

CHAPTER 4-8

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL



Figure 1. Deciduous branch tips of *Campylopus cryptopodioides*. Photo by Michael Lüth.

Vegetative Reproduction

Botanists have traditionally considered vegetative reproduction (Figure 1), a common mode among bryophytes, as making only limited contributions to genetic variability and new adaptation. But is this really the case, in particular, of bryophytes? Laaka-Lindberg *et al.* (2003) consider asexual propagules to have a significant role in bryophyte dynamics.

In view of the vegetative propagation sources, Scrosati (2002) has offered a new definition of **genet** to allow for those plants such as bryophytes and algae that routinely propagate from vegetative cells: "For clonal autotrophic macroorganisms, in general, genet may be defined as a free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces

ramets vegetatively during growth." In these organisms, only a few living cells may start a new plant. And it may be those very cells that are different, different in ways that endowed them, and them alone, to survive whatever killed the remainder of the plant. Through somatic mutations, individual cells may indeed be more adapted than the plant they occupy. And because of their small size, such fragments in bryophytes can be dispersed and serve as propagules. Each individual or part of an individual gametophore in the clone is capable of renewed growth upon relocation. However, while this scenario is theoretically possible, we have no clue how often it occurs.

While spores are the sexual means of reproduction and dispersal of mosses, providing a mechanism for

recombination and variation, it is likely that most mosses rely more heavily on various vegetative means for their propagation (Anderson 1963; Steere 1965; Schuster 1966; Longton 1976, 1982; Selkirk 1984; Schofield 1985). For example, in three *Octoblepharum* species in Panama, Korpelainen (1999) found that most populations consisted of a single genet, hence resulting from a single colonization event by one individual.

Longton and Schuster (1983) listed six basic means of asexual reproduction in bryophytes:

1. multiple gametophores from the protonema of one spore
2. decay of older gametophyte parts with the separation of younger parts
3. development of multiple shoots by rhizomes and stolons
4. development of gametophores from rhizoids
5. regeneration from fragments
6. production of specialized "propagula"

Such reliance is due in part to the difficulty of completing sexual reproduction in many bryophytes. Since nearly 60% of the bryophytes are dioicous (Wyatt & Anderson 1984), and the monoicous habit usually provides more opportunity for sexual reproduction than the dioicous habit, it is easy to understand the importance of vegetative reproduction (Schofield 1985). Furthermore, some widely distributed species have never been found with sporophytes.

Fragmentation

Only three bryophytes are known to produce sporophytes on the continent of Antarctica: *Bryum algens* (Filson & Willis 1975), *Bryum antarcticum* (Kanda 1981), and *Grimmia trichophylla* (Selkirk 1984). However, birds and other animals scratching among the plants dislodge numerous fragments (Selkirk 1984). When Selkirk (1984) set out Tauber traps (Tauber 1974) to collect the diaspores on the surface of the snow in the Antarctic, she found that only two species had been dispersed by specialized structures: *Ulota phyllantha* by gemmae (Figure 2) and *Dicranella cardotii* by stem tips. Most of the plants, however, had been dispersed by various fragments of leaves and stems. She further verified that many of these moss taxa were actually growing from vegetative fragments at all the types of sites she observed where bare, colonizable areas were available.



Figure 2. Brown gemmae of *Ulota phyllantha*. Photo by Michael Lüth.

Fragmentation is the simplest form of asexual reproduction, a method used by the Japanese for the

development of moss gardens (Ando 1971, 1987). Cells detached from virtually any part of a moss or liverwort are capable of regeneration into a new plant.

In Arctic Canada, Miller and Howe Ambrose (1976) estimated a total of 33,820 bryophyte fragments per cubic meter of granular snow! Of these, 97% were less than 2.25 mm, so small that airborne dispersal was likely. They found that almost all the viable fragments were leaf-bearing moss stem tips. Based on their experiments and the number of fragments available, they estimated that over 4000 viable propagules occurred per cubic meter of granular snow. They suggest that the same winds that serve to disperse these fragments serve as the agent to break the fragments from the plants.

Vegetative Diaspores

Correns (1899) examined 915 types of mosses with **vegetative diaspores** (specialized propagula of Longton and Schuster). Since then, usage of terminology has diverged among the countries of the world, and even within one country. In the recent Glossarium Polyglottum Bryologiae (Magill 1990), bryologists from around the world attempted to standardize terminology. In that edition, Magill used the concept of Goebel (1905) that divided vegetative diaspores into two groups based on their development at germination. He applied the term **propagula** to those diaspores that have an apical cell and can grow directly into a leafy shoot if the apical cell is reactivated (Figure 3, Figure 6). Unfortunately, this definition is clouded by its impracticality and because even these diaspores usually produce protonemata.



