

# CHAPTER 4-7

## ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES

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# CHAPTER 4-7

## ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES



Figure 1. *Marchantia polymorpha* showing both vegetative diaspores (gemmae in splash cups) and umbrella-like archegoniophores where sporangia and sexual spores are housed. Photo by Michael Lüth, with permission.

### Importance of Dispersal

Boedeltje *et al.* (2019) considered the vegetative diaspores of bryophytes to be of pivotal importance in colonization of new areas. These, however, are dependent on life history traits and habitat.

### Diaspores

Diaspores are everywhere and some are ready to grow. In bryophytes, **diaspores** are spores and other propagules, including fragments, that function in dispersal (see Figure 1). These may be airborne, drop within the parent colony, or become buried in a diaspore bank in the substrate. Some even are dispersed by animals or water. They serve both to increase colony size and to invade new places.

Nevertheless, spread of many species is dispersal limited. Sillett *et al.* (2000) found that nine species of bryophytes had colonized branches of Douglas fir (*Pseudotsuga menziesii*) from 1995 to 1999, with relatively rapid colonization in all age classes. Nevertheless, when bryophytes were transplanted to Douglas fir trees, they became more frequent on inoculated branches than on ones

not inoculated by the researchers. This suggests that these bryophytes were dispersal limited in colonizing the trees.

The importance diaspores is exemplified by the large number of bryophytes that occur on multiple continents. Of the 7567 accepted binomials for liverworts and hornworts, 2211 are found on more than one continent (Anders Hargborg, pers. comm. 23 February 2017). And of these, 20 are found on all 7 continents plus Oceania. Frey and Hensen (1995) considered dispersal of such importance that they proposed a life strategy system based on dispersal strategies. One strategy that differed from other systems was the **perennial stayers with diaspore years**. That is, some years have prolific reproduction, vegetative or sexual, whereas in other years these are more limited.

### Sampling Methods

To fully understand the role of diaspores we must sample them. The methodology influences what we sample, so it is worthwhile to examine these first.

The most commonly used means of sampling spores and other diaspores in the atmosphere is to place open

**Petri dishes** with a common bryophyte nutrient agar in the field at various heights and distances from a known source for a species. For shorter distances, one can use **glass slides** coated with glycerine. The spores usually cannot be identified by themselves, unless one has considerable experience and a good set of pictures and/or samples for verification. Hence, they must be germinated and the developing protonemata must be coaxed to develop and produce gametophores. Even then, one cannot be certain that the ensuing growth form is representative, since the light is artificial, may be too low or too high, certain growth factors available in its environment may be missing, and nutrients may be at inappropriate levels.

Other traps can include filters or air funnels in strategic positions that catch microbiota carried by drafts and other wind patterns. Each of these methods has its drawbacks, in addition to the problems of culturing and identification. Contamination is certain, density is low, and local micropatterns in air movements may be more influential in what they record in some cases than major pathways.

Levetin *et al.* (2000) compared the **Tauber trap** (Figure 2-Figure 3) with the **Burkard volumetric spore trap** (Figure 4-Figure 5), the latter a trap used in Antarctica (Lewis Smith 1991). The Burkard volumetric spore trap is used primarily for collecting airborne pollen, whereas the Tauber trap is used primarily to analyze deposition. They found a strong correlation between the pollen trapping recorded by the Tauber traps and the cumulative sums of average daily airborne spores/pollen from collections with the Burkard spore trap. Peck (1972) used the Tauber trap to sample pollen in turbulent flow water and found that under those conditions the collection efficiencies for individual taxa vary with both size and weight of the grains and velocity of flow. Smaller grains were trapped less efficiently than larger ones. As the water speed increased, grain characteristics had less effect, but the trapping efficiency decreased.

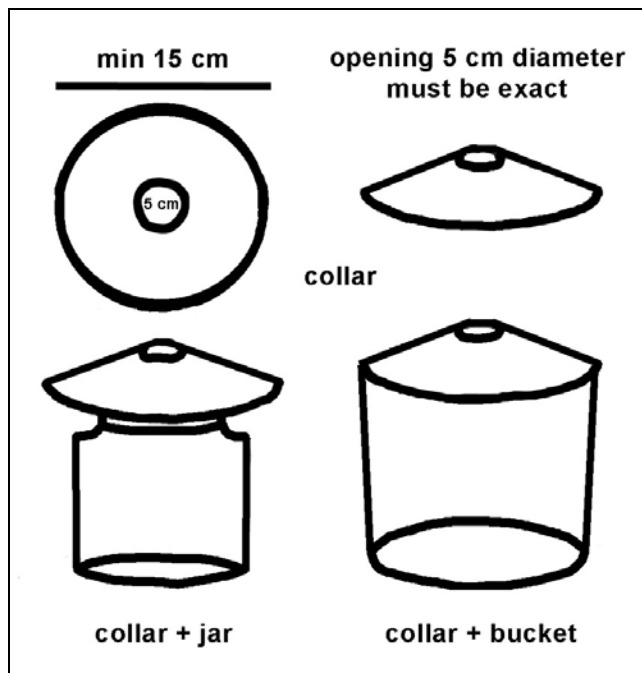


Figure 2. Tauber trap. Drawing based on Pardoe *et al.* 2010.

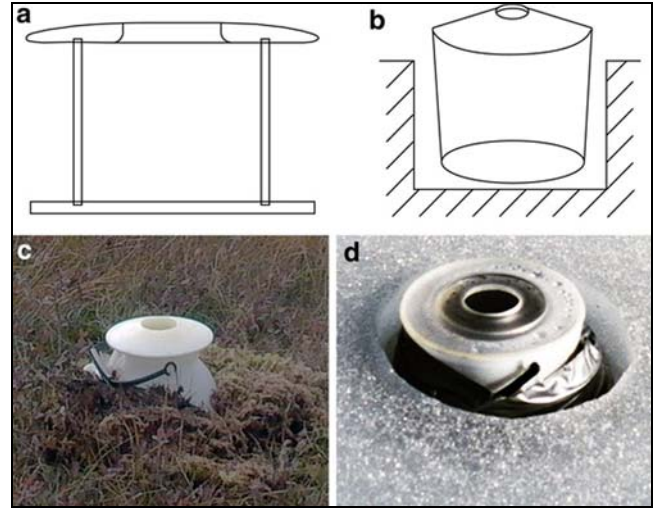


Figure 3. Tauber's original design (a & c) compared to the modification used with the Pollen Monitoring Programme (PMP) (b & d). Images from Pardoe *et al.* 2010, through Creative Commons.



Figure 4. Burkard volumetric spore trap. Photo by Burkard at <<http://www.burkard.co.uk/7dayst.htm>>, with permission.

More sophisticated samplers collect, filter, and concentrate the spores. One that has been used in bryophyte studies is the Rotorod sampler (Rotorod® Sampler 2009). This is a programmable instrument with a



timer that spins the head, bringing the pollen-collecting rods out by gravity. Its standard sampling is a 10% duty cycle, meaning that it samples for one minute out of every ten. A 5% duty cycle would collect for 30 seconds out of every ten minutes. Spores are collected on polystyrene rods pre-greased with silicone grease. To count the spores, the rod is placed in one of the deep grooves of a microscope stage adapter and a few drops of Calberla's stain applied. The rod is covered with a standard coverslip at the distal end of the rod and the spores are counted under a compound microscope at 400X. I am concerned that this rod is apparently intended to be used again and could easily have remnants of spores from a previous sampling, despite careful cleaning. A reticule can be used to aid in counting and to calibrate. The company has found that 400 spores are sufficient to get an accurate estimate of what is there.

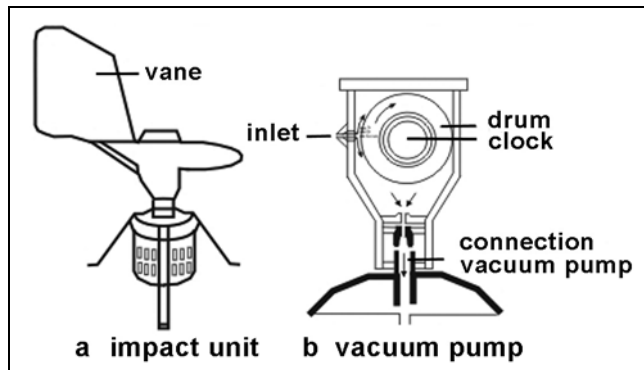


Figure 5. Burkard volumetric spore trap. Redrawn from Aerobiological Sampling, Universidad D Cordoba.

Nature provides her own traps that we can use, but these are varying pictures of time and not necessarily indicative of the present. In the Antarctic, snow provides an appropriate medium for analysis of deposition of diaspores (Lewis Smith 1991). And peatlands have been traditionally sampled for pollen as well as spores.

But not all evidence comes from trapping diaspores. Patterns of bryophyte distribution can help us to hypothesize the pathways and mechanisms. Lönnell (2011) summarizes indirect connections that can contribute to our understanding of dispersal:

1. genetic similarity between populations in different locations
2. successful colonization that can be connected through distribution patterns
3. diaspore longevity compared to species distribution
4. species composition with prevailing winds.

One problem with assessing the relative importance of asexual vs sexual reproduction is that we often misunderstand the mechanisms used by a species. Fritz (2009) demonstrated this for several pleurocarpous species. *Pseudoscleropodium purum* (Figure 6) and *Pleurozium schreberi* (Figure 7) are known for rarity of sporophytes, but Fritz found that genetic evidence of new gene combinations suggested that sexual reproduction followed by spore production was more common than suspected. This was further supported by finding frequent presence of both antheridia and archegonia.



Figure 6. *Pseudoscleropodium purum* with capsules in Bawsey Country Park, UK. Photo by Des Callaghan, with permission.



Figure 7. *Pleurozium schreberi* showing dying basal portion of stem that can result in the living portion becoming a separate plant, creating reproduction by cloning. Photo by Janice Glime.

## Diaspore Banks or New Arrivals?

Leck and Simpson (1987) examined the spore bank in a Delaware River, USA, freshwater tidal wetland. Their samples came from rainwater, 0-2 cm, 4-6 cm, and 8-10 cm depth in high marsh, cattail, and shrub forest. These samples revealed 14 moss species and 2 liverwort species. The most common bryophyte was a species of *Bryum*. The 0-2 cm samples had more species and greater densities, but no cover. The sample spores required longer germination times in culture than what is typical for seed bank spores and may explain the lack of cover on the tidal surfaces.

In a forested floodplain in Ohio, USA, McFarland and Wistendhal (1976) found six species of mosses, with *Eurhynchium hians* (Figure 8) being dominant. In this case, they considered low light levels and occasional flooding to promote protonemal growth. Samples of soil with plants and fragments buried under 10 cm of alluvium had good regrowth and appear to be important to the establishment of terrestrial mosses on these flood plains.

Diaspores for colonizing an area can arrive from elsewhere or be exposed from propagules that have been buried and dormant. In areas experiencing recolonization,



propagule sources can arrive quickly from **diaspore banks**, those buried propagules that have survived for long periods until such time as they are once again returned to a position with sufficient light and moisture to grow. In this case, travelling the distance means travelling down to a depth where they can survive until they once again experience a favorable location. This may mean not travelling too far so that they never again surface; in other cases, deeper is safer.



Figure 8. *Eurhynchium hians* in Europe. Photo by Michael Lüth, with permission.

Heinken *et al.* (2004) found three recolonization mechanisms at work in pine forest gaps in Central Europe. These were 1) advance of shoots from the edge of the gaps through clonal growth; 2) dispersal of detached individual shoots and clumps; 3) regeneration of what appeared to be dead stems from a soil diaspore bank. Each of the regenerating species seemed to be best at one of the strategies. Disturbance temporarily increased diversity as colonists succeeded on newly available ground before the perennial stayers were able to completely occupy the gap.

Arrival can account for differences in species dominance. In a boreal forest, *Pleurozium schreberi* (Figure 7) didn't show any diaspore limitation (Lloret 1994). *Dicranum scoparium* (Figure 9) cover was not influenced by proximity of its neighbors, but it did increase its colonization when the species was introduced by planting. In these forest sites, *D. scoparium* seemed to depend on the diaspore bank for its establishment. *Hylocomium splendens* (Figure 194), on the other hand, did depend on the presence of neighbors.

**Activation conditions** usually mean reaching not only sufficient moisture, but being exposed to light. Continued metabolic activity without light is certain death, but most species seem to have mechanisms to prevent germination until light is available. For example, diaspore banks of the forest floor can be activated for germination by disturbance that brings propagules into sufficient light and available moisture (Korpelainen *et al.* 2011). Such diaspore banks may be the source of rapid colonizers after forest harvesting (Caners *et al.* 2009), mining of peatlands (Poschold 1995), or other soil/substrate disturbances.



Figure 9. *Dicranum scoparium*. Photo by Janice Glime.

Even within the same habitat, the diaspore bank can differ based on the medium. In the bushland of western Australia, Biggs and Wittkuhn (2006) found 11 bryophytes in the soil and 13 in the litter. *Tayloria octoblepharum* var. *octoblepharum* (Figure 10) and *Rosulabryum campylotheceum* (Figure 11) only occurred in soil diaspore bank samples and *Lunularia cruciata* (Figure 12), *Fissidens serratus* (Figure 13), *Racopilum cuspidigerum* var. *convolutaceum* (Figure 14), and *Tortula antarctica* (Figure 15) only occurred in litter samples. *Bryum argenteum* (Figure 16) and *Rosulabryum billardieri* (Figure 17) were present in soil samples from all nine floristic types (including various types of woodlands, shrublands, heath, and mobile dunes); *Gymnostomum aeruginosum* (Figure 18) occurred in litter from all nine floristic types. As in other studies discussed herein, the diaspore bank housed some species that rarely occurred above ground, e.g. *Riccia* (Figure 97) and *Physcomitrium* (Figure 20). Among the familiar taxa from studies in other parts of the world were *Funaria hygrometrica* (Figure 178) and *Pohlia nutans* (Figure 36) in these Australian diaspore banks.



Figure 10. *Tayloria octoblepharum* with capsules. Photo by Janice Glime.





Figure 11. *Rosulabryum campylothecium*, a species common in soil diaspore banks but not in litter. Photo from British Bryological Society website, with permission.



Figure 12. *Lunularia cruciata* showing gemmae. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 13. *Fissidens serratus* germinating bud. Photo by Tom Thekathyl, with permission.



Figure 14. *Racopilum cuspidigerum*. Photo by Jan-Peter Frahm, with permission.



Figure 15. *Tortula antarctica* with capsules, a species for which spores occur in the litter but not in the soil of Australian bushland. Photo by M. Fagg, Australian National Botanic Gardens <[www.anbg.gov.au](http://www.anbg.gov.au)>, with online permission.



Figure 16. *Bryum argenteum* males. Photo by George Shepherd, through Creative Commons.



Figure 17. *Rosulabryum billardieri*. Photo by Tom Thekathyl, with permission.





Figure 18. *Gymnostomum aeruginosum*. Photo by John Game, through Creative Commons.

During (2001) considers that species such as *Micromitrium tenerum* (Figure 19) and *Physcomitrium sphaericum* (Figure 20) that require "episodically suitable habitats" persist in the diaspore bank as spores. In Mediterranean habitats where conditions permit winter annuals to persist, a sporebank is likewise an important source. On the other hand, in temperate forests and grasslands, long-lived shoots (especially pleurocarpous mosses) are rare in the diaspore bank even if numerous on the surface, whereas the short-lived species are typically over-represented in the diaspore bank, often as asexual propagules, awaiting small-scale disturbance.



Figure 19. *Micromitrium tenerum*, an ephemeral moss. Photo by Jan-Peter Frahm, with permission.



Figure 20. *Physcomitrium sphaericum* with protonemata, leaves, and capsules. Photo by Michael Lüth, with permission.

During (2001) considers that ruderal species often produce several types of propagules that are suitable for

different conditions. One such species is *Blasia pusilla* (Figure 21), which has stellate gemmae (Figure 22-Figure 23) that have two auricles with the nitrogen-fixing Cyanobacterium *Nostoc* (Figure 24) and large amylochloroplasts in the gemmae. Its second type of gemma is ellipsoid or ovoid (Figure 25) and produced in flask-shaped structures (Figure 21-Figure 26). They are filled with starch, proteins, and lipids but lack *Nostoc* (Duckett & Renzaglia 1993). The stellate gemmae are produced throughout the growing season, but do not survive the winter cold. The ellipsoid gemmae are not released until late summer or autumn and do survive winter, germinating in the spring. These latter gemmae are suitable for the diaspore bank, but their presence there does not seem to be documented (During 2001). It is likely that other taxa with multiple diaspore types likewise have a division of labor.



Figure 21. *Blasia pusilla* showing flask-shaped stalks with gemmae on top. Photo by Dick Haaksma, with permission.

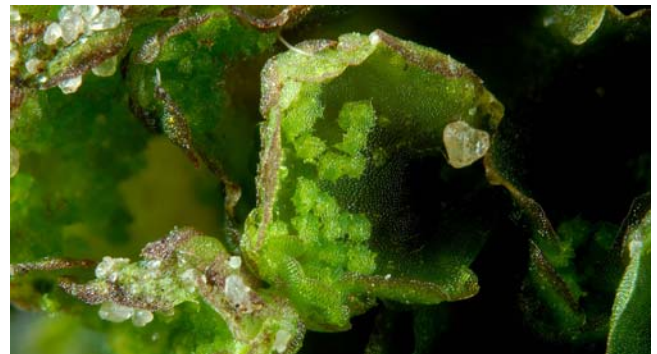


Figure 22. *Blasia pusilla* showing stellate gemmae. Photo by Dick Haaksma, with permission.



Figure 23. Stellate gemma of *Blasia pusilla* with *Nostoc* colonies. Photo by Dick Haaksma, with permission.





Figure 24. Thallus of *Blasia pusilla* with dark-colored *Nostoc* colonies. Photo by Walter Obermayer, with permission.

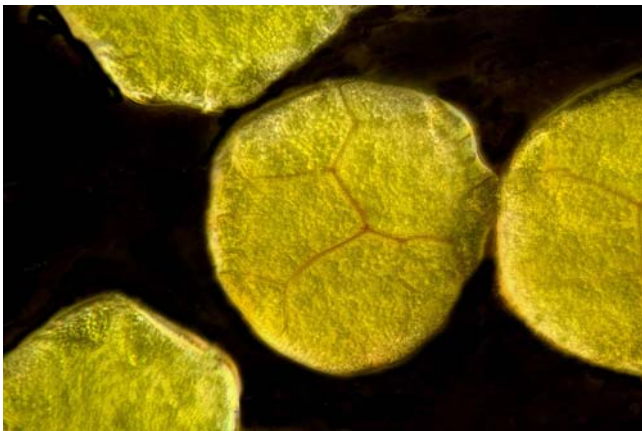


Figure 25. *Blasia pusilla* elliptical gemmae from the flask-shaped stalk. Photo by Dick Haaksma, with permission.



Figure 26. *Blasia pusilla* flask-shaped stalk with gemmae on top. Photo by Des Callaghan, with permission.

### Species Differences

Not all diaspores enter the diaspore bank equally. Representation in diaspore banks is not necessarily a good

indication of what grows at the surface. During (1997) found that species that were short-lived above-ground were usually over-represented in the diaspore bank, but perennial species tended to be absent or rare. These diaspore bank species tend to have large spores, but many are only represented by vegetative diaspores.

Lönnell (2011) reviewed dispersal literature and concluded that diaspore banks have little representation by even dominant pleurocarpous mosses, whereas the short-lived species that one can easily miss in the flora are common in the diaspore banks. This may account for the observations of Vitt (2006), who summarized previous studies and concluded that diaspore banks usually lack good representation of the extant community. Instead, he found that the species dominating the current community are generally rare or absent in the diaspore bank; rather, spores present in the diaspore bank represent pioneer species that are not present in more mature stages. This latter statement supports the conclusion of Lönnell (2011) that the short-lived species are the most common. Lönnell also found that larger diaspores are better represented than smaller ones. This latter strategy is useful for species that must await an opening, then accomplish their life cycle quickly before the competition arrives. During *et al.* (1987) demonstrated that even in diverse habitats in Spain, this bias holds true. They found tubers, gemmae, leaf fragments, and viable cells on decaying stems in the diaspore banks. Despite the mix of bryophytes growing on the surface, the diaspore bank was dominated by species with a colonist life strategy. On the other hand, Poschlod (1995) concluded that for disturbed (mined) peatlands, recolonization is from the diaspore bank.

During and ter Horst (1983) found 37 species in the diaspore bank of a chalk grassland. Among these the **acrocarpous** (having archegonia terminal on upright stems; mostly growing vertically) colonists were likewise the most frequent, despite dominance of **pleurocarpous** (having archegonia on short side branches; mostly growing horizontally) mosses and perennial liverworts on the surface. During (1990) suggested that high species diversity in chalk grasslands might be maintained by intermediate disturbances that cause a high turnover of species originating from the diaspore bank.

During and Moyo (1999; During 2003) found that in a Zimbabwean savannah, fire did not seem to harm the diaspore bank. Following disturbance by burning, only *Exormotheca holstii* (Figure 27), 2 *Riccia* spp (Figure 97), 2 *Archidium* spp (Figure 109) and *Bruchia* (Figure 28) emerged from soil samples near the surface in the middle of the rainy season (During & Moyo 1999; During 2003). Nevertheless, in soil samples representing the diaspore bank 11 liverworts and hornworts and 21 moss species were present. As seen in a number of other studies, taxa often were absent in the surface flora and appeared only when the right disturbance conditions occurred (During 2007). During and Moyo (1999) found that some rare species and even some species previously unknown for that region were conserved in the diaspore bank (During & Moyo 1999; Zander & During 1999).

