CHAPTER 13
DECOMPOSITION

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Figure 1. ***Adelanthus decipiens*** with fresh, green branches and older, decomposing brown branches. Photo by Michael Lüth, with permission.

Decomposition

If you were to ask the average person to name a plant that decays at the bottom while the top is green and continues to grow, most would have no clue or tell you that's not possible. These people, like most of my beginning students, when defining plants, have forgotten about bryophytes. This group of plants is unique in its ability to die at its base and continue life for years, or even centuries, from the parts above.

Although bryophytes are generally quite small, their slow rate of decomposition and their effect on decomposition of other plants can be important influences on ecosystem dynamics. For example, the genus ***Sphagnum*** (Figure 2), well known for its preservative properties, occupies 1/3 of the land on the planet and stores more carbon than any other single genus of plants (Turetsky *et al*. 2002). Decomposition in that system necessarily is important.

Although they lack the lignin that resists decay in tracheophytes, bryophytes are replete with many kinds of secondary compounds – compounds with no known metabolic function, but that seem to deter herbivores from consuming them. These same compounds, including many phenolics, are likewise active in inhibiting the organisms that would normally facilitate decomposition. In fact, bryophytes do have a slower decomposition rate than do tracheophytes (Scheffer *et al.* 2001). Turetsky (2003) considers this to result not only from the secondary compounds, but also from the low nitrogen concentrations in many taxa, an interpretation shared by Aerts *et al.* (1999), who demonstrated that ***Sphagnum*** (Figure 2)

leaves had lower N and P concentrations than other taxa and likewise had lower rates of litter decomposition.

Figure 2. ***Sphagnum fuscum*** hummock. Photo by Oscar Gran, through Creative Commons.

Aerts *et al*. (1999) also found that cellulose decomposition in bogs was lower than in fens and that the nutrient mineralization rate was greater in forested peatlands than in herbaceous peatlands. On the other hand, Coulson and Butterfield (1978) found that the rate of decomposition depended not on the substrate of peatland vs. mineral substrate, but on the kinds of plants being decomposed. Peat mosses can play a major role in determining what kinds of plants can live there, so they do play a role in the sequestration of carbon and the decomposition rate by limiting available nutrients and encouraging growth of evergreen shrubs.

It is not surprising that decomposition rates are affected by nutrient levels in the plants. The availability of nutrients influences the kinds of decomposers and the rate at which they act. Aerts *et al.* (2001) found that higher N concentrations caused higher potential rates of decay of ***Sphagnum*** litter (Figure 3); the rates were actually not significantly affected by nutrient additions. Rather, the higher N levels in ***Sphagnum*** and other litter led to lower P concentrations. Changes in these ratios can have serious effects on the carbon balance. ***Sphagnum***, as an ecosystem engineer, seems quite important in the decomposition process.

Figure 3. ***Sphagnum fimbriatum*** with capsules and senescent tissues. Photo by J. C. Schou, with permission.

Tsuneda *et al*. (2001) studied the degradation of cell walls in ***Sphagnum fuscum*** (Figure 2). They found that the **Ascomycota** fungi ***Acremonium cf. curvulum*** (Figure 4) and ***Oidiodendron maius*** were able to degrade the leaf cell walls in this species. ***Acremonium cf. curvulum*** first fragmented the outer wall layer, then removed it. Then the inner wall was mostly degraded and removed, the middle wall layer, consisting of bundles of microfibrils embedded in an amorphous matrix, experienced degradation and disappearance of the amorphous matrix. Finally, the microfibrils were degraded, causing holes in the cell wall. ***Oidiodendron maius***, on the other hand, did not degrade the wall in layers. Rather, it degraded all the components in a nearly simultaneous manner.

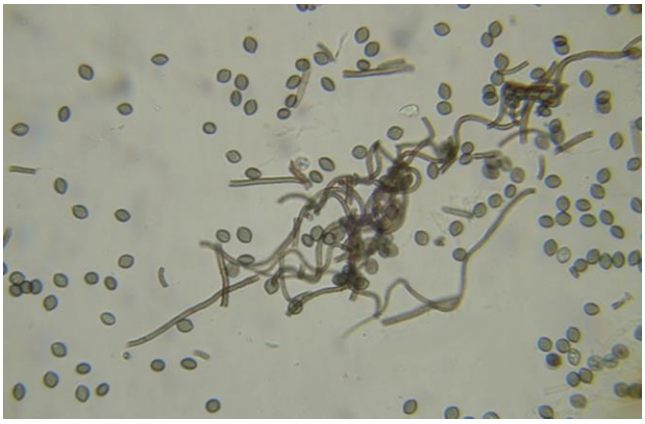

Figure 4. ***Acremonium*** ascospores, a fungus able to degrade ***Sphagnum fuscum*** leaf cell walls. Photo by Ninjatacoshell, through Creative Commons.

Decomposers

A wide array of organisms typically contribute to decomposition of plant material, with invertebrates, especially arthropods, breaking up the tissues into smaller fragments, and fungi and/or bacteria attacking the cellulose and other parts. This is not necessarily the order of activities, which can vary with habitat and available species. **Protozoa** can contribute in some habitats and complete the major groups generally involved.

But bryophytes do not seem to encourage all of these organism groups. Consumption of bryophytes is limited, most likely due to the many secondary compounds they produce (Asakawa 1990). Among liverworts, a variety of volatile oils may be the deterrent (Lohmann 1903, in Frankland 1974). It appears that animals play little role in the decomposition process of bryophytes (Frankland 1974; Coulson & Butterfield 1978).

On the other hand, a wide variety of parasitic and saprophytic fungi are known from bryophytes. Frankland (1974), reporting on earlier work of Racovitza (1959, in Frankland 1974), considered the decreasing order of importance of fungi to be **Ascomycetes** > **Fungi Imperfecti** > **Phycomycetes** > **Basidiomycetes** > **Mycelia Sterilia** > **Archimycetes**. Although some common fungi, like the Loculoascomycetes, may not penetrate the bryophyte host (Henderson 1972, in Frankland 1974), other studies have demonstrated the ability of fungi to penetrate and decompose bryophyte cells (Parke & Linderman 1980; Redhead 1981; Grasso & Scheirer 1981).

There are some indications that the number of fungal species on bryophytes is lower than the number on tracheophytes (Frankland 1974). Longton (1992) found that more than 50% of the bryophytes tested produced microbial inhibitors, perhaps explaining the reduced number of decomposer species found on ***Sphagnum*** (Figure 2), where *p*H is often too low for most bacteria to survive.

