

CHAPTER 4-8

ADAPTIVE STRATEGIES: TRAVELLING THE DISTANCE TO SUCCESS

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Figure 1. *Conostomum tetragonum* with capsules in the mountains of Norway where its spores become windborne more easily than those of bryophytes in the forest. Photo by Michael Lüth, with permission.

Diaspore Travel Distances

Although bryophyte spores are typically wind-dispersed, it appears that few actually travel very far. Most never actually become airborne (Wyatt 1977; Stoneburner *et al.* 1992). More typically, most of the spores fall within a meter or less (Crum 2001) of the capsule. It is likely that the bryophytes themselves act as spore traps, particularly for the neighboring plants of their own species. Pardoe *et al.* (2010), using mosses to compare trapping efficiencies, demonstrated that mosses serve as traps for pollen, suggesting that they should be traps for bryophyte spores as well.

But trapping spores and quantifying atmospheric spore rain is difficult at best, and the worldwide distribution of a number of taxa attests to the fact that these diaspores must at least occasionally travel great distances. There are tests of survivability for spores, but even less is known about vegetative diaspores.

Failure to Leave Home

Most spores will fall near the parent. In *Tortula truncata* (= *Pottia truncata*; Figure 2), 67% of the spores released fell within the parent clump and 70% within 2 m (Roads & Longton 2003). Further evidence of lack of gene flow to new locations is that there was little or no genetic variation within the individual clumps, but no genotypes were in common between the populations, suggesting that genes (including those in spores) from one population clump had not reached the other one. Sundberg (2005) found that for six species of *Sphagnum* (Figure 3), 8-32% of the spores that dispersed beyond the colony did not travel beyond the active release area of 3.2 m. Stoneburner *et al.* (1992) demonstrated this stay-at-home behavior experimentally for *Atrichum angustatum* (Figure 5). In that species, 94% of the spores were collected within 2 m of the colony center; 1% were found 15 m from the center. On the other hand, Miles and Longton (1990, 1992b) found

that more than 80% of the spores of *Atrichum undulatum* (Figure 6) and *Bryum argenteum* (Figure 7) travelled beyond their 2-m trapping distance.



Figure 2. *Tortula truncata* (= *Pottia truncata*) with capsules; most of the spores fall within the parent clump. Photo by Des Callaghan, with permission.



Figure 3. *Sphagnum fimbriatum* with capsules. Photo by David Holyoak, with permission.



Figure 4. *Tortula acaulon* (= *Phascum cuspidatum*) with capsules. Photo by Jan-Peter Frahm, with permission.

In *Tortula acaulon* (= *Phascum cuspidatum*) (Figure 4), 98% of the spores remained within the colony in this annual shuttle species (Roads & Longton 2006). This resulted in three of the five permanent quadrats having this species in them again in the second year. Many of the

second-year colonies overlapped with the position of the first-year colonies, suggesting that spores fell close to home.



Figure 5. *Atrichum angustatum* with immature capsules; most spores apparently travel more than 2 m. Photo by Janice Glime.



Figure 6. Gametophytes and sporophytes of *Atrichum undulatum*. Photo by Michael Lüth, with permission.



Figure 7. *Bryum argenteum* with capsules in Europe. Most spores are apparently able to travel more than 2 m. Michael Lüth, with permission.

Polytrichaceae

Atrichum undulatum (Figure 6) may not be a good example of dispersal distance in bryophytes due to its

presence of an epiphragm. This membrane, a characteristic of the **Polytrichaceae**, connects the 32 teeth and prevents spores from leaving from the top of the capsule, forcing them to leave between the teeth (Figure 8-Figure 9; see also Figure 61). Such a mechanism precludes the upward thrust that might be seen in some capsules where spores can travel upward directly. Rather, it is likely that spore dispersal in this species is facilitated by raindrops on the epiphragm, as is known for *Dawsonia* (Figure 10), limiting its dispersal (van Zanten 1973) both by the wet atmosphere and the horizontal ejection because they are not ejected high enough to reach the wind turbulence.

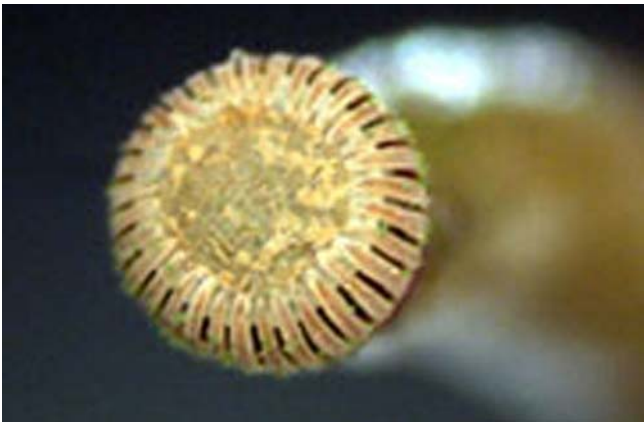


Figure 8. *Atrichum undulatum* showing epiphragm membrane extended across opening and attached to teeth like a trampoline. Photo from UBC website, with permission from Wilf Schofield.

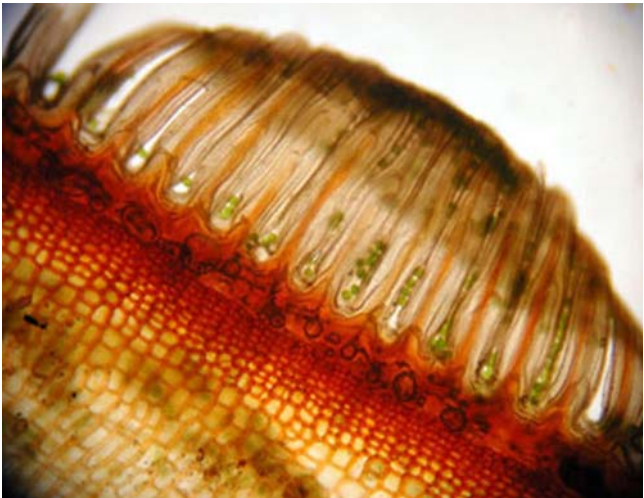


Figure 9. *Atrichum undulatum* with openings between peristome teeth showing spores. Photo from UBC website, with permission from Wilf Schofield.

Thus, based on limited data, it seems to be accepted that most bryophytes probably only disperse the majority of their spores within about 2 m (Table 1). But only a few spores need go farther to accomplish long-distance dispersal, and some species seem more able than others to accomplish this. Stoneburner *et al.* (1992) found that when air volume was increased, 4.5 million out of 25.8 million spores of *Atrichum angustatum* (Figure 5) from the colony reached the limits of their 15-m study area. Just think what would happen to spores caught in the updrafts of a forest fire or tornado!



Figure 10. *Dawsonia longiseta* with capsules. Photo by Niels Klazenga, with permission.

Table 1. Published maximum dispersal distances of bryophyte spores, based on direct measurements to traps. It is appropriate to consider that these spores will travel at least this far.

<i>Sphagnum subtile</i>	75-100 cm	McQueen 1985
<i>Tetraphis pellucida</i>	2 m	Kimmerer 1991
<i>Bryum argenteum</i>	>2 m	Miles & Longton 1992b
<i>Atrichum undulatum</i>	>2 m	Miles & Longton 1992b
<i>Tortula truncata</i>	>2 m	Roads & Longton 2003
<i>Ptilidium pulcherrimum</i>	2.5 m	Crum 2001
<i>Atrichum angustatum</i>	>15 m	Stoneburner <i>et al.</i> 1992

Evidence from a Road Cut

Miller and McDaniel (2004) used a novel method to estimate the distance and rate of dispersal that delivered new species to a new substrate. Using a highway construction site on Whiteface Mountain, New York, USA (Figure 11), they examined the bryophytes on concrete mortar there and found that it had increased the bryophyte diversity by 50% above that found on local rock substrata. The local and mortar bryophyte floras differed considerably. Many of these new species were typical of lower elevation forests, at least 5 km distant, where they were not on concrete. The new diversity suggested that these colonizers had arrived and established at the rate of at least one species per year during the 65 years since the highway construction. Miller and McDaniel concluded that for at least some bryophytes, dispersal over 5 km or more are routine events.



Figure 11. Whiteface Mountain, NY, with new-fallen snow at the summit. Photo from Wikimedia Commons.

Epiphytes

For epiphytes, dispersal must necessarily be more than a few meters for the species to survive natural die-off of forest trees, not to mention the ravages of harvesting. Snäll *et al.* (2003) found that the occurrence of the epiphyte *Orthotrichum speciosum* (Figure 12) in a fragmented forest landscape was most affected by shading, but also by connectivity to nearby tree patches, aspen (*Populus*) tree diameter, and forest vitality, suggesting that age of forest was a contributing factor, perhaps in providing more time for colonization. Furthermore, once either *O. speciosum* or *O. obtusifolium* (Figure 13-Figure 14) became established on a tree, the species remained there until the tree died. Local extinctions were entirely a function of the life of the host tree. Hedenäs *et al.* (2003) found that environmental variables seemed to have little influence on the epiphytes (including *O. obtusifolium*) in a *Populus tremula* stand. Rather, asexually dispersing species were more common than sexually dispersing ones. Sexually dispersing species tended to be more aggregated than the tree species, whereas the asexually dispersing ones had a distribution similar to that of their host.



Figure 12. *Orthotrichum speciosum* with capsules. Photo by Michael Lüth, with permission.



Figure 13. *Orthotrichum obtusifolium* on bark, a species that remains with its host tree until the tree dies. Photo by Michael Lüth, with permission.



Figure 14. *Orthotrichum obtusifolium* with gemmae on leaves. Photo by Michael Lüth, with permission.

The occurrence of *O. obtusifolium* (Figure 13-Figure 14) in the fragmented landscape was controlled by similar variables but with different relative importance. Unlike *O. speciosum* (Figure 12), colonization of *O. obtusifolium* was not affected by connectivity. Snäll *et al.* (2004a) found that there was significant kinship between individuals of both *Orthotrichum speciosum* and *O. obtusifolium* up to 350 m apart. Snäll and coworkers suggested that this indicated they were dispersal limited and might be threatened by current silvicultural practices. Nevertheless, this distance is superior to that of the species listed in Table 1, although it probably represents **stepping stone** dispersal, discussed below.

For the epiphyte *Neckera pennata* (Figure 15-Figure 16) the past history of its occurrence accounted for much of its current distribution, emphasizing the importance of nearby sources of diaspores (Snäll *et al.* 2004b). Snäll and coworkers (2004b) suggested that its dependence on connectivity, tree age, and tree diameter (a surrogate for tree age) indicate a restricted dispersal range for *Neckera pennata*. Its primary distribution at heights of less than 1.6 m on the tree could also be a response to the restricted dispersal range.



Figure 15. *Neckera pennata* on bark of *Thuja occidentalis*. Photo by Janice Glime.



Figure 16. *Neckera pennata* branch with capsules, a species that seems to be dispersal limited. Photo by Jan-Peter Frahm, with permission.

Disturbed and Short-lived Substrata

One might assume that short-lived substrata would drive selection for species that have good dispersal capability. It appears that *Ptilidium pulcherrimum* (Figure 17) from rotting logs in the coastal peninsula of northern Sweden has a somewhat better dispersal than the epiphytes mentioned above where the tree substrate is stable for a longer period of time. Söderström and Jonsson (1989) found that only 43% of the spores of log-dwelling *Ptilidium pulcherrimum* produced remained within 2.5 m of the source, suggesting that 57% were able to travel far enough to reach logs at a greater distance than that.



Figure 17. *Ptilidium pulcherrimum*, a log- and soil-dwelling species that relies on superior dispersal. Photo by Michael Lüth, with permission.

The soil-dwelling *Atrichum angustatum* (Figure 5) seems to be less adapted for dispersal than the log-dwelling *Ptilidium pulcherrimum* (Figure 17), with 94% of the spores of the former falling within 2 m of the colony center, and another 1% falling in the range of 15 m (Stoneburner *et al.* 1992). Hence, the soil-dwelling populations of *P. pulcherrimum* are prepared for dispersal to a greater distance as their habitat becomes uninhabitable. It is therefore not surprising to find it among the early colonizers of disturbed soil banks and other newly cleared soil in forests as well as on decaying logs.

Herben, *et al.* (1991), likewise using rotting logs, considered the number of spores needed to give rise to

enough new colonies that a bryophyte species could persist in this system of temporary habitat patches. To answer this question, they studied the invasive moss *Orthodontium lineare* (Figure 18) in southern Sweden. This species invades rotting wood, and based on model simulations, its success depends primarily on spore transport and establishment. Disturbance rate, competition, and colony growth are of lesser importance.



Figure 18. *Orthodontium lineare* with numerous capsules that help it to be an invasive species. Photo by David Holyoak, with permission.

If a species thrives in a periodically disturbed habitat such as an arable field or floodplain, then it needs a means of surviving and distributing to suitable substrata when favorable growing conditions occur. But the most favorable circumstances typically are those where it currently exists, and although it is likely that nearby areas are suitable, many distant areas most likely are not. Hence, such species are often adapted for rapid colonization and short-distance dispersal. With these considerations in mind, it is somewhat surprising that diaspore banks in these habitats are typically dominated by spores, such as those of *Physcomitrium sphaericum* (Figure 19; During 1997). On the other hand, habitats with small scale but somewhat regular disturbances usually have species that mostly reproduce asexually.



Figure 19. *Physcomitrium sphaericum* with capsules, a common species in diaspore banks. Photo by Li Zhang, with permission.

In peatlands, disturbances from mining are large scale and recolonization occurs on a bank of peat. The disturbance exposes deep peat where propagules have collected for centuries (Poschlod 1995). Poschlod found that some *Sphagnum* spores can germinate from these older peats following disturbance that exposes them to light. He found that the species appearing after these disturbances are typical of the original vegetation, are represented in the diaspore bank, and are often absent in the diaspore rain. This was likewise true in a dry heath, where the dominant bryophyte re-colonizer was *Campylopus pyriformis* (Figure 20-Figure 21).



Figure 20. *Campylopus pyriformis* with abundant capsules. Photo by Jan-Peter Frahm, with permission.



Figure 21. *Campylopus pyriformis* showing detached leaves that can serve as propagules. Photo by Michael Lüth, with permission.

Richards (1988) considered all substrata useful for bryophyte colonization in tropical forests to be impermanent. He therefore considered it important for those species inhabiting such substrata to have efficient short-distance dispersal. The same will be discussed below (Spore Size and Number) for *Archidium* (Figure 22) species, with large spores, cleistogamous capsules, and poor dispersal ability.

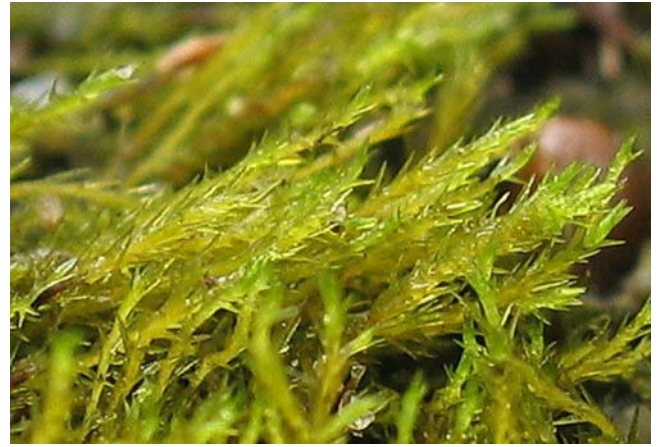


Figure 22. *Archidium alternifolium*. Photo by Andrew Spink, with permission.

Kubisch *et al.* (2014) summarized the importance of interacting factors in facilitating or preventing successful dispersal. Such factors include abiotic factors (wind, air currents) and adaptation to the new environment. They describe these as a "dynamic equilibrium of colonization and local extinction events." These principles should apply to bryophytes.

Long-Distance Dispersal (LDD)

For many bryophytes, there is at least indirect evidence that long-distance travel occurs. On Signy Island in the Antarctic, Marshall and Convey (1997) trapped spores of all five taxa of bryophytes at distances of 0.5-1 km from the nearest known sources, attesting to their ability to travel beyond a short distance. In this case, the spores were more abundant than bryophyte plant fragments in the trappings, and the representation of both was proportionately smaller than that of lichens.

A number of studies have demonstrated that typical bryophyte distance curves for spore dispersal are **leptokurtic** (Mogensen 1981). That is, they look like an exponential curve, but with a fat tail, *i.e.*, the numbers are greater close to the source and again at substantial distances than would be expected (Figure 23).

Lessons from Tracheophytes

Nekola and White (1999) took a comprehensive approach to evaluating the long-distance dispersal of bryophytes by comparing them to tracheophytes. They examined bryophytes in North American spruce-fir forests and Appalachian montane spruce-fir forests to estimate the rates of "distance decay." Predictably, the similarity of numbers compared to the source decreased significantly with distance. They found that the rate of similarity decay was 1.5-1.9 times as high for tracheophytes as for bryophytes, *i.e.*, bryophytes disperse farther. They considered that two factors cause distance decay: decrease in suitable habitat and limits to dispersal. Since the habitats were the same for both the bryophytes and the tracheophytes, it would imply that either the bryophytes have broader ecological amplitude for such factors as soil type, temperature, moisture, and day length, or they have greater dispersal ability. It is likely that both are true.

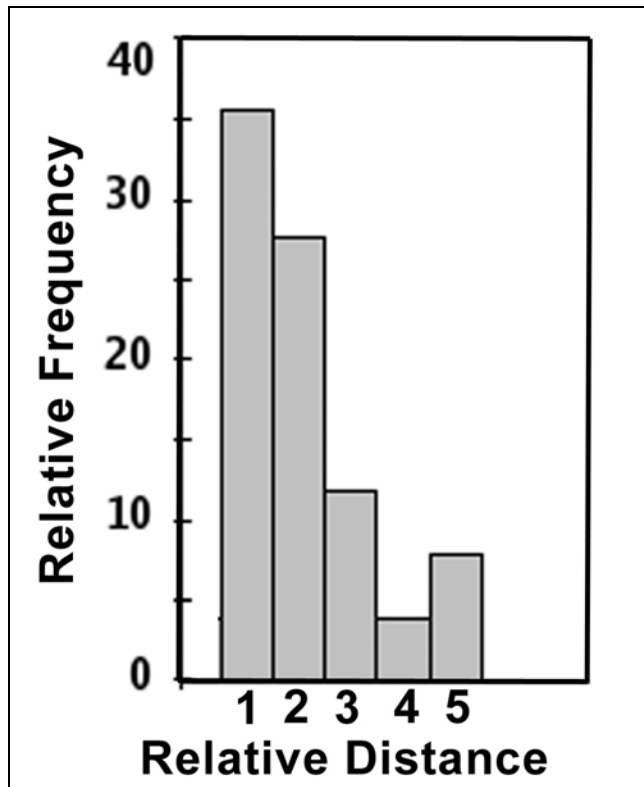


Figure 23. Hypothetical leptokurtic data graph showing asymmetrical distribution of data with a fat end on the right. Based on graph by Audrius Meskauskas through Wikimedia Commons.

Iwatsuki (1972) had a somewhat different perspective on the dispersal of bryophytes and their geographic isolation, particularly among the islands of eastern Asia. He considered the distribution of mosses to be comparable to that of tracheophytes and assumed that bryophytes lack an effective means of long-range dispersal. He also considered that bryophytes evolve very slowly, a factor that appears to be true for their morphology but not for their biochemistry and physiology (Glime 2011), and that this lack of evolution results in most moss species having wider ranges than the tracheophytes, *i.e.*, they have not evolved into new species. This perspective made sense based on our morphological understanding of species, but forty years later, with more recent techniques, we are learning that there are DNA differences and that many disjunct or distant populations represent microspecies that differ genetically, and presumably also biochemically. Hence, bryophytes have evolved to occupy somewhat different niches as they have spread to more distant lands. It seems that these wonderful plants have conjured up a million ways to confound us!

In support of Iwatsuki's 1972 premise, Mateo *et al.* (2013) examined the biogeographic regionalization of European bryophytes. They failed to support their first hypothesis, that regions defined for bryophytes would differ from those defined for other taxa due to the highly specific ecophysiology of the bryophyte group, thus adding credence to the suggestion of Iwatsuki. I'm not convinced that they have such a highly specific ecophysiology anyway. Mateo and coworkers concluded that their findings support a greater similarity between migration

patterns of tracheophytes and bryophytes than previously considered. They did, however, find that bryophytes had a substantially lower optimal number of clusters and an absence of nested patterns within primary bryogeographic regions, supporting their second hypothesis. Nevertheless, they cautioned that there are so many regions lacking data that such conclusions are tentative until some of the assumptions and data gaps can be removed.

Certainly some records confirm that bryophytes have broader distributions than do tracheophytes. Jerry Jenkins (Bryonet 6 March 2013) has observed the colonization of his own farmland and second-growth forest in New York State, USA. This area has been invaded by about 100 bryophyte species and a similar number of tracheophytes. He has found a striking contrast in the distributions of the invading species of these two groups. Approximately half of the bryophytes are species known from two or more continents, whereas most of the tracheophytes are restricted to North America, and many to eastern North America. This leads us to examination of the concept that "everything is everywhere."

Everything Is Everywhere!