Some species always seem to be there when the landscape is scoured for a road cut or for making a ski trail. Such is the case for *Trematodon ambiguus* (Figure 29). In fact, this species had been considered to be extinct in



Belgium and the Netherlands, but following large-scale disturbance it reappeared, apparently from a long-lived spore bank in the soil (During *et al.* 2006). The spores are somewhat large (~30 µm), not especially numerous in the capsule (~14,000), and emerged from soil samples taken at 0-3 cm.

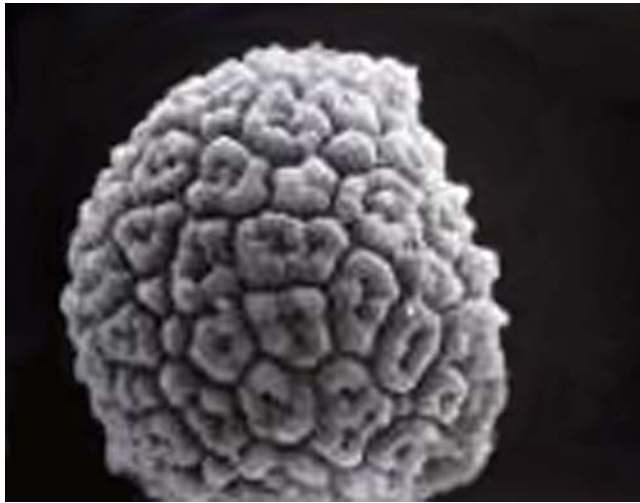


Figure 27. *Exormotheca holstii* spore, a propagule that can regenerate after fires in the Zimbabwe savannah. Photo by Laura Forrest, permission pending.



Figure 28. *Bruchia flexuosa*, a species that can emerge from the diaspore bank after fire. Photo by John Game, through Creative Commons.



Figure 29. *Trematodon ambiguus* capsules in an exposed soil bank along a new ski trail in Houghton, MI, USA. Photo by Janice Glime.

While not all bryophytes enter the diaspore bank equally, neither do they emerge equally. In a different road-cut study, Hassel and Söderström (1998) found that two species of *Pogonatum* behaved differently. *Pogonatum dentatum* (Figure 30) was most likely to occur on roads only 0-4 years old, whereas *P. urnigerum* (Figure 31) was more likely along roads more than 4 years old. At least for *P. dentatum*, frequency in the diaspore bank decreased with distance from parent colonies, suggesting that the diaspore bank is more important than diaspore rain.



Figure 30. *Pogonatum dentatum*, a species that appeared along new road cuts. Photo by Michael Lüth, with permission.



Figure 31. *Pogonatum urnigerum* with capsules and young male splash cups (unopened). This species appeared along road cuts more than 4 years old. Photo by Michael Lüth, with permission.

Some tuber-bearing mosses (Figure 35) seem to be especially dependent on diaspore banks. They may be very common in the diaspore bank, but absent on the surface until the soil is disturbed (During 1995). Where they do occur on the surface, maintenance of that population seems to depend on occasional recruitment from the diaspore bank. Nevertheless, they can still exhibit clonal behavior because the tubers are deposited near the parent on relatively long rhizoids.

### Arable Fields

In three cultivated fields of Switzerland, Bisang (1996) found *Anisothecium staphylina* (Figure 32), *Dicranella schreberiana* (Figure 33), *Bryum rubens* (Figure 34-Figure 35), *Pottia* sp (Figure 118), and *Phascum* sp (Figure 61) as common members of the soil diaspore banks. As is typical, some species were present in the diaspore bank but not



present among the flora of that field. Species of diaspores in these agricultural habitats varied most between localities.



Figure 32. *Anisothecium staphylina*, a species that appears after disturbance of cultivated fields in Switzerland. Photo by Michael Lüth, with permission.



Figure 33. *Dicranella schreberiana* with capsules, a species common in diaspore banks of arable fields. Photo by Michael Lüth, with permission.



Figure 34. *Bryum rubens* growth habit, a species common in arable fields in Switzerland. Photo by Michael Lüth, with permission.



Figure 35. Rhizoidal tubers on *Bryum rubens*. Photo by Jan-Peter Frahm, with permission.

### Ponds and Lakes

One common bryophyte in the mud of ponds and lakes is *Physcomitrium sphaericum* (Figure 20). This species is not a regular member of the flora surrounding these water bodies because it requires conditions that are not present annually: exceptionally warm, dry summers (Furness & Hall 1981). In fact, the spores will germinate only in the range of 15-35°C. Its appearance under those suitable conditions is possible only because its spores remain viable in the mud for a long time.

### Forests

The role of diaspore banks in various forested landscapes has been investigated through several studies. Caners *et al.* (2009) used mineral soil samples from mixed and coniferous stands of boreal mixed-wood forest in northern Alberta, Canada, to examine the role of these potential diaspore banks in reforestation after harvesting. Surprisingly perhaps, the composition of bryophyte species that were able to germinate related not to the forest types or harvesting intensity (measured by light regime), but to edaphic factors and, not surprisingly, to spatial proximity. Spatial proximity not only accounted for the species available, but also accounted for edaphic similarities. Nevertheless, light intensity had a significant influence on both the responses of individual species and on the species assemblages that arose.

In the boreal forest, Jonsson (1993) found 40 species, similar to the number found by During and ter Horst (1983) in chalk grasslands, of liverworts and mosses in the diaspore bank of an European *Picea abies* forest. The most abundant taxa were *Pohlia nutans* (Figure 36-Figure 37), *Sphagnum* spp. (Figure 47-Figure 52), and *Polytrichum commune* (Figure 88-Figure 89) / *Polytrichastrum longisetum* (Figure 38). In the boreal forest soil diaspore bank in southeastern Norway, Rydgren and Hestmark



(1997) found that *Plagiothecium laetum* agg. (Figure 39) and *Polytrichum* spp. (Figure 88-Figure 89) were the most frequent bryophytes germinating. Sean Robinson succeeded in growing new plants from a plant fragment of *Pohlia nutans* (Figure 37).



Figure 36. *Pohlia nutans* becoming established on sand. Photo by Des Callaghan, with permission.

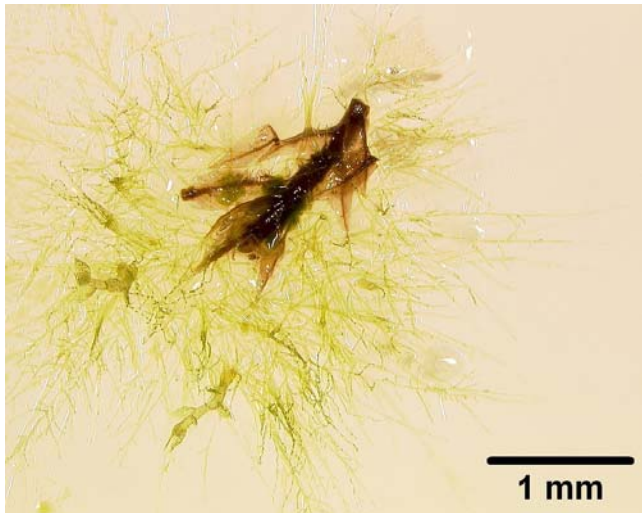


Figure 37. *Pohlia nutans* growth from fragments. Photo by Sean Robinson, with permission.



Figure 38. *Polytrichastrum longisetum* with capsules and mixed with *Campylopus* sp. Photo by David T. Holyoak, with permission.



Figure 39. *Plagiothecium laetum*. Photo courtesy of Betsy St. Pierre.

Forest gaps benefit from diaspore banks. Palisaar and Poschlod (2001) found that both forest and windthrow areas have a predominance of long-lived species, but the colonist strategist predominates in the diaspore bank, ready to take advantage of large, sunny gaps.

Tropical forest diaspore banks have rarely been studied, but it appears that their composition follows different patterns from those of other forests and periodically disturbed habitats. In lab cultures of diaspore banks from Brazil, bark (68) and decaying wood (55) species dominated, compared to soil species (22) (Maciel-Silva *et al.* 2012). Mosses were more numerous in both species and number of shoots than liverworts. Monoicous species were more common than dioicous species. Species that produced sporophytes and those producing gemmae were well represented in the diaspore banks. The biggest difference was that the diaspore banks represented the growing vegetation rather well.

When culturing samples from the diaspore bank of three Malaysian mountain rainforests, Bisang *et al.* (2003) found germination of more liverworts than mosses, especially from the lower altitudes, contrasting with the results of Maciel-Silva *et al.* (2012). These liverworts [*Cincinnulus* (as *Calypogeia*) *argutus* (Figure 40), *Mnioloma* (as *Calypogeia*) *fuscum*, *Lepidozia wallichiana* (Figure 41), and *Zoopsis liukuensis* (Figure 42)], were, as in the study of Maciel-Silva *et al.*, common taxa growing in the area. Stem fragments that had lost their chlorophyll seemed to be the diaspores that gave rise to *Isopterygium* sp. (see Figure 43) and cf. *Ectropothecium* sp. (Figure 44), but for other taxa they were unable to identify the type of diaspore.



Figure 40. *Cincinnulus argutus*, a species in tropical diaspore banks. Photo by Des Callaghan, with permission.



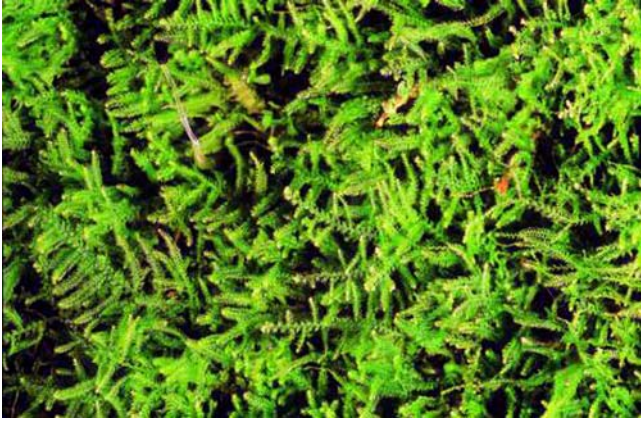


Figure 41. *Lepidozia wallichiana*, a species in tropical diaspore banks. Photo by Jia-Dong Yang, through Creative Commons.



Figure 44. *Ectropothecium perrotii*, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.



Figure 42. *Zoopsis liukuensis*, a species in tropical diaspore banks. Photo by Rui-Liang Zhu, with permission.



Figure 43. *Pseudotaxiphyllum elegans* with gemmae, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.

### Peatlands

In peatlands, recolonization is derived from diaspore banks and adjoining similar habitat. Sundberg and Rydin (2000) showed experimentally that 15-35% of *Sphagnum* spores could survive for 13 years when stored in humid conditions such as would be present in a peatland diaspore bank.

Campbell *et al.* (2003) found that in a regenerating Quebec, Canada, peatland, *Polytrichum strictum* (Figure 45) was widespread and its colonization showed no significant trends with distance from a living source. *Pleurozium schreberi* (Figure 46), *Sphagnum capillifolium* (Figure 47), and *Sphagnum fuscum* (Figure 48), on the other hand, only became frequent further from edges (> 20 m), suggesting that the right habitat conditions were absent at the edges. They explained the strong presence of *Polytrichum strictum* by the long fall times from capsule to substrate, coupled with its very small spores, facilitating its travel despite its low release height. Nevertheless, the diaphragm forces the spores out the sides, a position not conducive to aerial transport.



Figure 45. *Polytrichum strictum* with capsules in Europe, a species whose regenerating capacity does not seem to relate to distance from source. Photo by Michael Lüth, with permission.





Figure 46. *Pleurozium schreberi* in Michigan, USA. Photo by Janice Glime.



Figure 49. *Sphagnum angustifolium*, a species not detected in the diaspore rain of a regenerating peatland, but nevertheless present as a regenerant. Photo by Michael Lüth, with permission.



Figure 47. *Sphagnum capillifolium*, a species that did not regenerate close to the edges of the peatland. Photo by David Holyoak, with permission.



Figure 50. *Sphagnum papillosum*, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum fuscum* in Alaska, USA, a species that did not regenerate close to the edges of the peatland. Photo courtesy of Andres Baron Lopez.

On the other hand, *Sphagnum angustifolium* (Figure 49), *S. papillosum* (Figure 50), *S. cuspidatum* (Figure 51), *S. subsecundum* (Figure 52), *Pleurozium schreberi* (Figure 46), *Leucobryum* sp. (Figure 53), and *Chiloscyphus profundus* (= *Lophocolea heterophylla*) (Figure 54) were present in the vegetation and absent in the measured diaspore rain of the regenerating peatland (Campbell *et al.* 2003).



Figure 51. *Sphagnum cuspidatum*, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.





Figure 52. *Sphagnum subsecundum*, a regenerating species absent from the diaspore rain. Photo by Michael Lüth, with permission.



Figure 53. *Leucobryum glaucum* with capsules. Note the broken leaves lying on the surface of the cushion. Photo by Janice Glime.



Figure 54. *Chiloscyphus profundus*, a regenerating species absent from the diaspore rain of a peatland in Canada. Photo by Michael Lüth, with permission.

Poschlod (1995) conducted extensive studies comparing milled peatlands to natural raised bogs in the Bavarian foothills of the Alps. He found for those peatlands that recolonization apparently came entirely from diaspore banks, especially for *Sphagnum* species. That

genus was entirely absent in the spore rain sampled. In particular, *Sphagnum magellanicum* (Figure 55), *S. capillifolium* (Figure 47), and *Polytrichum strictum* (Figure 45) occurred in the diaspore rain in at least one of the six sites studied.



Figure 55. *Sphagnum magellanicum* in Europe, a species that regenerates from diaspore banks. Photo by Michael Lüth, with permission.

Among the bryophytes in these peatland diaspore banks, Poschlod (1995) found six species of liverwort fragments. Of these, five of these are species that develop tubers. Furthermore, *Cephalozia connivens* (Figure 56) and *Kurzia pauciflora* (Figure 57) have subterranean shoot axes and *Calypogeia* (Figure 58) species have a shoot axis near the surface. Duckett and Clymo (1988) likewise found liverwort shoot axes in bogs in Great Britain and estimated that regeneration came from peat layers that were 25-60 years old. Based on studies by Clymo and MacKay (1987), they ruled out downwash into deeper layers.



Figure 56. *Cephalozia connivens* in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.





Figure 57. *Kurzia pauciflora* in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.



Figure 58. *Calypogeia fissa*, a species that can persist in diaspore banks by its subterranean shoots. Photo by Hermann Schachner, through Wikimedia Commons.

Poschlod (1995) found all the *Sphagnum* species typical of raised bogs in the diaspore banks. Brown stems and branches of *S. capillifolium* (Figure 47) and *S. cuspidatum* (Figure 51) were able to regenerate from depths down to 15 cm. Peatland diaspore banks can be deep, with viable *Sphagnum* spores occurring as deep as 30 cm (Poschlod 1995). Poschlod (pers comm. 28 March 2013) concluded from this that the spores could survive more than two centuries!

### Delayed Germination – Dormancy

Propagules may survive diaspore banks through dormancy (Hock *et al.* 2004). In two open grasslands in Hungary, gemmae of a species in the *Bryum atrovirens* complex (Figure 59) and *Weissia controversa* (Figure 60) exhibited dormancy. Likewise, dormancy seemed to be present in the spores of *Tortula acaulon* (= *Phascum cuspidatum*) (Figure 61). Hock *et al.* suggested that dormancy may be relatively common for diaspores of species living in habitats with short-term periods of unfavorable growing conditions.

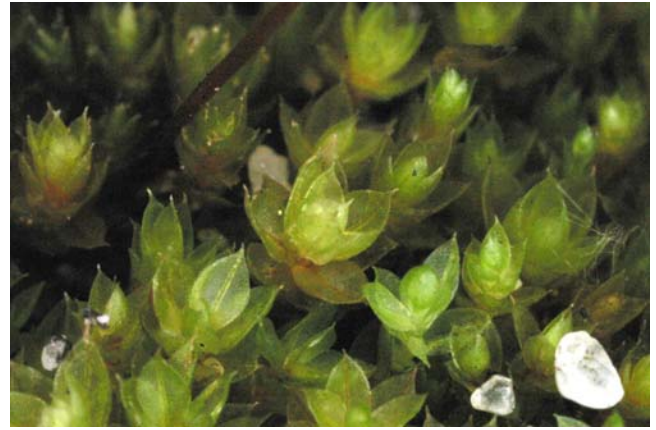


Figure 59. *Bryum atrovirens* aggregate. Photo by Jan-Peter Frahm, with permission.



Figure 60. *Weissia controversa* var. *controversa* with capsules. Photo by David Holyoak, with permission.



Figure 61. *Tortula acaulon* (= *Phascum cuspidatum*) with capsules. Photo by David Holyoak, with permission.

It is interesting that initially the highest number of species in the boreal forest diaspore bank arose from the mineral soil (9.9 per sample), but after four years the reverse was true (Jonsson 1993), with more arising from the humus, suggesting that some species have a delay mechanism that does not permit them to germinate right away. Watson (1981) suggested that *Polytrichum* species had the option of chemical inhibition to facilitate dormancy. Such delay mechanisms are known from flowering plants and include such factors as immature embryos (not applicable to bryophytes), chemical inhibitors



that must be washed away or removed by digestive enzymes of an animal (not yet shown for bryophytes but possible), or the need for hormones or vitamins from a fungal or bacterial partner [known for development of the gametophore in *Pylaisiella selwynii* (Figure 62) and several other moss species (Spiess 1977, 1979; Spiess & Lippincott 1978; Spiess *et al.* 1971, 1972, 1973, 1976, 1981a, b, 1982, 1984a, b, c, d, 1986, 1990)]. I have cultured *Fontinalis squamosa* (Figure 63) that produced protonemal gametophore buds in the presence of contamination while the cultures that remained sterile produced no buds. What other examples of bryophytes are out there in nature where a living partner is needed to provide some growth factor necessary for development to continue – or even start?



Figure 62. *Pylaisiella selwynii* on bark, a species that requires a bacterial partner to complete its development. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Fontinalis squamosa* in Europe, a species that may require a bacterial partner to develop protonemal buds. Photo by Michael Lüth, with permission.

Other factors relating to delay of germination may be habitat condition or suitable weather. For example, in *Sphagnum* (Figure 47-Figure 52), dormancy may be conditional, depending on weather (Sundberg & Rydin 2000).

This leads us to ask what conditions are needed to break dormancy. Obviously, water is needed, and for continued success, light is needed. But water may be insufficient for continued development, so the spore needs a way to prevent germination when conditions are not likely to remain suitable. Mogenson (1981) suggested that spore surface sculpturing may serve to prevent small quantities of water from activating the spore by creating

surface tension that prevents the water from penetrating the spore. However, this hypothesis seems not to have been tested.

*Blasia pusilla* (Figure 22-Figure 26) is one liverwort whose gemmae do not germinate right away when brought to the surface from a diaspore bank (During 2001). Gemmae of *B. pusilla* do not germinate until the spring after their production (Duckett & Renzaglia 1993), a phenomenon well known for seeds. This delay could be related to its storage of food reserves as protein, which is slower to metabolize than the starch or oils of other spores (Crum 2001). It seems likely to me that there are other bryophytes that have this delayed germination mechanism in spores or other propagules, especially in the **Anthocerotophyta** with their protein food reserves (Crum 2001). The leafy liverwort *Lophozia ventricosa* var. *silvicola* (Figure 64) changes its dormancy based on the time of production, with those gemmae produced in the spring germinating readily, but those produced later seem to lose germinability with time of production (Laaka-Lindberg 1999). A similar seasonal relationship is known for the forest floor tracheophyte *Melampyrum lineare*. If a propagule begins to convert its food reserves, loss of water could stop the process and prevent germination. This could only happen a few times before the reserves are used up, and a small propagule would lose its reserves sooner than a large one.



Figure 64. *Lophozia ventricosa*. Photo by Hermann Schachner, through Creative Commons.

Asexual propagules likewise display dormancy. We have witnessed the effect of parents on inhibiting development of vegetative propagules, *e.g.* the absence of germination of *Marchantia polymorpha* gemmae (Figure 65) while they remain on the parent. There seem to be few species where either spores or vegetative propagules can germinate while still in contact with the parent, and many species, for example *Funaria hygrometrica* (Figure 178), are unable to germinate near their parents due to chemical inhibitors leached from the parent. Could there be biochemicals in the environment that must leach out before germination occurs in some species?

Even freshly produced spores may have dormancy (**innate dormancy**), as in *Archidium alternifolium* (Figure 66). This dormancy is broken slowly and the mechanisms for breaking it are unknown (Miles & Longton 1992). Germination was less than 65% and increased as the spores aged, up to 4 years. This delay suggests to me that there



may be a chemical inhibitor that is removed by leaching. In *Sphaerocarpos texanus* (Figure 67), spores are dormant when released, but dormancy is broken by fluctuating temperatures, typically 35/20°C and may even have dormancy/non-dormancy cycles resulting from temperature fluctuations (McLetchie 1999).

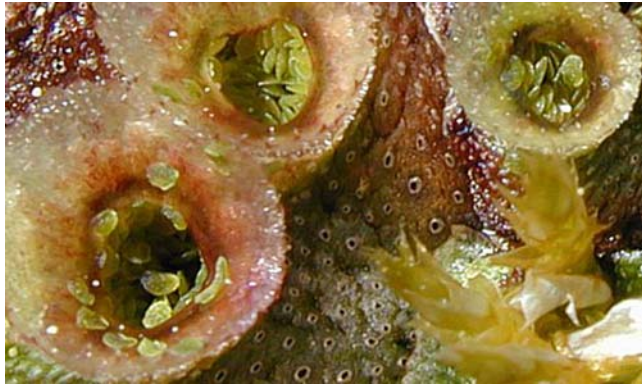


Figure 65. *Marchantia polymorpha* with gemmae. Photo by Michael Lüth, with permission.