However, it appears that even on ***Sphagnum*** (Figure 2), the number of taxa can be large. In a boreal bog in Alberta, Canada, 55 species of fungi were identified on *S. fuscum*, 36 of which were new records for ***Sphagnum*** (Thormann *et al*. 2001). It appears that this may be a poorly investigated habitat for fungi with many more taxa awaiting discovery. One reason for the large number of fungal taxa on ***Sphagnum*** may be their ability to utilize a wide range of carbon sources, including cellulose, tannic acid, and pectin.

The concentration of ergosterol is an indication of fungal presence (Uchida *et al.* 2001). Fungi are common among bryophytes, and Uchida *et al*. found that not only the brown moss litter of ***Hylocomium splendens*** (Figure 5), but also its living green shoots exhibited ergosterol. The interesting relationship for this species is that the ergosterol content of its litter from boreal and subalpine forests was about twice that of the cool temperate forest where the decomposition rate was faster.

Figure 5. ***Hylocomium splendens***, showing senescing brown portions and green shoots. Photo by Michael Lüth, with permission.

Penicillium (Figure 6) seems to be a common inhabitant of bryophytes. Mikola and Hintikka (1956) found it to be one of the more abundant fungi (3 species) on ***Pleurozium schreberi*** (Figure 7), along with ***Mucor*** (Figure 8) (3 species; 50% of the number of molds) and ***Trichoderma*** (see Figure 9-Figure 10) (40% of the number of molds). In the same experiment, a grass had the same species plus four more genera. Leaf litter lacked ***Trichoderma***, but had 8 species not found on the ***P. schreberi***, suggesting certain fungi may have a specificity for bryophytes.

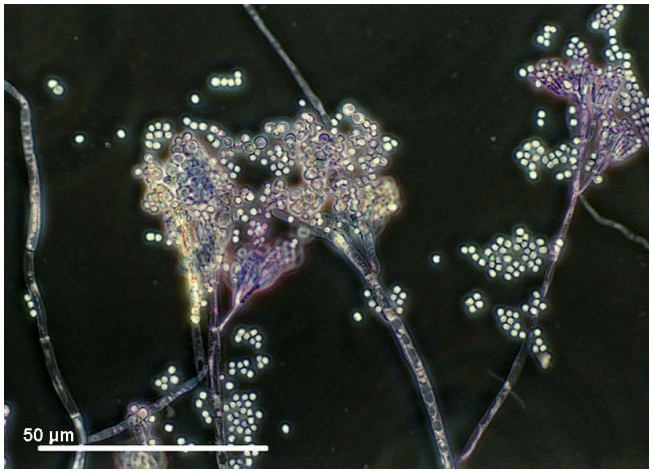

Figure 6. ***Penicillium*** sp. ***Penicillium spinulosum*** is inhibited by culture with ***Sphagnum***. Photo by Josef Reischig, through Creative Commons.

Figure 7. ***Pleurozium schreberi***, a common boreal forest species with several abundant fungal associates. Photo by Janice Glime.

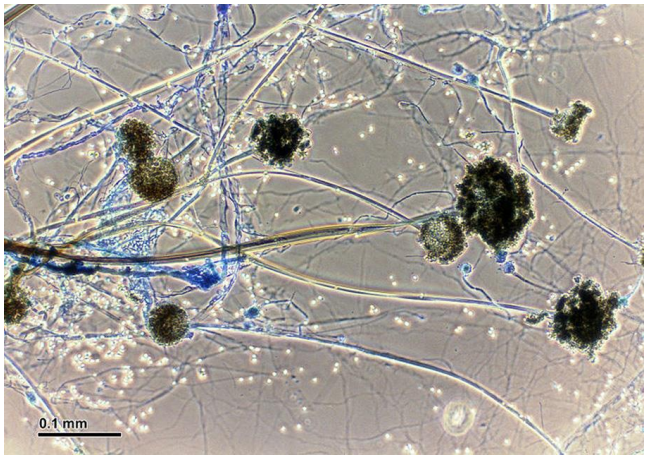

Figure 8. ***Mucor***, a common genus on ***Pleurozium schreberi***. Photo by Josef Reischig, through Creative Commons.

Figure 9. ***Trichoderma*** *aureoviride*. ***Trichoderma lignorum*** is inhibited by culture with ***Sphagnum***. Photo by Paul Cannon, through Creative Commons.

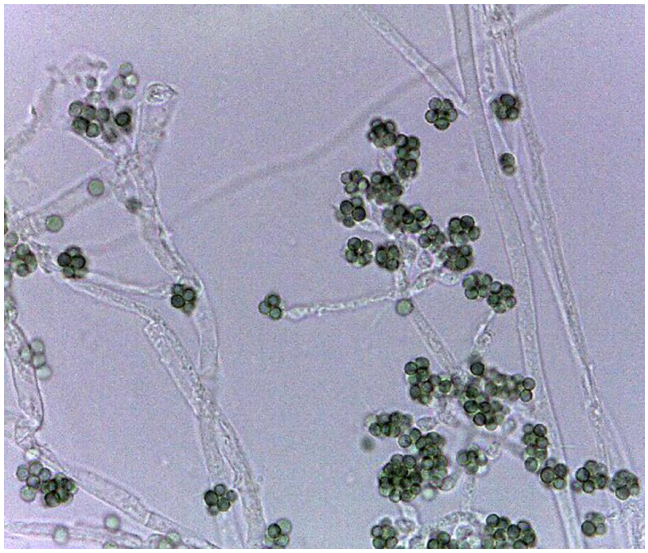

Figure 10. ***Trichoderma*** *harzianum*. ***Trichoderma lignorum*** is inhibited by culture with ***Sphagnum***. Photo by Andre Rodrigues, through Creative Commons.

Clymo (1965) concluded that micro-organisms were the chief agents in ***Sphagnum*** (Figure 2) decomposition, albeit slowly. As suggested earlier, the acidic conditions in most ***Sphagnum*** habitats do not encourage bacterial growth (Frankland 1974). Williams and Gray (1974) found that when the *p*H drops below 5, decomposers drop proportionally to the drop in *p*H. Nevertheless, in an acid peatland, even a four-year addition of simulated acid rain had no effect on the decomposition rate (Rochefort *et al*. 1990). Furthermore, ***Sphagnum*** itself is bacterial resistant, as noted by those using it for bandages in World War I. For example, only 6-8% of dry weight was lost in six months incubation of ***Sphagnum*** inoculated with ***Trichoderma lignorum*** (see Figure 9-Figure 10) or ***Penicillium spinulosum*** (see Figure 6) (Minchevich 1969, in Frankland 1974). ***Collybia dryophila*** (Figure 11), a fungus, causes a 30% loss of bryophyte dry mass in only four months; this fungus caused 53-56% loss in bryophytes while angiosperm litter lost only 46-69% (Mikola & Hintikka 1956, in Frankland 1974). Benda (1957, in Frankland 1974) found that associated organisms could be important. In her experiments, bacterial decomposition of ***Sphagnum*** protein occurred only when fungal symbionts of *Erica* were present.

