that the sucrose is insufficient to establish desiccation tolerance. Life forms may help some species slow dehydration, providing another protective measure. Carvalho *et al.* noted that in ***Fontinalis antipyretica*** (Figure 12) the growth form permits the plants to create numerous capillary spaces where water is held, permitting slow drying.

Gupta (1976) reported the leakage of 15 amino acids from ***Plagiochila asplenioides*** (Figure 39) following desiccation for 48 hours at 50% relative humidity, and rehydration. This was accompanied by the loss of 3 unknown compounds, nearly 10 carbohydrates, and 4 organic acids. He found that practically all the soluble compounds in the plant shoots were able to leak out during this dehydration-rehydration protocol, most likely through passive diffusion through leaky membranes.

Invaders in the Mix

Leakage from the cell indicates that there are holes in the cell membranes. That could make it possible for invading microbes to enter the cells, making new food supplies available to them, and perhaps more importantly, organic leakage providing food outside the cell, the latter demonstrated by Gupta (1977c). Gupta found that the burst of respiration following desiccation and rehydration was not a function of the cell, but rather increased respiration by the microbes that had gained more favorable conditions. This burst of respiration was exhibited on xerophytic [***Syntrichia ruralis*** (Figure 24; no significant change); ***Porella platyphylla*** (Figure 7) (2X)], mesophytic [***Mnium hornum*** (Figure 25; 2X)], meso- to hydrophytic [***Dichodontium palustre*** (Figure 42; 2.5X)], and hydrophytic [***Scapania undulata*** (Figure 8; 6X)] bryophytes.

Figure 42. ***Dichodontium palustre***, a species that may be submersed or in the splash zone. Photo by Hermann Schachner, through Creative Commons.

Polyribosomes and Protein Synthesis

Bewley (1974) found that when the aquatic moss ***Hygrohypnum luridum*** [Figure 43; probably ***Cratoneuron filicinum*** (Figure 41), as identified later] was desiccated, it did not matter if it was done quickly or slowly in a saturated atmosphere. Both of these conditions caused an irreversible loss of polyribosomes. Furthermore, the moss was unable to recover and resume protein synthesis when it was rehydrated. This is in contrast to the sequence of events and recovery in the drought-tolerant terrestrial moss ***Syntrichia ruralis*** (Figure 24).

Figure 43. ***Hygrohypnum luridum***, a moss on emergent rocks. Photo by Andrew Melton, through Creative Commons.

Gwozdz and Bewley (1975) considered the effects of fast and slow drying on ***Syntrichia ruralis*** (Figure 24) and its retention of polyribosomes. This desiccation-tolerant moss actually retained fewer polyribosomes when dried slowly, the ribosomes were more active than in the rapidly dried moss. The major protein synthesis occurs in the cytoplasm on rehydration. Hence, in the slowly dried mosses, this retention of synthetic capacities permits them to resume protein synthesis more quickly than in rapidly dried mosses. They found that the aquatic moss ***Hygrohypnum luridum*** [Figure 43; probably the moss later identified as ***Cratoneuron filicinum*** (Figure 41)] retained its polyribosomal and ribosomal activity during desiccation, but suffered great loss of activity on rehydration.

Non-autotrophic CO_2 Fixation

Not all CO_2 is fixed into carbohydrates for structure or storage. CO_2 fixation can also occur in the dark and is incorporated into amino acids (> 60% of total, mainly into aspartate, alanine, and glutamate) and organic acids (< 40%). ***Cratoneuron filicinum*** (Figure 41), a drought-sensitive species, and ***Syntrichia ruralis*** (Figure 24), a drought-tolerant species, fix CO_2 non-autotrophically at a rate of about 1.2 and 2.2 μmol h^{-1} g^{-1} dry weight, respectively (Dhindsa 1985). During drying these two species differ in their responses. The dark CO_2 fixation rate of ***S. ruralis*** does not diminish until the tissues lose about 60% of their original fresh weight. This dark fixation resumes immediately upon rehydration in this species, but not in ***C. filicinum***. Nevertheless, even in ***S. ruralis***, when dry plants are placed in nearly 100% relative humidity, the weight increases to only about 40% of the original hydrated weight and dark CO_2 fixation returns to only about 60% of that in the fresh moss. Dhindsa suggested that the immediate availability of NADPH, produced from NADH during dark CO_2 fixation, in drought-tolerant species may be important in repairing cellular damage through reductive biosynthesis of membrane components and other damaged cellular constituents.

Temperature Effects

Chlorophyll content can serve as a surrogate for cell health. Hearnshaw and Proctor (1982) used chlorophyll content to determine the loss of viability in seven species [***Anomodon viticulosus*** (Figure 44), ***Racomitrium aquaticum*** (Figure 45), ***R. lanuginosum*** (Figure 46), ***Tortella humilis*** (Figure 47), ***Andreaea rothii*** (Figure 48), ***Frullania tamarisci*** (Figure 49), and ***Porella platyphylla*** (Figure 7)] of bryophytes that were kept dry at temperatures ranging 20-100ºC from a few minutes to weeks or months. Although the different temperatures tended to affect all of them similarly, the time required for the same amount of damage differed widely. At 100ºC, the least resistant species suffered a 50% loss of chlorophyll in a few minutes or less. The more resistant species survived at 20 and 37ºC for weeks to months before experiencing 50% chlorophyll loss. Both ***Racomitrium*** species exhibited great tolerance at temperatures in the middle part of the range investigated, despite ***R. aquaticum*** occurring on moist, shaded rocks and ***R. lanuginosum*** occurring frequently in the tundra and tropical alpine areas, although these locations are frequently misty or humid.

Figure 44. ***Anomodon viticulosus***, a xeric species. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Racomitrium aquaticum***, a species of wet habitats. Photo by Hugues Tinguy, through Creative Commons.

Figure 46. ***Racomitrium lanuginosum***, a xeric moss. Photo by Hermann Schachner, through Creative Commons.

Figure 47. ***Tortella humilis***, a species of rock crevices near water. Photo by Bob Klips, with permission.

Figure 48. ***Andreaea rothii***, a rock-dwelling xeric moss. Photo by David T. Holyoak, with permission.

Figure 49. ***Frullania tamarisci***, a moss that can be exposed to a wide range of humidities. Photo by Tim Waters, through Creative Commons.

Pigment Responses

Like **e**migration and **im**migration, **emersion** is the process of exiting and **immersion** is the process of entering the water. These two processes affect mosses from different habitats differently. Peñuelas (1984b) found that aquatic moss species lost 50% of their chlorophyll in very few weeks of emersion, with pigments having OD430/OD665 being most sensitive. The phaeo-pigment proportion was sensitive to periods of rainfall and humidity. ***Cinclidotus fontinaloides*** (Figure 50) was the most tolerant species, ***Fontinalis antipyretica*** (Figure 12) the least. By contrast, all terrestrial mosses studied lost 50% of their chlorophyll content in the first week of immersion. Spitale (2009) even found that he could use pigments as indicators of the height above the water table, hence the moisture conditions, in spring systems.

Figure 50. ***Cinclidotus fontinaloides***, a species of emergent rocks that is relatively tolerant of desiccation. Photo by Hermann Schachner, through Creative Commons.

Fatty Acid Responses

Stewart and Bewley (1982) found that both the desiccation tolerant ***Syntrichia ruralis*** (Figure 24) and the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 41) maintained their fatty acid phospholipid composition during rapid drying. However, after slow drying, some unsaturated fatty acids decline. After slow drying, ***S. ruralis*** exhibits further decline of these fatty acids upon rehydration. Then, after ~105 minutes, they regain their original nondesiccated levels. After rapid desiccation, the decline is smaller and more transient. On the other hand, in ***C. filicinum*** most of the phospholipid unsaturated fatty acids decrease during rehydration, and these are never recovered. In contrast to ***S. ruralis***, ***C. filicinum*** exhibits very little incorporation of acetate or glycerol during rehydration.

Fatty acid concentrations vary widely among the bryophytes (Dembitsky & Rezanka 1995). For example, acetylenic fatty acid concentration in the wetland moss ***Calliergon cordifolium*** (Figure 51) was 6.6% but reached 80.2% in the floating thallose liverwort ***Riccia fluitans***. At the very least, these differences suggest that we need to look at the role of fatty acids as protective substances in bryophytes.

Figure 51. ***Calliergon cordifolium***; the genus ***Calliergon*** has algal fatty acids. Photo by Jerry Jenkins, Northern Forest Atlas, with permission.

ABA Mediation

Noting the ancestral terrestrial life style of bryophytes and their evolutionary history of going back and forth between terrestrial and aquatic environments, Wanke (2011) explored the role of the hormone ABA in submersed-emersed switches. This environmentally responsive hormone has been present throughout the plant kingdom from bryophytes to flowering plants. It can initiate the production of other hormones.

Whereas **heterophylly** (having more than one leaf type on same plant) is common between submersed and emergent leaves of tracheophytes, such heterophylly is rare among bryophytes. In the tracheophyte *Callitriche heterophylla*, **GA** (gibberellic acid, a growth hormone) induces cell elongation, causing emergent leaves to resemble submersed leaves (Deschamp & Cooke 1985). On the other hand, GA seems to induce **heterophylly** through a pathway with the gaseous hormone **ethylene**, and this antagonizes the synthesis of the hormone **ABA**. Thus, when aerial shoots of *Ludwigia arcuata* (Figure 52) were exposed to ethylene, they were induced to form leaves resembling submersed leaf morphology (Kuwabara *et al.* 2003; Kuwabara & Nagata 2006). Little work has been done with bryophytes and the effects of these three hormones. Yet we know that ACC, the ethylene precursor, has a significant effect on morphology and coloration in ***Fontinalis squamosa*** (Figure 1) and ***F. antipyretica*** (Figure 12) (Glime & Rohwer 1983). We need to investigate its role in emergent vs submergent morphology.

Figure 52. ***Ludwigia arcuata***, an aquatic tracheophyte that responds to ethylene concentrations to determine leaf shape. Photo by Shaun Winterton, through Creative Commons.

Added ABA in three bryophytes [mosses ***Physcomitrella patens*** (Figure 53) and ***Atrichum undulatum*** (Figure 54) and liverwort ***Marchantia polymorpha*** (Figure 55)] caused these bryophytes to exhibit a decrease in total chlorophyll and carotenoids (Vujičić *et al.* 2016). Effects on growth were unclear. It is likely that ABA has effects on desiccation tolerance in aquatic bryophytes, but much more research is needed to understand the role of this hormone in bryophytes.

Figure 53. ***Physcomitrella patens***, a moss that responds to added ABA by a reduction in total chlorophyll. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Atrichum undulatum***, a moss that responds to added ABA by a reduction in total chlorophyll. Photo by David T. Holyoak, with permission.

Figure 55. ***Marchantia polymorpha*** with gemmae cups, a liverwort that responds to added ABA by a reduction in total chlorophyll. Photo by Hermann Schachner, through Creative Commons.

Allocation Changes

Rice (1995) compared allocation and growth in pairs of aquatic and non-submersed species of ***Sphagnum*** (**Error! Reference source not found.**, **Error! Reference source not found.**). The submerged taxa all had greater relative growth rates and greater allocation to their photosynthetic tissues. The latter was expressed as higher whole plant chlorophyll content. In this genus, the greater allocation to photosynthetic processes was accomplished by fewer or smaller hyaline cells and a shift in the biochemical partitioning within the photosynthetic cells to favor light-reaction proteins. This latter factor was estimated from chlorophyll to nitrogen ratios. But these adaptations differed by species.

Light

Proctor (1990) considered most bryophytes to be shade plants, having low chlorophyll *a*/*b* ratios, and reaching light saturation at relatively low light levels. They behave as C_3 plants, despite their ability to dry out to water contents as low as 5-10% of their dry weight. Growth forms can have a profound effect on the ability for light capture. Proctor stated that "bryophyte growth-forms must represent an adaptive balance between water economy and needs for light capture and carbon and mineral nutrient acquisition."

Most bryophytes seem unable to tolerate high light intensities. Aquatic bryophytes are typically protected from light by water depth, and in woodland streams and small pools, also by canopy cover. At cool temperatures, high light can cause severe reactions in ***Fontinalis antipyretica*** (Figure 12), resulting in loss of chlorophyll or production of bright red pigments (Figure 56-Figure 58) (Glime 1984).

Figure 56. ***Fontinalis antipyretica*** red (especially upper middle) in cold water and high light 15 May 1982 near Rothenfels, Germany. Photo by Janice Glime.

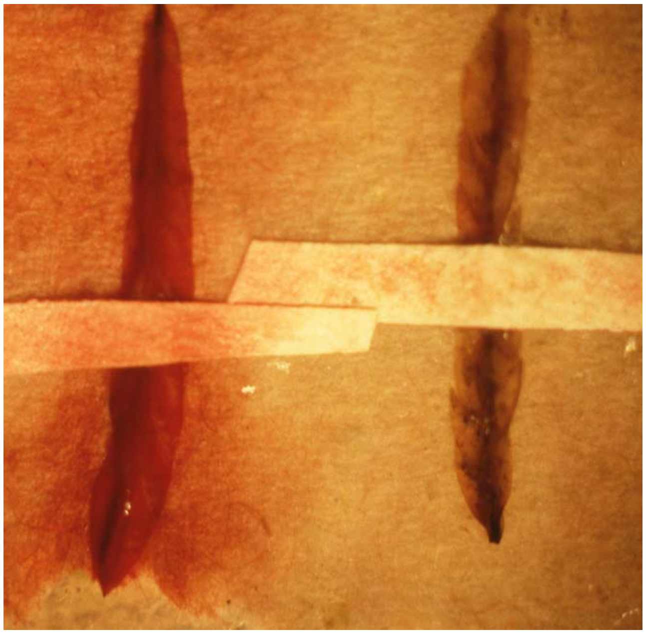

Figure 57. ***Fontinalis antipyretica*** red leakage in tropism experiment out of water, a response also seen in high light. Photo by Janice Glime.

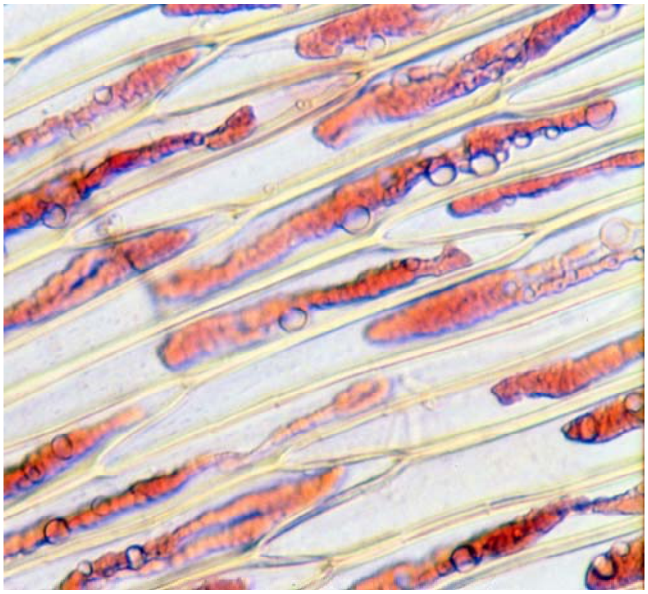

Figure 58. **Fontinalis antipyretica** red cells in tropism experiment out of water, a response similar to that in high light. Photo by Janice Glime.

Martin and Churchill (1982) found that both chlorophyll concentrations and *a*:*b* ratios were lower in bryophytes than for most tracheophytes. Those mosses collected from habitats with low light levels had higher chlorophyll concentrations and lower chl *a*:*b* ratios than those collected from high light levels. These differences suggest that changes in chlorophyll concentrations can adapt bryophytes to low or high light. Thus, we should expect mosses in forest streams to contain more chlorophyll than those in terrestrial habitats.

Bryophytes may have relatively low light optima. Using populations from the Keweenaw Peninsula of Michigan, USA, Glime and Acton (1979) found that the **Fontinalis duriaei**-periphyton association had its maximum productivity at 10ºC, 5400 lux. At 5400 lux it approached light saturation under the experimental conditions, whereas direct sunlight at noon can reach 120,000 lux (Wikipedia 2019).

The ability to survive with low growth rates in low light permits bryophytes to live at depths of water that are unavailable to their tracheophyte competitors. For example, Westlake and Dawson (1976) noted that **Fontinalis antipyretica** (Figure 12) became a significant part of the plant biomass at depths greater than 1 m in the River Frome. Light there is only 30% of incident light.

Burr (1941) concluded that **Fontinalis** (Figure 5, Figure 6, Figure 12, Figure 20) reaches its light compensation at 150 lux at 20ºC and at 40 lux at 5ºC. Nevertheless, some species are tolerant of high light, such as **Schistidium agassizii** (Figure 21) in Alaskan streams (Bowden *et al*. 1994) and others (Ormerod *et al*. 1994).

Marschall and Proctor (2004) concluded that, based on 39 species of mosses and 16 of liverworts, bryophytes are generally shade plants. This was supported by total chlorophyll, Chl *a*:*b* ratio, PPFD values at 95% saturation mostly <1000 µmol m-2 s-1, but bryophytes in general "are not inherently shade plants." They concluded that their low productivity in the sun, relative to tracheophytes, was most likely limited by CO_2 diffusion into the leaves. The greater area with ventilated photosynthetic tissue (Figure 59), such as that of **Polytrichum** (Figure 60), may account for the greater productivity of members of that genus.

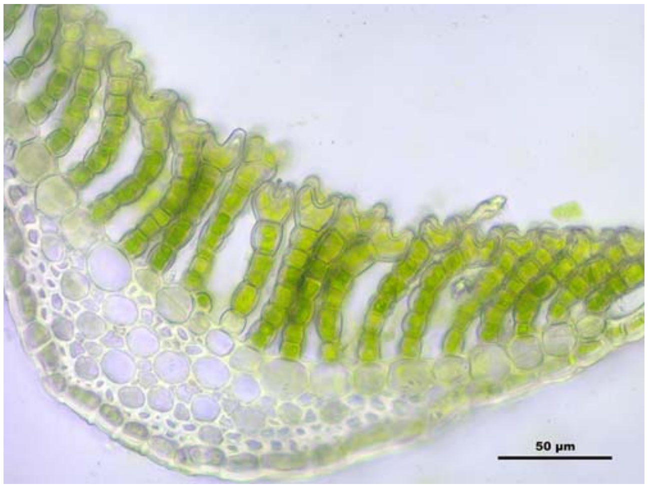

Figure 59. **Polytrichum commune** leaf cs showing the lamellae that create "ventilation" within the photosynthetic tissue. Photo by Hermann Schachner, through Creative Commons.

Figure 60. **Polytrichum commune**, a wetland species with greater productivity than most mosses, perhaps due to its ventilated photosynthetic tissue. Photo by Michael Lüth, with permission.

López and Carballeira (1989) found that the aquatic mosses **Fontinalis antipyretica** (Figure 12), **Brachythecium rivulare** (Figure 61), **Fissidens polyphyllus** (Figure 62), **Platyhypnidium riparioides** (Figure 10), and the leafy liverwort **Scapania undulata** (Figure 8) exhibited a higher chlorophyll concentration than some terrestrial bryophytes. In addition to responses to low light, chlorophyll content responded to both organic and metal pollution. In this regard, **Fontinalis antipyretica** was the most resistant and **Scapania undulata** the most sensitive among these species.

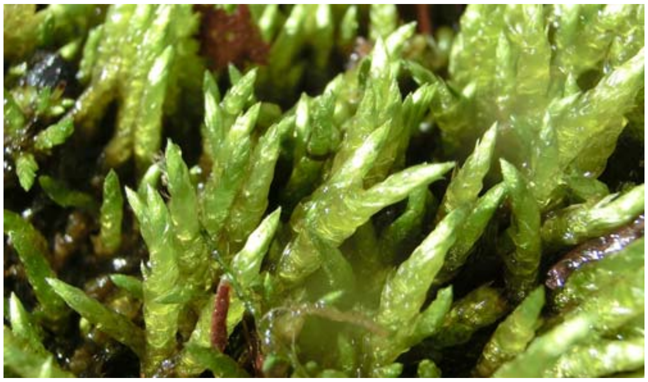

Figure 61. ***Brachythecium rivulare***, a wet habitat or emergent species with a higher chlorophyll content than most terrestrial bryophyte species. Photo by Michael Lüth, with permission.

Figure 62. ***Fissidens polyphyllus***, a species of wet cave walls and other wet habitats; it has a higher chlorophyll content than most terrestrial bryophyte species. Photo by David T. Holyoak, with permission.

Habitat Differences

Szarek (1994) found that other abiotic factors affected the chlorophyll *a* concentrations in mosses (and attached algae) in the Sucha Woda stream in the High Tatra Mountains of southern Poland. The lowest chlorophyll *a* concentrations were found in the high mountain part of the stream, whereas the lowest were found in the middle part. In that middle portion, significant differences in light intensity did not have any significant effect on the chlorophyll *a* content, suggesting that other factors were involved.

In the Kuparuk River of Alaska, USA, ***Schistidium agassizii*** (=***Schistidium alpicola***; Figure 21) exhibited little response to increases in light availability (Arscott *et al.* 2000). ***Hygrohypnum*** species (Figure 22, Figure 23, Figure 43), on the other hand, responded strongly to increases in light, helping to explain the distribution of these species in the Arctic.

In many locations, bryophytes are able to grow near lights in caves where the public have access. These are mostly terrestrial bryophytes growing on the walls of the caves. However, Thatcher (1949) found several typically aquatic or emergent mosses in Crystal Cave, Wisconsin, USA. Light where bryophytes grew ranged 269-9149 lux. Although Thatcher did not mention submersion for these species, the limestone cave supported the growth of ***Bryoerythrophyllum recurvirostrum*** (Figure 63), ***Leptodictyum riparium*** (Figure 64), ***Warnstorfia fluitans*** (Figure 18), and ***Brachythecium populeum*** (Figure 65), all of which can be submersed, as well as a number of terrestrial species. All of these "aquatic" species were new records for caves.

Figure 63. ***Bryoerythrophyllum recurvirostrum***, a basophile that can occur in limestone caves. Photo by Will Van Hemessen, through Creative Commons.

Figure 64. ***Leptodictyum riparium***, an aquatic moss that can occur in limestone caves. Photo by Hermann Schachner, through Creative Commons.

Patterson (1946) examined the osmotic values of bryophytes from different habitats, including a number of aquatic species, and found that these were correlated with the light intensity and not with the available moisture. The first and most typical of the behavior types was for species that became plasmolyzed at the same value after a dry period as when tested after a prolonged moist period. The second type was somewhat refractory toward plasmolyzing agents after a dry period and plasmolyzed at a somewhat greater concentration than when tested after a moist period. A third type exhibited a marked temporary increase of its refractory property. A fourth type failed to plasmolyze at any time after a dry period – a response that was at one time considered to be true of all bryophytes. A fifth type exhibited aberrant behavior, with the same specimen sometimes becoming plasmolyzed and at others failing to do so, suggesting that some sort of preconditioning could be involved.

Figure 65. ***Brachythecium populeum*** with capsules, a moss that lives on emergent rocks and that can occur in limestone caves. Photo by Hermann Schachner, through Creative Commons.

Chlorophyll and Accessory Pigments

The aquatic bryophytes generally have the same pigments as the green algae and tracheophytes (Martínez-Abaigar & Núñez-Olivera 1998). In general, bryophytes have chlorophylls *a* and *b*, typically 24 carotenoids, including the pure hydrocarbons α and β carotene and the oxygen-containing xanthophylls lutein, zeaxanthin, violaxanthin, and neoxanthin as the most frequent (Taylor *et al* 1972; Schmidt-Stohn 1977; Czeczuga 1980, 1985; Czeczuga *et al.* 1982; Huneck 1983; Farmer *et al.* 1988; Boston *et al.* 1991). ***Fontinalis antipyretica*** (Figure 12) is unusual in having **auroxanthin** (Bendz *et al.* 1968), but otherwise there is no "outstanding" difference between terrestrial and aquatic bryophytes (Martínez-Abaigar & Núñez-Olivera 1998).

As is often the case, the nature or nurture question is not a yes or no comparison. Both are important. The pigment composition of bryophytes, including that of aquatic bryophytes, is a product of both genetic and environmental factors (Martínez-Abaigar & Núñez-Olivera 1998). At that time, we knew little about the anatomical factors or physiological factors that permitted bryophytes to survive high light intensities, especially among aquatic bryophytes. Nevertheless, some factors seemed to be characteristic. Researchers have warned that it is important to use the tips of the bryophytes where the highest chlorophyll contents occur (Schmidt-Stohn 1977; Martínez-Abaigar & Núñez-Olivera 1998).

Water effectively filters out red light, increasing with depth, leaving predominantly green light, but also blue (Kirk 1994) to penetrate to greater depths. Green light causes an increase in chlorophylls and carotenoids in ***Fontinalis*** (Figure 5, Figure 6, Figure 12, Figure 20) (Czeczuga 1987). Evans *et al.* (1974) recognized the importance of light as an ecological factor, examining such bryophytes as ***Fontinalis antipyretica*** (Figure 12) and ***Pellia epiphylla*** (Figure 66). Potential pigments to facilitate photosynthesis in lakes and other deep-water habitats are present in ***Bryum pseudotriquetrum*** (Figure 67) from Pletwicki Lakes, Yugoslavia (Czeczuga 1971). These include the carotenoids α-carotene, cryptoxanthin, lutein (epoxy and free), zeaxanthin, violaxanthin, and neoxanthin.