Figure 66. *Archidium alternifolium*. Photo by Michael Lüth, with permission.



Figure 67. *Sphaerocarpos texanus* on disturbed soil. Photo by Adolf Ceska, with permission.

Dormancy relationships seem to be complex, making them difficult to predict. Kobayashi and Yamamura (2000) found that inbreeding caused an increase in dormancy, perhaps through complementation. But the spores have only one set of chromosomes, so this logic seems to fail. And under some conditions inbreeding leads to decreased dormancy – a combination of genes where dormancy is poor to start with? We also know examples where longevity of female spores is longer than that of male spores [McLetchie 1992 for *Sphaerocarpos texanus* (Figure 67)]. How does dormancy affect longevity?

The seed bank houses a set of seeds that represent a non-random set of genotypes. That is, at the seed bank level, there is selection. There is evidence that there are correlations among suites of characters such as temperature of response and seed longevity. Such relationships need to be explored for bryophytes. Furthermore, risk of predation by animals and attack by fungi are strong selection factors for seeds, but these likewise have received inadequate attention for bryophytes.

### Does Depth Matter?

Bisang (1996) compared germination of diaspores from above and below 25 cm for diaspores that were disturbed by regular ploughing to a depth of about 10-25 cm. In general, protonemata of mosses were less vigorous in soil samples from below 25 cm. Furthermore, *Eurhynchium hians* (Figure 8) and *Riccia* sp. (Figure 97) were present only to a depth of 15 cm.

### Benefits of Diaspore Banks

Diaspore banks that have a store of recent species are likely to provide the soil/substrate characteristics required for the successful re-establishment from diaspore growth, once they are in a position to obtain sufficient light and moisture. On the other hand, light conditions may differ from those when the diaspores were deposited, and the species represented are often different from those on the surface (During & ter Horst 1983; During 1997). Furthermore, the species richness of the bryophytes may be influenced by the species composition of tracheophytes that has developed while the diaspores lay dormant (Aude & Ejrnæs 2005). For the short-lived shuttle species of agricultural landscapes, even the soil characteristics may have changed due to agricultural practices of fertilizing, a condition that can be detrimental to many bryophytes adapted to low nutrient conditions.

### Tradeoffs

Diaspores, like any other novel solution, have their tradeoffs, although our understanding of these is very limited. During (2001) suggests that the lack of perennial bryophytes in the diaspore bank represents a tradeoff between adult longevity and diaspore longevity. Spore size is another potential tradeoff. Species with small spores such as *Funaria hygrometrica* (Figure 178) tend to have short viabilities in the soil (During 1987). During (2001) suggests that a similar tradeoff between dispersability and soil longevity could account for the scarcity of such weedy species as *Marchantia polymorpha* (Figure 1), *Bryum argenteum* (Figure 16), *B. bicolor* (Figure 68), and *Ceratodon purpureus* (Figure 69) in soil diaspore banks.



Nevertheless, Biggs and Wittkuhn (2006) found *B. argenteum* in the soil diaspore banks in all nine habitats in their study in western Australia. Could it be that this is a different microspecies?



Figure 68. *Bryum bicolor* with capsules, a species with good dispersability and poor diaspore longevity. Photo by Jonathan Sleath, with permission.



Figure 69. *Ceratodon purpureus* in southern Europe, a species with good dispersability and poor diaspore longevity. Photo by Michael Lüth, with permission.

Rather than small spores and good dispersal, During (2001) finds that the overall trend in diaspore banks is just the opposite. Those species that persist in the soil diaspore bank tend to have large spores (Jonsson 1993). This is a reasonable expectation because it would make it possible for these species to grow rapidly when they do germinate, taking advantage of the absence of competition from tracheophytes. Furthermore, many of these species have cleistocarpous capsules and short setae, making dispersal to any distance an unlikely event.

This presence of large spores in the diaspore bank is in contrast to that of seeds, where small seeds predominate. During (2001) suggests that seed predation on larger seeds and ease of dispersability of small spores may account for the difference in relationships. Furthermore, asexual diaspores are much more common among bryophytes.

## Spores vs Vegetative Dispersal

All bryophytes require dispersal in some form to continue the species as its current habitat changes or disappears. Spores may be especially important for colonizing epiphytic habitats and other vertical habitats

such as walls and cliffs, as well as being the primary source of propagules for forest clearings. Grime and coworkers (1990) contend that sporebanks are important in exploiting disturbed habitats, but even these sporebanks depend on aerial dispersal as well as local dispersal. These recolonization and new colonization events by spores are possible only because of the ease of dispersal of at least some of the spores.

Both spores and asexual diaspores provide the means by which bryophytes can reach new locations or spread in local ones. At some point, specialized asexual reproduction arose in photosynthetic organisms. Algae can make extensive use of fragmentation, and some algae have asexual spores. But bryophytes have developed specialized structures for their reproduction and never produce asexual spores, *i.e.*, they produce only meiospores.

We must ask then, what are the advantages of sexual vs asexual propagules, and under what circumstances? Newton and Mishler (1994) summarized our knowledge and pointed out that spores have a prerequisite of fertilization, and this process requires water. But spores usually disperse farther than vegetative propagules and germinate best in previously uncolonized substrates. Vegetative structures, on the other hand, can be produced even under stressful conditions, disperse well locally, and are more successful in germinating among existing colonies.

During (pers. comm. 5 January 2005), however, points out that in some cases, the role of spores in dispersal, particularly large spores, is very similar to that of asexual propagules, having short-range dispersal with greater chance of germination and establishment in a somewhat wider range of habitats. And if the species is **monoicous** (both sexes on same plant), it is likely that the spores resulted from selfing and thus have similar genetic makeup to that of any asexual diaspore that might be produced in the same species. Hence, there seems to be a trade-off in these species with large spores. There appears to be little advantage for them also to produce asexual structures for reproduction. This is especially true for annual shuttle species – these species may simply not have enough time to produce both, since many bryophytes typically do not have enough energy to produce sexual spores and vegetative diaspores at the same time, although they may ultimately be present at the same time.

Fritz (2009) tested the relative importance of asexual vs sexual reproduction in several species [*Pseudoscleropodium purum* (Figure 6), *Pleurozium schreberi* (Figure 7), and *Rhytidiadelphus squarrosus* (Figure 70)] where sporophytes are considered to be rare. First, he found that sporophytes were apparently not so rare, using molecular data to demonstrate that the level of genetic diversity was that to be expected from spore dispersal. In these small populations, the genetic structure showed positive correlations between genetic diversity of a population and sporophyte occurrence. It appears that there may be an energy tradeoff at work here, because Fritz found that in these three species, clonal plants were present primarily in small patches up to 6 m<sup>2</sup> and were restricted to populations where both antheridia and archegonia, as well as sporophytes, were absent, or where only one sex of gametangia was present. This would be a good contingency strategy – that of a **bet hedger**.





Figure 70. *Rhytidiadelphus squarrosus*. Photo by David Holyoak, with permission.

Pohjamo *et al.* (2006) compared spores and gemmae in the leafy liverwort *Anastrophyllum hellerianum* (Figure 71), where they are of equal size. Unlike the suggestion of During (pers. comm. 5 January 2005) that their dispersal distances would be equal, Pohjamo *et al.* found that dispersal distances differed, with gemmae travelling farther. Between 17.5 and 43.1% of the spores released and 0.64 and 4.8% of the gemmae available were deposited within 10 m of the central colonies. Rain had no effect on either dispersal pattern, but more gemmae were released on rainy days. This leaves us to wonder why gemmae travel farther. Perhaps their non-spherical shape causes them to be caught by the wind more easily, or to attach to animals more easily.

A number of species rarely produce capsules. If they likewise do not have any specialized reproductive structures, this presents a dispersal problem. But researchers continue to discover asexual means that were previously unknown or rarely described in floras. For example, despite the obvious presence of propagula in several species of *Aulacomnium*, these are seldom mentioned for *A. heterostichum* (Figure 72), but can be quite abundant in some populations (Imura *et al.* 1991; Figure 72). Such was the case for *Mnium stellare* (Figure 73), a species that rarely produces capsules in Europe. However, in 2012, Hugonnot and Celle discovered that it reproduces by leaf **fragmentation**. This is not just random fragmentation, but rather the result of both splitting (**schizogeny**) and breaking (**lysogeny**). In **lysogeny**, there is partial cell disintegration that facilitates the fragmentation. They suggested that **schizogeny** was probably the result of hydration of the middle lamella. In *Mnium stellare* the fragility of the leaves seems to be greater when the leaves are hydrated, rather than when they are dry. Hugonnot and Celle verified these fragments as legitimate dispersal units by showing that they readily germinated on wet peat. Other species are already known for their leaf fragmentation abilities, *e.g.* *Dicranum viride* (Figure 74), *D. fragilifolium* (Figure 75), *Tortella fragilis* (Figure 76).



Figure 71. *Anastrophyllum hellerianum* gemmae that are the same size as spores in this species. Photo by Des Callaghan, with permission.

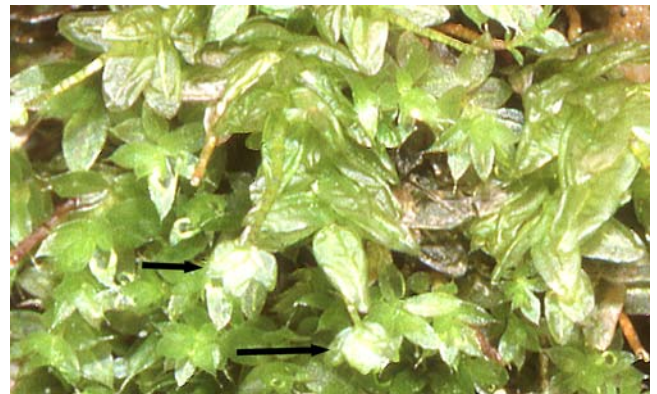


Figure 72. *Aulacomnium heterostichum* with propagules, indicated by the arrows. Note also the yellowish branch tips where these specialized leaves have been shed. Photo by Janice Glime.



Figure 73. *Mnium stellare* from the Khibiny Mountains, Apatity, Murmansk. Note the broken leaves at the arrows. Photo by Michael Lüth, with permission.





Figure 74. *Dicranum viride* showing broken leaves. Photo by Janice Glime.



Figure 75. *Dicranum fragilifolium* with broken leaf tips. Photo by Janice Glime.



Figure 76. *Tortella fragilis* with broken leaf tips. Photo by Michael Lüth, with permission.

Wang *et al.* (2012) used inter-sample sequence repeat markers and DNA sequences to investigate sexual vs asexual strategies in *Hypnum plumaeforme* (Figure 77) and *Pogonatum inflexum* (Figure 78). *Hypnum plumaeforme* reproduces primarily vegetatively. For this

species, the genetic diversity among island populations was significantly greater than that among lakeside populations where the habitat became available and isolated 50 years earlier, suggesting greater isolation among the island populations. *Pogonatum inflexum*, on the other hand, is frequently fertile, spreading primarily by spores. In this species there was no difference in genetic diversity between island and lakeside populations. Wang *et al.* (2012) considered this to be evidence that fragmentation of landscapes could increase genetic differentiation in species that have limited dispersal abilities, resulting in greater spatial differences in genetic structure.



Figure 77. *Hypnum plumaeforme* on bark, a species that reproduces primarily vegetatively. Photo by Janice Glime.



Figure 78. *Pogonatum inflexum*, a species that reproduces primarily by spores. Photo from the University of Hiroshima Digital Museum, with permission.

Understanding dispersal of bryophytes is complicated by their ability to disperse by more than one means. Furthermore, some species are not known to produce spores and others don't produce spores in some locations where only one gender is present. As an example, Bremer and Ott (1990) reported that nearly 40% of mosses in the Netherlands never or rarely produce spores. Nevertheless, the first bryophytes to colonize forests there are those that produce spores frequently, with those rarely producing spores [*Orthodicranum montanum* (Figure 79), *Rhytidiadelphus squarrosus* (=R. *lozeus*; Figure 80), *Thuidium tamariscinum* (Figure 81)] arriving 20 years later. In these forests, experiments suggest establishment from spores is very rare for perennial stayers. It is only in older forests that one can find species with large spores.



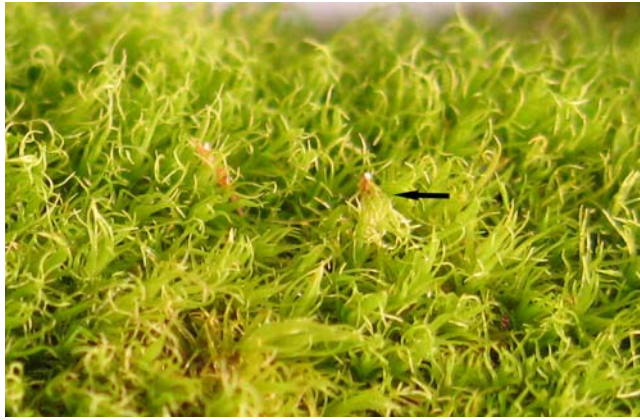


Figure 79. *Orthodicranum montanum* showing dislodged bulbil (**arrow**). This species can form entire colonies of bulbils or form larger gametophyte stems accompanied by these bulbils. Photo by Janice Glime.



Figure 80. *Rhytidiadelphus squarrosus* (= *R. loreus*) with capsules. Photo by David T. Holyoak, with permission.



Figure 81. *Thuidium tamariscinum*, a moss that seldom produces capsules. Photo by Brian Eversham, with permission.

It is widely accepted that bryophyte spores are important for long distance dispersal to colonize newly available habitats (Newton & Mishler 1994). The time required, however, may be centuries or even millennia. Longton (1997, 2006) sums up the differences as one of spores being able to establish new populations more easily and asexual propagules being of major importance in colony expansion and maintenance.

## Differences in Success

One question we might ask is why do some (actually many) bryophytes maintain both sexual and asexual reproductive propagules? Bengtsson and Ceplitis (2000) contend that for such a system to evolve and be maintained, the relative fitnesses of the sexual and asexual propagules must vary over the years. This would permit the most fit system to operate under the environmental conditions of that year. These conditions might be weather conditions, but they can also relate to competition, availability of bare soil, disturbance, herbivory, and other environmental factors. In this context, we might ask what hormonal changes occur in response to herbivory, or how does nutrient depletion affect asexual vs sexual reproduction? And if it is dry, will that stimulate asexual instead of sexual reproduction?

Frahm (2009) claims that there is no difference in effectiveness between sexual and vegetative propagation. He contends that the small size and weight of both spores and vegetative propagules would lead one to believe that both can be dispersed easily, thus supporting wide ranges for the species. Some species do have wide distribution, whereas others have very narrow ranges. And both of these categories include strictly vegetative reproducers and sexual (spore) reproducers. This disparity of ranges does not seem to relate to the abundance of propagules produced, with some species with high production of propagules demonstrating limited distribution and some sterile species having wide distribution (Frahm 2009).

But Callaghan and Ashton (2008) have arrived at a different conclusion for bryophytes in the British Isles. They found that among the 430 taxa there, range-size of both mosses and liverworts is significantly positively correlated with sporophyte production. But in seeming contradiction to this relationship, they found that **monoicous** (having both sexes on the same plant) moss species were rarer than **dioicous** (having the two sexes on different plants) species, suggesting that this rarity of monoicous taxa may be due to less fitness arising from self-fertilization.

Data on *Octoblepharum albidum* (Figure 82-Figure 83) demonstrate a different benefit than is typically attributed to gemmae. Their protonemata from gemmae grow faster than those from spores, most likely making their establishment more successful. On the other hand the spores produce more gametophytes. That is, one gemma produces one plant, but one spore produces many plants arising from multiple buds on a single protonema, at least for mosses.

It is not unusual for bryophytes to have more than one vegetative means of propagation. For example, *Rhytidium rugosum* (Figure 84-Figure 85) has three types of vegetative propagation: ramets (vegetative branches that separate by decay and disintegration when they are older; Figure 84); brood branches; and caducous branches (branches that easily break off as dispersal units; Figure 85). Pfeiffer *et al.* (2006) used AFLP fingerprinting to identify three clones from two plots, each having 2-15 samples with identical fingerprints. Presence of one clone in two plots indicates dispersal by vegetative diaspores. The close relationships between plots suggest that these plots were created through cloning, not spore dispersal.





Figure 82. *Octoblepharum albidum* with both capsules and gemmae (arrow). Photo by Li Zhang, with permission.



Figure 83. *Octoblepharum albidum* leaf with gemmae. Photo by Li Zhang, with permission.



Figure 84. *Rhytidium rugosum* showing dark bases of the ramet that will eventually decay and separate this piece (ramet) into a new plant. Photo by Michael Lüth, with permission.



Figure 85. *Rhytidium rugosum* demonstrating a dry branch that can easily be broken off (caducous) by a frisky squirrel. Photo by Michael Lüth, with permission.

Molecular data for *Pseudoscleropodium purum* (Figure 6) and *Pleurozium schreberi* (Figure 7) showed clonal reproduction [as in *Rhytidium rugosum* (Figure 84-Figure 85)] was an important part of their population dynamics (Fritz 2009). Fritz (2009) furthermore found possibilities for vegetative reproduction that had not yet been documented, including cloning, brood branches/branchlets, caducous shoot apices, and brood leaves (only in *P. schreberi*).

Löbel *et al.* (2009) compared mating systems and concluded that larger asexual diaspores enjoyed higher establishment rates at the cost of shorter dispersal distances, whereas the small sexual spores sacrificed establishment rate to achieve greater dispersal distances, a concept supported by the *Rhytidium rugosum* (Figure 84-Figure 85) study (Pfeiffer *et al.* 2006). This is an interesting contrast to that of Pohjamo *et al.* (2006) for the leafy liverwort *Anastrophyllum hellerianum* (Figure 71) where the vegetative gemmae travelled farther.

### Limits to Success

These inconsistencies based on propagule size and abundance lead us to the conclusion that the propagules of different species have different abilities to arrive and colonize in new locations, using attributes independent of size. As Frahm (2009) points out, it suggests that the germinating propagule is limited by narrow ecological niches, age of taxon, local extinction, or historical events such as ice ages. Caners *et al.* (2009) also found that microhabitat conditions determine the success of species once they arrive or get exposed from soil banks. **Edaphic** (soil) factors are especially important, as well as habitable space. Although successful species composition did not relate to forest type or harvesting intensity, Caners and coworkers found that light intensity had a significant influence on the success of individual species and thus has important management implications in reforestation. To further their assertion of the importance of soil, we might consider the conclusions of Bischler and Jovet-Ast (1981) that in the **Marchantiales** (Figure 1) morphological characters may not be important to survival and dispersal, but rather their adaptations are primarily "linked to biochemical and biophysical properties of the cell content."



With respect to soil characters, I must caution about an area of research that has received little attention. In a new location, differences in soil chemistry could cause morphological differences that could cause even an astute systematist to assume a different species. This can of course be sorted out by DNA fingerprinting, but there is little experimental evidence to address this question. A few studies have, however, demonstrated the plasticity of species under different environmental conditions. For example, Zastrow (1934) cultured a variety of species and showed that responses to water culture include loss of central strand, papillae, alar cells, and leaf border, as well as showing reduction in costa and chlorophyll. Alkaline conditions caused stem elongation between nodes compared to that in neutral and acid conditions. Buryová and Shaw (2005) cultured six populations of *Philonotis fontana* (Figure 86-Figure 87) under two light and two water regimes and observed that both light and water affected growth, but cell dimensions seemed unaffected. Responses differed not only according to treatment, but also showed genetic differences in their responses. But others have shown changes in the number of cell layers in the stem of *Fontinalis* (Figure 63) species (Sée & Glime 1984). Such plasticity makes tracking species dispersal pathways more difficult and our understanding is likely to remain under constant revision for some time to come as molecular data refute our earlier hypotheses.



Figure 86. *Philonotis fontana* in a wet habitat where it can become submerged. Leaves produced in these submerged conditions can be smaller and more widely spaced than those grown aerically. Photo by Michael Lüth, with permission.



Figure 87. *Philonotis fontana* showing brood bodies at the tip of the stem. Photo by Janice Glime.

In recent years, genetic/molecular methods are facilitating our understanding of the relative roles of asexual vs sexual means of reproduction in bryophytes (Shaw *et al.* 2002). For example, Derda and Wyatt (1990) measured 38 multilocus genotypes in populations of *Polytrichum commune* (Figure 88-Figure 89). They found that 69% of these genotypes were distributed evenly across the range of the species, with a mean genotypic diversity of  $0.546 \pm 0.042$ . This is a low value, coupled with potential for vegetative reproduction, and Derda and Wyatt used it to support the concept that spore-mediated gene dispersal in this species is limited. Van Zanten (1973) likewise asserted that dispersal of *Dawsonia* (Figure 90), another member of the *Polytrichaceae*, is limited due to the epiphragm that requires physical contact such as a raindrop to expel the spores.



Figure 88. *Polytrichum commune* with capsules. Photo by David Holyoak, with permission.

This chapter will consider each of these diaspore mechanisms and some examples of dispersal types among the bryophytes. Where possible (data are limited), we will examine what contributes to their success in getting established.



Figure 89. *Polytrichum commune* capsule showing epiphragm connected to teeth, forcing spores to exit the capsule from the sides. Photo by Michael Lüth, with permission.





Figure 90. *Dawsonia longiseta* with capsules. Photo by Niels Klazenga, with permission.



Figure 91. *Polytrichastrum formosum*. Photo by Tom Thekathyl, with permission.