Figure 11. ***Collybia dryophila***, a species that is able to decompose bryophytes. Photo by Dan Molter, through Creative Commons.

Küster (1968), on the other hand, did not consider peat to be the microbe-poor community that its antibacterial properties might suggest, reporting that the numbers were "much higher than originally assumed." He concluded that chemical composition, structure, moisture, and other factors determined the occurrence and nature of the microorganisms on peat.

Satake and Miyasaka (1984) reported the penetration of bacteria into the cell walls of the leafy liverwort ***Jungermannia vulcanicola*** (Figure 12-Figure 13). Satake and Shibata (1986) supported the role of bacteria in at least some bryophytes by demonstrating that the leafy liverwort ***Scapania undulata*** (Figure 14) exhibits bacterial invasion of its cell walls at both *p*H 6.4 and *p*H 4.2. Furthermore, they found no evidence of fungal presence on these aquatic leafy liverworts.

Figure 12. ***Jungermannia vulcanicola*** habitat. Photo courtesy of Angela Ares.

Figure 13. ***Jungermannia vulcanicola***, a species in which leaf cells are penetrated by bacteria. Photo courtesy of Angela Ares.

Figure 14. ***Scapania undulata***, an aquatic leafy liverwort that seems to be free of fungi. Photo by Michael Lüth, with permission.

Frankland (1974) suggested that *p*H may not be the limiting factor and concluded that the chemical composition of ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) walls determined its rate of decomposition. They are rich in pectin. Their cellulose and "lignin" are unusual. The cellulose actually hydrolyzes more readily than that of seed plants, but phenolic compounds such as sphagnol may serve as a microbial retardant. Reports of a lignin of unusual composition probably represent another phenolic compound, but its resistance to decay is still of importance.

Decomposition is not the only factor contributing to the disappearance of bryophyte tissue. Other factors in the Antarctic and elsewhere include wind erosion, leaching, and removal by skuas (Davis 1981). The losses to invertebrates are assumed to be minimal, but for some bryophyte taxa, it could be significant.

Phaeopigments

Phaeopigments have been used to indicate the degree of decomposition in algae and bryophytes. Bastardo (1980) examined ***Fontinalis*** (Figure 15) and other aquatic plants, demonstrating that the ratio of chlorophyll *a* to phaeopigment can be used to indicate plant vitality, with a ratio of less than 1 indicating irreversible decomposition. On the other hand, use of phaeopigments as an indicator of decomposition may be misleading. Martínez Abaigar *et al.* (1994) found that the degradation of chlorophyll in immersed bryophytes did not produce phaeopigments.

Figure 15. ***Fontinalis antipyretica***, a species in which a high phaeophytin to chlorophyll ratio can be an indicator of decomposition. Photo by Misha Ignatov, with permission.

Influential Factors

We have already seen that water is a major factor in the rate of photosynthesis. It appears that it may be the major factor in decomposition as well, with different taxa having different moisture requirements. Belyea (1996) showed that for ***Sphagnum capillifolium*** (Figure 16) this ideal water content was achieved in the zone of water fluctuation; for ***Racomitrium lanuginosum*** (Figure 17), it was just above the highest water level. For epiphytes, it appears that living on the north side of a tree may incur an advantage that increases the decomposition rate (Van Tooren 1988).

Figure 16. ***Sphagnum capillifolium***, a species for which the zone of water fluctuation is ideal for decomposition. Photo by Li Zhang, with permission.

Figure 17. ***Racomitrium lanuginosum***, a species that decomposes best just above the water level. Photo by Janice Glime.

Depth in the peat profile seems to have a major influence on ***Sphagnum*** (Figure 16) decomposition (Hogg 1993; Johnson *et al*. 1990). At a depth of 7-10 cm, nearly all hollow species had completely fragmented into stems and leaves. On the other hand, the hummock species, especially ***S. fuscum*** (Figure 2), remained completely intact to a depth of at least 25 cm. This relationship further supports the contention that hollow species decompose more rapidly than do hummock species (Limpens & Berendse 2003). But as observed by Belyea (1996), those in the zone of water fluctuation disintegrated the most rapidly and completely. Even when samples were moved from deep peat (50-100 cm), the hummock species still decomposed more slowly than did the hollow species (Hogg 1993). In older peat, decomposition reduces to 0%.

Peat seems generally to resist decay. Karunen (1981) demonstrated that ***Sphagnum*** (Figure 2) cell walls were resistant to both **autohydrolysis** and microbial decomposition. Some organisms, such as insects and fish, accomplish autohydrolysis by releasing enzymes (from dead cells) that cause them to digest themselves from the inside out. Nevertheless, not all species of ***Sphagnum*** exhibit equal resistance. Johnson and Damman (1991) indicated that the species are important in determining the decay rate. ***Sphagnum cuspidatum*** (Figure 18) in the hollows have a decay rate (16.9% mass loss) 1.5 times as fast as that of ***S. fuscum*** (Figure 2) (11.3% mass loss) in the hummocks. Even when the species were placed in each others' habitats, ***S. cuspidatum*** continued to have the faster rate. They suggested that the more rapid decay rate of hollow species like ***S. cuspidatum*** may initiate and maintain the hummock and hollow complex. In a separate experiment, Johnson *et al.* (1990) found that among three species, ***S. fuscum*** stems were the most decay resistant, ***S. rubellum*** (Figure 19) next, and ***S. balticum*** (Figure 20) least. Rochefort *et al.* (1990) likewise found that the decomposition rate was least at the top of the hummock and greatest for hollow species, suggesting that it was the slower decomposition rate that maintained the hummocks, not high production.

Figure 18. ***Sphagnum cuspidatum***, a hollow species with a faster decay rate than that of the hummock species ***S. fuscum***. Photo by Jutta Kapfer, with permission.

Figure 19. ***Sphagnum rubellum***, a species with a moderate decay resistance. Photo by Michael Lüth, with permission.

Figure 20. ***Sphagnum balticum***, a species with lower decay resistance than ***S. fuscum*** or ***S. rubellum***. Photo by Michael Lüth, with permission.

Water is not the only factor that differs at the top of the hummock. Because the hummock is not submersed often, if at all, it has only the small task of lowering the *p*H of the adhering water, whereas the hollow species may have their efforts of acidifying diluted by an entire lake. The result is that the hummocks exhibit the lowest *p*H in the peatland (Clymo 1963, Vitt *et al*. 1975; Clymo 1986), and this acidity most likely contributes greatly to the lower breakdown rate there.

