

CHAPTER 5-6

ECOPHYSIOLOGY OF DEVELOPMENT: FRAGMENTS

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CHAPTER 5-6

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Figure 1. *Dicranum viride*, a moss that fragments regularly by a row of abscission cells across the upper half of the leaf. Note the broken leaf tips. Photo by Michael Lüth, with permission.

Fragmentation

Fragmentation may be random pieces that break due to abrasion, decay, or animal severance, or they may be programmed genetically by means of an abscission layer such as demonstrated in *Dicranum viride* (Figure 1). In certain habitats, fragmentation may be a regular phenomenon, accounting for nearly all the reproduction.

Even fossil evidence supports the importance of fragments in the dispersal and reproduction of bryophytes (Miller 1985). And buried fragments often retain viability, providing the source for the flora when a disturbance returns an area to previous conditions (Wasley 2004).

Yet, when we diagram life cycles, fragmentation is usually ignored, and certainly for many flowering plants it is unimportant. However, in bryophytes it is often the fragments that perpetuate the species. Likewise, Giordana and coworkers (1996) found that regeneration from the

detached leaves was the major form of regeneration in moss *Pleurochaete squarrosa* (Figure 2). Other bryophytes, such as *Hyophila crenulata*, share their successful regeneration from fragmentation with other means such as gemmae (Olarinmoye 1981).

Mishler and Newton (1988) contend that in perennial mosses reproduction and spreading is almost entirely by means other than spores. Many populations exist for which capsules are unknown, particularly for dioicous taxa (having males and females on separate plants; unisexual). Even when all individuals in the population can produce both sexes (monoicous; bisexual), water is needed at the right time for sperm and egg to meet, so success rate will vary with habitat and with weather in a given year. Newton and Mishler (1994) suggest that vegetative reproduction, including specialized propagules, can occur

under more stressful conditions. Whereas spores germinate best on previously uncolonized substrates, vegetative reproductive units can do well even in contact with existing colonies. However, they suggest that such vegetative units cannot travel as far as spores – tradeoffs again.



Figure 2. *Pleurochaete squarrosa*, a moss that relies on detached leaves for regeneration. Photo by Michael Lüth, with permission.

Some mosses even provide special means to accomplish fragmentation. *Dicranum viride* (Figure 1), *D. fragilifolium* (Figure 3), and *Tortella fragilis* (Figure 4) have a weakened area of cells that break easily, releasing the upper portion of the leaf. This is so typical that these species can be identified by their chopped off appearance. Other species have **caducous** leaves (leaves that normally detach).



Figure 3. *Dicranum fragilifolium* on rock, showing broken leaves. Photo by Janice Glime.



Figure 4. Broken tips on leaves of *Tortella fragilis*. Photo by Michael Lüth, with permission.

The success of fragments within short range (Newton & Mishler 1994) is supported by experiments by Nehira and Nakagoshi (1987). They removed a community of bryophytes and found that the community became re-established within 1-2 years. Most of the growth occurred in spring and autumn despite little seasonal variation in propagule dispersal. Thallose liverworts and pleurocarpous mosses were able to regenerate more quickly than the acrocarpous mosses. Yet these same fragments may have been eaten or decayed before ever growing if the researchers had not removed the parent colony. Newton and Mishler (1994) found that at least for the dry habitat mosses they studied, the parent plants seemed to inhibit growth of the fragments, with growth commencing once they were separated.

Fragmentation is likely to determine success of the species in some environments. Miles and Longton (1990) found that *Funaria hygrometrica* (Figure 5) reproduced and spread easily by spores, whereas *Atrichum undulatum* (Figure 6) and *Bryum argenteum* (Figure 7) were likely to experience failure before sporelings produced gametophores. On the other hand, these latter two species freely accomplished regeneration from shoot fragments. This ability of *Atrichum* to regenerate easily from leaf fragments permitted it to dominate the ground cover rapidly after the construction of a parking lot on the Michigan Technological University campus (Glime 1982). *Funaria hygrometrica*, on the other hand, apparently manages to arrive, presumably by spores, and colonize charred ground within a year after a fire, as occurred after the big Yellowstone fire (Glime pers. obs.).



Figure 5. *Funaria hygrometrica*, demonstrating the prolific production of capsules. Photo by Niels Klazenga, with permission.