### Which Strategy Accomplishes More?

In a model designed for Bryozoa, not bryophytes, Karlson and Taylor (1992) provided criteria for dispersal that would seem also to apply to bryophytes. Dispersal involves a tradeoff between energy spent on probable success of short distance dispersal and the energy lost to provide an expansion of the species through long-distance dispersal. "Using a procedure which minimizes the extinction probability for the lineage (hence maximizing survivorship of the genetic individual)," they predicted that "a high proportion of dispersed offspring should be associated with high numbers of asexual offspring, a low risk of mortality to offspring during dispersal, and high local survivorship of offspring."

One consequence of vegetative reproduction and dispersal might be a loss of genetic diversity. Van der Velde *et al.* (2001) used the genetic structure of *Polytrichastrum formosum* (Figure 91) to assess this genetic diversity in sexual vs asexual reproduction. They found that the levels of microsatellite variability were, on average, lower than those known for most other plant species. Nevertheless, genotypic diversity within the populations studied was high. They interpreted this as an indication that sexual reproduction is an important determinant of the within-population genetic structure of *P. formosum*. Furthermore, Van der Velde *et al.* found no significant differences among microsatellite markers between populations or between regions (450 km in Denmark vs the Netherlands). They likewise interpreted this as evidence of sexual reproduction with high effective spore dispersal between populations, despite the well known ability of this species to reproduce clonally, supporting the interpretations discussed above for *Pseudoscleropodium purum* (Figure 6), *Pleurozium schreberi* (Figure 7), and *Rhytidiadelphus squarrosus* (Figure 70) (Fritz 2009). Members of the *Polytrichaceae* do not produce specialized asexual reproductive structures, and reproduction by fragments exists but is poorly known for most of the *Polytrichum/Pogonatum/Polytrichastrum* group (Figure 91).

The leafy liverwort *Orthocaulis attenuatus* (= *Barbilophozia attenuata*; Figure 92) provides another example of the tradeoffs. Korpelainen *et al.* (2011) found that diaspores of this species in the diaspore bank of a forest floor can be activated by disturbance. A disturbance as small as ant trails can favor the establishment of large gemmae over small spores for establishment. They found that these gemmae are effective at short distances, but not at mid-distances. For longer distances, spores are an effective means of dispersal. This short-distance gemmae dispersal provides compatible genotypes already adapted to this environment, but the tradeoff is the lack of genetic diversity and other problems attached to inbreeding.

### Lost Energy

Production of sporophytes is a cost in energy. First, it costs energy to produce antheridia and archegonia. Then it costs energy to nourish the sporophyte to maturity. Production of spores likewise costs energy. Therefore, this costly process needs to afford a significant advantage for the species to succeed and survive with this strategy through evolution.



Figure 92. *Orthocaulis attenuatus* (= *Barbilophozia attenuata*), showing gemmae at the tips of some branches. Photo by Michael Lüth, with permission.



Nevertheless, some species seem to produce sporophytes to no avail. Unfavorable conditions for development may make vegetative dispersal more important than dispersal of spores. In Nigeria, the widespread *Bryum coronatum* (Figure 93) produces abundant sporophytes, but it appears that they have a large failure rate (Egunyomi 1982). Among those in the study, 42% remained undehiscent even during the dry season when they normally discharge spores. Furthermore, 41% of the setae never developed capsules. Although the spore germination rate was 65-88%, protonemal growth was abnormal. The abundant production of axillary propagules is certainly important in those seasons, most likely frequent, when conditions during sporophyte development are less than ideal. This is a widespread species and sporophytes are most likely more important in other locations where conditions are more favorable for them.



Figure 93. *Bryum coronatum*, a moss with a large failure rate for sporophytes in Nigeria. Photo by Jan-Peter Frahm, with permission.

As already mentioned, for species that produce large numbers of spores that travel great distances, most of those spores will not reach a suitable substrate and microclimate, hence contributing to the loss of energy.

### Liverworts vs Mosses

Longton (1997) pointed out that the production of specialized asexual propagules is more common among (leafy) liverworts than among mosses. Gemmae are so common among leafy liverworts that their species often are identified by the structure and location of their gemmae. In the British liverwort flora, Laaka-Lindberg *et al.* (2000) found no association between production of asexual propagules and rarity, or with the monoicous vs dioicous condition. But those species that produce neither spores nor special asexual propagules are typically rare.

### Habitat Differences

#### Disturbed Habitats

Disturbance can play a selective role for species that may be mediated by tradeoffs between dispersal rate and establishment success. Kimmerer (1993) found that *Tetraphis pellucida* (Figure 94-Figure 95) benefitted from frequent disturbance, whereas suppressed disturbance caused it to become out-competed by other bryophytes. Its competitor, *Orthodicranum flagellare* (Figure 96), is

successful in colonizing gaps when there are other populations of the species nearby to contribute asexual brood branches. These germinate more rapidly than the gemmae of *Tetraphis pellucida* (Figure 94-Figure 95), making *O. flagellare* the better competitor.



Figure 94. *Tetraphis pellucida* gemmae in splash cups. Photo by Jan-Peter Frahm, with permission.

Flood plains, arable fields, and other regularly disturbed habitats are colonized by species that can lie dormant in diaspore banks during periods unsuitable for growth, or they must arrive quickly, colonize immediately, and complete their life cycles before the habitat is once again unfavorable. Such a habitat favors such species as thallose liverworts that can roll up their thalli, dry out, and resume growth from dormant terminal buds, as in *Riccia* (Figure 97). These are often invisible to the naked eye until those suitable growth conditions are provided, either in the field or in the lab. Kürschner and Parolly (1999) found that this community in Turkey consisted mostly of annual shuttle species and vegetative colonists that produced very large spores, retained spore tetrads, and/or produced asexual propagules, all of which survived in the diaspore bank during winter flooding and were able to re-establish the community quickly when the flood waters receded.

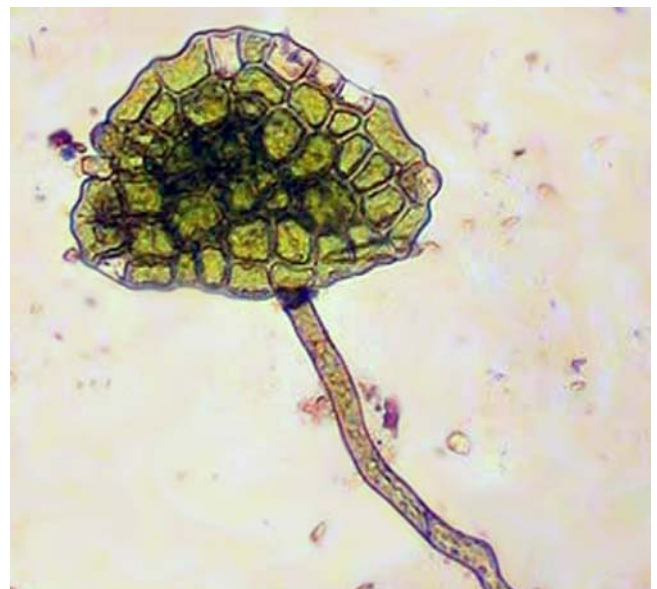


Figure 95. *Tetraphis pellucida* gemma germinating. Photo from UBC botany website, with permission.





Figure 96. *Orthodicranum flagellare* showing flagelliform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.



Figure 97. *Riccia bischoffii* var. *ciliifera* on drying mud. Photo by Jan-Peter Frahm, with permission.

Bijlsma *et al.* (2012) found *Ephemerum cohaerens* (Figure 98) and *E. serratum* var. *rutheanum* (Figure 99) in extensive beds where there was regular inundation and high flooding until May or early June, hence causing a setback to competing vegetation. They attributed the success of these species in these conditions to the flooding, life strategy, and soil characteristics. The large spores and tubers permitted these species to remain in the diaspore bank, whereas the rapid development of an extensive protonemal mat following the recession of flood waters gave them an establishment advantage. Their short life cycle permitted them to form plants in late summer and complete the life cycle to spore production in autumn.



Figure 98. *Ephemerum cohaerens* with perigonia. Photo by Dick Haaksma, with permission.



Figure 99. *Ephemerum serratum* with capsules. Photo by David T. Holyoak, with permission.

Arable fields are a man-made habitat that favors certain bryophyte species. This can be a suitable habitat for some members of the **Anthocerotophyta**, but changes in agricultural practices can make the habitat unsuitable. Following years of hornwort-unfriendly agricultural practices, new eco-friendly practices returned in some areas of Europe. Bisang *et al.* (2009) compared the presence of this hornwort group before and after the eco-friendly practices were established in the Swiss plateau and found the return of *Anthoceros agrestis* (Figure 100) and *Phaeoceros carolinianus* (Figure 101-Figure 102). The re-establishment of these two species apparently resulted from spores that remained persistent in diaspore banks through the many years of unfavorable conditions.

Other disturbed habitat colonizers, like *Marchantia* (Figure 103), are frequent in the diaspore rain (Gaur & Kala 1984; Ross-Davis & Frego 2004) and arrive almost continuously, ready to take advantage of the low competition. *Marchantia polymorpha* is one of the colonizers after a forest fire (Graff 1936). In their experiments on buried propagules in an old-growth forest, Ingersoll and Wilson (1990) found that most (88%) of the gametophores emerging were from vegetative sprouts. There were significantly more vegetative sprouts in the undisturbed treatments. The number of emergents responded inversely to an increase in disturbance, with exposure to sun causing a significant decline in the six most abundant species. Vegetative structures with shallow burial were lost in the fire treatment.



Figure 100. *Anthoceros agrestis* with splitting sporophytes exposing spores. Photo by Michael Lüth, with permission.





Figure 101. *Phaeoceros carolinianus* on disturbed soil. Photo by Michael Lüth, with permission.

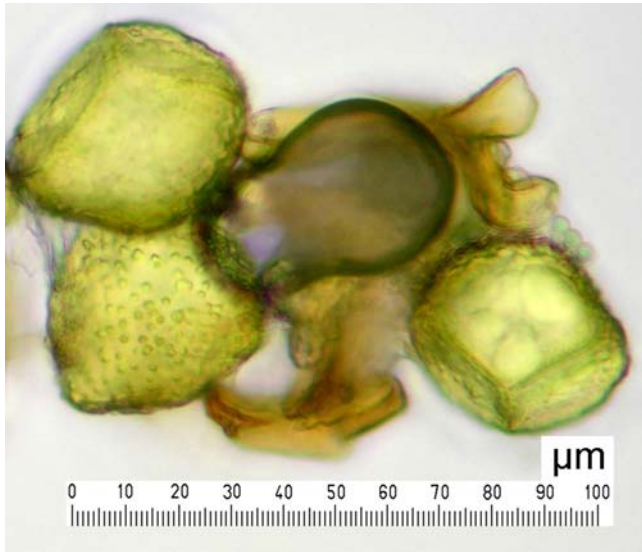


Figure 102. *Phaeoceros carolinianus* spores. Photo by David Wagner, with permission.

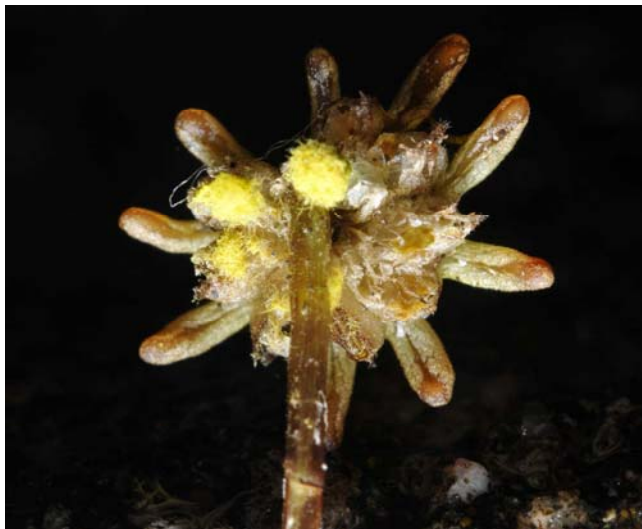


Figure 103. *Marchantia polymorpha* archegonial head showing spores and elaters. Photo by George Shepherd, through Creative Commons.

Unfortunately, our methods of determining what is in either diaspore banks or diaspore rain requires culturing, and this method is both time-consuming and incomplete, permitting us to identify the species if growth to a gametophore is successful, but often not permitting us to

identify the dispersal structure that produced it. And we might not provide the right conditions for its successful development.

### Epiphytes

Löbel and Rydin (2009) found that in epiphytic bryophytes, the conditions in the habitat influenced the production of sporophytes, but not that of asexual propagules. Furthermore, development of sporophytes had a negative effect on growth, whereas presence of asexual propagules did not. Further detriments to the sexual strategy arise from the need to reach a certain colony size before reproduction is effective; there is no threshold for the asexual reproduction. Thus, two sets of trade-offs arise: dispersal distance vs reproductive age and dispersal distance vs sensitivity to habitat quality. They considered that habitat turnover and connectivity may be more important selection pressures than species interactions.

The genus *Radula* (Figure 104), a leafy liverwort in which both monoicous and dioicous taxa exist, demonstrates a specific case for the advantages of asexual reproduction. In this genus that lives in a frequently dry environment, there was no correlation with either dioicy or epiphytism (Devos *et al.* 2011). Rather, there seems to have been a shift from sexual systems (dioicy to monoicy) among the facultative epiphytic taxa several times. Both facultative and obligate epiphytes in this genus produce gemmae equally, as well as dispersing gametophyte fragments. These asexual propagules may provide a pre-adaptive mechanism that permits the facultative epiphyte taxa to live on trees where frequent wetting and drying out are detrimental to the development of protonemata into buds and gametophores. Fragments and asexual propagules can skip this stage or use it only briefly before developing into a leafy plant. Devos *et al.* suggest that the larger size of these diaspores imposes a tradeoff by limiting dispersal distance.



Figure 104. *Radula lindenberghiana* with gemmae. Photo by Jan-Peter Frahm, with permission.

### Peatlands

Peatlands are unique habitats, and they seem to do lots of things differently. Poschlod (1995) examined the relative importance of spores and fragments in the recolonization of milled peatlands in the Bavarian foothills of the Alps. He found that spores were relatively unimportant in the diaspore rain, but that fragments did



appear in the spore traps. In particular, branches and leaves of *Sphagnum magellanicum* (Figure 55), *S. capillifolium* (Figure 47), and *Polytrichum strictum* (Figure 45) were captured in the traps in most of the study sites. Furthermore, diaspore bank samples were placed in pots and cultivated for more than one year. In these pots, only three species germinated and grew: *Betula* (birch tree), *Marchantia polymorpha* (Figure 103), and *Funaria hygrometrica* (Figure 178).

### The Antarctic

Harsh environments impose different selection pressures from the ones at play in more friendly environments. Lewis Smith and Convey (2002) offered evidence to refute the long-held hypothesis that bryophyte fertility decreases as latitude (and climate severity) increases. Using the maritime Antarctic (68-72° S lat) as an example, they demonstrated that a relatively high proportion of the bryophytes there were capable of producing sporophytes. At Marguerite Bay, 43% of the species (17 species of mosses, 2 of liverworts) were known to produce sporophytes; at Alexander Island it was 47% (16 species of mosses, 1 of liverworts). In more arid parts of the Antarctic continent, the number was less (33%). This is still considerably smaller than that found by González-Mancebo and Hernández-García (1996) for an altitudinal gradient in the Canary Islands, where most life cycle strategies had 70% fertility, with that of the perennial stayers being lower.

Not surprisingly, Lewis Smith and Convey (2002) found that most of the Antarctic fertile mosses in their study areas were short, monoicous acrocarpous species. For dioicous species, the problem arises of having both genders arrive on the island in sufficient proximity and having both mature at the same time under a different set of temperatures, day length, and moisture regime than at their source.

In this harsh Antarctic environment, spores were more abundant than bryophyte fragments in the Rotorod® samplers of Signy Island (Marshall & Convey 1997). Spore size did not seem to matter, with all five taxa occurring in samples 0.5-1 km from their nearest known sources. Nevertheless, the presence of spores was small compared to their represented ground cover and in comparison to the lichen propagules in the same samples. This extensive ground cover most likely resulted from vegetative spread after spore arrival.

### Plasticity of Spore Size

Habitat may matter as well in determination of successful spore size and means of reproduction within a species. Hassel and Söderström (2003) compared the spread of *Pogonatum dentatum* (Figure 105) in the mountains vs lowlands in Fennoscandia. The lowland plants seem to have a tendency to produce more but smaller spores (statistically non-significant) compared to the mountain plants. Nevertheless, establishment in the mountains seems rarely to occur from either spores or leaves whereas these two methods are frequent in the lowland. On the other hand, the diaspore bank is more important in the mountains because of the more regular and shorter disturbance intervals there. The diaspores of *P.*

*dentatum* are apparently too short-lived to survive the longer disturbance intervals in the lowlands.



Figure 105. *Pogonatum dentatum*. Photo by Jan-Peter Frahm, with permission.

### Seasons

In a study of airborne pollen and spores in Buenos Aires, Noetinger *et al.* (1994) noted that while spores are scarce throughout the year, they are mainly represented by the bryophytes, with the greatest densities in May to June. For seed plants, pollen density was dependent on phenology of the species, and densities corresponded with blooming seasons of the various groups. Latorre *et al.* (2008), in Mar del Plata city, Argentina, found an increase in pollen with an increase in temperature, reaching a maximum in early spring. Data differed among the trap types, with a negative correlation with wind using the Burkard trap and negative correlation with humidity using the Tauber trap. Data supporting such correlations with phenology and weather for bryophytes are meager. And some bryophytes retain their capsules for more than one year.

Marshall and Convey (1997) were surprised to find that spores were captured over a long time period on Signy Island in the Antarctic, including captures in the winter months. With availability of bare substrate, it is possible that spores could be redistributed from non-trapping surfaces throughout the year. Just what is going on during the seasons when most of us are not looking?

For *Polytrichastrum ohioense* (Figure 106) in the subalpine zone of the Yatsugatake Mountains, Central Honshu, Japan, capsules endure the winter in an immature stage, taking 13 months to mature and dispersing their spores in the following mid-July to mid-August (Ayukawa *et al.* 2002). In *Racomitrium africanum* (Figure 107), *Fissidens weirii* (as *Fissidens glauculus*), *Thuidium gratum*, and *Stereophyllum* sp. (Figure 108) in southwest Nigeria, sporophytes develop and mature at the end of the same rainy season (Oct/Nov & Dec) as that for fertilization (beginning of rainy season) (Odu 1981). Spores from mature capsules of these species all dispersed during and after the dry season (Nov-Apr).



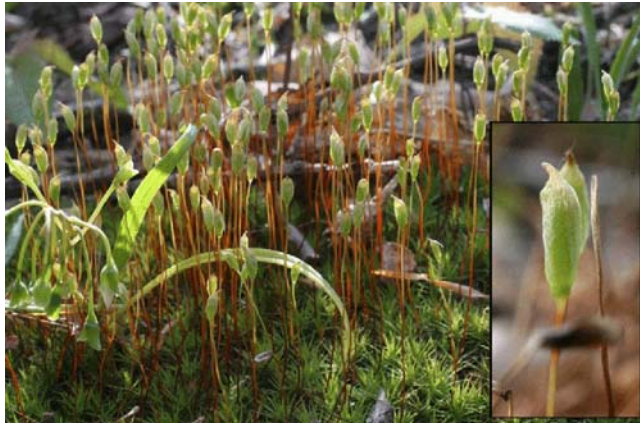


Figure 106. *Polytrichastrum ohioense* with capsules that take more than one year to mature. Photos by Bob Klips, with permission.



Figure 107. *Racopilum africanum* with developing sporophytes. Photo by Jan-Peter Frahm, with permission.



Figure 108. *Stereophyllum radiculosum* on bark. Photo by Scott Zona, through Creative Commons.

For *Archidium ohioense* (Figure 109), *Bryum coronatum* (Figure 93), *Fissidens minutifolius*, and *Trachycarpidium tisserantii*, also in southwest Nigeria, capsule dehiscence and spore dispersal occurred in September – October (Makinde & Odu 1994). But in this case, the stages of sporophyte development occurred during the rainy season, including capsule dehiscence and falling

of the capsules themselves. Not surprisingly, they found that the spores did not discharge easily from the cleistocarpous capsules of *A. ohioense* or *T. tisserantii*. In the Hiruzen Highlands of Japan, Nishimura (1993) found that dispersal dates for 34 species of mosses occurred in late autumn (late November) to early spring (early April); 12 occurred in late spring to summer (May to August) and 5 in autumn (September to November). One had no definite season and one had two dispersal seasons. In these examples, it appears that the season of dispersal is not random, but that conditions needed for one species may not be suitable for another. It is easy to understand that most small spores will benefit from dispersal when it is dry, permitting them to be carried by wind and air currents to new locations. For those with large spores that fall to the ground, a rainy season is beneficial for immediate germination and growth.



Figure 109. *Archidium ohioense* with capsules. Photo by Li Zhang, with permission.

Time of day matters and may help us to unravel the conditions favoring dispersal. For pollen, Pérez *et al.* (2003) found a maximum between 10:00 and 12:00 h, with a minimum at 18:00 h in Mar del Plata, Argentina. They suggested that optimal diurnal conditions for dispersal of arboreal pollen are high temperatures and low relative humidity. It is likely that this relationship could be applied on an annual scale and that it would also apply to bryophyte spores.

One seasonal advantage of asexual propagules is that they are generally produced throughout the growing season, whereas spores tend to be released during a limited time each year (During 2001).