Baas-Becking (1934) formulated this hypothesis for micro-organisms, promulgating the notion that "everything is everywhere, but, the environment selects." This concept will be discussed later (Interactions volume) for protozoa and small animals. But is the concept applicable to bryophytes, where single-celled spores are among these small, airborne propagules?

The concept of everything is everywhere assumes that small propagules are able to travel the world over, but that once they arrive, they must locate in a suitable environment to survive. Santos-González (2007) discussed this concept for fungi, which, like the bryophytes, can spread by single-celled spores. It is easy enough to show for both fungi and bryophytes that the environment selects, but to demonstrate that everything is everywhere is more challenging. Not only must we demonstrate that air patterns are capable of distributing and redistributing bryophyte spores (and even asexual propagules) to all locations, but we must also demonstrate that they survive the journey. Such experimentation has rarely been attempted.

Bryophyte species are generally more widely distributed than those of tracheophytes (Pisa *et al.* 2013).

Lazarenko (1958) considered the remote transport of moss spores as doubtful in explaining the formation of discontinuous moss ranges. Rather, he, like Iwatsuki (1972), asserted that moss distribution has followed the same principles as that of tracheophytes, following continental drift theory. He uses radiation of species from two distribution centers of *Syntrichia ruralis* (Figure 24) to illustrate the role of the separation of the continents. He rejects the significance of long-distance transport to explain such patterns. While I agree that he has offered a plausible explanation, I do not agree that it is the only one, and I consider it possible that *Syntrichia ruralis* could have been transported from a northern location prior to the Ice Age to

both Europe and North America or been transported at some point in time from one of those continents to the other, perhaps when the species was young, then diverged into the various lineages of similar species, resulting in several degrees of differences. Such transport could have occurred by wind passage. Nevertheless, Lazarenko argues that the ranges of mosses show the same zonal regularities as seed plants. While that may be true, many bryophytes have much wider distributions than seed plants, suggesting a different or easier mode of dispersal. Most bryologists do consider that many bryophytes are capable of long-range dispersal, accounting for the presence of many species on both sides of the Atlantic Ocean and others at both poles. Van Zanten and Pócs (1981) considered it likely that long-distance transport was common for spores under 25 μm . On the other hand, they considered transport across the equator to be difficult, if not impossible.

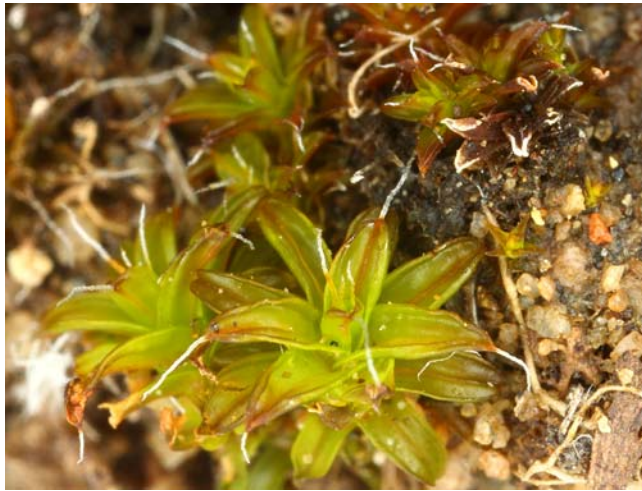


Figure 24. *Syntrichia ruralis*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Pisa *et al.* (2013) used *Bryum argenteum* (Figure 7) to demonstrate the Baas-Becking hypothesis. This species has a wide (**cosmopolitan**) distribution. They found that genetic diversity demonstrated environmentally driven genetic variation, with the greatest genetic diversity above 1900 m. There was a significant genetic variation correlation with elevation, but the genetic diversity did not correlate with geographic distance, supporting the concept of long-distance dispersal rather than stepping-stone distribution.

Spore Size and Range

One question that arises in dispersal is that of **effective size** of the dispersal unit. Because of their dominant haploid generation, bryophytes do not conform well to the general genetic models. Bengtsson and Cronberg (2009) investigated the size effect in bryophytes and found that the effective size corresponds well with the smallest size of scored individuals. When only a small number of sporophytes is produced by females in a male-dominated community, the decrease in effective size is most severe. They concluded that the **harmonic mean** (obtained by

dividing number of observations by reciprocal of each number in series) of diploid sporophytes per individual gametophyte is the more relevant measure in determining minimal size needed for effective dispersal.

One way to test "everything is everywhere" and support or refute Lazarenko's assertion is to examine the correlation between spore size and species range. This correlation remains to be done on a broad scale. And this correlation might not be instructive if nearly all bryophyte spores are small enough to travel everywhere. As Schuster (1969) concluded, the evidence of distributions seen at our present point in time does not really permit us to distinguish ancient overland dispersal from more recent dispersal by spores. Delgadillo (1993) discussed this same problem in trying to explain the bryogeographic relationships between the Neotropical flora and that of Africa, areas that share about 334 taxa. These decisions are complicated by rapid evolution vs slow evolution. It is interesting that while the Afro-American liverworts number 74 species, these are all in one family, the **Oxymitriaceae** (Figure 25) (Gradstein 2013). Nevertheless, these constitute about 5% of the Neotropical liverwort flora and 8% of the African liverwort flora. Gradstein treats these as primarily the result of long-distance dispersal.



Figure 25. *Oxymitra incrassata* (Oxymitriaceae), representing the only Afro-American liverwort family. Photo by Michael Lüth, with permission.

Distribution Stories

Schuster (1979) attempted to understand the distribution of liverworts in the Southern Hemisphere, where "old" families seem to predominate. He considered dispersal there to be the result of short-range or "step-wise" (referred to herein as "**stepping stone**") dispersal. This explanation relies on the separation of populations due to the fragmentation of Gondwanaland (Figure 26) and makes assumptions about the rate of speciation and efficiency of long-distance dispersal compared to the presumed geological background. Schuster (1982) explained the origin of plant groups in the southernmost Gondwanaland with the continental fragments (Figure 26) as "floating Noah's arks."

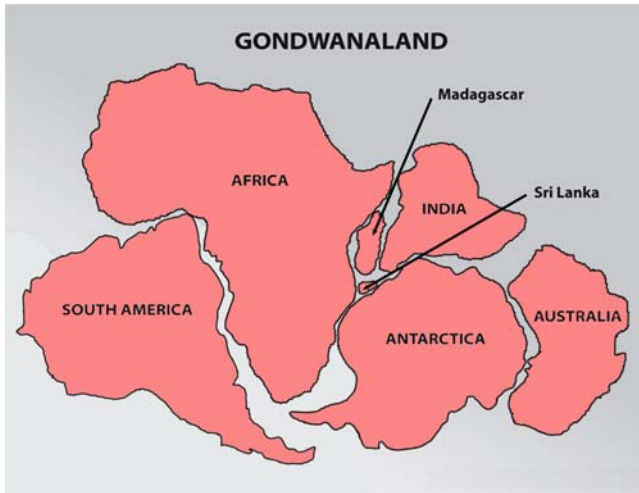


Figure 26. Gondwanaland breakup. Redrawn from Richard W. Hughes.

Ceratodon purpureus (Figure 27) arrived on one of the outer Aleutian Islands within less than a year of eruption (Rod Seppelt, Bryonet 11 March 2013). Surtsey was colonized by bryophytes by 1967 following the island's emergence from the sea off the Iceland coast in 1963 (Fridriksson & Magnússon 1992). However, the first vascular plant was found there in just two years after eruption, in 1965.



Figure 27. *Ceratodon purpureus* with capsules. Photo courtesy of GERALYN MERKEY.

In New Zealand populations of *Sphagnum plumulosum* (= *S. subnitens*; Figure 28), Eric Karlin, Jon Shaw, and Dick Andrus (Karlin *et al.* 2011) found that only two genetic signatures existed, representing two founding parents (Rogers 2011). In northwestern North America, they found 100% of the gene pool was derived from one individual! This means that to colonize the widespread areas in these two regions required considerable dispersal. They determined that this dispersal involved both vegetative fragments and spore dispersal. They also concluded that the spread of this species from Europe to North America and to New Zealand was by humans within the last 300 years, followed by non-human dispersal to reach their present ranges in those two regions.



Figure 28. *Sphagnum subnitens* with capsules. Photo by David Holyoak, with permission.

Island Colonization Stories

Surtsey, off the southeast coast of Iceland, provided a natural experiment in colonization following its volcanic emergence from the sea. The primary colonizers were mosses and lichens on the hardened lava and tracheophytes on ash. Colonization on Surtsey compared to Katmai in having few Cyanobacteria, but differed from Krakatau, where the primary colonizers were Cyanobacteria (Brock 1973). Tracheophytes arriving and becoming established were inversely proportional to the distance from the available source, the nearest being a rock 5.1 km away (Fridriksson 1987). However, distance to the mainland is more than 35 km.

Bryophyte invasion lagged behind that of tracheophytes. This may be the result of dispersal types, with most of the tracheophytes arriving with birds (Magnússon *et al.* 2009). Nevertheless, by 2008 on the block lava on the eastern part of the island, tracheophytes were still poorly represented. Instead, the lichen *Stereocaulon* and moss *Racomitrium* (Figure 29) predominated. By 1994, the Lesser Black-backed Gull invaded the southern barren lava and used the *Racomitrium* as nesting material. The effect of these birds in spreading the moss on the island is unknown.

The Northern Stockholm archipelago in the Baltic Sea can provide a test of dispersal and "everything is everywhere." Among the 19 islands, Sundberg *et al.* (2006) found 500 patches of *Sphagnum* in 19 species in 83 rock pools on 14 of these islands. The species richness on the islands correlated positively with island area and degree of shelter by surrounding islands, emphasizing the importance of habitat even when other locations might be more accessible. Supporting this habitat importance, they found that distance from mainland, connectivity, height, and age did not add to the predictability of the island flora. This suggests the importance of aerial dispersal over long distances. Furthermore, spore size did not add to the model, supporting my suggestion that most bryophyte spores might be small enough to be "everywhere." However, individual species did differ in the habitats they occupied, supporting the concept of "the environment selects." Species frequency (number of colonized islands and rock pools) was predicted primarily by spore output of the species on the mainland.



Figure 29. *Racomitrium lanuginosum* on rock. Photo by Janice Glime.

The choice of *Sphagnum* from these Baltic islands is a good one to support the Baas-Becking hypothesis. *Sphagnum* has no specialized asexual reproductive structures (Sundberg *et al.* 2006), although the importance of fragmentation in this genus is poorly known. Furthermore, only 2% of the *Sphagnum* patches on the islands produced sporophytes, and these were mostly on *Sphagnum fimbriatum* (Figure 30). Hence, we can be reasonably certain that there has been little or no stepping stone dispersal (discussed below) and that colonization is the result of spore dispersal from the mainland. Sundberg *et al.* concluded that the *Sphagnum* on the island is the product of centuries of colonization, but that it is not dispersal limited.



Figure 30. *Sphagnum fimbriatum* in Europe. Photo by Michael Lüth, with permission.

Reverse Colonization

For whatever reasons, ecologists have tended to consider islands to be the end of the journal for dispersal of species. But Bellemain and Ricklefs (2008) challenged that concept. They reasoned that if propagules could get to the island, their descendants could get from the island to the mainland. In most cases, we could expect their dispersal abilities to be as good as those of their ancestors. They supported this hypothesis with molecular phylogenies that revealed several examples of **reverse colonization** from islands to continents. But their work was based on animals. What does it mean for bryophytes?

Hutsemékers *et al.* (2011) addressed this question for spore-producing plants. They noted that arguments against reverse colonization focussed on the assumption that island colonizers lose their dispersal power and that back colonization is unlikely due to prior occupation of the niche. Using the Azores, Canary Islands, and Madeira, they found that the aquatic moss *Platyhypnidium riparioides* (Figure 31) does not lose its dispersal ability on the islands. This is not surprising since its primary means of dispersal is by fragments that travel downstream. They further found that mainland populations experienced a severe bottleneck during the last glacial maximum. Hence, instead of being dead ends for the propagules, these islands serve as major sources of biodiversity for postglacial recolonization of Europe, at least for this spore-bearing moss.



Figure 31. *Platyhypnidium riparioides* in a typical stream habitat. Photo by Hermann Schachner, through Creative Commons.

In the aquatic moss *Platyhypnidium riparioides* (Figure 31) there was a significant correlation between the strong genetic variation among populations at a regional scale and the genetic distances (Hutsemékers *et al.* 2010a). However, at a landscape scale, strong dispersal limitation seems to result different histories between southern and northern groups. Furthermore, ecological and genetic variation correlate, suggesting there is reproductive isolation among ecotypes.

Laenen *et al.* (2011) also supported the reverse colonization concept from nearby islands to Europe. They found that Macaronesia exhibited low rates of endemism for bryophytes. Using *Radula lindenberiana* (Figure 32) as a model, they found that European populations share a common Macaronesian ancestor, supporting the view that this island served as a source to repopulate the species in Europe in the postglacial time. They further suggested that the reduced size of bryophytes could account for the diminished amount of morphological variation in these Macaronesian populations. They concluded that islands such as these could have served as refugia during glacial times.



Figure 32. *Radula lindenbergiana*; European populations share a common Macronesian ancestor. Photo by Hermann Schachner, through Creative Commons.

I raised this question of reduced morphological variation many years ago and suggested that bryophytes diversified biochemically as they struggled to persist against the advances of herbivory, fungal attack, and competition with larger plants (Glime 2011). Laenen *et al.* (2014) suggested another explanation. They used statistical rate analysis with time calibration to support the hypothesis that both mosses and liverworts experienced bursts of diversification since the mid-Mesozoic. The current low number of extant species is the result of mass extinctions, with fossil finds not adequately representing their history.

Cronberg *et al.* (2006) explored the variation in the genetic clonal structure of the **dioicous** *Hylocomium splendens* (Figure 33). Using five 10x10 cm plots monitored for five years, they determined the allozyme haplotype of 157 ramets and those from an additional four neighboring plots. They found only four haplotypes within the plots. One female type occurred in all plots and one male type occurred in four plots. Genets were growing intermingled. Although sporophytes were abundant, they found no evidence of recruitment from spores. Their evidence suggests that clonal diversity within patches is determined by vegetative reproduction, in this case by branching and fragmentation. Among patches, sexual processes, *i.e.* production of spores, dominates diversity.



Figure 33. *Hylocomium splendens*, a species that has little recruitment from spores. Photo by Daniel Mosquin, with permission.

In their analysis of range disjunctions and speciation of the leafy liverwort *Leptoscyphus* (Figure 34), Devos and Vanderpoorten (2009) found that rather than having its evolution triggered by episodic shifts in habitat conditions, diversity in this liverwort genus seems to be the product of morphological and molecular divergence that has accumulated gradually. This contrasts sharply with the rapid diversification known in at least some tropical trees.



Figure 34. *Leptoscyphus normalis*, in a genus that seems to have accumulated its genetic diversity gradually. Photo by Jeremy Rolfe, through Creative Commons.

Hutsemékers *et al.* (2010b) noted that our traditional way of viewing maintenance, diversity, and evolution of aquatic plants has been:

1. decreasing or erasing patterns of isolation by distance
2. increasing outbreeding
3. resulting in downstream increase of genetic diversity.

In the aquatic moss *Platyhypnidium riparioides* (Figure 31), the geographic partitioning of genetic variation at the scale of the river basin and indirect measures of dispersal fail to support these principles. Instead, the results suggest an overall weaker dispersal ability of the moss compared to that of pollen or wind-dispersed seeds. Unlike the flowering plants, dispersal of sperm to the egg is more difficult in aquatic species of flowing water. Instead, dispersal of fragments is the more common means of arriving at new sites, accounting for the lower degree of diversity among sites for *Platyhypnidium riparioides*. But overall, bryophytes are considered to be more mobile than flowering plants (Preston & Hill 1999).

One of the predictions for island floras is that they would be subject to **Baker's Law**, that colonization by self-compatible organisms is more likely to be successful than colonization by self-incompatible organisms because of the ability for self-compatible organisms to produce offspring without "pollination" agents. By extension, this would mean that monoicous bryophytes would be more successful in colonization than dioicous taxa.

Patiño *et al.* (2013) examined whether loss of dispersal power and bias toward self-compatibility (Baker's Law) were true for island bryophytes. They found that life history traits of oceanic bryophytes differed statistically from those on continents. On the other hand, life history traits between continental bryophytes and those of continental islands were similar. In this regard, monoicous species of bryophytes were in significantly greater

proportion on oceanic islands than on continents. At the same time, oceanic islands had a greater proportion of species that produced specialized asexual propagules, favoring short-distance dispersal. Nevertheless, for the four species examined, the relative frequency of fertile shoots was higher on islands than on continents. They conclude that this evidence indicates a global loss of long-distance dispersal among oceanic island bryophytes, just as seen with the development of flightless birds!

Factors Contributing to Dispersal

Distance from Source

One of the most obvious factors limiting dispersal is distance to be travelled. Sundberg (2005) found that the spore deposition patterns of *Sphagnum* fit the inverse power law (deposition per unit area is proportional to the distance ($R^2 > 0.99$)). Nevertheless, when the curves were extended to infinity, they failed to account for all the spores dispersed. For example, in *Sphagnum squarrosum* (Figure 35), only 11% could be accounted for. Therefore, something else must be occurring. Sundberg suggests that this "something else" is thermal updraft.



Figure 35. *Sphagnum squarrosum* with capsules. Photo by Michael Lüth, with permission.

Sundberg (2012) used cotton cloth traps to assess the *Sphagnum* spore density in spore rain. He estimated that densities were approximately 6 million per m^2 over the season in a large area, but were only 1000 m^{-2} in Svalbard, northern Norway, indicating that all rains are not equal. Spore rain was strongly related to distance from source, especially relating to sources within 200 km. It is interesting that he found larger spores at isolated island sites, suggesting that they originated from distant, humid areas. In boreal areas, *Sphagnum* accounts for immense numbers of spores, a factor that accounts for its ability to colonize quickly in the wetlands there. Most striking to our consideration of long-distance dispersal is his estimate that 1% of the spores were of a trans- or intercontinental origin and that these spores originate from multiple locations.

Hutsemékers *et al.* (2008) used colonization of 52 slag heaps to assess distance and rate of travel of bryophytes. They found that the number of species per slag heap correlates significantly with time elapsed and area size. Of

these colonizers, 44% of the species were recruited from within 6 km. Recruitment from 6-86 km accounted for the remaining 56% that were recruited within 50 years. New slag heaps are mostly colonized by fugitive, weedy species. Those colonized for more than 50 years accumulated perennial species with a **stayer life strategy**. Rare species tend to occur at intermediate stages, experiencing a tradeoff between probability of dispersal and limitation by increasing competition.

Dispersal Pathway

Just as wind-pollinated trees are adapted to disperse their pollen in spring before the leaves come out on the trees to avoid that interference, bryophytes are limited in their dispersal by similar obstructions. Fenton and Bergeron (2006) found that *Sphagnum* (Figure 35) spore abundance in boreal forests of northwestern Quebec, Canada, was inversely correlated with local tree stand density, and suggested that this was evidence that wind intensity may play a role in limiting dispersal. I would add to that the ability of trees to serve as spore traps.

Renner (2004, 2005) used data on direction, strength, and speed of both sea currents and wind jets to explain dispersal of plants across the tropical Atlantic Ocean. He used data from genera, partly because of data availability and partly, as he argued, because families may have broken up (evolved) before dispersal and species had too much anthropogenic influence. Nevertheless, 110 genera contain species on both sides of the tropical Atlantic. Dispersal patterns and disjunctions can be related to water currents between Africa and South America and to exceptional westerly winds from northeastern Brazil to northwest Africa. Although dispersal by water in both directions seems to be more common for these genera than wind or animal dispersal, bryologists have considered the saltwater to be lethal to bryophyte spores. Furthermore, wind dispersal seems to have facilitated spread from South America to West Africa, but not in the opposite direction.

Air Currents

Van Zanten and Gradstein (1988) summarize the air currents that can facilitate long-distance dispersal:

4. dry air streams at relatively low altitudes (<3000 m)
5. hurricanes, tropical storms, or depressions
6. wet air streams at relatively low altitude (< 3000m)
7. dry air streams at high altitudes, *e.g.* jet streams (ca 10,000-12,000 m asl)

These means of transport vary in their limiting factors: high UV, desiccation, wet freezing, low atmospheric pressure, ozone. The two dry airstreams subject the diaspores to desiccation, with the jet stream causing dry freezing and strong UV radiation, but the low altitude transport has only moderate UV radiation. Likewise, the wet air stream at low altitude has even lower UV radiation due to absorption and reflection by clouds. Hurricanes and storms can have wet-freezing and lower atmospheric pressure, accompanied by different air composition. These storms are likely to be less effective for long-distance dispersal because of the heavy precipitation that can clean the air of the diaspores. The wet air streams at low

altitudes seem to be the safest mode of travel, with only moderate desiccation and low UV intensity.

Molecular Clocks

Molecular clocks have become useful tools to determine not only the pathway, but also the timing of transport of propagules (Renner 2005). Using molecular sequences (gene regions), one can estimate the age of a particular lineage and determine its approximate arrival time. Using fossils, models can analyze the change in substitution rates of a lineage by combining molecular data with known time constraints, particularly with fossils. These fossil/molecular "clocks" are termed **relaxed clocks**. These molecular clocks become effective tools that can be combined with information on prevailing wind and water currents, position of land mass, and size of land mass.