Figure 66. ***Pellia epiphylla***, a stream bank species. Photo by David T. Holyoak, with permission.

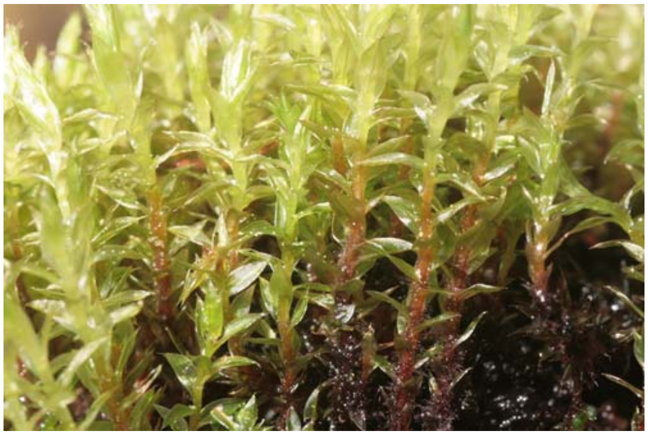

Figure 67. ***Bryum pseudotriquetrum***, a wetland species. Photo by Hermann Schachner, through Creative Commons.

Aquatic bryophytes have lower chlorophyll concentrations than do aquatic tracheophytes (Martínez-Abaigar & Núñez-Olivera 1998). Even the stream algae tend to have more chlorophyll than the bryophytes. The chlorophyll *b* and carotenoids serve as accessory pigments to capture the blue and green light and transfer it to the chlorophyll *a* action centers in the bryophytes (and other plants and algae). The chlorophyll *a*:*b* ratios of aquatic bryophytes typically range between 2 and 3 (Peñuelas 1984a, b; Peñuelas *et al* 1988; López & Carballeira 1989; Martínez-Abaigar *et al.* 1994). Tracheophytes typically have values between 2.4 and 3.7 (Martin & Churchill 1982). **Phaeophytins** may be produced as a result of stress that results in chlorophyll breakdown, but not all phaeophytin pigments are the result of breakdown.

Photosynthetic pigment concentrations change with the seasons (Martínez-Abaigar *et al*. 1994). These researchers analyzed pigment composition in 13 aquatic bryophytes from a variety of habitats. Chlorophyll content ranged 2.2-9.2 mg g^{-1} dry weight, 97-351 mg m^{-2} shoot area. These values were higher than those reported in terrestrial bryophytes, but lower than in tracheophytes. They were similar to those of epilithic river algae. Chlorophyll *a*/*b* ratios (2.1-2.8) and carotenoid indices of 1.72-2.11 were also significantly lower than those of tracheophytes. The researchers interpreted these differences as adaptations to shade in the bryophytes, as well as the lower physiological activity of the bryophytes. The phaeopigments had a positive correlation with the chlorophyll content, a result of the presence of functional phaeophytin *a* in photosystem II. Chlorophyll degradation in the emersed bryophytes did not produce phaeopigments. Furthermore, the phaeopigment ratios had little variation with season or habitat. Summer desiccation was the primary factor related to pigment cycles, with strong chlorophyll content decreases in summer, accompanied by a decrease in the Chl *a*/*b* ratio. When bryophytes were continuously wet, the seasonal cycle was more attenuated and correlated more with changes in light conditions caused mostly by changes in canopy coverage. If the bryophytes were permanently immersed in sun-exposed habitats, both chlorophyll content and chlorophyll *a*/*b* ratio were high in all seasons, suggesting high metabolic activity all year. The leaf specific area and leaf specific weight were both comparable to those of terrestrial bryophytes and served to indicate the proportion of non-photosynthetic tissues and were related to desiccation and light tolerance of the species.

Seasons

Seasonal light differences can cause a shift in dominance of the stream macrophyte flora. Everitt and Burkholder (1991) suggested that the dominance of the red alga *Lemanea* (Figure 68) during cool months was due to its greater tolerance of high light intensities. When leaves returned to the trees, ***Fontinalis*** (Figure 5, Figure 6, Figure 12, Figure 20) species were able to dominate in the warmer months.

Figure 68. ***Lemanea fluviatilis***, a red alga that thrives in streams in the cool months. Photo by J. C. Schou, with permission.

In the Riu Tenes, Catalonia, chlorophyll *a* increases in submerged mosses from December (after a dry period) to May (after a rainy period) (Peñuelas & Vallcorba 1988). On the other hand, the carotene:chl *a* ratio and phaeopigments increase following emergence. Thus, seasonal changes in pigment concentrations respond to microclimatic changes resulting from changes in the river level.

Martínez-Abaigar *et al*. (1994) analyzed seasonal changes in the photosynthetic pigments of 13 aquatic bryophytes. As in the study by López and Carballeira (1989), they found that chlorophyll contents (2.2-9.2 mg g^{-1} dry weight and 97-351 mg m^{-2} shoot area) were higher than those of terrestrial bryophytes, but were similar to those of epilithic river algae. They furthermore had a lower chlorophyll *a*:*b* ratio (2.1-2.8) and carotenoid index. In both bryophytes and algae, these are considered adaptations to shade conditions. They found that when chlorophyll degraded in the emersed bryophytes, no phaeopigments were produced. Furthermore, phaeopigments showed little variation with season or habitat. Seasonal differences were manifest as reduced chlorophyll in response to summer desiccation. This also caused a reduced chlorophyll *a*:*b* ratio, accompanied by an increase in the carotenoid:chlorophyll ratio. The seasonal cycles were less obvious in wet bryophytes, responding to changes in light conditions caused by leaf-out and leaf fall. For permanently submersed species, the chlorophyll content and chlorophyll *a*:*b* ratio were high in all seasons, indicating that these plants had a high metabolic state year-round.

Martínez-Abaigar and Núñez-Olivera (2011) found that the moss ***Fontinalis antipyretica*** (Figure 12) showed some damage from enhanced UV radiation, mostly as brown coloration, development of the central fibrillar body in the cells, chloroplast disappearance, and protoplasts that became vesiculose to vacuolized to hyaline (Martínez-Abaigar *et al*. 2004b), but they noted that these symptoms are common as signals of stress from other causes. The one specific response demonstrated was a change in cell wall color from yellow to orange-brown (Martínez-Abaigar & Núñez-Olivera 2011)

Pigment concentrations track the opening and closing of the canopy (Álvaro 2001). Concentrations of nutrients tend to be lowest in spring and highest in autumn. This is due to dilution from the greater flow in spring and can relate to growth cycles and low flow in autumn. Although the light changes, the temperature variation in streams is much less than in the terrestrial environment.

UV-B

UV-B radiation is increasing as a result of ozone depletion in the upper atmosphere. The lack of a thick cuticle or epidermis, and often absence of multiple cell layers, suggests that bryophytes should be particularly susceptible to damage from this increased radiation. In the aquatic environment, water can protect many species due to its ability to rapidly absorb the UV-B radiation and the canopy cover that diffuses much of it during the summer. But in mountain streams, the water may be insufficient to provide protection in this more exposed habitat.

Furthermore, at low temperatures, ***Fontinalis antipyretica*** (Figure 12) suffers greater UV damage, but the aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) does not seem to respond differentially to temperature under UV stress (Núñez-Olivera *et al*. 2004). There also seems to be a direct relationship between UV tolerance and desiccation tolerance (Martínez-Abaigar & Núñez-Olivera 2011). This seems to be particularly true for ***Fontinalis antipyretica*** as it is among the most sensitive to both.

Figure 69. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, an aquatic species that seems to be indifferent to temperature under UV stress. Photo by Jan-Peter Frahm, with permission.

Some early studies recognized that UV light could damage sporelings. Kinugawa (1966) explored the damage and dark recovery in sporelings of ***Bryum pseudotriquetrum*** (Figure 67). Arróniz-Crespo *et al.* (2008b) found age-specific physiological responses to UV radiation in ***Jungermannia exsertifolia*** subsp. ***cordifolia***, an aquatic leafy liverwort. In the presence of enhanced UV radiation, some coumarin compounds only accumulated in older tissues (C3), whereas others were only in younger tissues (C4). The newly grown shoots showed the highest concentrations of chlorophylls, carotenoids, MEUVACs, and C4 in response to elevated UV.

Rader and Belish (1997) transplanted ***Fontinalis neomexicana*** (Figure 70) in a 10-week field experiment in a mountain stream to determine the effects of higher UV-B radiation. They irradiated transplants from shaded and sun-exposed sites and found that those from the open site exhibited an "important reduction" in dry biomass. On the other hand, those from the shaded site showed no effect on biomass. But they failed to show any net growth, and all samples lost material in these natural settings.

By contrast, Núñez-Olivera *et al.* (2005) demonstrated that previous light acclimation influenced degree of damage by enhanced UV radiation, with shade samples showing more effect than sun samples. This apparent protection of sun-adapted plants was evident in the sensitive ***Fontinalis antipyretica*** (Figure 12), but not in the UV-tolerant ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69). As further evidence of acclimation, Martínez-Abaigar *et al.* (2009) collected the same species from high altitudes and lower altitudes, finding that those from high altitudes (with greater UV radiation) were more tolerant of UV radiation.

Figure 70. ***Fontinalis neomexicana***, a species in which sun-adapted populations can have a reduction in biomass accumulation when transplanted to the shade. Photo by Belinda Lo, through Creative Commons.

Martínez-Abaigar *et al.* (2003) considered the responses of ***Fontinalis antipyretica*** (Figure 12) and the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) to elevated ultraviolet-B radiation. The responses were different between these two species. There was little response to UV-A radiation. With increased UV-B, ***Fontinalis antipyretica*** exhibited decreased chlorophyll and carotenoid concentration, chlorophyll *a*:*b* ratio, chlorophyll:phaeopigment ratio, net photosynthetic rate, light saturation point, maximum quantum yield of PS II, and apparent electron transport rate. Dark respiration increased, as did the **sclerophylly index** (ratio between dry mass and surface area of bryophyte shoot; see Montefort *et al.* 2018). But ***Jungermannia exsertifolia*** subsp. ***cordifolia*** showed only a reduction in **Fv/Fm** (measurement ratio that represents maximum potential quantum efficiency of Photosystem II if all capable reaction centers are open) and an increase in pigmentation. The production of UV-B-absorbing compounds (pigments) had rarely been reported in bryophytes when Martínez-Abaigar *et al.* (2003) conducted this study, particularly aquatic ones. Based on these response differences, the researchers warned against treating all bryophytes as one functional group, as has often been done in ecology.

In their study of bryophytes in mountain streams, Arróniz-Crespo *et al.* (2004) found differences among the species. They furthermore differed between 9 of the 10 mosses and the 4 liverworts in this study. Liverworts presented high levels of methanol-extractable UV-absorbing compounds, whereas these were low in all mosses except for ***Polytrichum commune*** (Figure 59-Figure 60). As noted by Crespo (2006), possible defense mechanisms have been characterized as both **constitutive** (always present) and **induced** (made present in response to a stimulus), differing greatly between mosses and liverworts.

Sun and Shade Plants

Núñez-Olivera and coworkers (Núñez-Olivera *et al.* 2005; Arróniz-Crespo *et al.* 2005) studied responses of the moss ***Fontinalis antipyretica*** (Figure 12) and the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) to elevated UV-B, this time using sun- and shade-acclimated samples of each. Both sun and shade samples of ***Fontinalis antipyretica*** proved to be more sensitive than the liverwort following 78 hours of acclimation at 2ºC. Responses were similar to those of longer exposures (36-82 days). Shade samples were more sensitive only in ***Fontinalis antipyretica***, indicating some degree of acclimation in that species. For this species, Fv/Fm decreased 42% in the shade samples and only 27% in the sun samples at the end of the culture period. Neither sun nor shade samples of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** demonstrated significant differences between controls and UV-B-treated samples.

Soriano *et al*. (2019) assessed sun and shade adaptations and acclimation of stream bryophytes. These included ***Marchantia polymorpha*** subsp. ***polymorpha*** (Figure 55), ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69), and ***Fontinalis antipyretica*** (Figure 12). Of these, the two liverworts were more responsive to the radiation than the moss ***F. antipyretica***. Compared to shade plants of ***M. polymorpha***, they noted many changes in sun plants:

higher **sclerophylly** (condition of thicker or firmer leaves, *i.e.* thallus)
lower Chl *a* + *b* contents
higher Chl *a*/*b* ratios
higher ratios of (antheraxanthin + zeaxanthin): (violaxathin+ antheraxanthin + zeaxanthin)
lower Fv/Fm values
higher contents of methanol-soluble vacuolar UV-absorbing compounds (soluble UVACs)
higher values of ratio between contents of methanol-insoluble cell wall-bound UVACs and soluble UVACs
higher contents of insoluble *p*-coumaric and ferulic acids.

These responses reduced the light absorption, alleviated overexcitation, increased photoprotection by non-photochemical energy dissipation, provided UV screening and antioxidant capacity that increased UV protection, and resulted in photoinhibition. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** exhibited moderate differences between sun and shade populations, whereas those in ***F. antipyretica*** were indistinct. The response of the **xanthophyll index** (antheraxanthin + zeaxanthin):(violaxathin+ antheraxanthin + zeaxanthin) was the most consistent response.

Photoprotective Pigments

Several researchers have reported photoprotective pigmentation in aquatic bryophytes grown in high light situations. Glime (1984) discovered red ***Fontinalis antipyretica*** (Figure 12) growing in cold water in full sunlight. These same leaves also had less chlorophyll than those grown in the shade. They exhibited greater specific leaf weight and less specific leaf area than the typical shade leaves. Nevertheless, there was no significant difference in the chlorophyll *a*:*b* ratio between the sun-acclimated and shade leaves.

López and Carballeira (1989) compared five species of aquatic bryophytes [***Fontinalis antipyretica*** (Figure 12), ***Brachythecium rivulare*** (Figure 61), ***Fissidens polyphyllus*** (Figure 62), ***Platyhypnidium riparioides*** (Figure 10), and the leafy liverwort ***Scapania undulata*** (Figure 8)] and their responses to stresses. The five species had higher chlorophyll concentrations than "some" terrestrial bryophytes. The stresses of organic and metal pollution were effective at changing the pigment ratios. They found that ***F. antipyretica*** was the most resistant species; ***S. undulata*** was the most sensitive. But what effects do these pigment changes have on the ability of these bryophytes to tolerate UV-B radiation and even high intensity PAR?

Martínez-Abaigar and Olivera (2007) noted that climate change and increasing UV-B could affect stream bryophytes. ***Fontinalis antipyretica*** (Figure 12) is sensitive and may be more sensitive when receiving enhanced UV-B at low temperatures. Shade plants of this species are more sensitive than sun plants. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) is relatively UV-B tolerant. Two of the five UV-B absorbing compounds in this species increase with altitude from 110-1800 m asl. At 2000 m asl these liverworts have a high UV-B absorption, whereas the ***F. antipyretica*** has low absorbance. When Martínez-Abaigar *et al*. (2003) compared a liverwort and a moss, the leafy liverwort ***Jungermannia exsertifolia*** experienced only a decrease in Fv/Fm, suggesting that this ratio and the concentration of UV-absorbing compounds were the most responsive indicators. These two responses can explain the greater tolerance of ***J. exsertifolia*** to enhanced UV light. The liverworts such as ***Jungermannia exsertifolia*** subsp. ***cordifolia*** appear to have higher concentrations of both constitutive and inducible methanol-extractable UV-absorbing compounds than do mosses (Martínez-Abaigar & Núñez-Olivera 2011).

Martínez-Abaigar and coworkers (Martínez-Abaigar *et al*. 2004a, 2006; Martínez-Abaigar & Núñez-Olivera 2011) found that in mountain streams the effects of UV-B exposure depended on the bryophyte species, environmental factors such as temperature, and location (sun or shade, low or high altitude). The liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) was a good bio-indicator of the light conditions. Variables such as Fv/Fm, concentrations of individual UV-absorbing compounds, and DNA damage were indicative of UV-B growing conditions. The most consistent indicators of damage by UV-B seem to be decreases in Fv/Fm, chlorophyll:phaeophyton, and of lesser importance decreases in chl *a*/*b* and net photosynthesis (Martínez-Abaigar & Núñez-Olivera 2011).

There is a natural gradient of increasing UV-B radiation as one ascends to higher altitudes. Arróniz-Crespo *et al*. (2006) explored this natural relationship at elevations ranging from 1140 to 1816 m altitude. In ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69), they found two new caffeic acid derivatives: 5"(7"8"dihydroxycoumaroyl)-2-caffeoylmalic acid & 5"'-(7"8"dihydroxy-7-O-beta-glucosyl-coumaroyl)-2-caffeoylmalic acid. In addition, they found phaselic acid (both in cis- & trans- forms) and feruloylmalic acid. These showed a significant linear relationship with altitude. The two new compounds, maximal apparent electron transport rate through PS II, and maximal non-photochemical quenching all increased with altitude. At the same time, the photoinhibition percentage decreased. The researchers suggested that this increase in some of these secondary compounds may permit the tolerance of this liverwort to the UV-B irradiance at high elevations

Arróniz-Crespo *et al*. (2008a) further explored the possible substances that provided protection from enhanced UV radiation. After exposure to enhanced UV radiation for 82 days, they examined five hydroxycinnamic acid derivatives. They reasoned that in its high mountain habitat with high UV radiation and low temperatures, it must have something to protect it. In particular, it showed little damage to the Fv/Fm ratio or chlorophyll:phaeopigment ratio in response to elevated UV radiation. They attributed this stability to the presence of three hydroxycinnamic acid derivatives: p-coumaroylmalic acid, 5"-(7",8"-dihydroxycoumaroyl)-2-caffeoylmalic acid, and 5"-(7",8"-dihydroxy-7-O-ß-glucosyl-coumaroyl)-2-caffeoylmalic acid. These are apparently induced in the liverwort by exposure to UV radiation.

In a laboratory experiment, Martínez-Abaigar *et al*. (2009) cultured three leafy liverworts [***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69), ***Marsupella sphacelata*** (Figure 71), ***Scapania undulata*** (Figure 8)] and three mosses [***Brachythecium rivulare*** (Figure 61), ***Bryum pseudotriquetrum*** (Figure 67), ***Racomitrium aciculare*** (Figure 72)] under enhanced UV-B radiation (10.3 kJ m^{-2}) as would be expected with a 20% ozone depletion. After 20 days of culture, they found that the culture conditions had a greater influence than did the enhanced UV radiation. Responses to both factors depended on the species and the variable considered. Both photosynthetic pigments and photosynthetic performance were negatively affected by the culture conditions, but only in ***Marsupella sphacelata*** was growth impeded. Enhanced UV-B, on the other hand, did not affect photosynthetic performance, but did affect growth in ***Jungermannia exsertifolia*** subsp. ***cordifolia***. There was rarely any increase in UV-protective compounds under this level of UV-B. These species had been collected at high altitudes (1850-2000 m asl) and were most likely already acclimated to high UV-B levels. This study supports previous studies in indicating that the location and collection date are important in acclimation to UV-B.

Otero *et al*. (2009) analyzed 135 herbarium samples of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) from northern Europe for UV absorbance in methanolic extracts. They also analyzed five specific hydroxycinnamic acid derivatives – UV-absorbing compounds. This demonstrated that the UV absorbance and compound levels showed a positive correlation with year during the sampling period of 1850-2006. *p*-coumaroylmalic acid (C1) was the only compound showing a significant (and negative) correlation with the stratospheric ozone and UV irradiance for the period of available data. Most specimens were from July-August, but the highest stratospheric ozone occurred in June. Nevertheless, there was no long-term temporal trend. UV values were higher in June-July than in August. In short, levels of *p*-coumarolymalic acid did not suggest any significant temporal trend during the study periods for which data were available.

Figure 71. ***Marsupella sphacelata***, a species for which growth was impeded by enhanced UV-B radiation. Photo by Hermann Schachner, through Creative Commons.

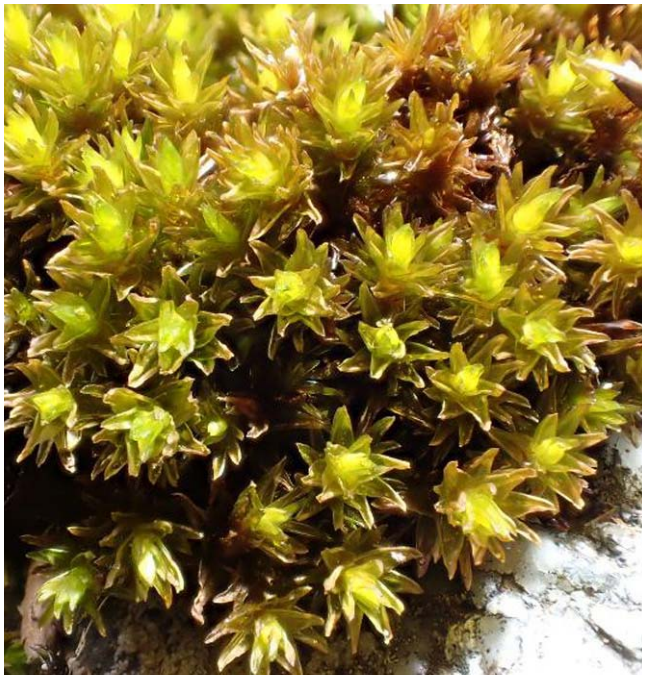

Figure 72. ***Racomitrium aciculare***, a species that responded more to culture conditions than to UV-B radiation enhancement. Photo by Hugues Tinguy, with permission.

In the Tierra del Fuego of Argentina, the high elevation means that UV-B is higher than in other aquatic habitats. After analyzing five liverworts and ten mosses from unshaded aquatic bryophytes, Otero *et al*. (2008) concluded, as had others mentioned here, that species differed. Spectral peaks ranged from none to 2 defined peaks, probably due to phenolic derivatives that could serve as both screening compounds and antioxidants. The absorbance curves of most liverworts were higher than those of most mosses. The liverworts ***Noteroclada***

confluens (Figure 73) and ***Triandrophyllum subtrifidum*** (Figure 74), in particular, showed higher bulk UV-absorption capacity in methanolic extracts. They concluded that while the accumulation of UV-absorbing compounds commonly protects liverworts against UV radiation, that rarely occurs in mosses.

Figure 73. ***Noteroclada confluens*** with antheridia, a species with higher UV-absorption capacity than that found in mosses. Photo by Li Zhang, with permission.

Figure 74. ***Triandrophyllum subtrifidum***, a species with higher UV-absorption capacity than that found in mosses. Photo by Shirley Kerr, with permission.

Cell Wall vs Soluble Compounds

Fabón *et al.* (2010) examined the cell compartments where hydroxycinnamic acid derivatives reside in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) as a response to elevated UV-B. The bulk UV absorbance of the soluble fraction was higher than that of the cell-wall-bound fraction. Absorbances by both fractions increased under elevated UV-B. Five different hydroxycinnamic acid derivatives were located in the soluble fraction, with two additional ones in the cell-wall-bound fraction, but only p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell-wall-bound fraction increased in response to elevated UV-B. Both maximum quantum yield of PS II and DNA were damaged more strongly when the UV-B was elevated. The researchers concluded that the soluble and cell-wall-bound fractions responded differently as protective mechanisms.

Fabón *et al.* (2012) found that **diel** (within 24 hours) differences existed in both the soluble and cell-wall fractions of UV-absorbing compounds in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69). They were able to respond within a few hours to radiation changes. Furthermore, components of the xanthophyll cycle made rapid and significant diel changes in response to high PAR, UV-A, and UV-B radiation. This causes dynamic photoinhibition responses and protection of PS II.

Soriano *et al.* (2019) concluded that the responses of aquatic bryophytes were influenced by both the **PAR** (photosynthetically active radiation) and UV radiation. They found that soluble UV-absorbing compounds (UVACs) generally had clearer responses than did the insoluble UVACs. They attributed this to the fact that insoluble UVACs are relatively immobilized in the cell wall. Under conditions close to ambient, sclerophylly and Chl $a + b$ content were influenced only by PAR and Fv/Fm. Luteolin and apigenin derivatives were determined by UV. The xanthophyll index was influenced by both types of radiation.

Montefort *et al.* (2018) found that mosses had lower levels of mainly vacuolar soluble UV-absorbing compounds (UVACs) but higher cell-wall-bound insoluble UVACs when compared to liverworts. This suggests that mosses should have greater tolerance of UV radiations, explaining their greater frequency in areas with high levels of UV radiation. Nevertheless, the relationships between UVACs and the ecological parameters they considered were weak. From this they concluded that UVACs might be primarily constitutive in bryophytes, *i.e.* depending on phylogeny more than on habitat. Nevertheless, water restrictions and high sun exposures increased sclerophylly, suggesting a physiological response.

UV Interactions

Martínez-Abaigar and Núñez-Olivera (2011) suggested that we might expect increased UV damage when heavy metals add to the stress. They were able to demonstrate this with cadmium and UV radiation in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69), with both causing loss of chlorophyll, strong inhibition of PS II, and an increase in the xanthophyll index, with greater effects under combined treatment. Cadmium affected the photosynthetic rate, but enhanced UV radiation did not. Both treatments increased the concentrations of UV-absorbing compounds.