## Are These Adaptations?

### Capsules and Setae

Setae develop first in **Bryophyta** and last in **Marchantiophyta** relative to the capsule. In either case, the elongated seta extends the spores farther above the plant (Figure 110), increasing the chances for them to be dispersed. Even in the **Anthocerotophyta**, where there are no setae, the elongate sporophyte matures from top down and dispels its spores from the top (Figure 100). Hence, we



might expect some differences in the length of the setae, with longer setae permitting spores to get farther from the parent bryophyte, and perhaps even hornwort sporophyte lengths, relative to dispersal needs. These may or may not correlate with characters of the capsule itself.



Figure 110. *Pohlia nutans* with nodding capsules and long setae. Photo by Michael Lüth, with permission.

We can list a number of differences among capsules that might contribute to their dispersal ability. Paramount among these is the means by which the capsule opens and dispels the spores. These will be discussed in some detail in the ensuing paragraphs, but one we might consider first is the drying of the capsule interior prior to spore expulsion. This process and its importance seem to lack experimentation except in *Sphagnum* (Figure 47-Figure 52), so some speculation is in order. Chater *et al.* (2011) have cited the regulation of stomatal behavior in photosynthetic organisms for 400 million years of evolution. Its role in leaves of tracheophytes is clear, but in bryophytes the sporophyte tissue is not in a leaf, and it is the sporophyte capsule that has the stomata (Renzaglia *et al.* 2000). However, it appears that as in the leaf, this tissue controls (perhaps permits is more appropriate) the loss of water. Recent evidence proposed by Duckett *et al.* (2010) suggest that we should consider the possible role of stomata in permitting the escape of moisture from the capsules of other mosses (Figure 111). Such drying leads to changes in capsule shapes and can contribute to the loss of the operculum, sometimes quite forcibly. This aspect of dispersal will be discussed in detail in another subchapter (4-9), but it may be helpful to keep this potential role in mind here as we examine dispersal strategies.

### Habitat Differences

Spore capsules in mosses (but not in liverworts) seem to differ considerably among species, and many of these seem to fall into habitat categories. As Vitt (1981) points out, the function of the sporophyte is to produce and disperse the spores as efficiently as possible. In this role, selection pressures should shape the sporophyte into the most effective organ for its growing conditions. These selective pressures differ significantly among the major habitat classifications of hygrophytic, mesophytic, and xerophytic.

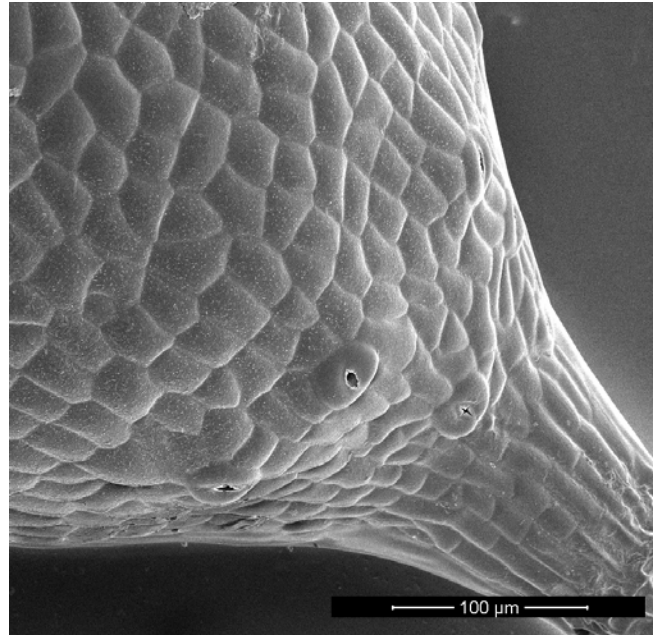


Figure 111. SEM of *Physcomitrella patens* stomata at base of capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

**Xerophytes** may be characterized by reduction of the sporophyte, including shorter seta length, broader and erect capsules, reduced or absent peristome including cleistocarpy, and large spores (Vitt 1981). These characters are often accompanied by a shortened life cycle that permits the xerophytes to avoid extended dry periods. As evidence, Vitt points out that this same group of adaptations has evolved in a number of unrelated mosses, including the acrocarpous genera *Bryobartramia*, *Viridivellus*, *Sporledera* (Figure 112), *Goniomitrium* (Figure 113), and pleurocarpous genus *Gigaspermum* (Figure 114). Others, including *Encalypta brevipes* (Figure 115), *Ditrichum* spp. (Figure 116), *Funaria* spp. (Figure 117), *Pottia* (Figure 118), *Stegonia* (Figure 119), *Trematodon* (Figure 120), and *Weissia* (Figure 121), lack the reduced life cycle but exhibit the other xerophytic adaptations.



Figure 112. *Cleistocarpidium palustre* (= *Sporledera palustris*) showing broad capsules. Photo by Jan-Peter Frahm, with permission.





Figure 113. *Goniomitrium acuminatum* subsp. *enerve*, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 114. *Gigaspermum repens*, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 116. *Ditrichum subulatum*, a species with an expanded capsule urn relative to others in the genus. Photo by Des Callaghan, with permission.



Figure 115. *Encalypta brevipes* Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.



Figure 117. *Funaria pulchella* showing expanded capsule urn. Photo by Michael Lüth, with permission.





Figure 118. *Pottia conica*, showing capsules with expanded urn. Photo by Jan-Peter Frahm, with permission.



Figure 119. *Stegonia latifolia* with slightly rounded capsules. Photo by Michael Lüth, with permission.



Figure 120. *Trematodon longicollis*, a moss of disturbed banks. Note the long neck and expanded urn. Photo by Li Zhang, with permission.



Figure 121. *Weissia controversa* var. *densifolia* showing swollen urn. Photo by Barry Stewart, with permission.

Mesophytic taxa, on the other hand, can have amplified capsules, as in the entomophilous members of the **Splachnaceae** (Vitt 1981; Figure 199). Vitt lists other taxa exhibiting sporophytic amplification are some **Dicranaceae** (as polysety; Figure 122), **Mniaceae** (Figure 124), **Hypnodendraceae** (Figure 123), and **Dawsonia** [amplified peristome (Figure 126) compared to other **Polytrichaceae** (Figure 89)]. The mesophytic group, not faced with the extremes of habitat, has taken multiple routes that preclude a clear definition of adaptations. Vitt (1979, 1981) included elongate, straight setae; curved, horizontal to pendent capsules that are smooth, cylindric, and have well-developed peristomes as common characters of mesic forest floor mosses. Example taxa include *Plagiomnium cuspidatum* (Figure 124) and *Timmia megapolitana* (Figure 127).



Figure 122. *Dicranum polysetum* with polysetous capsules. Photo by Janice Glime.





Figure 123. *Hypnodendron commutatum* showing the large capsule. Photo by Janice Glime.



Figure 125. *Cladomnion ericoides* from Pureora Forest, Taupo, NZ. Photo by Andy Hodgson, with permission.

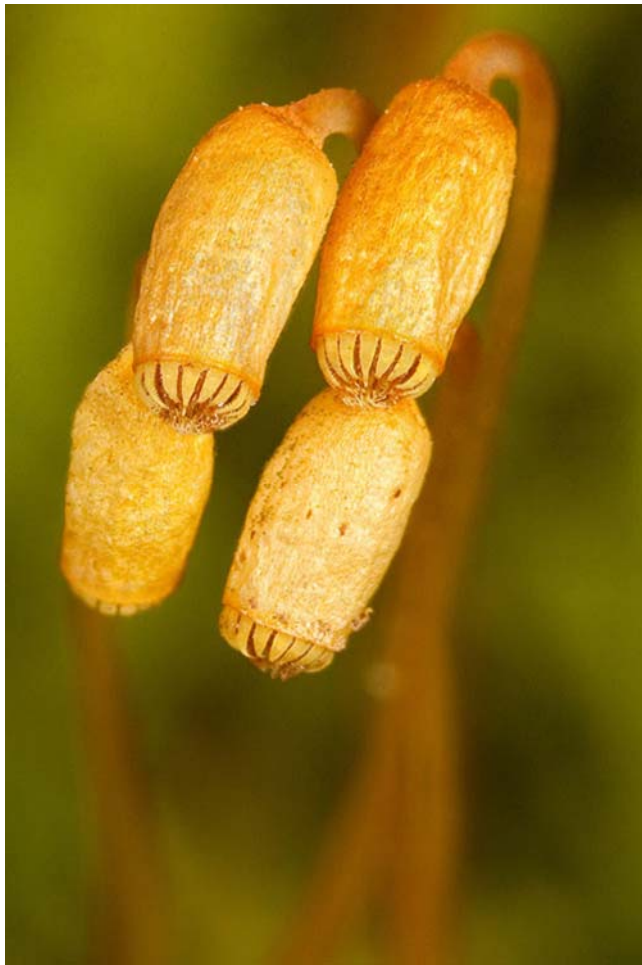


Figure 124. *Plagiomnium cuspidatum* illustrating the straight setae with smooth, cylindric, pendent capsules and well developed peristomes. Photo by Robert Klips, with permission.



Figure 126. *Dawsonia longifolia* capsule showing enlarged teeth. Photo from University of British Columbia Botany website, with permission.



Figure 127. *Timmia megapolitana*. Photo by Jessica M. Budke, with permission.

Epiphytes usually have xerophytic adaptations, but these differ from those of the edaphic species because dispersal is a different problem for these elevated taxa. *Cladomnion ericoides* (Figure 125) provides a good example of epiphytic adaptations with its short, stout setae (permitting leaves and perichaetial leaves to protect the capsule from desiccation); erect, ribbed, ovate-oblong capsules; and sheathing perichaetial leaves (Vitt 1981).

Many epiphytic members of the **Isobryales** share similar features with other bryophytes of vertical surfaces: *Haplohymenium* (Figure 128), *Andreaea* (Figure 129), *Fabronia* (Figure 130), *Grimmia* (Figure 197), *Tortula* (Figure 131), *Hedwigia* (Figure 132), *Orthotrichum* (Figure 133-Figure 135), *Ptychomitrium* (Figure 136), *Racomitrium s.l.* spp. (Figure 137), and *Tortella* (Figure 76), presumably adapting them to vertical substrates where humidity alternates between dry and wet periods and light intensity is higher (Vitt 1981). These habitat characteristics seem to favor the short, erect, ribbed capsules; short, stout



setae; reduced peristomes; and sheathing perichaetial leaves. Epiphytic *Orthotrichum*, on the other hand, seems to have evolved from ribbed [e.g. mesophytic *O. lyellii* (Figure 133) or *O. vittii* (Figure 134)] to smooth [e.g. xerophytic *O. pusillum* (Figure 135)] capsules (Vitt 1981).



Figure 128. *Haplohymenium triste* with lichens on bark. Photo by Bob Klips, with permission.



Figure 129. *Andreaea rothii* subsp. *falcata* showing valvate cylindric capsule. Photo by Barry Stewart, with permission.



Figure 130. *Fabronia ciliaris* with ovate capsules and short setae. Photo by Michael Lüth, with permission.



Figure 131. *Tortula canescens* capsules showing cylindrical shape and extended spiral peristome. Photo by Des Callaghan, with permission.



Figure 132. *Hedwigia ciliata* with short capsules on short setae and surrounded by perichaetial leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.





Figure 133. *Orthotrichum lyellii* with gemmae. Photo by Jonathan Sleath, with permission.



Figure 136. *Ptychomitrium polyphyllum* showing short seta and cylindrical capsule. Photo by Malcolm Storey at Discover Life, through Creative Commons.



Figure 134. *Orthotrichum vittii* showing ribs on capsule. Photo by Jan-Peter Frahm, with permission.



Figure 137. *Bucklandiella affinis* (= *Racomitrium affine*) with cylindric capsules, reduced peristome, and short setae. Photo by Michael Lüth, with permission.



Figure 135. *Orthotrichum pusillum* capsules. Note the nearly smooth (non-ribbed) surface of these capsules. Photo by Bob Klips, with permission.

Vitt (1981) considers two groups of mosses with submerged or emergent habits. Those with aquatic gametophytes and terrestrial sporophytes, often produced at times of low water levels, include, for example, *Scorpidium* (Figure 138), *Hygrohypnum* (Figure 139), *Platylomella* (as *Sciaromium*; Figure 140), *Drepanocladus* s.l. (Figure 142), and *Platyhypnidium riparioides* (Figure 141). These taxa have sporophytes that align with mesophytic bryophytes from the forest floor. On the other hand, the aquatic mosses with aquatic sporophytes [e.g. *Blindia* (Figure 143), *Fontinalis* (Figure 144), *Wardia* (Figure 145), *Scouleria* (Figure 146)] tend to have reduced or absent peristomes; ovate or oblong, smooth, immersed capsules; enlarged perichaetial leaves; and thick or leathery **exothecial** (outer capsule wall) cells.



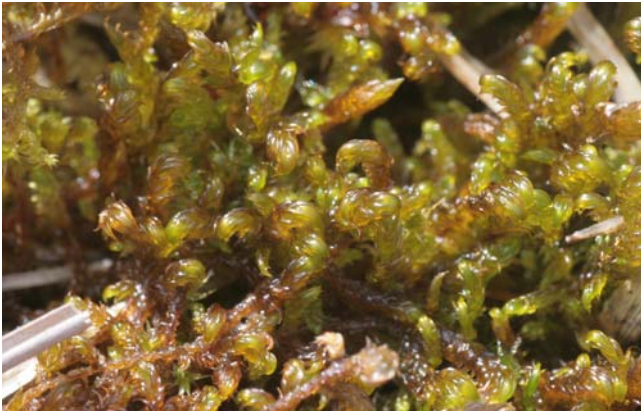


Figure 138. *Scorpidium cossonii*. Photo by Hermann Schachner, through Creative Commons.



Figure 139. *Hygrohypnum luridum* with emergent capsules. Photo by Michael Lüth, with permission.



Figure 140. *Platylomella lescurii*, a species that produces capsules at low water levels. Photo by Blanka Shaw, with permission.



Figure 141. *Platyhypnidium riparioides* showing emergent capsules. Photo by Andrew Hodgson, with permission.



Figure 142. *Warnstorfia* (previously *Drepanocladus*) *fluitans* with capsules. Photo by Biopix, through Creative Commons.

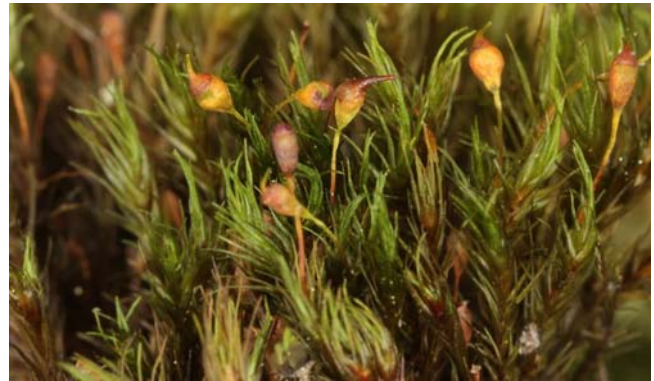


Figure 143. *Blindia acuta* showing ovate capsules common among submersed species. Photo by Jan-Peter Frahm, with permission.



Figure 144. *Fontinalis squamosa*, member of a genus that produces submersed, ovate, thick-walled capsules that have short stalks and enlarged perichaetial leaves. Photo by David Holyoak, with permission.





Figure 145. *Wardia hygrometrica* from the southwest Cape of Africa, showing oblong capsules typical of submersed species. Photo by Des Callaghan, with permission.



Figure 146. *Scouleria aquatica* with a submersed capsule typical of aquatic species. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.

### Anisospory

Mogensen (1981) points out that having **anisospory** (unequal spore sizes, in this case) creates different dispersal potential between males (small spores) and females (large spores). One would presume that small spores will disperse farther, hence making it more likely that males establish as single-sex populations in distant places. It also seems that there is an advantage in the production of dwarf males from these anisosporous male spores because some

of these will germinate on a female and thereby be close enough to accomplish fertilization. There is no equivalent advantage for the female spores to land on another member of the species because these are never known to produce dwarf plants that might somehow accomplish fertilization. Rather, in most cases, they will not germinate at all when landing on their own genotype.

### Spores and Spore Walls

Liverworts and mosses differ in the number of layers in the spore wall (Mogensen 1981). Both have **intine** and **exine**. The **intine** (Figure 147) is the inner wall and possesses the aperture that is responsible for the breakup of the spore wall during germination. The **exine** is the outer wall and thus protects the spore from the environment. The **perine** is present only in moss spores and is laid down on the outer surface of the spore. It is not produced by the spore, but rather, the surrounding sporophyte deposits the perine (Figure 148) material on the spore walls. This perine is of taxonomic value and one might assume that it has environmental significance, but little information is available to provide us with such correlations.

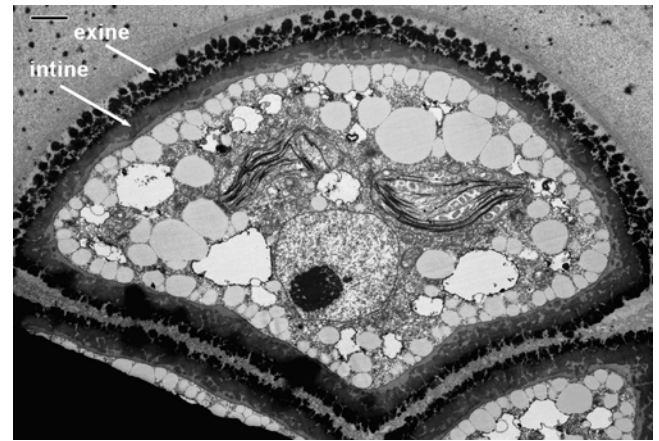


Figure 147. *Andreeaea rothii* TEM of spore. Photo courtesy of Karen Renzaglia.

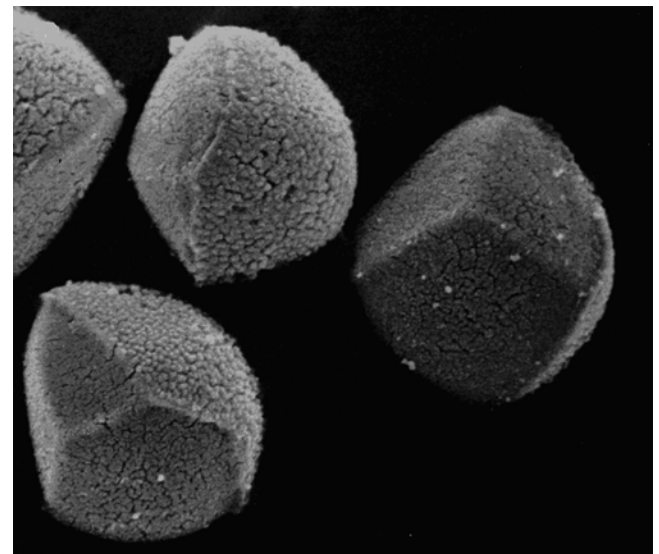


Figure 148. *Andreeaea rothii* spore SEM showing papillae (perine layer) laid down by the sporophyte. Photo courtesy of Karen Renzaglia.



Some speculation is in order so that we can develop hypotheses about this perine layer (Figure 148). This layer causes air to be trapped in spaces around the surface of the spore. So one hypothesis is that the spores trap air that makes them lighter in weight per unit volume, permitting them to float. What are the advantages gained by spaces so small that cohesion of water molecules prevents them from entering those spaces? Does this potential repellence of water prevent inappropriate germination? And what difference does the pattern make? Or could it be that this layer provides a food source for potential dispersal agents that pass the spore through the gut unharmed at some new location or simply carry the spores like ants do seeds with elaiosomes? Does the layer have any food value? Does it make adherence easier for both dispersal and attachment to substrate?

### Liverworts

Bischler and Jovet-Ast (1981) contend that adaptations in liverworts are primarily those of biochemical and biophysical properties of the cell content, hence making them more difficult to assess. Both the gametophyte and sporophyte produce specific **flavonoids** that may protect the developing gametes and spores from UV light (Suire & Asakawa 1980). They likewise synthesize secondary compounds that seem to deter predators and parasites. SEM images provided by William T. Doyle seem to provide evidence that they are also adapted by differences in the sculpturing of the spore wall (Figure 149-Figure 154).

Although liverworts lack a perine layer, spores of many species are not without decoration (Figure 149-Figure 154). Some of the leafy liverworts, e.g. *Frullania chevalieri* (Figure 152), have quite intricate and interesting patterns of papillae; others have deep sculpturing, as in *Fossombronia* (Figure 154).

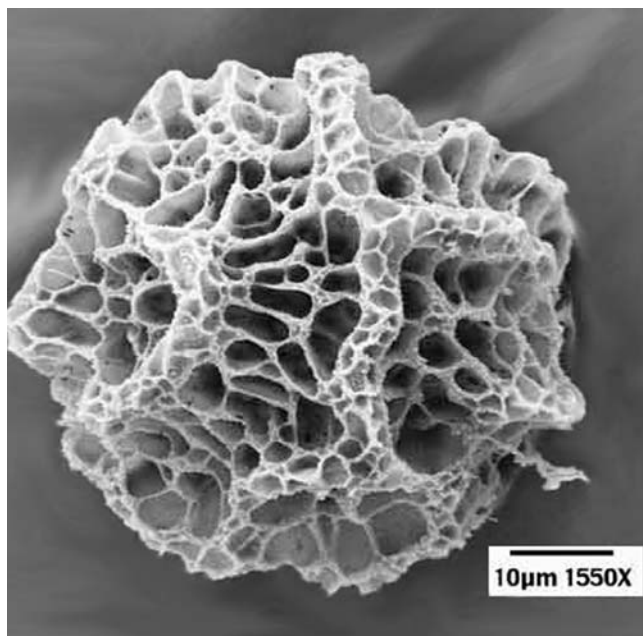


Figure 149. *Targionia hypophylla* distal spore wall SEM. Photo by William T. Doyle, with permission.