Even on rocks, where one might expect a small spore and protonema to have more success than a large fragment, it seems that fragments dominate the reproductive success. Keever (1957) did find that spores germinated on granite, but colonization through fragmentation was more rapid. One such rock-dwelling (and bark-dwelling) species is *Orthodicranum montanum* (Figure 8). Chrobak and Sharp (1955) established that this species grew well from leaf fragments. The proximal (basal) half of the broken leaf was more successful than whole leaves or the distal portion of the leaf (Figure 9).



Figure 6. *Atrichum undulatum* with drying plants that can break more easily than hydrated plants. Photo by Michael Lüth, with permission.



Figure 7. *Bryum argenteum*, a moss that easily loses its tips as dispersal units. Photo by Janice Glime.



Figure 8. *Orthodicranum montanum* on bark. Photo by Janice Glime.

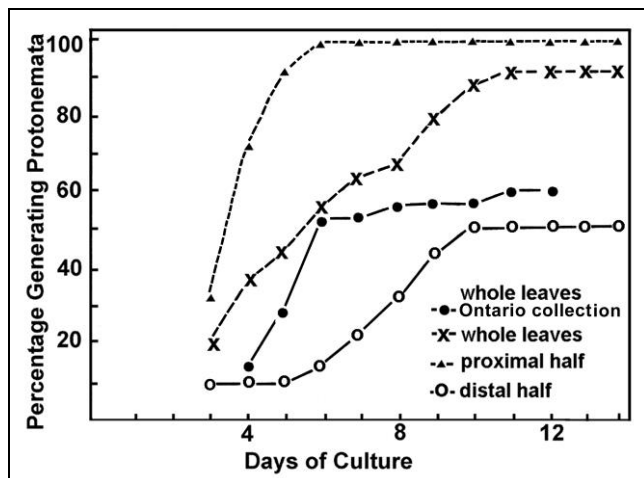


Figure 9. Success of producing protonemata from various leaf parts of *Orthodicranum montanum* from Michigan, USA, and Ontario, Canada. Redrawn from Chrobak & Sharp 1955.

Arctic and Alpine

Mogensen (1986) found that *Platydictya* (Figure 10) was dispersed in Greenland primarily by vegetative propagules and Bonde (1959) found viable *Polytrichum piliferum* (Figure 11) fragments among the wind-blown debris of a Colorado glacier. Lindskog and Eriksen (1995) found that the fragments of mosses, in particular, that were on the glacier reflected accurately the composition of the surrounding vegetation.



Figure 10. *Platydictya jungermannioides*. Photo by Des Callaghan, with permission.



Figure 11. *Polytrichum piliferum*, a moss that reproduces by fragments on the Colorado Glacier. Photo by David T. Holyoak, with permission.

McDaniel and Miller (2000) demonstrated the importance of fragments in alpine areas of the Adirondack Mountains of New York, USA, and suggested that fragments dispersed in winter might be a significant means of establishing new populations following spring snowmelt. It would certainly much easier for fragments to glide across a snow pack than to travel amid ground vegetation.

In the Arctic, fragments on the ice are common, and are easily moved around over the smooth surface, permitting rapid transport over considerable distances. Miller and Howe Ambrose (1976) found that fragments of mosses were distributed across the snow by wind on Bathurst Island in the Canadian high Arctic. They were able to grow these fragments in culture, with only 12% of the fragments producing evidence of viability by growth of protonemata, shoots, or rhizoids. The leaf-bearing tips of leafy shoots were the most likely to produce new growth. Nevertheless, this yielded an estimate of more than 4000 viable fragments per cubic meter of snow! Liverworts, however, did not fare as well, with only one fragment producing new growth. They surmised that such moss fragments may be "routine" in Arctic climates.

The importance of fragments may reach its climax in the Antarctic. In colonizing a new Antarctic volcanic island, fragments of *Campylopus* (Figure 12), *Marchantia*, (Figure 13) and *Bryum* (Figure 7) species seemed to be the most important means of arrival (Smith 1984).



Figure 12. *Campylopus pilifer* showing fragments formed by tips of plants. Photo by Michael Lüth, with permission.



Figure 13. *Marchantia polymorpha* with dead portions that can create fragments. Photo by Michael Lüth, with permission.

In Antarctica on Mt. Rittmann, *Pohlia nutans* (Figure 14-Figure 17) only establishes on geothermally heated ground (Skotnicki *et al.* 2002). The geothermal heat (17-35°C) permits the moss to survive. It is apparently dispersed only by fragments (Figure 16-Figure 17) from elsewhere in Antarctica.