When UV stress is combined with other stress factors, it becomes even a greater stressing agent. After 15 days of cultivation of the aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69), Otero *et al.* (2006) found that both cadmium and enhanced UV radiation caused the degradation of chlorophyll and a decrease in the maximum quantum yield of PS II, while resulting in an increase in the mechanisms of non-photochemical dissipation of energy (increase in the xanthophyll index). Cadmium proved to be more stressing than did enhanced UV radiation. The increased UV radiation caused the level of trans-*p*-courmaroylmalic acid to increase, whereas cadmium caused an increase in trans-phaselic and feruloylmalic acids. Furthermore, UV-B radiation caused DNA damage, but this was intensified in the presence of cadmium. Cadmium and other metals impair the DNA enzymatic repair mechanisms.

Photoinhibition

Maberly (1985) found no evidence of photoinhibition at 7 levels of photon irradiance and 5-6 CO_2 concentrations in ***Fontinalis antipyretica*** (Figure 12) during four months at ambient temperature. The light compensation point for these populations was generally lower than most published values. He noted the importance of the interaction between light intensity, CO_2 concentration, and temperature on the levels of net photosynthesis. Effects of increased light levels is dependent on availability of CO_2 and loss of carbon through photorespiration as the temperature rises.

On the other hand, Rader and Belish (1997) concluded that photoinhibition increases under 15-40% UV-B increase and may be harmful to aquatic mosses such as ***Fontinalis neomexicana*** (Figure 70). This species had no effects by increased UV-B in the shade (biomass 28.47 mg cm^{-2}), but in the open it produced lower biomass (19.57 mg cm^{-2}). Subsequently, Soriano *et al.* (2019) similarly indicated that photoinhibition can occur in aquatic bryophytes.

It appears that photoinhibition can even affect nitrification in streams, as noted in bryophyte enclosures of non-acidified streams in the alpine zone of the High Tatra Mountains along the border of northern Slovakia in the Prešov Region and southern Poland in the Lesser Poland Voivodeship (Kopacek & Blazka 1994).

Effects of Nutritional Status

The ability of plants to make various compounds depends on their nutritional status. Martínez-Abaigar *et al.* (2008) improved the phosphorus availability to the liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 69) and the moss ***Fontinalis antipyretica*** (Figure 12) to determine effects on several UV responses in lab experiments. After 36 days there were no differences between bryophytes in the P-enhanced and normal P conditions for any of the measured UV response factors, except for the vitality index OD430/OD410 in ***J. exsertifolia***. These bryophytes have low nutritional requirements, so it is likely that the additional P was not needed, particularly in the absence of any other nutrient additions.

Although the addition of phosphorus, typically a limiting nutrient in streams, helps to protect some microalgae, this has not been observed in aquatic bryophytes (Martínez-Abaigar & Núñez-Olivera 2011). In two bryophytes from mountain streams, an increase of P 1.7- to 3.7-fold did not alter the responses to enhanced UV radiation (Martínez-Abaigar *et al.* 2008). It might be instructive to test the same enhancement of P on lower elevation aquatic bryophytes that did not have any natural acclimation to UV radiation.

Temperature

Our field experience tells us that temperature can be a limiting factor for bryophytes, including those in streams. Ewart (1895-1897) contended that the ability to withstand temperature extremes is directly related to the moisture content of the plants. But studies that examine other effects on photosynthesis and growth in bryophytes are rare.

We have seen in subchapter 2-4 of this volume that temperature governs periods of growth and rhizoid production in species of ***Fontinalis***. Maberly (1985) noted that the slope of photosynthesis vs CO_2 concentration increased linearly as temperature increased, an observation that is consistent with the effects of boundary-layer resistance.

High Temperatures

Bryophytes in the water seem to be particularly susceptible to high temperatures. They are hydrated and thus are able to respire. But they are C_3 plants and as the temperature goes up, so does the photosynthetic product, but also so does the respiratory rate, only faster. Irmscher (1912) cultured many mosses at various temperatures and found that ***Fontinalis antipyretica*** (Figure 12) and ***F. squamosa*** (Figure 1) were still alive at 20ºC, but at 30ºC ***F. antipyretica*** was dead. ***Drepanocladus aduncus*** (Figure 19), a species that occurs in shallow water of lakes, pools, ditches, and fens, did not fare any better at these two temperatures. But the ***Fontinalis*** did not fare well at -15ºC, with both species dying in both submersed and turgescent conditions; at -10ºC, ***F. antipyretica*** survived.

My experience in the tropics is limited, but in the lowland forest streams there we would expect the combination of low light and high temperatures to cause respiration to exceed photosynthesis (Vitt & Glime 1984; Glime & Gradstein 2018). On the other hand, in higher elevations in the tropics, temperatures remain cool enough for a number of species to survive.

Carballeira *et al.* (1998) subjected ***Fontinalis antipyretica*** (Figure 12) to temperatures ranging 16ºC-34ºC. They found responses (pigment ratio, photosynthetic and respiratory rates) did not differ between mosses collected from a "normal" river and one subjected to abnormally high temperatures resulting from hotspring waters. They also subjected mosses to 30ºC for 2, 4, and 10 days, then transferred them to 16ºC for 40 days. Even those held at 30ºC for 10 days exhibited good recovery.

Nevertheless, Ceschin *et al.* (2012) found that few aquatic bryophyte species prefer higher temperatures. ***Hygroamblystegium fluviatile*** (Figure 75) and ***Leptodictyum riparium*** (Figure 64) exhibited temperature optima of 18ºC and above. Other species exhibited temperature preferences below 12ºC, including ***Palustriella commutata*** var. ***commutata*** (Figure 37), ***Cratoneuron filicinum*** (Figure 41), ***Fissidens viridulus*** (Figure 76), and ***Cinclidotus aquaticus*** (Figure 34).

Figure 75. ***Hygroamblystegium fluviatile***, a species with a high temperature optimum (18ºC) compared to other aquatic mosses. Photo by Michael Lüth, with permission.

Figure 76. ***Fissidens viridulus***, a species that prefers temperatures below 12ºC. Photo by Jan-Peter Frahm, with permission.

Sanford (1979) found that ***Leptodictyum riparium*** (Figure 64) exhibited branch proliferation under high temperature stress. This ability to produce new branches decreased later in the experiments. The apices of branches and the main axis seemed to be the most heat-resistant parts of this species. Glime and Carr (1974) found a similar resistance in the apices of ***Fontinalis*** in New Hampshire, USA (Figure 77). They were able to demonstrate this in ***Fontinalis*** species that were boiled for 12 hours per day for two weeks. The mosses were returned to their native stream and one stem produced a green leaf within the next year. All other leaves were dead or gone.

Figure 77. Labelled rocks with ***Fontinalis*** spp. from the Glime and Carr 1974 temperature experiment. Photo by Janice Glime.

Sanford *et al.* (1974) observed growth of ***Hygrohypnum ochraceum*** (Figure 23) in relation to temperature in the Sacramento River. When temperatures were above 26ºC, some of the stem tips died. After four weeks at 30ºC all plants died. The temperature optimum for growth ranged ~17-21ºC. Sanford (1979) found that ***Leptodictyum riparium*** (Figure 64) had its optimum growth at 23ºC, with death occurring at 33ºC.

Not surprisingly, species differ in their response to temperature. Arscott *et al.* (2000) found that ***Schistidium agassizii*** (Figure 21) could persist in the Kuparuk River, Alaska, with cold, low-nutrient conditions, but ***Hygrohypnum alpestre*** (Figure 22) and ***H. ochraceum*** (Figure 23) could not. In fact, the ***Hygrohypnum*** species were able to take advantage of the elevated light and temperatures (>20ºC) with greater net primary production. On the other hand, these two species were more affected by desiccation than was ***S. agassizii***.

Bryophytes are C_3 plants. This means that they have a low temperature compensation point and high levels of photorespiration as the temperature increases. Carballeira *et al.* (1998) found that ***Fontinalis antipyretica*** (Figure 12) did not exhibit any difference in physiological response to temperature between populations from a normal river and one with abnormally high temperatures. In fact, after exposure to temperatures of 30ºC for up to 10 days, these mosses showed good recovery after 40 days at 16ºC.

Elevated temperatures can change the absorption rate for substances in the water. Martins *et al.* (2004) found that some metal elements increase in their absorption, but others do not. For example, maximum biosorption capacity for cadmium by ***Fontinalis antipyretica*** (Figure 12) did not change with elevated temperatures, but for zinc the capacity increased with temperature from 11.5 mg g^{-1} at 5ºC to 14.7 mg g^{-1} at 30ºC.

Bryophytes are able to acclimate to temperatures through heat hardening. Temperatures above the optimum can increase their thermal resistance, as has been noted in flowering plants (Antropova 1974). For example, the wetland emergent ***Sarmentypnum sarmentosum*** (Figure 78) shifts its optimum temperature from 19ºC in July to 11ºC in August to 16ºC in September (Oechel 1976). This change seems to correspond to moisture availability. Vitt and Pakarinen (1977) likewise found moisture to be of major importance to emergent mosses in the High Arctic.

Figure 78. ***Sarmentypnum sarmentosum***, a wetland species that has seasonal changes in its optimum temperature. Photo by David T. Holyoak, with permission.

Low Temperatures

Limiting factors in streams are different from those on land and even some in lakes and ponds. And winter temperatures in temperate and arctic streams can be more severe while open water remains in a partially frozen stream. Our data from New Hampshire streams indicated the temperature of flowing water in one such partially frozen stream remained at 0.8-1.0ºC throughout the winter.

Temperature is an important stimulant in the production of pigments (Martínez-Abaigar & Núñez-Olivera 2018). Cold temperatures can cause the formation of red pigments, particularly in high light, as discussed above (Glime 1984). Presumably this protects the chlorophyll from high excitation when the temperature slows the physiological protections against photodamage.

Cold temperatures are not usually a problem in streams because the streams typically do not freeze to the bottom. And even if the mosses are frozen in ice, the ice and snow on top of the ice insulate them from lower temperatures. Growth can even occur at low temperatures. Sanford *et al.* (1974) found that in the Sacramento River, ***Hygrohypnum ochraceum*** (Figure 23) experienced growth at temperatures as low as 4ºC.

Dilks and Proctor (1975) also demonstrated the ability of the bryophytes to withstand sudden cold temperatures. Most of the tested species survived rapid cooling to -5ºC for 6 hours. They seem to be protected from intracellular freezing under normal cooling processes by withdrawal of water, most likely by extracellular ice crystals, much like events causing freezer burn in a deep freeze. But in the case of the bryophytes, this withdrawal prevents formation of ice crystals within the cells, thus preventing damage to the cell membranes and organelles. When temperatures warm, the water again enters the cells of the bryophytes and they return to normal activity unharmed. This is more easily accomplished when all leaf cells contact the atmosphere than in the multi-layered leaves of tracheophytes. On the other hand, the stream bank bryophytes ***Conocephalum conicum*** (Figure 35) and ***Pellia epiphylla*** (Figure 66) were killed by rapid cooling to -5ºC.

Fissidens fontanus (Figure 79) was killed when frozen in ice at -5ºC, but was able to maintain luxurious growth where it lived on rocks exposed to sub-zero temperatures above water (Lohammar 1954). Lohammar suggested that the basal portion was more resistant, thus permitting the above-water plants to survive. ***Fissidens crassipes*** (Figure 80) spread when the temperature of the Rhine was elevated 2ºC by industrial waste, eliminating most of the ice drift and revealing another cause of winter loss – destruction by ice flow (Florschütz *et al.* 1972).

Freezing can kill emergent mosses such as ***Drepanocladus*** cf. ***aduncus*** (Figure 19) and ***Sarmentypnum sarmentosum*** (Figure 78) (Priddle 1979). But they did survive in an Antarctic lake that did not freeze where they were growing. On the other hand, ***Fontinalis antipyretica*** (Figure 12) and ***Drepanocladus aduncus*** survived to -10ºC, whereas when turgescent these mosses died at that temperature, as did most of the terrestrial bryophyte species.

Figure 79. ***Fissidens fontanus***, a species that died at -5ºC in ice but survived and grew at even lower temperatures in air. Photo by Walter Lampa, through Creative Commons.

Figure 80. ***Fissidens crassipes*** with capsules, a species that spread when the temperature rose by 2ºC in the Rhine. Photo by Michael Lüth, with permission.

Optimum Temperatures

Dilks and Proctor (1975) used manometry to compare assimilation of bryophytes, including the aquatic species ***Fontinalis squamosa*** (Figure 1) and ***Nardia compressa*** (Figure 81), at various temperatures. In these experiments, the carbon dioxide concentrations were high, permitting the optimum temperature for net assimilation to occur at ~25-30ºC. The temperature compensation point occurred at ~35-40ºC. Unlike most of the terrestrial bryophytes, the aquatic moss ***Fontinalis squamosa*** had its optimum oxygen production (measure of photosynthesis) at 15-20ºC. The aquatic leafy liverwort ***Nardia compressa*** had its maximum photosynthesis at 20ºC.

Figure 81. ***Nardia compressa***, a leafy liverwort that can have its maximum photosynthesis at 20ºC. Photo by Hermann Schachner, through Creative Commons.

Other similar temperature optima have been reported in aquatic species. Zastrow (1934) found the optimum for wetland species in his study to be 15-20ºC. Saitoh *et al.* (1970) similarly found 20ºC to be the optimum for ***Fontinalis hypnoides*** (Figure 82). But the Keweenaw Peninsula, Michigan, populations of six species of ***Fontinalis*** indicated that these species could not sustain growth at temperatures above 15ºC for a long time. In fact, some [***F. neomexicana*** (Figure 70) and ***F. dalecarlica*** (Figure 5)] had maximum growth at 10ºC (Glime & Acton 1979; Glime 1982). The wetland species ***Sarmentypnum sarmentosum*** (Figure 78) can spend 10 months of the year experiencing temperatures above its low temperature compensation point due primarily to a very low respiration rate at low temperatures (Priddle 1982). On the other hand, the aquatic ***Racomitrium aquaticum*** (Figure 45) requires 64 days at 37ºC to experience 50% chlorophyll loss. At 20º it requires 200 days, whereas in the terrestrial ***R. lanuginosum*** (Figure 46) it requires 400 days.

Figure 82. ***Fontinalis hypnoides***, a species that can reach an optimum at temperatures as high as 20ºC. Photo by Jean Faubert, with permission.

Using manometry, Glime and Acton (1979) cultured ***Fontinalis duriaei*** (Figure 83) from Houghton County, Michigan, USA, with its associated periphyton at five temperatures from 1 to 20ºC and at 3 light levels (2400, 5400, 10,800 lux). At the mid light level, this population experienced its peak assimilation at 10ºC, a combination that would typically occur in its native stream shortly after snow melt and again in the autumn, the two periods when this population experiences its greatest growth in nature. The level of 5400 lux was indicated as the level of **light saturation** (light level where increasing the light does not increase photosynthetic rate) under the CO_2 conditions of the experiments. Further experiments are needed in which CO_2 gas is bubbled into the containers during measurement to avoid depletion.

Fontinalis antipyretica (Figure 12) and ***Leptodictyum riparium*** (Figure 64) in culture showed contrasting growth optima of 10ºC and 23ºC, respectively (Glime 1982), but in the study by Vanderpoorten *et al.* (1999) both species had similar broad ranges. In separate studies, Glime and Acton (1979) and Fornwall and Glime (1982) demonstrated acclimation to the temperature in species of ***Fontinalis***, as well as geographic differences, which could account for the differences observed by Vanderpoorten and coworkers.

Figure 83. ***Fontinalis duriaei***, a species that at 5400 lux experiences its peak assimilation at 10ºC. Photo by Michael Lüth, with permission.

Crombie and Paton (1958) found that temperature can affect seta elongation in liverworts. They found that if older sporophytes of the stream bank ***Pellia epiphylla*** (Figure 66) are left in the field until January or February, they will respond more rapidly to a temperature stimulus than those collected in early autumn. This could occur as a result of slow accumulation of growth hormones stimulated by temperature and/or light. Possible substances include IAA (Asprey *et al.* 1958), gibberellins (Brian & Hemming 1958), and 2,4-dichlorophenoxyacetic acid (Benson-Evans 1961).

While there are a number of experimental studies on the effects of temperature, the physiological responses outside photosynthesis and growth remain largely undocumented. My own experience suggests that at high temperatures the mosses lose color, suggesting chlorophyll damage. A secondary problem is that the higher temperatures can favor the growth of bacteria and algae, thus blocking light.

Bryophyte Antifreeze

Investigations on the fatty acid content of mosses indicate high levels of C_{22} acids, but low levels of C_{18} fatty acids that are typical of xerophytic mosses (Anderson *et al.* 1974). ***Fontinalis antipyretica*** (Figure 12) has the angiospermous type of fatty acids and the lowest concentration of algal fatty acids of any bryophyte tested (Karunen 1982). But the emergent ***Drepanocladus*** *s.l.* (Figure 19) was in the middle and ***Calliergon*** (Figure 51) had algal fatty acids. ***Fontinalis*** has the arachidonic acid prostaglandin (Asakawa, pers. comm.), a fatty acid known to be important in keeping footpads pliable in Arctic rodents (Prins 1981). Could these arachidonic acids help the aquatic bryophytes to survive at low temperatures?

Temperature Effects on Absorption

As we should expect, temperature affects absorption rate. But these effects on heavy metals are not all the same. In ***Fontinalis antipyretica*** (Figure 4), temperature had little or no effect on the absorption rate of cadmium, whereas zinc absorption increased with temperature from 11.5 mg g^{-1} moss at 5ºC to 14.7 mg g^{-1} moss at 30ºC (Martins *et al.* 2004). These temperature relationships will be discussed further in subchapter 2-7 of this volume.

Summary

Bryophyte lineages have been back and forth between land and water. This has provided them with a genetic background that gives rise to a variety of physiological adaptations. This is beneficial in permitting them to live where seasonal water level changes occur. Even the aquatic moss ***Fontinalis*** is able to survive in a dry stream for several months. When water returns, leaf and plant fragments can be dispersed and develop new plants. Stems, in particular, are highly resistant and can produce protonemata or rhizoids and branches.

When aquatic mosses are stranded out of water, they become pale, with less chlorophyll, but develop more chloroplasts. Chlorophyll *a* is damaged more than chlorophyll *b*. More chlorophyll is lost at higher temperatures. Damage to cellular membranes causes electrolyte leakage, especially potassium, as well as carbohydrates, amino acids, and other organic compounds. Some of these are reabsorbed upon rewetting. More sugar and less protein are produced during dehydration; the reverse is true during rehydration. Irreversible loss of polyribosomes occurs during dehydration. Amphibious species may develop denser tissues and more denticulations out of water. Heterophylly resulting from submersion vs emersion does not seem to occur in bryophytes, but experimentation is needed. Growth forms must balance light capture with water retention and drag reduction. Changes in allocation can result from changes in water availability.

Slow drying is important in survival; growth form can slow the rate. But amount of water lost seems to have the greatest effect on membrane integrity and photosynthesis. In a natural stream, where drying is usually slow, it can take 1-4 weeks to cause cellular damage. Emergent mosses take longer. There is a peak in photosynthesis during the initial phase of water loss. Photosynthetic efficiency is important in rate of recovery. The respiratory burst upon rewetting is shorter in wet-adapted species.

Truly aquatic species seem to have less desiccation tolerance, but laboratory studies must be viewed with caution because of the rapid rate of drying in most. Nevertheless, some aquatic species have pectic substances in the cell walls that permit rapid water intake, especially in the stems. Gibberellic acid, ethylene, and abscisic acid should be explored for their role in adaptations to immersion-emersion.

High light levels during emersion can stimulate production of colored pigments, especially red. Pigments in bryophytes are mostly the same as those in tracheophytes. Low light levels cause bryophytes to have more chlorophyll *b* and lower *a*:*b* ratios. Pigment concentrations change seasonally and track opening and closing of the canopy and periods of desiccation. Osmotic values seem to be correlated with light intensity, but not with moisture.

Increased UV-B causes a decrease in chlorophyll and carotenoid concentration, chlorophyll *a*:*b* ratio, chlorophyll:phaeopigment ratio, net photosynthetic rate, light saturation point, maximum quantum yield of PS II, and apparent electron transport rate, with an increase in protective pigmentation and a higher xanthophyll index. Defense mechanisms are both constitutive and induced. Acclimation occurs to some degree. Many liverworts seem to produce higher levels of methanol-extractable UV-absorbing compounds compared to most mosses. Hydroxycinnamic acid derivatives seem to be among the protective substances. Mosses tend to put more protective compounds in the cell walls, whereas the liverworts put them within the cells.

Enhanced UV-B can affect growth without affecting photosynthetic performance. Photoinhibition can increase. Negative effects of UV can increase when coupled with heavy metals. Nutrient levels often do not affect the response to UV-B, perhaps because of the slow growth and low needs for nutrients.

Most aquatic bryophytes prefer cooler temperatures, but optimum temperatures range 10º-30ºC. Nevertheless, they have good recovery after short periods of temperatures of 30ºC. And they are able to acclimate their photosynthetic rate. Freezing can kill emergent mosses. Temperature affects absorption rates of different nutrients and heavy metals differently. Higher temperatures can cause chlorophyll damage and invasion of periphytic bacteria and algae that block light. Fatty acids, especially arachidonic acid, may keep membranes pliable and protect the bryophytes from membrane damage at cold temperatures.

When light levels are low and temperatures high, respiration exceeds photosynthesis. There is an interaction between light intensity, CO_2 concentration, and temperature on the rate of net photosynthesis.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. Thank you to Josep Peñuelas for sending me the paper on the evolution of sclerophylly. Maria Arróniz-Crespo provided me with a needed paper. Javier Martínez-Abaigar has provided with many of the papers from his lab regarding UV-B radiation and pigmentation.

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CHAPTER 2-7

STREAMS: PHYSIOLOGICAL ADAPTATIONS – NUTRIENTS, PHOTOSYNTHESIS, AND OTHERS

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STREAMS: PHYSIOLOGICAL ADAPTATIONS – NUTRIENTS, PHOTOSYNTHESIS, AND OTHERS

Figure 1. ***Hygrohypnum alpestre*** showing bubbles produced by photosynthesis, a condition called **pearling**. Photo by Michael Lüth, with permission.

Nutrient Relations

Richards (1959) commented that "The mineral economy of bryophytes is a subject on which so little is known that a connected discussion is hardly possible." Whereas this statement is still largely true for terrestrial bryophytes, the effects of pollutants, including those that serve as nutrients, on stream bryophytes has received considerable attention. Hence, we do know a reasonable amount about the nutritional relations of stream bryophytes.

Many early studies on plants included the large aquatic moss ***Fontinalis antipyretica*** (Figure 2). Boresch (1919) examined the entry and emulsifying effect of various substances in the leaf cells of this species. Bode (1940) discovered photorespiration in the same species.

Arnon and Stout (1939) named three criteria to determine if an element is essential to a plant:

1. Deficiency of the element makes it impossible for the plant to complete its vegetative or reproductive cycle
2. It cannot be replaced by any other element.
3. The effect is not simply the result of interaction with other non-essential elements, organisms, *etc*.

Figure 2. ***Fontinalis antipyretica***, a common aquatic research organism. Photo courtesy of Betsy St. Pierre.

Hoffman (1966) published the effects of nutrient deficiencies on the terrestrial ***Funaria hygrometrica*** (Figure 3). However, a similar treatment for aquatic bryophytes seems to be missing. My student (Marr 1983, unpublished report) described the visible effects based on experiments with ***Fontinalis antipyretica*** (Figure 2) cultured at 5ºC in 24-hour light. The complete nutrient stock solutions are in Table 1. Table 2 lists the amounts of each stock in the experimental deficiency solutions.

Figure 3. ***Funaria hygrometrica***, a common bryophyte in lab studies, including nutrition. Photo by Michael Lüth, with permission.

Table 1. Stock solutions used to make complete and deficient solutions for culturing ***Fontinalis antipyretica***.

	Compound	g L^{-1}
A	$Ca(NO_3)_2 \cdot 4H_2O$	236.1
B	KNO_3	101.1
C	$MgSO_4 \cdot 7H_2O$	246.4
D	KH_2PO_4	136.1
E	$Ca(H_2PO_4)_2 \cdot H_2O$	2.52
F	K_2SO_4	87.2
G	$CaSO_4 \cdot 2H_2O$	1.72
H	$Mg(NO_3)_2 \cdot 6H_2O$	25.4
I Minor elements:		
	$MnCl_2 \cdot 4H_2O$	1.81
	H_3BO_3	2.86
	$ZnSO_4 \cdot 7H_2O$	0.22
	$CuSO_4 \cdot 5H_2O$	0.08
	$H_2MoO_4 \cdot H2O$	0.09
J	$Na_2FeEDTA$	5 mg Fe L^{-1}
K	$FeCl_3$	162.2

Table 2. Deficiency treatment stock added to 400 ml H_2O.