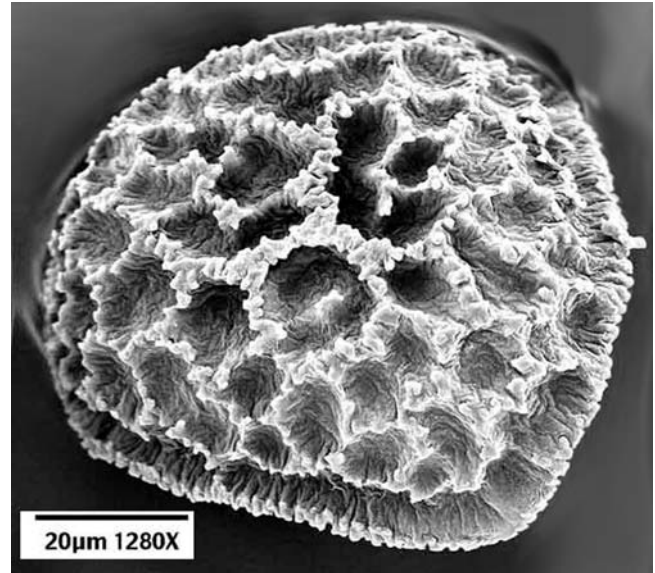


Figure 150. *Riccia cavernosa* distal spore wall SEM. Photo by William T. Doyle, with permission.

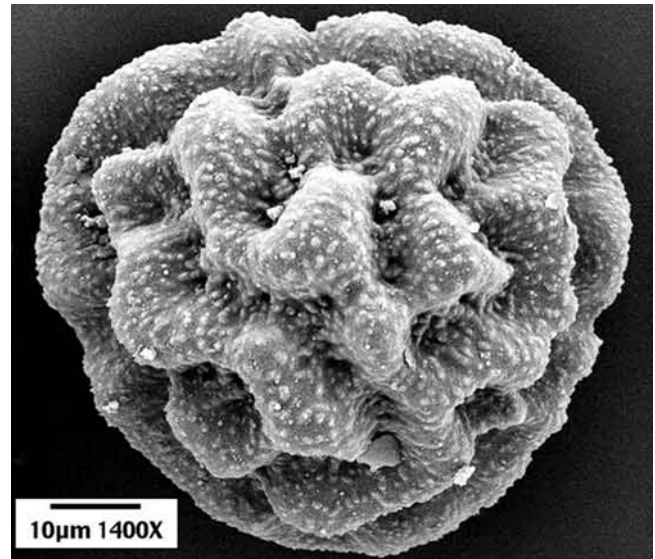


Figure 151. *Mannia californica* distal spore wall SEM. Photo by William T. Doyle, with permission.



Figure 152. *Frullania chevalieri* spore SEM showing the rosettes of papillae. Photo by Matt von Konrat, with permission.



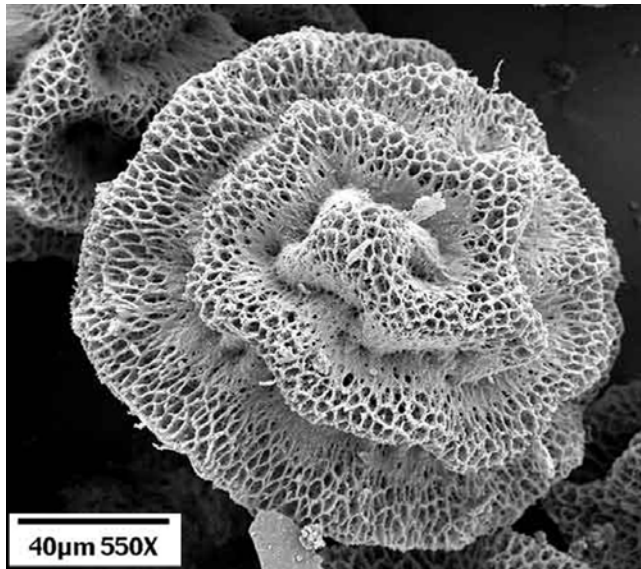


Figure 153. *Asterella californica* distal spore wall SEM. Photo by William T. Doyle, with permission.

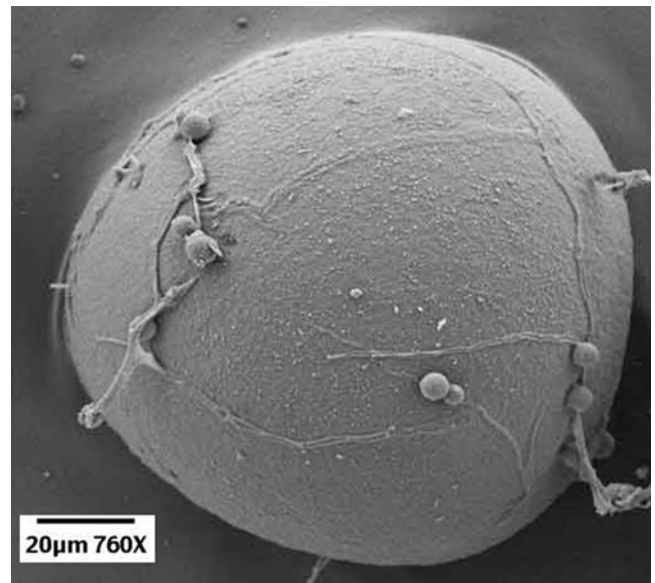


Figure 155. *Geothallus tuberosus* (Sphaerocarpaceae) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't require adherence on their landing surfaces. Photo by William T. Doyle, with permission.

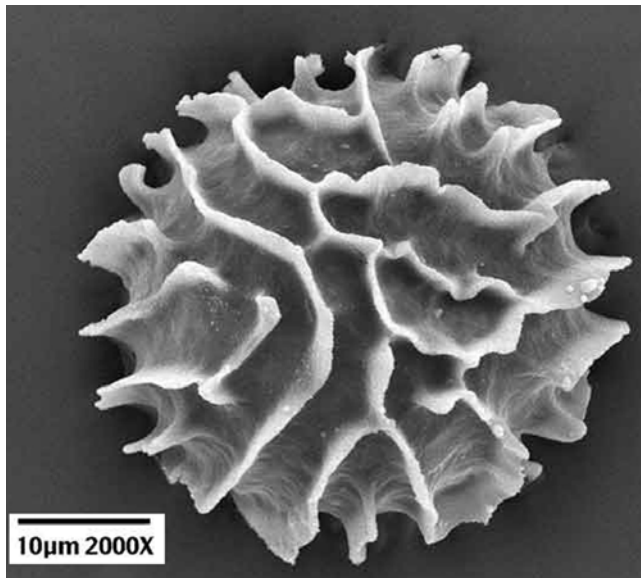


Figure 154. *Fossombronina pusilla* distal spore wall SEM. Photo by William T. Doyle, with permission.

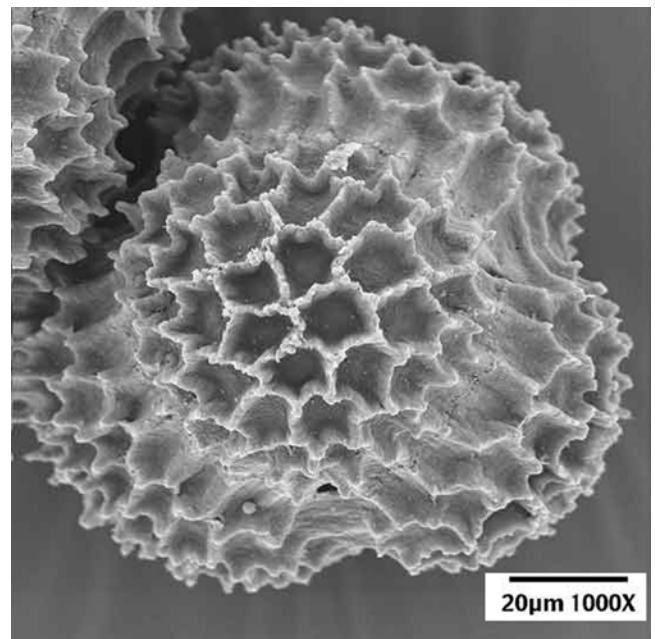


Figure 156. *Sphaerocarpos michelii* distal spore wall SEM. This species lives on damp soil of fallow fields, soils subject to seasonal flooding, and sandy soil of tall-grass prairies. Photo by William T. Doyle, with permission.

But what is the overall indication of these sculpturings? Van Zanten and Gradstein (1988) found no significant difference between the spore sculpturing of transoceanic and endemic Neotropical liverwort species, with both smooth (Figure 155) and finely **verrucose** (covered with warts or wart-like projections) spores (Figure 152) in both groups. On the other hand, they found that there were significantly more strongly verrucose spores among endemic species than among transoceanic species, regardless of size. Furthermore, species with strongly verrucose spores (Figure 156) are typically hygrophytic and terrestrial (a combination for species that live where they are submersed for short periods of time), suggesting to van Zanten and Gradstein that this sculpturing might aid in short-distance dispersal overland by water movements during heavy rainfall. Such a strategy could be useful for *Sphaerocarpos michelii* (Figure 156).

Bischler and Jovet-Ast (1981) attempted to assess reproductive adaptations for the **Marchantiales**. This group is characterized by large spores with an ornamented exine (e.g. *Asterella*; Figure 157). Few species of **Marchantiales** have specialized gemmae [e.g. *Marchantia* (Figure 1), *Lunularia* (Figure 158), *Blasia* (Figure 159) as exceptions], although these are common among leafy liverworts. The sporophyte is imbedded in or surrounded by gametophyte tissue, where it remains until the spores ripen. For many of the taxa, an archegoniophore is produced, hence raising the ensuing sporophyte above the thallus.



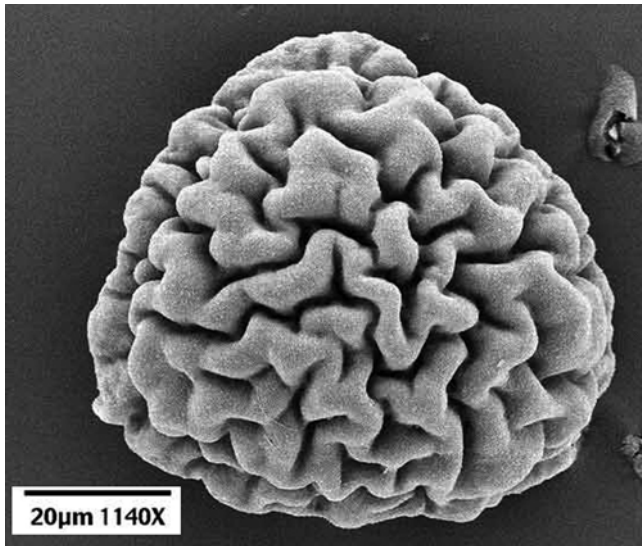


Figure 157. *Asterella palmeri* distal spore wall SEM, illustrating the highly decorated exine and large size. Photo by William T. Doyle, with permission.



Figure 158. *Lunularia cruciata* showing gemmae. Photo by Martin Hutten, with permission.

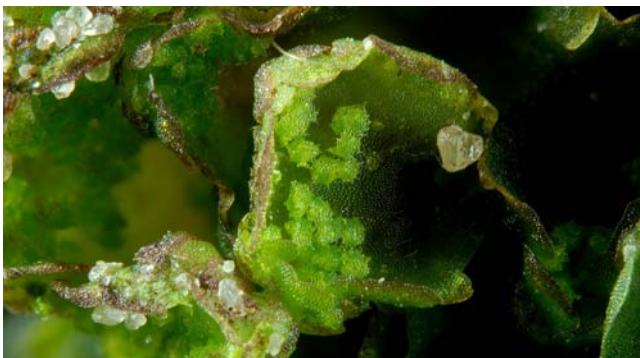


Figure 159. *Blasia pusilla* gemmae on the thallus surface. Photo by Dick Haaksma, with permission.

Elaters occur among the spores of both **Jungermanniales** and **Marchantiales**. These elongate structures twist in response to moisture changes and help in the dispersal in many of the taxa – or do they hinder it by entangling the spores (Figure 160) and forcing them to be dispersed as a mass? Little is known about the role of these elaters in dispersal – perhaps their primary role is in maintaining moisture in the capsule during spore development.

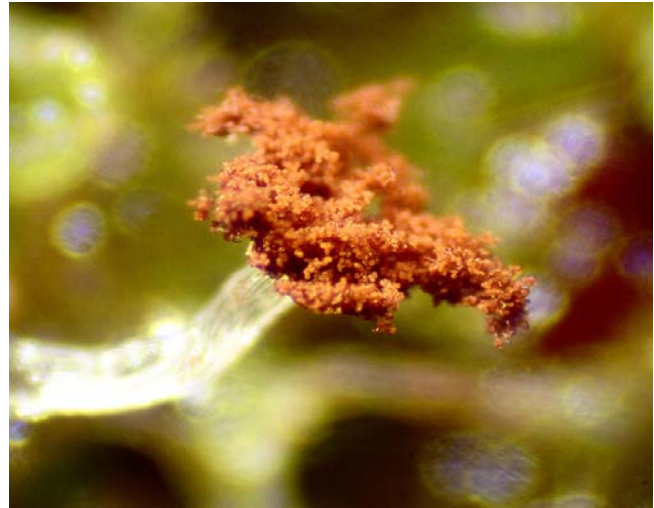


Figure 160. Open capsule of *Jungermannia* sp. showing spores and entangling elaters. Photo by George Shepherd, through Creative Commons.

### Monoicous vs Dioicous

One interesting result of the study by van Zanten and Gradstein (1988) is that among the Neotropical liverworts they considered, monoicy vs dioicy made a difference in dispersal. Gradstein (1985) found that 57% of the endemic **Lejeuneaceae** (Figure 161-Figure 162) are monoicous. In the **Jubulaceae** (Figure 163), only one transoceanic species is dioicous. Van Zanten and Gradstein (1988) concluded that if the species had spores larger than 35  $\mu\text{m}$ , then dioicism may create a serious reduction in its long-distance dispersal ability. They reasoned that for small spores there were better chances for transport by air currents, hence providing a greater chance for dioicous species with small spores to arrive near a partner of the opposite sex. To achieve the same opportunity for a partnership in species with larger spores would take a longer time. It is also important to recognize that the only dioicous species to achieve transoceanic dispersal in the Jubulaceae was *Frullania ericoides* (Figure 163), a species that is also the only one with gemmae. On the other hand, all the species in Lejeuneaceae that have gemmae are endemic.



Figure 161. *Cheilolejeunea trifaria* (Lejeuneaceae) from the Neotropics. Note the perianths, with a prominent one in the middle of the image. Photo by Michael Lüth, with permission.





Figure 162. *Cololejeunea cardiocarpa* (Lejeuneaceae) archegonia (left) and antheridia (right). Photo by Paul Davison, with permission.



Figure 163. *Frullania ericoides*, the only transoceanic member of **Jubulaceae** among neotropical liverworts, and the only member of **Jubulaceae** with gemmae there. Photo by Paul Davison, with permission.

### Ecological Adaptations

Not surprisingly, van Zanten and Gradstein (1988) found a positive correlation between Neotropical liverwort species range and xerophytic habitat. They found that correlation mainly related to large spore size. There was no similar relationship for species with small spores. Moreover, they found no relationship between spore drought tolerance and moisture level of the habitat. However, for sporelings there is a significant correlation with the average number of days for survival of desiccation, with 30 days for xerophytes, 25 for mesophytes, and 13 for hygrophytes. This suggestion that successful establishment may be more important than dispersal has appeared in other studies discussed herein.

Van Zanten and Gradstein (1988; Gradstein 2013) found that tropical lowlands have significantly more transoceanic species than at higher elevations. Most of these transoceanic species are members of the Lejeuneaceae and Jubulaceae, families with large, green spores. This requires some explanation since it is easier to get higher elevation species into the airstream, and large green spores suggest a need for immediate germination. But the lowland species are generally more widespread than are montane and alpine species, providing greater availability of these lowland species. Furthermore, this widespread habitat availability is in effect at the receiving

end as well, creating greater opportunity for a "stepping stone" effect in regions where there are oceanic islands with large areas of relatively low elevation.

### Persistent Protonemata

Some bryophytes retain their protonemata even after the leafy gametophores are well developed. These include *Buxbaumia aphylla* (Figure 164), *Discelium nudum* (Figure 165), various *Ephemerum* species (Figure 166-Figure 167), *Fissidens exilis* (Figure 168), *Pogonatum pensilvanicum* (Figure 169), *Schistostega pennata* (Figure 170) (Bob Klips, Bryonet 22 December 2021), *Rhizomnium* (Figure 171), *Tetraphis* (Figure 172) (Wolfgang Hofbauer, Bryonet 22 December 2021), *Diphyscium* (Figure 173) (Rob Gradstein, Bryonet 22 December 2021), *Ephemeropsis* (Figure 174), *Cololejeunea metzgeriopsis*, *Protocephalozia ephemeroides*, *Radula aguirrei*, *R. yanoella*, and *Viridivellus pulchellum* (Gradstein & Wilson 2008). *Fissidens magnicellulatus* from a damp, vertical soil bank in Zambia likewise has persistent protonemata (Bruggeman-Nannenga 2013). *Mittenia* (Figure 175), like *Schistostega*, has persistent protonemata that reflect light when struck by it at right angles (Stone 1961).



Figure 164. *Buxbaumia aphylla* capsules with persistent protonemata. Photo by Janice Glimme.



Figure 165. *Discelium nudum* masses of persistent protonemata. Photo by Andrew Hodgson, with permission.





Figure 166. *Ephemeron recurvifolium* showing capsule and protonemata. Photo by Rayna Natcheva, with permission.



Figure 167. *Ephemeron rutheanum* with attached protonema. Photo by Dick Haaksma, with permission.



Figure 168. *Fissidens exilis* with persistent protonemata. Photo by Jonathan Sleath, with permission.



Figure 169. *Pogonatum pensilvanicum* with protonemata and young sporophyte. Photo by Charlie Davis, through Creative Commons.



Figure 170. *Schistostega pennata* persistent protonema. Photo courtesy of Misha Ignatov.



Figure 171. *Rhizomnium punctatum* with persistent protonemata covering canyon wall, Hocking Hills OH, USA. Photo by Janice Glime.





Figure 172. *Tetraphis pellucida* protonemal flaps on the persistent protonema. Photo from Botany Website, UBC, with permission.



Figure 173. *Diphyscium foliosum*, in a genus with a persistent protonema. Photo by Michael Lüth, with permission.

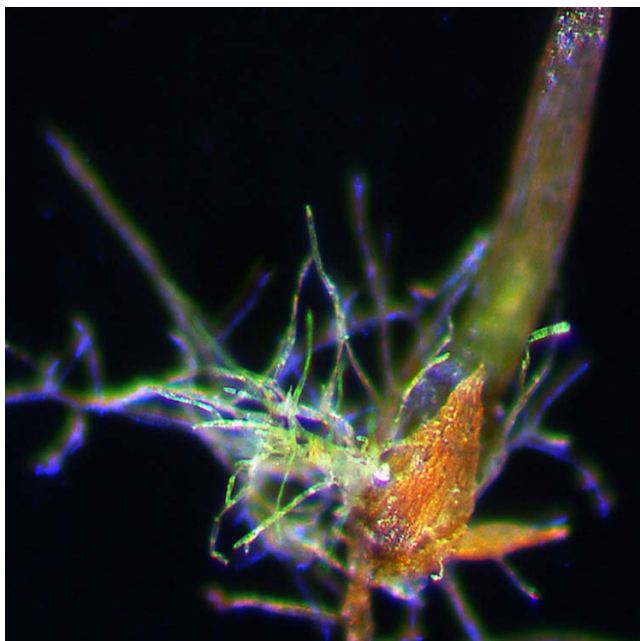


Figure 174. *Ephemeropsis trentepohlioides* leaves and persistent protonema. Photo by Larry Jensen, with permission.

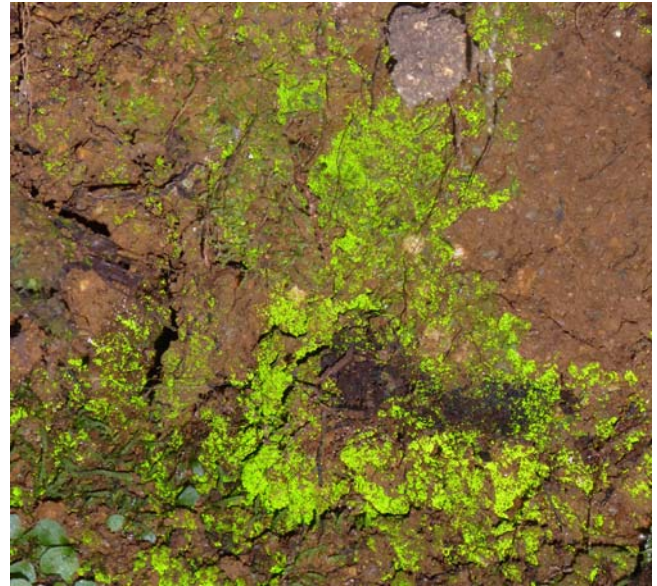


Figure 175. *Mittenia plumula* persistent protonemata. Photo courtesy of David Glenn.

When Furuki and Iwatsuki (1989) described the liverwort *Mizutania* as a new genus, they considered that the gametophyte thallus might actually be a persistent protonema.