Weather

One might assume that wind dispersal is going to be affected by weather. Fungi might serve as a model for expectations of the effect of weather on bryophyte dispersal. In a study on fungal dispersal, Gregory and Hirst (1957) determined that airborne spore concentrations were dependent on weather and the phenology of the local flora. Lönnell (2011) considered horizontal wind speed and thermal updrafts/turbulence as factors that influence the dispersal distances.

Fungi demonstrate the importance of intermittent and gusty wind in spore dispersal (Aylor 1990). And like wind-pollinated trees, canopy plants with leaves can trap the spores and thus must be avoided unless they are indeed the target. For tropical bryophytes, this may be the case, but in temperate zones, tracheophyte leaves are rarely the target substrate. Hence, like the windborne pollen seeking a stigma, the bryophyte pollen must avoid the canopy traps in order to travel any great distance. Aylor points out the importance of gusts of wind in once again removing trapped spores and putting them back into the air. He assumes that gusts can enhance the air movement by a factor of five in the canopy compared to the average air movements. In the fungi, and likely in the bryophytes, half the spores that have ventured only a few meters from their source can escape the canopy if they are released from mid-canopy or higher. If this premise holds, then epiphytes gain considerable dispersal advantage by their high starting location.

A further simulation shows that fluid motion such as that of smoke can cause an ejection type of flow that enhances spore escape from its source. In fact, Aylor (1990) contends that movement of smoke (and similar cloud-type movements of spores) create features similar to release from the top of the canopy. Aylor suggests that the most difficult aspect to model is the "takeoff" from the source and "integration into the transport process," in the bryophyte case being from the capsule.

Fires

I must wonder if forest fires play any role in distribution. Certainly there are tremendous updrafts (Figure 36), but are there updrafts that are cool enough for diaspores to survive? Based on my observations in

Yellowstone after a massive fire, I have to suspect there might be. There were patches of trees burned on one side, but live on the other, suggesting that bryophytes might also survive there but be subjected to the updrafts. But better evidence came from patches of *Pleurozium schreberi* (Figure 37) that were burned on part of a clump but green and healthy only millimeters away. Surely those nearby burned portions were creating updrafts, even if only small ones. It took only a glance at the mountainside to understand the patchiness of the burn itself. Surely these patches of fire created considerable turbulence that could thrust diaspores for considerable distances. If the soot can reach a location, so can the diaspores. And the smoke itself might offer protection from UV light. We need to examine temperature and air movement patterns to further assess the feasibility of these updrafts as dispersal agents.



Figure 36. Wildfire in California, USA. Photo through Wikimedia Commons.



Figure 37. 1989 view of *Pleurozium schreberi* next to burned soil from a 1988 fire at Dunraven Pass, Yellowstone, Wyoming, USA. Photo by Janice Glime.

Diaspore Characteristics

Not all bryophytes are created equal. Individual characteristics can determine the likelihood of the spores becoming part of the spore rain. Lönnell (2011) lists diaspore size, shape, weight, type of abscission (active or passive), abscission height, and abscission time to contribute to dispersal distances.

Most experiments on bryophyte dispersal have suffered from distance limitations of only a few meters. Lönnell *et al.* (2012) conducted a novel experiment in which they eliminated the possibility of multiple spore sources by isolating a pot of *Discelium nudum* (Figure 38) on a raised bog where its normal clay habitat was unavailable. Hence there was little possibility of other colonies contributing to the experiment. Pots of clay, numbering 2000, were placed at various distances between 5 and 600 m from the mother colony. Within 10 m of the mother colony, the mean colonization rate was greater than 50%. In the 10-50 m range, the colonization rate dropped sharply, but for pots between 50 and 600 m the colonization rate was stable, ranging 1-3%. The estimated number of spores (2-6 per m²) in that most distant segment was commensurate with the spore output of the mother colony. Lönnell considered this to be evidence that the majority of spores of this species escape the parent colony to travel greater distances. Thus, establishment into new locations at distances measurable in kilometers is likely for this and probably a number of other species with similar spore output and dispersal characteristics.



Figure 38. *Discelium nudum* with red antheridia. Photo by David T. Holyoak, with permission.

Work by Hutsemékers *et al.* (2008) adds credence to this assertion of kilometers of dispersal. Using 52 slag heaps in Belgium as pristine soil, they tracked the invasion by bryophytes to heaps at various distances and inferred rate of dispersal by the distance and time of arrival. As expected, the number of species per slag heap is significantly correlated with area size of the heap and time since colonization. It is the weedy species that arrive first, exercising a superior dispersal ability and generally large numbers of spores.

Evidence from Geophysics

Diffusion Models

Levin (1992) contends that generalized diffusion models can explain dispersal of seeds, pollen, and even invertebrate larvae, where winds, currents, and gravity play the major roles. Even organisms that are able to use detailed environmental cues may be dispersed primarily according to diffusion models. Adding habitat-dependent movement can improve the model. Nevertheless, an adequate model can be developed on diffusion alone to explain the spread of oaks and muskrats (Skellam 1951)!

However, Levin (1992) suggests that the diffusion model does not apply well on broader scales and that more refined models are needed. He lists the percolation model for fragmented habitats (Gardner *et al.* 1987; Durrett 1988), the correlated random walk for the movement of insects (Kareiva & Shigesada 1983), or clonal growth for branching organisms (Cain 1990, 1991).

It is likely that models mentioned by Levin (1992) apply as well to a number of bryophyte species. Certainly clonal growth is common among bryophytes and can account for small-scale distribution patterns. The percolation model or the correlated random walk may account for distribution of *Splachnaceae* (dung mosses; Figure 39-Figure 40), where the fly may follow a random pattern of visiting dung piles, but the moss dispersal would be closely correlated to that pattern. It would seem as if these fly-dependent taxa might disperse in a manner similar to that of host-specific parasites.



Figure 39. *Splachnum ampullaceum* capsules on dung in southern Europe. Photo by Michael Lüth, with permission.



Figure 40. Fly visiting capsules of *Tayloria mirabilis* near Cape Horn. Photo by Adam Wilson NYBG, through public domain.

Numerous phytogeographic papers have suggested dispersal patterns over broad areas and linked modern distribution patterns to earlier geologic events. Since major air movement patterns are known, and Van Zanten's work (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981)

provides us with data on aerial survivorship of a number of species, it should be possible to test the diffusion model on bryophytes.

Dust Storms

In their discussion of the global transport of dust, Griffin *et al.* (2002) describe the massive movement of bacteria, viruses, and fungi along with suspended dust particles (and soil pollutants). Just as an example, they estimate that about 13 million metric tons of sediment from Africa land in the North Amazon Basin of South America in a year. Just one dust storm can deliver 200 metric tons.

Charles Darwin, in 1846, expressed the situation as follows: "From the several recorded accounts it appears that the quantity of dust which falls on vessels in the open Atlantic is considerable and that the atmosphere is often rendered quite hazy; but nearer to the African coast the quantity is still more considerable. Vessels have several times run on shore owing to the haziness of the air; and Horsburgh recommends all vessels, for this reason, to avoid the passage between the Cape Verd Archipelago and the main-land." (in Griffin *et al.* 2002). Miles Berkeley (in Griffin *et al.* 2002) concluded that the trade winds could carry fungal spores for thousands of kilometers. German scientists, in 1908, found that the most common bacteria were highly pigmented and all were spore-forming (Griffin *et al.* 2002), suggesting adaptations for aerial dispersal. By 1921, the record height for finding viable bacteria was 21 km above the earth. But these collections had been over land. Finally, in the mid 1930's, Fred Meier, a scientist with the U.S. Department of Agriculture, persuaded Charles Lindbergh to contribute to our knowledge by flying a plane with a metal arm holding microscope slides with a sterile coating of oil while he flew over uninhabited ice, water, and mountains from Maine, USA, to Denmark. These collections revealed fungal spores, pollen, algae, diatoms, and insect wings. Meier then planned sampling over the Caribbean Sea and the Pacific Ocean, but he died in a plane crash in 1938 while doing fieldwork. All these data suggest that bryophytes, too, could enter the jet stream and accomplish long-distance travel.

Not All Storms Are Equal

The next important revelation was that storms of tropical origin were far more likely to enter the upper atmosphere than those of polar origin, carrying nearly 100 times as many fungal spores (Griffin *et al.* 2002). Microbes in the dust in the Virgin Islands show a ten-fold increase during African dust storms. Then a new record for height was set – 77 km above the Earth's surface for some pigmented fungal spores. Of more relevance to the bryophytes is the presence of pollen grains, which might be expected to have similar size and structure to that of bryophyte spores, at 17-19 km above the Earth. This understanding of particle movement is important to our understanding of bryophyte distributions, helping to explain why some tropical bryophytes may appear in polar geothermal areas.

Aloina Example

Numerous authors have attested to the long distance travelling capabilities of bryophyte spores. Kimmerer

(1991) found that many spores were trapped 2 m from the plants and contended that spores ensured long-distance dispersal. Pettersson (1940) filtered spores from precipitation in Finland, then grew them to identify them. Large numbers of spores from *Aloina brevirostris* (Figure 41) were present, as well as those of *A. rigida* (Figure 42), but the genus *Aloina* was unknown in Finland. Both species prefer calcareous substrata and thus are limited in their distribution. Pettersson suggested that they came from Siberia, citing the absence of *A. rigida* in nearby European countries, but Persson (1944) and Bergeron (1944) both rejected that hypothesis.

Persson argued that Pettersson ignored the other species that accompanied the *Aloina* (Figure 42). Among these, *Bryum pallens* (Figure 43), *Leptobryum pyriforme* (Figure 44), and *Marchantia polymorpha* (Figure 45) present no problem, all being common in both Europe and Siberia. However, *Metzgeria* was not known from Siberia, although *Echinomitrium furcatum* (= *Metzgeria furcata*) (Figure 46) is common in Europe. Persson's second argument was that the *Aloina* spores were quite common in the rain (est. at least 60,000,000,000 / km²). That would be an incredible number to come from such a distance as Siberia. The final complication was that an *Aloina* from neighboring European countries had been misidentified as *Aloina ambigua* when in fact it was *Aloina rigida* (Figure 42), making a European origin of *Aloina rigida* quite possible; furthermore, he considered identification of *Aloina rigida* without capsules to be difficult, if not impossible.

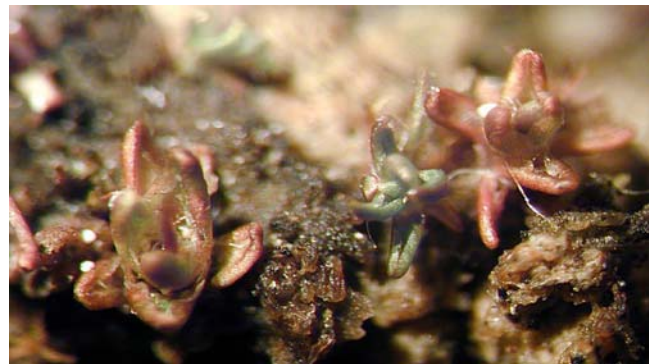


Figure 41. *Aloina brevirostris* gametophytes. Photo by Michael Lüth, with permission.



Figure 42. *Aloina rigida* gametophytes and sporophytes. Photo by Michael Lüth, with permission.



Figure 43. *Bryum pallens* showing red pigmented phase. Photo by David T. Holyoak, with permission.



Figure 44. *Leptobryum pyriforme* with capsules. Photo by Michael Lüth, with permission.



Figure 45. *Marchantia polymorpha* with gemma cups. Photo by Michael Lüth, with permission.

Bergeron's (1944) arguments against a Siberian origin for the *Aloina* (Figure 42) were meteorological rather than biological. First, the weather conditions in Siberia during the preceding week were not likely to have had the force needed to bring the spores into the airstream where they were needed to travel to Finland. Second, rather, the air masses arriving on the day in question originated to the north from other European countries. Third, the air masses leaving the Siberian region did not travel in the direction of

Finland. Fourth, the conditions at the collecting site in Finland on the days of sampling did have the right weather conditions to bring down spores, and these were most likely to have come on air currents from the NNW or SSE, either of which would have traversed areas where *Aloina* grows and neither of which would have passed over Siberia or joined forces with air from that region. There are lots of factors to consider when attempting to determine the origin of propagules.



Figure 46. *Echinomitrium furcatum* (= *Metzgeria furcata*) in Europe. Photo by Michael Lüth, with permission.

Size and Falling Velocity – Distance and Laws of Physics

The first condition of passive dispersal by wind for a diaspore is to get caught by the wind before reaching the ground. For the tiny distances that bryophyte diaspores fall to their substrate, this is a challenge. The laws of physics would predict that atmospheric density of dispersed spores will decrease with increasing distance and increasing height from the colony.

For whatever reason, it appears that when spores exit hanging capsules they can rebound and are elevated (Figure 47) (Cronberg *et al.* (2008)). This gives the spores from hanging capsules the same advantage as those from upright capsules. But what causes this upward movement?



Figure 47. *Bryum argenteum* spore release, showing upward movement of spores. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

This can be helped somewhat by animals (I'm guessing especially squirrels and other rodents) that bump them and cause clouds of spores to become airborne. In rangeland, hoofed mammals surely contribute. Once airborne, the falling velocity is important. Small spores like those of bryophytes typically have a falling velocity less than those of larger objects, permitting them to stay airborne longer and have greater opportunity for capture by moving air.

One approach to examining long-distance dispersal is to develop a trajectory model. Trackenberg (2003) developed such a model (PAPPUS) to consider the potential of wind as a dispersal vector. The model included effects of topography, turbulence (including thermal updrafts), and weather conditions. Simulations included initial release height and falling velocity. It improved on most approaches by modelling turbulence. The model was tested against distances measured in the field. Trackenberg considered that sunny weather with thermal turbulence and updrafts would cause a high proportion of long-distance dispersal, even in periods of low horizontal wind speed.

Not only does the model suggest that sunny weather with thermal turbulence and updrafts may be most important, Trackenberg (2003) concluded that stormy weather may have little importance for long-distance dispersal, especially for species with falling velocities less than 1.5 m s^{-1} . Horizontal wind speed seemed to have no effect on diaspores dispersing more than 100 m; frequency of updrafts was positively correlated. I became aware of this importance myself during a blizzard. I'm not suggesting that spores get distributed in blizzards, but the wind patterns can be seen then without equipment. My "aha" moment came as I watched wind and snow swirl around my house and carve a funnel in the snow, raising the snow into the airstream. While this 1 m wide funnel was caused by an L corner of my house, smaller funnels can occur around rocks and other obstructions where bryophytes grow. Snow is a good marker for wind patterns, and it is common for us to see the snow "falling" upward as wind whirls around buildings and other obstructions. Such wind conditions are not restricted to winter. If it is not a rainy day, such conditions would seem ideal for getting the spores away from the ground and putting them into the airways.

Trackenberg (2003) considered the improved predictability of his model to result not only from the addition of turbulence to the model but also to the effect of topography. Those bryophytes that are elevated either by living on trees, rocks, or walls or by living at high elevations have a greater chance of entering the atmosphere. This improvement is in part due to the slow falling velocity of the tiny diaspores of bryophytes. With falling velocities of less than 1.5 m s^{-1} , unstable atmospheric conditions and thermal updrafts under low humidity provide the greatest contributions to dispersal. If diaspore abscission is coupled with these conditions (**xerochasy**), bryophytes can optimize their dispersal capabilities.

In their predictions for immigration into a milled peatland, Campbell *et al.* (2003) assumed that diaspores released from higher altitudes are typically exposed to greater wind velocities (Greene & Johnson 1996) and thus are likely to be carried farther. As discussed above, this probably only matters once they have been lofted into the

wind stream by updrafts or other short-distance mechanisms. To determine terminal velocity, Campbell *et al.* (2003) assumed a density of 1 (Gregory 1973) and applied Stoke's law for a sphere with a low Reynolds number. They also assumed that propagules with a slower falling velocity (including bryophytes) and/or with a higher release height from the ground would have a greater probability of dispersing into the mined peatland (Campbell *et al.* 2003; Trackenberg *et al.* 2003). Trackenberg and coworkers warned against using morphology as an indicator of dispersal ability, emphasizing the importance of location of growth and consequent falling distance and upwinds as being of greater importance. For plants in general, Campbell and coworkers found that dispersal distance was most sensitive to falling velocity and weather conditions. Since bryophytes in general have slow falling velocities, we might expect weather to be of greatest importance for them.

Evidence from Restoring Peatlands

Campbell *et al.* (2003) assessed the immigration potential of plants into a mined peatland in southeastern Quebec, Canada. They selected 32 species, including both bryophytes and tracheophytes, as potential colonizers, based on presumed dispersal capabilities. They developed an index of immigration potential based on:

- propagule release height
- falling time (propagule release height/settling velocity)
- propagule wing loading (probably not applicable to bryophyte spores, but possibly to gemmae and bulbils).

Their evidence supported these attributes. Those bryophytes with the higher immigration potentials by wind were usually the more frequent colonizers in the mined peatlands. *Sphagnum capillifolium* (Figure 48) and *Sphagnum fuscum* (Figure 49), however, were exceptions, with less than a 1% occurrence but relatively high immigration potential. Campbell *et al.* (2003) attributed this to an establishment problem. Rochefort (2000) found that *Sphagnum* is particularly vulnerable to drought and the instability of the substrate in the early establishment stages. But Campbell *et al.* found that mosses in general had less of a recolonization constraint than did the herbaceous species in this environment.

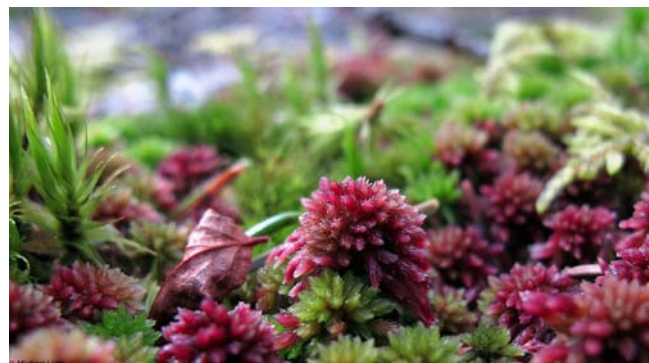


Figure 48. *Sphagnum capillifolium*. Photo by Michael Lüth, with permission.



Figure 49. *Sphagnum fuscum*. Photo by Michael Lüth, with permission.

Disjunct Distributions

The large number of disjunct taxa in the Andes and Atlantic coastal region of Brazil might lend support to the air current hypothesis (Gradstein & Reiner-Drehwald 2007). Major flyways for birds, especially raptors, often follow mountain ridges because these areas often have air currents that propel the birds forward, saving energy on long migrations. It is reasonable to assume they can similarly provide "flyways" for bryophyte diaspores.

Directional (**anisotropic**) dispersal seems to play a role in Southern Hemisphere distribution. Using data from global winds coverage from the National Aeronautics and Space Administration SeaWinds scatterometer, Muñoz *et al.* (2004) found that the correlation of floristics of bryophytes, lichens, and ferns with wind patterns and wind connectivity is stronger than the correlation with geographic proximity, suggesting that spores travel with the wind.

There seems to be an interesting contrast between the arrival of two species of bryophytes [*Ulota phyllantha* (Figure 50) and *Sanionia uncinata* (Figure 51)] on Macquarie Island in the Antarctic. *Sanionia uncinata* has spores only 10-18 μm in diameter, whereas *Ulota phyllantha* has cigar-shaped spores 100 μm long. As Rod Seppelt pointed out on Bryonet (6 March 2013), *U. phyllantha* occurs abundantly on the coastal rocks along the western side of Macquarie Island (Antarctica) but is rarely seen on the east coast. Its distribution on the island has led to the assumption that it has been distributed by the jet stream from southern South America. On the other hand, *Sanionia uncinata* appears to have migrated to Macquarie Island from Australia or New Zealand, matching their genotypes, and differing genetically from other subAntarctic island populations to the east that seem to match the southern South America-Antarctic Peninsula genotypes (Lars Hedenäs, Bryonet 6 March 2013). This migration, contrary to prevailing winds and having a larger dispersal unit, suggests that dispersal by wind will not always follow prevailing winds. Wind directions do change, and Rod Seppelt (Bryonet 6 March 2013) explained that cyclonic low pressure cells can center off the southwest side of Tasmania, pass through the southeast mainland Australia, miss New Zealand and reach to the Ross Sea area of Antarctica. These heavy winds are likely to carry all sorts of propagules from Australia and New Zealand to Antarctica, thousands of kilometers away. Furthermore, during drought periods, huge dust clouds in

Australia can reach New Zealand, no doubt carrying spores along with the dust.



Figure 50. *Ulota phyllantha* with capsules. Photo by David T. Holyoak, with permission.



Figure 51. *Sanionia uncinata* with capsules. Photo by David T. Holyoak, with permission.

Shaw (1982) provides us with more convincing evidence of "everything is everywhere" and the flyway hypothesis. The rare circumboreal *Plagiobryum zieri* (Figure 52) has been found in the Huehuetenango Province of Guatemala, far from its nearest neighbor in Colorado, USA. Shaw suggested that the tendency of the spores in this species to remain in tetrads may be a preadaptation to its ability to survive such long-distance travel and become established in its high altitude homes.

