

CHAPTER 4-10

ADAPTIVE STRATEGIES: VEGETATIVE PROPAGULES

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CHAPTER 4-10

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

Vegetative Reproduction

Vegetative reproduction comes in many forms. These range from breakage of leaves and stems that have become brittle through desiccation to specialized gemmae that occur on leaves or special stems and are nurtured by the parent plant, ready to go when finding a suitable substrate, to tubers that occur on roots and protonemata.

Such asexual structures seem to have evolved through **heterochrony** (developmental change in the timing of events, leading to changes in size and shape), including **neoteny** (retention of juvenile characteristics in adults of species) Newton & Mishler 1994). Hence, we can see gemmae that look like reduced leaves, as in *Aulacomnium* (Figure 2).

We might assume that in disturbed habitats, such as industrial areas, vegetative means to reproduce might offer advantages over more fragile-seeming protonemata necessitated by spore dispersal. But this is not always true. Nordhorn-Richter (1982) found the extent of bryophyte distribution in an industrial area of Germany was not improved by presence of asexual propagules except among members of *Plagiothecium* (Figure 3-Figure 4). On the other hand, vegetative reproduction offers the advantage of being ready to start developing an adult plant, reaching maturity much more quickly than a plant from a spore. Furthermore, bryophytes produce asexual propagules at a younger age than that needed for sexual reproduction.



Figure 2. *Aulacomnium palustre* gemmae that are modified leaves. Photo by Zen Iwatsuki, with permission.



Figure 3. *Plagiothecium laetum*. Photo by Christian Peters, with permission.



Figure 4. *Plagiothecium laetum* leaves with scattered gemmae. Photo by Kristian Peters, with permission.

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."

Frey and Kürschner (2011) shortened and summarized this list, identifying three types of asexual reproduction that are recognized today:

1. asexual reproduction *s. str.* by **regeneration** from somewhat specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and by production of specialized propagules (gemmae, protonemal brood cells, tubers)
2. **fragmentation** of plants or parts of plants into essentially unspecialized fragments
3. **clonal** reproduction (cloning from branches, stolons, and rhizomes).

Cloning results when a branch of a protonema or a plant becomes separated from its parent. This can occur by decay of the protonema or disintegration of plant modules. In gametophores, cloning requires the formation of **ramets** (individuals, "daughter plants"). Frey and Kürschner (2011) consider cloning to be a "keystone factor for asexual reproduction, habitat colonization, and habitat maintenance." While this cloning mechanism is not dispersal in the usual sense, it does contribute to placing the species in new locations. For example, when we (Zhang, Raeymaekers, and Glime, unpublished) mapped the locations of *Pleurozium schreberi* (Figure 5) in m² plots and followed them yearly for five years, we found that they appeared to "move" from one location to another within the plot, often changing position by several centimeters, sometimes forming two clumps.



Figure 5. *Pleurozium schreberi* in the boreal forest. Photo by Janice Glime.

Although sexual reproduction may provide the opportunity for new gene combinations, a number of bryophytes [*e.g.* *Cyrtomnium hymenophylloides* (Figure 6; Miller & Mogensen 1997)] persist without any evidence of sexual reproduction. In reviewing the literature, Rolstad & Gjerde (2003) considered that some bryophytes have poor dispersal capability due to the absence of spore production. In this case, vegetative diaspores and even fragments

maintain the species and carry it to new locations. As in *C. hymenophylloides*, the absence of sexual reproduction may only occur through part of its range, whereas other species seem never to produce capsules (Miller & Mogensen 1997). Rather, in *C. hymenophylloides* of North America and Greenland new growth arises from axillary and apical buds that appear to be the principal means of reproduction. Miller and Mogensen assumed that these were dispersed by wind but considered that water and gravity were also possible. It is interesting that populations may be all male, or more typically, all female.



Figure 6. *Cyrtomnium hymenophylloides*. Photo by Michael Lüth, with permission.

In general, not counting fragmentation, there seems to be only one type of asexual reproduction within a species (Li Zhang, Bryonet 16 March 2010). Nevertheless, many exceptions occur. Pressel *et al.* (2007) reviewed the propagules in *Bryum* (see below) and related genera. In this genus one can find rhizoidal and chloronemal tubers, axillary bulbils, chloronemal brood cells, and foliar and protonemal gemmae. *Ptychostomum* (= *Bryum*) *capillare* (Figure 7) and *Bryum dichotomum* (Figure 8) have three types, but only one type has been found in any individual at a given time (Imura 1994). However, Zhang found two types on the same individual of *Fissidens* sp. (Figure 9-Figure 12, Figure 117) – rhizoidal gemmae and tubers. Gemmae (Figure 10-Figure 12) in this species come in a variety of shapes and types. *Octoblepharum albidum* (Figure 13) has three modes (Zhang *et al.* 2003). In this species, new plants can grow from the leaf tips where first rhizoids are produced and then buds. These buds grow into plants and may, in turn, produce another "generation" of leaf-tip shoots, much like the walking fern *Asplenium rhizophyllum*. These walking mosses may constitute 5-20% of the population. *Leucobryum glaucum* (Figure 14-Figure 15; *Leucobryum* Figure 16) has a similar behavior in which the terminal rosette of leaves may produce rhizoids and new plants. But in this case, so far as is known, the new plants drop off and grow if they land on a suitable substrate.



Figure 7. *Ptychostomum* (= *Bryum*) *capillare* wet, a species that can produce caulonemal, rhizoidal, or leaf gemmae. Photo by David Holyoak, with permission.



Figure 8. *Bryum dichotomum*, a species with chloronemal, rhizoidal, and leaf gemmae. Photo by Michael Lüth, with permission.



Figure 9. *Fissidens taxifolius*. Photo by David Holyoak, with permission.



Figure 10. *Fissidens flaccidus* axillary gemmae on stem. Photo by Ida Bruggeman, with permission.



Figure 11. *Fissidens macaoensis* rhizoidal tuber. Photo by Li Zhang, with permission.

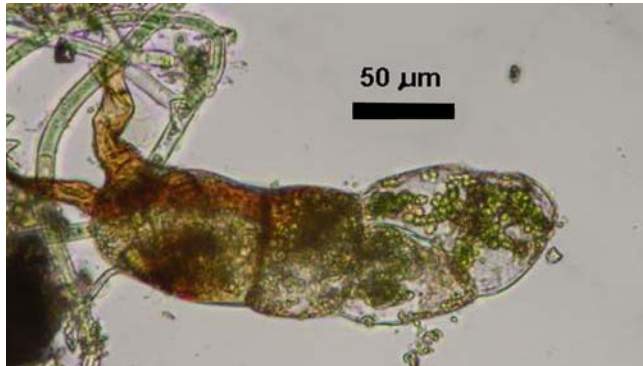


Figure 12. *Fissidens tenellus* bud. Photo by Tom Thekathyl, with permission.



Figure 13. *Octoblepharum albidum*, a moss that can grow new plants at its leaf tips, creating a walking fern type of reproductive strategy. Photo by Michael Lüth, with permission.



Figure 14. *Leucobryum glaucum* with young apical rhizoids. Photo by Nancy Ironsides, with permission.



Figure 15. *Leucobryum glaucum* with mature apical rhizoids that can serve as propagules. Photo by Sean Edwards, with permission.



Figure 16. *Leucobryum* showing rhizoids developing from leaf tips. Photo courtesy of Andi Cairns.

Pfeiffer *et al.* (2006) identified three types of vegetative morpho-types in the pleurocarpous moss *Rhytidium rugosum* (Figure 17): **ramet** (individual plant that has grown vegetatively from another individual, *i.e.*, a

branch, becoming part of a clone of that plant) that can become separated when they decay, brood **branch**, and **caducous** (easily detached) shoot apex. They demonstrated successful dispersal of vegetative diaspores through AFLP (amplified fragment length polymorphism) fingerprinting, wherein samples from one clone occurred on both studied plots in Germany. Furthermore, the close relationship of the fingerprinting between the two plots suggest clonal rather than sexual (spore) origin for the populations.



Figure 17. *Rhytidium rugosum* from Europe, showing what appear to be several ramets. Photo by Michael Lüth, with permission.

Dispersal of vegetative propagules seems to be more of a passive process than that of spores. Few special mechanisms are documented for removal of asexual propagules from the plant. *Tetraphis pellucida* (Figure 18-Figure 19), with apical gemmae in splash cups is a notable exception among mosses, with *Marchantia* (Figure 20-Figure 21) and *Lunularia* (Figure 22) species likewise having gemma splash cups. Others easily "pop" as they become detached by some intruder bumping them, as in *Dicranum flagellare* (Figure 23). The extent of transport by animals that brush against them has seldom been documented.



Figure 18. *Tetraphis pellucida* with gemma splash cups. Photo by Andrew Spink, with permission.



Figure 19. Gemma of *Tetraphis pellucida* showing protonema developing from it and lack of an apical cell. Photo from Botany website, UBC, with permission.



Figure 20. *Marchantia alpina* with gemma cups in Norway. Photo by Michael Lüth, with permission.

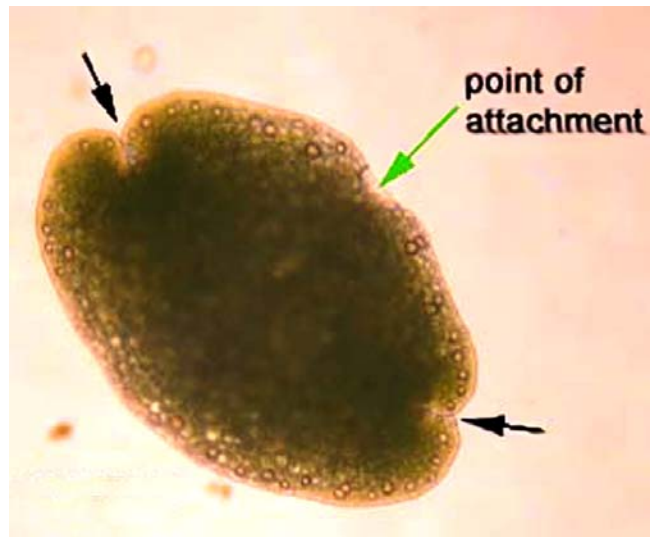


Figure 21. *Marchantia polymorpha* gemma showing notch (arrow) where growth begins. Photo by Kavita Uttam UBC, with permission.



Figure 22. *Lunularia cruciata* showing gemma splash cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 23. *Dicranum flagellare* showing flagelliform branches that serve as propagules. It is accompanied by several species of the lichen *Cladonia*. Photo by Robert Klips, with permission.

Herben (1994) considers habitat to be the important parameter for assessing the role of the reproductive mode of bryophytes, with those in small and unstable habitats showing more frequent formation of propagules. Löbel and Rydin (2009) found that among epiphytes the habitat conditions had no influence on production of asexual propagules, whereas they did influence sporophyte production. Furthermore, sexual colonies had to reach a specific size before they could reproduce sexually, whereas there was no such limit for asexual reproduction. Despite the dispersal limitations of large asexual diaspores, asexual dispersal is still common among epiphytes, with higher growth rates for the asexual diaspores partially compensating for the limited dispersal. Furthermore, habitat turnover most likely favors asexual diaspores that start growth rapidly.

Löbel and Rydin (2009), working in the temperate zone, further considered that competition was not an important character in the epiphytic habitat because of the difficulty of dispersal and ability to spread vegetatively. Yu and Wilson (2001) pointed out the importance of patchiness and arrival times in plants, a concept that seems appropriate for bryophytes, especially epiphytes. They suggest that "trade-offs between different stages of colonization could be far more common in nature than a trade-off between competitive ability and colonization ability."

Botanists have traditionally considered vegetative reproduction (Figure 1) 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 genetic 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 bryophytes, 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* (Figure 13) species in Panama, Korpelainen (1999) found that most populations consisted of a single genet, hence resulting from a single colonization event by one individual.

Clones can be very important in recolonization of minor disturbances. Frego (1996) reported on four boreal bryophytes and their ability to do so. *Pleurozium schreberi* (Figure 5) often has pure colonies in black spruce forest (*Picea mariana*). But it also has colonies with minor species as seeming invaders (Figure 24). Frego found that these minor species are able to persist by occupying small disturbance gaps in the *P. schreberi* colony. All of the species were able to colonize by encroachment of vegetative shoots. Propagules were important for this encroachment. *Pleurozium schreberi* was the most rapid colonizer, probably due to a combination of rapid growth and abundant vegetative propagules.



Figure 24. *Pleurozium schreberi* (center) and *Dicranum polysetum* (lower left), a common species combination in the boreal forest. Photo by Janice Glime.

Such reliance on asexual reproduction 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.

Dispersal potential is a major limiting factor on the distribution of bryophytes (Pohjamo *et al.* 2006). Hence, those species with mixed reproductive strategies have a greater chance of success. Pohjamo *et al.* suggest that such mixed strategies are particularly useful in a heterogeneous landscape where different means of reproduction have different levels of success in each of the microhabitats, and possibly in different years. Traditional thinking suggests that long distance dispersal is generally best by spores, whereas vegetative dispersal places the diaspores close to the parents, generally in the same environment. But what occurs when both are the same size?

Using trapping techniques, Pohjamo *et al.* (2006) tested this propagule size relationship for the leafy liverwort *Anastrophyllum hellerianum* (Figure 25-Figure 26), a dioicous inhabitant of **decorticated** (lacking bark) logs in their study area. This species produces gemmae on the branch apices, and these gemmae approximate the size of the spores. In their study, spore dispersal had little dependence on distance in the field or forest. The dispersal of gemmae was more strongly dependent on distance in the open than in forest sites. Rainy periods favored gemmae deposition compared to dry periods, perhaps due to effects of splashing. But weather seemed to have no effect on the dispersal pattern of either spores or gemmae. Gemmae provided the advantage of nearly continuous availability, whereas spore dispersal was seasonal. The striking revelation from this study is that gemmae, at least those of the same size as spores, can contribute to long-distance dispersal.

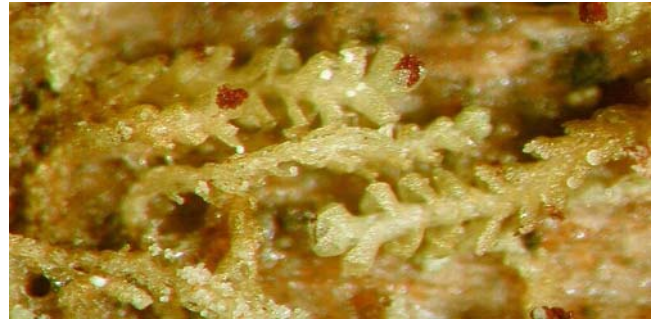


Figure 25. *Anastrophyllum hellerianum* with gemmae. Photo by Michael Lüth, with permission.



Figure 26. *Anastrophyllum hellerianum* gemmae. Photo by Des Callaghan, with permission.

Adaptations

There seems to be little information on adaptations of asexual propagules for dispersal or establishment. Thiers (1988) examined morphological adaptations of tropical rainforest **Jungermanniales**, including diaspores. She found that these diaspores had a secretion of sticky mucilage with discoid gemmae production. We can guess at some adaptations – projections that help bulbils adhere, dense starch storage in gemmae, thicker cuticles to reduce water loss, physiological ability to withstand desiccation, hormones (ABA) to induce dormancy, but these are guesses and remain to be tested as actual factors.

Fragmentation

Bryophytes have the ability to produce new plants from almost any part, making fragmentation a viable means of reproduction. Such a process requires that at least some cells lose their specificity (**dedifferentiate**), then differentiate into a new plant (Giles 1971). Giles considered that as long as cells remain on the parent plant, they will not dedifferentiate. But there are some indications among the leafy liverworts that such detachment is not always necessary before new plantlets are able to grow, particularly if the leaf is attached to a fragment rather than an attached plant (Fulford 1936; Glime 1970). This might suggest that the cells require a continuing source of an inhibitor to prevent dedifferentiation.

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. This is true of leaves in which the tips dehisce to function as propagules (Reese 1997). Some of these devices are highly specialized, as for example, the caducous branchlets of *Leucodon andrewsianus* (Figure 27) where sporophytes are unknown (Reese & Anderson 1997).