Figure 14. *Pohlia nutans* below old mine on Svalbard (Arctic). Photo by Michael Lüth, with permission.



Figure 15. *Pohlia nutans* on Svalbard (Arctic), a species often spread by fragments. Photo by Michael Lüth, with permission.

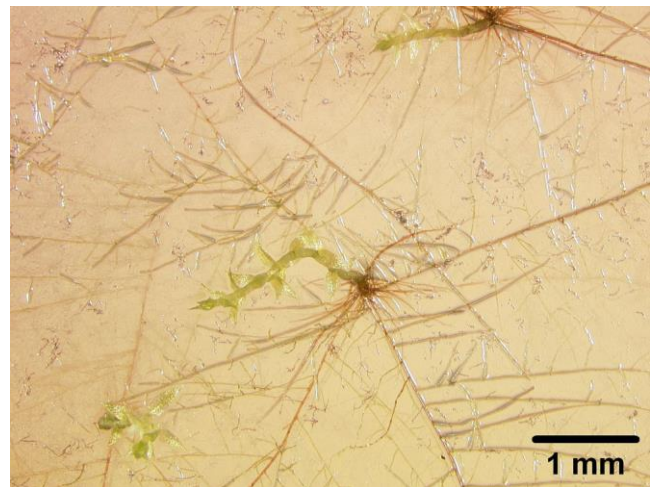


Figure 16. *Pohlia nutans* fragment and protonemata with buds and developing gametophores. Photo by Sean Robinson, with permission.

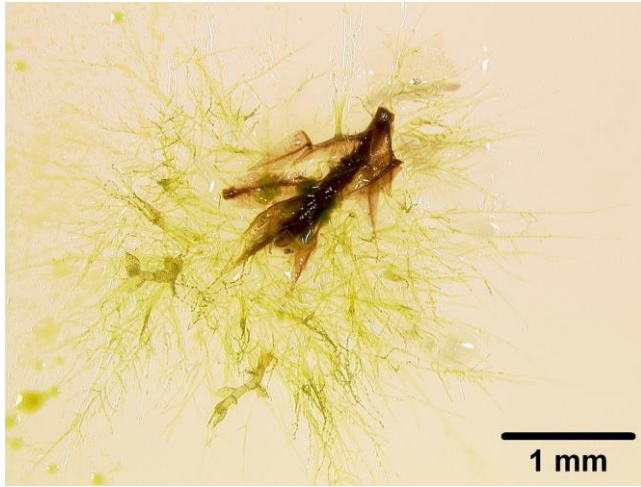


Figure 17. *Pohlia nutans* fragment and protonemata with buds and developing gametophores. Photo by Sean Robinson, with permission.



Figure 18. Fragments of *Fontinalis dalecarlica* caught in ice of a stream. Fragmentation appears to be its primary form of dispersal and new establishment. Photo by Janice Glime.

Streams and Other Aquatic Habitats

In flowing streams, sporophytes seem rare, and asexual propagules seem to be unimportant. However, significant dispersal can occur from fragments during spring runoff, and entire clumps as well as branches and smaller fragments become impinged on rocks and roots in the stream. The larger surface area of fragments makes it more likely that they will become lodged than will the small spores and asexual propagules. Glime *et al.* (1979) demonstrated that for *Fontinalis duriaei* these actually do become established in nature, occasionally even achieving upstream movement (by feet of bears?).

For aquatic mosses and liverworts, fragmentation may be the only means of reproduction for many years before appropriate conditions exist for completing sexual reproduction. In dioicous mosses such as *Fontinalis*, sexual reproduction seems to be so infrequent as to be totally ineffective as a means of providing dispersal units (spores), whereas fragments are numerous during times of ice melt and high water (Figure 18; Conboy & Glime 1971, Glime *et al.* 1979, Glime & Knoop 1986). Even when spores are produced in this genus, the spore faces numerous challenges in becoming located where its subsequent protonema will neither be washed away nor desiccated, and sufficient light will be available for development. Since there is no documentation of the occurrence of any protonema of any *Fontinalis* species in the field, we can only conjecture about the success of reproduction by spores in this genus.