Kälviäinen *et al*. (1985) supported the difference between species by demonstrating biochemical differences. The two ectohydric forest mosses underwent a rapid decay and possessed a dominance of short-chain hydroxy acids. The two ectohydric ***Sphagnum*** species were highly resistant to decay and possessed a dominance of long-chain hydroxy acids in their walls. Changes in biochemistry may result in differences in rates. ***Sphagnum fuscum*** (Figure 2) has considerably more hydroxy acids in the 9-12 cm segments than in the 0-0.5 cm segment (Ekman & Karunen (1982).

Fontinalis seems to be somewhat different in this regard. The sterolesters of ***Fontinalis antipyretica*** (Figure 15) are rapidly hydrolyzed during decay (de Leeuw *et al*. 1976).

Rate

Decomposition rates of bryophytes have been difficult to measure. The tiny bryophyte leaves are often lost through the holes of mesh bags, making the litter bag method used for tree leaves less reliable for bryophytes. Nakatsubo *et al*. (1997) used the annual rate of litter production and the amount of litter accumulated to calculate the decomposition rate in ***Hylocomium splendens*** (Figure 5) in boreal and subalpine forests. They estimated the litter production rate based on the moss shoot growth. While this method gave larger estimates than those usually obtained by the litter bag method, it relies on the assumption that litter production occurs at the same rate as shoot production. Over a long period of time, this assumption probably provides a fairly accurate estimate, but in any given year the estimate could be quite disparate.

Bryophytes are known for their slow decomposition. For example, ***Pseudoscleropodium purum*** (Figure 21) has a much slower rate than does the grass *Brachypodium pinnatum* under the same conditions (Kilbertus 1968). The feather moss ***Pleurozium schreberi*** (Figure 7) can require 5-12 years to decay (Weetman & Timmer 1967). But ***Hylocomium splendens*** (Figure 5) lost 10-24% of its biomass per year in Northern Hemisphere boreal and subalpine forests (Nakatsubo *et al*. 1997).

Figure 21. ***Pseudoscleropodium purum***, a species with a much slower decay rate than the grass *Brachypodium pinnatum*. Photo by Janice Glime.

All indications are that bryophyte decomposition is slow [Russell 1990 – tundra (Figure 22); Verhoeven & Toth 1995 – ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18); Hobbie 1996 – tundra; Sand-Jenson *et al*. 1999 – Arctic lakes (Figure 23); Liu *et al*. 2000 – montane moist evergreen broad-leaved forest (Figure 24); Moore *et al*. 2007 – temperate peatlands (Figure 25); Turetsky *et al*. 2008 – ***Sphagnum*** in boreal peatlands (Figure 23); Lang *et al*. 2009 – subArctic]. As a result, bryophytes become a nutrient sink compared to other plant species in most ecosystems. This implies that they get most of their decomposition nutrients from litter decomposition of tracheophytes, not from recycled nutrients from their own tissues.

Figure 22. Arctic tundra at Svalbard. Photo by Gary Bembridge, through Creative Commons.

Figure 23. Arctic tundra lakes and peatlands. Photo by Sphinx through Creative Commons.

Figure 24. Broadleaf evergreen Laurel forest Photo by Inkaroad, through Creative Commons.

Figure 25. Temperate peatland. Photo by Janice Glime.

Rejment-Grochowska and Misztal-Cieliczko (1975) examined the decomposition of the moss ***Climacium dendroides*** (Figure 26). They found that moss decay increases with depth in the 12 cm examined. Temperature undoubtedly plays a role, with an increase from April to August, then decreasing to November when the study ended. Nakatsubo *et al*. (1997) demonstrated that rates of decomposition of the moss ***Hylocomium splendens*** (Figure 5) decreased with altitude, but at boreal sites the rates were similar to those of the subalpine sites, despite the lower mean annual temperatures. They found a log-linear relationship between the annual mass loss rate and the cumulative value of monthly mean air temperatures higher than 0°C.

Figure 26. ***Climacium dendroides***, a species in whih decay increases with depth. Photo by Michael Lüth, with permission.

In the Antarctic, where ground at 20-30 cm is permanently frozen, decomposition above the frozen portion is less than 1% per year. By the time it becomes part of the permafrost zone, about half the original material has decomposed (Fenton 1980). It took approximately 40 years to decompose half of the moss ***Polytrichum strictum*** (Figure 27) in the upper 15 cm. But this low rate may not be representative. This species has an intrinsically low decomposition rate.

Time, of course, has an effect on the rate. Johnson and Damman (1991) found a much faster rate during the first 10 months than in the months 10-22 after the onset of the experiment. When tested in the anoxic (submerged) zone, ***Sphagnum fuscum*** (Figure 2) actually had less total decomposition (9.1%) in months 10-22 than in the first 10 months (10.6%), whereas ***Sphagnum cuspidatum*** (Figure 18) increased slightly from 15.1% to 16.1%.

Figure 27. ***Polytrichum strictum***, a moss that forms deep cushions. Photo by Michael Lüth, with permission.

Extreme heat may have a negative effect on decomposition in bryophytes (Ohlson 1987). In a Swedish mire, rates of decomposition differ spatially. This may in part be due to temperature differences. Clymo (1965) showed that ***Sphagnum papillosum*** (Figure 28) that was dried at 105° C exhibited less subsequent decay than did material that dried in air. This may have been due to death of associated microorganisms.

Figure 28. ***Sphagnum papillosum***, a species that decays less after being subjected to 105°C. Photo by 1 James K. Lindsey, with permission.

One explanation for the slowdown in decay rate may be types of constituents that still remain (Coulson & Butterfield 1978). In ***Hylocomium splendens*** (Figure 5), the oldest and most decomposed tissues exhibited a slight increase in polymerized lipid monomers (Kälviäinen *et al*. 1985).

Cellulose and hemicellulose content change during decomposition (Küster 1968). For ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) the hemicelluloses changed from 16% in relatively undecomposed peat to 10% in well-decomposed plants. Celluloses had a similar decline from 19% to 11%. Such changes affect the kinds of organisms required for or attracted to the moss for decomposition and these changes affect the rate of decay.

As readily obtainable nutrients are consumed by the decomposers, more recalcitrant kinds become a greater proportion of the remaining components. Nadkarni (1984) demonstrated considerably higher nutrient content of N, P, Ca, Mg, K, and Na in live compared to dead parts of epiphyte mats [including bryophytes, *Selaginella* (Figure 29-Figure 30), and *Polypodium* (Figure 31) on *Acer macrophyllum* (Figure 32). However, these changes in concentrations could reflect re-distribution of nutrients to growing parts of the plants. But one of the biggest decreases is in Ca, an insoluble nutrient that is not readily moved within plants, suggesting that some of these changes may result from loss during decomposition. During (1990) demonstrated that bryophytes in calcareous grasslands released nutrients in summer as a result of partial die-back and decomposition. Damman (1988) found that as the age of decomposing ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) increases, tissue N concentrations increase. Malmer and Wallén (1993) supported this observation with their evidence that N is conserved in decomposing ***Sphagnum***. N becomes depleted in the litter at the bottom layer where decomposition has led to disintegration, but below that layer (litter deposition level) the concentration of N increases once more with depth (in the decay decrease level).