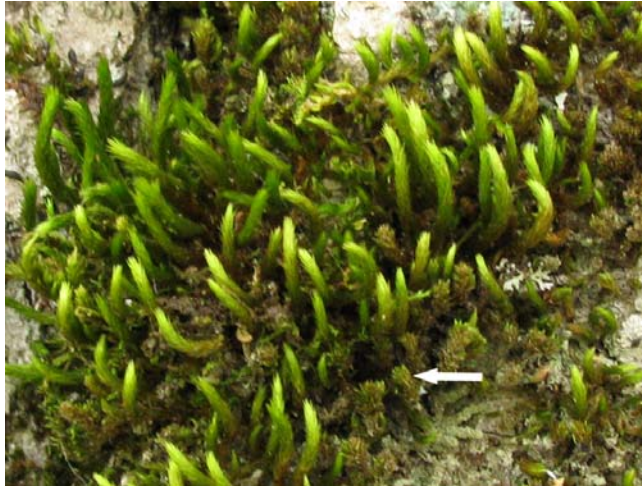


Figure 27. *Leucodon andrewsianus* on bark near Twin Lakes, Michigan. Arrow indicates caducous branchlets. Photo by Janice Glime.

Correns (1899) recognized the importance of the regenerative capacity of vegetative parts. They have historic importance in fossils as well. Miller (1985) reported fossil evidence that the dispersal and establishment of mosses had occurred as gametophyte fragments, suggesting that this is an ancient mechanism of reproduction and dispersal. This contention was supported by Lindskog and Eriksen (1995) who found fossil plant fragments in the debris layers of the ice core of a glacier in northern Scandinavia. These fragments compared well with the composition of the surrounding vegetation. Olga Belkina has supplied me with photographs indicating the presence of fragments and the establishment of colonies of *Hygrohypnella polaris* (Figure 28-Figure 30) on a glacier at Svalbard (Belkina & Mavlyudov 2011). Mosses are scattered across the glacier, as shown in Figure 31.

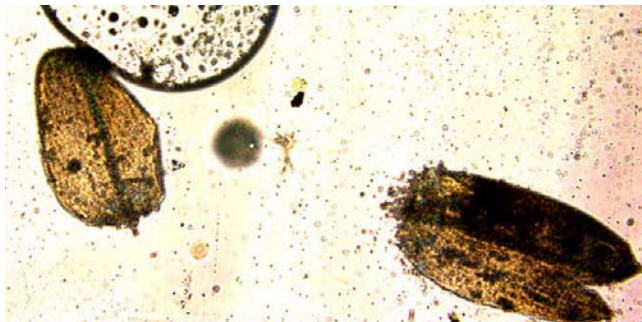


Figure 28. Fragments of *Hygrohypnella polaris* from glacier. Photo by Olga Belkina, with permission.



Figure 29. *Hygrohypnella polaris* on glacier. Photo by Olga Belkina, with permission.



Figure 30. Lower surface of *Hygrohypnella polaris* cushion with green branches and pedestal near it on glacier, indicating that it has been overturned and begun growth on the opposite side. Photo by Olga Belkina, with permission.



Figure 31. Austre Grønfyordbreen glacier with the moss *Hygrohypnella polare* in the foreground. Photo by Bulat Mavlyudov, with permission.

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 juniperinum* (as *P.*

alpestre) (Figure 32), 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* (Figure 33-Figure 34) was readily apparent. In *Atrichum undulatum* (Figure 43) and *Bryum argenteum* (Figure 35), many spores germinated, but often the gametophores failed to develop. Rather, those species, like the *Polytrichum juniperinum* (Figure 32), regenerated more easily from fragments.



Figure 32. *Polytrichum juniperinum* (= *P. alpestre*), a species that forms new shoots easily from apices. Photo by Des Callaghan, with permission.

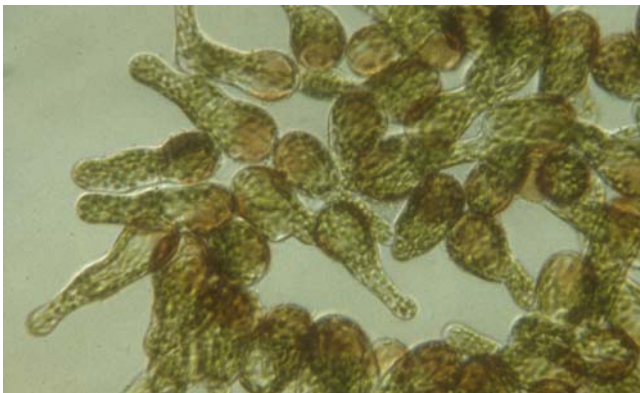


Figure 33. Germination of spores of *Funaria hygrometrica*. Photo by Janice Glime.

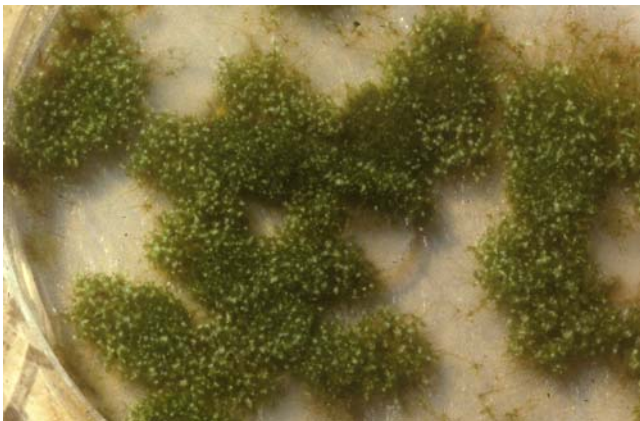


Figure 34. Young plants of *Funaria hygrometrica* germinated from spores. Each clump is the result of one spore, demonstrating the large number of vegetative reproduction by buds on the protonemata. Photo by Janice Glime.



Figure 35. *Bryum argenteum*, a species with caducous tips but spores that often fail to germinate. Photo by George Shepherd, through Flickr Creative Commons.

Leaves and Stems

Peter Poschlod (pers. comm. 6 March 2013) considers fragmentation to be the most important dispersal diaspore in peatlands, citing the absence of *Sphagnum* spores in traps, but the frequent presence of vegetative fragments (Poschlod 1995). Furthermore, he has regenerated protonemata and shoots from leaf fragments of both *Sphagnum* from peatlands (Poschlod & Pfadenhauer 1989) and brown mosses from fens (Poschlod & Schrag 1990).

In most cases, regeneration from fragments starts with a protonema. Longton and Schuster (1983) reported that even apparently dead or dark, moribund lower shoots of *Pleurozium schreberi* (Figure 5) and *Bryum argenteum* (Figure 35) are capable of producing protonemata. Clymo and Duckett (1986) likewise reported the development of protonemata and/or shoots from lower shoot tissues that appeared to be dead or moribund. Using cores from at least 30 cm depth of *Sphagnum papillosum* (Figure 36), *S. magellanicum* (Figure 5), and *S. recurvum* (Figure 37) they were able to culture numerous new shoots. They estimated that the fragments in the cores were 25-60 years old. The growths appeared to arise from both fragments and spores, with the latter producing protonemata first. Nevertheless, some protonemata arose directly from old stems, whereas most of the growths from fragments directly produced stems and leaves. Regeneration required both light and air, explaining the lack of growth prior to removal through coring. These cores also gave rise to five species of leafy liverworts, but it is unclear if these came from fragments, gemmae, or spores.

Polytrichum species seemed to be inalcitrant to growth from leaf fragments, but in 1980, Wilmot-Dear succeeded in demonstrating regeneration from leaves in four species of the former *Polytrichum*, growing them at 20°C in a 12:12 light:dark cycle. *Polytrichum commune* (Figure 38), *P. juniperinum* (Figure 32), and *Polytrichastrum formosum* (Figure 39) developed long, much-branched secondary protonemata that produced buds. *Pogonatum urnigerum* (Figure 40) directly developed buds with no initial protonema. *Polytrichum piliferum* (Figure 41) produced short, unbranched protonemata, each with a single terminal bud. These regenerants arose

primarily from the large cells at the bases of lamellae, but some arose from the basal cells of the lamellae themselves. In *Pogonatum urnigerum* regeneration tended to decrease from the tip to the base of the leaf, whereas in *Polytrichum* and *Polytrichastrum* it decreased from base to tip. Only *Pogonatum aloides* (Figure 42), a species with persistent protonemata, did not regenerate from leaves. Wilmot-Dear advised that more experiments should be conducted on temperature prior to regeneration. *Atrichum* seems to regenerate from leaves rather easily. Gemmell (1953) reported leaf regeneration in *Atrichum undulatum* (Figure 43). I have seen it in *Atrichum angustatum* (Figure 44).



Figure 36. *Sphagnum papillosum*, a species that can regenerate from 30 cm cores. Photo by Michael Lüth, with permission.



Figure 37. *Sphagnum recurvum*, a species that can regenerate from 30 cm cores. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.



Figure 38. *Polytrichum commune*, a species that can grow from leaf fragments. Photo by James K Lindsey, with permission.



Figure 39. *Polytrichastrum formosum*, a species that can grow from leaf fragments. Photo by James K. Lindsey, with permission.



Figure 40. *Pogonatum urnigerum*, a species in which regeneration decreases from apex to base. Photo by David Holyoak, with permission.



Figure 41. *Polytrichum piliferum*, a species that regenerates protonemata from leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

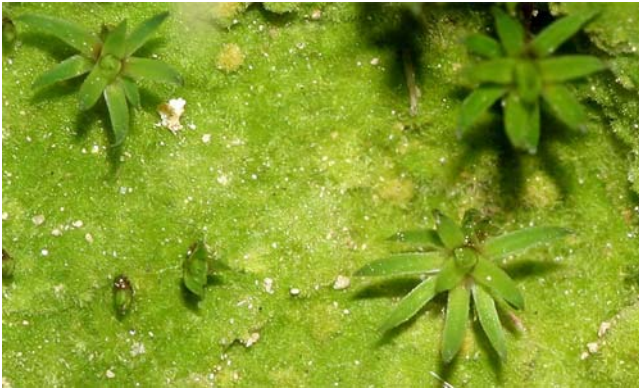


Figure 42. *Pogonatum aloides* with persistent protonemata. Photo by Walter Obermayer, with permission.



Figure 43. *Atrichum undulatum* from Gratiot River, MI, USA. These leaves can grow new plants from fragments. Photo by Janice Glime.



Figure 44. *Atrichum angustatum* with dry plants, protonemata, and buds. Photo by Janice Glime.

Newton (1972) likewise found differences in regeneration from detached leaves in *Mniaceae* species. Those of *Plagiomnium undulatum* (Figure 45)

experienced more rapid regeneration than did *Mnium hornum* (Figure 46). Fragments of both species survived frost before and during regeneration. But males failed to survive desiccation of young gametophyte regenerants from leaves, whereas 77% of the females survived.



Figure 45. *Plagiomnium undulatum*, a species with relatively rapid regeneration from detached leaves. Photo by Hermann Schachner, through creative Commons.



Figure 46. *Mnium hornum*, a species with somewhat slower regeneration from detached leaves. Photo by Bob Klips, with permission.

Early reports of regeneration from deciduous leaves or branches of leafy liverworts are provided by Cavers (1903) and Watson (1964, p. 94). I have observed the development of a young plant from a leaf in the stream-dwelling leafy liverwort *Scapania undulata* (Figure 47-Figure 48; Glime 1970). In this case, some of the plantlets developed from the center of the leaf while it was still attached to a stem fragment (Figure 48). This was not an isolated incident – several such plantlets or buds were collected in debris in drift nets being used to capture stream insects. It is interesting that this collection occurred on 1 March in Plymouth, NH, USA, before the spring melt. At this time most of the plants would be completely submerged and the stream would typically have a moderate flow from intermittent snow melt. Greatest stream flow usually occurs in this area in early April, providing a dispersal means for the plantlets. The species typically grows submersed or on rocks where it is kept moist most of the year by flowing water that splashes against the rocks. *Bazzania denudata* (Figure 49) develops plantlets on normal leaves still adhering to the plant (see Figure 50) (Fulford 1936), as in the case of *Scapania undulata* (Figure 47-Figure 48). *Plagiochila* (Figure 51), on the

other hand, can form similar growths, but these usually occur on deciduous leaves (Schuster 1960, 1966).



Figure 47. *Scapania undulata* in a typical habitat on a rock in a stream where it is nearly always wet. Moving water can easily break off fragments in this location. Photo by Dick Haaksma, with permission.

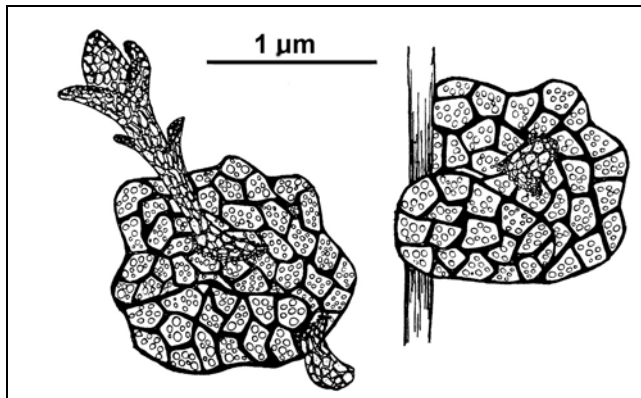


Figure 48. Detached leaf (left) with two developing plantlets and attached leaf (right) with beginning plantlet on *Scapania undulata*. Drawing courtesy of Flora Mace.



Figure 49. *Bazzania denudata*, a leafy liverwort that produces plantlets from normal leaves, but that also has fragile thin branches (shown here) projecting from beneath the stems and looking denuded. Photo from UBC Botany website, with permission.

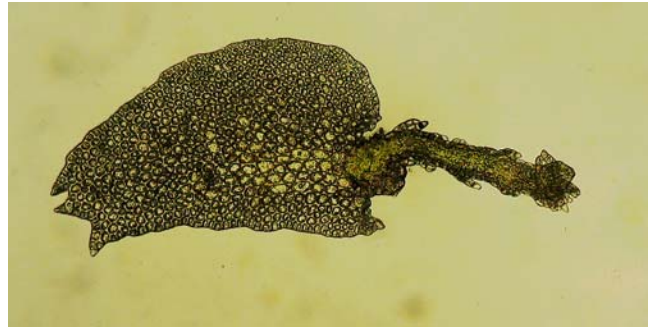


Figure 50. *Bazzania adnexa* leaf fragment with germling. Photo by Tom Thekathyl, with permission.



Figure 51. *Plagiochila asplenioides*, member of a genus that forms growths on its deciduous leaves. Photo by Dick Haaksma, with permission.

Herbarium specimens often are not as dead as they look, and even bryophytes in nature in desert types of habitats can remain desiccated for many years. Maheu (1922) rehydrated *Syntrichia ruralis* (Figure 52) after 14 years of continuous desiccation. The shoots of this species regenerated from their leaves.



Figure 52. *Syntrichia ruralis* hydrated, a species that regenerated from leaves after 14 years of desiccation. Photo by Misha Ignatov, with permission.

Stark *et al.* (2004) found that dried plants do not regenerate as quickly as fresh material. In the desert moss *Syntrichia caninervis* (Figure 53), fresh material

regenerated in 3-14 days (Figure 54). They used juvenile, green, yellow-green, and brown leaves, representing 0, 2, 6, and 12 years old respectively, to determine regeneration. The 0-2-year-old leaves had somewhat greater viability, regenerated more quickly, and extended their protonemal filaments farther in the 58 days of the experiment. They likewise produced shoots more quickly and accumulated a greater biomass. They also found that female leaves were more likely to produce a shoot than were male leaves. The sexes did not differ in time required to produce a protonema, linear extension of the protonema, or in rate of biomass accumulation. Nevertheless, protonemata derived from male leaves tended to emerge more quickly and produce greater total biomass, ultimately resulting in predominately protonemata. As a consequence, females had a higher success of shoot production, perhaps explaining rarity of males in *S. caninervis*.



Figure 53. *Syntrichia caninervis*, a species that is very desiccation tolerant and regenerates from leaves. Photo by John Game, through Creative Commons.



Figure 54. *Syntrichia caninervis* regeneration from leaf. Photo courtesy of Lloyd Stark.