Soln.	A	B	C	D	E	F	G	H	I	J	K
Complete	5	5	2	1	0	0	0	0	1	1	0
-K	7.5	0	2	-	50	0	0	0	1	1	0
-P	7.5	0	2	0	0	20	0	0	1	1	0
-Ca	0	15	2	1	0	0	0	0	1	1	0
-N	0	0	.5	0	50	20	200	0	1	1	0
-Mg	5	5	0	1	0	10	0	0	1	1	0
-S	5	5	0	1	0	0	0	.5	1	1	0
-Fe	5	5	2	1	0	0	0	0	1	0	0
-Minor	5	5	2	1	0	0	0	0	0	1	0
$FeCl_3$	5	5	2	1	0	0	0	0	1	0	1
1/4 strength											

Marr found that the complete nutrient solution resulted in most shoots appearing normal and healthy in most of the 3 basal and 3 apices in each of the replicate culture jars, but 4 apical pieces had brownish tips and 1 basal piece had brownish leaf margins. Deficiency symptoms were similar to those of tracheophytes:

-K: all samples bright green, but some slightly pale
-P: all dark green, some with scattered chlorotic leaf tips
-Ca: all pale yellow-green with hint of brown
-N: all pale green
-Mg: all looked normal
-S: all looked normal
-Fe: all had bright red stem bases; few red in leaf bases
-Minors: all normal except 8 brown apices
$FeCl_3$: all had yellow-brown leaves, bright green stems
1/4 strength: all normal

The changes in stem color with the two iron treatments are interesting and have taxonomic implications since stem color is sometimes used for recognition. The lack of effect by culturing with no minor nutrients may reflect the slow growth rate coupled with the ability to store and move the nutrients to growing tissues.

Buck and Brown (1978) warned that typical methods used in measuring bryophyte nutrients could cause misleading results because of leakage of water-soluble nutrients from the cell. If the bryophytes are dried first, this leakage is even greater. Nevertheless, vigorous washing is required to remove particulate matter collected on the bryophyte surface (Figure 4).

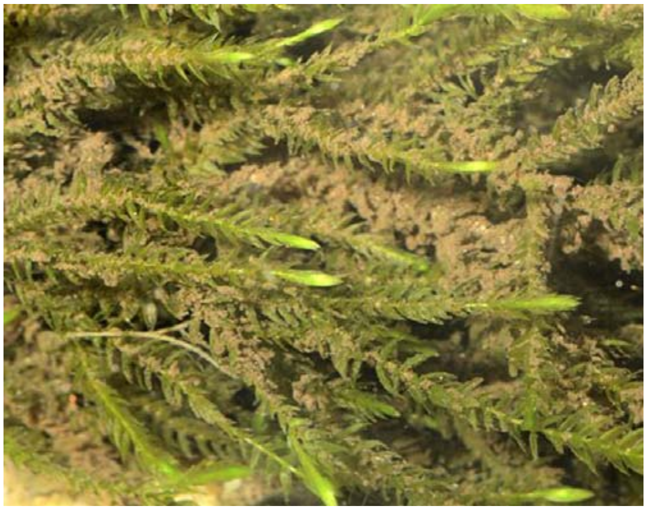

Figure 4. ***Fontinalis antipyretica*** exhibiting dense detritus accumulations that can occur with organic pollution. Photo by J. C. Schou, with permission.

In ***Cratoneuron filicinum*** (Figure 5) from a stream bank, little zinc and magnesium were lost from desiccated cells. Buck and Brown (1978) suggested that this low loss was due to the large proportion of the sample that was stem or branch tissue, whereas the losses typically occur from the 1-cell-thick leaves. Potassium, on the other hand, was readily lost from the leaves, and this needs to be done before the bryophytes are dried because it will glue itself to the bryophyte as it dries..

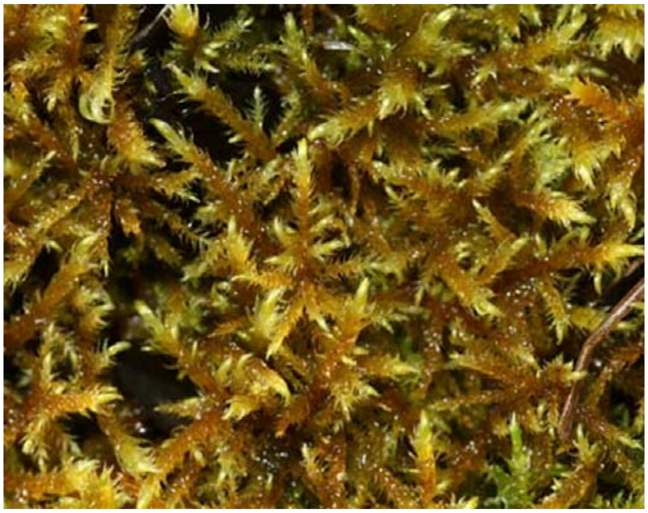

Figure 5. ***Cratoneuron filicinum*** showing a large proportion of stem and branch tissue. Photo by Barry Stewart, with permission.

Noting that bryophytes are the main primary producers in mountain streams, Álvaro (2001) considered them to have great utility as bioindicators of contamination, nutrient or otherwise. Their lack of thick cuticle, roots, or lignified vascular system, perennial life strategy, high mineral absorption capacity, simple structure, and wide distribution make them more suitable than most of the tracheophytes. Álvaro assessed the mineral nutrients and photosynthetic pigments of 12 permanently submerged aquatic bryophytes from different streams of the Iregua River basin in northern Spain. The concentrations of N, P, K, Ca, Mg, Fe, and Na were measured in the streams. Their concentrations in the bryophytes depend on internal factors such as the physiological activity, the specific capacity for accumulation, the delicacy of the tissues, and the growth cycle. Typically, the lowest concentrations occur in spring and the highest in autumn, but are influenced by the growth cycle and flow (causing dilution or concentration and determining the rate of delivery).

Samecka-Cymerman *et al* (2007) measured Al, Be, Ca, Cd, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, Pb, and Zn in the stream mosses ***Fontinalis antipyretica*** (Figure 2), ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7). These bryophytes came from streams running through granites/gneisses, limestones/dolomites, and sandstones in the Tatra National Park of Poland. PCA analysis grouped bryophytes by mineral concentrations that coincided with rock types. Those from granites/gneisses exhibited higher concentrations of Cd and Pb. Those from sandstones had higher concentrations of Cr. And those from limestones/dolomites had higher concentrations of Ca and Mg. We can suppose from these data that the dominant species of bryophytes in these streams may be adapted to higher concentrations of these elements, but that they do not necessarily require those concentrations. For this reason, the bryophytes can serve as ecological indicators when analyzed for their mineral content and thus serve as monitors for accumulations that occur over an extended period of time. This can be particularly useful when the input of an element is intermittent, but knowledge of its overall presence through time is needed.

Figure 6. ***Platyhypnidium riparioides*** with capsules, a species with 2-phase kinetics for phosphorus enzyme activity. Photo by J. C. Schou, through Creative Commons.

Figure 7. ***Scapania undulata***, an emergent species that seems to be tolerant of elevated heavy metal concentrations. Photo by Michael Lüth, with permission.

In the Brandon Pithouse Stream of northeast England, mosses were the most abundant phototrophs (Ellwood & Whitton 2007). The stream experienced seasonal changes in its dissolved N and P. The filtrable N and P were mostly organic, but it appears that with the high N:P ratio, only the organic P was important for the mosses. This peaked in late spring during the two study years. Axenically cultured plants exhibited higher PMEase and PDEase (both phosphorous enzymes) activities when grown with organic P than when grown with inorganic P.

Vanderpoorten and Palm (1998) reported that aquatic bryophytes are able to integrate sudden increases in nutrients in oligotrophic streams during floods, suggesting greater productivity than that which could be sustained during the other times of the year.

Several acetylenic acids have been identified from mosses. These can contribute to the production of triglycerides in nutrient-stressed mosses (Swanson *et al.* 1976), although that phenomenon seemed to be associated with more terrestrial mosses rather than aquatic ones (Anderson *et al*. 1974). In ***Fontinalis antipyretica*** (Figure 2), an early study revealed the presence of 9,12-octadecadien-6-ynoic and 11,14-eicosadien-8-ynoic (Anderson & Gellermann 1975). Later, Dembitsky and

Rezanka (1995) demonstrated a wide variation in the percentage of acetylenic fatty acids among the aquatic bryophyte fatty acids, from 6.6% acetylenic fatty acids in the moss ***Calliergon cordifolium*** (Figure 8) to 80.2% in the thallose liverwort ***Riccia fluitans*** (Figure 9).

Figure 8. ***Calliergon cordifolium***, a moss with only 6.6% acetylenic fatty acids. Photo by Jerry Jenkins, Northern Forest Atlas, with permission.

Figure 9. ***Riccia fluitans***, a thallose liverwort with the high level of 80.2% acetylenic fatty acids among its fatty acids. Photo by Andy Newman, through Creative Commons.

Nitrogen

Schwoerbel and Tillmanns (1964) demonstrated that ***Fontinalis antipyretica*** (Figure 2) was able to assimilate ammonium from nutrient solutions of NH_4Cl, with *p*H decreases dependent on the intensity of the assimilation. They found that the tracheophytic aquatic plant ***Callitriche hamulata*** (Figure 10) increases its ammonium assimilation with increases in *p*H, suggesting that it could take up undissociated molecules of NH_4OH. But our understanding of aquatic bryophyte usage of ammonium is limited to relatively few species.

Figure 10. ***Callitriche hamulata***, a species that assimilates more ammonium at higher *p*H levels. Photo through Creative Commons.

Kopacek and Blazka (1994) assessed the ammonium uptake of bryophytes in alpine streams of the High Tatra Mountains in Slovakia. They found that the uptake length decreased with the decreasing stream discharge, and that it was negligible in acidified streams. In non-acidified streams about 50% of the added ammonium underwent nitrification. The maximum ammonium uptake rates in the experiment ranged 6-11 mg m^{-2} h^{-1} and were comparable to those of two *in situ* experiments (8 & 12 mg m^{-2} h^{-1}). Mean uptake rates for ammonium were not related to the *p*H of the stream water. However, nitrification did experience significant photoinhibition in the non-acidified streams.

Vanderpoorten (2000) also noted that different populations of ***Hygroamblystegium tenax*** (Figure 11) exhibited different response curves in their responses to ammonium nitrogen, suggesting multiple ecotypes. Using DNA markers, Vanderpoorten revealed great variation in Amplified Fragments Length Polymorphism between populations of this species, with some showing greater affinities to ***H. fluviatile*** (Figure 12). Thus, it appears that the aquatic bryophytes have both genetic differences and the ability to acclimate through physiological changes in response to variable nutrient availability.

Figure 11. ***Hygroamblystegium tenax***, an oligotrophic species. Photo by Jerry Jenkins, Northern Forest Atlas, with permission.

Figure 12. ***Hygroamblystegium fluviatile***, a species of less oligotrophic streams than those of ***H. texax***. Photo by Michael Lüth, with permission.

Later, Schwoerbel and Tillmanns (1974, 1977) found that ***Fontinalis antipyretica*** (Figure 2) is able to assimilate both nitrate and ammonium, but that ammonium is used preferentially when both are present. While ammonium is being used, nitrate reductase activity is repressed. When the same plants were then given only nitrate, the nitrate reductase activity resumed.

Melzer and Kaiser (1986; Melzer 1980) compared nitrate levels in various aquatic macrophytes, including the moss ***Fontinalis antipyretica*** (Figure 2). The moss had the lowest levels of nitrate. Whereas some tracheophytes had accumulation amplification up to 131 times compared to the water, the moss had only 1.24. Nevertheless, N can be limiting for ***Fontinalis novae-angliae*** (Figure 13). When our lab (unpublished) cultured this species in stream water vs stream water with nitrate added to make 100 mg L^{-1} nitrate, the mosses in the added nitrate solution became much darker green in color and at least looked healthier (Figure 13).

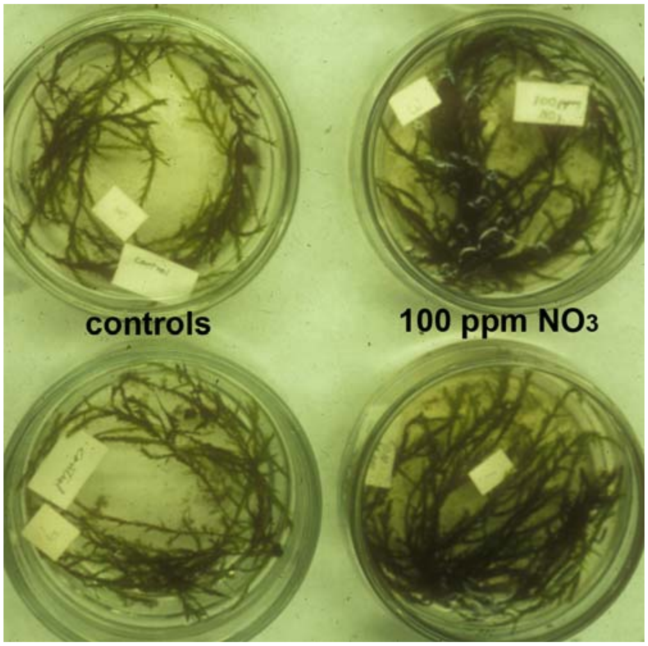

Figure 13. ***Fontinalis novae-angliae*** in stream water controls and stream water with added nitrate, showing much deeper green color in the amplified nitrogen. Photo by Janice Glime.

Some bryophytes are able to use amino acids as nitrogen sources (Keilova-Kleckova 1959). This is also known for the aquatic moss ***Taxithelium*** sp. (Figure 14-Figure 15) (Alghamdi 2003), but experiments using amino acids as a nitrogen source are rare.

Figure 14. ***Taxithelium planum*** on mangrove roots in a flood plain. Photo by Andi Cairns, with permission.

Figure 15. ***Taxithelium planum***, in a genus that is known to be able to use amino acids as a nitrogen source. Photo through Creative Commons.

In an old-growth forest stream in Oregon, USA, Ashkenas *et al.* (2004) found that residence time of labelled N in the stream was very short (3-12 minutes) and that it travelled only 35-55 meters at detectable levels. The predominant organisms involved in this uptake were aquatic bryophytes and biofilms on large woody debris (**epixylon**; Figure 16). On the other hand, they found that 49% of that nitrogen was exported from the stream to the terrestrial environment.

Figure 16. Large woody debris such as that which can provide substrate for bryophytes and algae in streams. Photo by Janice Glime.

Phosphorus

Arscott *et al*. (1998) added phosphorus to a portion of the Kuparuk River, Alaska, USA, in the summer annually for 15 years. They followed the responses of two genera of bryophytes, ***Schistidium agassizii*** (Figure 17-Figure 18) and ***Hygrohypnum*** spp. (Figure 1, Figure 59, Figure 72-Figure 73) As noted by Benstead *et al*. (2007) the aquatic bryophyte cover greatly increased, but required 8 years of enrichment to reach such high cover. It likewise took 8 years of recovery to approach reference levels, with the help of storms that scoured the mosses from the recovering portion.

Figure 17. ***Schistidium agassizii*** in its habitat on emergent rocks. Photo by Michael Lüth, with permission.

Figure 18. ***Schistidium agassizii***, a common species in unfertilized portions of the Kuparuk River, Alaska, USA. Photo by Des Callaghan, with permission.

Slavik *et al*. (2004) reported that following 8 years of phosphorus fertilization in the Kuparuk River the bryophytes replaced the epilithic diatoms (Figure 19) as the dominant primary producers. This new coverage of mosses affected the ammonium uptake rates, the benthic gross primary productivity, the habit structure, and the abundance and composition of insect species.

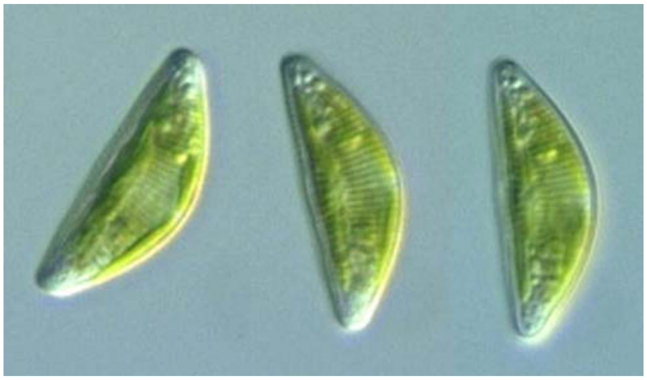

Figure 19. ***Cymbella minuta***, one of the major rock-dwelling diatoms in the Kuparuk River, Alaska. Photo by Yuuki Tsukii, with permission.

Schistidium agassizii (=***S. alpicola***; Figure 17-Figure 18) and ***Hygrohypnum*** spp. (Figure 1, Figure 59, Figure 72-Figure 73) became extensive in the P-fertilized portion of the stream, but only ***S. agassizii*** was common in the unfertilized reaches (Bowden *et al*. 1994; Arscott *et al*. 1998). The productivity of the epilithic algae was greater than that of the bryophytes when measured as net primary productivity per unit of chlorophyll *a*, suggesting a more efficient photosynthesis in these algae, perhaps due to the more complex structure of the bryophytes. But the areal rates for the ***Hygrohypnum*** species were 2-4 times that of the epilithic algae, accounting for 80% of the primary productivity in the P-fertilized portions, but for only 9% in the unfertilized portions. Arscott and coworkers concluded that ***Schistidium agassizii*** uses a subsistence strategy, whereas the ***Hygrohypnum*** species are opportunists.

Steinman (1994) reported on the effects of phosphorus enrichment on the leafy liverwort ***Porella pinnata*** (Figure 20-Figure 21) in two woodland streams in eastern Tennessee, USA. The P:C ratio in this liverwort in Walker Branch was not affected by enrichment, but the P:N ratio increased significantly. In Sludge Creek, where the N:P ratio of the water was much smaller, both the P:C and P:N ratios in the liverwort increased significantly following addition of phosphorus.

In four upland streams in northern England, Ellwood *et al*. (2008) found that moss phosphatase activities were among the most variable parameters in these streams. They found a significantly positive relationship between phosphatase activities and aqueous organic nitrogen, but not with aqueous organic phosphorus. There was a significantly positive relationship between the phosphodiesterase:phosphomonoesterase ratio and the aqueous organic nitrogen, between phosphatase activities and tissue phosphorus concentration, and between phosphatase activities and the tissue N:P ratio.

Figure 20. ***Porella pinnata*** on tree in floodplain. Photo by Paul Davison, with permission.

Figure 21. ***Porella pinnata***, a species that responds positively to P additions where P is in low concentration in the water. Photo by Ken McFarland and Paul Davison, with permission.

Turner *et al*. (2001) found that all shoot tips from twelve terrestrial and aquatic mosses in their northern England and Sweden study exhibited PMEase activity in the shoot tips, but not all exhibited PDEase activity. The mean optimum *p*H for PMEase was 5.9; for PDEase it was 5.7. Vmax values differed between Sweden and England. In their assessment of ***Fontinalis antipyretica*** (Figure 2) and ***Platyhypnidium riparioides*** (Figure 6) these mosses exhibited a 2-phase kinetics for PMEase and PDEase. **Km** (substrate concentration at half-maximal enzymatic velocity) and **Vmax** (reaction rate when enzyme is fully saturated by substrate) were dependent on the substrate concentration. They found that PMEase activity was located in the cell wall.

Christmas and Whitton (1998) compared the concentrations of N and P in ***Fontinalis antipyretica*** (Figure 2) and ***Platyhypnidium riparioides*** (Figure 6) at headwater and downstream sites of the River Swale-Ouse, northeast England. Mosses in the headwaters exhibited the greatest variability of N and P concentrations, and these were the lowest concentrations in the mosses among the sites. Both elements increase in the stream water downstream. However, the N:P ratio was highest in the headwaters (14.9), decreasing to 6.8 downstream for ***F. antipyretica***. Likewise, for ***P. riparioides*** this ratio decreased from 12.5 to 5.5 with downstream sampling. The PMEase (phosphomonoesterase) was greater at *p*H 5.5 than at *p*H 7.5 or 9.5. The greatest activity was in the headwaters and in the summer. When the tissue P concentration was low or the N:P ratio was high, the PMEase activity was greatest, suggesting an acclimation mechanism.

Martínez-Abaigar *et al*. (2002b) examined the physiological effects of KH_2PO_4 on the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 22). The levels of both P and K in the liverwort tissues were significantly higher in the more enriched cultures. However, the accumulation of P increased through time, whereas that of K fluctuated. The researchers presumed that K was subject to leakage from its cells, whereas P continued to accumulate. Although P can be a good indicator of environmental conditions, it can reach a saturation point. Furthermore, additional P did not result in any increase in photosynthesis, perhaps because P was not limiting initially or because even as P increased there were other limiting conditions such as other nutrients, light, CO_2, or temperature. In fact, net photosynthesis declines then tissue P exceeded 0.45% of dry mass, indicating that it had become toxic. The concentration of chlorophyll was not affected by P enrichment, but the chlorophyll *a*/*b* ratio and the proportion of chlorophylls to phaeopigments suggested phosphorus toxicity at those levels. This toxicity level could explain the disappearance of this liverwort from streams polluted with phosphorus and permit us to use this species as a biological indicator. In anoxic situations the liverwort is apparently unable to absorb the P, presumably because the mitochondrial respiration is blocked. After three days, P is lost from the tissues, perhaps due to membrane damage (or inability to repair them) in the anoxic conditions.

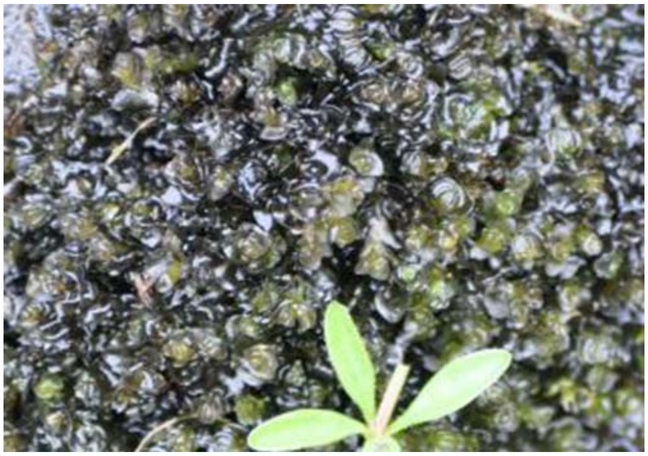

Figure 22. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a liverwort that can benefit from addition of both P and K. Photo by Andy Hodgson, with permission.

Finlay and Bowden (1994) demonstrated the importance of P in Arctic tundra stream bryophytes. Two species of ***Hygrohypnum*** (Figure 1, Figure 59, Figure 72-Figure 73) and ***Fontinalis neomexicana*** (Figure 23) were much more abundant in the riffles of P-fertilized portions of the Kuparuk River, Alaska, USA, but much less common in fertilized pools. In unfertilized portions of the river, they were absent. The researchers used artificial bryophytes to test the role of epiphytes and determined that whereas growth at low P concentrations was severely limited, in the fertilized pools growth of the bryophytes was limited by epiphytes. Epiphyte cover was 4-4.5 times as great in the fertilized pools compared to fertilized riffles. In the unfertilized pools and riffles, the stem tips of ***Hygrohypnum*** species failed to elongate, whereas in fertilized pools and riffles, stem elongation not only occurred, but did not differ based on presence of moving water after 32 days. Stem tips of ***Fontinalis neomexicana*** elongated in all sites. The ***F. neomexicana*** in fertilized riffles had significantly greater growth (4.7±0.1 cm) compared to that in unfertilized riffles (2.1±1.1 cm), but growth of tips in control pools (2.8±0.8 cm) did not differ significantly from that in fertilized pools (2.7±0.9 cm). These observations support my observations of aquatic bryophytes in pool culture wherein growth of epiphytes increases to the detriment of the mosses. Similarly, Arscott *et al*. (1998) reported an increase in productivity rates for ***Hygrohypnum*** species from control values of 2.3 g C h^{-1} to 6.3 g C h^{-1} in fertilized reaches of the Kuparuk River.

Figure 23. ***Fontinalis neomexicana***, a species for which growth rate increased with the addition of P to the water. Photo by Rambryum, through Creative Commons.

Using 10 "strictly aquatic" bryophyte species from the Rhine Rift, Vanderpoorten *et al*. (1999) found a strong correlation between absorption of ammonia N and phosphate P with stream temperature deviation. ***Chiloscyphus pallescens*** (Figure 24), ***Apopellia endiviifolia*** (syn.=***Pellia endiviifolia***; Figure 25), and ***Hygroamblystegium tenax*** (Figure 11) were oligotrophic in comparison to ***Hygroamblystegium fluviatile*** (Figure 12), ***Cinclidotus danubicus*** (Figure 26), ***C. riparius*** (Figure 27), and ***Fissidens crassipes*** (Figure 28). ***Leptodictyum riparium*** (Figure 29), ***Fontinalis antipyretica*** (Figure 2), and ***Platyhypnidium riparioides*** (Figure 6) were more frequent in eutrophic (high nutrient level) streams, but tolerated a broad spectrum of nutrients. Birch *et al*. (1988) found that the River Wear, northeast England, experienced a marked increase in the moss ***Leptodictyum riparium***, noting that it is a species typical of sites with organic pollution. ***Leptodictyum riparium*** can be associated with raised nitrate concentrations (Chatenet *et al*. 2000) and other forms of eutrophication (Hussey 1982; Birch *et al*. 1988; Gecheva *et al*. 2017). García-Álvaro (1999) indicated that ***Platyhypnidium riparioides*** was similarly an indicator of eutrophic conditions.

Figure 24. ***Chiloscyphus pallescens***, an oligotrophic leafy liverwort. Photo by Hermann Schachner, through Creative Commons.

Figure 25. ***Apopellia endiviifolia*** male plants, an oligotrophic species of stream banks. Photo by Hermann Schachner, through Creative Commons.