Figure 29. ***Selaginella oreganum***, a common epiphyte in the Olympic Peninsula, WA . Photo by Janice Glime.

Figure 30. ***Selaginella oreganum***, a tracheophyte species that accompanies bryophytic epiphytes on *Acer macrophyllum*. Photo by Janice Glime.

Figure 31. ***Polypodium glycyrrhiza***, a species that often accompanies epiphytic bryophytes on *Acer macrophyllum*. Photo by Keir Morse, through Creative Commons.

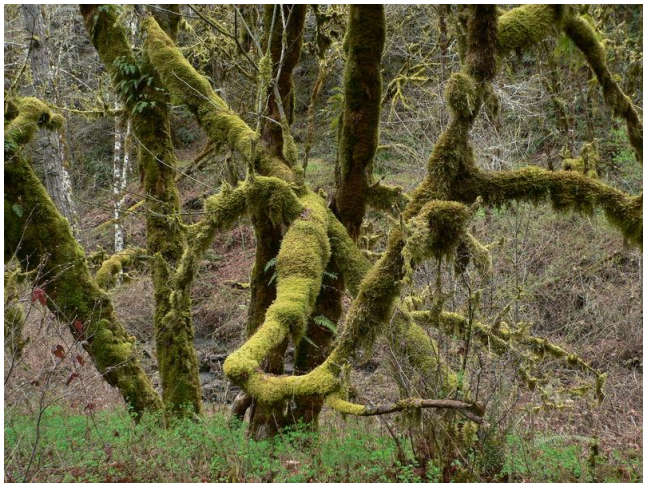

Figure 32. ***Acer macrophyllum*** with bryophytic epiphytes. Photo by Walter Siegmund, through Creative Commons.

Damman suggested that P deficiency might limit the decomposition rate. However, Coulson and Butterfield (1978) found that for ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18), increased concentration of P caused a reduction in its decomposition rate. Such releases could favor different groups of organisms for subsequent decomposition. Increased N levels, on the other hand, seemed to increase the decomposition rate.

It appears that in ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) the ratio of N:C is more important than the absolute level of N in the plants (Limpens & Berendse 2003). This ratio affects the litter quality, with greater decomposition when the N:C ratio is higher.

Habitat within an ecosystem can play a significant role. Decomposition of epiphytic bryophytes in a tropical montane forest at Monteverde, Costa Rica, was significantly less than that of forest floor taxa (Clark *et al*. 1998). The first year, the epiphytes were reduced by 17%, reaching only 19% reduction by the end of the second year. At the same time, forest floor bryophytes lost 29% to decomposition the first year and 45% by the end of the second year. These differences most likely reflect differences in water availability, but they also support the N story. Within the first three months the bryophyte forest floor litter lost 47% of its N; the remaining N seemed to be

recalcitrant. Similar recalcitrance occurred in epiphytes, which typically trap significant amounts of N-containing dust from the atmosphere, then convert it to biomass and lock it up. Reduction in available N could contribute to the slowdown of decomposition with time.

The decomposer population likewise changes with time, further modifying the decay rate. For ***Pleurozium schreberi*** (Figure 7), Mikola and Hintikka (1956) found bacterial densities of 10 million per ml after 20 days, a reduction to 1 after 50 days, up to 40 after 80 days, and back down to 10 after 130 days. The molds had a more consistent pattern, exhibiting declining numbers with time.

The decline in decomposition rate with time seems to be a fairly common occurrence among bryophytes. Clark *et al*. (1998) showed a decline in rate from the first to second year in various northern hemisphere populations of ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18), ***Dicranum*** (Figure 33), mixed bryophytes (from Costa Rica), and ***Calliergonella*** (Figure 34). Only a population of ***Sphagnum*** from North Sweden deviated, increasing its decomposition rate in the second year. Van Tooren (1988) likewise demonstrated a decline in the decomposition rate of ***Calliergonella cuspidata*** (Figure 34) after six months. Concomitantly, there was a drastic drop within the first two months in both N and P as a percent of that originally present. Nevertheless, after the first two months, both the N and P content eventually increased as a percent of the remaining dry weight.

Decomposition rates of ***Hylocomium splendens*** (Figure 5) varied with site (Uchida *et al*. 2001). The most recent two years of growth were green from all sites. However, two-year-old segments were green in the Canadian boreal forest and the Mt. Fuji subalpine forest, but were senescing from Mt. Tsurugi. By the third year, decomposition had slowed in the boreal and subalpine forests, with the 5-year-old segments on Mt. Fuji exhibiting ~80% of the weight of the largest segment. On Mt. Tsurugi, on the other hand, rapid decomposition had rendered the 5-year-old segment to be less than half the weight of the largest segment.

Figure 33. ***Dicranum fragilifolium*** showing older brown parts that will decompose slowly over time. Photo by Michael Lüth, with permission.

As we can see from these examples, decomposition rates vary widely between habitats and geographic areas. Likewise, the onset of senescence and decomposition varies with locality and habitat. ***Eurhynchium oreganum*** (Figure 35) in Douglas fir forests (Figure 36) of Oregon, USA, begins decomposition at age 3 (Binkley & Graham 1981), whereas those in Washington don't turn brown until age 6 (Frye 1928). In the same Washington forest, ***Hylocomium splendens*** (Figure 5) lives 8 years before its lower parts begin to decompose. But moss tissue may remain alive even after it has become brown (Longton 1972), moving nutrients to younger parts (Eckstein & Karlsson 1999).

Figure 34. ***Calliergonella cuspidata***, a species that experiences a decline in decomposition after six months. Photo by David Holyoak, with permission.

Figure 35. ***Eurhynchium oreganum***, a species that begins decomposition at age 3 in Oregon and age 6 in the neighboring Washington. Photo by Adolf Ceska, with permission.

Figure 36. Douglas fir forest in Vancouver, BC, Canada. Photo by Janice Glime.

We might expect decomposition in the Antarctic to be slow. Baker (1972) found that ***Chorisodontium aciphyllum*** (Figure 37-Figure 38) on Signy Island had an approximately linear decomposition rate, averaging 2% per year.

Figure 37. ***Chorisodontium aciphyllum***, a species that decays at approximately 2% per year in the Antarctic! Photo by Peter Convey, with permission.

Figure 38. ***Chorisodontium aciphyllum***, a species that decays at the rate of 2% per year in the Antarctic. Photo by Jan-Peter Frahm, with permission.