Regenerants

Many leafy liverworts produce **regenerants** (new plants) (Barbara Crandall-Stotler, Bryonet 24 April 2021). In *Lophocolea* sp., these are produced along the leaf edges (Figure 55) (Emmett Judziewicz, Bryonet 23 April 2021). These tend to occur as the growing season is ending or the plant is in a less than favorable habitat (Barbara Crandall-Stotler, Bryonet 24 April 2021), such as this *Lophocolea* species (Figure 55) growing at a higher, drier, cooler than usual altitude. The regenerants develop like a sporeling (Figure 56), causing the leaves to resemble the juvenile leaves of the species. In *Lophocolea* sp., these are bilobed (Figure 56). These regenerants are able to re-establish the population once suitable growing conditions return.

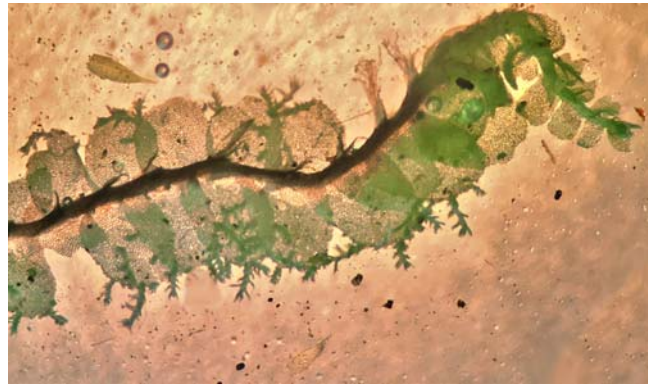


Figure 55. *Lophocolea* sp. with regenerants, found at Acacia koa kīpuka at 1700 m on Mauna Loa, Hawaii. Photo by Emmett Judziewicz and Virginia Freire, with permission.



Figure 56. *Lophocolea* sp. with regenerant. Photo by Emmett Judziewicz and Virginia Freire, with permission.

Protonemata

Protonemata have been largely ignored in the ecology of bryophytes. This is not surprising due to their inconspicuous nature, difficulty in identification, and often short life. But Pasiché Lisboa (2014) has contributed to our knowledge by studying their dispersal potential in the moss *Callicostella belangeriana* and *Taxiphyllum taxirameum* (Figure 57). Spores from wild-collected capsules were cultured axenically to get protonemata in the lab. These

protonemata were placed on cardboard and splashed by three sequential drops of dyed water from 1 and 2 m height. This resulted in dispersal up to 80 cm, and it was more likely that a protonema hit by a drop would move than that it would remain stationary. These dispersed protonemata had a high survival rate, and even though most stayed within 10-12 cm, it provides an additional means for a colony to spread. I do wonder if the same dispersal would occur from soil instead of cardboard.



Figure 57. *Taxiphyllum taxirameum* with capsule, a species for which raindrop dispersal of spores has been demonstrated up to 80 cm. Photo by Bob Klips, with permission.

Perianths

But leaves and branches are not the only dispersal units through fragmentation. In *Lophozia* (= *Gymnocolea*) *inflata* (Figure 58), non-fertile **perianths** (leaves surrounding female reproductive structures) 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, the perianths 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. Perianths of *Chonecolea doellingeri* likewise are easily dislodged, but these do not become inflated (Schuster 1966).

Calyptrae

Britton (1902) reported that *Fissidens fontanus* (as *Octodicerus julianum*) (Figure 59) is able to regenerate from its calyptra, producing protonemata. The capsules of this species fall off just before maturity while they are still green and the calyptra is still attached. Together they are able to float, hence creating a potential dispersal unit of the

calyptra. Its vegetative dispersal capabilities may account for its widespread occurrence in many kinds and locations of aquatic habitats.

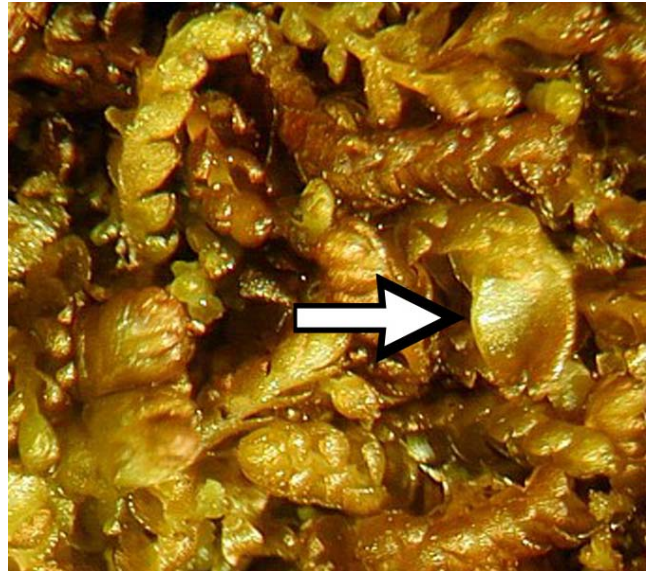


Figure 58. Perianth (arrow) of *Lophozia* (= *Gymnocolea*) *inflata*. Photo by Michael Lüth, with permission.



Figure 59. *Fissidens fontanus*, a species that can regenerate from its calyptra. Photo by Jan-Peter Frahm, with permission.

Kortselius *et al.* (2017) reported that the aquatic moss *Fissidens fontanus* is known to achieve asexual reproduction through the calyptra, developing gametophytes.

Wynne and Budke (2012) took the calyptrae one step further in *Funaria hygrometrica* (Figure 62). They looked at the ability of the calyptra to produce protonemata as a function of time and discovered several things: 1) The calyptrae remain alive and capable of producing protonemata for at least 28 days after detachment from the capsule; 2) the younger calyptrae produced significantly more protonemata than the oldest of three developmental stages.



Figure 60. *Fissidens fontanus* calyptrae with germination. Photo courtesy of Hans Kruijer.



Figure 61. *Fissidens fontanus* calyptra with germination. Photo courtesy of Hans Kruijer.



Figure 62. *Funaria hygrometrica* young sporophytes with calyptrae. Photo by Michael Lüth, with permission.

Involucres

The **involucre** (protective sheath originating from thallus and surrounding single gametangium or sporophyte) is not a structure one would normally consider as a dispersal unit. Nevertheless, in *Metzgeria* (Figure 63), this seems to be the case (Kuwahara 1968, 1973). Eight species in this genus, including *M. acuminata*, *M. agnewii*, *M. arborescens*, *M. filicina*, *Echinomitrium* (= *Metzgeria*) *furcata* (Figure 64), *M. grollei*, *M. imberbis*, and *M. liebmanniana*, all have demonstrated the ability to grow branches from female involucres into normal vegetative thallus. These liverworts have come from Europe, Africa, South America, and North America, suggesting that the phenomenon might be present in other taxa that produce involucres. Since these are early papers, it is likely that other examples are known. But do these have any significance for fragmentation and dispersal?



Figure 63. *Metzgeria conjugata* with sporophyte and basal involucre. Photo from Botany website, University of British Columbia, BC, Canada, with permission.



Figure 64. *Metzgeria furcata*, a species that can regenerate from the involucre. Photo by Des Callaghan, with permission.

Paraphyses

Many mosses produce paraphyses that surround the antheridia and archegonia. These are usually considered to

help maintain more constant moisture conditions than would be possible without them, help to squeeze sperm out of the antheridia, and may also function to protect against frost, solar radiation, and herbivore damage. But the presence of chlorophyll in a structure that would not seem to need it caused Correns (1890) and Hill (1903) to suspect that they might also serve as propagula. Hill even observed protonema-like branching in paraphyses (Figure 65) from *Rhodobryum roseum* (Figure 66-Figure 67). But early attempts to actually grow new plants from these paraphyses failed (Heald 1898; LaRue 1930).

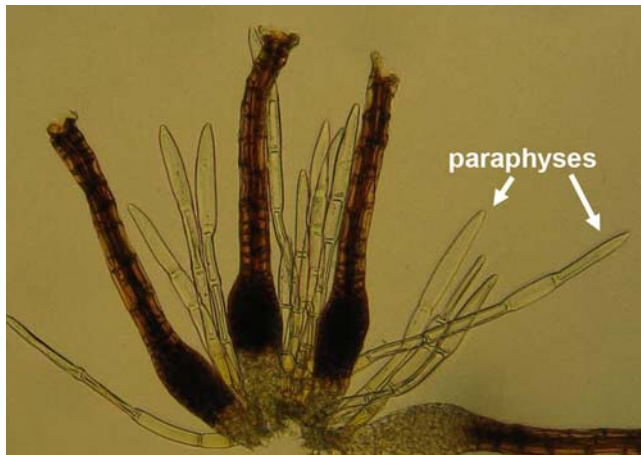


Figure 65. *Zygodon intermedius* archegonia among paraphyses. Photo by Tom Thekathyl, with permission.

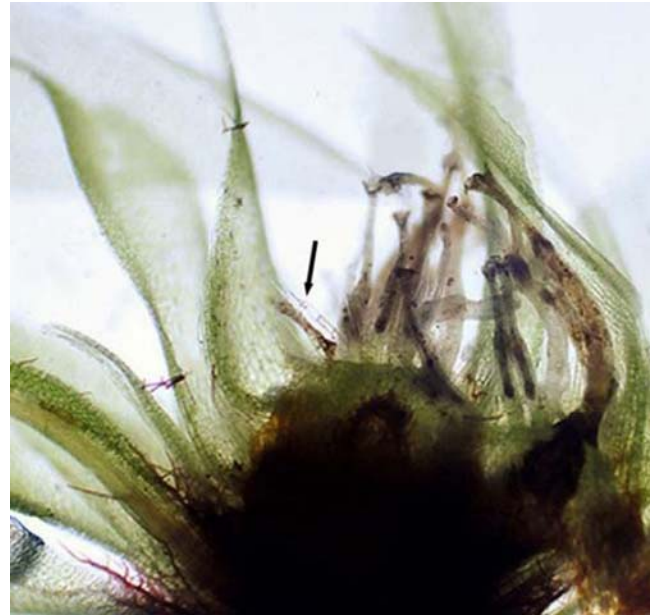


Figure 67. *Rhodobryum roseum* perichaetium. Arrow indicates paraphysis. Photo by George J. Shepherd, through Creative Commons.

Finally, Reese (1955), also convinced that a regenerative function was implied by the presence of chlorophyll in the paraphyses, managed to culture paraphyses of three species and successfully produce regeneration: *Ptychostomum* (= *Bryum*) *capillare* (Figure 7) 10%; *Aulacomnium palustre* (Figure 68) 12.5%; *Funaria hygrometrica* (Figure 69) 25%. *Ptychostomum capillare* and *Funaria hygrometrica* required only one month for the first evidence of regeneration, whereas *Aulacomnium palustre* required two months. Reese suggested that the ease of obtaining regenerants from these three mosses suggests that other mosses with green paraphyses might also regenerate in this way. But this leaves one question remaining, how are they dispersed?



Figure 66. *Rhodobryum roseum*, a moss in which paraphyses can develop protonemata. Photo by Hermann Schachner, through GNU Free Documentation.



Figure 68. *Aulacomnium palustre* in MI, USA. Photo by Janice Glime.



Figure 69. *Funaria hygrometrica* with young sporophytes. Photo by Andrew Spink, with permission.

Falling Epiphytes

In the tropics, where epiphytes abound, bryophytes can fall from the canopy. Within dense canopies, these bryophytes can fall to another branch that is within their tolerance range for light, temperature, and humidity. Others will fall to the ground. Clumps of plants in the Neotropics ranged in size from 90 cm³ to 36,000 cm³ with the number of individual plants per clump ranging 2-9 (Matelson *et al.* 1993). Unfortunately for us, data for bryophytes were not separated from the general assessment. Matelson *et al.* found that these falling epiphytes can contribute to the NH₄⁺ and K⁺ of the forest floor. There were no significant differences in longevity among the eight plant categories (bryophytes being one category), suggesting that perhaps some of the bryophytes could continue to live and possibly be re-dispersed by wind or animals.

Moss Balls

Some fragments get dispersed by snow and ice and may even blow around as moss balls on glaciers. McDaniel and Miller (2000) reported both bryophyte and vascular plant fragments in late-spring snowbeds in the Adirondack Mountains, NY, USA. The alpine fragment diversity far exceeded that from a forested site, and the bryophyte diversity exceeded that of the vascular plants. Among the bryophytes, 82% were sufficiently healthy and complete to permit identification to genus or species. An interesting revelation was the presence of liverworts from the alpine samples, suggesting that their absence from late-glacial sediments may be due to the fossilization process (taphonomy) rather than their absence in the flora or their inability to disperse by fragments. Although rare, some of the fragments in the alpine areas came from lower elevation balsam fir and red spruce-balsam fir forests. Fragments deposited on the snow would be available for immediate establishment when the snow melted, with cool temperatures and plenty of water to get started. The bryophytes will be there when the glaciers melt.

Cushions of mosses from large basalt outcrops can create moss balls when they become detached from their substrate (Pérez 2010), particularly due to activity of the Dark-rumped Petrels (*Pterodroma phaeopygia*) that burrow

to make nests under outcrops. Such detachment can be facilitated by rainfall, desiccation, wind, frost, and animal disturbance. These balls can form as the clumps are transported down steep slopes (26-34°) by geomorphic processes such as frost (especially needle ice activity), runoff, and wind. At the Haleakala crater, Maui, Hawaii, USA, these balls contained *Grimmia trichophylla* (Figure 71) and *G. torquata* (Figure 72). Pérez found that the larger mosses tended to become flattened because they were less disturbed by needle ice, hence remaining immobile for longer periods of time. These potential moss balls generally moved less than 100 cm (83%); only 5% moved 200-839 cm. Trapping of dust grains and small soil particles, combined with water-holding capacity of the mosses, created a greater water storage capacity in these balls (310%) compared to that in the soils of the site (16.8%). Pérez interpreted this as a self-replicating dispersal system on these slopes.



Figure 70. *Pterodroma phaeopygia* (Galapagos Petrel, Dark-rumped Petrel) that burrows and disrupts mosses, causing moss balls to form. Photo by Lip Kee, through Creative Commons.



Figure 71. *Grimmia trichophylla* on a boulder. Clumps such as this are easily broken off and can become moss balls. Photo by Michael Lüth, with permission.



Figure 72. *Grimmia torquata*. Once free, a clump can become a moss ball; lower branches grow toward the center of an upside down plant. Photo by Michael Lüth, with permission.

I have seen moss balls that fell from the talus slopes near the Red River in New Mexico, USA. There were numerous balls on the ground near the base of the slope, some quite rounded and others irregular in shape (Figure 74-Figure 73).



Figure 73. Detached moss ball formed by rolling down the talus slope shown in Figure 74. Photo by Janice Glime.

Animals – Breaking or Ingesting Bryophytes

Some fragments have a little help from the animals in the vicinity. We are finding an increasing number of animals that ingest bryophytes, including insects, earthworms, molluscs, rodents, and occasionally larger mammals. (See next subchapter.)

Extreme Environments

In extreme environments, fragments may be important in dispersal. They can be produced under the most harsh conditions and be blown around in an arrested state until landing in a suitable microhabitat.

Antarctic & Arctic

On the continent of Antarctica, only three bryophytes were known to produce sporophytes: *Bryum pseudotriquetrum* (as *Bryum algens*; Figure 75) (Filson & Willis 1975), *Henediella heimii* (as *Bryum antarcticum*; Figure 76) (Kanda 1981), and *Grimmia trichophylla*

(Figure 71; 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* (Figure 77) by gemmae (Figure 77-Figure 79) 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 74. Talus slope near the Red River, New Mexico, USA, a source of mosses that roll down the slopes and across the valley below, breaking off tips and becoming rounded moss balls. Photo by Janice Glime.



Figure 75. *Bryum pseudotriquetrum*, one of three bryophytes known to produce sporophytes in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 76. *Hennediella heimii* with capsules, a species that produces capsules in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 77. Brown gemmae of *Ulota phyllantha*, a dispersal unit found in Tauber traps in the Antarctic. Photo by Michael Lüth, with permission.