Such disjunctions as 28 species of bryophytes common to Central America and the Himalaya Mountains (Sharp 1974) likewise lend credence to long distance dispersal of bryophyte diaspores. They not only support "everything is everywhere," but also emphasize the importance of the "environment selects."



Figure 52. *Plagiobryum zierii* from southern Europe. Photo by Michael Lüth, with permission.

Finding a species at both poles of the Earth tends to make one think of long-distance dispersal, and *Pohlia nutans* (Figure 53) not only supports the concept that "everything is everywhere," but it clearly supports the "environment selects." Present in Iceland in geothermal areas, common in the Northern Hemisphere, and present on the geothermal areas of the continent of Antarctica, it is the epitome of the environment selects because it is absent in other (non-geothermal) habitats in Antarctica (Skotnicki *et al.* 2002). The Antarctic populations of *P. nutans* exhibit low levels of genetic diversity (RAPD & DNA sequences of conserved nuclear ribosomal RNA), supporting the conclusion that they have been derived from a single dispersal event leading to vegetative growth, mutation, and stepping stone dispersal within the continent, a pattern also discernible for the geothermal *Campylopus pyriformis* (Figure 21, Figure 54).



Figure 53. *Pohlia nutans* with abundant capsules. Photo by Michael Lüth, with permission.

Lewis Smith (1991) considered southern South America to be a continuous source of diaspores for the Antarctic and attributes this to relatively frequent storms that track eastward over the southeast Pacific Ocean. They gain momentum over the southern part of South America where they pick up spores. Sometimes a blocking anticyclone over the South Atlantic Ocean deflects the winds, sending them off to Antarctica.



Figure 54. *Campylopus pyriformis* with capsules. Photo by Michael Lüth, with permission.

Perhaps the best explanation is one from Schofield and Crum (1972), that continental drift, long-distance dispersal, and fragmentation of a previously continuous landscape all have been considered meritorious explanations. But "no single hypothesis is sufficient to accommodate all species within any disjunctive pattern." Nevertheless, many of the bryophyte disjunctions are similar to those of tracheophytes, suggesting that similar mechanisms are at play.

Long-range dispersal in bryophytes is supported primarily by their distribution patterns and our knowledge of air movement patterns and the ability of updrafts to carry particles of various sizes. Survival of a number of taxa at atmospheric low temperatures and UV radiation suggests that such long distances may occur, but probably infrequently.

Stepping Stones

It is likely that many species disperse through relatively short distances most of the time, reaching distant locations eventually through a series of dispersal events from location A to location B, then from location B to location C, a means I shall call **stepping stones**, as that term has been used in the literature several times.

At least in some species, we can document evidence of a stepping stone means of species range expansion. For example, Derda and Wyatt (1999b) found that *Polytrichum commune* (Figure 55-Figure 56) had a high mean genetic identity between populations (0.867-0.998), but that there was significant differentiation among regions that increased with distance. This, coupled with region-specific genotypes, suggested that this species dispersed from location A to location B and then from location B to location C, *i.e.*, the "stepping stone" method. At the same time, some distant populations had multilocus genotypes that were very similar, suggesting that an occasional long-distance dispersal event had occurred.



Figure 55. *Polytrichum commune* in its typical abundance, facilitated by new shoots from rhizomes. Photo by Christopher Tracey, through Creative Commons.

Bischler and Boisselier-Dubayle (1997) provide us with an example that supports the concept of stepping stones. They found that in liverworts, there are few differences among the alleles within a population. Rather, intrapopulation differences are more typically an expression of phenotypic plasticity. But over a larger area, a species typically consists of a series of small populations that are reproductively isolated from each other, presumably due to dispersal limitations on the sperm. They considered that these facts are consistent with repeated dispersal and founder events. Further variation can arise from genetic drift. They found a contradiction in the restricted gene flow between populations and the limited genetic differences among geographically disjunct populations.



Figure 56. *Polytrichum commune* with abundant capsules that provide spores for long-distance travel. Photo by David T. Holyoak, with permission.

Could it be that rather than stepping stones or multiple dispersal events there could have been a single event that left a number of isolated founder populations that were further divided by genetic drift? Such a proposal is not unreasonable. We know that certain weather events can carry dust for long distances [for example from the Sahara in Africa to Texas in the USA or to California, USA

(Reardon 2013) or to southern England (Ken Adams, Bryonet 6 March 2013)] or change the usual direction of weather patterns. Tornadoes can certainly pick up propagules and drop them off in a number of distant locations, sometimes far distant. Hurricanes can make similar deposits, particularly on oceanic islands. Bischler and Boisselier-Dubayle (1997) point out that liverworts have lower levels of genetic variability than do mosses. Rather, they seem to respond to habitat variation by more non-genetic responses through plasticity. Although they consider this to support a history of repeated dispersal and founder events, it does not rule out the possibility of a single dispersal event populating a number of isolated locations, then differing due to genetic drift, founder principle, or subsequent genetic modification. Their success may be due to a genetic complement that permits phenotypic plasticity.

Disjunct distributions always raise questions as to their causes – extinctions, land drift, or incomplete dispersal? Delgadillo (1987) reported that there is evidence of "extensive floristic exchange" in Mexico among the major alpine areas of the Neovolcanic Belt. However, floristic differences and ages among the mountains indicate that dispersal has not been unidirectional nor occurring through a single event. This would seem to indicate that it is not a **flyway** unless air currents change directions, perhaps with seasons. Nevertheless, this range of mountains seems to have provided a **barrier** to the dispersal of some mosses in a north-south direction, but not in the opposite direction. This might be interpreted as an example of "the environment selects," but more ecological information is needed to support that conclusion. In any case, it is likely that mountains present barriers to species that disperse through "stepping stone" pathways and that are unable to survive the climate of the mountain tops.

Dispersal by birds for any instance seems to be discounted by many researchers for a number of regions. Cruden (1966) sums up some of the concerns for transport of seeds:

1. Internal carriage is highly unlikely because it takes at least a month for migration from, for example, California, USA, to Chile, whereas the gut contents are dispelled within a few hours.
2. External carriage is likewise unlikely because the birds frequently preen themselves.
3. The disjunct plant groups do not seem to have any special qualifications for long-distance dispersal. Rather, they live in open, unstable habitats; their seeds can be dispersed by animals; and they are self-compatible.

But some of the objections applied to bird dispersal for tracheophytes do not seem to apply as well to bryophytes. It is unlikely that internal carriage of bryophyte diaspores occurs on long flights, but it could occur in a stepping stone fashion. External carriage is more likely. If a bird in fact walked through a patch of dispersing capsules, numerous spores could adhere. Because of their fine nature and small size, it seems unlikely that preening could remove all of them, and some are also likely able to continue adherence even through the splashing of a bird's bath. Furthermore, like seed plants, only a single spore is needed in the right place to begin a new population, and the birds are likely to

seek out the same kind of habitat as the one where the spore first joined the journey, *i.e.*, a suitable habitat. Cruden (1966) has noticed a correspondence between wintering areas of the birds and plant distributional ranges. He likewise suggests that mountain hopping has been undervalued as a possible migrational route for the plants, in some cases at least following the flyways of the birds. Whereas shorebirds seem to satisfy the long-distance requirements, mountain hopping could account for distribution by a larger number of birds. This latter mechanism could follow the long-distance travel on a shore bird, and at least for bryophytes, seems like a plausible mechanism.

Gene Flow

Gene flow is an indirect measurement of dispersal. While it cannot tell us distance values, it can suggest the magnitude of gene dispersal, hence spore dispersal (assuming that spore dispersal is greater than gamete dispersal). Gene flow results in increased genetic variation within the population and prevents that population from exhibiting genetic differentiation from other populations. For *Leucodon temperatus* and *L. luteus*, both epiphytes, the gene diversity between populations relative to the total diversity was low (Akiyama 1994). Akiyama interpreted this as evidence of extensive gene flow between populations. He considered the low genetic divergence to be a result of their epiphytic habitat, which would suggest that lots of new invasions by spores occurred.

Genetic diversity can be maintained even as a result of small remnant populations in *Trichocolea tomentella* (Figure 57). The apparent infrequent gene flow among populations of this species indicates that it suffers dispersal limitations, even on a small spatial scale. On the other hand, new colonization within a population is not affected by its isolation, suggesting that it benefits from random short-range dispersal of fragments. It furthermore appears to have a long life span that permits it to spread through branching. On the other hand these characteristics suggest that it is not a good colonizer because of its limited dispersal.



Figure 57. *Trichocolea tomentella*, a leafy liverwort. Photo by Michael Lüth, with permission.

Korpelainen *et al.* (2005) evaluated gene flow in bryophytes in a broader context. They found that most bryophyte species (*i.e.*, mostly mosses) have a fair amount of gene flow between populations, based on the genetic differentiation that exists among populations. That suggests that there is a fair amount of invasion of populations by spores of other populations.

On the other hand, Derda and Wyatt (1990, 1999a, b) found genetic evidence in *Polytrichum* species to indicate that distribution of genetic variation by spores was limited. For *P. commune* (Figure 55-Figure 56) the mean genotypic diversity was 0.546. For *P. piliferum* (Figure 58) the mean genetic diversity within populations was only 0.037 (Derda & Wyatt 1999a), whereas in *P. commune* it was 0.061 (Derda & Wyatt 1999b). Derda and Wyatt (1999b) concluded that long distance dispersal did occasionally occur, based on "region-specific multilocus genotypes" that occasionally occurred distant from the apparent parent population. The fact that this species has a worldwide distribution suggests it is capable of at least some long-distance dispersal. More commonly, it appeared that genotypes moved from location to location in a "stepping-stone" fashion. As one would expect, the genetic similarities between regions generally decreased with the distance between the regions. Evidence from *Polytrichum juniperinum* (Figure 59) and *P. strictum* (Figure 60) suggests that dispersal distances and gene flow may depend in part on latitude (Derda & Wyatt 2003). For *P. juniperinum*, Derda and Wyatt found that spore dispersal in the upper Midwest and Pacific Northwest of the USA and Canada was apparently low and relatively less effective south of the Pleistocene glacial margins, whereas colonization from distant refugia seems to have been more effective in the northern latitudes. Members of the **Polytrichaceae** are unique in having an **epiphragm** stretched across the peristome teeth, providing only tiny holes from which spores can be dispersed (Figure 61). Van Zanten (1973) considered that long-range dispersal was unlikely in the **Polytrichaceae** genus *Dawsonia* (Figure 10), citing horizontal spore ejection by raindrops or other agents that strike the mature capsule. It is likely that other members of the family suffer the same problem.



Figure 58. *Polytrichum piliferum* with young capsules. Photo through GNU free documentation license.

Polytrichum strictum (Figure 60), a species that has often been treated as a subspecies of *P. juniperinum* (Figure 59), has some of the highest gene diversity levels

known for mosses (HTP = 0.205), with strong regional partitioning of the genetic structure (Derda & Wyatt 2003). This might be explained by the lack of re-invasion of spores into a colony, permitting genetic drift and gene divergence. This lack of re-invasion is consistent with the poor spore dispersal predicted by Van Zanten (1973).



Figure 59. *Polytrichum juniperinum*. Photo by Li Zhang, with permission.

The story for *Hylocomium splendens* (Figure 33) in Scandinavia seems to be quite different from that of *Polytrichum* (Figure 58-Figure 61). Cronberg *et al.* (1997) found that among populations from four vegetation zones, eleven out of thirteen loci screened by allozyme electrophoresis demonstrated variation. The relative differentiation among the populations was low ($G(ST) = 0.073$), indicating a high level of gene flow between populations. Furthermore, although the Subarctic-alpine population was apparently a single widespread clone, it was comprised of many rare genotypes that often occurred together within 10 x 10 cm patches. Cronberg *et al.* concluded that this population had spread by dispersal of vegetative fragments. In the lowland populations, identical genotypes often occurred in multiple patches, which Cronberg *et al.* interpreted to indicate that these had arisen by independent sexual recombinations, not dispersal. Hmm...Why not by fragments?



Figure 60. *Polytrichum strictum* with male splash cups. Photo by Kristian Peters, through GNU free documentation license.

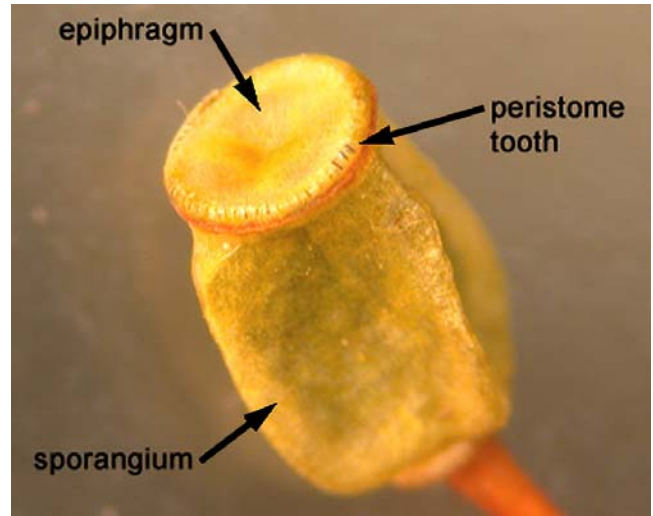


Figure 61. Capsule of *Polytrichum commune* showing epiphragm stretched across the 64 short teeth. Photo with permission from Botany Website, UBC.

It appears that even annual shuttle species that would seemingly rely on dispersal of much more than a few meters may have little genetic mixing between populations. Roads and Longton (2003) found no field germination of spores in *Tortula acaulon* (= *Phascum cuspidatum*; Figure 4) and spores only inconsistently produced gametophytes in *Tortula truncata* (as *Pottia truncata*; Figure 2). As discussed above for the latter species, 67% of the spores never left the clump and 70% were deposited within 2 m. Nevertheless, that left 30% to be deposited farther away. However, there were no genotypes in common between populations and no variation within populations, suggesting that all members of the population had come from a single spore or clone.

Grundmann *et al.* (2007) obtained what seems like conflicting data for *Pleurochaete squarrosa* (Figure 62). Using allozymes, they showed no isolation by distance, but using DNA sequence data instead, there was evidence of isolation based on distance. Shaw (1995) used 15 allozyme loci to assess *Scopelophila cataractae* (Figure 63) and concluded that it was native to both America and Asia, having spread by long-distance dispersal.



Figure 62. *Pleurochaete squarrosa* wet. Photo by David Holyoak, with permission.



Figure 63. *Scopelophila cataractae*, a species that seems to have spread by long-distance dispersal. Photo by David T. Holyoak, with permission.

Many bryophytes exhibit little variation within populations and reasonable variation between populations, suggesting that most within-population members are derived from the same clone. Genetic differences between populations suggest that most have arisen by a single invasion of a single propagule.

Spore Size and Number

Size matters. Aerosols – particles suspended in air like those in smoke – disperse easily to great distances, but the particles typically have a diameter less than 5 μm (Lönnell 2011). Size affects the terminal velocity of falling objects, with increasing size causing a greater terminal velocity (Lönnell 2011). But does this have any meaning for a bryophyte propagule? And if so, how is it affected by updrafts, vortices around the substrate, hydration, or surface ornamentation?

There seems to be an assumption that dispersal declines rapidly as diaspore size increases. As Frahm (2009) reminds us, bryophyte spores, typically only one cell, mostly range in size from 7 μm to 100 μm . Schmidt (1918) considered that spores smaller than 20 μm are easily dispersed, a position supported by van Zanten and Pócs (1981) who thought the small spore size permitted them to lift into the air column more easily. Mogensen (1981) tells us that theoretically, wind that would carry a 20 μm spore for 1000 km would only carry a 55 μm spore approximately 40 km. But experimental evidence for this seems to be lacking, and the large spore size of some ephemeral taxa, such as *Ephemerum* (Figure 64-Figure 65), would seem to suggest that occasionally these large spores do travel. In fact, van Zanten and Gradstein (1988) found no correlation between spore size and species range for neotropical liverworts. They cited three species with some of the largest spores [*Brachiolejeunea phyllorhiza*, *Cheilolejeunea unculoba*, and *Leucolejeunea xanthocarpa* (Figure 66) as having transoceanic distribution

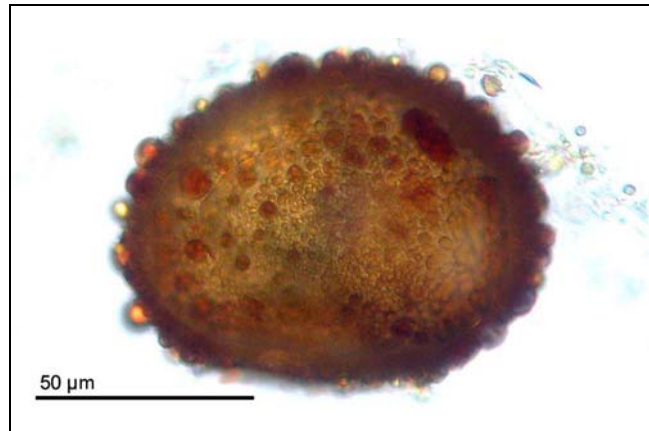


Figure 64. *Ephemerum serratum*. **Upper:** Leafy gametophytes with capsules. **Lower:** One spore. Photos by Michael Lüth, with permission.

In describing dispersal of testate amoebae in the Arctic and Antarctic, Wilkinson (2001) found that the large species (up to 230 μm) were confined to only one of those areas, whereas the cosmopolitan species had a maximum size of 135 μm . Size matters. The same principle of smaller travels farther should be applicable to bryophyte propagules. But most bryophyte spores have a diameter that is less than 50 μm (Lönnell 2011; Figure 67), with liverworts generally having larger spores than mosses, presenting a greater number of species with spore diameters in the 40-100 μm range than do mosses. Among the species for which I could easily find numbers, the liverworts tended to produce fewer spores than the mosses, a factor one might expect to accompany larger spores (Table 2).



Figure 65. *Ephemerum serratum* (formerly *E. minutissimum*) spores. Photo by David T. Holyoak, with permission.



Figure 66. *Leucolejeunea xanthocarpa*, a transoceanic species with large spores. Photo by Jia-Dong Yang, through Creative Commons.

Despite the widespread assumption that small spores lift more easily, hence disperse more easily, than large spores (Van Zanten & Pócs 1981), there seems to be no empirical evidence for the assumption (McIntosh 1997).

McIntosh points out that producing smaller spores permits production of more spores, and just by that increase, the probability of going farther increases.

In their examination of 24 Asian bryophytes, He and Zhu (2010) concluded that mosses have a higher spore output than liverworts (Table 2). They further observed an inverse relationship between spore size and spore number, a conclusion also supported by Lönnell (2011; Figure 68). This is especially borne out in the genus *Archidium* (Figure 22), which may have as few as four spores and these are the largest found among bryophytes (Crum 2001).

Noguchi and Miyata (1957) asserted that mosses that have abundant spores can have wide geographic ranges, but tend to have rather confined habitats. This relationship might relate to spore size, with small spores being more abundant than larger ones. And small spores do not bring with them the nutritional reserve that could give them a good start in their new location. Could this be the explanation for their "confined habitats?"

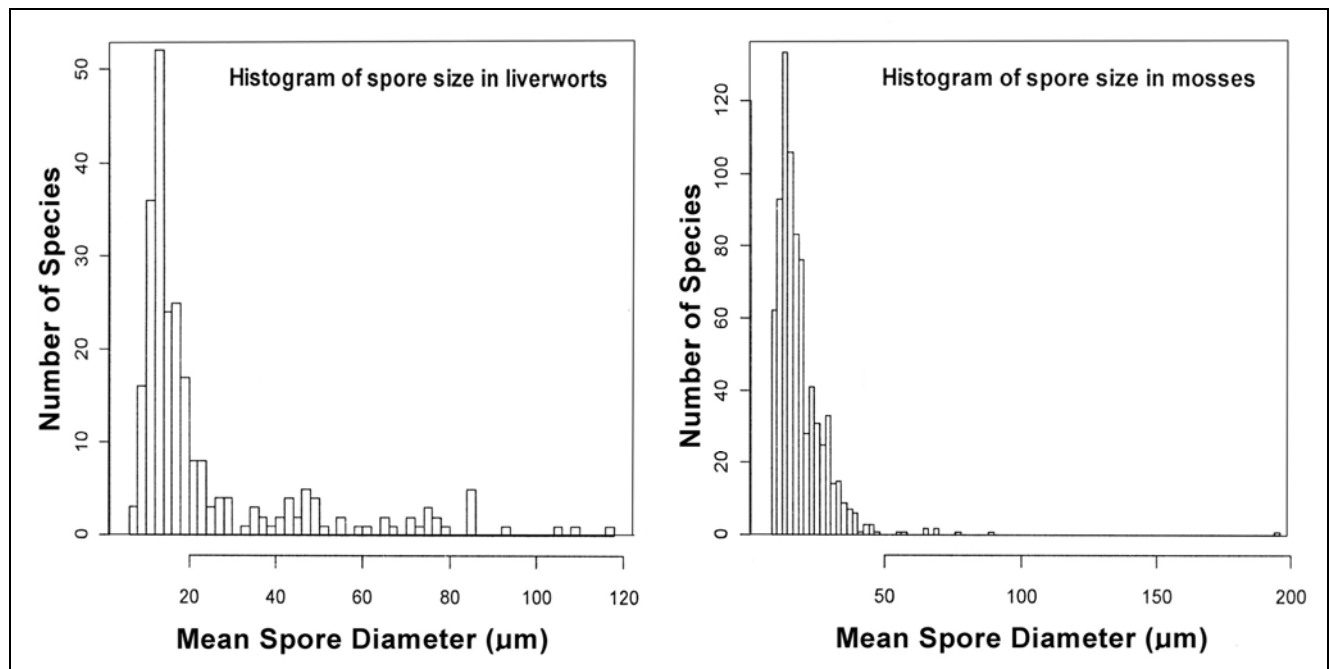


Figure 67. Comparison of spore size distributions in liverworts and mosses. Redrawn from Lönnell 2011.