It may be fairly typical that decomposition of forest floor bryophytes is at a pace similar to that of growth. For example, ***Hylocomium splendens*** (Figure 5) exhibits apical growth equivalent to the loss from the distal segments (Callaghan *et al*. 1978). Zhang (1998) used mapped permanent plots on Isle Royale, Michigan, to track yearly changes in boreal bryophytes for four years. He likewise found that decomposition was approximately replaced by new growth, resulting in little change in cover from one year to the next, but often considerable change in position of the clump.

As might be expected, temperature is an important contributor to the rate of decomposition, as shown for peat decomposition in Scotland (Chapman & Thurlow 1998).

Habitat Differences

Forests

Forests are known for their relatively rapid decomposition of deciduous leaf litter. Decomposition in conifer forests is notably slower (Berg 1984). But where do the bryophytes fit in?

Liu *et al*. (2000) compared decomposition of bryophytes [***Homaliodendron scalpellifolium*** (Figure 39), ***Symphyodon perrottetii***, ***Herbertus*** sp. (Figure 40), and ***Bazzania albicans***] with that of three dominant non-conifer tall tree species and an understory bamboo in southwest China. The tracheophyte decomposition rates seem to be controlled by initial concentrations of lignin, N, and P rather than by leaf morphology. Nutrient and lignin concentrations were less important in bryophyte decomposition. Furthermore, the trees all decayed faster than the bamboo, and the bamboo decayed faster than the bryophytes. The rate constants of canopy litter ranged 0.50-0.64, that of bamboo 0.40, and that of bryophytes 0.22. Turnover time for the canopy species ranged 1.55-2.0 years, for bamboo 2.50 years, and for bryophytes 4.55 years.

Figure 39. ***Homaliodendron flabellatum***. ***Homaliodendron scalpellifolium*** decays more slowly than the bamboo or three tree species studied in southwest China. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.

Figure 40. ***Herbertus*** sp., a genus that decays more slowly than the bamboo or three tree species studied in southwest China. Photo by David Elckhoff, through Creative Commons.

Peatlands

It seems that more is known about decomposition of bryophytes in peatlands than from all other ecosystems combined (Collins 1973; Heal & French 1974; Heal *et al*. 1981; Davis 1986; Grandmaison & Laflamme 1986; Lieffers 1988; Russell 1990; Chmielewski 1991; Johnson & Damman 1991; Santelmann 1992; Gignac & Vitt 1994; Bowden *et al*. 1999; Table 1). That is attributable to the

large area of the Earth's surface covered by peatlands and their importance in those ecosystems.

Table 1. Percent decompositional rates of peatland bryophytes. From Bowden *et al*. 1999.

Rate (% y^{-1})	Species	Location	Reference
0.04-3	moss	Arctic	Russell 1990
5	*Sphagnum fuscum*	Arctic	Roswall *et al*. 1975
4	*S. balticum*		
7	*S. lindbergii*		
5	*Drepanocladus schulzii*		
7	*Dicranum elongatum*		
1.5	moss	Antarctic	Davis 1986
1.3-2.4			Baker 1972
0.1-8.3			Fenton 1980
2	*Chorisodontium aciphyllum*	Signy Island	Collins 1973
14	*Sanionia uncinata* (dry)		
25	*S. uncinata* (wet)		

Thomas and Pearce (2004) suggest that cation exchange may be responsible for preventing decay in deep peat. Conditions in the deep peat are anoxic. When mono- and di-valent cations were added to deep peat, a reduction in emissions of methane and CO_2 follows. Decay could be stimulated by adding a carbon source, but not by added NH_4^+. The researchers concluded that the cation limitation is limited to the deep peat and could explain the decay rate differences between anoxic surface and deep peat.

In northern peatlands, the maintenance of unfrozen bogs and fens creates habitat heterogeneity where these wetlands are interspersed among areas of permafrost mounds. Thus, their presence affects the hydrology, topography, thermal regime, and community structure (Turetsky 2004). Turetsky determined that the internal lawn peat produces more CO_2, hence has more decomposition, than other peatland types. The composition of the peat, as suggested earlier, plays a major role in the rate of decomposition, with acid-insoluble material and the ratio of this material to nitrogen being of primary importance when looking at the broadscale of peatlands. However, within a given peatland, the soluble proximate fractions are better predictors of the decompositional rate. Permafrost stability is important in determining the plant and soil environment, which in turn controls litter inputs, quality of organic matter, and ultimately, decomposition rates.

Peatlands are famous for their emission of methane, causing concerns that global warming will raise the methane emission, which will in turn increase the global warming effect (Weltzin *et al*. 2001). But peatlands can also consume methane. Yavitt *et al.* (1990) demonstrated that ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) -derived peat from 0-40 cm exposed to aerobic conditions consumed methane (CH_4), presumably due to consumption by aerobic microorganisms, whereas the same peat maintained under anaerobic conditions at 19ºC for 40 hours produced 0.5-1.0 µM L^{-1} peat h^{-1}. Under these two conditions, CH_4 emission of 6.8 mmol m^{-2} d^{-1} and CH_4 consumption of 5.4 mmol m^{-2} d^{-1} demonstrate a net increase of CH_4 to the atmosphere.

Methane emission could experience further enhancement due to various environmental pollutants that enhance the rate of decay. among these concerns are increaing temperaturea and acid precipitation. Rochefort *et al*. (1990) examined the effects of simulated acid rain on ***Sphagnum fuscum*** (Figure 41), ***Sphagnum magellanicum*** (Figure 42), and ***Sphagnum angustifolium*** (Figure 43). During the first two years, production of ***Sphagnum*** was enhanced, but after that it declined to its original rates. Decomposition was unaffected during the four years of application. Furthermore, it appears that the hummocks are maintained by a higher rate of production and lower rate of decomposition than that of the hollows in that Ontario, Canada, poor fen.

Figure 41. ***Sphagnum fuscum***, a hummock top species. Photo by Michael Lüth, with permission.

Figure 42. ***Sphagnum magellanicum***, a species in which acid rain does not affect decomposition rate. Photo courtesy of Betsy St. Pierre.

Figure 43. ***Sphagnum angustifolium***, a species in which acid rain does not affect decomposition rate. Photo by Jan-Peter Frahm, with permission.

In a *Betula*-carr, conditions were suitable for growth of ***Sphagnum recurvum*** var. ***mucronatum*** (Figure 44) (Brock & Bregman 1989). This species proved to have one of the highest productivity rates of peatmosses. On the other hand, loss of mass during breakdown in this species in the wetland forest was low. N, P, and especially K reduced faster than did the biomass during decomposition, but a large proportion of N and P remained after 12 months. This was consistent with the observation that little damage had occurred to the cells, and colonization by micro-organisms was poor.