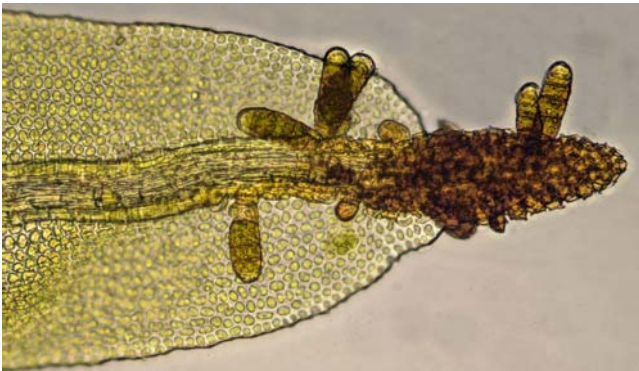


Figure 78. *Ulota phyllantha* gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

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. Cold air and desiccating conditions make the plants more fragile and contribute to the breakage.



Figure 79. *Ulota phyllantha* gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

Alpine

Many bryophytes seldom or never produce sporophytes in harsh environments such as that of alpine summits, requiring them to rely on asexual means for reproduction and dispersal. Robinson and Miller (2010) compared two species of *Sphagnum* from the Adirondack Mountains and other high altitude sites in eastern North America. These two species [*S. pylaesii* (Figure 80), *S. tenellum* (Figure 81)] live in similar habitats, but their life strategies differ. Robinson and Miller used 17 microsatellite loci to infer dispersal from the gene flow estimates. Branch fragments of *S. pylaesii* were coated with UV-fluorescent dye and released from two alpine summits. Fragments were located after 12 and 24 h and 1 week using UV LED light sources in the evening. Both species exhibited more genetic variation than expected. However, the species differed, with *S. pylaesii* having high differentiation and low gene flow between populations throughout its North American distribution. *Sphagnum tenellum* was less differentiated and showed higher levels of gene flow. Robinson and Miller concluded that fragments played an important role in transport both on summits and to other alpine summits.



Figure 80. *Sphagnum pylaesii*, a species that can be dispersed by branch fragments. Photo by Michael Lüth, with permission.



Figure 81. *Sphagnum tenellum* with capsules. This is a species that exhibits greater gene flow than *S. pylaesii*, perhaps due to its capsule production. Photo by Dick Haaksma, with permission.

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 83, Figure 95). Unfortunately, this definition is clouded by its impracticality and because even these diaspores usually produce protonemata.

Köckinger and Kucera (2007) considered that *Barbula amplexifolia* (Figure 82) reached the Austrian Alps by vegetative gemmae across the cold Pleistocene steppes from Central Asia. They support this conclusion by the absence of male plants and sporophytes in the Alps and the low level of morphological and anatomical variability. They suggest that extensive road construction through the forests may be facilitating their recent increase in distribution.



Figure 82. *Barbula amplexifolia* with capsules in India. Photo by Michael Lüth, with permission.



Figure 83. Deciduous branches (**propagula**) of the moss *Campylopus pilifer*, representing a common means for its reproduction. Photo by Michael Lüth, with permission.

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 19, Figure 95). 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:

1. **Deciduous shoot apices** (Figure 35, Figure 84) 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* (Figure 35) and *Campylopus sinensis* (= *C. japonicus*) (Figure 84).

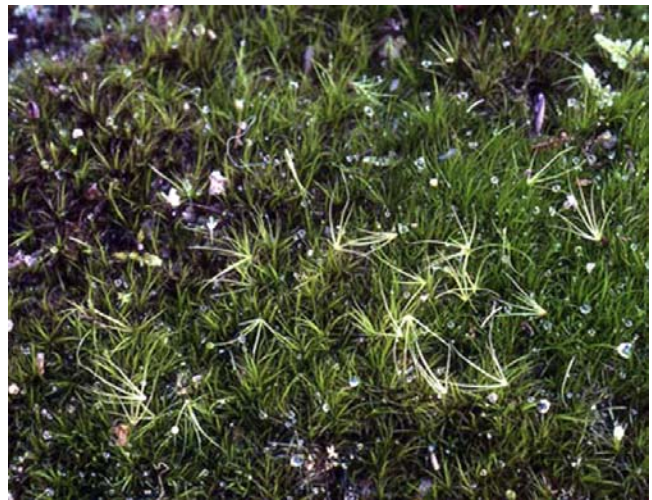


Figure 84. *Campylopus sinensis* (= *C. japonicus*) with broken tips. Photo from Hiroshima University website, with permission.

2. **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. A good example of these is in *Pterigynandrum filiforme* (Figure 85; Bergamini 2006). Although such branches are not common among pleurocarpous bryophytes, they can also be found in *Pseudotaxiphyllum* (= *Isopterygium*) *elegans* (Figure 86), *Leucodon*

sciuroides (Figure 87), *Platygyrium repens* (Figure 88-Figure 89), and *Pseudoleskeella nervosa* (Figure 90).



Figure 85. *Pterigynandrum filiforme*. Photo by Dick Haaksma, with permission.



Figure 86. *Pseudotaxiphyllum* (= *Isopterygium*) *elegans* with caducous filiform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.



Figure 87. *Leucodon sciuroides* var. *sciuroides*. Photo by David Holyoak, with permission.



Figure 88. *Platygyrium repens* with bulbils at tips of branches. Photo by Dick Haaksma, with permission.

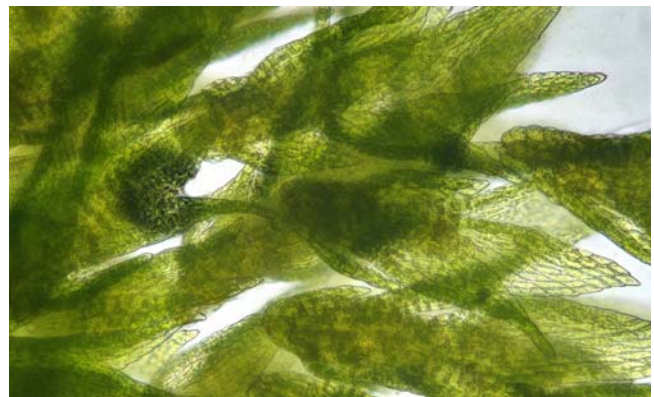


Figure 89. Microscope view of *Platygyrium repens* bulbil branches. Photo by Dick Haaksma, with permission.



Figure 90. *Pseudoleskeella nervosa* showing bulbils (caducous branchlets) at branch tips. Photo by Hermann Schachner, through Creative Commons.

3. **Flagella** 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. These are common in *Dicranum flagellare* (Figure 23).
4. **Bulbils** (Figure 91-Figure 95) 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* (Figure 91-Figure 94).

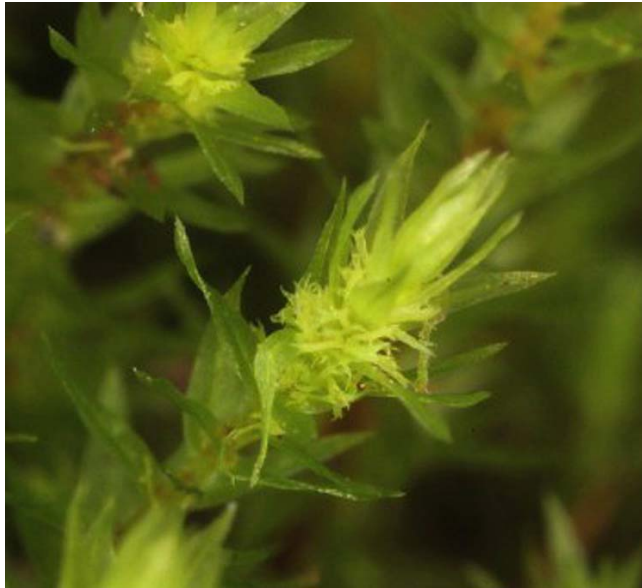


Figure 91. *Pohlia flexuosa* with flagelliform bulbils. Photo by Jan-Peter Frahm, with permission.



Figure 92. *Pohlia bulbifera*. Photo by David T. Holyoak, with permission.



Figure 93. *Pohlia bulbifera* bulbils in leaf axil. Photo by Des Callaghan, with permission.



Figure 94. *Pohlia filum* with bulbils in Europe. Photo by Michael Lüth, with permission.

Gemmae can be filamentous, spindle-shaped, globular, discoid, or multi-horned (Figure 95). They occur on various parts of the gametophyte and sometimes have pale, thin-walled cells at the base. Protonemal 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* (Figure 98-Figure 99) and *Syntrichia laevipilum* (as *Tortula pagorum*; Figure 96-Figure 97), the caducous leaves are on short branches at the axils of upper leaves (Imura & Iwatsuki 1990). *Thuidium cymbifolium* (Figure 100) produces caducous flagella (Akiyama 2009).

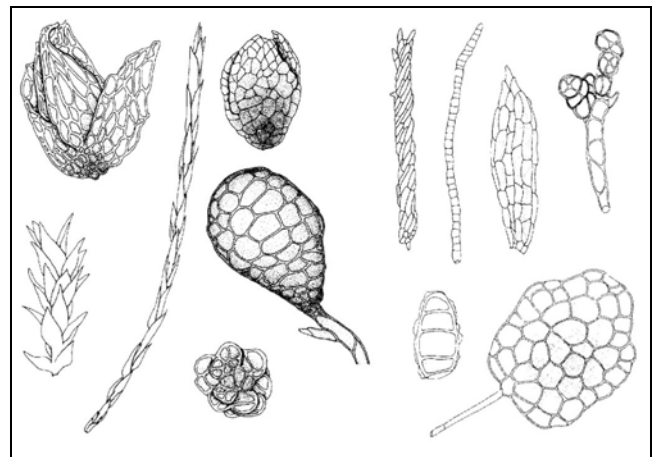


Figure 95. Propagula and gemmae of selected bryophytes. Redrawn from Imura and Iwatsuki (1990).



Figure 96. *Syntrichia laevipilum* (= *Tortula pagorum*) with caducous leaves in the axils of upper leaves. Photo by Robert Klips, with permission.

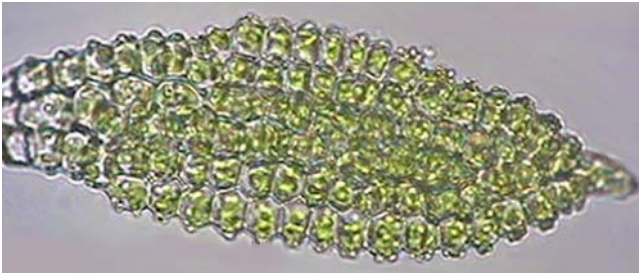


Figure 97. Caducous leaf gemma from axils of upper leaves of *Syntrichia laevipilum*. Photo by Paul Davison, with permission.



Figure 98. *Campylopus fragilis* with short branches having caducous leaves in the axils of upper leaves. Photo by David T. Holyoak, with permission.



Figure 99. *Campylopus fragilis* with caducous leaves and branches. Photo by Jan-Peter Frahm, with permission.



Figure 100. *Thuidium cymbifolium* with capsules, a species that forms caducous flagella for asexual reproduction. Photo by Li Zhang, with permission.

2. **Endogenous gemmae** (Figure 101-Figure 111) 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 101. *Heterogemma* (= *Lophozia*) *capitata* leafy plant with sporophyte; this species produces endogenous gemmae (Figure 102). Photo by Jan-Peter Frahm, with permission.



Figure 102. *Heterogemma* (= *Lophozia*) *capitata* with endogenous gemmae on leaf margin. Photo modified from web site of Paul Davison <www2.una.edu/pdavis/bryophytes.htm>, with permission.



Figure 103. *Scapania nemorea* in Europe showing apical gemmae. Photo by Michael Lüth, with permission.



Figure 107. *Scapania nemorea* leaf gemmae. Photo by Dick Haaksma, with permission.



Figure 104. *Scapania nemorea* showing mature apical gemmae. Photo by Dick Haaksma, with permission.



Figure 108. *Lophozia ventricosa* with leaf gemmae. Photo by Jan-Peter Frahm, with permission.

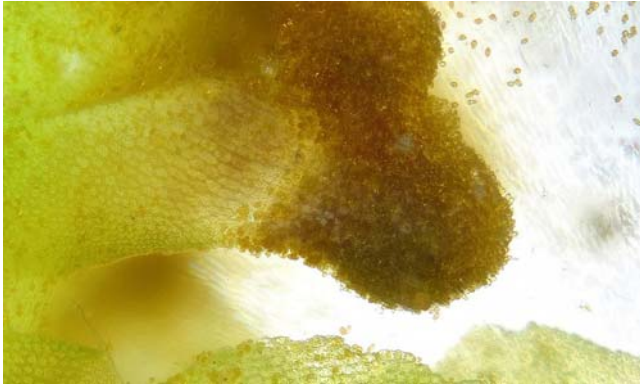


Figure 105. *Scapania nemorea* gemmae on leaf. Photo by Dick Haaksma, with permission.



Figure 109. *Jubula* (= *Radula*) *complanata* with gemmae on leaf margins. Photo by Walter Obermayer, with permission.



Figure 106. *Scapania nemorea* gemmae on leaf margin. Photo by Paul Davison, with permission.



Figure 110. *Jubula* (= *Radula*) *complanata* gemmae. Photo by Walter Obermayer, with permission.

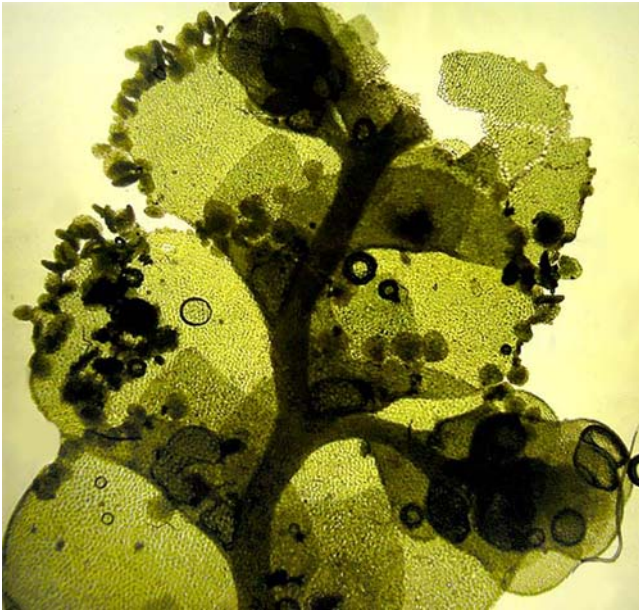


Figure 111. *Jubula* (= *Radula*) *complanata* leaves with gemmae. Photo by Walter Obermayer, with permission.

Stem and Leaf Gemmae

As one might expect, at least in some cases, the environmental conditions can have a strong effect on forms and numbers of gemmae. For example, the species *Bryum dichotomum* has several forms that previously have been named as different species (Dolnik 2006). These species, including the synonym *B. bicolor* (Figure 112), have been separated based on the forms and numbers of gemmae. Dolnik germinated the bulbils in culture in the greenhouse under a variety of conditions. In the form of *B. dichotomum* identified as its synonym *B. barnesii* (Figure 113-Figure 114), environmental conditions had no effect on number of bulbils per leaf axil, but the shape varied with seasonal variability, causing taxonomists to initially consider them to be different species. Both these bulbils and those developing on protonemata can float for several days and remain viable, providing a potential means of long-distance dispersal to locations along streams and shorelines where water levels vary.



Figure 112. *Bryum dichotomum* (*B. bicolor* form). Photo by Michael Lüth, with permission.



Figure 113. *Bryum dichotomum* (*B. barnesii* form) with bulbils in leaf axils. Photo by Kristian Peters, with permission.

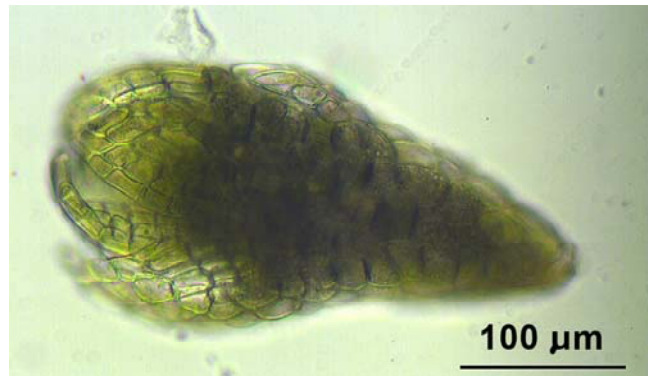


Figure 114. *Bryum dichotomum* (*B. barnesii* form) bulbil from leaf axils. Photo by Kristian Peters, with permission.