Table 2. Numbers of spores per capsule in a variety of bryophytes. Liverwort taxa are in bold face.

<i>Archidium</i>	4-28	Ingold 1959	<i>Dicranella varia</i>	71,450	He & Zhu 2010
<i>Riccia gougetiana</i>	192	Schuster 1966	<i>Ditrichum pallidum</i>	79,160	He & Zhu 2010
<i>Riccia glauca</i>	220	Schuster 1966	<i>Jungermannia truncata</i>	84,150	He & Zhu 2010
<i>Riccia crystallina</i>	246	Schuster 1966	<i>Trematodon longicollis</i>	85,800	He & Zhu 2010
<i>Leptocolea</i> (=Cololejeunea)			<i>Lophozia ventricosa</i>		
<i>magnilobula</i>	257	He & Zhu 2011	var. <i>silvicola</i>	86,000	Laaka-Lindberg 2000
<i>Sphaerocarpos michelii</i>	760	Schuster 1966	<i>Chiloscyphus profundus</i>		Jonsson & Söderström 1988
<i>Acrolejeunea emergens</i>	<1000	He & Zhu 2011	= <i>Lophocolea heterophylla</i>	93,000	
<i>Trocholejeunea sandvicensis</i>	1450	He & Zhu 2010	<i>Orthocaulis</i> (=Barbilophozia)		Jonsson & Söderström 1988
<i>Fossombronia foveolata</i>			<i>attenuata</i>	115,000	
var. <i>cristula</i>	1660	He & Zhu 2010	<i>Sphagnum lindbergii</i>	129,545	Sundberg 2002
<i>Sauteria alpina</i>	2100	Schuster 1966	<i>Sphagnum palustre</i>	130,000	He & Zhu 2010
<i>Reboulia hemisphaerica</i>	2410-2500	Schuster 1966; Patidar <i>et al.</i> 1987	<i>Ceratodon purpureus</i>	100,000-120,000	Kreulen 1972
<i>Monosolenium tenerum</i>	3160	He & Zhu 2010	<i>Grimmia pulvinata</i>	200,000	Ingold 1959
<i>Pellia epiphylla</i>	4500	Schuster 1966	<i>Sphagnum squarrosum</i>	243,000	Sundberg & Rydin 1998
<i>Ptychanthus striatus</i>	5038	He & Zhu 2011	<i>Tetraplodon angustatus</i>	250,830	He & Zhu 2010
<i>Conocephalum conicum</i>	5300	Schuster 1966	<i>Rhynchostegium serrulatum</i>	280,000-700,000	Ingold 1959
<i>Tortula acaulon</i>			var. <i>confertum</i>	250,000-750,000	Ingold 1974
<i>Phascum cuspidatum</i>	5500	Ingold 1959	<i>Tetraphis pellucida</i>	348,300	He & Zhu 2010
<i>Preissia quadrata</i>	8000	Schuster 1966	<i>Scapania</i> (=Diplophyllum)		
<i>Targionia hypophylla</i>	1196-7385	Patidar <i>et al.</i> 1987; He & Zhu 2010	<i>albicans</i>	400,000	Schuster 1966
<i>Physcomitrium courtoisii</i>	8760	He & Zhu 2010	<i>Polytrichastrum alpinum</i>	440,000-873,000	Convey 1994
<i>Anthoceros agrestis</i>	>17,000	Bisang 2001	<i>Atrichum undulatum</i>	450,000	Ingold 1959
<i>Sphagnum tenellum</i>	18,500	Sundberg & Rydin 1998	<i>Funaria hygrometrica</i>	55,800-495,000	Nakosteen & Hughes 1978; He & Zhu 2010
<i>Pohlia elongata</i>	20,700	He & Zhu 2010	<i>Polytrichastrum sexangulare</i> var. <i>vulcanicum</i>		
<i>Cephaloziella varians</i>	14,000-23,750	Lewis Smith & Convey 2002	(= <i>Pogonatum sphaerothecium</i>)	516,200	He & Zhu 2010
<i>Lophocolea cuspidata</i>	23,900	Schuster 1966	<i>Dicranum scoparium</i>	523,500	He & Zhu 2010
<i>Reboulia hemisphaerica</i>	25,000	Schuster 1966	<i>Haplocladium microphyllum</i>	675,830	He & Zhu 2010
<i>Ptilidium pulcherrimum</i>	27,400	Jonsson & Söderström 1988	<i>Pogonatum dentatum</i>	712,000	Ingold 1959
<i>Schistostega pennata</i>	36,000	Ingold 1959	<i>Scapania undulata</i>	1,000,000	Schuster 1966
<i>Anastrophyllum hellerianum</i>	42,000	Pohjamo & Laaka-Lindberg 2003	<i>Tortula muralis</i>	1,000,000	Ingold 1959
<i>Sphagnum rubellum</i>	54,000	Sundberg 2002	<i>Polytrichum juniperinum</i>	1,400,000	Kreulen 1972
<i>Riccardia</i> sp.	56,400	He & Zhu 2010	<i>Buxbaumia viridis</i>	1,000,000-9,000,000	Wiklund 2002
<i>Sphagnum papillosum</i>	62,250	He & Zhu 2010	<i>Polytrichastrum formosum</i>	2,200,000	Ingold 1959
<i>Sphagnum junghuhnianum</i>	68,750-73,300	He & Zhu 2010	<i>Buxbaumia aphylla</i>	5,500,000	Ingold 1959
			<i>Polytrichum commune</i>	8,983,000	He & Zhu 2010
			<i>Dawsonia lativaginata</i>	80,000,000	Kreulen 1972

Lönnell (2011) compared spore sizes among spore-producing organisms, considering those of bryophytes to range 10-50(-100) μm , fungi 3-10(-300) μm , and ferns 30-100 μm . Crum (2001) gives a broader range from 5 (*Dawsonia*; Figure 10) to 310 (*Archidium*; Figure 22) μm , but few are greater than 30 μm . The generalization still holds that those taxa that produce small spores produce lots of them and those with large spores produce few (Schuster 1984) (50 million in *Dawsonia*, 4 in *Archidium*; (Table 2).

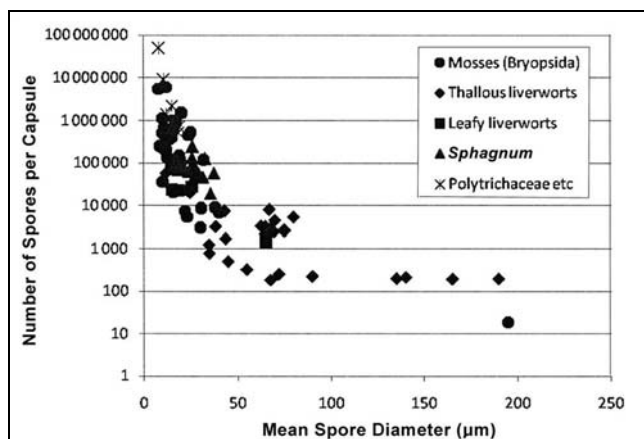


Figure 68. Inverse relationship of number of spores produced per capsule to spore size. Redrawn from Lönnell 2011.

Large Spores

Archidium (Figure 22), as a genus, sets the record for spores size in mosses. This larger size permits it to maintain a large food reserve that becomes available when the moss germinates. In its open habitat, this permits it to develop quickly and complete its life cycle before conditions once again become unfavorable for growth. *Archidium brevinerve* has the largest average spore diameter (235 μm); *A. ohioense* (Figure 69) has the largest measured spore (310 μm) (Snider 1975). In Europe the most widespread species in the genus is *A. alternifolium* (Figure 22) with an average spore size of 162 μm and range of 139-223 μm (Boros *et al.* 1993). Among the liverworts, *Asterella* has spores 135-160 μm in diameter (Figure 70). *Sphaerocarpos* (Figure 71-Figure 72) sheds its spores in tetrads, making those spore dispersal units quite large. They furthermore are highly decorated, creating air spaces that could increase surface area without adding weight and increasing floatability. Some spores are **precocious** (Figure 75), *i.e.*, germinating within the spore wall and typically before leaving the capsule. Such spores are consequently larger and presumably heavier, as for example those of *Tuyamaella molischii* (Lejeuneaceae; Figure 73-Figure 75) that are up to 140 μm long (Rui-Liang Zhu, Bryonet 6 March 2013).



Figure 69. *Archidium ohioense* with sporophytes. Photo by Li Zhang, with permission.

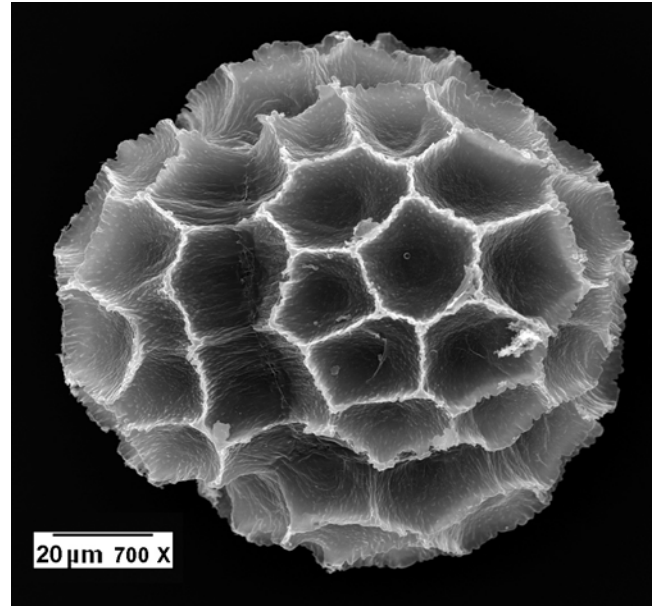


Figure 72. *Sphaerocarpos texanus* spore SEM, showing highly decorated wall. Photo courtesy of Karen Renzaglia.

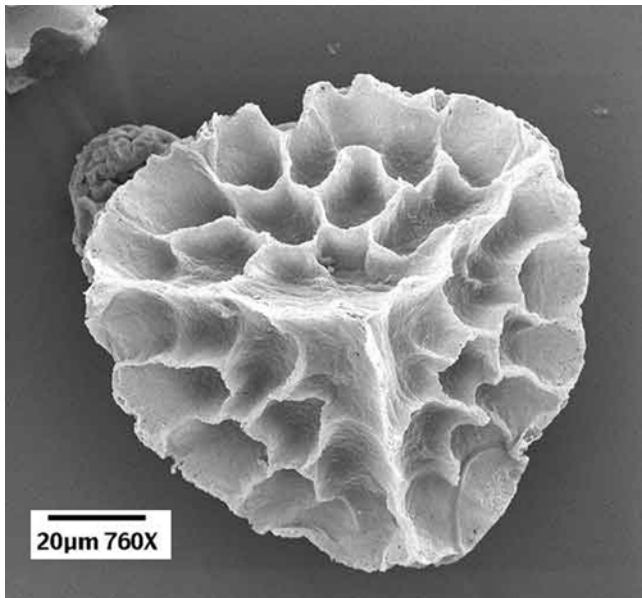


Figure 70. *Asterella bolanderi* spore proximal view SEM. Photo by William T. Doyle, with permission.



Figure 73. *Tuyamaella molischii* var. *molischii*, an epiphyllous liverwort from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.



Figure 71. *Sphaerocarpos michelii*. Photo by Jan-Peter Frahm, with permission.



Figure 74. *Tuyamaella molischii* var. *molischii* capsules from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

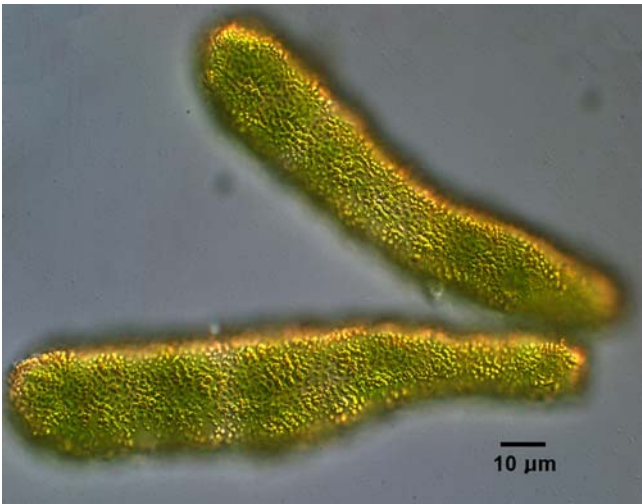


Figure 75. *Tuzymaella molischii* var. *molischii* precocious spore development, from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

In *Archidium alternifolium* (Figure 22), little or no protonema develops when the spore germinates (Miles & Longton 1992a). Rather, a germling shoot arises from the dehiscing spore(!), or shortly thereafter from a short protonema. This ability most likely arises through the complements of an adequate food supply in the large spore, precluding the need for a protonema to store such energy before a shoot can be formed. But other factors might also be at play. Could it be that necessary hormones to stimulate the shoot growth are carried in this large spore, sacrificed in small spores to make room for the little bit of nutrient matter it can provide? Such hormones, in the case of small spores, might then be provided by the protonema, or in the surrounding environment (see discussion on Delayed Germination in subchapter 4-7).

It appears that the large size of the spore in *Archidium alternifolium* (Figure 22) might afford other advantages as well. When Miles and Longton (1992a) cultivated the spores on agar, germination spanned a period of several months. Furthermore, the spores remained viable for up to four years following field collection of fresh material. But it is interesting that in the field these spores seem to lack what it takes for any dispersal. Rather, they remain in the capsule, attached to their parent plants. Despite the spore longevity and size, according to Miles and Longton, it is the fragments that predominate in the diaspore bank and form the recolonizing population following disturbance.

Convey and Lewis Smith (1993) suggested that large spore sizes observed in short-lived species may be important in local colonization in the Antarctic. Those taxa that are annual or short-lived invest more in spore dispersal than those in most perennial taxa. Nevertheless, on Signy Island in the Antarctic, spore size did not seem to influence dispersal potential in the five taxa identified (Marshall & Convey 1997).

For whatever reason, acrocarpous spores of Michigan, USA, mosses are generally smaller (mostly <25 μm in diameter) than those of pleurocarpous taxa (mostly >25 μm), based on sizes provided by Crum (1973). These evolutionary trends may not relate to habitat, but we do know that pleurocarpous mosses are perennial and rely less on spores for their reproduction than do many of the

acrocarpous taxa. Having larger spores provides more energy for a better start in life. Liverwort taxa may have a similar division between leafy and thallose taxa, if Schuster's table (Table 3) on spore size is any indication, but the number of taxa represented is far too small to draw any generalizations.

Table 3. Spore size (μm) in liverworts. The first six are leafy. Based on Schuster (1966).

<i>Scapania</i> (= <i>Diplophyllum</i>) <i>albicans</i>	10-14
Blepharostomaceae	8-16
<i>Chiloscyphus</i> (= <i>Lophocolea</i>) <i>cuspidata</i>	14-16
<i>Scapania undulata</i>	15-20
<i>Selaginella</i> (= <i>Herbertus</i>) <i>adunca</i>	25
Ptilidiinae	15-65
<hr/>	
<i>Sphaerocarpos michelii</i>	30-40
<i>Pellia epiphylla</i>	50-60
<i>Sauteria alpina</i>	60-70
<i>Preissia quadrata</i>	60-75
<i>Ricciella</i> (= <i>Riccia</i>) <i>crystallina</i>	65-80
<i>Reboulia hemisphaerica</i>	60-90
<i>Conocephalum conicum</i>	70-90
<i>Riccia glauca</i>	80-100
<i>Riccia gougetiana</i>	180-200

The number of spores per meter square is a function not only of the number of spores per capsule, but also the density of the capsules present. Some of these numbers are enormous (Table 4).

As already noted, spore number is determined not only by the number per capsule, but also by the number of capsules produced. More capsules can correlate with wider dispersal and wider distribution. Robinson (1990) pointed out this relationship in the **Leucobryaceae**, where *Octoblepharum albidum* (Figure 76) typically has many sporophytes and has one of the widest distributions in the family. In many genera in this family, sporophytes are reduced, but propagation by leaves and leaf fragments is common. Robinson suggests that birds and other arboreal animals could facilitate dispersal among the epiphytic members of the family.

Spore size is an integral part of life history strategies. Longton (1988) summarized some of these relationships for arid regions. He found that perennial stayers are typically acrocarpous mosses with small spores, long spores, and "other features promoting dispersal." Annual shuttle species, conversely, produce large spores, often in submersed capsules, promoting rapid germination and establishment *in situ*, but not well adapted for dispersal. Perennial shuttle species are mostly marchantialian liverworts with large spores. Fugitives stay at a given site and are able to do this by having small, easily dispersed spores.

Jenkins *et al.* (2007) attempted to use existing data from many data sets to answer the question of size vs dispersal distance. They divided organisms into active and passive dispersers, defining active dispersers as those that arrived at a new location under self-propulsion. This includes most vertebrates and arthropods, but many other animals depend primarily on passive sources. Plants, including bryophytes, are mostly passive dispersers.

Jenkins and coworkers found that active dispersers, as expected, dispersed significantly farther and were significantly greater in size ($P < 0.001$). Passive dispersers, on the other hand, had random dispersal distances compared to mass/size. They concluded that while size is important for active dispersers, it is not for passive dispersers. But could there still be a relationship for dispersal units less than a certain size that permits them to be dispersed by air currents? Jenkins *et al.* consider that dispersal-size relationships for microbes cannot be tested by direct observation. Perhaps that for bryophytes will be somewhat easier. In their analysis for passive dispersers, Jenkins and coworkers used organisms weighing in the range of 10^{-8} to 10^{-9} g, dominated by plant seeds. This hardly seems a good model for bryophytes with single-celled spores as their dispersal agents.

Table 4. Number of bryophyte spores per m^2 . Liverwort taxa in bold face.

<i>Anthoceros agrestis</i>	14 mil/ m^2	Bisang 2001
<i>Sphagnum</i>	16 mil/ m^2	Sundberg 2002
<i>Atrichum undulatum</i>	37 mil/ m^2	Longton & Schuster 1983
<i>Pleurozium schreberi</i>	100 mil/ m^2	Longton 1976
<i>Ptilidium pulcherrimum</i>	20-300 mil/ m^2	Jonsson & Söderström 1988
<i>Grimmia pulvinata</i>	7,400 mil/ m^2	Longton & Schuster 1983
<i>Tortula muralis</i>	38,300 mil/ m^2	Longton & Schuster 1983



Figure 76. Capsules of the epiphytic *Octoblepharum albidum*. Photo by Janice Glime.

Spore Weight

Hughes *et al.* (1994) developed a set of provisional conclusions regarding the relationship of dispersal mode and other attributes of plants and their habitats. Although these were developed with seed plants in mind, examining them for bryophytes might be instructive in developing our own hypotheses. They concluded that seeds larger than 100 mg tend to be adapted for dispersal by vertebrates, whereas those less than 0.1 mg tend to be unassisted.

Bryophyte spore weights do not seem to have been a priority for bryologists, so it is necessary to estimate. Most spores range from 20 to 100 μm in diameter (Boros *et al.*

1993). A 20 μm spore has a radius of 10 μm . Knowing that, we can calculate its weight by assuming it is a sphere, starting by determining the volume ($V = 4/3 \pi r^3$). Hence, the volume would be $4.188 \times 1000 = 4188$ cubic microns. Assuming that a spore is mostly water, and knowing that the weight of water is 1000 g per liter, a cubic micron is 10^{-15} L or 10^{-9} μL . Hence, 1 cubic micron weighs 10^{-12} grams or 10^{-3} nanograms. A 20 μm spore would weigh only 4.2×10^{-9} g (0.0042 μg , or 4.2 nanograms) when fully hydrated ($V = 4/3 \pi r^3 = 4188$ cubic μm ; 1 cubic $\mu m = 10^{-9}$ μl ; 1 $\mu l = 1$ μg of water; 1 μg weighs 1 million picograms). Using a sphere as our model, we can derive the formula:

$$\begin{aligned} \text{spore weight} &= 4/3 \pi r^3 (10^{-3}) \text{ nanograms} \\ \text{or} \\ \text{spore weight} &= 4/3 \pi r^3 (10^{-6}) \mu g \end{aligned}$$

It is rather easy to do this calculation at <<http://www.wolframalpha.com>> and inserting "weight of sphere of water 20 microns in diameter."