Dedifferentiation

Dedifferentiation is the process involved in the return of a cell to its embryonic state (Figure 19). It is necessary before a mature cell can form into a different kind of cell, or into a protonema, permitting the development of new plants from fragments. In bryophytes, virtually all cells seem to have the ability to undergo dedifferentiation once they have been isolated from the intact plant (Giles 1971). This is not the case for cells such as xylem elements of tracheophytes, which no longer have protoplasm and hence are non-living.



Figure 19. *Warnstorfia fluitans* leaf fragment with rhizoid that has dedifferentiated and redifferentiated into a different kind of cell. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Moss fragments seem to retain their polarity, resulting in protonemata at the apical end and rhizoids at the basal end, but inverting them causes the base to act as the apex and vice versa (Westerdijk 1907), suggesting a gravimetric response by some growth factor. Mosses tend to have more regenerative ability at the base of the gametophyte than at the apex. Their sporophytes, however, are strongly polar in regeneration (von Wettstein 1924). Liverworts, on the other hand, seem to be much more strongly polar, and new growth is nearly restricted to the apical end of the gametophytes, but the sporophyte seems to lack polarity (Giles 1971). This strong polarity of the liverwort gametophyte regeneration, however, decreases with tissue age (Kreh 1909).

Earliest known reports on regeneration from bryophyte fragments come from Necker in 1774 (Giles 1971). Kreh (1909) showed that for liverworts, every part of the plant except the antheridia could regenerate. Nevertheless, few reports of liverwort regeneration from fragments are known. In mosses, even the seta will regenerate into a protonema, forming diploid gametophytes (von Wettstein 1924).

It is common for the nuclei to increase in size in dedifferentiating cells (Giles 1971). The dedifferentiation process involves a sort of "budding" of the chloroplasts and mitochondria, producing more of these organelles. At the same time, nucleolar volume increases only in regenerating cells. We now understand that the nucleolus is not an organelle in its own right, but rather that it is the site of extensive protein synthesis, hence staining more densely. This is an indication of building activity in the regenerating cell.

In *Campylopus pyriformis* (Figure 20) fragments, it is the chloronema that gives rise to buds, with no caulonema forming. By contrast, and unlike the growth from a spore, the caulonema of *Plagiomnium affine* (Figure 21) grows nearest the plant fragment and the chloronema is the farthest and youngest tissue (Sironval 1947; Bopp 1959a,b; Giles 1971). The ensuing buds develop, therefore, nearest the leaf fragment from the caulonema. Up to 100 secondary protonemata may originate from the dedifferentiated leaf cells of a single leaf in this species.



Figure 20. *Campylopus pyriformis* showing fragments of branch tips. Photo by Michael Lüth, with permission.



Figure 21. *Plagiomnium affine*, a moss that develops protonemata from fragments. Photo by Janice Glime.

Secondary Protonemata from Fragments

Secondary protonemata are those produced from mature tissues that have been damaged or cut. Hence, these protonemata develop on fragments. At first thought, one might expect that these would behave in the same way as primary protonemata (produced from a spore), but further consideration should remind us that fragments provide a large store of nutrients, including energy sources, from the plant fragment.

Like primary protonemata, the secondary protonemata of the moss *Tortula modica* is negatively gravitropic in the dark (Ripetskyj *et al.* 1999). When placed in the light, the apical parts of the protonemata begin to branch and apical cells of side branches and main protonemal filaments frequently differentiate as buds. One might consider this event as being possible because of the energy sources available from the fragment. When the fragments were illuminated from below, an intensity of at least $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ was necessary to induce phototropism and light-directed development of branch buds and directed growth of side branches. In lower light intensities the apical cells grew away from the light (*i.e.*, away from gravity as well).

To further understand the role of spore grown vs secondary protonemata, Wagner and Sack (1998) grew the moss *Ceratodon purpureus* from protoplasts. In these protoplasts, the emerging filament was mostly gravimorphic, with more than 66% of the filaments emerging above the horizontal. The tip-growing cells of these filaments began to exhibit a gravitropic response within 1-2 cell divisions. But in these filaments, plastid sedimentation did not occur, contrasting with dark-grown filaments.

Gravity Effects

As we might expect, based on studies on protonemata, secondary protonemata also respond to gravity. In *Tortula modica*, the secondary protonemata are negatively gravitropic in the dark (Ripetskyj *et al.* 1999). In the light, these protonemata branch near the apical cells and these branch tips typically differentiate as buds. A light intensity of at least $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ was required to induce phototropism in apical cells, cause light-directed initiation of branch primordia, and direct development of side branches and bud initiation. At lower light intensities, the apical cells grew away from light (*i.e.* negatively gravitropic).