In the genus *Fossombronia*, two species are known to produce budlike vegetative propagules from leaf cells (Zhang *et al.* 2003). In South Africa, *Fossombronia gemmifera* has this behavior (Cargill 2000). In Australia, sterile plants of *Fossombronia cerebriformis* produce adaxial leaf gemmae at the bases of leaves (Scott & Pike 1984).

Newton (2002) found flagelliform propagules that were ready for dispersal in *Pilotrichella flexilis* (Figure 115). These developed from primordia in leaf axils where they had minute juvenile leaves and in some cases rhizoids were present on some branchlets. Although miniature branches often serve as propagules, this is the first time they are known to develop from moss leaves (Schuster 1966). In *P. flexilis* these develop directly from the alar cells and do not develop protonemata. The phenomenon of developing miniature shoots from leaf cells is known among the liverworts in the genus *Plagiochila*.



Figure 115. *Pilotrichella flexilis*, a species that has flagelliform propagules (miniature branches) developed from primordia in leaf axils. Photo by Claudio Delgadillo Moya, with permission.

Rhizoidal Gemmae

As I began working on this section, I quickly realized I had a nomenclature problem. I had a number of images of rhizoidal tubers – no problem there. But I also had a number labelled **rhizoidal gemmae**, all from bryologists. All but one of these gemma images resembled the tubers. After consulting the *Glossarium Polyglottum Bryologiae*, I was comforted to learn that in mosses, rhizoidal tubers were defined as gemmae born on rhizoids. But one of these images was quite different, that of *Fissidens macaoensis* (Figure 116-Figure 118). In this species, the rhizoidal gemmae are elongate filaments that are narrow at the base and expand toward the tips (Figure 117; Zhang & Hong 2011). And it develops **rhizoidal tubers** (Figure 118) at the same time, a seemingly unique character among mosses. Zhang and Hong suggest that these two types of gemmae on the soil surface could be an adaptation that permits easy dispersal up to several hundred m during floods created during the typhoon season in Macao, China.



Figure 116. *Fissidens macaoensis*, a tiny species with both rhizoidal tubers and rhizoidal gemmae at the same time. Photo by Li Zhang, with permission.

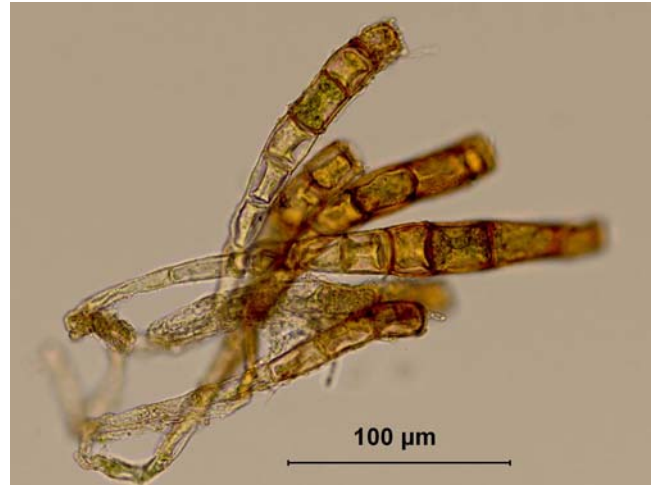


Figure 117. *Fissidens macaoensis* rhizoidal gemmae. Photo by Li Zhang, with permission.

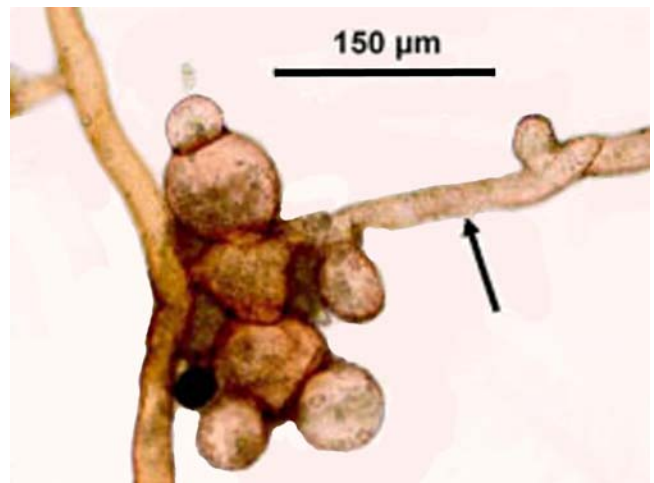


Figure 118. *Fissidens macaoensis* rhizoidal tuber. Photo by Li Zhang, with permission.

Risse (1986) observed the development from rhizoidal gemmae of *Dicranella rufescens* (Figure 119) and reviewed the rhizoidal gemmae of 82 European moss species and 3 additional ones from outside Europe (Risse 1987). Pressel *et al.* (2007) reviewed the protonemal propagules in *Bryum* (Figure 120-Figure 121, Figure 127-Figure 130) and related genera. Lepp (2008) reports over 100 species with rhizoidal gemmae, but most likely there are many more that have not been investigated.



Figure 119. *Dicranella rufescens* with rhizoidal gemmae. Photo by David T. Holyoak, with permission.



Figure 120. *Bryum* rhizoid with gemma tubers. Photo courtesy of Javier Abaigar Martinez.

Nordhorn-Richter (1984a) discovered that many parts of bryophytes, including asexual propagules, could be distinguished with the fluorescence microscope. She found this to be especially important in finding rhizoidal tubers and other propagules in the genus *Pohlia* (Nordhorn-Richter 1984a-d, 1985, 1988).

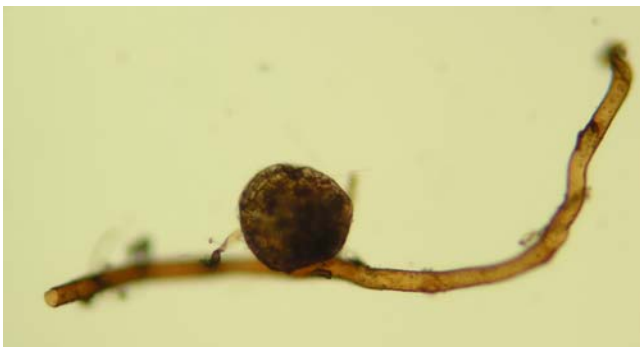


Figure 121. *Bryum* rhizoid gemma tuber. Photo courtesy of Javier Abaigar Martinez.

Whitehouse (1961) reported rhizoidal gemmae from *Henediella* (= *Tortula*) *stanfordensis* (Figure 122) in Cornwall, Great Britain, and later Reese (1967) reported them in *Chenia leptophylla* (= *Tortula vectensis*; Figure 123-Figure 124) from North America. *Henediella stanfordensis* forms a band nearly 1 km long on the coast

near Lizard Point. Male plants seem to be absent, so this species depends on its gemmae, also chloronemal gemmae, and probably fragments. It is a winter annual, surviving the summer primarily through these rhizoidal gemmae.



Figure 122. *Henediella stanfordensis*. Photo by Paul Wilson, with permission.



Figure 123. *Chenia leptophylla*. Photo by Jonathan Sleath, with permission.

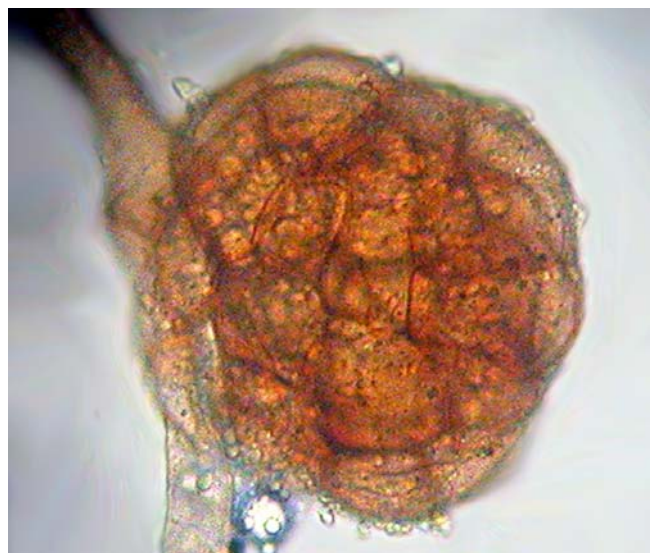


Figure 124. *Chenia leptophylla* rhizoidal tuber. Photo by Jonathan Sleath, with permission.

Rhizoidal Tubers

Rhizoidal tubers (Figure 125-Figure 131) occur on the rhizoids and are usually filamentous, branched, or spherical and have diverse origins. Whitehouse (1966) described these for 29 species of European mosses. He considered them to be a means of survival in arable fields and a means of dispersal for taxa living by streams. These often occur on species where sporophytes are unknown. Arts (1994) reported both rhizoidal tubers and protonemal gemmae in nine species of *Ditrichum* (Figure 125-Figure 126). They are common in the genus *Bryum* (Figure 127-Figure 130), and are likewise known in *Pohlia* (Figure 131). Arts (1986a) cultivated tubers of *Fissidens dubius* (= *F. cristatus*; Figure 132) and established that they are drought resistant. The large tubers of *Campylopus pyriformis* (Figure 133) 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.



Figure 125. *Ditrichum cornubicum*, a species with rhizoidal tubers. Photo by David T. Holyoak, with permission.



Figure 126. *Ditrichum cornubicum* rhizoidal tuber. Photo by David T. Holyoak, with permission.



Figure 127. *Bryum canariense* rhizoidal tubers exposed in the soil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

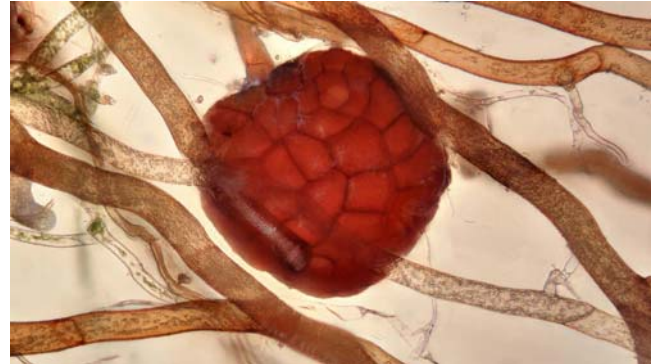


Figure 128. *Bryum bornholmense* rhizoidal tubers. Photo by Dick Haaksma, with permission.

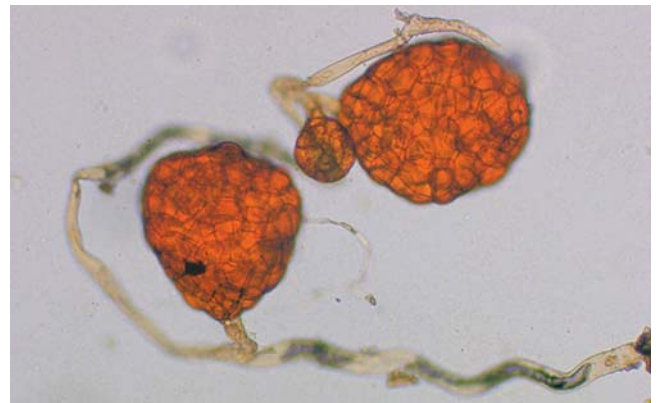


Figure 129. *Bryum tenuisetum* rhizoidal tubers. Photo by Chris Hesse, with permission.

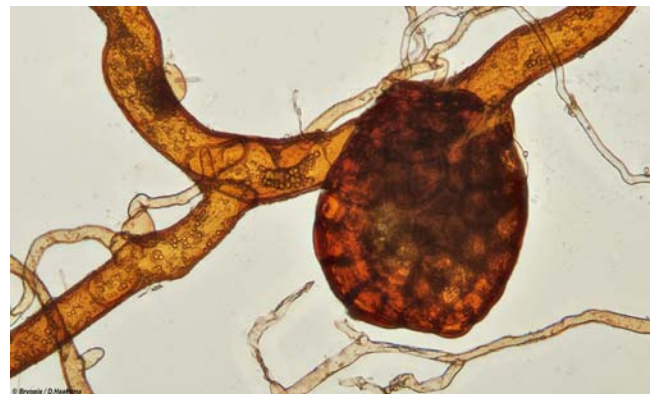


Figure 130. *Bryum torquescens* rhizoidal tuber. Dick Haaksma, with permission.



Figure 131. *Pohlia wilsonii* rhizoidal tuber. Photo by Guillermo M. Suárez.



Figure 132. *Fissidens dubius*, a species with drought-resistant rhizoidal tubers. Photo by Bernd Haynold, through Creative Commons.

Protonemal Gemmae

Because of identification difficulties, we seldom examine protonemata closely in the field. Hence, to many of us, protonemal gemmae are all but unknown. Nevertheless, Pressel *et al.* (2007) consider them to be relatively common. These protonemal gemmae occur in a variety of families. The moss *Trematodon brevicalyx* (Bruchiaceae) produces them (Dhingra & Chopra 1983) and they are known in 36 species of *Bryum* (Chopra & Rawat 1977; Pressel *et al.* 2007).

It is likely that many species have protonemal gemmae or other reproductive structures that remain to be discovered. For example, these were unknown until recently in the Splachnaceae. Following the discovery of protonemal bulbils in *Splachnum ampullaceum* (Figure 134) (Mallón *et al.* 2006), Martinez and Price (2011) studied the development of the protonemata of the epiphytic *Tayloria rudolphiana* (Figure 135), likewise a member of the Splachnaceae. In culture, they observed protonemal brood cells for the first time in this species, occurring at the ends of caulonemal filaments where they formed chains of short, somewhat thick-walled spherical cells. These brood cells developed after four months in culture and had abundant chloroplasts and some lipid droplets.



Figure 133. *Campylopus pyriformis* with caducous leaves, also producing rhizoidal tubers. Photo by Michael Lüth, with permission.



Figure 134. *Splachnum ampullaceum* with capsules. Photo by David Holyoak, with permission.



Figure 135. *Tayloria rudolphiana*, a species that produces chains of spherical protonemal brood cells at the ends of caulonemal filaments. Photo by Jan-Peter Frahm, with permission.

Zygodon forsteri (Figure 136) is only known from beech bark (*Fagus sylvatica*), often occurring with *Z. viridissimus*, and is rare (Adams & Rumsey 2005). *Zygodon forsteri* occurs on rain tracks on trees, on roots in places that collect water, and on callus tissue where squirrels make grooves that aid establishment (Figure 139-Figure 140). The authors suspect that slug herbivory on the capsules of *Z. forsteri* is responsible for poor reproduction, but they have documented that the running water disperses its bountiful chloronemal gemmae.



Figure 136. *Zygodon forsteri* with capsules that may be eaten by slugs. Photo by César Garcia, with permission.



Figure 137. *Zygodon viridissimus* on bark. Photo by J. C. Schou, with permission.



Figure 138. *Zygodon viridissimus* leaf with gemmae that may help it to compete with *Zygodon forsteri*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 139. Beech knothole callus. Photo from pxfuel, with online permission.

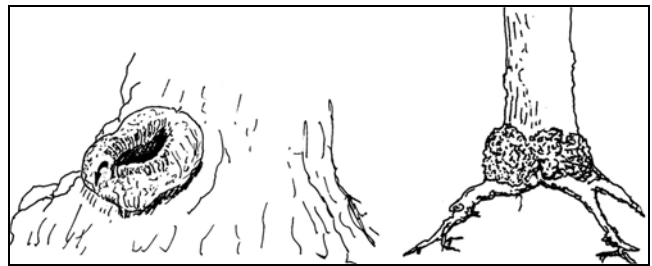


Figure 140. *Zygodon forsteri* (right) on callus tissue (left). Photo modified from Adams *et al.* 2005, with permission.

Even the aquatic moss *Fontinalis antipyretica* (Figure 158) produces protonemal gemmae (Ares *et al.* 2014). Thus far, this has only been observed in culture, but few or no observations have been made in the field. These are produced in ageing and desiccating cultures, and the authors suggest that in nature they may be produced in response to diminishing water levels.