Figure 3. Deciduous branches (**propagula**) of the moss *Campylopus pilifer*, a common means for its reproduction. Photo by Michael Lüth.

Magill (1990) likewise used the concept of Goebel to define **gemmae** as vegetative diaspores with no apical cell and that always must begin growth with a protonemal phase (Figure 5, Figure 6). These units then include caducous leaves and endogenous gemmae, as well as those specialized, oval, round, or irregularly shaped structures we have always called gemmae in the strictest sense.

Among the **propagula**, Imura and Iwatsuki (1990) identified four aboveground types (Figure 6):

Deciduous shoot apices (Figure 4a) result from an area weakened by a cleavage in the cell walls. These often already have rhizoidal initials at their basal parts. Such shoot apices occur in *Bryum argenteum* and *Campylopus japonicus*.

Caducous branchlets (caducous = deciduous) seem like deciduous shoot apices, except that they are branchlike structures with minute leaves and are attached to the parent plant by one-celled stalks.

Flagella (Figure 4b) are slender branches with reduced leaves and occur in the axils of upper leaves. The basal portion is multicellular, thus separating them from caducous branchlets.

Bulbils (Figure 4c) usually occur on one-celled, short stalks and have what appear to be partially developed leaves. Some are round and bulb-like, others are thread-like. They are common in *Pohlia*.

Rhizoidal tubers (Figure 4d) occur on the rhizoids and are usually filamentous, branched, or spherical and have diverse origins. They occur in species of *Bryum*, *Pohlia*, and *Fissidens*, among others.