Figure 26. ***Cinclidotus danubicus***, a species of less oligotrophic streams than those of ***Chiloscyphus pallescens***. Photo by Michael Lüth, with permission.

Figure 27. ***Cinclidotus riparius***, a species of less oligotrophic streams than those of ***Chiloscyphus pallescens***. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Fissidens crassipes***, a species of less oligotrophic streams than those of ***Chiloscyphus pallescens***. Photo by Michael Lüth, with permission.

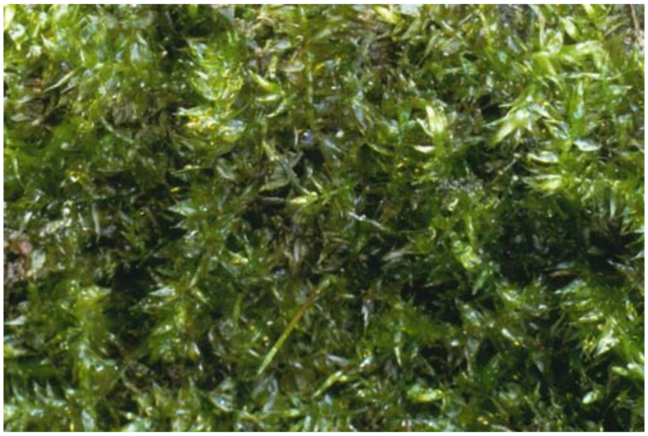

Figure 29. ***Leptodictyum riparium***, a species of less oligotrophic streams than those of ***Chiloscyphus pallescens***. Photo by Jan-Peter Frahm, with permission.

In Bear Brook, at the Hubbard Brook Experimental Forest, New Hampshire, USA, Meyer (1979) found that bryophytes and sediments are retention sites for processing of dissolved P. But Fisher and Likens (1973) have shown that the bryophytes contribute only 1% of the total energy in this stream. Algae and tracheophytes are absent. More than 99% of the energy results from **allochthonous** (originating from outside the stream) sources (mostly litter and substances carried by the surface and subsurface waters).

Similarly, Bunn *et al*. (1989) found that aquatic mosses were of only tertiary importance as a source of energy in a tundra river system. Instead, most of the energy was derived from terrestrial sources.

Locations in Plant

Brown and Buck (1979) have provided us with good insight into the location of cations within the bryophyte tissues. These should hold for aquatic as well as terrestrial bryophytes. Potassium, a very soluble nutrient, is dissolved within the cells. Calcium, on the other hand, has poor solubility and is bound to exchange sites in the cell wall. Magnesium is present in all these locations. When the bryophyte is desiccated, the cell membranes become damaged and leak soluble ions, thus causing the leaves to lose potassium and some magnesium. Most of the magnesium becomes bound to cell wall exchange sites. The retention of potassium within the cells upon drying is related to the availability of water in the bryophyte's habitat.

García-Alvaro *et al*. (2000) assessed element concentrations (N, P, K, Ca, Mg, Fe, & Na) in the 3-cm apices of ***Platyhypnidium riparioides*** (Figure 6). These were sampled from 17 populations of the Iregua River in northern Spain. These element concentrations were significantly correlated with the concentrations in the water, differing between the upper siliceous reaches and the human impact and $CaCO_3$ of the middle and lower reaches. These elements differentiated into the mainly intracellular ones (N, P, & K) and those that are primarily exchangeable (Ca & Mg). The more soluble elements N, P, and K exhibited a linear relationship between tissue content and water content. But for Ca and Mg, a saturation curve relationship was present. Thus this moss exhibited enrichment for N, P, and K, but not for Ca and Mg. They provided arguments that this species could acclimate to changing water chemistry conditions by altering the uptake efficiency.

García-Álvaro (1999) noted that nitrogen, calcium, and potassium are the most abundant elements and that those found in their study were comparable to those in other aquatic bryophytes. The elemental concentration was lowest in spring. ***Fontinalis antipyretica*** (Figure 2) and ***F. squamosa*** (Figure 30) exhibited the highest concentrations of the most mobile elements (N, P, K) in the apical portions. The least mobile elements (Ca, Mg, Fe) were concentrated in the basal portions. These locations suggest that soluble (mobile) elements are moved about in the plant. It does not explain the accumulation of the least mobile elements at the base, and it suggests some mechanism to determine the direction of movement for at least some elements.

Figure 30. ***Fontinalis squamosa***, a species that exhibits high concentrations of the most mobile elements (N, P, K). Photo by Hermann Schachner, through Creative Commons.

In a mid-Wales headwater stream, Chapman *et al.* (1996) found no biological removal of nitrate or potassium from the water in winter. However, ***Sphagnum*** (Figure 31) apparently contributed to temporary retention of potassium through cation exchange.

Figure 31. ***Sphagnum torreyanum***, a species sometimes found in streams. ***Sphagnum*** species can contribute to retaining potassium temporarily through their cation exchange sites.

Fischer (1948) compared the leaves of the moss ***Fontinalis antipyretica*** (Figure 2) and the tracheophyte ***Elodea canadensis*** (Figure 32). The older leaves of both species have a lower viscosity of cytoplasm. Potassium content decreases sharply in older leaves, especially compared to calcium content, consistent with observations on terrestrial tracheophytes. Fischer interpreted the changes in viscosity and mineral salt content as decreased hydration of the aging plasma micelle.

Miyazaki and Satake (1985) examined the uptake of inorganic carbon and nitrogen by two leafy liverworts in Kashiranashigawa, an acid stream in Japan. ***Solenostoma vulcanicola*** (Figure 33) and ***Scapania undulata*** (Figure 7) had similar uptake activities, with both exhibiting the highest uptake in the tips of the shoots. Uptake decreased gradually toward the base. For ***S. vulcanicola*** carbon uptake at the shoot tip in light was 10.4×10^{-4} C g dry wt^{-1} h^{-1}, whereas it was 8.1×10^{-4} g^{-1} for ***S. undulata***. Nitrate uptake was less than ammonium uptake in the tips, suggesting that these liverworts use ammonium as their major N source.

Figure 32. ***Elodea canadensis***, an aquatic species that has more potassium in younger leaves than in older ones. Photo by Kristian Peters, through Creative Commons.

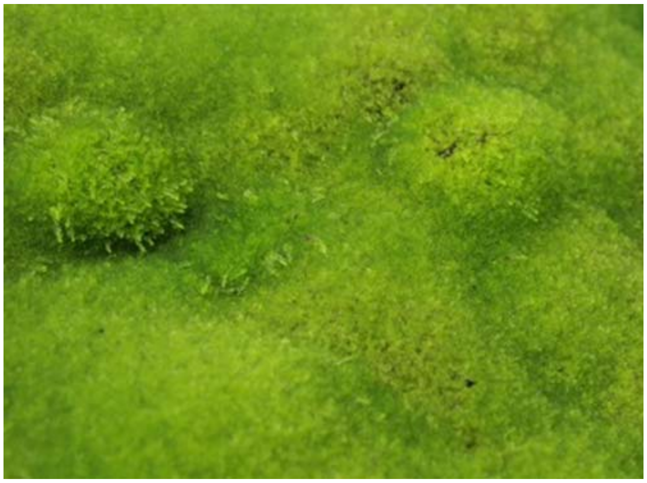

Figure 33. ***Solenostoma vulcanicola*** habitat in an acid stream in Japan. This species takes up nutrients at the tips and apparently uses ammonium preferentially over nitrate. Photo courtesy of Angela Ares.

Martínez-Abaigar *et al.* (2002a) found that ***Fontinalis antipyretica*** (Figure 2) had a higher nitrogen concentration, perhaps due to greater physiological activity related to its more rapid growth. ***Fontinalis squamosa*** (Figure 30), on the other hand, had a greater accumulation of iron. The three relatively insoluble elements Ca, Mg, and Fe increased significantly from the apex to the base, consistent with uptake over time. The more physiologically active and soluble (mobile) elements N, P, and K were in greatest concentrations in the tips.

Pollution Effects

In a study of 30 highly seasonal river sites in Bulgaria, both hydromorphological river alterations and eutrophication led to loss of bryophyte species and decreased bryophyte abundance (Gecheva *et al.* 2017). Pleurocarpous mosses became the most prevalent type. Eutrophication favored increase in ***Leptodictyum riparium***

(Figure 29), an observation also true of filter beds in water reclamation works (Hussey 1982).

Pollution can provide toxic substances, but it can also provide limiting nutrients. And it can affect uptake rates and nutrient balance within plants. For example, organic pollution can cause a net loss or cause uptake of N and P to cease, resulting in photosynthetic decline (Martínez-Abaigar *et al*. 1993). This was followed by changes in pigment composition and phaeopigment ratio. The most sensitive species tested was ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 22), ***Fontinalis antipyretica*** (Figure 4) the least, and ***Brachythecium rivulare*** (Figure 34) demonstrated intermediate sensitivity.

Figure 34. ***Brachythecium rivulare***, a species with intermediate sensitivity to pollution. Photo by David T. Holyoak, with permission.

Heavy Metals

Bidwell (1979) noted that micronutrients may be toxic if taken in large quantities. Many heavy metals such as manganese, copper, zinc, and molybdenum fall into this category. **Micronutrients** are those nutrients needed only in small quantities. These are often components of enzymes.

Satake *et al*. (1984) reported a number of inorganic elements in several aquatic bryophytes from New Caledonia. Those assessed included B, Na, Mg, Al, Si, P, K, Ca, Sc, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Br, Sr, Mo, Cd, and Sb in the shoots of ***Ectropothecium zollingeri*** (Figure 35), ***Vesicularia inflectans*** (Figure 36), and ***Lopholejeunea*** sp. (Figure 37) from streams. Not all elements could be detected by the ICP analysis method. Others were detectable but the concentrations were too low for the concentrations to be determined. Differences occurred between the acidic streams and those that were not acidified. Iron, in particular, exhibited a considerable difference.

Figure 35. ***Ectropothecium zollingeri***, a species that absorbs inorganic elements differently in acidic and non-acidic streams. Photo by Jan-Peter Frahm, with permission.

Figure 36. ***Vesicularia montagnei***; ***V. inflectans*** is a species that absorbs inorganic elements differently in acidic and non-acidic streams. Photo by Tan Sze Wei Aquamoss website <www.aquamoss.net>.

Figure 37. ***Lopholejeunea subfusca***, a species that absorbs inorganic elements differently in acidic and non-acidic streams. Photo by Yang Jia-dong, through Creative Commons.

Glime and Keen (1984) explored the effects of copper on several species of aquatic mosses. Copper is an essential nutrient, but it becomes toxic at higher concentrations. Glime and Keen used Chlorophyta medium (Prescott 1968) to culture these bryophytes for 14 days, adding copper to make concentrations of 0.01, 0.1, 1.0, and 10.0 mg Cu L^{-1}. They found that for ***Platyhypnidium riparioides*** (Figure 6), symptoms of toxicity began at 0.01 mg Cu L^{-1}, as demonstrated by a loss of chlorophylls *a* and *b* (Figure 38). The same was true for ***Fontinalis duriaei*** (Figure 39) (for chlorophyll *b*, but chlorophyll *a* took an initial dip, then increased, before exhibiting a declining curve of chlorophyll *a* loss (Figure 40). Both ***Fontinalis gigantea*** (Figure 41) and ***F. dalecarlica*** (Figure 42) exhibited an initial chlorophyll *a* and *b* rise at 0.01 mg L^{-1} compared to that of controls, suggesting that the medium had copper levels that were not optimal for these two moss species (Figure 43 and Figure 44 respectively).

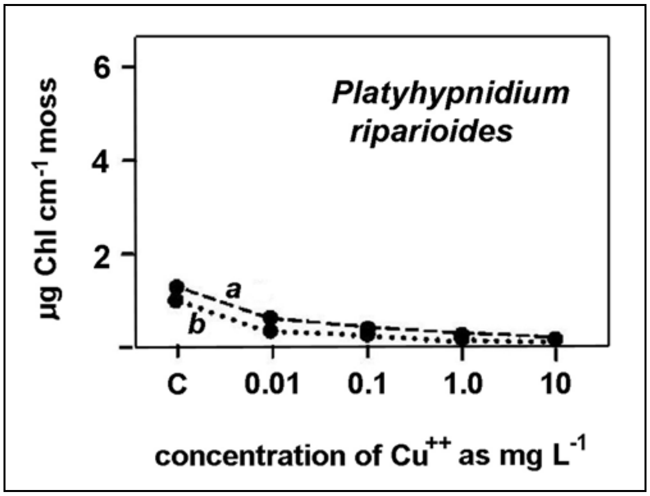

Figure 38. Effect of Cu ions on chlorophyll *a* and *b* concentrations in ***Platyhypnidium riparioides***. Redrawn from Glime & Keen 1984.

Figure 39. ***Fontinalis duriaei***, a species that is sensitive to copper. Photo by Michael Lüth, with permission.

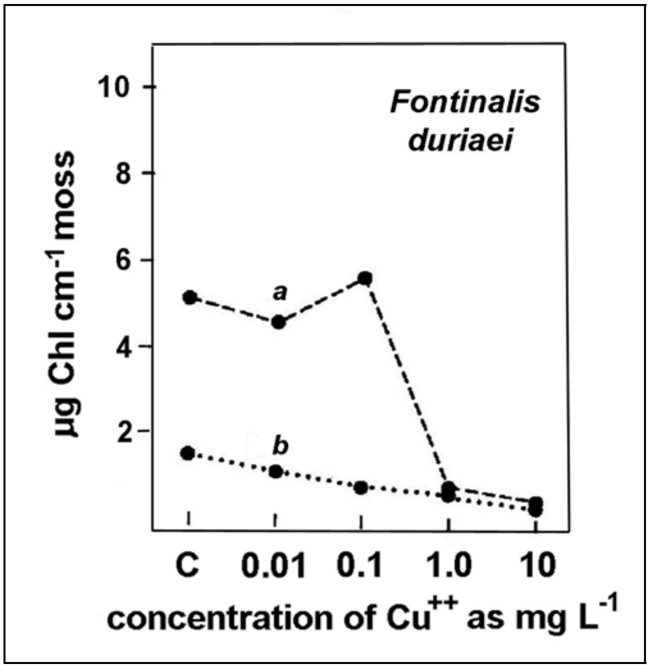

Figure 40. Effect of Cu on chlorophyll *a* and *b* concentrations in ***Fontinalis duriaei***. Redrawn from Glime & Keen 1984.

Figure 41. ***Fontinalis gigantea*** in Massachusetts, USA, a species that may benefit from some added copper, but that is damaged at higher concentrations. Photo courtesy of Glenn Krevofsky.

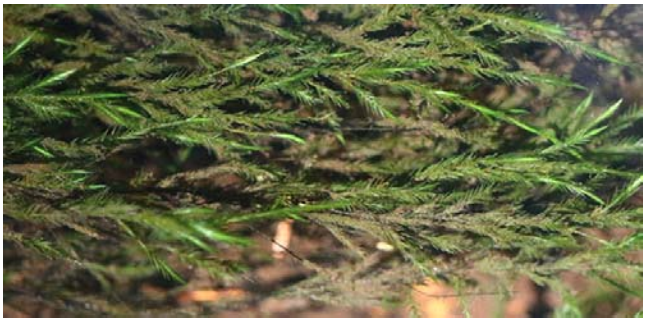

Figure 42. ***Fontinalis dalecarlica***, a species of acidic streams, but is damaged at *p*H 3.0. Photo by Jean Faubert, with permission.

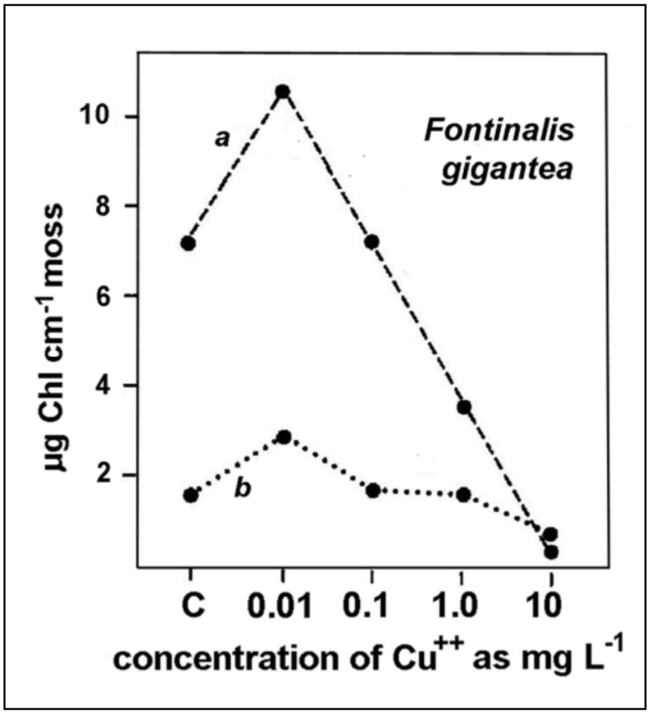

Figure 43. Effect of Cu on chlorophyll *a* and *b* concentrations in ***Fontinalis gigantea***. Redrawn from Glime & Keen 1984.

The measurements of chlorophyll as affected by added copper were evident externally as loss of color in the mosses (***Fontinalis*** spp.; Figure 45-Figure 46). Glime and Keen (1984) also found cellular changes in leaves with high levels of copper. In the controls, the protoplasm with its chloroplasts filled the leaf cells (Figure 47). A small addition of Cu (0.01 mg L^{-1}) caused an increase in chlorophyll (Figure 48). At 1 mg Cu L^{-1}, the leaf cells of ***Fontinalis dalecarlica*** (Figure 47-Figure 49) exhibited only minor damage compared to the controls (Figure 49), whereas the cells of ***F. duriaei*** were clearly plasmolyzed and most of the green color was gone (Figure 50). At 10 mg Cu L^{-1} the leaf cell contents of ***F. dalecarlica*** (Figure 42) again filled the cells but the contents were brown with little structure being visible (Figure 51). The loss of plasmolysis at this concentration suggests severe membrane damage.

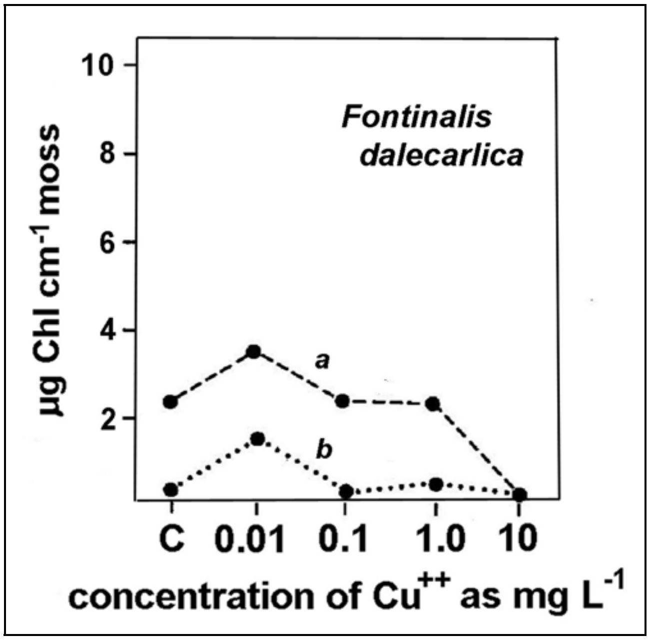

Figure 44. Effect of Cu on chlorophyll *a* and *b* concentrations in ***Fontinalis dalecarlica***. Redrawn from Glime & Keen 1984.

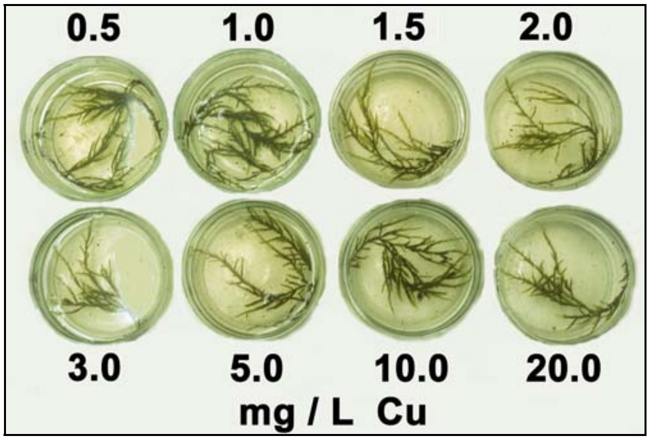

Figure 45. ***Fontinalis novae-angliae*** responses to various Cu concentrations showing loss of green color at branch tips. Photo by Janice Glime.

Figure 46. ***Fontinalis novae-angliae*** in 3 mg L^{-1} Cu, showing loss of green color, especially at the tips of the branches. Photo by Janice Glime.

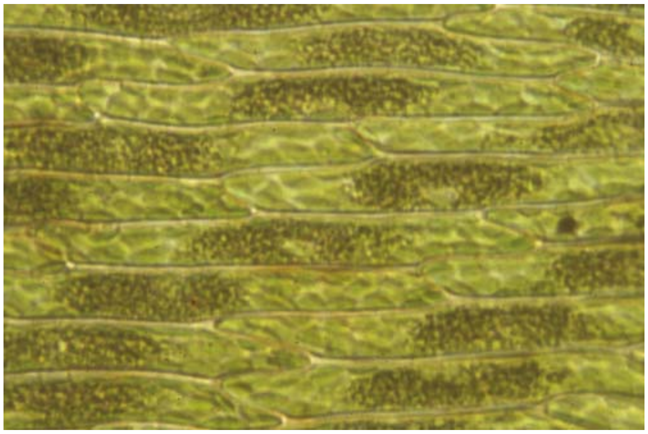

Figure 47. ***Fontinalis dalecarlica*** healthy leaf cells in Control culture medium. Photo by Janice Glime.

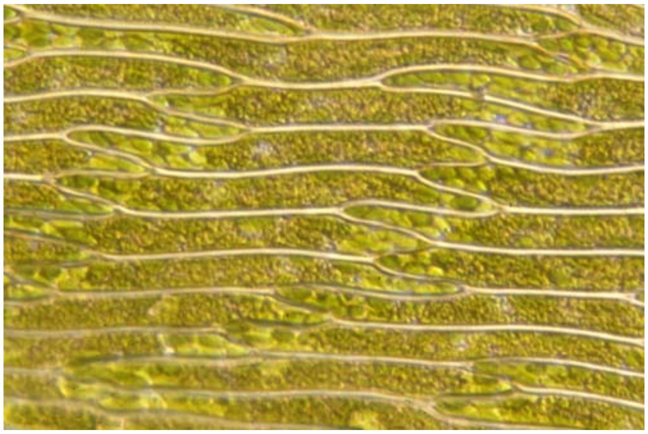

Figure 48. ***Fontinalis dalecarlica*** leaf cells at 0.01 mg Cu L^{-1}. At this concentration, both chlorophylls increased in concentration compared to the controls. Photo by Janice Glime.

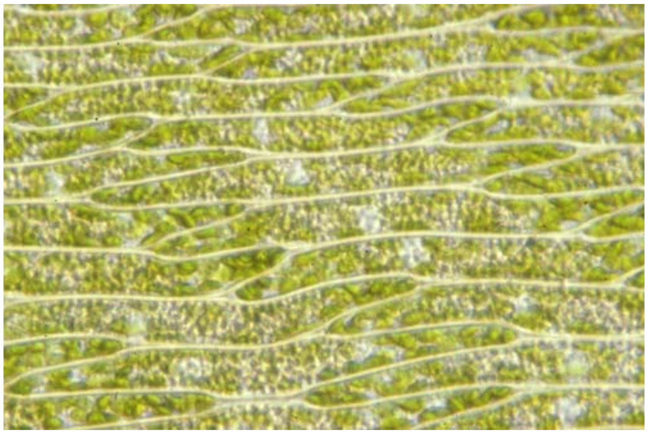

Figure 49. ***Fontinalis dalecarlica*** exhibiting beginnings of damage in culture medium with 1 mg Cu L^{-1}. Photo by Janice Glime.

Claveri and Mouvet (1995) found that a concentration of 90 µg L^{-1} copper exposure for 12 days at 29ºC resulted in denaturation of chlorophyll in ***Platyhypnidium riparioides*** (Figure 6). As they increased the water temperature from 7 to 29ºC, the moss vitality decreased, but the copper uptake and release did not change. They concluded that copper uptake is not related to photosynthesis.

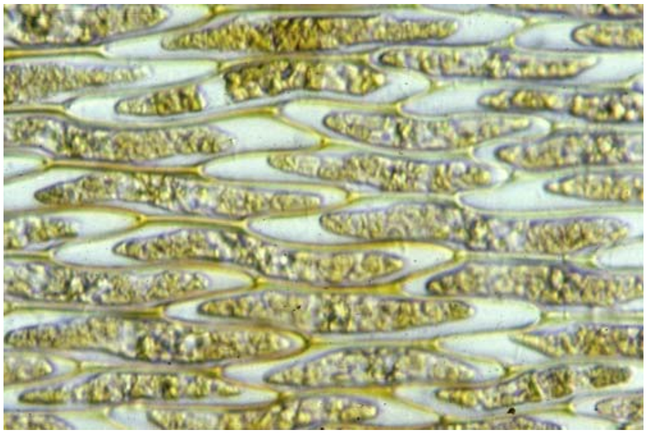

Figure 50. ***Fontinalis duriaei*** plasmolyzed leaf cells in culture medium with 1 mg Cu L^{-1}. Photo by Janice Glime.