*Protocephalozia ephemeroideis* is a liverwort and consists of a mat of numerous branched filaments that give rise to very short, leafy sexual branches; it has been found only once – in 1854 in Venezuela (Gradstein & Wilson 2008). In *Pogonatum* (Figure 169), many species are represented by a mat of protonemata with only scattered leafy plants (Wyatt & Derda 1997). Protonemata in *Ephemerum* (Figure 166-Figure 167) produce long-lived tubers. Pressel *et al.* (2013) suggest that in their lake margin homes in the British Isles, these provide an alternative means of perennating that allows them to survive inundation when it occurs prior to sporophyte production.

In *Rhizomnium punctatum* (Figure 171), the protonemata are the dominant phase in the life cycle and remain persistent when leafy gametophores arise (Duckett & Ligrone 1994). Those produced by spores and those produced from excised leaf bases are the same. They produce gemmae on side branches and then secondary gemmae by proliferation. The gemmae germinate readily and the filaments are strongly adherent to solid objects. The protonemata are the dominant phase in the life cycle.

Stone (1985a) described an unusual persistent protonema in *Archidium thalliferum* in Australia. This protonema is cushion-shaped and thalloid, but composed of short-celled filaments. The thalloid structure has differentiated layers with functions of protection, photosynthesis, and possibly storage. The upper layer of filaments is greyish-white and protects the chlorophyllose tissue beneath it. The middle portion provides dense chlorophyll concentrations with large spaces among the protonemal filaments that would facilitate photosynthesis much like a mesopyll. The basal portion has colorless cells and is rich in oils, possibly serving as a storage organ. The filaments break off easily and could potentially serve as propagules, but their ability to regenerate remains to be demonstrated. The rhizoids produce gemmae and both the



rhizoids and the gemmae store oil. Stone suggested that these and the oil-filled spores might remain viable for years when rainfall was insufficient for successful germination. Upright gametophores may remain buried within the cushion. *Archidium minutissimum*, also in Australia, has persistent protonemata, but these do not form cushions and may be found on the ground or among the leaves (Stone 1985b).

Pursell and Allen (2017) found that the ephemeral *Fissidens exilis* (Figure 168), one of smallest species of *Fissidens* in eastern North America, grows from persistent protonemata on bare, usually disturbed soil. More recently, Kwon *et al.* (2019) found that *Fissidens protonemaecola* similarly produces a persistent protonema. The species occurs on shaded soil in Korea, where it produces small, bud-like shoots scattered on the protonemata. It is also known from China, Japan, and Taiwan.

Duckett and Pressel (2013) reported *Discelium nudum* (Figure 165) as a pioneer on unstable clay banks. It seems to persist or arrive as unicellular, colorless, starch-filled rhizoidal tubers (with up to 20 µm diameter starch grains) *ca* 1 cm below the surface. These diaspores are exposed on new clay surfaces when winter causes leaves of the vegetation to disintegrate. The diaspores are both abundant and germinate rapidly, a reproductive strategy that gives the *Discelium* a competitive advantage. The persistent chloronemata lack gemmae, but their spread is rapid.

The **Ephemeraceae** typically occur in sunny or partly shaded areas on disturbed soil where they face little competition from mosses or larger plants. They appear as patches of green protonematal filaments with occasional tiny leafy gametophores. Their asexual reproduction is mostly by protonemal fragments, but rare thick-walled elongate, swollen protonematal segments may detach and persist on or in the soil.

In *Bryum* (Figure 176) species with persistent protonemata, protonemal gemmae and tubers are in greatest production in winter when sporophytes are still immature (Pressel *et al.* 2007). Protonemal gemmae arise within only weeks, whereas sporophyte formation takes at least a year. The most rapid protonemal production is evident in species in arable fields in autumn, and in these species the gemma production is transient. The persistent protonemata grow in places where leafy gametophores are unable to flourish. Pressel *et al.* suggested that this persistence was due to low irradiance. This behavior is similar to that of *Dicranoweisia cirrata* (Figure 177), wherein the gemmiferous protonemata form in conditions with high nutrients. In *Bryum* species, the spores are packed with lipids and are long-lived, whereas the gemmae are filled with starch and presumed to be short-lived.

Thus it appears that persistent protonemata provide different advantages in different species. Their ability to produce vegetative propagules seems to be common, providing a means of reproduction in habitats where spores might not succeed due to their smaller size and therefore smaller amounts of stored nutrients. But their nutrient strategies seem to differ. In species like *Rhizomnium punctatum* (Figure 171) the rock substrate is low in nutrients, whereas in fallow fields some *Bryum* (Figure 176) species persist as protonemata on a soil substrate rich in nutrients. Some of the persistent protonemata are

present only in one or few species in a genus, whereas others characterize an entire order. Protonemal propagules have received insufficient attention in most bryophyte species, so overall statements as to the adaptive advantages of persistent protonemata with propagules would seem to be premature.

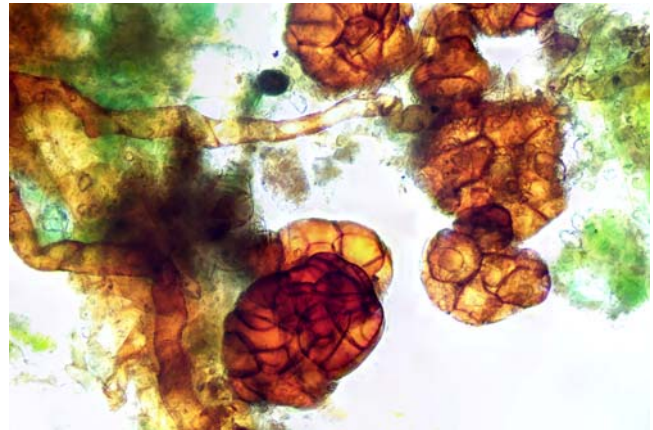


Figure 176. *Bryum klinggraeffii* tubers on the persistent protonemata. Photo by Claire Halpin, with permission.



Figure 177. *Dicranoweisia cirrata*, a species with a persistent protonema. Photo from Biopix, through Creative Commons.

## Who Is Travelling?

We seem to have a reasonable understanding of the algae that we are likely to encounter in diaspore rain, with genera like *Chlamydomonas* and *Chlorella* likely to show up in that translucent glass jar in which you are starting to root a plant. In fact, the water in most such glass jars will turn green before the plant has enough roots to put it in soil due to the arrival and successful colonization of *Chlorella*. But I was surprised to find we scarcely have similar information for bryophytes.

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



Anyone who has watched a disturbed area, peered at the cracks in the sidewalk, or investigated an area after a fire knows that one of the first bryophytes to arrive is often *Funaria hygrometrica* (Figure 178). To add to this list of habitats, this was the first moss to arrive and become established on the volcano Surtsey when it arose from the sea off the coast of Iceland (Schwabe 1974). This moss seemed to benefit from having its protonemata colonized by nitrogen-fixing Cyanobacteria, particularly members of the group *Schizothrix* (Figure 179)/*Plectonema* and members of the *Nostocaceae*, particularly *Anabaena* (Figure 180).



Figure 178. *Funaria hygrometrica* on rocky substrate in southern Europe. Photo by Michael Lüth, with permission.



Figure 179. *Schizothrix lenormandiana*. Photo from Cyanosite as freeware.



Figure 180. *Anabaena* sp., a common symbiont with some bryophytes. Photo by Janice Glime.

One test of the dispersal ability of bryophytes is to compare the spore rain with the extant species in the area. This will indicate those that are able to disperse there, but are unable to become established. This can be further tested by culturing the propagules to see if germination might be successful if different, and hopefully more appropriate, conditions are provided.

Certainly some species are more common in the diaspore rain than others. Leitaó *et al.* (1996) and Santos *et al.* (1996) used agar traps to identify cryptogamic organisms from the atmosphere in Coimbra, Portugal. These included many non-bryophytes, but 75% of those collected were spores <25 µm (Santos *et al.* 1996). In addition to non-bryophytes [Cyanobacteria, Chromophyta (Ochrophyta), Chlorophyta, and Pteridophyta], Santos and coworkers isolated the liverworts *Fossombronia angulosa* (Figure 181-Figure 183) and *Pellia epiphylla* (Figure 184) and the mosses *Leptodictyum riparium* (Figure 185), *Bryum dunense* (Figure 186), *Ditrichum* sp. (Figure 187), *Gymnostomum aeruginosum* (= *G. calcareum*; Figure 188), *Pottia* sp. (Figure 189), and *Trichostomum brachydontium* (Figure 190). *Bryum dunense* forms axillary bulbils and *Leptodictyum riparium* is monoicous and produces abundant capsules.



Figure 181. *Fossombronia angulosa* with capsule, a species of liverwort found in agar traps. Photo by Des Callaghan, with permission.



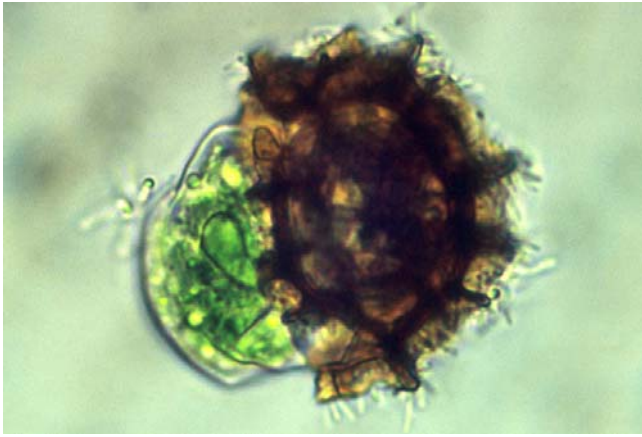


Figure 182. *Fossombronina angulosa* spore germination. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.



Figure 183. *Fossombronina angulosa* protonema. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.



Figure 184. *Pellia epiphylla* with sporophytes. Photo by Hermann Schachner, through Wikimedia Commons.



Figure 185. *Leptodictyum riparium* with capsules. Photo by Michael Lüth, with permission.



Figure 186. *Bryum dunense*, one of the mosses distributing airborne propagules trapped in Coimbra, Portugal. Photo by Jan-Peter Frahm, with permission.



Figure 187. *Ditrichum pallidum* with capsules. Photo by Li Zhang, with permission.





Figure 188. *Gymnostomum aeruginosum* with capsules, a species found in the diaspore rain in Portugal. Photo by Hermann Schachner, through Wikipedia Commons.

and identified spores of *Marchantia* (Figure 103), *Conocephalum* (Figure 191), *Pellia* (Figure 184), and *Metzgeria* (Figure 192) among the predominately fungal spores (65.5%) and flower pollen (23.9%). The liverworts in the spore rain were characteristic of the species growing in the area, so local dispersal could not be ruled out.



Figure 191. *Conocephalum conicum* with archegoniophores. Photo by Janice Glime.



Figure 189. *Tortula modica* (= *Pottia intermedia*) in Europe. Photo by Michael Lüth, with permission.



Figure 192. *Metzgeria decipiens* spores and elaters. Photo by Tom Thekathyl at Blue Tier, with permission.



Figure 190. *Trichostomum brachydontium* showing dry (left) and wet (right). Photos by Michael Lüth, with permission.

Gaur and Kala (1984) tested what is in the spore rain compared to what is growing in the Himalayan alpine zone of India. They used adhesive-coated slides at 3600 m asl

The most comprehensive study seems to be that of Ross-Davis and Frego (2004;

Table 1). They examined the propagule sources of forest floor bryophytes in two mature mixed-wood forests in southeastern New Brunswick, Canada. The bryophyte communities in the two forest locations they studied revealed 36 bryophyte taxa. They found 51 taxa in the diaspore rain and diaspore bank. They furthermore found seasonal differences in the diaspore rain. Of the extant species present, 36% were absent in both the spore rain and the diaspore bank. Both communities were dominated by the feather mosses *Pleurozium schreberi* (Figure 193) and *Hylocomium splendens* (Figure 194), and these two species were present in both the spore rain and the buried diaspore bank. But the dominant taxon in the diaspore bank was *Sphagnum* (Figure 195), which was not present among the extant flora in either location. Up to 22 species from the diaspore bank were able to germinate after a six-hour culture. The aerial diaspore composition was 62% similar between the two locations, whereas the diaspore bank had only 34% similarity.



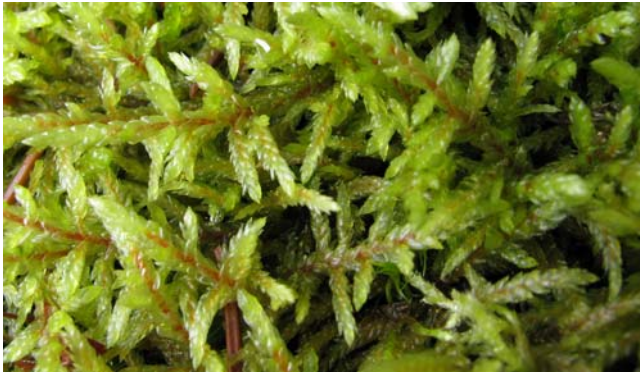


Figure 193. *Pleurozium schreberi*, a species that appears in both diaspore banks and diaspore rain. Photo by Janice Glime.



Figure 194. *Hylocomium splendens* in autumn. Petr Brož, through Creative Commons.



Figure 195. *Sphagnum* protonemata and young plant. Photo by Andras Keszei, with permission.

Table 1. Bryophytes found in diaspore banks and aerial banks in southeastern New Brunswick, Canada. Diaspores were collected in two locations in mixed forest. Species that were in at least one of the diaspore samples at both locations are in **bold**. **DB** indicates buried diaspore bank. **DR** indicates aerial diaspore rain. Based on Ross-Davis & Frego 2004.

<i>Amblystegium serpens</i>	<b>DB</b>	<b>DR</b>	<i>Herzogiella striatella</i>	<b>DR</b>
<i>Atrichum crispum</i>	<b>DB</b>	<b>DR</b>	<i>Hypnum imponens</i>	<b>DR</b>
<i>Atrichum</i> spp.		DR	<i>Hypnum pallescens</i>	<b>DR</b>
<i>Aulacomnium palustre</i>		DR	<i>Hypnum</i> spp.	DR
<b><i>Bazzania trilobata</i></b>	<b>DB</b>	<b>DR</b>	<i>Isopterygiopsis pulchella</i>	DR
<i>Blepharostoma trichophyllum</i>	DB		<i>Leptobryum pyriforme</i>	DB
<i>Brachythecium reflexum</i>	DB		<i>Leptodictyum riparium</i>	DR
<i>Brachythecium starkii</i>	DB	DR	<b><i>Marchantia polymorpha</i></b>	<b>DB</b>
<i>Brachythecium</i> spp.		DR	<i>Mnium stellare</i>	DB
<i>Bryum pallescens</i>		DR	<i>Nowellia curvifolia</i>	DR
<i>Callicladium haldanianum</i>	DB	DR	<i>Philonotis fontana</i>	DB
<i>Campylium hispidulum</i>	DB	DR	<b><i>Platydictya subtilis</i></b>	<b>DR</b>
<b><i>Campylium stellatum</i></b>	<b>DB</b>	<b>DR</b>	<b><i>Platygyrium repens</i></b>	<b>DR</b>
<i>Cephalozia lunulifolia</i>	DB		<b><i>Pleuridium subulatum</i></b>	<b>DR</b>
<b><i>Cephalozia</i> spp.</b>	<b>DB</b>	<b>DR</b>	<b><i>Pleurozium schreberi</i></b>	<b>DB</b>
<i>Cephaloziella</i> spp.		DR	<b><i>Pohlia</i> spp.</b>	<b>DB</b>
<b><i>Ceratodon purpureus</i></b>	<b>DB</b>	<b>DR</b>	<i>Polytrichum commune</i>	DB
<i>Chiloscyphus profundus</i>			<b><i>Polytrichum</i> spp.</b>	<b>DR</b>
(= <i>Lophocolea heterophylla</i> )		DR	<i>Pseudobryum cinclidioides</i>	DB
<i>Dicranella rufescens</i>	DB		<i>Ptilidium pulcherrimum</i>	DB
<i>Dicranum polysetum</i>	DB		<i>Sanionia uncinata</i>	DR
<i>Dicranum scoparium</i>	DB	DR	<b><i>Sphagnum</i> spp.</b>	<b>DB</b>
<i>Ditrichum flexicaule</i>	DB		<i>Syzygiella</i> (=Jamesoniella)	
<i>Frullania oakesiana</i>		DR	<i>autumnalis</i>	DR
<i>Funaria hygrometrica</i>		DR	<i>Thuidium delicatulum</i>	DR
<b><i>Geocalyx graveolens</i></b>	<b>DB</b>	<b>DR</b>		

But these studies are very local and tell us little about what species are most likely to be encountered in the

atmosphere. There are certainly not enough studies to assess the types of characters that seem to contribute to



their presence. May I suggest, then, that the most likely entrants into the aerial realm are those diaspores (mostly spores) that are small, light weight, perhaps have surface waxes or papillae that increase their surface area and buoyancy without adding proportional weight, and have some means of getting away from the capsule and into the air stream, such as the explosive expulsion of spores from a *Sphagnum* capsule (see Chapter 4-9). Research by Sundberg (2012) on *Sphagnum*, discussed in Chapter 4-8 under Everything is Everywhere, supports my last suggestion, but I have little support to offer for my other suggestions. They must also have a means to survive desiccation and protection against UV radiation. Testing these should provide for an interesting set of experiments. But first, we must find out what is in the spore rain around the world. This will be challenging because the concentrations are quite low. For example, Lewis Smith (1991) found no exotic bryophyte spores in the Antarctic air space, yet new volcanic land that was heated became colonized by species not known for more than 1000 km, suggesting that the diaspores are there in the diaspore rain but are too dilute to be sufficiently captured by our sampling methods.

## Spore Dispersal Mechanisms

We might think of spore dispersal as having the same potential mechanisms as pollen dispersal, but some caveats exist. The flowers have carried the variety of dispersal agents to extremes, utilizing birds, bats, a variety of insects, water, gravity, and wind, and to a lesser extent, other mammals and invertebrate animals. To accomplish this great diversity, especially among the animal vectors, the flowers have spent tremendous energy in the production of attracting organs (the flowers themselves) that have colors, shapes, odors, and rewards that beguile their benefactors. Among the bryophytes, such extravagant expenditures of costly energy and biomass are rare, but some do exist (see subchapter 4-8).

For the seed plants, Hughes *et al.* (1994) concluded that plant growth form and stature can exclude certain dispersal modes. Since bryophytes generally are shorter in stature than their tracheophyte counterparts, we could expect all of them to exclude certain types of dispersal such as being eaten by large mammals. But some bryophytes could get around this problem by growing on trees, should any be suitable food for tall mammals. Their growth forms are such that they easily trap spores that pass by them, so the elevation of the capsule on a seta in most species seems necessary to reduce self-entrapment.

The third conclusion of Hughes *et al.* (1994) was that the availability of specific dispersal vectors seems to have no influence on dispersal mode. That conclusion needs some consideration, and dispersal vectors will be discussed in a later subchapter. But the wide range of dispersal vectors available to seed plants seems to have little similarity to the dispersal modes used by or even available to bryophytes in the same habitats, largely due to the small size of both the bryophyte plants and the propagules (Hughes *et al.* 1994).

Finally, Hughes *et al.* (1994) concluded that attributes of the physical environment rarely are important except

indirectly through influencing plant stature and seed size. We have discussed above the meager evidence to support the influence of the physical environment on spore size in bryophytes; for example, it does seem that ephemeral habitats may have placed a selection pressure for larger spores [e.g. Bijlsma *et al.* 2012 for *Ephemerum* spp. (Figure 98)]. Living among other vegetation that can trap the spores, including forest canopies, may prevent them from getting into the air stream. I do wonder if bryophytes that live high on vertical surfaces (Figure 196) may be influenced in their success by the greater opportunity for wind carriage due to greater wind velocity, as shown for seeds by Greene and Johnson (1996). Perhaps there is a relationship to spore size and in some cases to the plant overall structure in such habitats.



Figure 196. *Tortella fragilis* at Khibiny Mountains, Apatity, Murmansk, demonstrating a vertical substrate at a high elevation where it might more easily become windborne. Photo by Michael Lüth, with permission.

## Sporophyte Adaptations for Dispersal

Hedenäs (2001) elevated the role of dispersal in evolution and considered spore dispersal to be one of the two functions causing differences in character state frequencies among various environments. He considered such spore dispersal to be related to **shape** and **orientation of capsules**, **annulus**, **appearance of exostome** and **endostome**, **spore size**, **spore maturation time**, and **seta length**. One might ask if aquatic mosses in general have short or absent setae, as in *Fontinalis* (Figure 144), thus reducing the chance of drag dislodging the capsule before maturity, and do epiphytes truly more commonly have erect capsules?

Stark (2001) compared capsule adaptations of two Mojave Desert species of mosses. They differed both in morphology and in period of distribution. The *Grimmia orbicularis* capsule (Figure 197) is inclined, short, and broad, releasing its spores over about 6 months; its position on nearly vertical rock surfaces permits it to drop the opercula and liberate spores quickly. The ground-dwelling *Syntrichia inermis* (Figure 198) releases its spores from a single cohort of capsules over a period of three years. Dispersal of the operculum and spores is less certain for this soil-dwelling species, and the operculum detachment period can last up to 2.5 years.





Figure 197. *Grimmia orbicularis* from southern Europe, showing the short, broad, inclined capsule and the vertical substrate. Photo by Michael Lüth, with permission.



Figure 198. *Syntrichia inermis* growing on soil. Photo by Jan-Peter Frahm, with permission.

Crawford *et al.* (2009) found an evolutionary relationship between separate sexes and small spores, although this might be backwards since it appears that evolution in mosses tends to go from the dioicous condition to the monoicous one through doubling of the chromosome number (often through the failure of meiosis) or addition of a sex chromosome. Hence, we might consider that large spores are more common in monoicous taxa, a phenomenon that might result from the doubling of chromosome number.