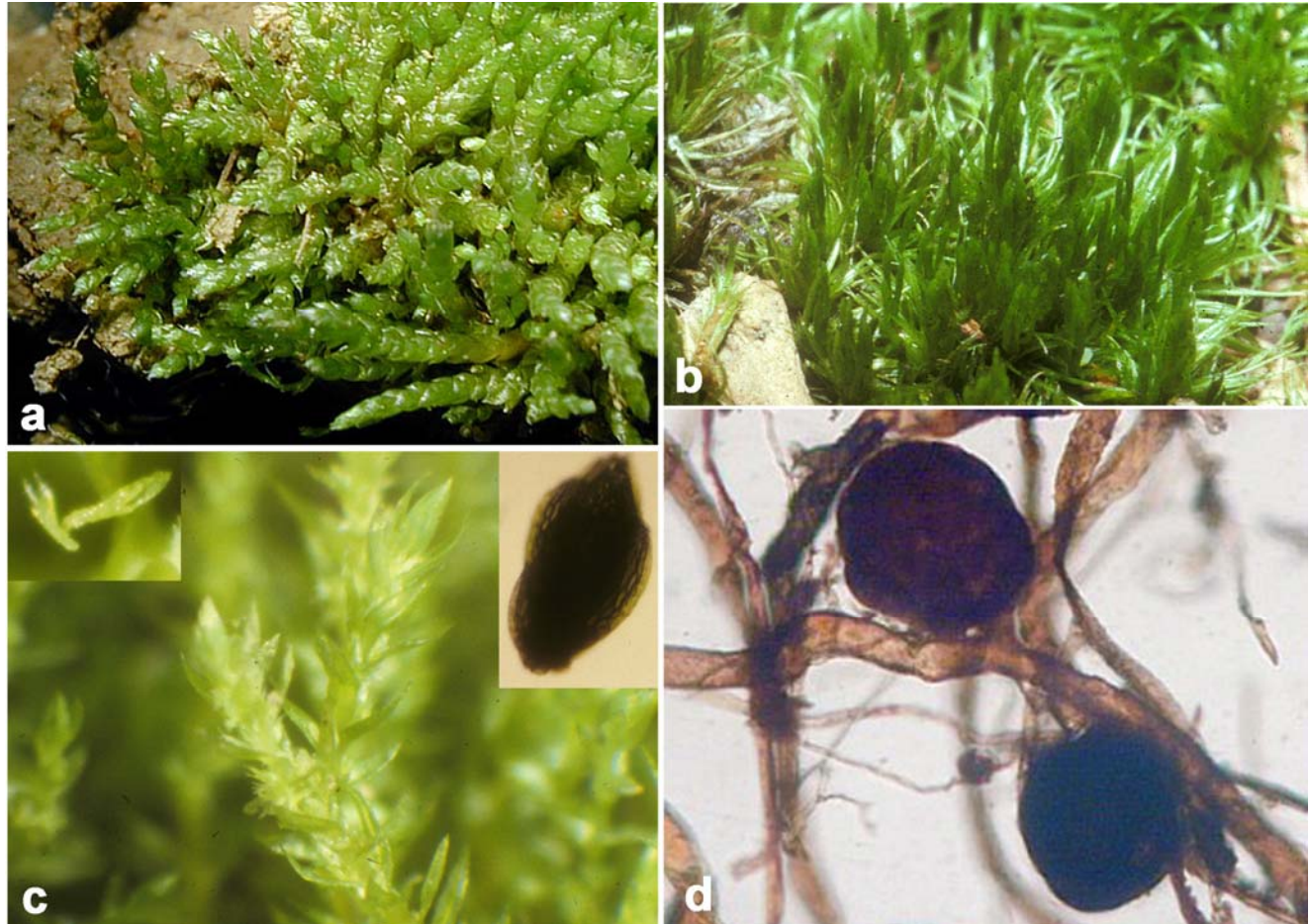


Figure 4. Propagula and rhizoidal tubers. **a.** Deciduous shoot apices of *Bryum argenteum*. Photo by Michael Lüth. **b.** Flagelliform branches of *Orthodicranum flagellare*. Photo by Janice Glime. **c.** Bulbils of *Pohlia annotina* varieties. Photos by Janice Glime. **d.** Rhizoidal tubers of *Bryum radiculosum*. Photo by Michael Lüth.



Figure 5. Gemma of *Tetraxis pellucida* showing protonema developing from it and lack of an apical cell. Photo with permission from www.botany.ubc.ca/bryophyte/LAB8.htm.

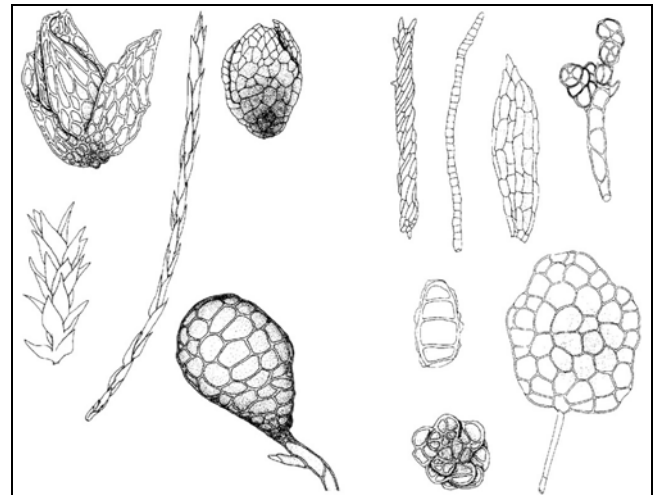


Figure 6. Propagula and gemmae of selected bryophytes. Redrawn from Imura and Iwatsuki (1990).

Gemmae can be filamentous, spindle-shaped, globular, discoid, or multi-horned. They occur on various parts of the gametophyte and sometimes have pale, thin-walled cells at the base. Pronematal and rhizoidal "gemmae" are usually labelled **bulbils** on materials from biological supply houses. Two types of gemmae can be identified based on their origin on the plant:

1. **Caducous leaves** are very specialized leaves of reduced size that may or may not differ from normal leaves in basic structure. In *Aulacomnium*, most of the taxa produce special branches with gemmae (caducous leaves) that are easily detached, reduced leaves (Imura *et al.* 1991). In *Campylopus fragilis* and *Tortula pagorum*, the caducous leaves are on short branches at the axils of upper leaves (Imura & Iwatsuki 1990).
2. **Endogenous gemmae** (Figure 7) are produced inside a cell initial. Most of the taxa among the mosses with these structures are in the Grimmiaceae, but they are common among the liverworts, often occurring as patches of non-green color at leaf tips or margins.



Figure 7. *Lophozia capitata*. **Upper:** Leafy plant with sporophyte. Photo by Jan-Peter Frahm. **Lower:** Endogenous gemmae on leaf margin. Photo with permission, modified from web site of Paul Davison, www2.una.edu/pdavis/bryophytes.htm.

Because vegetative reproduction tends to be more successful than that from spores, having fragments or specialized structures can be a safety net. For example, in experimental plantings of *Polytrichum alpestre*, Miles and Longton (1990) could find no evidence that spores germinated in the field. However, new shoots formed readily from shoot fragments. In the same experiment, production of shoots from spores in the short-lived *Funaria hygrometrica* was readily apparent. In *Atrichum undulatum* and *Bryum argenteum*, many spores germinated,

but often the gametophores failed to develop. Rather, those species, like *Polytrichum strictum* (= *P. alpestre*), regenerated more easily from fragments.