Spores that are 100 μm in diameter would weigh 0.524 μg and often travel only downward by gravity, as in *Archidium* (Figure 22). Since bryophyte spores therefore fall in the less than 0.1 mg category, they support the hypothesis of Hughes *et al.* (1994) that diaspores less than 0.1 mg tend to be dispersed unassisted. Nearly all of the spores of bryophytes are apparently unassisted in their dispersal (*i.e.*, unassisted by animals, with only undirected wind and water for assistance).

Even at 300 μm diameter in *Archidium* (Figure 22) (Snider 1975), the spores of such bryophytes would weigh only 14.1 μg . Spores are usually dry when they travel, making them even less in weight.

The formula provides an estimate of the maximum weight of a spore with the density of water. Most spores are not fully hydrated and the spores may be slightly flattened into a tetrahedron with one rounded side. Whitaker and Edwards (2010) assumed a spore shape of a tetrahedron with a circular base to calculate the weight of a *Sphagnum* spore and determined a weight of 1.7 nanograms for a spore with a base diameter of 28 μm . If we assume that this spore is all water and spherical with a diameter of 28 μm , it would weigh 11.5 nanograms, a rather substantial difference in estimation caused not only by the shape assumption, but also by the water assumption.

Spores vary in weight between species, even at the same spore sizes. These variations depend on food reserves and water content (Jeff Duckett, Bryonet 6 March 2013). Green spores are short-lived, commonly remain hydrated, and typically store their food as starch, giving them a specific gravity greater than 1 and making them heavier than brown spores. Brown spores are generally smaller, long-lived, and use both protein and lipid reserves. They are usually very dehydrated and have a specific gravity considerably less than 1. Hence, green spores usually sink in water; brown ones usually float and, presumably, more easily become airborne.

But Gradstein (Bryonet 11 March 2013) argues that green vs non-green spores from nearly 100 tropical species do not correlate with range sizes or with long-range dispersal, based on an experimental study (van Zanten & Gradstein 1988). No differences correlated with drought or

low temperatures for exposures from a few hours to a year or more.

We can estimate weight by the size of the spore, but as noted, not all spores are created equal. The specific gravity is a more important measure of the transportability than the weight (mass) alone. Peter Poschlod (pers. comm. 6 March 2013), like Duckett, points out that some spores float on water whereas others sink. Among the ones that sink immediately are those of *Sphagnum*. Using spore traps in peatlands, Poschlod (1995) was unable to find any *Sphagnum* spores. Rather, the traps produced vegetative parts, especially those of *Sphagnum* (Figure 77). Dry *Sphagnum* is especially light weight and easily becomes airborne, as I witnessed one day while watching ants trying to repair their mound during a windstorm. In grasslands, on the other hand, vegetative diaspores tended to be the exception. Nevertheless, in the grasslands it appeared that grazing animals, especially sheep, transported the mosses, particularly ones such as *Abietinella abietina* (Figure 78) that in Central Europe does not produce capsules.



Figure 77. *Sphagnum* protonemata growing on a *Sphagnum* branch in the field. Photo by Andras Keszei, with permission.

Survival and Longevity

Some spores, under the right conditions, can survive extremely long periods (Table 5). Gubin *et al.* (2003) reported viable moss spores from permafrost sediments in northeast Eurasia, citing ages of tens to thousands of years of preservation.



Figure 78. *Abietinella abietina*, a species that seems to be transported by sheep in grasslands. Photo by Michael Lüth, with permission.

Van Zanten and Pócs (1981) surmised that spores from taxa in dry habitats had a generally greater drought resistance than those from wet habitats. Since liverworts tend to live in wetter habitats, grow where there is less air turbulence, and have larger spores, they further concluded that moss spores should be expected to travel farther.

Most spores that arrive at a given area will not have travelled terribly far. The majority will land within a few cm to a meter of the parent, but some are carried by air currents to far off places. In this longer transport, they will be subjected to high UV radiation and extremes of moisture and temperature.

Table 5. Known longevity for bryophyte spores, based mostly on Crum 2001 and arranged from least to most. Liverworts are in bold face.

Lejeuneoideae	7-8 d	Gradstein 1994
<i>Cyathodium tuberosum</i>	9 mos	Tiwari 1935
<i>Conocephalum conicum</i>	<1 mo	Crum 2001
<i>Plagiochasma intermedium</i>	<1 yr	Crum 2001
<i>Blepharostoma trichophyllum</i>	1 yr	Crum 2001
<i>Polytrichastrum alpinum</i>	16 mos	Crum 2001
<i>Marchantia polymorpha</i>	<17 mos	O'Hanlon 1926
<i>Riella americana</i>	17 mos	Studhalter 1931
<i>Grimmia elatior</i>	17 mos	Crum 2001
<i>Mannia fragrans</i>	<18 mos	Inoue 1960
<i>Targionia hypophylla</i>	18 mos	O'Hanlon
<i>Grimmia muehlenbeckii</i>	18 mos	Crum 2001
<i>Physcomitrium pyriforme</i>	2 yrs	Meyer 1941
<i>Preissia commutata</i>	>2 yrs	Teodoresco 1929
<i>Anomodon longifolius</i>	29 mos	Crum 2001
<i>Sphagnum</i>	3 yrs	Chalaud 1932
<i>Riella paulsenii</i>	3 yrs	Porsild 1902
<i>Brachythecium velutinum</i>	1.5-4 yrs	Herguido & Ron 1990
<i>Blindia acuta</i>	4 yrs	Crum 2001
<i>Microbryum starckeanum</i>	4.75 yrs	Lesage 1918
<i>Bucklandiella (=Racomitrium sudeticum)</i>	7 yrs	Crum 2001
<i>Aloina ambigua</i>	9 yrs	Llo Stark, pers. comm.
<i>Dicranoweisia cirrata</i>	9 yrs	Malta 1922
<i>Funaria hygrometrica</i>	11 yrs	Hoffman 1970
<i>Riella capensis</i>	13 yrs	Studhalter 1931
<i>Riella affinis</i>	16 yrs	Tenge 1959
<i>Ceratodon purpureus</i>	16 yrs	Chalaud 1932
<i>Anoetangium aestivum</i>	19 yrs	Malta 1922
<i>Oedipodium</i> sp.	20 yrs	Chalaud 1932
<i>Dicranella</i> sp.	50 yrs	Chalaud 1932
<i>Ricciocarpos natans</i>	50 yrs	Conrad 1996

Sphagnum in experiments suggest that *Sphagnum* spores may have a half-life of 1-20 years, but that individual spores may survive for several decades and possibly even centuries (Sundberg & Rydin 2000). Refrigerated spores retained 15-35% viability for 13 years.

Some of the records of spore longevity from herbarium specimens have been suspect due to the possibility for contamination. However, Bristol (1916) reported germination of spores and development of protonemata from spores that had been collected from the top 24 cm of soil in Great Britain 49 years earlier and stored in bottles.

Egunyomi (1979) tested the germination success of tropical moss spores that had been stored at room temperature for various periods of time from 1-3.5 years. Of the 22 species tested, 15 failed to germinate at all. Five species had better than 50% germination. He chose four of

these (*Microcampylopus nanus*, *Weissia papillosa*, *Mittenothamnium overlaetii*, *Weisiopsis nigeriana*) that had been stored at least two years for further experimentation of extreme conditions for 4 weeks: -2°C, 8°C, continuous immersion in water at room temperature, alternate wetting and air drying every 24 hours. None of the species at -2°C survived for 4 weeks. At 8°C, all survived four weeks, with survival percentages ranging 43-81%. Continuous immersion, like the -2°C, resulted in 0% survival after 4 weeks, but alternate wetting and air drying resulted a range of 45-76% survival with the success ranks by species being the same as in the 8°C treatment.

Atmospheric Conditions – UV and Desiccation

It is likely that conditions that favor the dispersal of protozoa and algae also favor the dispersal of bryophyte spores. Hence, we might expect cloudy or overcast skies to help filter UV light (Schlichting 1961). Fires and volcanoes can put particulates in the atmosphere, likewise serving as UV filters. Clouds also can prevent severe desiccation.

Drought Tolerance

Drought tolerance has the greatest correlation with transoceanic distribution (van Zanten & Gradstein 1988). Van Zanten and Gradstein found that only 5% of the transoceanic species had lost the ability to germinate after five days (the minimum time calculated for crossing the Atlantic), whereas 32% of the endemic species exhibited that limitation. Among the transoceanic species, half were able to germinate after 70 days, whereas among the endemic species only half could still germinate after 25 days. Six transoceanic species could still germinate after 100 days of desiccation: *Anastrophyllum auritum* (60% germination), *Andrewsianthus jamesonii* (50%), *Gymnocoleopsis multiflora* (50%), *Herbertus subdentatus* (Figure 79) (40%), *Dumortiera hirsuta* (Figure 80) (10%), and *Chiloscyphus* (as *Lophocolea*) *muricata* (Figure 81) (5%). Some even lasted 150 days. Nevertheless, three endemic species germinated after 100 days of desiccation: *Cephalozia crassifolia* (Figure 82) (10%), *Marchantia chenopoda* (Figure 83-Figure 84) (80%), and *Fossombronia* sp. (Figure 85) (80%), with the latter species even germinating after 150 days. These three endemic taxa have large, dark-colored spores, suggesting they could also survive UV light, but van Zanten and Gradstein suggest that these are probably adaptations for surviving adverse climatic periods, not long-distance dispersal.



Figure 79. *Herbertus subdentatus*, a species with 40% germination after 100 days desiccation. Photo by Michael Lüth, with permission.



Figure 80. *Dumortiera hirsuta* thallus with archegoniophore, a species whose spores had 10% survival of desiccation for 100 days. Photo by George Shepherd, through Creative Commons.



Figure 81. *Chiloscyphus muricatus*, a species whose spores had 5% survival of desiccation for 100 days. Photo by Andrew Hodgson, with permission.

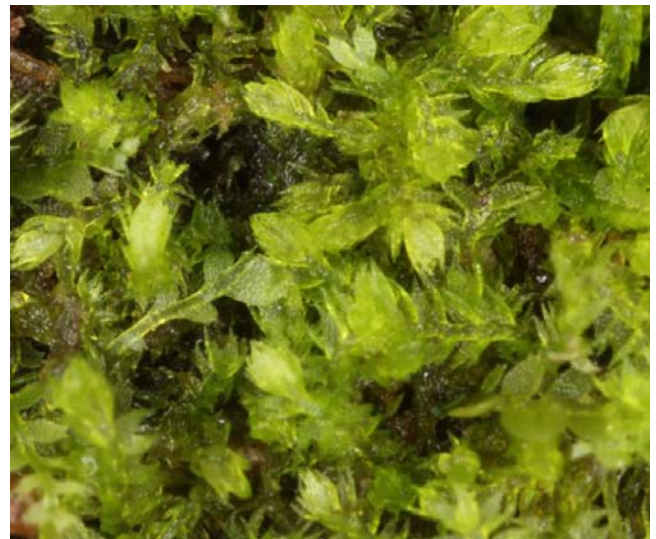


Figure 82. *Cephalozia crassifolia*, an endemic species whose spores had 10% survival of desiccation for 100 days. Photo by Jan-Peter Frahm, with permission.

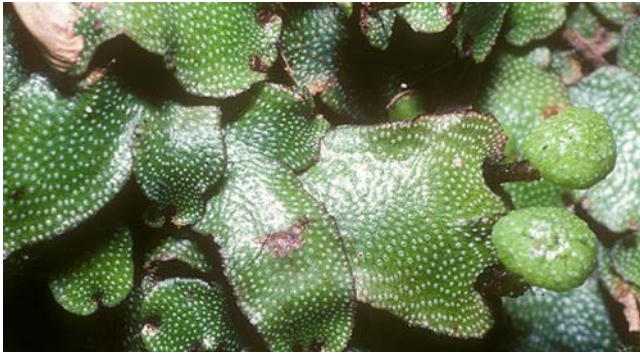


Figure 83. Thallus and antheridiophores of *Marchantia chenopoda*, an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Janice Glime.



Figure 84. *Marchantia chenopoda* with archegoniophore and gemma cups. Photo by Janice Glime.



Figure 85. *Fossombronina japonica*, genus with an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Li Zhang, with permission.

The liverwort *Gymnocoleopsis multiflora* has unusual spores that are very durable despite thin spore walls and hygrophytic habit (van Zanten & Gradstein 1988). Both spores and sporelings are fairly resistant to UV radiation, as well as being very durable. These appear to be adapted to the high alpine habitat where it lives. By contrast, *Riccardia amazonica* and *Stictolejeunea balfourii* live in the understory of wet primary rainforest and their spores have very poor drought resistance. Such examples suggest that the spore adaptations may be more related to the habitats of the parents than to dispersal capabilities. In fact, most of the transoceanic species van Zanten and Gradstein tested came from more open habitats such as forest margins – habitats that would require more of the

same habitat adaptations as long-distance space travel, and where getting into the airstream may be easier than in the forest.

Frost Resistance

Van Zanten and Gradstein (1988) found that spores of transoceanic species had significantly better frost tolerance than endemic species, especially among spores that were desiccated for one week before the freezing treatment. Those spores that had been dried had better resistance in small-spored species than in large-spored ones, suggesting again that small-spored species should travel farther.

Nevertheless, wet freezing does not seem to favor the transoceanic species more than the endemic species (van Zanten & Gradstein 1988). Hence, it is not likely to affect the dispersability of liverworts. Interestingly, fresh spores are less likely to survive dry freezing, and this danger is more pronounced in the endemic species.

UV Protection

The greatest danger, considered by van Zanten (1976) and van Zanten and Gradstein (1988), is that of UV radiation damage. This poses a special problem because dry conditions that make them light in weight are also usually sunny conditions. Schlichting (1961) considered the greater success of UV-sensitive organisms (algae and protozoa) under humid and cloudy conditions to be due to the diminished impact of UV radiation, a concept supported by van Zanten and Gradstein. The added moisture also counteracts the severe desiccation often experienced in the upper atmosphere. The fact that algae have been collected by aircraft from 2000 m above the Earth suggests that bryophyte diaspores likewise occur there. Schlichting (1958) even reported viable moss spores from fingerbowls exposed at 2 m above the ground over periods of 45 minutes to 32 hours.

But we also know that UV light is used to kill cells, and bryophyte spores are no exception. Van Zanten and Gradstein (1988) tested the effects of UV radiation on spores in nearly 100 tropical liverwort species by flying them from Amsterdam to Los Angeles on the wings of a commercial 747 jet. Only two species, both from above 3000 m asl in the Andes, survived the journey, suggesting that the jet stream is not an available avenue to most species, at least among liverworts. This greater resistance to UV damage displayed by high altitude species may explain the distribution of species along mountains – perhaps a better explanation than the flyway explanation. But the two aspects could work together. In short, most species seem to be unable to survive the dosage of UV radiation required for long-distance dispersal under most conditions.

Some spores travel with chlorophyll. But van Zanten and Gradstein (1988) found no correlation between chlorophyll presence and species range. Furthermore, they found no relationship between precocious germination and local dispersal or between non-green and long-distance dispersal. There also seemed to be no dormancy effect.

Some spores have dark pigments; others have cuticular ridges or other extrusions, including papillae. It would be interesting to correlate those characters with success of the spores in travelling long distances where they must survive the greater desiccation and UV light of the atmosphere.

We need to understand just what levels of UV are present under dispersal conditions, what levels kill spores and other diaspores, and how long the exposure must last to cause damage. On the other side, we need to understand what characteristics of spores protect them from this damage, how moisture affects that damage potential, and is there a set of conditions and adaptations that would permit long-distance dispersal.

Liverwort Spore Survival

Fulford (1955 in Schuster 1966) considered that spore survival of leafy liverworts was short, but she actually had only one citation (Figure 86; Bernstein 1928) – for one species (*Blepharostoma* sp; Figure 87) – to back up this assumption; since then we have learned that some have considerable longevity. Inoue (1960) tested spore longevity in six liverwort taxa (Table 6) and found survival up to 18 months in three of them. Malta (1922) failed to obtain germination of spores from *Plagiochila asplenioides* (Figure 88) or *Pellia epiphylla* (Figure 89-Figure 90) after four years or of *Preissia quadrata* (Figure 91) after eight years of storage. Nevertheless, as van Zanten and Gradstein (1988) have demonstrated, those species with transoceanic distributions typically have longer viability.

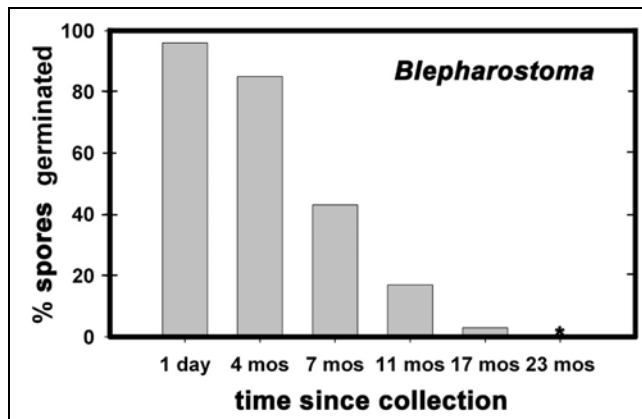


Figure 86. Decline in spore germination in *Blepharostoma* from the first day after collection onward. * refers to one spore that germinated out of 512 after 23 months. Based on data from Bernstein 1928.

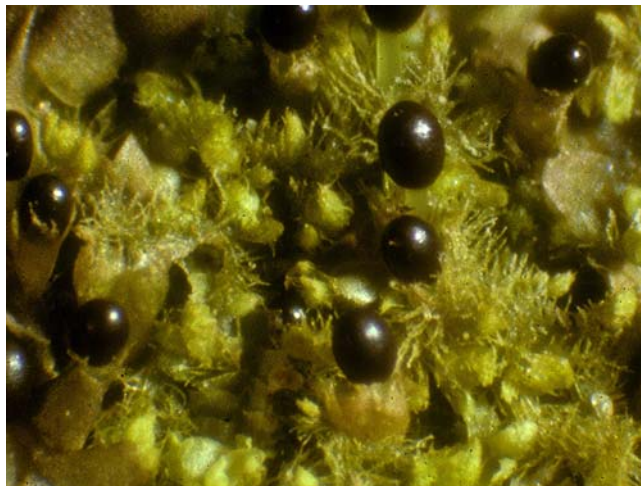


Figure 87. *Blepharostoma trichophyllum* with capsules, a species with short spore survival. Photo by Janice Glime.

Table 6. Percentage of spore viability in Marchantiales. From Inoue (1960).

	1 mo	6 mos	12 mos	18 mos
<i>Reboulia hemisphaerica</i>	100	100	95	11.3
<i>Plagiochasma intermedium</i>	-	48	0	0
<i>Mannia fragrans</i>	100	100	76	0.0
<i>Marchantia polymorpha</i>	100	100	87	43
<i>Marchantia paleacea</i>	100	100	72	21
<i>Conocephalum conicum</i>	0	0	0	0



Figure 88. *Plagiochila asplenioides*; spores failed to germinate after four years of storage. Photo by Dick Haaksma, with permission.



Figure 89. *Pellia epiphylla* with sporophytes; spores failed to germinate after four years of storage. Photo by Kristian Peters, with permission.



Figure 90. *Pellia epiphylla* spore. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

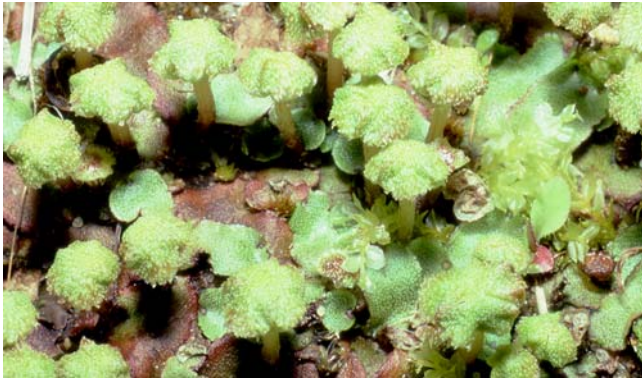


Figure 91. *Preissia quadrata* with archegoniophores; spores failed to germinate after eight years of storage. Photo by Janice Glime.

Schuster (1983) has suggested that many liverworts that survive as relict populations are limited in their dispersal success by being dioicous, being unable to withstand desiccation, and lacking asexual reproductive structures. He suggested further that successful dispersal can be enhanced by 1) formation of sexual propagules (*Lophozia-Scapania* model), 2) production of large numbers of very small spores per sporophyte (numerically overwhelming), 3) dispersal of spores mixed as monads, diads, and tetrads (*Haplomitrium* model) (see Figure 92), 4) spores permanently united in tetrads (*Cryptothallus-Sphaerocarpos* model), 5) acquisition of desiccation tolerance coupled with numerical overwhelming (xerothermophyte model), and 6) monoicium (*Calypogeia-Isopaches* (= *Lophozia bicrenatus-Cololejeunea* model).

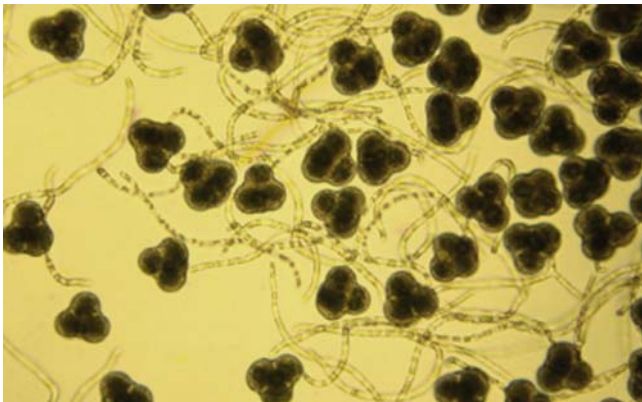


Figure 92. *Porella navicularis* spore tetrads as they appear after meiosis and before separation. From botany website, University of British Columbia, with permission.

