Glime, J. M. 2017. Adaptive Strategies: Life Cycles. Chapt. 4-6. In: Glime, J. M. Bryophyte Ecology. Volume 1. Physiological Ecology Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 5 June 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

CHAPTER 4-6

ADAPTIVE STRATEGIES: LIFE CYCLES

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Figure 1. Strap-shaped leaves of males and capsules with perichaetial leaves of females of the dioicous moss *Diphyscium foliosum.* Photo by Michael Lüth, with permission.

Life Strategies

By now it must be obvious to you that to understand the life strategies of bryophytes, one must first understand the life cycle (*e.g.* Figure 1). Frahm and Klaus (2001) state that bryophytes are able to react quickly to such events as climatic fluctuations because of their short life cycle and ease of dispersal by spores. It is likely that when all other plant life has perished from some Earth catastrophe, it will be the bryophytes that persist, surviving as spores or other propagules until conditions return to safety and once again surrounding the earth due to their ability to travel great distances as "dust."

By definition, the life cycle includes reproduction. However, even such a widely used term has ambiguities. In bryophytes, we shall use this term to refer not only to the sexual reproduction that results from union of sperm and egg (ultimately resulting in spores produced by meiosis), but also to the multitude of **asexual** (vegetative) means by which bryophytes are able to make more, physiologically independent plants (Mishler 1988). This definition separates reproduction, which can permit relocation, from growth, which implies the increase in size of a physiological individual (Söderström 1994). On the other hand, growth can ultimately result in reproduction, as is the case when the plant branches and is physiologically connected, but later the branches separate and become physiologically independent. As you can see in Figure 2, the degree of reproduction by propagules depends on habitat. Among British habitats, short-lived habitats (wood, bark, farmland, dung) have the highest degree of propagular reproduction (that is, by vegetative means) (Herben 1994). On the other hand, the habitats with the greatest percent of the species are in the middle of the range of propagules.

Using the principle that extreme conditions might provide the best test of the limits of an organism, we learn that in the maritime Antarctic, bryophytes seem to have enhanced sexual reproduction (Lewis Smith & Convey 2002). This is contrary to the generally accepted belief that bryophyte fertility decreases toward the poles. Rather, 43% of the bryophytes (19 species) in Marguerite Bay and

47% of those on Alexander Island are known to produce capsules. But Lewis Smith and Convey attribute this to favorable microclimatic conditions. Nevertheless, in this extreme environment, the large majority of mosses with capsules were short, monoicous, acrocarpous taxa, suggesting that the predominance of dioicous taxa in more temperate climates may be possible because the environment is less stressful. In the more extreme environments of the Antarctic continent, the numbers of species producing capsules at similar latitudes (68-72°S) are much less (33%).

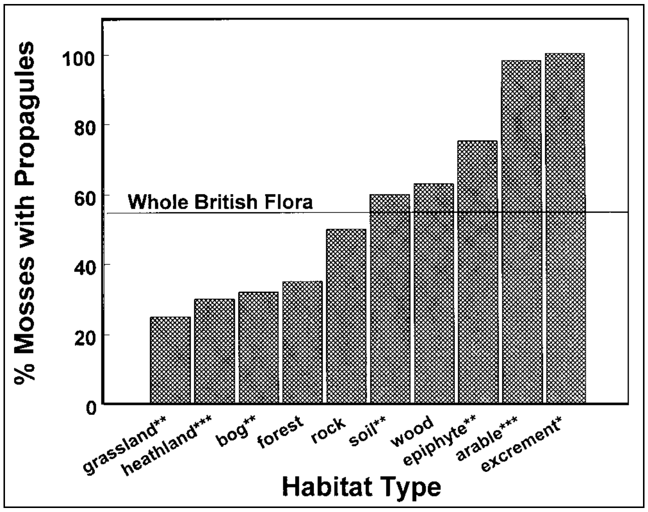

Figure 2. The percent of mosses that form spores or gemmae frequently or commonly in selected habitats of Great Britain. Asterisks indicate degree of significance (Chi-square test) when compared to the whole moss flora of Great Britain (* = P<.05, **=P<.01, ***=P<.001). Redrawn from Herben (1994), based on data from Smith (1978).

Although life cycle strategies are obviously important, especially in extreme habitats, life forms and growth forms may be more important. During and Lloret (1996) found that within individual sites in Spain, species with the same life strategy exhibited similar patterns, and that between locations, growth forms differed more than life cycle strategies.