Figure 141. *Fontinalis antipyretica* chloronemal gemma. Photo modified from Ares *et al.* 2014.

The production of protonemal gemmae seems to be environmentally controlled. Vashistha and Chopra (1984) found that in *Didymodon recurvus* the production of protonemal gemmae was favored by low light and high temperature, whereas high light and low temperature resulted in development of gametophore buds. This experimental observation is consistent with the assertion of Whitehouse (1980). He found that the protonemata of *Barbula trifaria*, *Gyroweisia tenuis*, and *Eucladium verticillatum*, as well as those previously reported in *Schistostega pennata* (Edwards 1978), seem to be

adaptations for survival and propagation at low light intensities of deep shade. Perhaps this is a mechanism to provide an opportunity for dispersal from an unfavorable location to one with more favorable light?

Pressel and coworkers (2007) found that in culture the protonemal gemma production increased with high nutrient availability and suggested that this may be true in nature as well. They assumed that the protonemal gemmae were both less long lived and less desiccation tolerant than tubers. They suggested that these diaspores helped in initial establishment as well as local spread of the species. The role in the diaspore bank and longevity of these structures remain to be investigated.

It is interesting that development of protonemal gemmae may also be controlled by the hormone **IAA** (Ahmed & Lee 2010). Ahmed and Lee found that both IAA and kinetin controlled the production of gemmae vs gametophore buds in *Palustriella decipiens* (= *Cratoneuron decipiens*) cultures from chopped up gametophores, serving as concentration-based external regulators. This does not necessarily imply that the same behavior would occur from protonemata produced by spores because chopped plants could provide hormones that might not be available to a spore germling.



Figure 142. *Bazzania trilobata* showing stolons with very reduced leaves. Photo by Dick Haaksma, with permission.

Liberation Mechanisms

Even the mechanisms of liberating the diaspores differ among species. Duckett and Ligrone (1992) identified five liberation mechanisms:

1. random breakage of thin-walled stalk cells
2. formation of new internal walls that separate from old
3. severance along middle lamella of basal cell with or without rounding off of cells
4. formation of highly specialized abscission (**tmema**) cells
5. breakage along intercalary region of thin-walled living cells

In contrast to these specific liberation mechanisms, rhizoidal gemmae lack any separation mechanism, being freed only by decay of the filament that has produced them.

Some bryophytes don't require any special cells or mechanisms to release fragments. For example, the leafy liverwort *Pycnolejeunea* will lose a shoot with only a light touch. Others may produce special branches that release with only a touch. This adaptation usually results from reduction in number of cells at the point of attachment. The ease-of-breakage method includes many leafy liverworts. One such species is *Lejeunea cardotii* that grows in mats on tree trunks and dead wood. Its stems produce small-leafed branches and these may in turn produce more small-leafed branches. These are fragile and break off easily. Other leafy liverworts, e.g. *Bazzania trilobata* (Figure 142), likewise get such specialized branches, often originating from under the branch.

Protonemal Gemmae

Most of the protonemal gemmae separate from the parent **chloronema** (part of protonema giving rise to buds) by a **tmema** (abscission) cell (Figure 147-Figure 149). Other taxa with this tmema mechanism include *Mielichhoferia bryoides* and *Rhodobryum roseum* (Figure 66). Other bryophytes use **schizolysis** to detach their gemmae. This requires the splitting from the parent plant by **lysis** of the cellular connections through rupture of adjoining cell walls. Genera with this strategy include *Epipterygium* (Figure 143), *Plagiomnium* (Figure 144), *Rhizomnium* (Figure 145), and *Mnium* (Figure 146).



Figure 143. *Epipterygium tozeri*, representing a genus that uses lysis to disconnect its gemmae. Photo by David T. Holyoak, with permission.



Figure 144. *Plagiomnium affine*, representing a genus that uses lysis to disconnect its gemmae. Photo by Michael Lüth, with permission.



Figure 145. *Rhizomnium punctatum*, representing a genus that uses lysis to disconnect its gemmae. Photo by Li Zhang, with permission.



Figure 146. *Mnium arizonicum*, representing a genus that uses lysis to disconnect its gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Tmema

A **tmema** (Figure 147-Figure 149) is a specialized abscission cell that permits portions of a protonema to operate independently and create a position of easy breakage (Correns 1899; Duckett & Ligrone 1992). This mechanism seems to be important in the release of protonemal gemmae, with a variety of different developmental patterns (Duckett & Ligrone 1992). Schnepf (1992) reported these from the chloronemata of *Funaria hygrometrica* (Figure 150), where they serve to fragment the protonemal filaments. In *Zygodon* (Figure 151-Figure 152), *Bryum pallens* (= *B. flaccidum*; Figure 153), and *Dicranoweisia cirrata* (Figure 154), they occur at

the bases of axillary gemmae, and they are characteristic of foliar gemmae in *Calymperes* (Figure 155-Figure 156) (Duckett & Ligrone 1992).



Figure 147. Protonema with short tmema cell where protonema can break apart. Photo by Jaime Goode, permission pending.



Figure 148. **Tmema cells** (colorless) and **brachyocytes** (short green) of *Physcomitrella patens* protonema. Photo courtesy of Anne Genau through Stefan Renfing. Marco Göttig set up the ABA treatment that induced these cell formations.

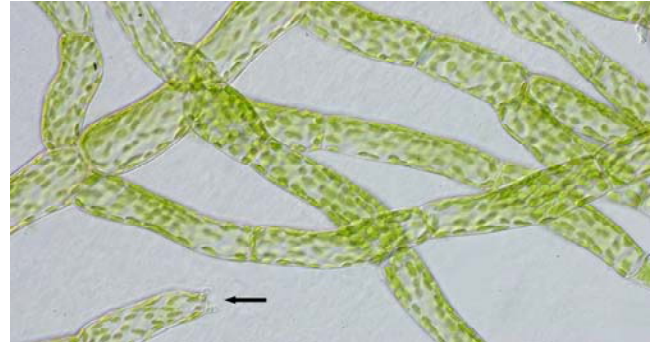


Figure 149. *Physcomitrella patens* protonema, showing broken cell that was a **tmema** (arrow). Photo by Anja Martin, Labor Ralf Reski <en.wikipedia.org/wiki/Ralf_Reski>, through Creative Commons.

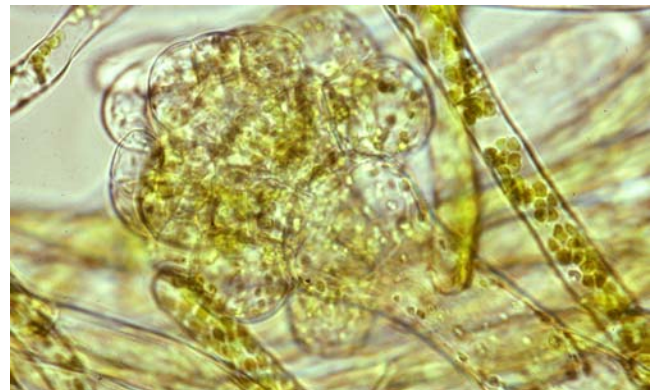


Figure 150. *Funaria hygrometrica* protonema with bud. Photo by Martin Bopp, with permission.



Figure 151. *Zygodon conoideus* growing on bark. Photo by Michael Lüth, with permission.



Figure 152. *Zygodon conoideus* gemmae. Photo by David Holyoak, with permission.



Figure 153. *Bryum pallens* (= *Bryum flaccidum*) with axillary filamentous gemmae, each attached by a tmema cell. Photo by Kristian Peters, with permission.



Figure 154. *Dicranoweisia cirrata* with capsules, a species that produces axillary gemmae with tmemata. Photo by Michael Lüth, with permission.



Figure 155. *Calymperes erosum* with leaf gemmae. Photo by Li Zhang, with permission.

The tmema cell in *Funaria hygrometrica* protonemata results from unequal cell division and is followed by the loosening of the old proximal cell wall (Bopp *et al.* 1991). Addition of 10 μM IAA prevents the formation on tmemata, indicating that the formation of this cell results from inadequate IAA. The result of this fragmentation is to create several separate protonemata. In gemmae, the tmemata connect the gemmae to the plant and permit its abscission (Figure 156-Figure 157) (Stapper 2006).

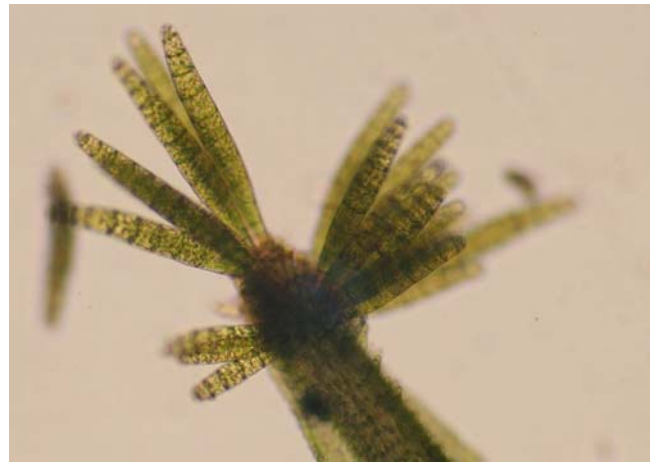


Figure 156. *Calymperes erosum* leaf with gemmae attached by tmemata. Photo by Li Zhang, with permission.



Figure 157. Tmema at base of brood bodies of *Dicranum tauricum*. Photo by N. J. Stapper, with permission.

Diaspore Bank

Unfortunately, it is difficult to determine whether spores or asexual diaspores contribute to the growth of new plants from the diaspore bank. During (1995) suggested that tubers of some moss species may be very abundant in the diaspore bank, and as seen earlier in the discussion of diaspore banks, these species often are not represented above ground or are sparse there. During contends that such populations seem to rely completely on occasional recruitment. Long rhizoids help to extend the range of some species within a location. He considers population regulation of these species to be a density-dependent mortality of the tubers in the soil.

The forest is often disturbed, whether by fire or by harvesting. Bryophytes are important in maintaining soil moisture and as reservoirs of nutrients that often get released toward the later part of the growing season. Following disturbance, forest floor bryophytes are often recovered from diaspore banks. Caners *et al.* (2009) cultured mineral soil samples from both mixed and coniferous forest stands in northern Alberta, Canada, following harvesting. They found that forest type was not the determinant of the species composition, nor was harvesting intensity. Rather, edaphic variables and geographic space determined the regenerant flora. Nevertheless, light intensity exerted a significant influence on both the species responses and the species assemblages. Low light caused significant reduction in richness and cover of acrocarpous mosses – the fugitive, colonist, and shuttle life-history strategies. Pleurocarpous mosses (perennial stayers), on the other hand, seemed unaffected by light intensity. Higher light intensities supported significantly greater **Shannon diversity** and the frequency of reproduction. Caners *et al.* concluded that diaspore banks were an important repository for forest floor species and provided a source for recovery after harvesting.

Ross-Davis and Frego (2004) found 10 of the 36 species of a forest floor community in both the diaspore bank and the aerial diaspore rain. Of the extant taxa, 36% were not present in either diaspore source. The two dominant mosses, *Pleurozium schreberi* and *Hylocomium splendens*, were present in both the diaspore bank and aerial diaspore rain.

Hence, bryophytes are able to colonize disturbed areas from both the diaspore bank and from the diaspore rain. These two sources contain both spores and vegetative propagules, but not necessarily both from the same species. Distinguishing which type of diaspore germinated is quite difficult and is not usually included in diaspore bank studies.

The Antarctic undoubtedly has many well-preserved bryophyte diaspores buried in the ice and deep in bryophyte mats. Bergstrom and Selkirk (1999) were able to culture propagules from substrate samples 5.5 cm deep on Macquarie Island. They succeeded in germinating 15 bryophyte taxa. They hypothesized that bryophytes that arrived on bare patches in the field, they were able to colonize stable ground but unable to colonize areas subject to surface movement. Instead, some of these propagules became buried. Spherical moss balls, however, were tolerant of the surface movement and disturbance. Of the 15 species that germinated, 10 were not local and came

from populations at the warmer lower altitudes. They suggested that such propagules will permit areas respond quickly to climate change by providing species that were tolerant to the new climate.

Propagule Dispersal Distances

It appears that little is known about actual distances that vegetative propagules might travel. Although studies have suggested that the distances are short, *i.e.* measured in centimeters rather than meters (Kimmerer 1991, 1994; Kimmerer & Young 1995), it appears that extensive measurements are lacking. Kimmerer (1991) found that gemmae of *Tetraphis pellucida* (Figure 18-Figure 19) travelled to a maximum of 10 cm in her study, and that 50% fell within 1 cm. 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* (Figure 158) vegetative dispersal, one piece had re-established upstream about 20 m from its origin, presumably carried there by some animal (bear or human?).



Figure 158. *Fontinalis antipyretica*, a moss that spreads vegetatively by rhizomes and disperses by fragments. Photo by Andrew Spink, with permission.

Convincing evidence of long-distance propagule dispersal is that of *Marchantia polymorpha* (Figure 159) on the crater of Deception Island, Antarctica. The crater was formed in 1969, exposing new ground following the eruption. In 1971, Young and Kläy reported this species on the new ground approximately 1000 km from the nearest known population in South America. No other colonies on Deception Island of this conspicuous liverwort were known to the scientists. Perhaps more surprising, the thallus had the distinctive dumbbell shape that is typical of a young thallus developed from a gemma! This example supports a conclusion of rapid long-distance dispersal that in this case arrived at a suitable habitat. (Let's hope this wasn't a case of inadvertent human dispersal!)



Figure 159. *Marchantia polymorpha* with gemma cups. Photo by Andrew Spink, with permission.

Propagule Survival/Longevity

The first question that comes to mind for long-distance dispersal of vegetative propagules is whether they can survive. These are living, often active fragments, gemmae, bulbils, and other structures that may or may not be dormant. Presumably, living fragments would be the least adapted among these to survive the conditions of the stratosphere. Studlar *et al.* (2007) tested fragment survivability by sending four mosses into the stratosphere on a weather balloon. These were subjected to temperatures as low as -30°C over a period of 4 hours, 2 of which were in the stratosphere. Subsequent culture for 28 days in the lab revealed the ability of these species to survive the stratosphere ride. *Sphagnum magellanicum* (Figure 160), *S. fallax* (Figure 161), and *Atrichum angustatum* (Figure 44) all regenerated with secondary protonemata and juvenile shoots. *Sphagnum girgensohnii* (Figure 162), however, did not. These results suggest that at least some vegetative diaspores, including fragments, could travel by wind into the stratosphere.



Figure 160. *Sphagnum magellanicum* in Europe, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.



Figure 161. *Sphagnum fallax*, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.

Some bryophytes may survive in a dry state for years, providing a larger set of opportunities for the wind or water to distribute them to new locations. Whitehouse (1984) reported that tubers of *Anisothecium* (= *Dicranella*) *staphylinum* (Figure 163) survived in stored soil for 50 years. Zander (1979) successfully cultured *Anoetangium* (Figure 164), *Barbula* (Figure 165), *Desmatodon s.l.* (Figure 166), *Didymodon* (Figure 167), *Gymnostomum* (Figure 168), *Hymenostylium* (Figure 169), *Leptodontium* (Figure 170), *Molendoo* (Figure 171), *Oxystegus* (Figure 172), *Pleurochaete* (Figure 173), *Pseudocrossidium* (Figure 174), *Tortella* (Figure 175), *Tortula* (Figure 176), and *Trichostomum* (Figure 177) species, all members of **Pottiaceae**, from herbarium plants (not spore) specimens. These were all less than 5 years old.



Figure 162. *Sphagnum girgensohnii* at Lake Perrault, MI, USA, a species that did not survive travel in a weather balloon. Photo by Janice Glime.



Figure 163. *Dicranella staphylinum* on soil, a species that can survive storage in soil for 50 years. Photo by Michael Lüth, with permission.



Figure 164. *Anoctangium aestivum* with capsules, a species cultured from herbarium specimens less than 5 years old. Photo by Jan-Peter Frahm, with permission.



Figure 167. *Didymodon rigidulus* in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 165. *Barbula unguiculata* with water on setae and capsules. This species was cultured from herbarium specimens less than 5 years old. Photo by Adnan Erdag, with permission.