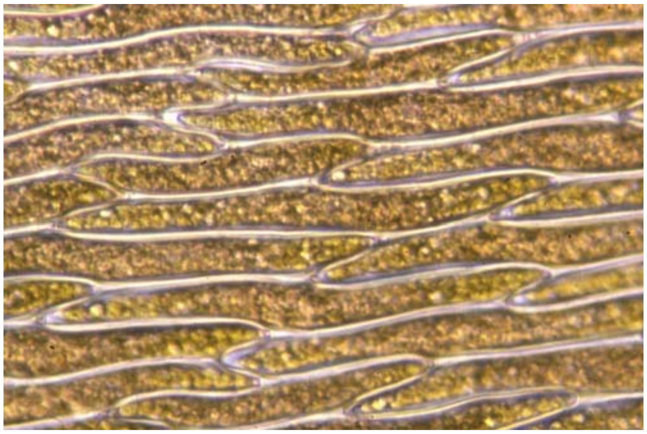

Figure 51. ***Fontinalis dalecarlica*** deplasmolyzed leaf cells in culture medium with 10 mg Cu L^{-1}. Photo by Janice Glime.

Recently researchers have been exploring the role of glutathione in protecting plants from stressors (Bruns *et al.* (2001). This includes their role in heavy metal detoxification. Bruns and coworkers found that the glutathione pool increased significantly during the first two days of added 100 µmol L^{-1} Cd(II) in both terrestrial and aquatic bryophytes. They found that Cd(II) induced an increase in the glutathione pool of ***Fontinalis antipyretica*** (Figure 2). At the same time, cysteine and γ-glutamyl-cysteine increased, but did not reach a high level. Uptake indicated fast regulation of the equilibrium between the plant surface and the medium. This was followed by slow migration of the Cd to intracellular sites in the moss. There the Cd is stored primarily in the vacuoles as phosphate precipitates. The sulfur content also increased during Cd exposure, and the Cd is chelated by SH groups. These cellular activities provide detoxification of heavy metals.

Because of their ability to take in heavy metals during all seasons of the year without suddenly releasing them has made aquatic bryophytes useful organisms for heavy metal biomonitoring. Caines *et al.* (1985) found that aquatic bryophytes in acid streams in Scotland could bioconcentrate the metals aluminium, manganese, and zinc, but that increased H^+ concentrations caused a decrease of metal concentrations in the aquatic bryophytes. Thus, the bryophytes that can help to clean up heavy metals in streams may be unable to accomplish their beneficial work when acid rain also accompanies the metal pollution.

In the Ore Mountains of eastern Germany, Samecka-Cymerman *et al*. (2002) assessed heavy metals and nutrients in the mosses ***Platyhypnidium riparioides*** (Figure 6) and ***Fontinalis antipyretica*** (Figure 2) and the liverwort ***Scapania*** sp. (Figure 7). All investigated elements (Ni, Cr, Co, Zn, Mn, Pb, Cd, Cu, Ba, Al, V, Ca, Mg, K) except Sr were elevated in the bryophytes. Furthermore, Cd (195 mg kg^{-1}), Cu (233 mg kg^{-1}), Zn (22,500 mg kg^{-1}), Pb (595 mg kg^{-1}), and Co (140 mg kg^{-1}) were in concentrations that seriously exceeded background values. The researchers furthermore demonstrated that the bryophytes retained part of the metal loading even after the pollution ceased and the streams returned to levels found in cleaner rural areas.

Heavy metals can cause the loss of soluble essential nutrients such as potassium or cause the release of nutrient cations, such as Mg, on the ion exchange sites. Vázquez *et al*. (1999) examined the locations of heavy metals in shoot tips of ***Fontinalis antipyretica*** (Figure 2), ***Scapania undulata*** (Figure 7), and ***Fissidens polyphyllus*** (Figure 52). They found that in most instances the greater concentration was in the extracellular component compared to the intracellular compartment. The particulate fraction content was negligible. The liverwort ***Scapania undulata*** has a high affinity for the metals on its extracellular sites. On the other hand, the moss ***Fissidens polyphyllus*** has a relatively low affinity. By contrast, the latter species has the highest intracellular content after incubation in the heavy metal solution. The heavy metals caused considerable loss in intracellular K, most likely due to membrane damage. Extracellular Mg also decreased in the heavy metal solutions, probably due to displacement on the cation-binding sites. The greatest losses of intracellular K occurred in ***S. undulata***, followed by ***F. antipyretica***. However, ***S. undulata*** had the lowest losses of extracellular Mg.

Figure 52. ***Fissidens polyphyllus***, a species with a low affinity for heavy metals. Photo by Janice Glime.

López and Carballeira (1993) similarly found that the leafy liverwort ***Scapania undulata*** (Figure 7) had the highest accumulatory capacity when compared to the mosses ***Fontinalis antipyretica*** (Figure 2), ***Platyhypnidium riparioides*** (Figure 6), and ***Brachythecium rivulare*** (Figure 34) with intermediate capacities. Nevertheless, they considered the latter two species to be more useful for bioindication. Although the relationship between metal in the bryophytes and that in the water was low, it was statistically significant for all metals except Co in ***F. antipyretica*** and Cd, Pb, and Co in the other three bryophytes. The low relationship can relate to intermittent concentrations in stream water, whereas the bryophytes accumulate and do not represent a single point in time. Like Caines *et al*. (1985), López and Carballeira found that *p*H was a modifying factor in how the bryophytes responded to the metals. Other modifying factors include sulfate concentration, nitrite, ammonia, and filtrable reactive phosphate.

Carballeira and López (1997) then applied this information to field assessment of heavy metals (Cd, Cr, Cu, Co, Ni, Pb, Zn, Fe, and Mn) in 36 rivers of Galicia, Spain. Using five bryophytes, they found that the liverwort ***Scapania undulata*** (Figure 7) and moss ***Platyhypnidium riparioides*** (Figure 6) indicated the highest background levels, with concentrations significantly exceeding those in ***Fontinalis antipyretica*** (Figure 2) and ***Fissidens polyphyllus*** (Figure 52) for nearly all metals tested. Substrate lithology clearly influenced levels of some metals in ***S. undulata*** and ***F. polyphyllus***.

Vázquez *et al*. (2000) explored the effects of acidity and metal concentration on accumulation of metals on and in the moss ***Fontinalis antipyretica*** (Figure 2). Using transplanted mosses that were subsequently sampled after 1 to 35 days, they determined the metal levels in the extracellular and intracellular compartments. As in other studies, they found that in acid water the uptake is distinctly lower than in near-neutral water. They suggested that competition of H^+ ions for the extracellular binding sites accounted for the lower concentration of metal cations. Furthermore, there was a rapid release of metal ions from the intracellular component. As found in other studies, K^+ was lost from within the cell and Mg^{++} was lost from the extracellular component. Ca^{++} was lost from both components, suggesting damage to the cell wall (or at least to the cell membrane).

*p*H

As already noted by Vázquez *et al*. (2000), in addition to its strong effects on obtaining CO_2 for photosynthesis, *p*H can also influence the uptake rate of metal ions into the mosses (Martins *et al*. (2004). The maximum biosorption capacity for both cadmium and zinc was at a *p*H of 5.0. On the other hand, zinc sorption increased when water hardness with added $CaCO_3$ increased from 101.1 to 116.3 mg L^{-1}. As the hardness increases further, the calcium effectively competes with the zinc and reduces its sorption. The presence of Ca ions had no affect on cadmium uptake.

Burr (1941) concluded that ***Fontinalis*** (Figure 2, Figure 4, Figure 23) is more productive in bicarbonate than in CO_2, but finding any mechanism to explain such a relationship has been elusive. Allen and Spence (1981) concluded that there was a gradation of bicarbonate users, not a "user" vs "non-user," among aquatic plants. This, in fact, makes some sense for this genus.

Farmer *et al.* (1986) tested 15 species of freshwater macrophytes for activities of RUBISCO and PEP carboxylase. RUBISCO was the most active in all species, including the moss ***Fontinalis antipyretica*** (Figure 2) and some liverworts. This is consistent with the behavior of C_3 plants.

Vieira *et al.* (2018) analyzed bryophyte communities in 474 river reaches in Mediterranean climates of six European countries. They found that calcium and magnesium were the most notable chemical influences on the types of communities present. These are both indicators of hard water and typically a *p*H above neutral.

Acidification changes the communities of bryophytes in streams. Liming of both natural and polluted acid streams can alter these communities (Brandrud 2002). In Sweden and Norway, Brandrud found that adding lime typically permits re-establishment of species such as ***Fontinalis*** spp. (Figure 2, Figure 4, Figure 23) that are acid-sensitive. The critical level of *p*H seems to be about 5.5, particularly for species that depend on availability of HCO_3^-, including many of the tracheophytes. On the other hand, bryophytes [*e.g.* ***Nardia compressa*** (Figure 53) and ***Sphagnum auriculatum*** (Figure 54)] may be negatively affected because of their need for free CO_2 for photosynthesis.

Figure 53. ***Nardia compressa***, a leafy liverwort, a species requiring free CO_2. Photo by Hermann Schachner, through Creative Commons.

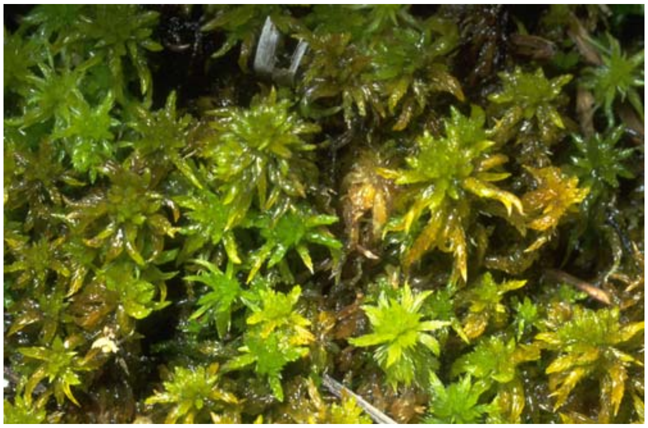

Figure 54. ***Sphagnum auriculatum***, a species that may be negatively affected by *p*H above 5.5 because of its need for free CO_2. Photo by Jan-Peter Frahm, with permission.

Photosynthesis and Growth

Hanson and Rice (2014) introduced the book *Photosynthesis in Bryophytes and Early Land Plants* by asking two questions: "What is it about bryophyte growth form and physiology that has allowed them to persist through time and radiate into every terrestrial ecosystem, even dominating some of them? What can we learn from modern bryophytes to address this question and to predict how plants will respond to future environmental change?" Certainly bryophyte growth and photosynthetic responses provide a major part of the answers to these questions.

Many of the early experiments on photosynthesis in bryophytes were conducted on aquatic species. These were often used to determine the various influences of environmental factors on the photosynthesis of aquatic plants and provided us with some of our early foundations regarding photosynthesis. Plaetzer (1917) investigated temperature effects on both assimilation and respiration in water plants, including ***Fontinalis antipyretica*** (Figure 2) and ***Cinclidotus aquaticus*** (Figure 55). Harder (1921) examined limiting factors in carbonic acid assimilation, using ***Fontinalis*** (Figure 2, Figure 4, Figure 23) and ***Cinclidotus*** (Figure 26-Figure 27) among their experimental organisms. Wehner (1928) examined the physiology of photosynthesis in ***Fontinalis***. Iversen (1929) studied the influence of *p*H on macrophytes in Danish waters, including the aquatic bryophytes ***Chiloscyphus*** (Figure 24), ***Drepanocladus*** *s.l* (Figure 56)., ***Fontinalis***, ***Nardia*** (Figure 53), ***Riccia*** (Figure 9), ***Ricciocarpos*** (Figure 57), ***Scapania*** (Figure 7), and ***Scorpidium*** (Figure 58). Bode (1940) looked at the effects of various wavelengths on photosynthesis and discovered what appears to be the first record of **photorespiration**, noting that there was respiration in light that was different from that in dark in ***Fontinalis antipyretica*** (Figure 2). Auerbach *et al.* (1972) developed an apparatus for using IRGA to measure CO_2 metabolism in ***Fontinalis antipyretica*** (Figure 2, Figure 4) and verified its effectiveness by the changeover from light to dark and back to light.

Figure 55. ***Cinclidotus aquaticus***, a moss that inhabits emergent boulders. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Drepanocladus aduncus***, a moss that can occur in ditches. Photo by Hermann Schachner, through Creative Commons.

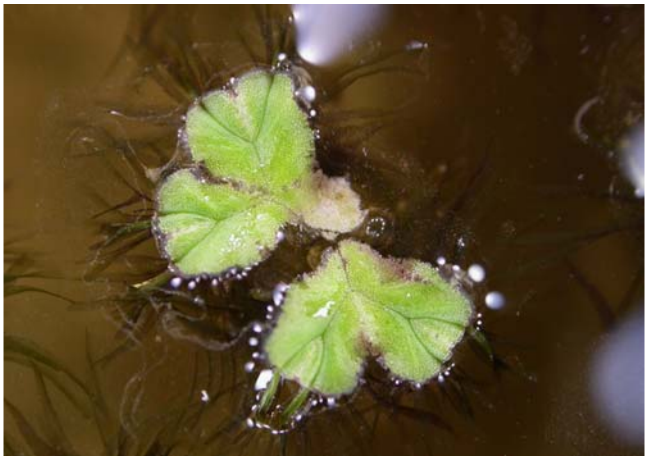

Figure 57. ***Ricciocarpos natans***, a floating thallose liverwort. Photo by Shaun Winterton, through Creative Commons.

Figure 58. ***Scorpidium scorpioides***, an emergent moss. Photo by Joanne Redwood, through Creative Commons.

Bryophytes typically are physiological shade plants with low chlorophyll *a*:*b* ratios (Proctor 1990). They become light-saturated at relatively low irradiance. Thus, they are well adapted for aquatic conditions. Their growth forms must balance water economy with light, carbon, and nutrient capture, the latter three often being limiting in the aquatic environment.

Conditions for existence may not always be those that promote growth. Survival can occur for long periods of time with no photosynthesis or growth. Thus, a fragment can arrive and survive, but not become established.

Glime (2014a) summarized published parameters that are important in determining photosynthetic rate in aquatic bryophytes. These include CO_2 concentrations, *p*H, boundary layer resistance, loss of light intensity with depth, loss of red light with depth (shifting to a greater percentage of green light), nutrients concentrations – especially nitrogen and phosphorus, sedimentation, periphyton, detritus, water level fluctuations causing desiccation, and temperature.

Sanford *et al*. (1974) found that temperature was among the important factors affecting growth of ***Hygrohypnum ochraceum*** (Figure 59). When the temperatures exceeded 26ºC, some stem tips died, and after four weeks at 30ºC, all died. But at temperatures at low as 4ºC, the mosses thrived and grew. Their optimum growth range for growth was 7-21ºC.

Figure 59. ***Hygrohypnum ochraceum***, a species in which temperature is an important factor affecting growth. Photo by S. H. Studdard, through Creative Commons.

One of the differences that bryophytes experience during photosynthesis is the lack of **lacunae** (unspecified spaces; Figure 60, Figure 61) within the leaves, although some thallose liverworts do have lacunae (Figure 60). In tracheophytes, these air spaces permit the leaves to refix respired CO_2. Westlake (1978; Kelly *et al*. 1981) noted that time lag between cessation of light and cessation of photosynthesis was very short, only ~2-7 minutes, a consequence of having no air spaces within the leaves. When Søndergaard (1979) compared the refixed CO_2 in ***Fontinalis antipyretica*** (Figure 2) to that in the tracheophytes ***Elodea canadensis*** (Figure 32), ***Dortmanna lacustris*** (syn. = *Lobelia dortmanna*; Figure 62), and ***Littorella uniflora*** (Figure 63), the ***F. antipyretica*** and ***Elodea canadensis*** had the lowest efficiencies. ***Elodea*** has few lacunae; ***Fontinalis*** has none. Søndergaard (1981) also demonstrated that for ***Fontinalis antipyretica*** the loss of C was greater in the dark than in the light. There was an initial burst in CO_2 in the light, after which the loss rates decreased little.

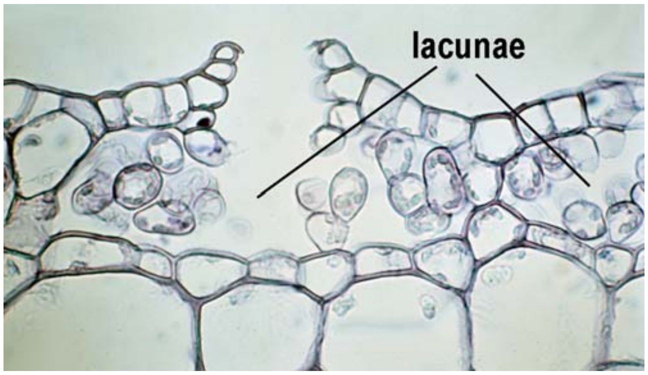

Figure 60. ***Marchantia polymorpha*** thallus cs showing lacunae with photosynthetic cells, associated with a pore. Photo by Wilhelm Barthlott, with permission.

Figure 61. ***Polytrichum juniperinum*** leaf lamellae CS showing air spaces. Photo courtesy of John Hribljan.

Figure 62. ***Dortmanna lacustris***, a species with greater CO_2 refixation efficiency than ***Elodea canadensis*** or ***Fontinalis antipyretica***. Photo by Przykuta, through Creative Commons.

Figure 63. ***Litorella uniflora***, a species with greater CO_2 refixation efficiency than ***Elodea canadensis*** or ***Fontinalis antipyretica***. Photo by Vallez, through Creative Commons.

Patterns of Allocation

The pattern of allocation can be an adaptation to environmental conditions present in the aquatic environment (Rice 1995). This determines the delegation of the carbon fixed to cell structure, hyaline vs photosynthetic cells, stem vs leaf tissue, and defense compounds.

Water Content

Among those factors important for photosynthesis and growth is the water content. Ueno and Kanda (2006) explored these relationships in Arctic populations of ***Calliergon giganteum*** (Figure 64), using IRGA to measure photosynthesis. They found that the maximum net photosynthetic rate was 1.2-1.6 mg CO_2 g^{-1} h^{-1}. At half this maximum net photosynthetic level, the water content was 980%, whereas at the optimum level it was 1500-1700% of dry weight. These values were the highest thus far reported for wetland mosses, suggesting that this species has a strong adaptation to hydric conditions.

Figure 64. ***Calliergon giganteum***, a species with an optimum of 1500-1700% of dry weight water content for photosynthesis. Photo by Misha Ignatov, with permission.

Respiration

One of the most notable discoveries in early studies on ***Fontinalis*** was that of **photorespiration**. Bode (1940) reported that there was a respiration present in the light that was different from that in the dark, and this appears to be the first discovery of photorespiration. He noted that ***Fontinalis antipyretica*** (Figure 2) carries out most respiration in blue light and photosynthesizes most in red light. But red light attenuates quickly as it passes through water. Bode also reported that chlorophyll respiration of this species increases in red light, but xanthophyll and carotene respiration increases in blue light.

Azcćon-Bieto *et al.* (1987) used cyanide resistance of respiration in two aquatic bryophytes and an alga to show that their respiratory resistance was lower (25-50%) compared to that of tracheophytes (>50%). They interpreted this to mean that the photosynthetic tissues of these aquatic autotrophs have a considerable capacity for alternative pathways. But understanding these alternatives has been elusive.

Peñuelas *et al.* (1988) found that aquatic bryophyte shoots had a higher rate of respiratory oxygen uptake (53-66 μmol O_2 g^{-1} DW h^{-1}) than did stems of flowering plants, but it was lower than those for flowering plant leaves. The cyanide-resistant respiration suggested the existence of an alternative pathway to the usual cytochrome system in all the plants and algae studied.

Steemann Nielsen (1947) cautioned that ***Fontinalis*** (Figure 2) had quite variable respiratory rates, making long experiments necessary. On the other hand, it has practically no C resource reserves that complicate measurements of photosynthesis in terrestrial tracheophytes.

Maberly (1985) examined the roles of photon irradiance, CO_2 concentration, and temperature in the aquatic moss ***Fontinalis antipyretica*** (Figure 2). Using 7 levels of photon irradiance and 5-6 concentrations of CO_2 at the ambient temperature of the collection site, Maberly measured photosynthesis in 4 months during the year. They found no evidence of photoinhibition, and light compensation was low compared to values for this species published elsewhere. The CO_2 compensation was typical of that for C_3 plants (those plants that initially store carbon from CO_2 in a 3-C compound and that are unable to store CO_2 in compounds used to complete the photosynthetic cycle later). They found that the slope of photosynthesis vs CO_2 concentration increases linearly with temperature in a manner that is consistent with the effects of boundary layer resistance. These measurements clearly demonstrated the interaction of temperature, CO_2 concentration, and irradiance on the rate of photosynthesis, emphasizing the need to consider all three factors when determining the upper and lower limits of net photosynthesis.

Winter Temperatures

Atanasiu (1968) reported on the photosynthesis and respiration of bryophytes in winter. Photosynthesis in some bryophytes occurs under ice (Bowes & Salvucci 1989), a condition wherein light levels are quite low.

Measurements indicate that the truly aquatic ***Fontinalis antipyretica*** (Figure 2) and ***F. squamosa*** (Figure 30) have their greatest vitality in winter, a time when both light levels and temperatures are low, hence reducing respiratory loss (Beaucourt *et al.* 1999; Beaucourt 2000). Furthermore, photosynthesis does not seem to be affected by internal concentration of nutrients or pigment composition. Beaucourt and coworkers reported that the chlorophyll concentration of ***Fontinalis antipyretica*** and ***F. squamosa*** in the studied European sites was similar to that found in terrestrial bryophytes and tracheophytes. Growth could occur throughout the year, but varied by season. Greater breadth of the metabolic capacity helps to account for the broader distribution of ***F. antipyretica*** when compared to that of ***F. squamosa***. Both species have only moderate nutritional requirements, permitting them to live in **oligotrophic** (having relatively low concentrations of plant nutrients) waters. They have low chl *a*: chl *b* ratios, typical of shade plants, and only limited photoprotective capacity. Nevertheless, their pheophytinization indices indicate a "good degree of vitality." Thus, these shade-adapted plants have rates of photosynthesis and respiration similar to those of shade-adapted tracheophytes. These are accompanied by low **apparent quantum yields** (measure of how many molecules of a certain substance such as H_2O_2, dissolved inorganic carbon, *etc.* can be produced per photon absorbed by, for example, colored dissolved organic matter), low **compensation points** (incorporated C = C lost in respiration), and low **saturation points** (level of light at which more light does not increase photosynthesis). They also develop photoprotective mechanisms at low irradiances and non-photochemical damping. These factors, along with their electron transport rate, indicate that the two aquatic mosses suffer from photoinhibition at relatively low light levels.

CO_2

Blackman and Smith (1910) were early researchers on the photosynthesis of aquatic plants, including bryophytes. They found that in ***Fontinalis*** (Figure 2, Figure 4, Figure 23) the assimilation increased steadily and proportionally as the CO_2 concentration increased. Then it stopped abruptly at ~0.023 g CO_2 assimilation per hour. They interpreted this as a limit set by the light intensity, creating a CO_2 saturation point for that light intensity. Compared to ***Elodea*** (Figure 32) in the same study, the ***Fontinalis*** was consistently less efficient in its uptake of CO_2. They suggested that the lack of an internal atmosphere limited the uptake in the moss. Consistent with the concept of limiting factors, they considered that whatever was in least supply imposes the limit to photosynthesis. The concept is based on Liebig's 1840 **Law of the Minimum** (Odum 1959), stating that growth is controlled by the scarcest resource, not the total amount of resources available.

A variety of factors interact to determine the level of photosynthesis that aquatic plants can achieve. These include use of alternative sources of CO_2, alternative sources of carbon besides CO_2, carbon-concentrating mechanisms, adaptations to achieve net photosynthesis in low light, and morphological adaptations to increase absorption of inorganic carbon and nutrients (Boston *et al.* 1989; Bowes & Salvucci 1989; Madsen & Sand-Jensen 1991).

Bowes and Salvucci (1989) considered plasticity in the photosynthetic metabolism to be an important adaptation in submersed aquatic macrophytes. They considered dissolved inorganic carbon, light, and temperature to be the main constraints, but *p*H, oxygen, and mineral nutrients may also contribute to the constraints. Because of low CO_2 diffusion rates, aquatic macrophytes typically have low light requirements and low photosynthetic rates. Photosynthesis in some occurs under ice and in some at 35ºC. Their plasticity is most recognizable in their variable CO_2 compensation points, in part because of their photorespiration. Nevertheless, alternate ways of obtaining or storing CO_2 have not been discovered in bryophytes.

CO_2 or Bicarbonate Use – or Not

James (1928), who included ***Fontinalis antipyretica*** (Figure 2) in his studies on CO_2 assimilation, noted that measurements of CO_2 uptake had assumed that all aquatic plants absorbed CO_2 only and could not use bicarbonate, but that this was a false assumption, at least for tracheophytes. Nevertheless, this question continued to puzzle those who studied photosynthesis in aquatic bryophytes (Ruttner 1947, 1948; Steeman Nielsen 1947; Steeman Nielsen & Kristiansen 1949; Stålfelt 1960a).