Adaptations for Survival

Many bryophyte spores seem to be particularly endowed to survive extremes during their travels. The first evidence of this is that they have resisted decay and remain in huge numbers in deposits from the Silurian and Devonian periods. But biochemical evidence tells us more of their survival capabilities. Each spore obtains a **callose** (glucose polymer related to cellulose) deposit before the **exine** (outer layer of spore) completely forms (Crum 2001). Then the exine attains a **polysaccharide** deposit impregnated with **sporopollenin** (that waxy substance similar to cutin that covers pollen). Last, the **intine** develops with cellulose and other polysaccharides. Once

the formation of the wall is complete, **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, and **Bryopsida** spores deposit a **perine** layer that creates ornamentation. As Crum (2001) describes it, this layer is the "detritus" from the walls of the spore mother cells and remains of the columella. Thus, liverworts and hornworts, lacking a columella, also lack the perine deposit. It is the sporopollenin layer that affords all these spores their resistance to water and decay (Crum 2001).

There is considerable documentation that under the right conditions, some spores can survive for considerable periods. Green spores, typical of species that occur in moist habitats, have a shorter viability due to their higher metabolic rate (Crum 2001). Green spores store starch as their food reserve, but yellow spores, those of longer viability, typically store oils and these species are common in drier habitats. Marin (1981) reported that among 120 species of mosses, green spores were more common (87%) than non-green spores. All epiphytic mosses had green spores, whereas non-green spores occurred in taxa of drier or disturbed soils and rocks. Some taxa use protein for their food reserves [the liverwort *Blasia* (Figure 93-Figure 94) and hornworts], but this form seems to be slower to metabolize and cannot be used for quick growth (Crum 2001).



Figure 93. *Blasia pusilla* from Europe, a species that stores its food reserves as protein. Photo by Michael Lüth, with permission.



Figure 94. Open capsule of *Blasia pusilla* showing spores and elaters. Photo by Walter Obermayer, with permission.

Sundberg and Rydin (2000) found that buried *Sphagnum* spores could survive at least three years at various depths in peat. Curiously, light-colored spores of *S. balticum* (Figure 95) and *S. tenellum* (Figure 96) had higher survivorship than the darker spores of *S. fuscum* (Figure 49) and *S. lindbergii* (Figure 97), suggesting possible differences in stored food reserves. Spore size did not seem to influence longevity between species, but within a single species (*S. balticum*, *S. tenellum*) the small spores from small capsules seemed to have a greater longevity than those from medium-sized and larger capsules, something that seems counter-intuitive.



Figure 95. *Sphagnum balticum* with capsules in southern Europe. Photo by Michael Lüth, with permission.



Figure 96. *Sphagnum tenellum* with capsules, a species where spores from smaller capsules survive longer. Photo by Dick Haaksma, with permission.



Figure 97. *Sphagnum lindbergii* with capsules, a species with dark-colored spores that survive shorter periods than light-colored spores of accompanying species. Photo by Michael Lüth, with permission.

Survival in Water

Waterways offer a means of rapid dispersal. In streams they can carry diaspores great distances. In flood plains (Figure 98), diaspores can be buried in mud or travel with a river, germinating at some later point in time when they somehow reach the surface. Spores and gemmae require light to germinate, permitting these diaspores to remain dormant as long as their energy stores permit and their ability to fend off other organisms that might use them for a food source (bacteria, fungi, small animals).



Figure 98. Eroded material transported by water to River Baihe, a tributary of Yellow River Tibet. Such flood plains can house dormant bryophyte diaspores that are ready to grow when the water recedes. Photo by Sven Bjork, with permission.

To test the viability of spores and fragments of bryophytes from various habitats, Dalen and Söderström (1999) stored sets of these from *Ceratodon purpureus* (Figure 27), *Codriophorus* (= *Racomitrium*) *aciculare* (Figure 99), *Dicranoweisia crispula* (Figure 100), *Oligotrichum hercynicum* (Figure 101), and *Schistidium rivulare* (Figure 102), and for six months in water or dry. All species except *S. rivulare* exhibited reduced spore germination frequencies at all time intervals when stored in water compared to stored dry. *Schistidium rivulare*, a species that includes rocks in the splash of rivers and streams, demonstrated longer spore survival than did the other species. This species also had the highest regeneration frequencies from fragments. Nevertheless, diaspores of all these species survived at least some time in the water. In all species, the regeneration frequencies of fragments tended to be lower than those of spores. On the other hand, fragments did not experience any reduction in survival when stored in water compared to stored dry.

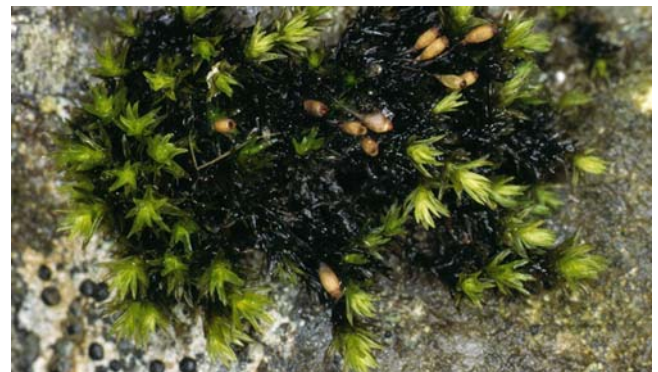


Figure 99. *Codriophorus* (formerly *Racomitrium*) *aciculare* with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.



Figure 100. *Dicranoweisia crispula* with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.



Figure 101. *Oligotrichum hercynicum* with capsules from southern Europe, a species whose spores survive a short time in water. Photo by Michael Lüth, with permission.



Figure 102. *Schistidium rivulare* with sporophyte, a species whose spores and fragments survive well in water. Photo courtesy of Betsy St. Pierre.

Survival of Spores vs Asexual Diaspores

Egunyomi (1978) compared viability of spores with that of gemmae in *Octoblepharum albidum* (Figure 76, Figure 103). He found that spores retain high viability for more than 8 months at temperatures of 22-30°C, 60-75% humidity, whereas gemmae lose viability at about 6 months under those conditions. Germination did not occur in darkness, suggesting that the propagules would not germinate within a diaspore bank. Nevertheless, some germination occurred in as little as 1 lux, suggesting that the species might be able to germinate among a heavy plant cover, but the question remains whether it could grow enough to survive and thrive there. Furthermore, if spores or gemmae were exposed to light, then cultured in dark, a light intensity of 800 lux for 48 & 36 hrs respectively was necessary for them to germinate at all.



Figure 103. *Octoblepharum albidum* gemmae. Gemmae of this species survive for a shorter period than do the spores at temperatures of 22-30°C and 60-75%. Photo by Li Zhang, with permission.

Germination of spores from herbarium specimens suggest that weedy species may remain viable longer than other taxa. *Ceratodon purpureus* (Figure 27) spores were the oldest to germinate – after 16 years (Malta 1922) – but this species surprisingly does not appear in the diaspore bank (Lönnell 2011). Most of the spores in the study by Malta did not germinate if they were more than 10 years old, and the greatest number were viable for only 5 years. In fact, within only 50 days of dry storage, a 30-40% loss in viability can occur (Löbel 2009). But perhaps it is the unnatural storage conditions of a lab or herbarium that causes such loss of viability. For *Sphagnum* spores, 15-35% survived 13 years of storage in humid, refrigerated conditions (Sundberg & Rydin 2000). On the other hand, tubers of *Anisothecium* (= *Dicranella*) *staphylinum* (Figure 104) remained viable for 50 years of storage (Whitehouse 1984). Keever (1957) found that herbarium specimens of *Grimmia laevigata* (Figure 105) still had 20% viability after ten years. Malta (1922) found survival of 19 years in plants of *Anoetangium aestivum* (Figure 106) and Maheu

(1922) found protonemal growth from plants of *Syntrichia ruralis* (Figure 24) after 14 years of storage.



Figure 104. *Anisothecium* (= *Dicranella*) *staphylina* in Europe, a species whose tubers remained viable for 50 years of storage. Photo by Michael Lüth, with permission.



Figure 105. *Grimmia laevigata* with capsules in southern Europe, a species whose plants retained 20% viability after ten years of storage. Photo by Michael Lüth, with permission.



Figure 106. *Anoetangium aestivum* from Europe, a species whose plants survived for 19 years in a herbarium. Photo by Michael Lüth, with permission.

Species from flood plains and other disturbed habitats may have some of the longest dispersal times. They may have considerable distances to traverse to reach a new location, and they may have long periods of unsuitable habitat requiring long survival. *Riccia* provides a good example of such a need. Breuil-Sée (1993) found that specimens of *Riccia macrocarpa* from Tunisia survived in a dry state in the herbarium for more than 23 years. Within three days of rehydration they exhibited new cells at the apices.

Long-distance Survival

Van Zanten, in his numerous papers on dispersal (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981), has shown the possibilities for long-range dispersal based on experimental evidence of survival. Van Zanten (in Gradstein & Pócs 1989) showed that New Zealand **endemics** (growing only in that area) had less resistant spores than those of wide-ranging taxa and that spores of tropical moss species, especially lowland rainforest taxa, are less resistant to drought than are temperate taxa, but surprisingly, the tropical taxa survive wet-freezing at -30°C! Tropical liverworts had similar relationships, but in general were less viable under extreme conditions than were the mosses (Van Zanten & Gradstein 1987). Trans-oceanic liverworts from Colombia have better resistance to desiccation and wet-freezing than endemic taxa. Nevertheless, only spores of *Marchantia chenopoda* (Figure 83), of the 61 species tested, survived travel on the wing-tips of an airplane. But death rates were also very high for the spores transported inside the wing. Van Zanten and Gradstein concluded that jet-stream altitudes were not favorable to long-distance dispersal, but that travel in wet air currents at high altitudes was a possibility for most of these liverworts. Dry air currents were more lethal.

Van Zanten (1977b, 1978b) found one puzzling relationship in longevity. After testing survival of drought, dry freezing, and wet freezing (up to 3 years), he found that spores from Northern Hemisphere bryophyte species tended to have a longer viability than those from the Southern Hemisphere. Not surprisingly, species with restricted distributions tended to have shorter periods of viability than species that occurred on multiple continents.

It appears that some spores, perhaps even the majority, can survive for many years provided they remain dry and in the dark. A false start in which they become hydrated and begin germination can be fatal if they are not permitted to continue development and produce sugars photosynthetically.

Establishment Success

As Brent Mishler pointed out on Bryonet (6 March 2013), particulate matter from China commonly reaches California. Dust from the Sahara reaches Texas. The opportunities for worldwide dispersal seem sufficiently common that most bryophytes should be everywhere, but "the environment selects." Once the propagules enter the transport stream, they must survive, arrive, germinate, and establish (SAGE).

Greater success of spores as a means of establishment through dispersal seems to be correlated with a lower age of first reproduction and greater phenological flexibility, but suffers a tradeoff, being correlated with decreased longevity (Longton 1997). For the conservation of rare species, the conditions of establishment upon arrival are particularly important (Cleavitt 2005). Hutsemékers *et al.* (2008) determined that rare species not only require specific habitat conditions, but that they typically are unable to compete. Therefore, when new habitats, such as slag heaps, are created, the rare species tend to enter at intermediate stages, after establishment of widespread species, but before the perennial competitors become established.

Buck (1988), in his study of the Tepui of Venezuela, hypothesized that the lack of moss flora on the summit of the Tepui was due to lack of dispersal from great distances and that available spores came from surrounding lowlands. Thus, failure of a diverse moss flora on the summit must be due to lack of adaptation for germination and survival on the summit. He was fortunate enough to be able to test this hypothesis when he discovered a "world within a world" on top of a Tepui. A sinkhole, 352 m wide and just as deep, provides a haven away from wildly fluctuating moisture and temperature conditions of the summit. In this sunken world, a forest similar to that of the lowland exists. He did indeed find that the moss flora in this sunken forest reflected that of lowland and not that of the summit, supporting his hypothesis that it was ecological conditions and not lack of dispersal that created the depauperate flora.

Germination success seems to be a major problem for spores, and much less so for vegetative propagules. Miles and Longton (1990) found no evidence of spore germination for *Polytrichum strictum* (Figure 60) in the field, but did find new shoots arising from vegetative fragments. By contrast, in *Funaria hygrometrica* (Figure 107-Figure 109), spore germination and establishment occurred frequently. Intermediate results were evident in *Atrichum undulatum* (Figure 6) and *Bryum argenteum* (Figure 7), with frequent regeneration from shoot fragments, and spores germinating, but sporelings usually failed to develop. Shoots seemed to develop easily in the latter two from protonemata planted in the field.

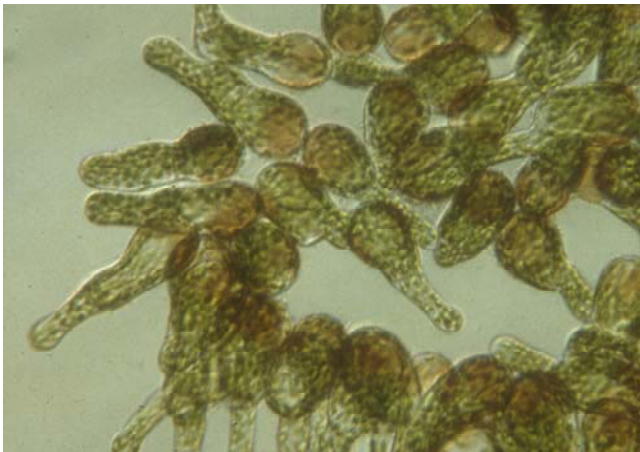


Figure 107. *Funaria hygrometrica* germinating spores on agar, demonstrating the ease of germination of many spores. Photo by Janice Glime.

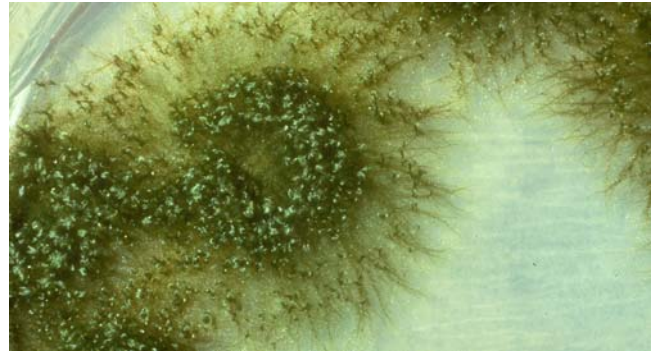


Figure 108. *Funaria hygrometrica* cultures. Each donut-shaped colony developed from a single spore, demonstrating how easily this moss can spread upon arrival. Photo by Janice Glime.



Figure 109. *Funaria hygrometrica* capsules, demonstrating the prolific production of capsules and spores. Photo by Li Zhang, with permission.

In the Negev Desert, it may be the ants in the genus *Messor* (Figure 110) that ensure the success of at least some moss spores (Loria & Herrnstadt 1980). They carry the capsules of *Crossidium crassinerve* (Figure 111) away to their nests, thus greatly increasing the likelihood that at least some spores will arrive in a suitable site for protonematal survival.



Figure 110. *Messor barbarus*, an ant that carries moss capsules, hence dispersing spores. Photo by José Miguel León Ruiz, through Creative Commons.



Figure 111. *Crossidium crassinerve* with a young sporophyte that might later be used in an ant's nest. Photo by Michael Lüth, with permission.



Figure 113. *Tortula muralis*, a species that has poor germination in company of its parents. Photo by Kruczy89, through Creative Commons.

Spores can be a means of surviving while competitors make living conditions impossible. Newton and Mishler (1996) found evidence of inhibition by mature plants on the germination of spores. However, if something were to destroy those mature plants, the sporebank could provide a new source of propagules for re-establishment. In fact, it appears that mature plants can have a sneaky way of prolonging time until germination of their spores. Mishler and Newton (1988) found that germination rates of both *Dicranum* (Figure 112) and *Tortula* (Figure 113) were greatly lowered on substrates of their parents. Although both *Dicranum* (Figure 98) and *Tortula* were severely affected by the presence of their parents, fragments were less affected than spores. *Dicranum* had an even greater inhibitory effect than did *Tortula*. Mishler and Newton compared this to the inhibitory effect that female *Dicranum scoparium* (Figure 112) has on spores that produce dwarf males when they germinate on the female plants. Mishler and Newton (1988) found that spores did better in continuously hydrated conditions, whereas fragments fared better when they had occasional drying.



Figure 112. *Dicranum scoparium* on the forest floor where it grows dwarf males on its own leaves. Photo by Janice Glime.

Keever (1957) found that spore germination of *Grimmia laevigata* (Figure 105) does occur on granite rock, but even there, fragments were more successful. One factor that influences the success of fragments vs spores is state of hydration, and this may have played a role in the establishment of *Grimmia laevigata*.

Hedderson (1992) found that rare mosses in the Terra Nova National Park, Newfoundland, Canada, were typically representatives of temperate, Arctic-montane, or montane floras. They are species at the edges of their ranges. He found that dispersal potential was negatively associated with rarity. These species have a narrow range of habitats and therefore are likely to have establishment problems.

Adherence

Arrival on the proper substrate is pretty much the end of the transport part of the story for most substrata, but for epiphytes and bryophytes on other vertical surfaces, or for those in flowing water, the problems don't end there. They must next adhere so that wind and rain don't take them once again on their journey. Van Zanten and Gradstein (1988) found that for Neotropical liverworts, the spore surface of epiphytes typically had finely verrucose spores with rosettes of large papillae (Figure 114). They suggested that these decorations were an adaptation that permitted them to adhere to rough surfaces such as bark. Epiphyllous and desert taxa, on the other hand, typically have spores that lack these rosettes (Figure 115). Both groups may gain further advantage by having precocious spore germination (Figure 75), permitting them to continue growth upon landing and gain a wider surface of adhesion.

Adherence may also be a problem in some aquatic habitats, such as streams and flood plains. But here the relationship is not so clear. Spores of *Riella* (Figure 116) are clearly spiny, possibly permitting them to adhere to the substrate more easily, but those of *Fontinalis* (Figure 117), a genus that typically adheres to rocks or underwater roots, are nearly smooth, having only small, rounded papillae.

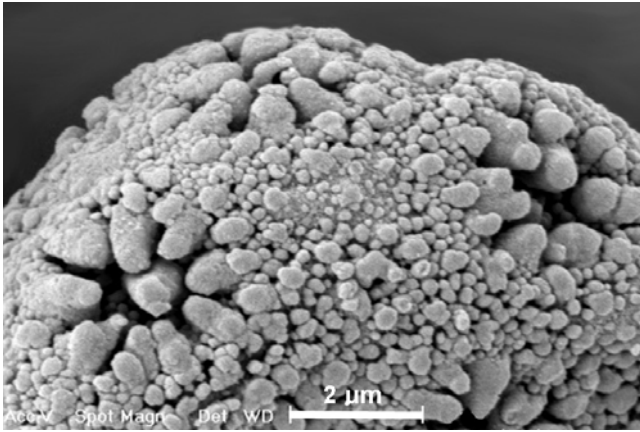


Figure 114. *Frullania chevalieri* spore SEM showing the rosettes of papillae. This spore exhibits characteristics that are common among epiphytes. Photo by Matt von Konrat, with permission.

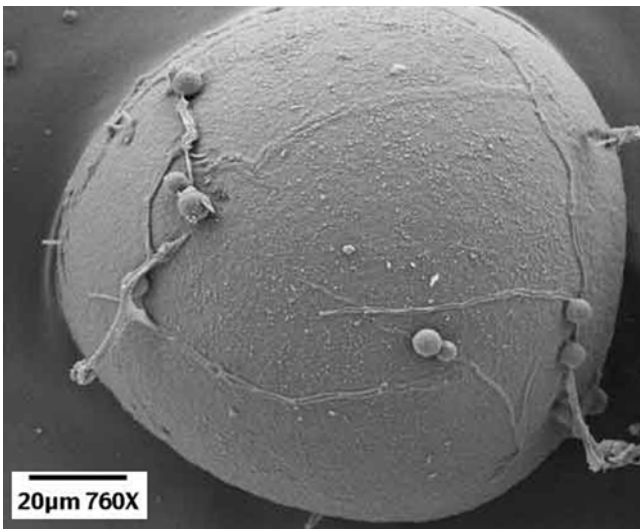


Figure 115. *Geothallus tuberosus* (Sphaerocarpaceae) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't travel far and don't have adherence problems on their landing surfaces. Photo by William T. Doyle, with permission.