Most bryophyte spores are wind dispersed, carrying many, probably most, to unsuitable habitats, but usually assuring that at least some will not land among their parents. Nevertheless, some bryophytes have evolved ingenious dispersal mechanisms. The simple bryophytes lack the resources to create such large and elaborate structures as flowers, but have, even so, in some cases (*e.g.* *Splachnaceae*, Figure 199) created highly visible and odiferous attractions to their dispersal vectors, as described in Chapter 4-9 of this volume. Nevertheless, most bryophytes seem to rely on wind and gravity as their primary dispersal agents. To this end, **mosses** have developed elaborate **peristome** teeth (Figure 200) that move in response to moisture changes and that tend to facilitate spore dispersal in dry air when the greatest opportunity for wind dispersal prevails (Bonnot 1978). The teeth are covered by an **operculum** (Figure 201) that seals the capsule and that is usually shed in response to drying and shrinkage of the capsule. It appears that this mode is highly successful, and the exceptions to wind dispersal are few.



Figure 199. *Splachnum rubrum* capsules displaying their showy hypophysis that attracts flies. Photo by Michael Lüth, with permission.



Figure 200. *Brachythecium velutinum* capsules showing double peristome. Photo by Dick Haaksma, with permission.



Figure 201. *Brachythecium populeum* capsules showing opercula. Photo by Des Callaghan, with permission.

One of the features of sporophytes that has fascinated my students is the twisting of the seta. When a dehydrated moss with sporophyte intact is hydrated, the seta of many species, *e.g.* *Dicranella heteromalla* (Figure 202), will gyrate in a spiral fashion, loosely coiling and uncoiling as its cells become hydrated, presumably unequally. Unfortunately, I have not observed that this has any effect on spore dispersal and must wonder if it is simply a consequence of the anatomy with no adaptive consequence at all. I am constantly reminded by the bryophytes that "all life has a twist in it."





Figure 202. *Dicranella heteromalla* with capsules and twisted setae that gyrate when the moisture changes. Photo by Biopix, through Creative Commons.

Sundberg (2005) examined capsule size in *Sphagnum* (Figure 203) to determine its possible role in dispersal distance. He tested four species of *Sphagnum* and found that the diameter of the capsule containing the spores was negatively correlated with the proportion of spores remaining in the capsule after dehiscence (5-16%), negatively correlated with those being deposited within the colony (2-14%), and negatively correlated with those being deposited between the colony edge and the outer sampled perimeter of 3.2 m (7-22%). These negative correlations imply that the larger diameter of the capsule somehow facilitates a greater dispersal distance.



Figure 203. *Sphagnum fimbriatum* with capsules that have lost their opercula. Photo by David T. Holyoak, with permission.

Thiers (1988) described morphological adaptations of the dispersal of liverwort propagules in the order **Jungermanniales** to their tropical habitat. These included **precociously** germinating spores (spores that germinate within the capsule; Figure 204-Figure 205), followed by a prolonged protonemal stage, and culminating in a **neotonic** life cycle (reproducing at an early developmental stage).

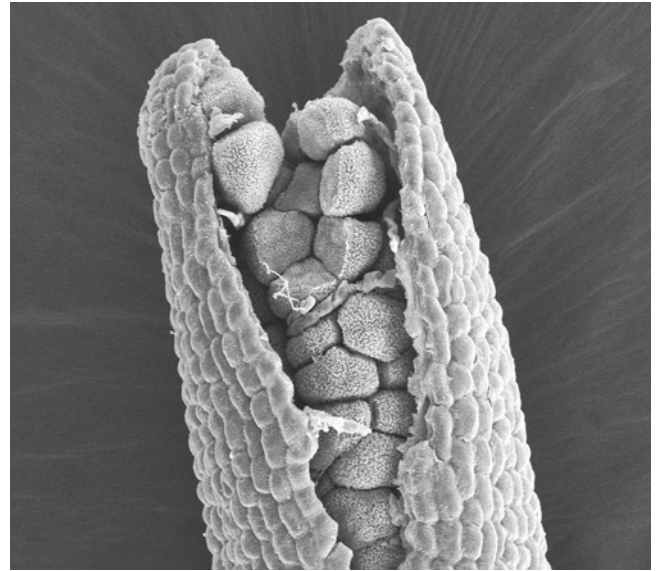


Figure 204. *Dendroceros* multicellular spores in capsule. Photo courtesy of Karen Renzaglia.

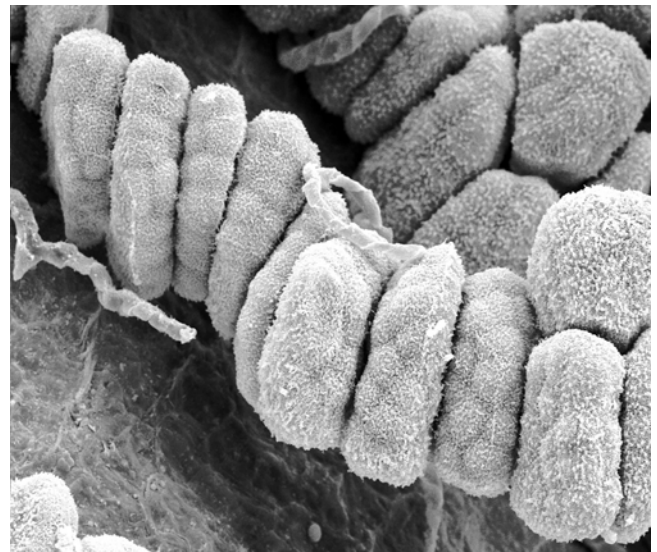


Figure 205. *Dendroceros* sp. (Anthocerotophyta) with stacks of multicellular spores, showing **precocious germination**. Photo courtesy of Karen Renzaglia.

### Role of Peristome

The peristome teeth have various patterns of movement, with some resting inward and others resting outward. The structure of the teeth often causes uneven shrinkage as they dry, causing them to pulsate or even twist. Patterson (1953) described three behavior types for peristome teeth:

1. teeth wherein outer teeth either exclusively or predominately bend inward [*Ceratodon* (Figure 206), *Barbula* (Figure 207), *Pylaisia* s.l. (Figure 208)]
2. teeth with outer teeth shrinking exclusively or predominately bending outward [*Grimmia* (Figure 209), *Orthotrichum* (Figure 210-Figure 211), *Dicranum* (Figure 212)]
3. teeth that oscillate strongly as they change from shrunken to swollen states [*Amblystegium* (Figure 213), *Hypnum* (Figure 214), *Neckera* (Figure 215), *Bryum* (Figure 216)]





Figure 206. *Ceratodon purpureus* peristome, where teeth mostly bend inward. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

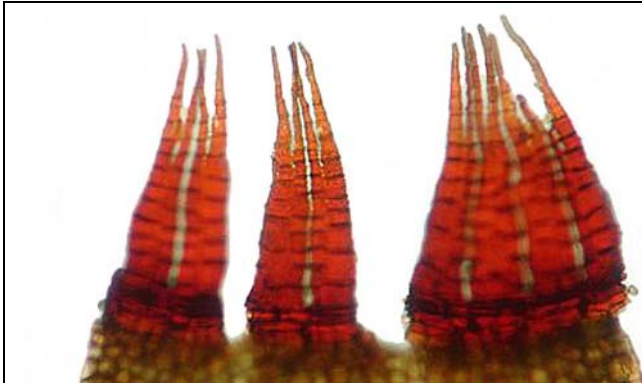


Figure 207. *Barbula amplexifolia* peristome from India, a species whose teeth bend inward. Photo by Michael Lüth, with permission.



Figure 208. *Pylaisiella polyantha* sporophytes showing teeth bending inward. Photo by Des Callaghan, with permission.



Figure 209. *Grimmia ungeri* with capsules showing outward-pointing teeth. Photo by Michael Lüth, with permission.



Figure 210. *Orthotrichum diaphanum* with capsules showing reflexed (outward-bending) teeth. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

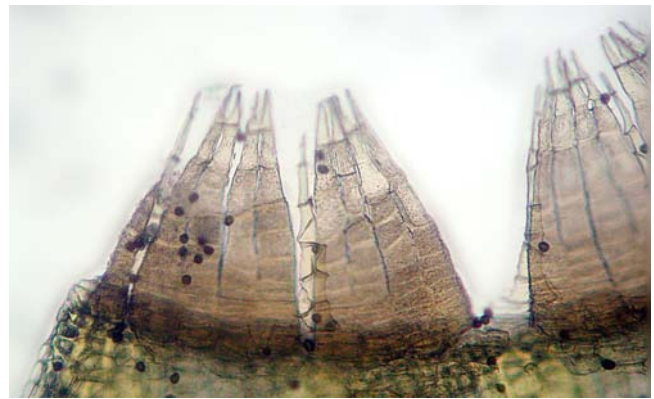


Figure 211. *Orthotrichum alpestre* peristome. Photo by Michael Lüth, with permission.

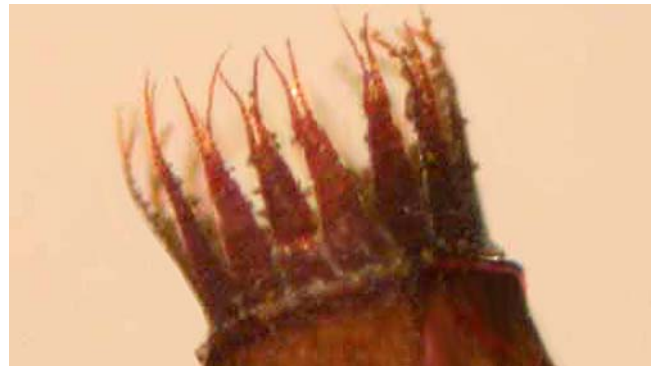


Figure 212. *Dicranum scoparium* peristome with teeth that bend outward upon drying. Photo from UBC botany website, with permission.





Figure 213. *Amblystegium subtile* with capsules showing teeth that flex as they change moisture states. Photo by Hermann Schachner, through Creative Commons.



Figure 214. *Hypnum cupressiforme* capsule showing peristome with teeth that flex as they change moisture states. Photo by Malcolm Storey, through Creative Commons on Discover Life.



Figure 215. *Neckera pennata* branch with capsule and teeth that oscillate in response to moisture changes. Photo by Dale A. Zimmerman, Herbarium, Western New Mexico University, with permission.

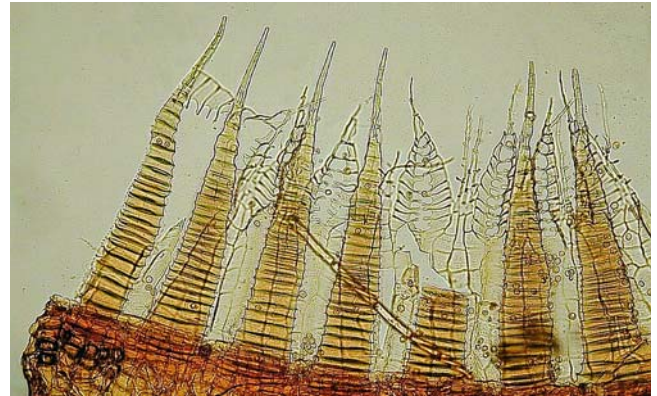


Figure 216. *Bryum caespitium* peristome, with teeth that flex as they change moisture states. Photo by Michael Lüth, with permission.

Schnepf *et al.* (1978) described the movement of the outer peristome in the moss *Racopilum intermedium* (Figure 217). This movement arises from different swelling velocities of the outer plates and inner ridges of wall thickenings. These swelling differences arise from the suberin-like substances and wax lamellae enclosing the ridges. There is no suberin-like material in the plates.



Figure 217. *Racopilum intermedium* with capsules. Photo by Michael Lüth, with permission.

Estébanez *et al.* (2002) determined that strongly bound lipids, phenolics, and non-cellulosic polysaccharides were responsible for the movement of the teeth in *Arctoa fulvella* (Figure 218), *Grimmia decipiens* (Figure 219), *Grimmia pulvinata* (Figure 220), *Schistidium rivulare* (Figure 221), *Bucklandiella sudetica* (= *Racomitrium sudeticum*; Figure 222), *Ptychomitrium sinense* (Figure 223), *Glyphomitrium humillimum* (Figure 224), and *Venturiella sinensis* (Figure 225).



Figure 218. *Arctoa fulvella* with capsules. Photo by Andrew Hodgson, with permission.





Figure 219. *Grimmia decipiens* with capsules. Photo by Henk C. Greven, Doorn, The Netherlands, with permission.



Figure 222. *Bucklandiella sudetica* showing reflexed peristome teeth. Photo by Hermann Schachner, through Creative Commons.



Figure 220. *Grimmia pulvinata* with capsules and teeth pointing outward. Photo by Michael Lüth, with permission.



Figure 223. *Ptychomitrium sinense* in dry state. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 221. *Schistidium rivulare* with capsule showing outward-pointing teeth and operculum attached by columella. Photo courtesy of Betsy St. Pierre.



Figure 224. *Glyphomitrium humillimum* with capsules. Photo by Okayama Prefectural Nature Conservation Center, permission pending.





Figure 225. *Venturiella sinensis* with capsules. Photo from Hiroshima University, with permission.

*Takakia ceratophylla* (Figure 226) has a dispersal mechanism that is unusual among mosses. The capsule has a spiral line of dehiscence. At maturity, when the capsule splits, this suture causes a spiral twisting that seems to help in spore dispersal (Higuchi & Zhang 1998). In many of the mosses, the annulus becomes modified as the capsule dries. For example, in *Ludorugbya springbokorum* the annulus rolls inwards, nearly covering the opening of the capsule (Hedderston & Zander 2007). Upon wetting, it rapidly everts, expanding the capsule opening. This exposes the two-sized spores within.



Figure 226. *Takakia ceratophylla* capsule showing spiral split. Photo by Ken McFarland, with permission.

Some bryophytes do not typically shed the operculum, but instead rely on disintegration of the capsule wall. *Buxbaumia aphylla* (Figure 227) seems rarely to shed the operculum (Glime & Liao, pers. obs.). Instead, the capsule cracks across its broad, flat upper face, peeling back to expose the spores (Figure 227). Eventually the tissue peels away, permitting the spores to escape. The protonema in this species produces sporophytes every year, and in Newfoundland, these sporophytes, which must overwinter to release the ripe spores in spring, can suffer high mortality from sudden frosts (Hancock 1973). *Diphyscium* (Figure 228) has a capsule with a similar small opening, but it does seem at least to shed the operculum. If it relies on the capsule splitting, I have not yet been able to observe it.



Figure 227. Capsules of *Buxbaumia aphylla* showing peeled away capsule wall on upper capsule. Photo by Janice Glime.



Figure 228. *Diphyscium foliosum* females with capsules showing shed operculum and teeth. Photo by Michael Lüth, with permission.

From my own observations, I concluded that *Fontinalis* (Figure 144) depends on abrasion for loss of the operculum. In spite of its beautiful lattice teeth, the operculum remains intact and winter-borne capsules become abraded by the silt load of melt waters. This abrasion removes sufficient tissue for spore dispersal to occur. In the absence of abrasion, the capsules seem to be so impregnated with phenolic compounds that the suture between the operculum and capsule body firmly glues them



together. But others have observed the beautiful teeth and spore dispersal, so my observations may only be of the unsuccessful capsules that remained after the others had dispersed their spores.

### Cleistocarpy

In some mosses, the capsules have no peristome or operculum, a condition known as **cleistocarpy**. Such is the case for *Archidium ohioense* (Figure 109) and *Trachycarpidium tisserantii* (Makinde & Odu 1994). As already noted, these two species had poor spore release, compared to that of the two peristomate mosses, *Fissidens ovatifolius* (as *Fissidens minutulus*; Figure 229) and *Bryum coronatum* (Figure 93). All four species benefitted in their savannah habitat in Nigeria by having a rapid maturation cycle for their capsules.



Figure 229. *Fissidens ovatifolius*. Photo by Jan-Peter Frahm, with permission.

In *Archidium* (Figure 109), the cleistocarpous capsule hides on a short seta among the leaves. At maturity, the capsule wall ruptures by decomposition, permitting spores to escape (Lönnell 2011). Lönnell suggests that this method of spore exposure and the large size of the spores are not supportive of wind dispersal and that use of another agent, perhaps water, is more likely. *Riccia* species likewise have large spores (Figure 230). Their presence in flood plains and other habitats that periodically get reasonably inundated with running water suggests that the same may be true for them.

Herrnstadt and Heyn (1988) have pointed out to us that a similar elaborate, complex, **sexine** (outer, sculptured layer of exine) spore wall pattern is common to a large percentage of the species that have cleistocarpous capsules or lack a peristome. These cleistocarpous species typically are small mosses, annual, terrestrial, and living in open habitats, particularly in the Mediterranean and adjacent arid regions. They furthermore have capsules that are immersed in the perichaetial leaves and possess large spores [(25) 30-40  $\mu\text{m}$ ]. Does this mean that this spore wall pattern has an adaptive value in arid regions?

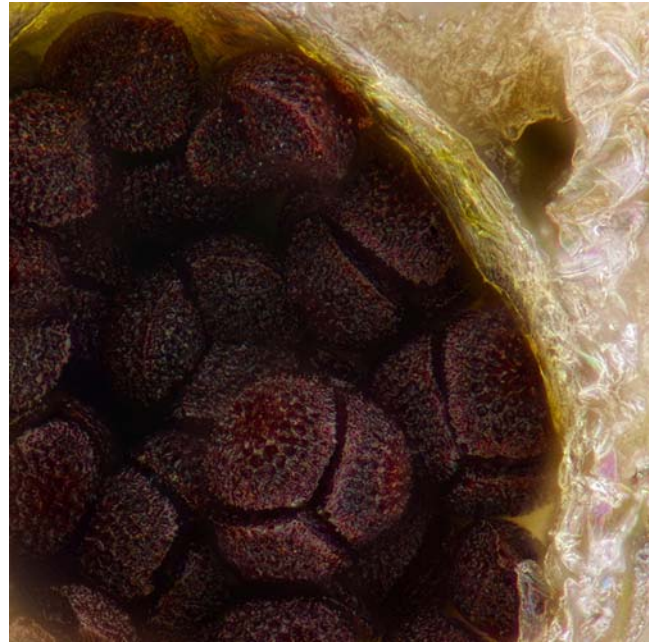


Figure 230. *Riccia sorocarpa* showing the large, highly pigmented spores. Photo by Des Callaghan, with permission.

### Summary

**Diaspores** include both spores and other propagules that serve in dispersal. These are typically sampled by exposed agar plates, glass slides with glycerine, or traps, including Tauber and Burkard traps.

Spores are usually smaller than vegetative diaspores and are therefore the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. But spores require fertilization as a prerequisite and therefore nearness of males and females. Vegetative diaspores continue in production under stressful conditions, but spores do not. Fragmentation is common in many species and seems only to require dry conditions; animals can help both in fragmenting and in carrying these propagules.

The success of dispersal and range size seems to be related to the abundance of sporophyte production. On the other hand, genetic information, at least for some species (especially **Polytrichaceae**), suggests that vegetative dispersal may be more important, even in species that produce abundant spores, perhaps due to spore dispersal limitations.

Dispersal success requires a tradeoff between energy spent on short-distance but energy-rich diaspores and energy wasted for a few of many spores produced that succeed in long-distance dispersal. Vegetative reproduction requires a tradeoff between likely success and loss of genetic diversity. Liverworts, as a group, seem to spend more energy on asexual reproduction than do mosses.

Disturbance can create conditions for vegetative growth, bring buried diaspores to the surface where they can germinate, and disperse propagules for short or long distances. Some species are especially adapted to



disturbances such as fires, floods, cold events, and even ants.

Diaspore banks are important for species that live in disturbed habitats. The spores of species that are regularly disturbed, such as floodplains, are typically large and these species may have rhizoidal tubers or other forms of rhizoidal propagules. For those that grow in areas of unpredictable disturbances, taxa that are easily dispersed, such as *Funaria hygrometrica* and *Marchantia polymorpha*, are often important colonizers and can survive in spore banks as well as arriving through aerial dispersal. Representation in the diaspore banks often does not reflect the species at the surface, but rather has a strong bias toward acrocarpous species and species of early successional stages.

**Peristome teeth** in mosses, an **explosive capsule** in *Sphagnum*, and **elaters** in liverworts help in dislodging spores and dispersing them. Other factors influencing dispersal are capsule size, shape, and orientation, annulus, exostome, endostome, spore size, maturation time, and seta length. Some rely on splitting of the capsule, including **cleistocarp**. Strongly bound lipids, phenolics, and non-cellulosic polysaccharides contribute to peristome movement. Flood plain species tend to have large spores that permit a rapid life cycle. Dioicous species tend to have smaller spores, permitting them to travel farther on those occasions when sexual reproduction is successful. In some species, the spore size varies with altitude.

Maturation time can be important. For most spores, a dry atmosphere is favorable for longer distance dispersal. For vegetative propagules, some are favored by rain and others by dry wind.

It is likely that many species have spores that can survive years of dormancy, and some may survive hundreds of years while dry and in the dark. Those that start to germinate, then dry out again, will most likely die. Spores are also kept dormant by their parents, most likely due to chemicals from the parents.

## Acknowledgments

This chapter has benefitted greatly from the wonderful discussion on Bryonet in March 2013. Thank you also to the helpful comments of a novice bryologist, Tatiany Oliveira da Silva, on places that needed to be clearer for international and novice readers. Karen Renzaglia provided images that I requested for specific purposes. William T. Doyle gave me permission to use any of his wonderful SEM images of liverworts and hornworts. Steve Trynoski offered several suggestions after a critical reading of this subchapter.

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