Figure 44. ***Sphagnum recurvum*** var ***mucronatum***, a species in which N, P, and especially K reduce faster than the biomass during decomposition. Photo by Jan-Peter Frahm, with permission.

The role of ***Sphagnum*** (Figure 42-Figure 45) in slowing decomposition is emphasized by the experiments of Verhoeven and Toth (1995). Using litter bags and laboratory experiments, they compared the decomposition rates of *Carex* litter from a base-rich fen with that of ***Sphagnum fallax*** (Figure 45) from a base-poor fen. In all experiments, the *Carex* litter decomposed significantly faster than did the ***Sphagnum*** litter. But more to the point, when ***S. fallax*** was added to *Carex* litter, the rate of loss of *Carex* mass slowed significantly. They concluded that *Sphagnum* acid, a phenolic compound, was responsible by inhibiting the growth of microorganisms.

Figure 45. ***Sphagnum fallax*** with capsules, a species that has not only a slow decomposition rate, but it reduces decomposition in litter of other species in contact with it. Photo by David T. Holyoak, with permission.

Arctic

Mass loss of non-***Sphagnum*** Arctic mosses correlated with the initial N in the plants, a phenomenon that may relate to their nutritive value to the decomposers (Lang *et al*. 2009).

Tundra

Freeze-thaw cycles in the tundra can affect the microbial activity on peat and other bryophytic substrata. Wynn-Williams (1982) compared dry and wet sites in the Signy Islands of Antarctica under ***Polytrichum strictum*** (Figure 27) and ***Chorisodontium aciphyllum*** (Figure 37-Figure 38). In the tundra biome, bryophytes are of major biomass importance, averaging 30% cover, but often reaching 100% in wetter areas (Russell 1990), so their decomposition rates have a major influence on those ecosystems. A high standing crop biomass results from low decompositional loss rates, with initial annual loss rates commonly below 10%. The long growing season at sub-Antarctic wet sites can support up to 1000 g m^{-2} yr^{-1}.

Antarctic

In the Antarctic, it appears that substrate and moisture are the primary regulators of the decompositional rate, with temperature having little effect (Wynn-Williams 1985; Smith & Walton 1986). Using ***Polytrichum*** (Figure 27) and ***Drepanocladus*** (*sensu lato*) (Figure 46) peat, Wynn-Williams demonstrated consistent differences in respiration rates. Furthermore, the lack of correlation between O_2 uptake and CO_2 release suggests that anaerobic CO_2 production occurs under wet conditions.

Figure 46. ***Drepanocladus longifolius***. In theAntarctic, CO_2 production in this genus occurs under wet conditions and temperature has little effect on rate. Photo by John Game, through Creative Commons.

Davis (1986) examined the decomposition of Antarctic mosses using litter bags. In a 2-year period, ***Polytrichum strictum*** (Figure 27) and ***Chorisodontium aciphyllum*** (Figure 37-Figure 38) from a moss turf community and ***Sanionia uncinata*** (Figure 47), ***Calliergon sarmentosum*** (Figure 48), and ***Cephaloziella varians*** (Figure 49) from a moss carpet community exhibited a decomposition rate of 1.5% per year. This was consistent with the low rate of decomposition of cotton strips inserted into the bryophyte clumps, indicating a low decomposition potential. The decomposition potential, from highest to lowest, for the

five species was ***S. uncinata***, ***C. aciphyllum***, ***C. sarmentosum***, ***P. strictum***, and ***C. varians***. The time required for 50% decomposition of the cotton strips buried among these bryophytes varied from 1-2 years for ***S. uncinata*** and ***C. aciphyllum*** to 3-4 years for ***P. strictum*** and ***C. varians***, with low temperatures, low *p*H, and short active season contributing to their slowness. Other differences affecting differing rates among sites, depth, and species resulted from temperature, nutrient status, water content, and available oxygen.

Figure 47. ***Sanionia uncinata***, a species that has an decomposition rate of 1.5% per year in the Antarctic. Photo by Michael Luth, with permission.

Figure 48. ***Calliergon sarmentosum*** emerging from the water. Photo by Michael Lüth, with permission.

Figure 49. ***Cephaloziella varians***, a species that has an decomposition rate of 1.5% per year in the Antarctic. Photo by Kristian Peters, with permission.

Streams

While impacts of grazers and other decomposers on leaf litter in streams are relatively well known, virtually nothing is known about decomposition of bryophytes in streams (Bowden *et al*. 1999). Yet bryophytes often comprise the predominant in-stream vegetation and must therefore play a significant role in its internal nutrient cycling.

Bowden *et al*. (1999) suggested that stream bryophytes may not produce litter in the traditional sense. Rather, biomass is lost to fragmentation, consequently dispersing tissues that could potentially form new plants in new locations. But in slower streams, fragmentation is less extensive, and accumulations of senescing and dead tissues could contribute significantly to ecosystem structure.

Suren and Winterbourn (1991) compared common bryophytes in and near New Zealand streams, revealing that content of lipids, carbohydrates, and N is similar to that of grasses, shrubs, and tree foliage. However, content of holocellulose, crude fiber, and ash may be slightly higher overall in bryophytes, suggesting there might be slightly more resistance to decomposition. Furthermore, antibiotic compounds such as phenolics, terpenes, and flavonoids may inhibit decomposition (Markham & Porter 1983; Geiger 1990; Gorham 1990; Herout 1990; Markham 1990; Russell 1990; Glime 2006).

It appears that the only study designed to measure the rate of decomposition of stream bryophytes [***Schistidium agassizii*** (Figure 50); ***Hygrohypnum*** spp. (Figure 51)] is that described in Bowden *et al*. (1999) for the Kuparuk River, Alaska, USA (Figure 52). These bryophyte rates are far faster than the yearly rates presented in Table 1 and furthermore show that the rates do not differ greatly from those of the tracheophyte leaves in the same study.

Figure 50. ***Schistidium agassizii***, a species with decomposition rates similar to those of the tracheophyte leaves nearby. Photo by Michael Lüth, with permission.

Figure 51. ***Hygrohypnum ochraceum*** in a stream waterfall. Photo by Michael Lüth, with permission.