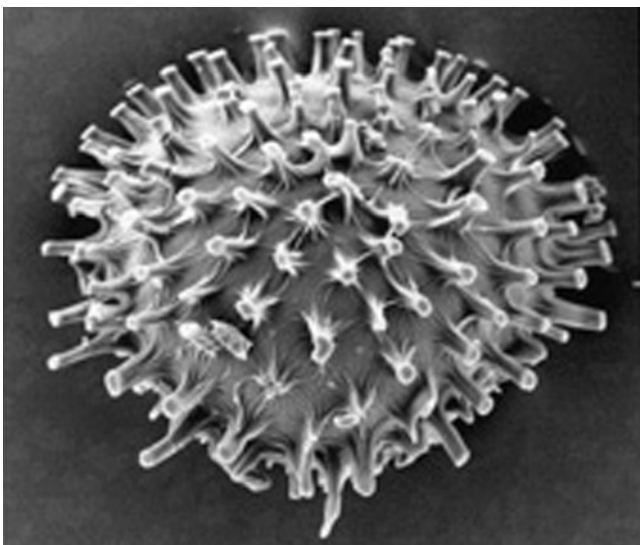


Figure 116. *Riella americana* spore SEM. Photo by William T. Doyle, with permission.

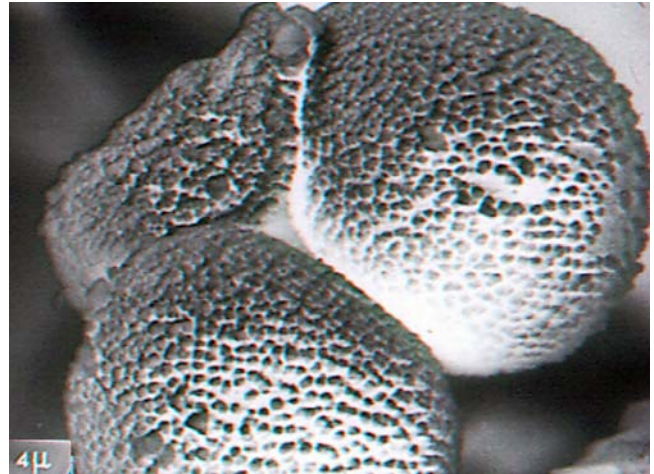


Figure 117. *Fontinalis squamosa* spore tetrad SEM. Photo by Janice Glime.

Conditions Matter

It is clear that survival while getting there is only part of the battle. Although the spores may arrive in viable condition, they may not succeed in germinating. Hassel and Söderström (1999) collected spores from *Pogonatum dentatum* (Figure 118) and germinated them in the laboratory. They had 96.6% germination within 21 days. They tested success in the field by sewing spores from 0.5, 1, and 2 capsules on 37 replicate quadrats of 10x10 cm. Considering the large estimated number of spores per capsule of 712,000, germination success was abysmal, with means of 11, 10, and 12 shoots produced, respectively, in the first year. They suggested that they had exceeded maximum density for successful protonemata. But it could also mean that some other field condition was not conducive to protonema development.

During (1986) found a similar problem in *Funaria hygrometrica* (Figure 107-Figure 109). In the greenhouse, shoots emerged from chalk grassland soil samples, even after two years, but in the field, none emerged. During considered that this failure in the field might be due to insufficient water or nutrients.



Figure 118. *Pogonatum dentatum* in Norway. Photo by Michael Lüth, with permission.

Drought tolerance of liverwort sporelings is significantly different between transoceanic and endemic species. This is a critical period for many species, with 30% of transoceanic species germinating after 50 days of desiccation and 30% of endemic species reduced to 30% germination after only 13 days. Both groups have a sporeling longevity of only about half that of spore longevity.

The problem of crowding, as suggested by Hassel and Söderström (1999) for *Pogonatum dentatum* (Figure 118), is only one problem faced by germinating spores close to the parent, and is one of little significance for long distance dispersal. The low numbers are more likely due to other problems in the field as well, including perhaps too much UV light, insufficient nutrients or moisture, or unsuitable temperatures. Noguchi and Miyata (1957) pointed out that at least some mosses with wide geographic ranges have abundant spores but are confined in their frequency by having rather specific habitats.

Multiple factors contribute to the success of a species upon its arrival. The conditions required for germination and development of the protonema and gametophore buds may differ, and are all part of the niche of a species, a topic that will be discussed in more detail in another volume. But it is appropriate to consider some examples here as we define limits of establishment.

Wiklund and Rydin (2004) compared spore establishment of two forest bryophytes, one [*Neckera pennata* (Figure 15-Figure 16)] an epiphyte and the other [*Buxbaumia viridis* (Figure 119)] an inhabitant of decaying logs. Using *in vitro* experiments, they determined that *Neckera pennata* was less successful at germinating at a low pH than was *Buxbaumia viridis*. The tradeoff was that *N. pennata* exhibited earlier germination at low water potential and survived longer when desiccated. They suggested that the higher pH would speed up germination and enable the spores to exploit short moist periods. This niche separation at the time of establishment is often not apparent by the range of tolerance of mature plants but can be critical to establishment of spores.



Figure 119. *Buxbaumia viridis* capsules on log. Photo by Hermann Schachner, through Creative Commons.

Sphagnum spores under wet, anaerobic conditions had much lower survivorship (dying within 2-3 years) than those under wet or periodically desiccated aerobic conditions, suggesting that respiration not only continued but was necessary for their survival (Sundberg & Rydin

2000). Refrigerated spores lasted up to 13 years. This infra-species size difference, coupled with the ability to survive freezing in upper atmosphere conditions, might permit the small spores, already better adapted for long-distance transport, to survive the greater time they are likely to be in transport.

Sphagnum provides a good example of the need for a specific nutrient. Despite the apparently good longevity of spores of *Sphagnum* species, few protonemata (Figure 77) have been observed in the field (Sundberg & Rydin 2002). Sundberg and Rydin attribute this absence to the need for phosphorus in greater concentrations than that typically found in natural waters. Various peat substrata were tested and it appeared that the amount of phosphate released was the determining factor in successful germination. Moose dung increased the success rate, as did litter from *Betula pubescens*. *Pinus sylvestris* litter did not help.

It appears that *Sphagnum* has other establishment needs as well. *Sphagnum* spp. fragments that arrived at a restoration project were unable to succeed unless they joined a *Polytrichum strictum* (Figure 120) carpet (Groeneveld *et al.* 2007). Apparently the carpet was important in keeping the developing *Sphagnum* moist. Groeneveld *et al.* considered that buffering of the temperature, making it cooler in daytime and warmer at night, may have been important as well.



Figure 120. *Polytrichum strictum* with *Sphagnum* growing between the stems. Photo by Andrew Hodgson, with permission.

Cleavitt (2002) tested the stress tolerance of fragments of pairs of rare and common species of mosses in view of their asexual dispersal potential. Habitat specificity in the three common species was more likely to correspond to physiological differences. For example, the common *Mnium spinulosum* (Figure 121) was intolerant of high light conditions and therefore only became established in the deep shade of conifer stands. The common *Bryum pseudotriquetrum* (Figure 122) was intolerant of desiccation and only became established on stream banks and other moist areas. The striking observation was that the rare *Mielichhoferia macrocarpa* (Figure 123) was tolerant of both high light and desiccation, but had the slowest rate of recovery, suggesting that some other factor contributed to its rarity, such as competition during its slow recovery, or insufficient time to recover in natural conditions before again suffering desiccation. And other factors in the environment could also be important establishment factors.



Figure 121. *Mnium spinulosum* from Europe, a species intolerant of high light conditions during establishment. Photo by Michael Lüth, with permission.



Figure 122. *Bryum pseudotriquetrum* with capsules from Europe, showing its typical wet habitat, here along a stream. Photo by Michael Lüth, with permission.



Figure 123. *Mielichhoferia macrocarpa*, a species tolerant of high light and desiccation, but one that has poor establishment success. Photo © Robin Bovey at PhytoImages website, with permission.

Bryophytes can be slow colonizers compared to some of the other taxa. Nevertheless, on Surtsey, they were among the first arrivals on the solidified lava. The typically early colonizers among the Cyanobacteria were remarkably scarce. Their most common locations were near steam vents, usually near moss clumps, particularly *Funaria hygrometrica* (Schwabe 1974; Figure 107-Figure 109). These nitrogen-fixing blue-green bacteria were especially attached to the protonemata. The moss *Racomitrium* (Figure 29), however, seemed to inhibit the growth of Cyanobacteria.

Slow Establishment

As we have noted above for *Mielichhoferia macrocarpa* (Figure 123), slow recovery may account for the lack of success in some species that arrive by diaspores. Leck and Simpson (1987) noted this problem for species recovered from a wetland diaspore bank. They identified 14 mosses, 2 liverworts, 7 ferns, and 1 horsetail, with *Bryum* sp (Figure 122) and the fern *Onoclea sensibilis* having the greatest densities. The highest densities occurred in the surface samples. Germination of spores and/or growth of these diaspores was slow compared to that required for seeds from seedbanks and they considered this slowness to be a factor in the absence of the bryophyte species on the surfaces of the wetlands.

Dispersal Limitation

A number of studies suggest that dispersal limitation is the best explanation for the patterns of abundance and distribution of bryophytes in some fragmented habitats (Pharo & Zartman 2007). But edge effects can also play an important role. Because of their small size, fast colonization-extinction rates, high substrate specificity, and dominant haploid condition, Pharo and Zartman consider them to be ideal model systems for testing the effect of fragmented landscapes on bryophyte community structure.

Nearness of source has been shown repeatedly as an important determinant of colonization, although Hylander (2009) found no relationship between colonization rate and nearness to mature forest stands for boreal forest bryophytes. This nearness component was well illustrated by Zartman and Shaw (2006) in their study of two epiphyllous species [*Radula flaccida* (Figure 124), *Cololejeunea surinamensis*] in the Amazon tropical rainforest. While extinction rates were the same for these species in both fragmented and continuous forests, colonization rate was much greater in the continuous forest sites (Figure 125).

Kimmerer (2005) demonstrated the importance of dispersal at a small scale in the colonization of treefall mounds in the Adirondack Mountains, USA. When spores and fragments of *Polytrichum ohioense* (Figure 126), *Dicranella heteromalla* (Figure 127), *Atrichum angustatum* (Figure 5), *Diphyscium foliosum* (Figure 128), and *Pogonatum pensilvanicum* (Figure 129) were sown on the mounds, these species became established, with the highest success occurring with fragments. Under natural conditions, only 1-2 of a possible 13 species established on any single mound and likewise, in the experiment, sown propagules were far more successful than natural dispersal to mounds with no added propagules.

Kimmerer considered this to be strong evidence of dispersal limitation on treefall mounds.



Figure 124. *Radula flaccida* with gemmae, an epiphyllous species that does best in continuous forest. Michaela Sonnleitner, with permission.

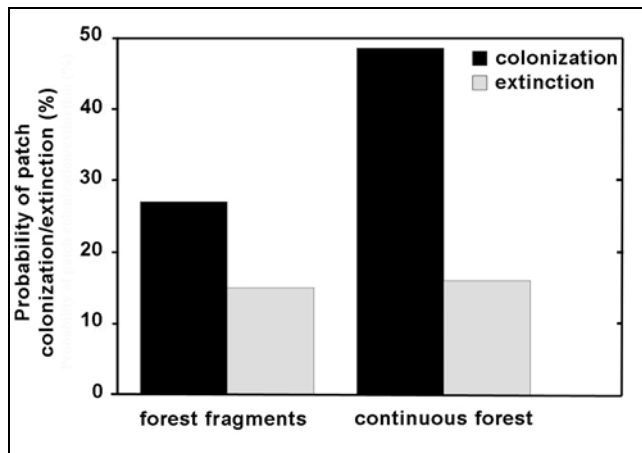


Figure 125. The colonization and extinction rates of *Radula flaccida* and *Cololejeunea surinamensis* on epiphylls in the Amazon tropical rainforest. Data for the two liverworts were very similar and thus were combined. Redrawn from Zartman & Shaw 2006.



Figure 126. *Polytrichum ohioense*, a species that seems to be dispersal limited when colonizing treefall mounds. Photo by Janice Glime.



Figure 127. *Dicranella heteromalla* on a soil bank. Despite its numerous capsules, its fragments are more successful at establishment on treefall mounds. Photo courtesy of Eric Schneider.



Figure 128. *Diphyscium foliosum* male plants (green) and female capsules and perichaetial leaves. Fragments are more successful in establishment than are spores. Photo by David Holyoak, with permission.



Figure 129. *Pogonatum pensilvanicum* with capsules on a soil bank. Note the ground cover of protonemata and absence of leafy gametophytes. Photo by Bob Klips, with permission.

Recolonization

In some habitats, bryophytes are among the first organisms to colonize a disturbed site. These are generally fugitives and other species that cannot tolerate the competition of tracheophytes. They take advantage of the sun but must tolerate greater drying than the species living in forested habitats. But they must also have good dispersal capabilities to arrive there and thrive before the competition arrives.

Arrival in disturbed habitats can be extensive, as Greven (1994) observed in an experimental garden. Between 1972 and 1991, 91 species arrived in the garden. The greatest number of taxa occurred on the chalk soils (40 spp), with peat having the fewest (6 spp). Even several rare taxa arrived.

In an urban environment, a community can re-establish itself in 1-2 years (Nehira & Nakagoshi 1987). Thalloid liverworts and pleurocarpous mosses were the first to regenerate, ahead of the acrocarpous mosses. This is somewhat unusual as the acrocarpous mosses typically have more asexual diaspores than do pleurocarpous mosses, but regeneration may have occurred from remnants and fragments, a dispersal mechanism common among pleurocarpous taxa. Regrowth occurred primarily in the spring and autumn, despite little seasonal variation in the number of airborne diaspores, suggesting the importance of rainfall and perhaps cool temperatures.

Forests

The slow rate of recolonization in harvested regrowth forests is illustrated by the smaller number of species present, presumably due to the slow rate of dispersal and establishment of species common in old-growth forests (Cooper-Ellis 1998). In the Central Cordillera of Colombia, Corrales *et al.* (2010) considered the dispersal of propagules among the various forest types to be the primary mechanism driving the regional pattern of bryophyte distribution.

Proximity to other suitable bryophytes seems to be a major factor in what species will become established after a disturbance. Even in the limited microcosm of a leaf, Cobb *et al.* (2001) found that bryophytes colonizing *Acer macrophyllum* leaves (epiphyllous) in Olympia, Washington, USA, after experimental removal of the epiphylls, were primarily due to lateral encroachment (75%). Only ~8% of the exposed area had been recolonized one year after removal of bryophytes, reaching 27% after three years. The 25% not colonized by encroachment included incompletely removed plant parts and aerially dispersed diaspores.

On the other hand, in young boreal forest stands, there was no indication of higher colonization by bryophytes close to the mature stands where bryophytes were undisturbed (Hylander 2009). Following a forest fire, bryophytes that recolonize can either arrive anew or survive the fire. Survival of the fire could be the result of migrating to a safe site during the fire (*i.e.*, local dispersal to safety) or by enduring the conditions (Hylander & Johnson 2010). Endurance can be due to wetness, burial, or positioning in the protection of logs, rocks, or other blockades to the fire. Hylander and Johnson (2010) found an average of three refugia per 50 x 50 m reference plot,

with a mean of 4.8 bryophytes associated with them. But in the area that had been burned, only a mean of 1.5 species could be found in the refugia. However, other factors seemed to be more important than refugia. There was no correlation between the number of refugia and the number of forest species that colonized the plots. The refugia were mostly on rocky or mesic sites, not wet sites. The importance of these refugia most likely depends on the intensity and nature of the fire. A ground fire will have a very different effect from a crown fire.

Schmalholz and Hylander (2010) examined a similar question regarding the role of forest floor refugia in response from clear-cut logging. They found survival differences based on microtopography. The shelter of boulders and stumps resulted in significantly more survival (~30%) than on level forest floor (10%) for transplanted bryophytes. These boulders and stumps also resulted in less change in species composition.

Evidence from Europe suggests that the same forest can be colonized by a bryophyte species multiple times. Cronberg *et al.* (2002) found repeated recruitment among populations of *Hylocomium splendens* (Figure 33) on 10 Baltic islands. He identified 103 haplotypes among 694 shoots with number of clones increasing significantly with increasing age of the islands. He likewise showed that the number of genotypes of *Plagiomnium affine* (Figure 130) correlated with the age of the forest stand in Europe (Cronberg 2005). Using 23 allozyme loci and six populations of *P. affine*, they sampled 602 shoots and found 16 haplotypes. Among these, 12 were unique to single populations. Allelic richness and diversity were significantly correlated with forest age at the ramet level but not quite so at the genet level.



Figure 130. *Plagiomnium affine*, a species for which the number of genotypes correlates with forest age. Photo by Michael Becker, through Creative Commons.

Patch Fragmentation

Logging has an impact on the distribution of bryophytes. Isolated patches that remain may be invaded by new species and disturbed areas will both lose old species and gain new ones. In the temperate rainforest of British Columbia, Canada, Baldwin and Bradfield (2007) compared bryophytes on the forest floor, downed logs, and tree bases. They found that the dispersal-limited groups

such as perennial stayers and the microclimate-sensitive groups declined in species richness or frequency as patch size decreased. These microclimate-sensitive groups included those from closed canopy, log-dwelling species, and liverworts. Colonists and open canopy species showed little relationship to patch size. In the patch size range of 0.6–63.6 ha, most of the patch size effects disappeared when the three smallest patches (0.6–1.8 ha) were not included in the analysis. Therefore, patch sizes of at least 3.5 ha seem to provide suitable habitat to sustain the diversity of bryophyte functional groups in this temperate rainforest habitat. It is likely that part of this decrease in diversity is due to dispersal limitation.

Summary

Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. Epiphytes gain height through their host. However, the majority of spores seem to land within 2 m of their parents. It follows that spore density in the atmosphere decreases with distance from the source and increases with height of the colony.

Members of the **Polytrichaceae** have a membrane connecting their teeth and disperse spores by disturbance such as rain drops. These are ejected horizontally and apparently do not travel far.

Bryophytes that live on temporary and disturbed substrata, such as logs and arable land, require either good dispersal or the ability to survive in diaspore banks.

Tracheophyte dispersal models have limited applications to bryophyte dispersal. Bryophyte spores are much smaller than seeds and lack multiple layers of tissues to protect them. Vegetative diaspores may mimic some of the elongate shapes, but spores tend to travel farther than vegetative propagules.

Bryophytes seem to support the concept that "everything is everywhere, but the environment selects." Unfavorable light, photoperiod, substrate, temperature, and moisture conditions can prevent establishment of a species once it arrives. This concept is supported by the small size of spores, the distribution patterns, and patterns of establishment on newly formed islands.

Molecular Clocks can be used to estimate time of arrival and help us to trace the dispersal routes.

Weather, dust storms, and fires can play a significant role in creating air currents, protecting from UV, and maintaining moisture.

Even diffusion models can help us understand dispersal, but size, falling velocity, and access to the air stream all have roles in the distance travelled. Long-range dispersal is facilitated by wind, requiring updrafts to get spores into the atmosphere. There the spores must survive UV light, desiccation, and extremes of temperature, especially sub-freezing temperatures. In some areas there is clear evidence of **stepping stone** progression once the first propagule arrives and succeeds in the area.

Small spores travel the farthest; large spores provide more energy for the start of growth. Spores

range from 5 μm in *Dawsonia* to 310 μm in *Archidium*, with numbers per capsule ranging from 4 in *Archidium* to 50 million in *Dawsonia*. Most bryophyte spores range about 20–100 μm and hence weigh about 0.004 μg to about 0.52 μg , all falling in the size category where wind dispersal is expected. Few animal dispersers are known for bryophytes. Most spores seem to fall within 2 m of their parents, but only a few need be caught into updrafts in order to accomplish long-distance dispersal. Limited **gene flow** between populations, demonstrated by genetic variation between them, suggests that most populations arise from a single propagule and that there is little mixing. This is further supported by the lack of genetic variation within populations.

Height of origin, such as epiphytes or species on walls and boulders increase dispersal effectiveness. Many dispersal periods are correlated with dry weather, especially for small spores, but at least in some locations, spores can be trapped from the atmosphere year-round. Some capsules require more than a year to develop whereas others mature in a few weeks. Few data exist that identify the species of atmospheric travellers, but certainly *Funaria hygrometrica* is one of them. Often the spores that are travelling are different from the species of a particular environment.

Long-distance dispersal is limited by drought tolerance and UV radiation (lethal for most species). For Neotropical liverworts, there is no dispersal advantage based on spore size, bisexuality among small-spored species, presence of chlorophyll, verrucosity of spore wall, and presence of gemmae. Bisexuality seems to have a positive advantage in large-spored (>35 μm) species. Species with greater source distributions and greater area of suitable destination habitats have greater dispersal potential. Dark-colored spore walls may protect against UV radiation. **Callose** deposits on the spore, waxy **sporopollenin** on the surface, and in most mosses a **perine** layer, all may contribute to protection of the spore.

Wet freezing has equal effect on transoceanic and endemic species. Both spores and sporelings survive longer with good drought tolerance. Among large-spored species (>25 μm), xerophytes survive dispersal better than mesophytes or hygrophytes. Dispersal by water is possible in many taxa, with survival times ranging from a few days to many months. **Spore longevity** is known from 7 days to 50 years.

Once arriving, spores and vegetative diaspores must adhere. For spores, verrucose surfaces can facilitate catching on something, such as tree bark.

Because of the limits of dispersal, ability to remain viable in soil banks, and changes in environmental conditions, the bryophytes that become established following a disturbance may differ considerably from the original flora.

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