Callose Formation

Scherp *et al.* (2001) documented the formation of callose in tissue fragments in all groups of multicellular photosynthetic organisms, including bryophytes. They found that in bryophytes and other multicellular green plants, callose is a regular component of the developing septa in juvenile cells during cytokinesis. Wound callose did not occur in cells that already had callose in the newly formed septa.

Establishment

It appears that fragments may survive better in water than spores, thus providing an additional means of long-distance dispersal. Dalen and Söderström (1999) tested

five species of mostly terrestrial mosses and found that in all five taxa, regeneration frequency of fragments was lower than that of spores, but that fragments survived as well in water as they did dry, whereas spores did not.

Light quality and intensity may be influential in success of fragments. Dagar and coworkers (1980) found that for the thallose liverwort *Riccia discolor* regeneration is best in diffused light. Red light can induce regeneration; far-red inhibits it (Giles & von Maltzahn 1967, 1968). There is evidence the red/far-red system may affect the "budding" or division of the chloroplasts (Hahn & Miller 1966), and its reversibility suggests that phytochrome may be active during the process. Little else seems to be known about light effects specifically on fragments, so these phenomena may be restricted to certain taxa or habitats.

When dispersal occurs over long distances, it is quite likely that only one gender will arrive, making its survival dependent on asexual means. As discussed elsewhere, fragments seem to provide the easiest means by which bryophytes can be propagated for gardens, so one should expect that nature makes widespread use of this ability as well. When a plant is damaged, the damaged surface will often produce protonemata and/or rhizoids (LaRue 1942) and subsequently develop a new leafy gametophore. In other cases, the new plant may develop directly with no protonemal intermediary, as in the leafy liverwort *Scapania undulata* (Figure 22) that developed from a leaf fragment (Figure 23; Glime 1970).



Figure 22. *Scapania undulata* growing in its streamside, wet habitat. Photo by Michael Lüth, with permission.

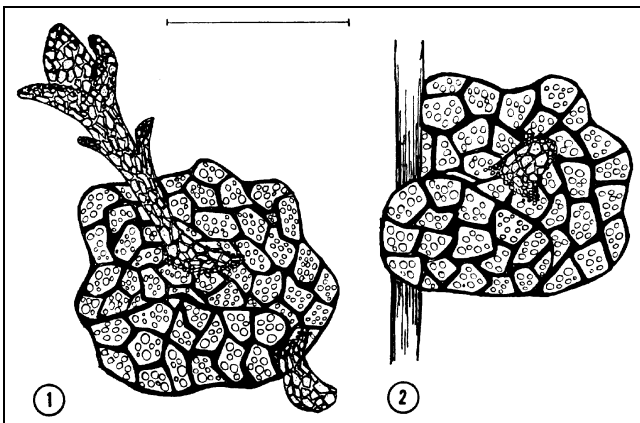


Figure 23. *Scapania undulata*, leafy liverwort known to reproduce from fragments. 1: Young plant growing from detached leaf. 2: Bud of young plant growing on leaf still attached to living stem. Drawings by Flora Mace.

It is the parent plant that determines which of these will develop – chloronema, caulonema, or rhizoids. Knoop (1984) tells us that small explants result in reversion to an early developmental stage wherein single leaf cells behave like spores and form chloronemata. On the other hand, large fragments revert back only to caulonemata, or go directly to buds and gametophore plants. Furthermore, apical leaves regenerate more easily than basal leaves (Gay 1971). It is puzzling that in *Plagiomnium undulatum* (Figure 24), basal leaves regenerate only from the lamina, apical cells from the costa, whereas apical ones regenerate only from the costa (Schröder *et al.* 1970).



Figure 24. *Plagiomnium undulatum*; basal leaves regenerate from the lamina, apical cells from the costa. Photo by Janice Glime.

Mishler and Newton (1988) demonstrated that fragments can require conditions opposite to those required for spores. In their study, *Syntrichia princeps* (Figure 25) fragments were slightly more successful when they experienced periodic drying, whereas the spores required continuously hydrated conditions. With such requirements, it is easy to understand why fragments are more successful on rocks and sand than are spores. Mishler and Newton attribute this success to the ability of fragments to produce a protonemal mat and new shoots much more rapidly than could spores. Furthermore, as mentioned earlier, the existing plants exhibited a much stronger inhibitory effect on the spores than on the fragments.