Animal Dispersal

The dispersal of vegetative parts by animals may be an important mode of travel, at least occasionally. McGregor (1961) observed *Riccia rhenana* attached to the carapace of a large snapping turtle. When I (Glime) grew *Conocephalum conicum* in my garden room in the company of a box turtle, it spread quickly around the room, something it never did in the absence of the turtle. But eventually the zebra finches discovered the liverwort and each day it grew smaller, with triangles cut from its edges. Alas, the birds seemed to be agents of destruction and not dispersal because it soon disappeared completely.

Various insects use fragments of mosses and lichens to build "houses" that they carry on their backs. Slocum and Lawrey (1976) report that the green lacewing larva (*Nodita pavidata*) carries about a "packet" of camouflage constructed of bits of lichen, lichen soredia, pieces of bark, pollen grains, fungal spores, moss gametophyte fragments, and other debris. They demonstrated that the lichen fragments were viable but did not test the mosses. It is likely that they not only were alive, but that some of these fragments also would land somewhere and grow. Larvae of Diptera (flies, especially craneflies) and Trichoptera (caddisflies) construct houses of various shapes and may incorporate bryophyte fragments in them, as will be discussed later in the chapter on animals.

Dispersal in the guts of earthworms (During *et al.* 1987; van Tooren & During 1988) can surely at times beat the 10 cm record of Kimmerer, and other invertebrates that eat bryophytes will deposit fragments in new locations. These could be distances of centimeters to hundreds of meters. Not only earthworms, but moles, voles, and ants have underground activities that can bring diaspores from their dormant state below ground to a position of activity above ground. Van Tooren and During (1988) found that eight species of bryophytes survived and appeared frequently in castings from earthworms (*Allobophora caliginosa*, *A. chlorotica*, and *Lumbricus terrestris*). Since the light travels at most only a few centimeters into the soil, these diaspores remain dormant until some disturbance brings them to the surface and light. The species that survived the enzymes, crushing, and scarification of the earthworm guts, then grew to be identified, were *Pottia* spp., *Pottia lanceolata*, *Weissia* spp., *Anisothecium schreberianum*, *Ephemerum recurvifolium*, and *Bryum klinggraeffii*. *Bryum rubens*, common in the castings, never produces capsules in the area and presumably survived as rhizoidal tubers. Most of the other taxa probably also survived as vegetative diaspores except for *Pottia* sp. and *Weissia* sp., which probably originated from spores.

Rhizoidal tubers (Figure 4d) occur on a number of taxa of bryophytes. Arts (1986a) cultivated tubers of *Fissidens cristatus* and established that they are drought resistant. The large tubers of *Campylopus pyriformis* are likewise drought resistant and contain large quantities of starch (Arts 1986b). Their dark color may indicate antiherbivore compounds or may serve as a filter against light, decreasing chances of germination under a small amount of soil.

Edwards (1978) and Risse (1987) found protonemal gemmae of *Schistostega pennata* (Figure 8) attached to the legs of mites. The gemmae, like the spores of this species, are very sticky (Ignatov & Ignatova 2001). While mites themselves most likely do not travel far, they can become passengers on other animals – birds and mammals – that might travel considerable distances.

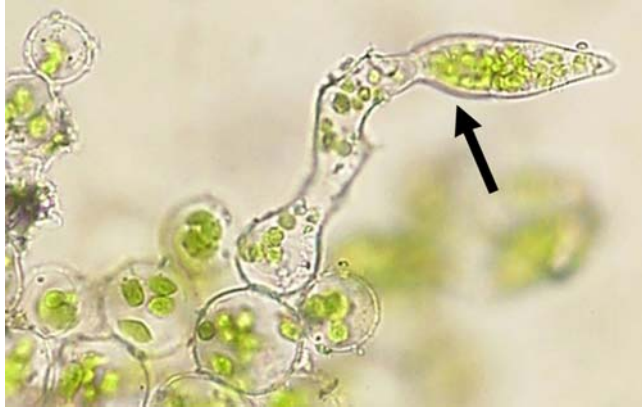


Figure 8. Protonemal gemma (**arrow**) of *Schistostega pennata*. Photo by Misha Ignatov.

Zhang *et al.* (2002) observed spider mites (*Tetranychus* sp.) eating the gemmae of *Octoblepharum albidum* in Hong Kong (Figure 9). It is possible that some of these gemmae will get trapped among the hairs on the legs, thus getting transported by the mite.



Figure 9. Spider mite (*Tetranychus* sp.) feeding on gemmae of *Octoblepharum albidum* in Hong Kong. **Arrow** indicates bases remaining where gemmae have been chewed. Photo from Zhang *et al.* (2002); permission pending.