Figure 168. *Gymnostomum aeruginosum* with capsules in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 166. *Tortula hoppeana* (syn.=*Desmatodon latifolius*) from the mountains in southern Europe. This species was cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 169. *Hymenostylium recurvirostrum* in India, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 170. *Leptodontium flexifolium* in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 173. *Pleurochaete squarrosa* wet, a species cultured from herbarium specimens less than 5 years old. Photo by David T. Holyoak, with permission.



Figure 171. *Molendoa hornschuchiana* in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 174. *Pseudocrossidium revolutum*, a species cultured from herbarium specimens less than 5 years old. Photo by Proyecto Musgo, through Creative Commons.



Figure 172. *Oxystegus cylindricus* subsp. *hibernicus*, a species cultured from herbarium specimens less than 5 years old. Photo by Jan-Peter Frahm, with permission.



Figure 175. *Tortella flavovirens* in southern Europe. Photo by Michael Lüth, with permission.



Figure 176. *Tortula muralis* with water drops in Dunblane, Scotland. This species was cultured from herbarium specimens less than 5 years old. Photo courtesy of Peggy Edwards.



Figure 177. *Trichostomum brachydontium*, a species cultured from herbarium specimens less than 5 years old. Photo by Barry Stewart, with permission.

Buried propagules must somehow remain dormant in an environment (diaspore bank) 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 again. 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* (Figure 13). 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* (Figure 178-Figure 183), 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 tolerance of these species and the extraordinary survival abilities.



Figure 178. *Leptobryum pyriforme* with capsules, a species with tubers that can survive two years in a freezer. Photo by Michael Lüth, with permission.



Figure 179. *Leptobryum pyriforme* with tubers from wet meadow and stagnant ditch Minnesota, USA. Photo by Jan Janssens, with permission.



Figure 180. *Leptobryum pyriforme* rhizoidal tuber. Photo by Victoria Rozhina.

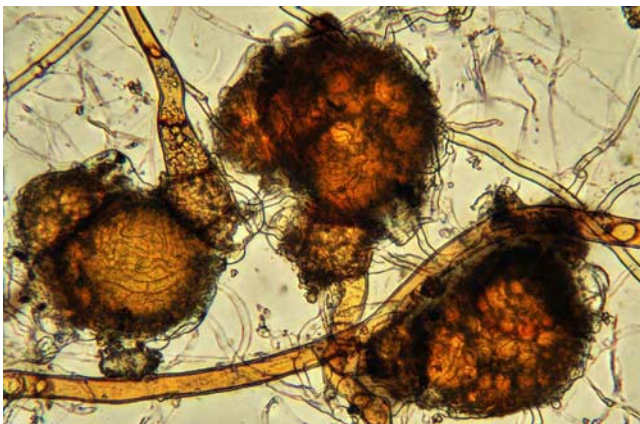


Figure 181. *Leptobryum pyriforme* rhizoidal tubers. Photo by Dick Haakma, with permission.

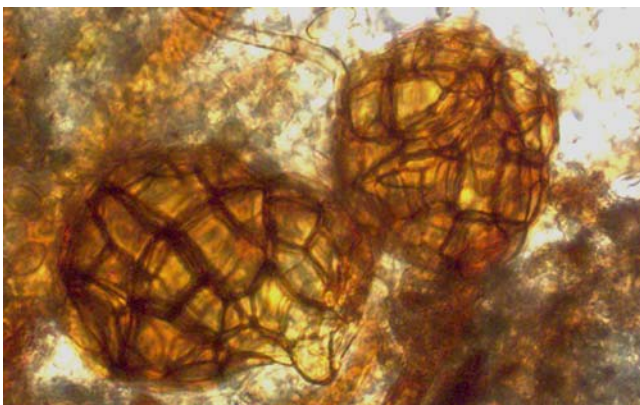


Figure 182. *Leptobryum pyriforme* rhizoidal tubers. Photo by Victoria Rozhina.

John Spence (Bryonet 22 November 2010) actually tested long-term viability of tubers in *Rosulabryum capillare* (Figure 184) and *Gemmabryum* (= *Erythrocarpa* sp.; Figure 185). Tubers of these species remained viable up to 15 years and germinated in distilled water and normal daylight. Such propagules can remain dormant in soil banks and other locations, germinating after unknown periods of time when they are disturbed and brought to the surface (e.g. During 199). Although there are a number of studies on propagules from such situations, the longevity of

these propagules is unknown. Herbarium specimens provide a means of checking longevity, but the conditions of a herbarium are quite different from the natural habitat. And even if the propagules could survive the conditions there, they may become dinner for hungry invertebrates.

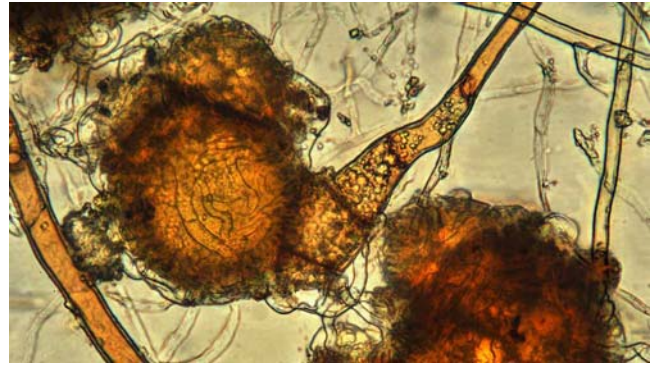


Figure 183. *Leptobryum pyriforme* rhizoidal tubers. Photo by Dick Haakma, with permission.



Figure 184. *Rosulabryum capillare* with capsules, a species whose rhizoidal gemmae can survive at least 15 years. Photo by Tom Thekathyl, with permission.



Figure 185. *Gemmabryum dichotomum* with bulbils. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Mishler and Newton (1988) experimented with four *Tortula* *s.l.* species (Figure 96-Figure 97; Figure 122-Figure 124) 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 dipteran 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 as viable propagules. Insect guts can have extremely high or extremely low *pH* (Nation 2002) 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 potential of a delayed response of the moss to such a detrimental gut environment is exemplified by our experiment on *Fontinalis duriaei* (Figure 186). In an experiment to determine if rainbow trout (*Oncorhynchus mykiss*) 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 187), 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.

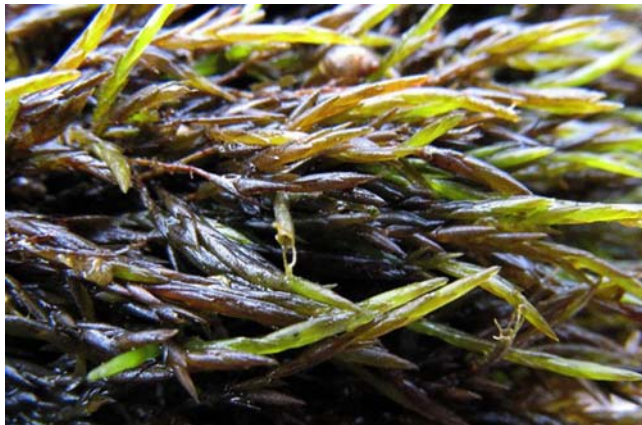


Figure 186. *Fontinalis duriaei*. Photo by Jan-Peter Frahm, with permission.



Figure 187. Feces packet from rainbow trout, containing *Fontinalis duriaei* that has lost its green color 24 hours after its egestion. Photo by Janice Glime.

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.

One prerequisite for propagules with long dormancy or lengthy travel is desiccation tolerance. Understanding this is necessary for cryopreservation to maintain species that may become extirpated in the future. Rowntree *et al.* (2007) have used cryopreservation successfully for many species and in doing so have added greatly to our understanding of the mechanisms the bryophytes are able to use to survive. They have found that survival can be enhanced by pretreatment with ABA and sucrose, the latter perhaps providing an energy source upon rehydration. Surprisingly, the pioneer moss *Ditrichum plumbeicola* had low survival of cryopreservation and likewise responded poorly to pretreatment. With further experimentation, they discovered that the pretreatment with sucrose and ABA caused significant changes in the protonemata. Growth was greatly reduced and propagules had pronounced morphological and cytological changes. Although most cells died, those that survived were markedly different from normal. The surviving cells had thick walls that were darkly pigmented and there were numerous small vacuoles and lipid droplets in the cytoplasm. When there was no ABA-sucrose pretreatment, desiccation and cryopreservation caused minimal cytological changes. These untreated tissues returned to their pre-dehydration state within 2 hours of rehydration. On the other hand, rehydration was normal once ABA and sucrose were removed from the pretreated propagules. Rather, these propagules (from the protonemata) became highly desiccation and cryopreservation tolerant, a behavior similar to that of rhizoids that function as perennating organs in the field. Rowntree and coworkers considered this as evidence that the propagules used ABA to increase their desiccation tolerance.

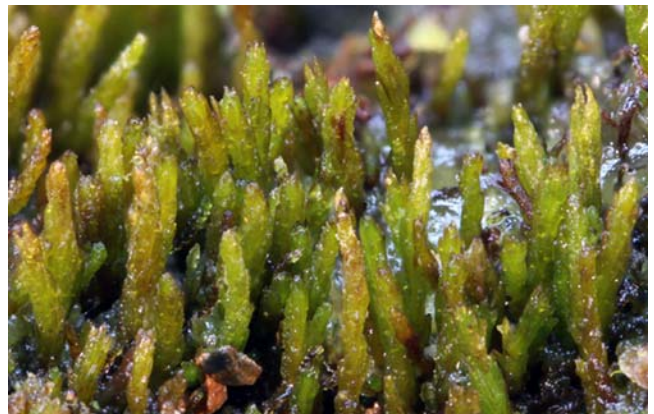


Figure 188. *Ditrichum plumbeicola*, a species with low cryopreservation survival. Photo by Des Callaghan, with permission.

In *Marchantia inflexa* (Figure 189) both water and desiccation affect mortality (Chris Stieha, Bryonet 27 February 2016). In his lab, there was less than 10% mortality of gemmae maintained in water for three months, but 20% mortality after only four days of desiccation. In the field they can turn brown within an hour of desiccation. Stieha *et al.* (2014) found that male plants of this species produce the most gemmae and more quickly when compared to females, but the male gemmae have less ability to survive desiccation. Gemmae in this species can move up to 20 cm from the parent plant in a light rain, permitting expansion of the population.



Figure 189. *Marchantia inflexa*, a species whose gemmae survive well in water but tolerate little desiccation. Photo by Scott Zona, with permission.

Propagule Establishment

Once a propagule reaches its final resting place, it must begin growth and become established (Figure 190). Due to both edaphic and climatic differences, the success of this establishment is less predictable as the distance increases (Karlson & Taylor 1992; Ronsheim 1997; Laaka-Lindberg *et al.* 2003).



Figure 190. Gemmae germinating. Photo by Li Zhang, with permission.

The conditions at germination can be critical. Risse (1987) tested rhizoidal gemmae of mosses, citing their importance in environments that are frequently disturbed by natural or anthropogenic influences. McCutcheon (1978) reported that light is required for germination, and that if the gemma of *Bryum rubens* (Figure 191-Figure 194) becomes imbibed for more than ten days without receiving light, it will die. Its fat storage reserves are

depleted in 15 days, so that imbibition can trigger that loss. Furthermore, after imbibition, tubers become sensitive to desiccation and do not regain their pre-germination tolerance if they have entered their pre-germination phase (imbibed) for more than 12 hours.



Figure 191. *Bryum rubens* rhizoidal gemmae. Photo by Ariel Bergamini, with permission.



Figure 192. *Bryum rubens* rhizoidal gemmae along stem rhizoids. Photo by Ariel Bergamini, with permission.

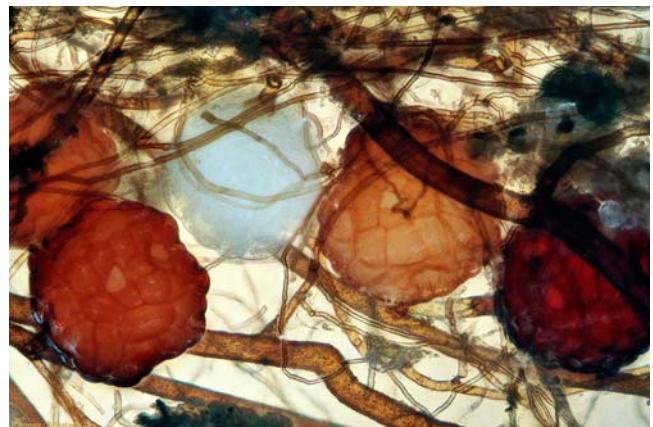


Figure 193. *Bryum rubens* rhizoidal tubers in various stages of maturity, showing how prolific they can be. Photo by Dick Haaksma, with permission.

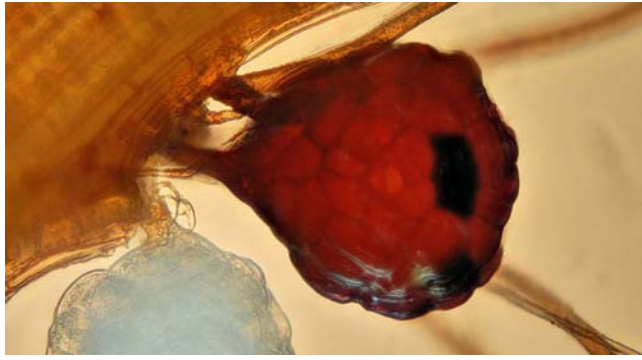


Figure 194. *Bryum rubens* rhizoidal tubers. Photo by Dick Haaksma, with permission.

Desiccation

A key factor in establishment is maintenance of sufficient moisture in early stages of development to permit development of a reproductive adult. An interesting example of this is *Pseudoscleropodium purum* (Figure 195). One habitat where this species grows is on ant hills of the yellow meadow ant, *Lasius flavus* (Figure 196), that is, on the north-facing sides of the ant hills (King 2003). Fragments detached by grazing animals are common on the mounds. After experimentation, King concluded that inability to establish on the south-facing side was most likely due to desiccation and metabolic drain leading to cell death. Transplanted adult mosses, on the other hand, seemed capable of survival.



Figure 195. *Pseudoscleropodium purum*. Photo by Michael Lüth, with permission.



Figure 196. The yellow meadow ant, *Lasius flavus*. Photo through Creative Commons.

Inhibitors

Gemmae do have a safeguard against competing with their parents. Most are inhibited by the presence of the parent (Figure 197) and are often even inhibited by related species [e.g. *Bryum rubens* (Figure 191-Figure 194) by *Bryum alpinum* (Figure 198) (McCurtcheon 1978)]. Ashton and Raju (2001) demonstrated inhibition of rhizoidal gemmae in *Gemmabryum* (= *Bryum*) *violaceum* (Figure 199) by the soil associated with the parents, but gemmae germinated while still attached if placed in fresh soil. This suggests that whatever served as the deterrent may have accumulated in the soil to a greater level than that in the plant. It would be interesting to attempt growing these in the same soil with charcoal as an adsorbant.



Figure 197. *Lunularia cruciata* showing ungerminated gemmae on thallus. Both *Marchantia* and *Lunularia* inhibit the germination of the gemmae on the parent. Photo by Martin Hutten, with permission.



Figure 198. *Bryum alpinum* showing competition. Photo by David T. Holyoak, with permission.

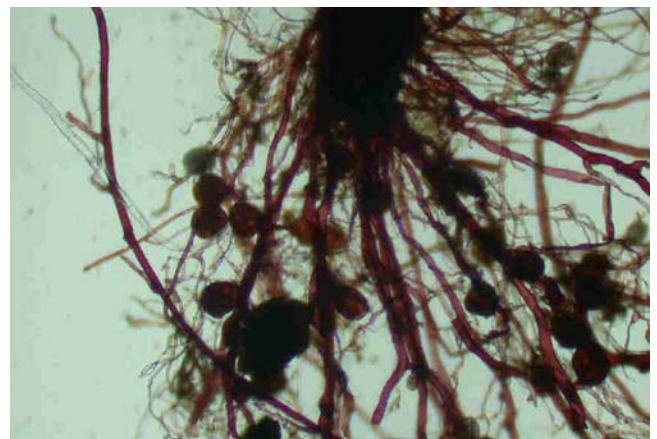


Figure 199. *Gemmabryum violaceum* with rhizoidal tubers. Photo by David T. Holyoak, with permission.