Stålfelt (1960b) noted that contributors to the publication *Handbuch der Pflanzenphysiology. V. Die* CO_2-*assimilation* had shown the dependence of CO_2 assimilation on light, temperature, and carbonic acid, noting the interactions of external and internal factors in CO_2 assimilation. Nevertheless, the ability of some aquatic bryophytes to thrive in alkaline streams where free CO_2 is scarce, still lacks explanation today.

Madsen and Sand-Jensen (1991) also puzzled over the relationship between CO_2 concentration and net photosynthesis in aquatic plants, including mosses. They found that it was a more gradual relationship than that predicted by **Michaelis-Menten kinetics** (equation relating reaction velocity to substrate concentration). This suggested that other factors besides activity of carboxylation enzymes were at play in regulating photosynthesis. When CO_2 concentrations in the medium are low, photosynthesis is restricted by the slow diffusion rate into the plant at the carboxylation site. The maximum possible photosynthetic capacity seems to be limited by the enzyme activity or turnover of intermediates in the carbon reduction cycle, including limitations by ATP and reducing agents. But for many of the aquatic macrophytes (~50% of those tested), bicarbonate can be a source of carbon for photosynthesis. A number of researchers have failed to find any use of bicarbonates by aquatic bryophytes (Bain & Proctor 1980). Bain and Proctor used the rise in *p*H as an indicator of photosynthetic uptake of CO_2. They found equilibrium values around *p*H 8.0-9.0, a limit that indicates the mosses are CO_2 limited and unable to use bicarbonate. By comparison, four known bicarbonate-using macrophytes reached equilibrium at *p*H 10.1 to 10.9. The hornwort ***Anthoceros husnotii*** (Figure 65), on the other hand, reached its maximum *p*H value at 9.5 in 2.0 mM $NaHCO_3$, suggesting a possible uptake mechanism for bicarbonate. ***Anthoceros***, a member of **Anthocerotophyta**, has pyrenoids (Figure 66), and these have been considered as possible CO_2-concentrating organelles (Smith & Griffiths 1996; Raven *et al.* 2018).

Figure 65. ***Anthoceros agrestis***; maximum photosynthesis of ***A. husnotii*** reached a *p*H of 9.2. Photo by Jean Faubert, with permission.

Figure 66. Cells of **Anthocerotophyta** showing doughnut-shaped pyrenoids. Photo by Chris Lobban, with permission.

Some aquatic plants, particularly the isoetids, have a carbon-concentrating mechanism that permits the binding of CO_2 at night for later use. As noted, we know that among the bryophytes, the **Anthocerotophyta** (Figure 65) have a CO_2-concentrating mechanism in the pyrenoid. However, no such structure is known in the aquatic bryophytes outside this phylum. Is there some other mechanism for trapping CO_2 or for converting bicarbonates?

Raven *et al.* (1998) found that most bryophytes tested were typical C_3 plants. However, two of the aquatic mosses, ***Fissidens*** *cf.* ***mahatonensis*** and ***Fontinalis antipyretica*** (Figure 2) behave as if they have a CO_2-concentrating mechanism. Furthermore, in running water there seems to be little restriction of CO_2 fixation due to CO_2 diffusion.

As noted by Madsen and Sand-Jensen (1991), one option exhibited by tracheophytes is the development of floating or aerial leaves, giving them access to atmospheric CO_2. To my knowledge, such a possibility has not been explored in bryophytes. But consider the bryophytes that are partly submersed and partly emergent on rocks. They remain fully hydrated through splash, but have access above the water line to atmospheric CO_2. This provides two possibilities. The CO_2 could be taken into exposed leaves and transported to other parts of the plant, or the CO_2 could be incorporated into intermediate or even final products and then transported to sites where it is needed. Many studies indicate that bryophytes are able to transport substances throughout the plant, so the latter explanation is feasible. Both hypotheses remain to be tested, possibly through tracer studies of labelled atmospheric CO_2.

Madsen *et al.* (1993a) demonstrated that net photosynthesis of stream macrophytes declined 34-61% as flow velocity in a stream increased from 1 to 8.6 cm s^{-1}. At the same time dark respiration increased 2.4-fold over that range. These included the moss ***Fontinalis antipyretica*** (Figure 2, a species considered unable to use bicarbonates. But how does this relate to CO_2 usage?

Madsen *et al.* (1993b) suggested that plant species with a high ability to extract carbon typically, possibly through bicarbonate use, had low RUBISCO activity, low chlorophyll concentrations, and low surface to volume ratio. This was particularly true for marine algae. Those species with low ability to extract carbon exhibited an opposite pattern. Madsen and coworkers suggest that it costs less to accomplish carbon assimilation in plants with a CO_2- concentrating mechanism. These relationships have not been investigated in bryophytes and should be investigated, especially in the **Anthocerotophyta** (Figure 65).

Having emergent parts permits some semi-aquatic bryophytes to obtain atmospheric CO_2 in their growing tips, but this is not an available option for truly aquatic species. Mosses such as ***Fissidens grandifrons*** (Figure 67) can live in waterfalls where exposure to atmospheric gasses is more common, but they can also exist and grow in completely submersed conditions in alkaline water where one would not expect to find any free CO_2 (Glime & Vitt 1987). So how do these mosses obtain the carbon needed for photosynthesis?

Figure 67. ***Fissidens grandifrons***, a moss that can grow completely submersed in alkaline streams. Photo by Janice Glime.

One possibility is CO_2 from sediments and adhering microbes, as reported by Madsen and Sand-Jensen for tracheophytes (1991). In some tracheophytes, the sediments can contribute more than 90% of the total carbon uptake. But many of these tracheophytes have pumping mechanisms that move the CO_2 from the sediments, through roots or tubers, to upper parts of the plants. Such a mechanism does not seem possible in bryophytes because of their lack of **lacunae** (spaces) in the stems where they could carry the CO_2 to leaves.

Sanford *et al.* (1974) concluded that CO_2 from the bacterial flora was important for the growth of ***Hygrohypnum ochraceum*** (Figure 59) in the Sacramento River, California, USA. In their experiments, an increase in dissolved CO_2 promoted an increase in elongation. Furthermore, the moss was less abundant in areas of the river that had a lower CO_2 level.

Nevertheless, in the cold waters of glacial melt streams such as those where Glime and Vitt (1987) found ***Fissidens grandifrons*** (Figure 67), we would expect the transformation of evolved CO_2 or loss to the atmosphere to be slowed by the low temperature. With no epidermis or thick waxy cuticle to interfere with CO_2 absorption (bryophytes often do have a cuticle – Green & Lange 1995), we could expect the moss to grab the CO_2 before all could be lost to the atmosphere or the bicarbonate-carbonate pathway in the water. But again, we have no evidence to support this hypothesis. I would guess that the rapid flow of these glacial streams does not facilitate the accumulation of organic silt. The microbes on the mosses have not been examined.

Another possibility that has not been explored is the possibility that the cation exchange sites on moss leaf cells could create an environment in which bicarbonate is converted to CO_2 due to lowering of *p*H at the leaf surface. We know that bryophytes (not just ***Sphagnum*** – Figure 54) have cation exchange. That means that the cell walls, including those on the surface, release hydrogen ions, thus creating a microenvironment of lower *p*H.

Or perhaps the carbonic anhydrase in the moss leaf cells (see Steemann Nielsen & Kristiansen 1949; Arancibia & Graham 2003). is able to convert bicarbonates in contact with the moss leaves to CO_2 at the leaf surface. Could this be sufficient to effect the change of bicarbonates, and even carbonates to release free CO_2 at the moss surface?

But the controversy continued. Osmond *et al.* (1981) found that delta ^{13}C values were consistent with the hypothesis that ***Fontinalis antipyretica*** (Figure 2) used almost exclusively free CO_2 in photosynthesis. Rather, they considered that the boundary layer diffusion and bicarbonate uptake may determine the assimilation rate. Their data on differences in different flow rates seemed to confirm this.

When attempting to test the reliability of radiocarbon dating of aquatic mosses, MacDonald *et al.* (1987) got a surprise. They found ^{14}C dates in the moss ***Drepanocladus longifolius*** (Figure 68) that were considerably older than the plant macrofossils of terrestrial species. The ^{14}C of living ***D. longifolius*** in the lake was less than 85% modern. Could the CO_2 used by the mosses come from sediment decomposition that releases older ^{14}C?

Figure 68. ***Drepanocladus longifolius***, a species in which extant plants have ancient carbon, suggesting use of CO_2 from the sediments. Photo by John Game Flickr Creative Commons.

Burr (1941) concluded that ***Fontinalis*** (Figure 2, Figure 4, Figure 23) is more productive in bicarbonate than in CO_2, but finding any mechanism to explain such a relationship has been elusive. Allen and Spence (1981) concluded that there was a gradation of bicarbonate users, not a "user" vs "non-user," among aquatic plants. This, in fact, makes some sense for this genus.

Farmer *et al.* (1986) tested 15 species of freshwater macrophytes for activities of RUBISCO and PEP carboxylase in photosynthesis. **RUBISCO** (enzyme present in plant chloroplasts, involved in fixing atmospheric CO_2 during photosynthesis and in oxygenation of resulting compound during photorespiration) was the most active in all species, including the moss ***Fontinalis antipyretica*** (Figure 2) and some liverworts, a usage consistent with C_3 plants.

While we are speculating, we might also consider the possibility of organic sources of carbon such as amino acids. We know that aquatic mosses can take up amino acids (Alghamdi 2003), but this would again require sediments, adhering organisms, or amino acids suspended in the water. And can they serve as a carbon source for photosynthesis in addition to their role as a nitrogen source? Are there other organic acids that can serve as photosynthetic carbon sources?

We have tended to underestimate the evolutionary changes in bryophytes (Glime 2011). While tracheophytes were developing all sorts of structural diversification, bryophytes were limited by their lack of lignin and consequent small size. Lacking these options would put more selection pressure on biochemical innovations. This is evidenced by the wide range of biochemical defenses against herbivory. The bryophytes have had even longer than tracheophytes to diversify. Why should we expect them to have evolved fewer adaptations? Rather, with selection pressures acting on a generation with only one set of chromosomes, we should expect more beneficial change to persist while unbeneficial ones can more easily be eliminated. We should pay more attention to their biochemical-physiological adaptations.

*p*H

Early studies on aquatic bryophytes indicated that many had a restricted *p*H range (Iversen 1929). Negoro (1938) reported on bryophyte associations in minerotrophic acidic waters in Japan. The *p*H can be an important limiting factor for bryophyte colonization (Apinis & Lacis 1936), especially in water. It affects the solubility of CO_2 in the water. It can also affect the solubility and availability of other nutrients. Steemann Nielsen (1952) examined several aquatic species, including ***Fontinalis antipyretica*** (Figure 2) and ***F. dalecarlica*** (Figure 42), regarding their persistence at extreme *p*H values. Acidity has been sufficiently important that Tremp and Kohler (1993), among others, advocated using water mosses as indicators of acidification to monitor rivers.

Tremp *et al.* (2012) looked at the factors that were important in defining bryophyte communities. Among these, *p*H is an important determinant of the bryophyte flora. This is reflected in the bicarbonate/ionic strength, affecting the availability of CO_2. It is manifest in distinctly different bryofloras in hard and soft water.

For example, Westlake (1981) considered the presence of ***Fontinalis*** (Figure 2, Figure 4, Figure 23) in hard water to be an anomaly. This conclusion was based on the need for this moss to obtain its carbon for photosynthesis as free CO_2, with no indication that it can use bicarbonates.

Steemann Nielsen (1952) experimented with the effects of lowering the *p*H on the photosynthesis and coloration of several species of ***Fontinalis*** (Figure 2, Figure 4, Figure 23). After populations of ***Fontinalis dalecarlica*** (Figure 42) were cultured at *p*H 3.0-3.1 for 23 hours, photosynthesis was strongly reduced. The leaves, however, still appeared fresh and green. At *p*H 2.1 the photosynthetic rate decreased further. After 80 minutes the leaves still appeared normal, but after 21 hours the green color was almost totally gone. ***Fontinalis antipyretica*** (Figure 2) had even less ability to endure low *p*H. In fact, this species lost its green color completely after 22 hours at *p*H 3.0. On the other hand, at *p*H 3.1 for only 80 minutes, ***F. antipyretica*** recovered completely when transferred to less acid water. At *p*H 4.0 there was only a slight decrease in photosynthesis after one hour. At *p*H 6.5, there was no decrease after 20 hours. Sorensen (1948) reported a field *p*H range of 5.5-8.2 for this species. It appears that the main factor separating suitable *p*H ranges for these two species is the ability to obtain sufficient CO_2, but at low *p*H levels ***F. antipyretica*** can suffer severe chlorophyll damage.

Much of our understanding of the effects of acid waters on bryophyte communities has come from studies on acid rain effects. Elwood and Mulholland (1989) found that both biomass and productivity of epilithic algae and bryophytes seemed to increase when the stream water *p*H declined to sustained levels below 5.0, whereas at the same time the fish and macroinvertebrates declined. The benefits of this lower *p*H might be in the greater availability of free CO_2 at those levels.

Turner *et al.* (2001) used phosphatase activities as a measure of *p*H effects. Enzymes such as these have optimal ranges for temperature and *p*H and can cease activity when very far out of that range. They found that in the aquatic mosses, phosphomonoesterase (PMEase) activity was at its optimum activity at *p*H 5.0. For phosphodiesterase (PDEase) the optimum was at *p*H 5.7. Staining suggested that the PMEase activity occurred in the cell wall of most of the moss species. Not all species exhibited PDEase activities.

Tessler *et al.* (2013) also identified Ca and Mg as important factors in determining bryophyte distribution. These two minerals are indicators of streams with a higher than neutral *p*H. They also found that bryophyte tissue concentrations of phosphorus were significantly correlated with *p*H. This was particularly pronounced for ***Fontinalis*** *cf.* ***dalecarlica*** (Figure 42) at low *p*H, with PMEase activity in the range of 4-7 being mostly indifferent to the *p*H level. The PMEase activity of ***Scapania undulata*** (Figure 7) likewise varied inversely with *p*H level, peaking at intermediate *p*H, but the activity also varied with the source of the water in the same *p*H range. ***Hygrohypnum ochraceum*** (Figure 59) seemed indifferent to the source of the water, having maximum PMEase activity at a *p*H of 5. Some species [***Andreaea rothii*** (Figure 69), ***Marsupella emarginata*** (Figure 70)] had relatively narrow *p*H optima in a low *p*H range, typically with peak PMEase activity at the lowest pH conditions tested, while others had narrow ranges at neutral levels [*e.g.* ***Hygrohypnum ochraceum***, ***Racomitrium aciculare*** (Figure 71)]. Species such as ***Hygrohypnum eugyrium*** (Figure 72-Figure 73) had a broad *p*H tolerance range.

Figure 69. ***Andreaea rothii***, a rock-dwelling species with a narrow low *p*H range. Photo by Michael Lüth, with permission.

Figure 70. ***Marsupella emarginata***, a species with a narrow low *p*H range. Photo by Štěpán Koval, with permission.

Figure 71. ***Racomitrium aciculare***, a species with a narrow *p*H range around neutral. Photo by Michael Lüth, with permission.

Figure 72. ***Hygrohypnum eugyrium*** habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Hygrohypnum eugyrium***, a species with a broad *p*H range. Photo by Hermann Schachner, through Creative Commons.

Some bryophytes seem to be more typical in acidic streams. This is true for ***Scapania undulata*** (Figure 7) and ***Nardia compressa*** (Figure 53) in Wales (*p*H 5.2-5.8) (Ormerod *et al*. 1987). ***Fontinalis*** (Figure 2, Figure 4, Figure 23), on the other hand, is more typical of streams with a *p*H of 5.6-6.2. But ability to tolerate a particular *p*H seems to differ geographically. In the streams of northeastern USA, ***Fontinalis*** species are common in acidic streams (*p*H 4.0-4.5). But in Wales, ***Fontinalis squamosa*** (Figure 30) is common, whereas that species does not occur in the northeastern USA. Furthermore, it is likely that physiological races are separated geographically and behave differently.

In the travertine streams of the French Alps and Britain, 26 mosses and 8 liverworts were documented in a *p*H range of 6.9-8.3 (Pentecost & Zhang 2002). The most common species were ***Eucladium verticillatum*** (Figure 74) and ***Palustriella commutata*** (Figure 75).

Figure 74. ***Eucladium verticillatum***, a common species on travertine rock with a *p*H range of 6.9-8.3. Photo by Michael Lüth, with permission.

Figure 75. ***Palustriella commutata***, a species that is able to grow in alkaline water. Photo by Michael Lüth, with permission.

Scorpidium scorpioides (Figure 58), ***S. cossonii*** (Figure 76), and ***S. revolvens*** (Figure 77) often occur in locations of high conservation value in Wales (Graham *et al*. 2019). These species are typical of springs and seepages and seem to form two distinct groups. ***Scorpidium cossonii*** characterizes one and ***S. revolvens*** the other, based on *p*H and electric conductivity. Habitats in Wales have a higher *p*H than those in Scandinavia.

But productivity is not the only factor affected by *p*H. Hargreaves *et al*. (1975) found that moss protonemata were more abundant than mature gametophytes in highly acidic streams with a *p*H value of 3.0 or less.

The *p*H also affects the solubility and uptake of heavy metals. Henricksen *et al*. (1988) concluded that it was a liverwort that served as a buffer and as a reservoir of aluminum. Massive amounts of aluminum were released at *p*H < 5. Both mosses and liverworts in the stream carry out ion exchange of base cations and aluminum during acid episodes. These ion exchange sites release base cations during acid episodes, neutralizing the additional H^+ in the water. Aluminum was a major contributor to this buffering.

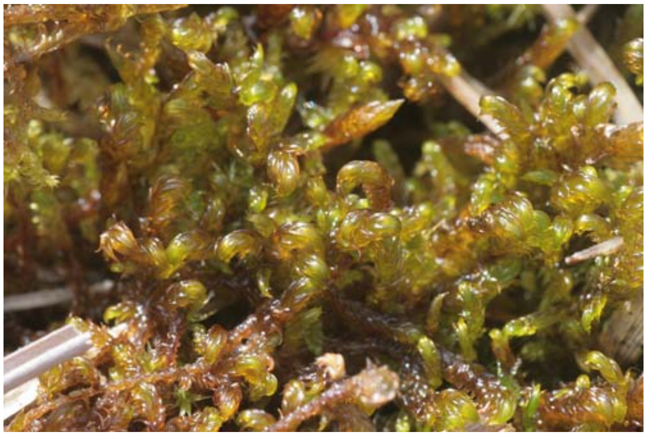

Figure 76. ***Scorpidium cossonii***, a species characteristic of springs and seepages. Photo by Hermann Schachner, through Creative Commons.

Figure 77. ***Scorpidium revolvens***, a species characteristic of springs and seepages. Photo by Hermann Schachner, through Creative Commons.

When Davies (2007) exposed shoot tips of ***Fontinalis antipyretica*** (Figure 2) to sulfate concentrations for 21 days at various levels of water hardness, the mosses did not respond well. They experienced significant reductions in shoot length, dry weight, and chlorophyll *a* and *b* concentrations in soft water. As the hardness as $CaCO_3$ increased, the negative effects of sulfate toxicity decreased.

Boundary-layer Resistance

Boundary resistance can prevent CO_2 from crossing into the bryophyte leaf. Jenkins and Proctor (1985) used wind tunnel evaporation measurements to assess the boundary-layer resistance to the photosynthetic uptake of CO_2 in aquatic bryophytes. They found resistances of the leafy liverworts ***Nardia compressa*** (Figure 53) and ***Scapania undulata*** (Figure 7) to range 35 to 5 s mm^{-1} (siemens = unit used to measure electrical conductance) and 70 to 9 s mm^{-1}, respectively, at water velocities of 0.02-0.2 m s^{-1}. For the streamers of ***Fontinalis antipyretica*** (Figure 2), resistance is about 180 - 15 s mm^{-1} over the range of water velocity of 0.01 to 0.2 m s^{-1}. They estimated that boundary layer resistance limits photosynthesis at stream velocities below about 0.01 m s^{-1} in ***Fontinalis*** and below about 0.1 m s^{-1} in the mat-forming species. They considered the mat growth form of the liverworts to minimize the boundary-layer resistance at high velocities while minimizing drag. On the other hand, the streamers of ***Fontinalis*** permit it to maximize surface area under limiting levels of boundary-layer resistance.

While ***Fontinalis*** (Figure 2, Figure 4, Figure 23) continued to confound the issue of obtaining CO_2 in alkaline water, another ***Fissidens***, ***F. grandifrons*** (Figure 67), emerged as doing something different. This species is known to do well in streams with high *p*H (*e.g.* Glime & Vitt 1987). Peñuelas (1985) again investigated the ability of these two species to use bicarbonates and CO_2 as carbon sources for photosynthesis. He found that in $NaHCO_3$ solutions, ***Fontinalis*** was able to increase the *p*H to a maximum of 9.6, corresponding to a CO_2 compensation point of 1.1 mmol m^{-3} CO_2. This increase in *p*H is too great to be explained by CO_2 uptake alone. In fact, although the net photosynthesis decreased at high levels of *p*H, it did not reach zero until the *p*H reached 10.10 for ***Fissidens grandifrons*** and 11.8-12.0 in ***Fontinalis antipyretica*** (Figure 2)! Photosynthesis was even increased at greater bicarbonate concentrations when CO_2 was held constant. This led Peñuelas to conclude that these two bryophytes could use bicarbonate. The question still remained – how?

Yet, in 1989, Prins and Elzenga (1989) still stated that bryophytes could not use bicarbonates. They suggested three ways by which some aquatic plants might be able to use bicarbonates:

1. carbonic acid symport
2. external acidification of bicarbonate into CO_2
3. increase in rate of conversion of bicarbonate into CO_2 by carbonic anhydrase.

We know that bryophyte leaves (not just ***Sphagnum*** – Figure 54) conduct cation exchange (Glime *et al.* 1982), so this mechanism could be used to accomplish #2. Still, in 1991, Raven considered any CO_2-concentrating mechanism in bryophytes to be absent or poorly developed. In 1994, based on an extensive literature survey, Raven *et al.* further stated that in streamer mosses such as ***Fontinalis antipyretica*** (Figure 2), the entry of CO_2 is limited only by rates of CO_2 diffusion into the moss; they still acknowledged no use of bicarbonate by this moss. So why couldn't they use all three methods simultaneously?

Diving Bell

One novel idea is that mosses may use their photosynthetic air bubbles (Figure 1) like a diving bell. It is typical to find photosynthesizing aquatic mosses and liverworts covered in tiny air bubbles, a phenomenon known as **pearling**. If they are able to work like a diving bell, the bubble with a high concentration of photosynthetic O_2 would trade its O_2 for CO_2 that is dissolved in the water, thus creating a gaseous environment containing CO_2 at the leaf surface. Such mechanisms are used, in reverse, to keep diving insects and spiders alive under water, sometimes as long as an hour. But the insects carry their "bells" of oxygen-rich air under water, then breathe in O_2 and expel CO_2. As the O_2 concentration diminishes, more diffuses into the diving bell from the water, and the CO_2 from their respiration diffuses from the diving bell into the water. The same mechanism should work for bryophytes, but this mechanism assumes that there is free gaseous CO_2 in the water column, not bicarbonate or carbonate. Thus, if it works at all, it presumably works only at lower *p*H levels where free CO_2 exists ... or perhaps at higher *p*H levels where microbial contributions are available on the surface of the bryophyte. Could microbial respiration at night by periphyton be contained in a diving bell, later to be exchanged for O_2 in the daytime?

Ecotypes

I have already noted the possibility of ecotype differences. For example, ***Hygroamblystegium fluviatile*** (Figure 12) and ***Fontinalis antipyretica*** (Figure 2) had similar trophic responses to eutrophication in two calcareous lowland streams, and both reached their maximum occurrences in oligotrophic water (Vanderpoorten & Durwael 1999). On the other hand, ***Hygroamblystegium tenax*** (Figure 11), ***H. fluviatile***, ***Fissidens crassipes*** (Figure 28), and ***Fontinalis antipyretica*** had distinctly different response curves in different hydrographic networks, suggesting the presence of physiological races or ecotypes in these species. Such differences could account for the widespread and varied habitats of some species.

Seasons and Phenology

Most stream bryophytes occur as **perennials** and can be found during all seasons of the year (Vieira *et al.* 2014). They may disappear or diminish during ice breakup or heavy runoff and spates, but otherwise, they must respond to changes in their environment through changes in their physiological behavior. Vieira and coworkers proposed that since bryophytes are able to withstand natural seasonal desiccation and have perennial life-strategies permitting them to be assessed any time of year, they can be suitable tools for the characterization of reference conditions.

The environment can signal that it is time to change physiological activity through a number of mechanisms. We have discussed many aspects of nutrients and their variable availability throughout the year. Temperature, light intensity, and photoperiod also offer potential signals to changes in physiological activity.

Glime and coworkers (Glime 1982; Glime & Raeymaekers 1987) have measured differences in number of reproductive structures, growth rates, and rhizoid productions of ***Fontinalis*** (Figure 2, Figure 4, Figure 23) species in various seasons and modelled these changes based on light and temperature. They found that temperatures ranging from 5 to 15ºC favored branching, but that the optimum temperature differed among species. Branching is greatly reduced in pool conditions compared to that in flowing water. More rhizoids were produced at temperatures above 10ºC, coinciding with periods when water levels were lowest, permitting more opportunity for attachment without fighting heavy flow. Rhizoid production can co-occur with branch production. These life strategies will be further discussed in the next subchapter.