Mollusks such as slugs eat bryophytes, but their sticky surfaces also cause fragments to adhere, causing their dispersal. *Orthodicranum flagellare* (Figure 4b) lives on logs and stumps where snails can readily gain access and contribute to dispersal of the flagelliform branches that serve as propagules (Stolzenburg 1995).

Cattle and other farm animals are able to transport terrestrial taxa wedged in their hooves, causing certain species to frequent cattle trails and ruts made by machinery (Crum 1973). In Hungary, geese are known to carry such fugitives as *Riccia frostii* on their feathers, feet, or muddy bills, making these common – you guessed it – along goose trails. It appears that hitch hiking is a common mode of travel for *Riccia* – in Michigan, USA, *R. sullivanii* and *R.*

cavernosa (Figure 10) are often dwellers along disturbed soil of 2-track roads, suggesting a vehicular means of dispersal.

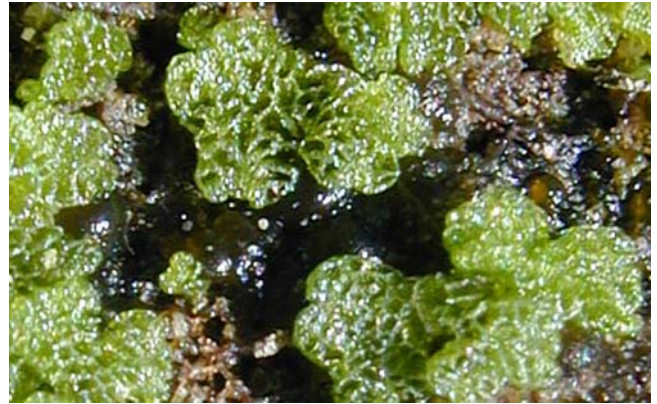


Figure 10. Thalli of *Riccia cavernosa* on disturbed soil. Photo by Michael Lüth.

Heinken *et al.* (2001) actually examined the coats and hooves of 15 roe deer (*Capreolus capreolus*) and 9 wild boars (*Sus scrofa*) from deciduous forests in Germany. They found 102 stem fragments and four leaves in these coats and hooves. Mean fragment length was 3.6 mm, but ranged 0.5-35 mm. The fragments came from just twelve species of terrestrial bryophytes, most prominently *Brachythecium velutinum*, *Hypnum cupressiforme*, and *Eurhynchium hians*. Robust acrocarpous species were absent.

The introduction of the aquatic liverwort *Ricciocarpos natans* (Figure 11) into Norway may be the result of transport by waterfowl or some other form of epizooic transport (Skulberg 1978). This has been shown for a number of algae that travel on the feathers and feet of ducks, arriving in viable condition (Schlichting 1958). Such organisms are also dispersed by aquatic insects (Stewart & Schlichting 1965, 1966; Stewart *et al.* 1970). Both mechanisms seem reasonable for bryophyte spores and leaf fragments, or even small branches.



Figure 11. Thalli of *Ricciocarpos natans* floating with the duckweeds *Lemna minor*, *Wolffia* sp., and *Spirodela polyrrhiza*. Since duckweeds are common foods for waterfowl, it is likely that *Ricciocarpos* gets mixed in with the food and stuck to feathers or feet as the birds wade and eat. Photo by Janice Glime.

McGregor (1961) actually found evidence that ducks indeed disperse living bryophytes. A fragment of *Riccia*

fluitans was attached to a feather at the back of the neck of a pintail duck that was soon to become a hunter's dinner.

Even mammals may eat (perhaps not intentionally) bryophytes, as indicated by ^{14}C studies on animal remains of late Pleistocene large herbivorous mammals (Ukraintseva 1979). But we have no evidence that these bryophyte fragments remain viable after passing through the digestive tract.

Bryophyte vegetative structures generally are not adapted for animal dispersal. Nevertheless, just by their location they are likely to be carried on animal hooves, turtle carapaces, slug slime, insect guts, hairs of mites and spiders, and stuck to feathers and beaks of ducks. Nest-building birds that line their nests with mosses often drop pieces, or the moss can even grow while within the nest. It appears that most vegetative parts do not survive the guts of most animals well, but some do and can thus be carried to new locations.

Human Dispersal

Bryum argenteum (Figure 4a) is commonly dispersed by humans. It has deciduous shoot apices that apparently attach to shoes and other clothing as well as to small animals. Clare and Terry (1960) used matchbooks in an elegantly simple experiment to demonstrate dispersal in this species. They "walked" the matchbook across patches of *B. argenteum*, then across soil. As a control, they walked matchbooks that had not contacted *B. argenteum* across other patches of soil. The *B. argenteum* became established on the plots where the matchbook had previously visited the mosses, but not on the others.