Figure 25. *Syntrichia princeps*, a moss whose fragments fare better with periodic drying. Photo by Jan-Peter Frahm, with permission.

On the other hand, both spores and fragments can be inhibited by the presence of mature plants (Mishler & Newton 1988). *Dicranum* (Figure 1, Figure 3) seemed to be more inhibitory than *Syntrichia princeps* (Figure 25), perhaps relating to the dry habitat of the latter. They considered that at least some of this inhibition was due to chemical exudates.

In an aquatic habitat, Florschütz and coworkers (1972) found that fragments of *Fissidens crassipes* (Figure 26) produced caulonemata, this time on moist bricks. This ability permitted them to spread rapidly in response to a rise in water temperature.



Figure 26. *Fissidens crassipes* growing on rock. Photo by Michael Lüth, with permission.

Regeneration often occurs from small leaf fragments that have begun to decay. This could be an indication that an inhibitor has been lost, or some colonizing microorganism could be providing a hormonal signal that starts the development. When growing *Leucolejeunea clypeata* on Ca-free media, Geldreich (1948) discovered that only contaminated leaves of Ca-deficient plants produced regenerants. It was only mature or old and necrotic leaves that regenerated, and these Ca-deficient leaves had oil bodies that were characteristic of old, senescent leaves. Since the contaminating microorganisms were typical of soil flora, and regenerants of this species are known in nature (Fulford 1947), perhaps the microorganisms do indeed play a role in providing the necessary stimulus.

Liverworts rarely regenerate from fragments. Occasionally a leaf may produce a new plant, as for example that of *Scapania undulata* (Figure 22-Figure 23), an aquatic leafy liverwort mentioned earlier (Glime 1970). Could it be that liverworts dry out too rapidly and cells lose their viability before new plants can arise? Would this explain the accomplishment of this aquatic species?

Growth Regulators

Like all other developmental processes, hormones and other growth regulators influence the developmental pathway of fragments. Patidar and coworkers (1987) found that 0.03 ppm gibberellin can stimulate regeneration in the thallose liverwort *Targionia hypophylla* (Figure 27). Concentration is of course important; at 0.1 ppm gibberellin is inhibitory to *T. hypophylla*.



Figure 27. *Targionia hypophylla*. Photo by Michael Lüth, with permission.

Few studies seem to have centered specifically on growth regulators of fragments, yet many in vitro studies are actually studies of fragments, particularly those of pleurocarpous mosses. Presumably, the same growth regulation applies to fragments as to the intact plants covered earlier. Yet, literature on the wound response seems to be lacking, as is literature on the remarkable ability of some fragments to persist under extremely stressful conditions. For example, we have grown *Fontinalis flaccida* from specimens dried for three months under herbarium conditions (ca. 30% relative humidity). In another case, *Fontinalis novae-angliae* that had been boiled for about 12 hours daily for two weeks developed new leaves on one portion of the remaining stem when it was returned to its native stream (Glime & Carr 1974). And what permits a partially decayed stem to suddenly spring forth a new plant after it has been uncovered from many years of burial (During *et al.* 1987)?

Using the aquatic moss *Palustriella decipiens* (Figure 28-Figure 29), Ahmed and Lee (2010) experimented with a wide range of IAA and kinetin concentrations on fragments. They found that protonemal gemma production varied with concentration, but was best at 10^{-8} M IAA and kinetin. Higher concentrations caused the gemmae to become brown. Low concentrations of IAA and kinetin induced bud formation.



Figure 28. *Palustriella decipiens*, an aquatic moss that regenerates from fragments and protonemata of those fragments respond to applications of IAA + kinetin to produce buds. Photo by Michael Lüth, with permission.



Figure 29. *Palustriella decipiens* protonemata with gemmae, produced at 10^{-8} M kinetin. Photo by Ahmed and Lee, with permission.

Animal Dispersal

Dispersal by animals is scarcely known in the bryophytes. Yet, we must suppose that the various activities of animals contribute to bryophyte movement. Various aquatic insects, especially Trichoptera (caddis flies), use mosses or liverworts in their cases, so the insect will carry the bits around wherever it goes. When drift carries the insect downstream, the moss goes too, and if the insect crawls upstream in the quiet interface at the bottom, the moss comes along. Lacewings [*Leucochrysa* (*Nodita*) *pavida*] carry viable bryophytes (and lichens) on their backs as camouflage (Slocum & Lawrey 1976).