Steinman and Boston (1993) followed the photosynthetic rates and phosphorus uptake of aquatic bryophytes in a woodland stream in Tennessee, USA, for 13 months. The most abundant bryophyte was the leafy liverwort **Porella pinnata** (Figure 20-Figure 21), with **Brachythecium** cf. **campestre** (Figure 78) and **Amblystegium** (**Hygroamblystegium**?; Figure 11-Figure 12) following in abundance. The bryophyte abundance peaked in late summer, but was reduced by a severe winter storm. **Porella pinnata** exhibited significantly greater area-specific photosynthetic rates than did the other bryophyte species and exceeded the periphyton in P uptake. However the periphyton significantly exceeded the other autotrophs in biomass-specific photosynthesis and P uptake rates.

Figure 78. **Brachythecium campestre**, a common bryophyte in a woodland stream in Tennessee, USA. Photo by Jerry Jenkins, Northern Forest Atlas, with permission.

Kelly and Whitton (1987) measured shoot growth of **Platyhypnidium riparioides** (Figure 6) in the Northern Pennines, England. Growth occurred in every month, with the maximum in spring and minimum in winter. Autumn experienced a second, smaller peak.

Everitt and Burkholder (1991) observed the seasonal dynamics of the macrophyte communities for a stream flowing over granite in North Carolina, USA. Bryophytes were not dominant, but **Fontinalis** sp (Figure 2, Figure 4, Figure 23) occurred. In the shaded sites, **Fontinalis** dominated in the warm seasons, but the red alga **Lemanea australis** (see Figure 79) dominated during the cool seasons.

Figure 79. **Lemanea fluviatilis**; **L. australis** dominates in winter and **Fontinalis** in the summer in a North Carolina, USA stream. Photo by J. C. Schou, with permission.

Núñez-Olivera *et al.* (2001) questioned whether seasonal variations in nutrient contents of aquatic bryophytes were due to internal or external measures. The elements N, P, Na, and Fe showed the most frequent annual cycles. Typically, the lowest concentrations appeared in spring and the highest in autumn. These seasonal cycles depended on the interactions of both internal and environmental factors. Growth in the bryophytes [**Fontinalis antipyretica** (Figure 2), **F. squamosa** (Figure 30), **Jungermannia exsertifolia** subsp. **cordifolia** (Figure 22), and **Apopellia endiviifolia** (Figure 25)] caused a dilution of the element concentrations in the bryophyte tissues. Seasonal changes occurred in the environment, causing changes in the element concentrations resulting from runoff, decomposition, changing flow rates, and litter input. Unlike those of heavy metals, the concentrations of elements in the bryophytes did not correlate well with those in the stream water.

Beaucourt *et al.* (2001) concluded that growth in **Fontinalis antipyretica** (Figure 2) and **F. squamosa** (Figure 30) was determined by both genetic and environmental factors. They found higher growth in early autumn and spring. We found similar growth patterns in **Fontinalis hypnoides** (Figure 80) and **F. duriaei** (Figure 39) (Glime & Acton 1979; Glime 1980, 1982; Fornwall & Glime 1982). **Fontinalis antipyretica** exhibited a higher growth rate than did **F. squamosa**, a factor that could contribute to some differences seen in seasonal nutrient uptake (Beaucourt *et al.* 2001).

Figure 80. **Fontinalis hypnoides**, a species with its highest growth in early autumn and spring. Photo by Jean Faubert, with permission.

Martínez-Abaigar *et al.* (2002a) used **Fontinalis antipyretica** (Figure 2) and **F. squamosa** (Figure 30) to track the seasonal variation in N, P, K, Ca, Mg, Fe, and Na in a mountain stream in Spain. The two species had similar elemental concentrations. **Fontinalis antipyretica** (Figure 2) had a higher nitrogen concentration, perhaps due to greater physiological activity related to its more rapid growth. Concentrations of K, Fe, P, and N increased in every plant segment and increased through summer and autumn, then decreased through winter and spring. The concentrations in the plants seemed to depend on the growth cycle, having only scattered correlations with water conditions.

We might expect ice to be a problem for aquatic bryophytes. Frahm (2006) observed that aquatic mosses can overwinter in ice. This does not appear to cause any physiological problems for high altitude or high latitude stream bryophytes, but the problems caused by dislodgment of the mosses have been discussed in an earlier subchapter.

Kalacheva *et al*. (2009) assessed the seasonal changes of polyunsaturated acids (PUFA) in ***Fontinalis antipyretica*** (Figure 2) from the Yenisei River in Siberia. The relative content of acetylenic acids in fatty acids remained high throughout the year, but achieved its peak in summer. These are highly specific (unique) to the mosses and can serve as biochemical markers in trophic interactions. The relative content of PUFA from the omega3 group was greatest in spring, whereas the omega6 group varied little throughout the year.

Pejin *et al*. (2012) examined fatty acids in the mosses ***Atrichum undulatum*** (Figure 81) and ***Hypnum andoi*** (Figure 82) in winter. They identified eight fatty acids using the chloroform/methanol extraction, one of which was arachidonic (6.21% of total methanol extractions). They considered ***A. undulatum*** to be a good winter source of linoleic acid and alpha-linolenic acid. Kajikawa *et al*. (2008) reported that the thallose liverwort ***Marchantia polymorpha*** (Figure 83) uses linoleic and α-linolenic acid to synthesize arachidonic and eicosapentaenoic acids, respectively.

Figure 81. ***Atrichum undulatum***, a good winter source of linoleic acid and alpha-linolenic acid. Photo by Michael Lüth, with permission.

Fatty acids seem to vary considerably among bryophytes, even when species are closely related. For example, the floating liverwort ***Riccia fluitans*** (Figure 9) exhibited a new acetylenic acid (Vierengel *et al*. 1987), but other tested members of the family **Ricciaceae** (floating liverwort ***Ricciocarpos*** – Figure 57) and other thallose liverworts outside the **Ricciaceae** had no detectable acetylenic fatty acids (Kohn *et al*. 1988). However all 12 species of the genus ***Riccia*** exhibited acetylenic fatty acids.

One study has examined the fatty acid composition of a number of aquatic bryophytes (Dembitsky & Rezanka 1995). The acetylenic fatty acids in triacylglycerols ranged from 6.6% in the moss ***Calliergon cordifolium*** (Figure 8) to 80.2% in the liverwort ***Riccia fluitans*** (Figure 9). It is not unusual for bryophytes to produce high amounts of very long-chain polyunsaturated fatty acids such as arachidonic acid and eicosapentaenoic acid (Lu *et al*. 2019). These are likewise common in marine algae, but are rare in tracheophytes. These fatty acids are typically amplified under conditions of biotic or abiotic stress.

Figure 82. ***Hypnum andoi***, a good winter source of linoleic acid and alpha-linolenic acid. Photo by James K. Lindsey, through Creative Commons.

Figure 83. ***Marchantia polymorpha***, a species that uses linoleic and α-linolenic acid to synthesize arachidonic and eicosapentaenoic acids, respectively. Photo by Michael Lüth, with permission.

Huneck *et al*. (1982) assessed the essential oils in the aquatic leafy liverwort ***Scapania undulata*** (Figure 7). The total essential oils ranged only from a low of 0.92 % dry weight in August to a high of 1.39 % in March when sampled from this liverwort in a small stream in a Thuringian Forest in Germany. But the relative constituents varied more widely, with longipinanol reaching its lowest of ~4% of the essential oils in May to a high of ~25% in April. It was always of the lowest concentration, whereas longiborneal was always exhibited the highest concentration except in August when the third oil, longipinene, slightly exceeded it.

Ellwood *et al*. (2007) found a summer/autumn increase in Km and Vmax of bryophytes that corresponded with the seasonal decrease in the phosphate supply in a northern England stream. PMEase and PDEase detection indicated that this phenomenon was widespread among mosses. The influence of the epiphytes appeared to be negligible. Instead, it is seasonal responses of the enzyme activity to changes in the nutrient supplies and requirements.

Given the importance of pigment concentrations in acclimating to light intensities, it is not surprising that these vary with the seasons in aquatic bryophytes (Martínez-Abaigar *et al*. (1994). Using 13 aquatic bryophytes, Martínez-Abaigar and coworkers found chlorophyll contents ranging 2.2-9.2 mg g^{-1} dry weight and 97-351 mg m^{-2} shoot area. Phaeopigment ratios differed little with seasons or habitat. However, as noted earlier, a strong decrease occurred in chlorophyll content and chlorophyll *a*/*b* ratio in summer, apparently due to desiccation. Those bryophytes that were continuously wet had less dramatic seasonal cycles, and these correlated with changes in light conditions.

For forested streams, light intensities vary widely between summer under the canopy and winter when the leaves are gone and the snow and ice are highly reflective. The aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 22) from a mountain stream in Spain exhibited little difference between years during the three years of study (Núñez-Olivera *et al*. (2009). However seasonal changes were apparent. New shoots in summer and autumn had a high Fv/Fm ratio and accumulated higher amounts of several hydroxycinnamic acid derivatives than during winter and spring. No DNA damage was evident at any time. Increase of *p*-coumaroylmalic acid was most responsive to increase in UV-B radiation and was an indirect indicator of ozone loss from the stratosphere.

A similar study on ***Bryum pseudotriquetrum*** (Figure 84) and ***Fontinalis antipyretica*** (Figure 2) yielded similar results (Núñez-Olivera *et al*. 2010). Like the leafy liverwort ***Scapania undulata*** (Figure 7), neither moss species exhibited DNA damage, apparently due to an efficient DNA repair mechanism. Both species exhibited responses to UV-B by increased activity of the xanthophyll cycle and increase in bulk UV absorbance of methanol-extractable UV-absorbing compounds, MEUVAC. Changes in chlorophyll fluorescence parameters were less distinctive. ***Bryum pseudotriquetrum*** exhibited both MEUVAC and kaempferol 3.7-O-diglycoside responses to radiation levels while ***Fontinalis antipyretica*** did not exhibit any correlation with any environmental variables. Furthermore, ***B. pseudotriquetrum*** exhibited 3-4X the MEUVAC concentration compared to that of ***F. antipyretica***.

Reproductive Signals

Reproductive organs are difficult to observe in aquatic species and little research relates to their phenology or signals for their development. I (Glime 1984, 2014b) cultured ***Fontinalis dalecarlica*** (Figure 42) from a population at Highlands, North Carolina, USA for 16 weeks to determine phenological signals. Using 4 photoperiods at 8ºC and 1560 lux in artificial streams, I determined that this species behaves as a quantitative short-day (long night) plant. Archegonia were first produced in the regime of 6 hours of light, 18 hours of darkness, but in the longer photoperiods (shorter dark periods), an equal number of archegonia were present at the end of the 16 weeks. Longer photoperiods favored growth, branching, and rhizoid production. But at the longest photoperiod (18 hours light, 6 hours dark), both growth and branching were reduced.

Figure 84. ***Bryum pseudotriquetrum***, a species that exhibited both MEUVAC and kaempferol 3.7-O-diglycoside responses to radiation levels. Photo by Michael Lüth, with permission.

One surprise I found was that aerated mosses were able to produce more archegonia than did the submersed mosses (Glime 1984, 2014b). But this in fact could be adaptive for stream mosses. In this stream, male populations usually occupied different rocks from the females. Swimming from one rock to another would seem to be an improbable occurrence for the tiny male sperm in flowing water. Furthermore, could they really put on the brakes and stop at an appropriate female colony? By living above the water, sperm could be splashed by the turbulent water of the riffles and land on a clump of female mosses above the moving water, thus permitting the sperm to swim to the nearest female. Thus, having aerial archegonia seems to be adaptive for fertilization success.

See Chapter 2-5 of this volume for a discussion of life strategies in stream bryophytes.

Periphyton

Fisher and Likens (1972) noted that the measurement of photosynthesis of the moss component in Bear Brook, New Hampshire, USA, included the productivity of the attached periphyton. This is a problem in measuring productivity of aquatic mosses anywhere. My personal experience indicates that the bryophytes are typically covered with periphyton (Glime & Acton 1979), and attempts to remove them often damage the bryophytes or are ineffective. Furthermore, even if the periphyton are removed, we have modified the system. CO_2 from respiring bacteria could compensate for CO_2 limitations in the water. Competition for light and nutrients could reduce productivity, as well as competition for CO_2.

We have already noted that epiphytic algae tend to increase on bryophytes at warmer temperatures. These likewise can block light and compete for CO_2, thus reducing the bryophyte productivity. Among these we typically find members of the blue-green bacteria (**Cyanobacteria**). Some of the macrophytes have a high uptake of the toxins from the **Cyanobacterium *Microcystis*** (Figure 85) (Pflugmacher 1653). In a study of four macrophytes, the grass *Phragmites communis* (Figure 86) had the greatest uptake. The moss ***Vesicularia dubyana*** (Figure 87) had a much lower uptake. Furthermore, when this species was followed in the succeeding hours, it initially experienced an oxygen decrease, thus a productivity loss. However, after half a day it had recovered and after nine days the oxygen production and consumption had returned to normal levels.

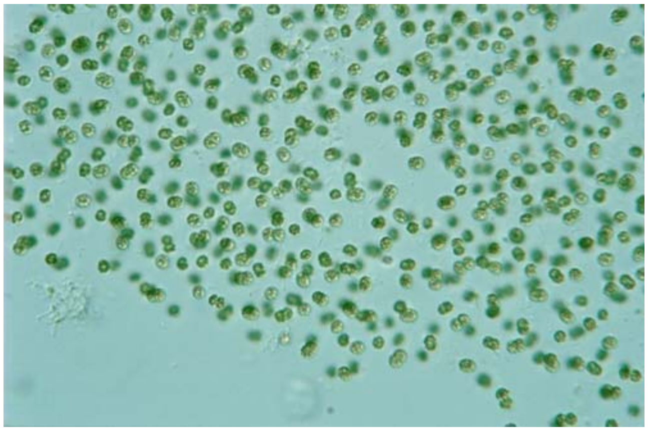

Figure 85. ***Microcystis***, a blue-green bacterium that produces toxins that can affect aquatic plants. Photo by Yuuki Tsukii, with permission.

Figure 86. ***Phragmites communis***, a species with high uptake of CO_2, especially compared with the aquatic moss ***Vesicularia dubyana***. Photo by Lazaregagnidze, through Creative Commons.

Herbivory and Pathogens

Lodge (1991) noted that researchers had put forward the hypothesis that macrophytes offer poor food quality due to low protein content. Nevertheless, macrophytes, including the aquatic bryophytes, are grazed. Lodge points out that often the grazers destroy more tissues than they eat. In any case, bryophytes are often the victims of consumption.

Figure 87. ***Vesicularia dubyana***, a moss with a low uptake of ***Microcystis*** toxins. Photo by Tan Sze Wei, AquamossNet.

Some researchers have assumed that bryophytes were not eaten because of low nutritional quality. However, this is not necessarily true (Liao & Glime 1996). ***Fontinalis antipyretica*** (Figure 2) produces the most total phenolics in the summer in the Keweenaw Peninsula of Michigan, USA, when herbivores are the most abundant. The phenolics are the lowest in spring when the growth of the moss is most rapid. Consumption rate on this species was lowest when the phenolic content was at its highest levels. The phenolic contents were also higher in sunny and intermediate habitats than in shady ones. This may be a defensive (stress) response in the higher light intensity where there is more UV radiation and potentially higher temperatures.

Acetylenic acids, noted above, are known for their antifungal properties against human pathogens (Xu *et al.* 2012), so it is likely that they are also effective against potential bryophyte pathogens.

Some mosses seem to be able to protect other mosses from herbivory. ***Fissidens fontanus*** (Figure 88) in northern Europe seems to be able to survive only when it is mixed with ***Fontinalis*** (Figure 2, Figure 4, Figure 23) (Lohammar 1954). Snails are common in the environment, but snails seem to avoid ***Fontinalis***, as demonstrated in aquaria, thus protecting the more edible ***Fissidens fontanus***.

Figure 88. ***Fissidens fontanus***, a species that benefits from growing with ***Fontinalis*** as an antiherbivore agent. Photo by Walter Lampa, through Creative Commons.

In the early stages of biochemical research, Marsili and Morelli (1968) noted the presence of triterpenes in the moss ***Thamnobryum alopecurum*** (Figure 89), a streambank moss. Such compounds are typically used as chemical defenses. For example, Toyota *et al*. (1999) isolated an eudesmane-type sesquiterpenoid from the aquatic leafy liverwort ***Chiloscyphus polyanthos*** (Figure 90).

Figure 89. ***Thamnobryum alopecurum***, a streambank moss with triterpenes. Photo by Hermann Schachner, through Creative Commons.

Figure 90. ***Chiloscyphus polyanthos***, a leafy liverwort with a eudesmane-type sesquiterpenoid. Photo by Hermann Schachner, through Creative Commons.

Parker *et al*. (2007) noted that stream mosses could provide refuges for stream macroinvertebrates. In their study, the large consumers ***Branta canadensis*** (Canada geese; Figure 91) and ***Procambarus spiculifer*** (crayfish; Figure 92) selectively consumed *Podostemum ceratophyllum* (riverweed; Figure 93) while ignoring the accompanying ***Fontinalis novae-angliae*** (Figure 93), despite the greater abundance (89% of biomass) of the moss. On the other hand, the number of macroinvertebrates on the mosses was twice that of the riverweed. In experiments, the researchers found that C18 acetylenic acid, octadeca-9,12-dien-6-ynoic acid, from the moss deterred the feeding by the crayfish. On the other hand, in lab feeding assays the amphipod ***Crangonyx gracilis*** (Figure 94) and isopod ***Asellus aqus*** (Figure 95) consumed significant amounts of the moss while rejecting the riverweed. These invertebrates were likewise not deterred by the extracted C18 acetylenic acid.

Figure 91. ***Branta canadensis***, a large consumer that avoids ***Fontinalis***, thus protecting the invertebrates living there. Photo by Lystopad, through Creative Commons.

Figure 92. ***Procambarus spiculifer***, a species that avoids eating ***Fontinalis***. Photo by Supertiger, through Creative Commons.

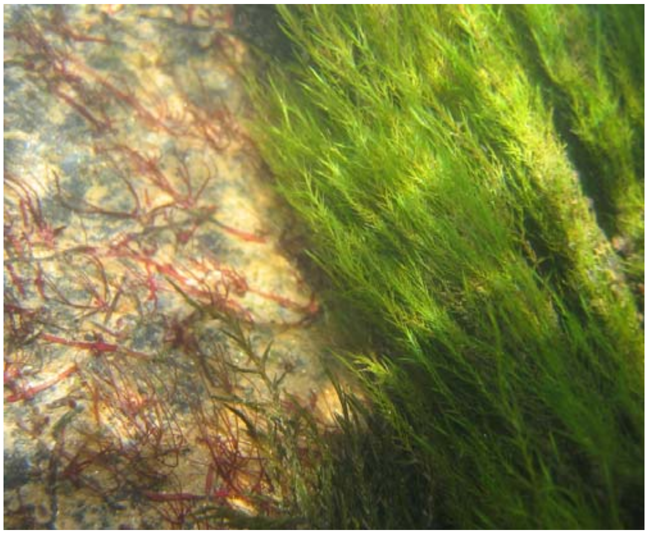

Figure 93. ***Podostemum ceratophyllum*** (**left**) and ***Fontinalis novae-angliae*** (**right**), the latter protecting invertebrates from grazing by geese. Photo by John Parker, with permission.

Figure 94. ***Crangonyx*** sp.. an amphipod that feeds on ***Fontinalis***. Photo from CBG Photography Group, Centre for Biodiversity, through Creative Commons.

Figure 95. ***Asellus aquaticus***, isopods that feed on ***Fontinalis***. Photo by M. J., through Creative Commons.

Living in water makes the bryophytes an excellent habitat for many microbes. By trapping sediments and providing substrate for periphyton, they become an outstanding dinner table for these microbes. But plants can be subject to attack from microbes, so it is predictable that a well-adapted plant in this environment will have mechanisms to prevent it from being attacked by them. Little has been done, beyond the antibacterial activity of ***Sphagnum*** (Figure 54), to determine this capability in aquatic bryophytes. However, research on the terrestrial ***Physcomitrella patens*** (Figure 96) has revealed several such defense mechanisms (Ponce de León & Montesano 2017). In fact, evidence indicates that these same mechanisms are conserved in flowering plants. These researchers found cell wall defenses that become activated through a MAP kinase cascade. Once pathogens begin their attack, the moss activates production of ROX and induces an HR-like reaction while increasing the levels of some hormones. It is likely that aquatic bryophytes have similar, but probably partially unique, mechanisms.

Figure 96. ***Physcomitrella patens*** with springtails; ***P. patens*** has chemical defenses against microbes. Photo by Bob Klips, with permission.

There is a much greater discussion of various interactions of stream bryophytes and invertebrates, including insects, in Volume 2, *Bryological Interaction*.

Summary

Although bryophytes require lower nutrient levels than do most tracheophytes, they can still experience limiting conditions. Their ability to accumulate ions makes them suitable bioindicators. Nutrient levels tend to be lowest in spring and highest in autumn. Nitrogen and phosphorus impose the most likely limitations and are typically low in stream habitats. At least some species can use ammonium as an N source, especially at higher *p*H levels. This seems to be influenced not only by the environment, but also by genetic variation within the species. And even within an individual, the ability to use nitrate vs ammonium can switch dependent on availability. Mosses exhibit little amplification of stored nitrate relative to the water compared to that of some tracheophytes. Evidence suggests that the P:N ratio might increase with P enrichment. Tissue concentration of P increases with time in enriched water, but K seems to be subject to leakage and its levels fluctuate in the tissues.

Potassium occurs dissolved in the cells. Calcium is bound to exchange sites in the cell wall. Magnesium is present in both locations. Thus potassium and magnesium are lost when the cells become desiccated and the membranes damaged. The soluble elements N, P, and K occur in the highest concentrations and are most mobile, having their highest concentrations in the apical portions. The least mobile elements (Ca, Mg, Fe) are highest in the basal portions. Species might be able to acclimate to changing water chemistry conditions by altering the uptake efficiency.

Heavy metals can cause damage to chlorophyll, loss of cellular organization, disruption of the nucleus, and plasmolysis. At even higher concentrations, deplasmolysis can occur. Locations of cytoplasmic vs cell wall can differ by species of bryophyte. Heavy metals can cause membrane damage and loss of K. Competition by H^+ on external exchange sites seems to be responsible for lower metal uptake in acidic water.

Many early photosynthetic studies were done on aquatic bryophytes, especially ***Fontinalis***. These included temperature effects on both assimilation and respiration, limiting factors in carbonic acid assimilation, influence of *p*H, effects of various wavelengths on photosynthesis, discovery of photorespiration, and use of IRGA to measure CO_2 metabolism.

Bryophytes are typically shade plants, having low chlorophyll *a*/*b* ratios. In the water they are usually limited by light, carbon, and nutrients. But their photosynthesis and growth are also affected by *p*H, boundary layer resistance, loss of red light in deeper water, sedimentation, periphyton, detritus, hydration state, water level fluctuations that cause desiccation, and temperature. Their growth temperature optima are generally 10-20ºC.

Although aquatic bryophytes are able to live in alkaline waters where free CO_2 concentrations are very low, and they seem to have alternative CO_2 pathways, we still don't understand how these work. Lack of internal air spaces prevents the re-use of respired CO_2.

Aquatic species are often characterized by low apparent quantum yields, low compensation points, and low saturation points. They can suffer from photoinhibition at relatively low light levels. The slope of photosynthesis vs CO_2 concentration increases linearly with temperature and may account for photoinhibition at low light levels. For forest species, light levels before freeze-over are higher in winter.

In the cold of winter, aquatic bryophyte photosynthesis seems to be unaffected by internal concentration of nutrients or pigment concentration. On the other hand, winter seems to be the period of greatest vitality for those in the water. Photosynthetic plasticity permits the bryophytes to photosynthesize and grow at these low temperatures.

CO_2 has a low diffusion rate in water, favoring low light requirements and variable CO_2 compensation points. At high *p*H levels, free CO_2 quickly converts to other carbon-containing compounds, severely limiting bryophyte photosynthesis. A number of aquatic tracheophytes are able to use bicarbonates in these conditions, but any direct evidence for this pathway in bryophytes has been elusive. One possibility is grabbing CO_2 emitted from sediments or bacterial respiration before it gets converted. CO_2 from such sources remains longer in cold water. Some periphyton can provide CO_2, but they also block light.

Typically, boundary layer resistance limits photosynthesis at stream velocities below about 0.01 m s^{-1} in ***Fontinalis*** (streamers) and below about 0.1 m s^{-1} in the mat-forming species. CO_2 could be held in a diving bell, exchanged for photosynthetic O_2, but the CO_2 must come from somewhere, possibly microbial respiration.

Aquatic bryophytes can be active year-round, making them superior organisms for biomonitoring compared to most aquatic tracheophytes. Nevertheless, rhizoid production, branch growth, and biomass gain can occur under different conditions. Higher growth in spring seems to benefit from greater nutrient levels, more light, plenty of water, and cool temperatures. On the other hand, nutrient concentrations in the plants seem to correlate with the growth cycle, not the water conditions. Fatty acid types and concentrations vary with season, as do pigment concentrations. Day length can signal the onset of sexual organ development.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa.

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