There are several documented cases of bryophytes dispersed by humans. One of the most recent reports is that of Ireland and Shchepanek (1993) for the spread of *Hyophila involuta* (Figure 12) in Canada. This species was known only from a few localities in Ontario. However, it is growing abundantly on the sides of most of the locks in the Rideau Canal and the authors suspect that it arrived in both Michigan and Canada from more southern localities by travelling there on boats. The locks are constructed of limestone and sandstone or concrete, and the plants seem to get started along the mortar seams.



Figure 12. Gametophytes of *Hyophila involuta* growing on concrete. Photo by Michael Lüth.

I still recall Iwatsuki commenting in Japan that he didn't need to check what was growing on the concrete retaining walls along the roads – it was all *Hyophila*. However, on the locks in Ontario it is nearly devoid on the

concrete blocks, occurring predominately on the limestone and sandstone blocks which are more similar to the construct in Japan). In the Ontario locks, it grows only below the water level, sometimes even on the bottom of the locks. Frequent wetting and drying and low light intensity seem to favor its growth, but the plants must also survive seven months out of the water in winter when the locks are drained. These plants never have sporophytes, and with only one report of sporophytes in the United States, it appears that they rely on their numerous multicellular gemmae.

Golf courses and picnic areas seem to be common sites for invasive species because they get considerable foot traffic from a wide range of locations. In Auckland, New Zealand, *Fissidens taxifolius* was first reported under a picnic table (Espie 1997). Also in New Zealand, *Rhytidiadelphus squarrosus* first appeared on a Dunedin golf course in 1975, presumably arriving with foot traffic.

Bryophytes used for packing can escape and become established, as in the case of *Pseudoscleropodium purum* (Figure 13), in widely ranging parts of the world (Allen & Crosby 1987). Further uses for packing will be discussed in the chapter on uses.



Figure 13. Gametophyte of *Pseudoscleropodium purum*, a widely transported packing material. Photo by Michael Lüth.

In South Africa, *Fontinalis antipyretica* was introduced to provide habitat for aquatic insects, and like many aquatic tracheophyte introductions, it soon clogged waterways, not to mention ousting the native insects adapted so well to bare rocks (Richards 1946).

Water Dispersal

Water aids in the dispersal of bryophytes in multiple ways. Aquatic mosses most likely depend primarily on water dispersal. *Fontinalis* species in streams are faced with the problem of having spores lodge in a suitable place to begin new growth, whereas branches can easily get caught against rocks or snagged by submerged branches and roots, giving them an opportunity for new establishment. In the winter, aquatic mosses can get frozen in the ice. When the ice breaks up, chunks may carry a number of fragments downstream where some may become impinged on similar substrata (Figure 14).



Figure 14. Fragments of *Fontinalis dalecarlica* frozen in ice that has broken up in a New Hampshire headwater stream. Photo by Janice Glime.

In *Gymnocolea* (Figure 15), non-fertile perianths become more globose and are shorter than the fertile ones, and they develop a line of dehiscence where they are constricted at the base (Schuster 1966). Almost any disturbance will break them free. On dry days, these may drop to the ground, but more typically, when they are struck by raindrops, these become free, or may already be free, and with their included air bubble they easily float. Such perianths then are carried away by water. But one could argue equally well that this light weight would permit them to be carried by wind should they be broken free on a dry and windy day. However, there is little documentation of regeneration from liverwort parts, so we can only guess that these perianths are able to form new plants.

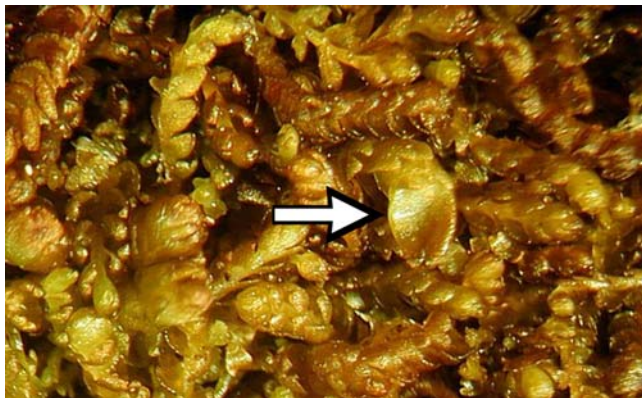


Figure 15. Perianth (arrow) of *Gymnocolea inflata*. Photo by Michael Lüth.