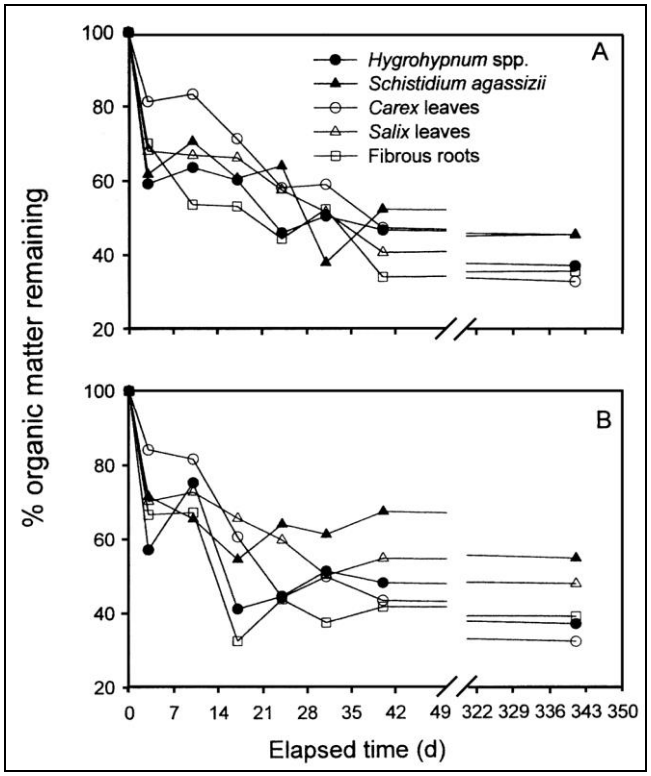

Figure 52. Mean percent of original organic matter of bryophytes, tracheophyte leaves, and roots remaining after six weekly intervals and one year when placed under rocks in the Kuparuk River, Alaska, USA. n = 5. **A =** control; **B =** fertilized portion of stream. Modified from Bowden *et al*. 1999.

Ecologists have traditionally considered that consumption of bryophytes by invertebrates was minimal. Nevertheless, consumption does occur and contributes to the removal of bryophyte tissue. Suren and Winterbourn (1991) found that of 23 invertebrate taxa in alpine streams in New Zealand, only 14 contained bryophytes in their guts. Furthermore, only the cranefly ***Limonia hudsoni*** (Figure 53; **Tipulidae**) and caddisflies ***Zelandopsyche ingens*** and ***Oeconesus similis*** (Figure 54) commonly consumed them. Suren and Winterbourn (1991) showed that bryophytes (***Fissidens rigidulus*** (Figure 55), ***Cratoneuropsis relaxa*** (Figure 56), ***Bryum blandum*** (Figure 57), ***Plagiochila retrospectans*** (Figure 58), and ***Hepatostolonophora paucistipula***) contained more refractory and indigestible compounds than did the common riparian tracheophyte plants nearby (*Chionochloa pallens*, *C. flavescens*, *Hebe subalpina*, *H. odora*, *Nothofagus solandri* var. *cliffortioides*, *Blechnum capense*, and *Marsippospermum gracile*), making the bryophytes less nutritious.

Figure 53. ***Limonia phragmitidis*** adult. Larvae in this genus are among the few insects that consume aquatic bryophyte litter. Photo by James K. Lindsey, with permission.

Figure 54. ***Oeconesus*** larva, one of the few insects that consume aquatic bryophyte litter. Photo by Landcare Research, through Creative Commons.

Figure 55. ***Fissidens rigidulus***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Bill & Nancy Malcolm, with permission.

Figure 56. ***Cratoneuropsis relaxa***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Jan-Peter Frahm, with permission.

Figure 57. ***Bryum blandum***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Niels Klazenga, with permission.

Figure 58. ***Plagiochila asplenioides***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Tim Waters through Creative Commons.

Lakes

In cold lakes, particularly those in polar regions, bryophytes may be the only form of macrovegetation (Sand-Jenson *et al*. 1999). In these frigid waters, with their low nutrients and short ice-free season, bryophytes are able to form dense stands, occupying great depths. Sand-Jenson and coworkers used changes in the size and density of leaves as markers to indicate growth and decomposition in Char Lake and North Lake in the Canadian High Arctic. The annual growth was remarkably constant (~10 mm shoot^{-1}), combined with slow decomposition. The slow growth rate, however, is at least partly offset by the greater longevity of the mosses in these communities.

Epiphytes

Of all the ignored bryophytes in the world, epiphytic taxa (Figure 59) have probably been most ignored by ecologists. However, in the tropics, a number of ecologists have recognized their importance in nutrient retention and cycling. Clark *et al*. (1998) examined the ecological role of epiphytic bryophytes in a tropical montane forest of Monteverde, Costa Rica. They found net production to be 122-203 g m^{-2} yr^{-1} while decomposition from litterbags after one and two years in the canopy was 17 ± 2% and 19 ± 2% mean ± 1 SE), suggesting that the bryophytes may have a significant retention time for nutrients. However, approximately 30% of the N content was released rapidly, contributing short-lived spikes in the N input to the underlying ecosystem. On the forest floor, approximately 47% of the N was lost in fhe first three months from green shoots! However, the N that remained in the litter was recalcitrant. Since bryophytes retain inorganic N from atmospheric deposition, they play a major role in altering the amount of available N to the system by transforming it to highly recalcitrant forms.

Figure 59. In the tropics even small branches can sport bryophytic epiphytes like ***Schlotheimia tecta*** growing with a bromeliad. Photo by Michael Lüth, with permission.

Role

It is too early to define a clear role for bryophytes in nutrient cycling through decomposition in ecosystems. Evidence from epiphytes suggests that leakage of N compounds from senescing bryophytes may be a significant

contribution of the nutrient pool for other epiphytes and throughfall recipients (Clark & Nadkarni 1992).

While our understanding of such roles in the terrestrial ecosystems is meager, our understanding in aquatic systems is nearly non-existent, as noted by Bowden *et al*. (1999). Their role in the regeneration of nutrients in streams is essentially unknown and there seem to be almost no published rates of bryophyte decomposition in stream ecosystems.

Summary

Bryophytes, unlike tracheophytes, die from the bottom up, with apical regions continuing to live and grow as their lower parts decompose. Compared to tracheophytes, their decomposition rate is relatively low, most likely due to recalcitrant cell wall components and secondary metabolites acting as antiherbivore/antibiotic compounds. Loss of nitrogen appears to be initially rapid, then becomes relatively unavailable, further limiting attractiveness to decomposers. Changes in the internal composition of the decomposing bryophyte appear to slow its rate of decomposition after the first year.

Bacterial decomposition may be limited in peatlands by the low *p*H, but it appears that fungi can be abundant, some being unique to bryophytes. Nevertheless, bacteria are able to penetrate the cell walls of at least some aquatic leafy liverworts, presumably contributing to their decomposition.

Phaeopigments may be an indicator of degree of decomposition, but their use for such purposes appears to be unreliable in aquatic systems.

Water seems to be the primary factor affecting rate of decomposition, but it acts in consort with *p*H, cell constituents, temperature, species of bryophyte, and available microorganisms.

Rates of decomposition vary widely, with peatland decomposition ranging from 0.04 to 25% per year. Similarly, the Antarctic exhibited a low rate of 1.5-2% per year. Tropical epiphytes may reach about 18% in a year.

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