Bears, beaver, and other animals can get mosses tangled among their toes and carry them for miles. Birds carry them off to build nests. I have even concluded that the turtle in my garden room was responsible for the distribution of *Conocephalum conicum* (Figure 30) all over the room from the single spot where it had been planted. When the turtle died, the spread of the liverwort stopped. In a field experiment, I found fragments of tagged *Fontinalis duriaei* (Figure 31-Figure 32) upstream from their initial location, a movement that could only have been effected by animals such as bears or humans.



Figure 30. *Conocephalum conicum* showing evidence of herbivory (arrows) that could lead to dispersal of fragments. Photo by Janice Glime.



Figure 31. *Fontinalis duriaei* held by Janice Glime, demonstrating how easily mosses might be dispersed by flowing water and trapped by branches and roots in the water. Photo by Zen Iwatsuki, with permission.



Figure 32. *Fontinalis duriaei* fragment. Photo by Janice Glime.

It is likely that rodents contribute to dispersal, although they may do more harm than good. I have watched chipmunks run across my moss garden and kick up clumps as they ran. Nancy Ironsides (Bryonet 10 June 2011) found rhizoids on the apical leaves of *Leucobryum glaucum* (Figure 33) and attributed these to disturbance by animals. Péntzes Kónya (2003) considered "big wild animals" to be major dispersers of *Leucobryum juniperoideum* (Figure 34) during dry periods. The caducous leaves function as gemmae by producing rhizoids (Figure 35) and forming new plants, especially during the rainy spring, but the disturbance of dry mosses seems to outpace the regeneration from disturbed plants.

Others may spread bryophytes as they eat them (Slack 1936, Mutch & Pritchard 1984), particularly if they only digest the surface organisms and return the moss fragments with their feces. Suren and Winterbourn (1991) found that 14 aquatic invertebrate taxa had bryophyte fragments in their guts, and two tipulid larvae regularly consumed bryophytes. I tested the hypothesis that rainbow trout, known to strike at anything, could serve as dispersal agents by eating the aquatic *Fontinalis duriaei* (Figure 31-Figure 32). However, the fish could not be tempted to strike at or eat the moss, even when it housed numerous aquatic insects. Finally, we force fed the fish. The moss was

delivered back as feces in a neat, cylindrical package with bright green moss (Figure 36). At last it seemed we had demonstrated a potential upstream dispersal mechanism! But, alas, we were surprised the following day to find that the moss had lost all its color, even though it was maintained in a gallon jar of its own stream water at a cool temperature. It does not appear that rainbow trout are likely dispersal vectors after all!



Figure 33. *Leucobryum glaucum* with apical rhizoids on leaves. Photo by Nancy Ironsides, with permission.



Figure 34. *Leucobryum juniperoideum* cushions. Photo by Michael Lüth, with permission.



Figure 35. *Leucobryum juniperoideum* with leaf rhizoids after overturn by cattle. Photo courtesy of Erika Pénez-Kónya.



Figure 36. Feces of rainbow trout consisting primarily of *Fontinalis duriaei* as a result of force-feeding. Photo by Janice Glime.

I have watched larvae of the **Rhyphidae** dipteran eat wet, dirty (most likely with diatoms) mosses and observed fragments of green moss come out the other end, clean. These fragments would be ideal propagules, although not dispersed very far, but I did not culture them to see if they met the same fate as the trout package.

Further discussion of bryophyte fragment dispersal is in the adaptations subchapter on dispersal.

Summary

Fragmentation results from random breakage or from genetically programmed cleavage areas on leaves, buds, or stems. For perennial mosses, especially pleurocarpous mosses, it is typically the primary means of spreading. Arctic/alpine and aquatic habitats may rely primarily on this type of reproduction. Fragments are more likely to become established than spores and survive better in water than do spores. Their establishment can be inhibited by the presence of mature plants, but they have a greater competitive ability than spores.

Regeneration from mature cells requires **dedifferentiation** and may begin as protonemata, rhizoids, or both. Light quality and intensity may play a role in early development. Little is known about growth regulation, but gibberellin can stimulate regeneration in at least some bryophytes. Dispersal can be accomplished by wind, water, and animals, sometimes because the animal transports the bryophyte for use in a nest or house.

Acknowledgments

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