Splash Cups

The best-known method is that of the **gemma cup** or **splash cup**. Several bryophytes have specialized cups where the gemmae are produced and from which they are subsequently dispersed by raindrops (Figure 16, Figure 17). The splash cup mechanism seems to be engineered to maximize the distance its contents can splash, thus forming an effective dispersal mechanism with the help of raindrops. Its significance was apparently not recognized until Buller (1942) described its function in the bird's nest fungus, *Cyathus*. Brodie (1951) followed up on the observations of Buller and noted that splash cups commonly form 60-70° angles with the horizontal, the cups have a broad basal attachment, and the dispersed objects

are lenticular. The latter, of course, is not true of sperm, but gemmae in the splash cups of the moss *Tetraphis pellucida* (Figure 16) and the liverworts *Lunularia cruciata* and *Marchantia polymorpha* (Figure 17) are lenticular. It seems to be a common feature for the splashing to carry its contents about 60 cm in *L. cruciata*, *M. polymorpha*, and *Polytrichum* (Brodie 1951), but in *T. pellucida*, they seem only to go about 10 cm (Kimmerer 1991). Brodie (1951) considered *T. pellucida* too frail to benefit from raindrops striking its apex, finding that the plants bent under the weight.



Figure 16. Gemmae cups of the moss *Tetraphis pellucida*. Photo by Janice Glime



Figure 17. **Upper:** Lens-shaped gemmae of *Lunularia cruciata*. Photo by Jan-Peter Frahm. **Lower:** Lens-shaped gemmae of *Marchantia polymorpha*. Photo by Michael Lüth.

Gravity

Whereas spores are light weight and therefore easily lofted away on a slight air current, vegetative structures are much more bulky and heavy. Shed parts, unless caught in a

gust that can even blow heavy maple fruits up into the air, are likely simply to fall to the ground. This seems to be a common means for structures like gemmae, deciduous perianths, and other bulky forms of brood bodies and fragments.

Propagule Dispersal Distances

It appears that little is known about actual distances that vegetative propagules might travel. Although many studies have indicated that the distances are short, it appears that measurements are lacking. Kimmerer (1991) found that gemmae of *Tetraphis pellucida* travelled to a maximum of 10 cm in her study. But surely moss balls (see subchapter on growth forms) can travel great distances. And fragments of bryophytes on glaciers likewise travel hundreds of feet, and potentially much more. In my study on *Fontinalis* vegetative dispersal, one piece had established upstream about 20 m from its origin, presumably carried there by some animal (bear or human?).

Propagule Survival

Buried propagules must somehow remain dormant in an environment that varies both their temperature and their state of hydration. The only factor they lack for germination appears to be light. Risse (1987) reviewed 82 species of European mosses with rhizoidal propagules and demonstrated that tubers and rhizoidal gemmae do not germinate in absence of light. Their germination is dependent upon the intensity of light, not the photoperiod. If the propagules are hydrated for more than ten days without successful germination they do not survive. After fifteen days, their fat reserves are depleted. Furthermore, imbibition of water causes the gemmae to lose their dormancy and become sensitive to dehydration, causing irreversible damage if they are more than 12 hours into their pre-germination phase when they dry out. This can explain the absence of viable propagules in the first cm of soil where frequent wetting and drying are certain.

Egunyomi (1978) found that spores have longer storage longevity than do gemmae for *Octoblepharum albidum*. Even at room temperature and 60-75% humidity, spores were viable after eight months, but gemmae began to lose viability at six months. Light is of utmost importance for germination, with only 8.0% of gemmae germinating at 1 lux, but 90% at 1375 lux.

Imura and coworkers (1992) experimented with the rhizoidal tubers of a moss (*Leptobryum pyriforme*) found on the ice surface of a lake near the Syowa Station in the Antarctic. Both protonemata and leafy shoots developed from these tubers after the tubers had been stored for two years in a freezer. This illustrates the tremendous plasticity of these species and the extraordinary survival abilities.

Mishler and Newton (1988) experimented with four *Tortula* species and found that fragments, while being less successful at germination than spores, usually developed numerous stems, whereas the spores did not during the 2.5 months of experiments. The protonemata looked different between the spore-derived and the fragment-derived ones. Perhaps they differed physiologically and those derived from spores required a day length or other condition not present in the experiment.

I have observed diatom-covered mosses being eaten by a Diptera larva in the Rhyphidae family. These went in

"dirty" and came out the other end clean and still bright green. But I have no evidence that these actually survived the digestive tract. Insect guts can have extremely high or extremely low pH to adapt them to digestion of the few remaining nutrients in detritus, and the particular diet of this larva suggests it might be so-adapted. These extreme pH levels are likely to be detrimental to the living cells of the moss. The delayed response of the moss to such a detrimental environment is exemplified by our experiment on *Fontinalis duriaei*. In an experiment to determine if rainbow trout could be dispersal agents of *F. duriaei*, we brought in fresh moss with lots of aquatic insects, but the fish did not eat the moss, so we force-fed it. The moss was expelled later through the anus in a neat cylindrical package (Figure 18), still bright green. We isolated it in a cooled jar of its own stream water, but 24 hours later, the moss had lost its green color and appeared to be dead.