Risse (1987) suggested that this inhibition might be caused by sugars, particularly mono- and disaccharides, shown by McCutcheon (1978) to inhibit tuber germination in *Bryum rubens* (Figure 191-Figure 194). Christianson (2000) showed that ABA (abscisic acid) is able to inhibit bud formation in *Funaria hygrometrica* (Figure 200), so it could also be the cause of inhibition by parents. This same self-inhibition (inhibition by parents) is known from *F. hygrometrica* (Figure 200). On the other hand, the cytokinin hormones leaked from one individual can stimulate bud formation on other nearby individuals of the same or related species (Bopp 1982).



Figure 200. *Funaria hygrometrica* showing the distinct margins where colonies contact each other. Photo by Janice Glime.

ABA is a common hormone in tracheophytes, having a variety of functions. It is best known in bryophytes as a responder to desiccation. Mallón *et al.* (2006) examined the effect of various concentrations of ABA on the production and behavior of gemmae in *Splachnum ampullaceum* (Figure 134). This species is best known for its ability to attract flies that disperse it among piles of dung, but its ability to produce vegetative propagules was previously unknown. The researchers managed to induce both brood cells and chloronemal bulbils in their protonemal cultures, as well as vegetative propagules, and their results suggest a bet-hedger strategy. The brood cells produced new chloronemal filaments when they were transferred to new media. There was a direct positive relationship between the concentration of ABA and brood cell formation, while at the same time increasingly inhibiting the growth of the protonemata. Furthermore, no buds developed on protonemata grown on media with ABA. Mallón and coworkers suggested that production of the vegetative structures on the protonema might be a desiccation response and would permit the plant to spread rapidly, a behavior that might also help to conserve moisture, if not then, in the future.

Establishment and Rarity

Cleavitt (2002) attempted to determine the factors that contributed to rarity of species [*Mielichhoferia macrocarpa* (Figure 201), *Didymodon johansenii*, and *Mnium arizonicum* (Figure 146)] and compared three rare

and common species pairs in the Front Ranges of Alberta, Canada. She found that propagule viability did not relate to establishment ability. Rather, establishment of rare species may be a function of a complexity of mechanisms that create a narrow realized niche. For example, *Mielichhoferia macrocarpa*, which occurred in the darkest and wettest sites, was tolerant of high light intensity and desiccation, suggesting that additional factors narrowed its establishment niche. She suggested that the broader apparent physiological tolerance found in these rare species may be due to their greater reliance on asexual reproduction. This suggests that we should look for other physiological factors and dispersal as causes of rarity.

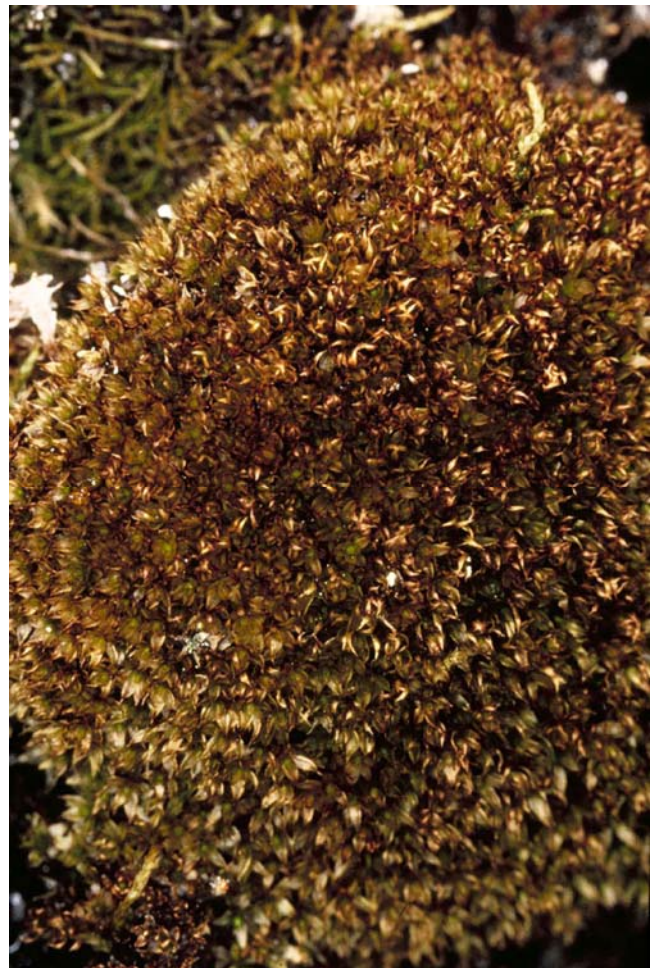


Figure 201. *Mielichhoferia macrocarpa*, a species that appears to have broad environmental tolerances, but with limiting requirements of some factor(s). Photo by Robin Bovey, with permission through Dale Vitt.

In contrast, Cleavitt (2002) found that the three common species [*Mnium spinulosum* (Figure 202), *Bryum pseudotriquetrum* (Figure 203), *Didymodon rigidulus* (Figure 204)] were more likely to occupy habitats that agreed with their physiological requirements. *Mnium spinulosum* was limited by high light and thus occurred only in deeply shaded conifer stands; *Bryum pseudotriquetrum* was intolerant of desiccation and was thus found in moist areas such as stream banks.



Figure 202. *Mnium spinulosum*, a common species that is intolerant of high light and lives in conifer forests. Photo by Michael Lüth, with permission.



Figure 203. *Bryum pseudotriquetrum* at streamside. Photo by Michael Lüth, with permission.



Figure 204. *Didymodon rigidulus*, a common species. Photo by Michael Lüth, with permission.

Cleavitt (2002) suggests that rare species may have broader physiological tolerance because they rely on vegetative reproduction largely as fragments. In particular, they have a high tolerance to desiccation in both whole colonies and in fragments. This suggests that they may be rare due to dispersal limitations, slow establishment rates

that permit competitors to overpower them, or special environmental factors that were not examined.

Reproductive Problems

But the problems don't end with germination or even successful production of gametophores. These gametophores must likewise be able to reproduce, whether by vegetative means or spores. This is particularly problematic for dioicous species because they must have the successful invasion of both male and female spores for any further reproduction by spores to occur. And if they did arrive at a distant location by spores, it is likely that this is their primary means of dispersal. The same problem exists for vegetative propagules. For dioicous taxa, it is possible that only one gender arrives, whether by specialized structures or by fragments.

Perhaps there are species where the spores travel in tetrads, as is known for *Haplomitrium gibbsiae* (Figure 205) (Van Zanten & Pócs 1981). Nevertheless, a tetrad of spores is larger and hence sacrifices ease of transport by air currents. Van Zanten and Pócs suggest that this limitation might also be overcome by having spores remain in relatively compact clouds during transport – a notion that is certainly worthy of consideration. We need to consider if this compact cloud approach might also work for vegetative diaspores.



Figure 205. *Haplomitrium gibbsiae*, a species where spores travel in tetrads. Photo by Jan-Peter Frahm, with permission.

Epiphytes

It is hard enough to land in the right microhabitat on the ground, but even more challenging to land on a vertical surface. Hence, highly structured bark has more chance of trapping the somewhat large vegetative propagules. But the problems are just beginning at landing. The vertical surface of almost anything is subject to drying, and tree trunks are particularly exposed. Fortunately, the tropical cloud forests manage to maintain a higher moisture content than other types of forest habitats and thus are endowed with dense bryophyte cover on everything (Figure 206).

As one can imagine, establishment of tracheophytes can be more difficult than that of bryophytes. Hence, many depend on bryophyte establishment to provide them with a suitable substrate (Nadkarni *et al.* 2000). Nadkarni and co-workers dropped epiphytic bryophyte fragments 50 cm

above branches of saplings and mature trees of *Ocotea tonduzii*. Only 1% of these fragments were returned for the six months of the experiment. During the same time period, branches in the canopy with intact epiphyte loads retained 24% and branches that had been stripped of their epiphytes retained 5%. They found that a larger surface area and presence of other bryophytes helped in the retention of the fragments.



Figure 206. Mossy forest, Malaysia, where high moisture levels make it easy for epiphytic bryophytes to establish. Photo by Vita Plášek, with permission.

Rosso *et al.* (2001) found that *Antitrichia curtispindula* (Figure 207-Figure 209) grows faster in the canopy (60% faster) than in the understory, making it easier for it to become established there than when it falls on lower branches. These researchers considered that its absence in young stands may be due to dispersal limitations compared to that in old growth stands. In old growth stands it has both greater height to launch dispersal and more time to get there.



Figure 207. Habitat of the epiphytic *Antitrichia curtispindula*. Photo by Michael Lüth, with permission.



Figure 208. *Antitrichia curtispindula* growth form. Photo courtesy of Karen Golinski.



Figure 209. *Antitrichia curtispindula* on a branch. Photo courtesy of Karen Golinski.

Symbionts Needed

For some bryophytes, a symbiotic relationship is important to survival. *Blasia pusilla* (Figure 210) and *Cavicularia densa* (Figure 211) have solved this problem by producing gemmae that include their *Nostoc* symbiont (Figure 212) (Rikkinen & Virtanen (2008). Others benefit from the presence of soil Cyanobacteria such as *Anabaena variabilis* and *Nostoc muscorum*, as is the case for *Funaria hygrometrica* (Rodgers & Henriksson 1976). These Cyanobacteria are able to capture atmospheric nitrogen and make it usable for the bryophytes.

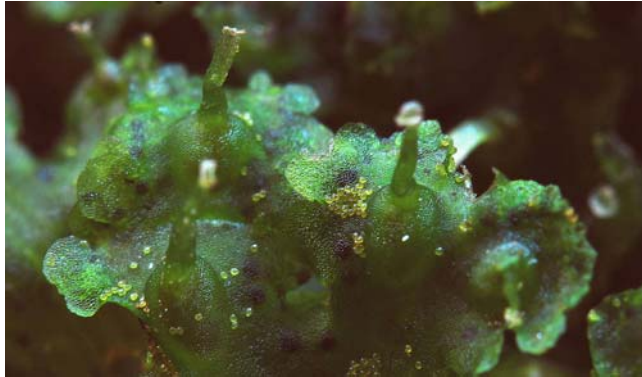


Figure 210. *Blasia pusilla* with *Nostoc* colonies (dark blue). Photo by Dick Haaksma, with permission.



Figure 211. *Cavicularia densa* with gemmae and *Nostoc* colonies. Photo from Digital Museum Hiroshima University, with permission.

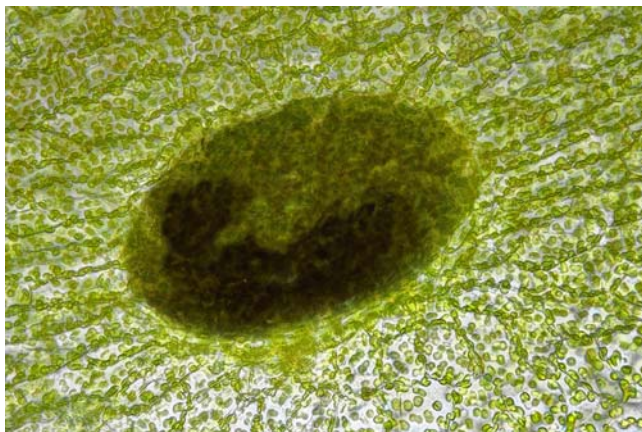


Figure 212. *Nostoc* colony on *Blasia pusilla* thallus. Photo by Dick Haaksma, with permission.

Other bryophytes need fungal partners (Figure 213) (Bidartondo *et al.* 2003; Martinez-Abaigar 2005; Bidartondo & Duckett 2010; Pressel *et al.* 2010; Bidartondo *et al.* 2011; Desirò *et al.* 2013). Although there

have been a number of studies on fungi associated with various bryophytes, these have not dealt with the need for partners at the time of establishment of vegetative diaspores. Are vegetative dispersal structures able to carry their partners with them? Even if so, the conditions must be right for such a partner to flourish along with the bryophyte.

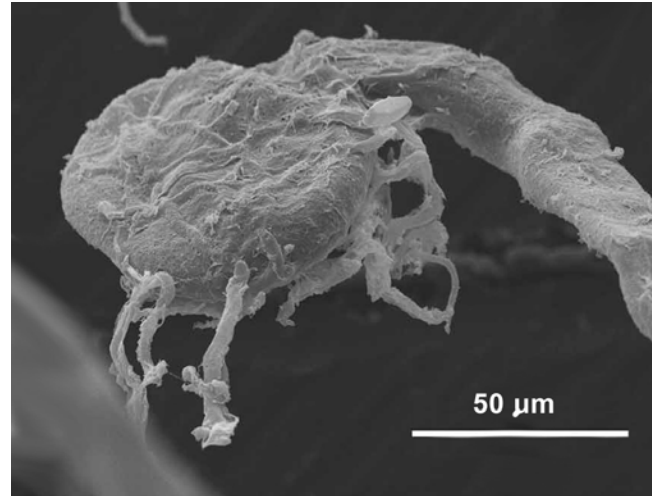


Figure 213. *Mylia anomala* rhizoid tip with symbiotic Ascomycete. Photo courtesy of Silvia Pressel, Robert Ligrone, and Jeffrey Duckett.

A somewhat similar problem occurs for *Dicranum flagellare* (Figure 23) on logs. It seems to be dispersal limited and can only colonize gaps caused by disturbance when other populations occur nearby (Kimmerer 1994). Therefore, older forests where there are more colonized logs provide a better source of propagules for dispersal. But once it reaches a substrate, it germinates much more rapidly than *Tetraphis pellucida* (Figure 18-Figure 19) and persists there longer, perhaps through competition.

Bacteria are important for the development of some bryophytes from spores (Spiess *et al.* 1984), so it is likely that these are also needed for some propagules to complete development, particularly those forming protonemata first.

Tradeoffs

Size matters in dispersal of propagules, but it invokes a tradeoff. Small propagules have the advantage of being produced in large numbers, *e.g.* 500-700 gemmae per leaf in *Scapania nemorea* (Figure 103-Figure 107) with 1-celled gemmae or 1000-7000 1-celled gemmae in *Lophozia ventricosa* var. *silvicola* (Figure 108) compared to only 15-45 in *Jubula* (= *Radula*) *complanata* (Figure 109-Figure 110) with discoid, multicellular gemmae (Laaka-Lindberg *et al.* 2003). Larger gemmae, on the other hand, have a greater chance for successful establishment where they arrive due to more stored energy.

It is also possible that the vegetative tissues of the vegetative diaspores may provide greater protection against germination in the wrong environment. Spores need only light and water to germinate. Hence, when they are brought to the surface and get a good rain, they germinate. As far as we understand, they do not, as spores, detect whether any other aspect of the environment is suitable. Some vegetative propagules, on the other hand, may be

able to detect inappropriate conditions of pH, insufficient nutrients, absence of a fungal partner, absence of hormones from associated bacteria, inappropriate temperature, or toxic metals and other substances. Examining these possible controls on germination of vegetative propagules may help us to understand both longevity of diaspores in the diaspore bank and the comparative success of spores vs vegetative diaspores.

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 and many kinds of protonemata produce gemmae.

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. But vegetative diaspores have few mechanisms that aid in their liberation and dispersal. Among these are **tmema**, small cells that form a weak link and permit breakage.

Propagules must survive the desiccation, temperatures, and UV light of travel, be able to remain dormant upon arrival until the habitat or weather is suitable for germination, then survive after germination for the dispersal to be successful. Some have inhibitors such as ABA. Some require bacteria or fungi as partners. Some must land and become attached to vertical substrates. The usually larger vegetative structures sacrifice long distance dispersal for the ability to carry more with them and become established more easily. In addition to ABA, sucrose may also help in the survival of desiccation.

Acknowledgments

This chapter has benefitted from several email discussions with Peter Poschlod, especially on *Sphagnum*. Thank you to Bryonettors for interesting discussions on diaspores. A special thanks to Stefan Rensing and his associates Marco Göttig and Anne Genau for inducing and photographing the tmema cells for this chapter.

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