Figure 18. Feces packet from rainbow trout, containing *Fontinalis duriaei* that has lost its green color 24 hours after its egestion. Photo by Janice Glime.

Van Tooren and During (1988) identified bryophytes from the digestive tract of earthworms in the Netherlands. Among these, tubers of *Bryum klinggraeffii*, *Bryum rubens*, and *Dicranella schreberiana* successfully germinated, but in general, there was high mortality among tubers and other vegetative structures. Van Tooren and During suggested that spore survival was higher than vegetative diaspore survival in earthworm guts, but they did not have quantitative measures of this. It is possible that it was greater numbers of spores that made it appear so.

Ross-Davis and Frego (2004) examined the propagule rain in southeastern New Brunswick, Canada, forests that were managed for timber production. Using emergence, they identified 51 species in the aerial rain and soil propagule banks. Only 36 of these were extant species in the area sampled. The air-borne species were more similar to the extant vegetation than were the buried taxa, attesting to the readiness of the diaspore bank for changes in the conditions.

Vegetative propagula are less likely to survive travel through the gut than spores, and they may be more susceptible to damage when they begin to germinate as well. Hydration without successful germination can kill them. But if they are able to germinate successfully, both fragments and specialized propagula have better chances than spores of producing gametophores, albeit only one per propagule. Propagule banks typically reflect not only the present vegetation, but also past vegetation, providing ready sources following disturbance.

Effects of Grazing

Ericson (1977) followed the changes in moss cover in Scandinavia for four years and discovered that rodents played a major role in the changes. Only the mosses on windthrows and tree stumps maintained constant cover. The fascinating realization was that different species seemed to suffer declines and increases in different years. In 1974, *Ptilium crista-castrensis* suffered 73% reduction and *Dicranum scoparium* suffered 57%. However, in 1975, the strongest decrease was in *Hylocomium splendens*, which suffered 49% reduction, while *P. crista-castrensis* increased 43% and *D. scoparium* increased 70%! Ericson felt that this might indicate increased growth as a response to fragmentation caused by grazing. In experiments with *Fontinalis*, I have observed that stems with broken tips will often produce several apical branches. However, to increase cover values so significantly, it would seem that at least some dispersal must have been effected.

In 1974 and especially in 1975, following heavy grazing in 1973, *Dicranum scoparium* had spread to areas where no *D. scoparium* occurred in 1973 (Ericson 1977). Rodents appear to have been the agent of both fragmentation and dispersal.

Ericson (1977) felt that several types of regeneration were common. *Polytrichum commune* and *P. juniperinum*, as well as others, can recolonize from protonemata, juvenile plants, and rhizoid fragments (Meusel 1935, Wigglesworth 1947). *Hylocomium splendens* (Correns 1899) and species of *Dicranum* (Meusel 1935) grow easily from broken parts of stems, and *Polytrichum commune* and species of *Dicranum* regenerate from isolated leaves (Correns 1899).

Summary

Vegetative reproduction includes fragments, gemmae, and vegetative diaspores. A genet is therefore those individuals that arise from a single zygote, parthenogenetic gamete, or spore and that produce branches vegetatively. There are six basic means of **reproducing vegetatively**: 1) **multiple gametophores** from the protonema of one spore, 2) decay of older gametophyte parts with the **separation of younger parts**, 3) development of **multiple shoots by rhizomes and stolons**, 4) development of **gametophores from rhizoids**, 5) regeneration from **fragments**, 6) production of **specialized propagula**. The success of vegetative propagation is due to selection in the face of the difficulty of accomplishing sexual reproduction in a terrestrial environment. **Fragmentation** is especially common among pleurocarpous, perennial mosses where the dioicous condition and small spore size reduce the success of sexual reproduction. Such fragments can reach densities of 4000 viable propagules per cubic meter of snow. **Propagula** differ from **gemmae** in having an apical cell that can grow directly into a leafy shoot without a protonema stage. **Propagula** include **deciduous shoot apices, caducous branchlets, flagella**, and **bulbils**. **Rhizoidal tubers** can occur underground.

Animal dispersal includes insects, mites, slugs, animal hooves, turtles, ducks, and nest-building birds. However, none of the bryophytes seems to be especially adapted for this mode of dispersal. Humans disperse

bryophytes through their own shoes and vehicle tires and through packing materials.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed.

Although most bryophytes are best adapted to wind dispersal, even of fragments and specialized propagules, gravity accounts for the short distances to which most of these travel.

Acknowledgments

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