Clonal Growth

At the mature end of the gametophytic cycle, bryophytes can form masses of related individuals, or clones. **Clones** can be defined as groups of individual plants created by fragmentation, viviparous bulbils, or apomictic seeds (Callaghan *et al.* 1992), whereas if gene flow is present the groups of plants are called **populations** (Harper 1977). In other words, clones have the same genetic makeup as the plant from which they were derived. In addition to these tracheophytic means, bryophytes create clones through multiple buds on the protonemata. But, as already discussed, somatic mutations render even these "clonal" derivations to be variable in genetic makeup.

Callaghan, *et al.* (1992) attribute to clonal growth the ability to sequester space and increase fitness of the populations. Among the benefits are persistence; spread of development and reproduction over time and environmental conditions; risk-spreading between **ramets** (individual members of clone) of the same type, thus increasing chances for survival of the genotype; protection of disadvantaged ramets that might later survive in the face of adversity; increased precision with the sequestering of space and dispersal of ramets; ability to monopolize resources for the benefit of the genotype. They furthermore include mobility, but I question whether this is much of a gain when compared to the alternative of wider distribution of propagules away from the parent.

One possibility that has barely been explored is the increase of genetic variability through production of these haploid genets. We had long assumed that the limited morphological development of the Bryophyta and Marchantiophyta reflected a limited genetic diversity, a case to be expected when the dominant generation is haploid and asexual reproduction is common. However, contrary to our expectations, moss populations are characterized by a high degree of isozyme variation, as shown for ***Ceratodon purpureus*** (Figure 3) (Shaw & Beer 1999). Cultivation of spores from one specimen of ***Drepanocladus*** (*Warnstorfia*) ***trichophyllus*** produced four distinguishably different morphologies (Sonesson 1966).

Figure 3. Color and leaf shapes of *Ceratodon purpureus*. **Top:** Green, broad leaf, hydrated form, **Middle:** Green, lanceolate leaf, hydrated form. **Lower:** Reddish dry form with capsules. Photos by Michael Lüth, with permission.

Velde and coworkers (2001) addressed this question of genetics of clonal relationships in ***Polytrichastrum formosum***. They determined that identical genotypes between spatially separated shoots were almost never present, whereas identical genotypes among **genets** (branching of gametophytes resulting from clonal growth of rhizomes) was extensive. However, this view of the genet has some problems. Scrosati (2002) pointed out that somatic mutations are predictably common, giving rise to genetic mosaics within any connected genet. To deal with this lack of genetic homogeneity, Scrosati suggested that **genet** should be defined as a "free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth." Nevertheless, it appears that even in adjacent populations of spore-producing plants, genetic variation is minor. In another example, populations of ***Funaria hygrometrica*** (Figure 4) growing in close proximity on contaminated tailings of a copper mine displayed very low levels of genetic variability, but had extensive morphological plasticity (Shaw & Bartow 1992).

Figure 4. Crowded ***Funaria hygrometrica*** with its abundant capsules. Photo by Michael Lüth, with permission.

During and van Tooren (1987) attempted to explain this paradox of genetic diversity in vegetatively reproducing taxa. Referring to earlier views of bryophytes as evolutionary failures, they contended that bryophytes in fact have high genetic variability, yet maintain their populations almost entirely by asexual means. They suggest that even though sexual reproduction, when it occurs, results in huge numbers of spores, establishment from spores in the field seems to be very difficult. Rather, they suggest that "remarkably rapid fine-scale dynamics" of many bryophyte populations may account for their ability to maintain a high degree of genetic variability.

Itouga and coworkers (1999) provide data on genetic variability in the liverwort ***Conocephalum japonicum***. They consider both the species and populations to have low genetic diversity values of **Hes** (species genetic diversity) = 0.008 and mean **Hep** (population genetic diversity) = 0.008±0.003. Between populations diversity was likewise low with **Gst** (coefficient of genetic differentiation) = 0.062. They used this low diversity as an indication that reproduction by gemmae predominated over sexual reproduction by spores.

Velde and coworkers (2001) considered this strategy of producing clonal genets to be one that provided increased longevity for the genet that accompanies increased reproductive capacity. Nevertheless, they showed that male reproductive success in ***Polytrichastrum formosum*** is determined primarily on spatial distance from females. In fact, these populations achieved their success primarily through sexual reproduction, facilitated by the ability of sperm to disperse to distances measured in meters rather than mm or cm.

Foraging and Sharing

The reproductive advantages of ramets may be enhanced by other advantages found more recently, at least in tracheophytes. In seed plants, the ability to relocate photosynthate from plant parts in the light to shaded parts has been demonstrated (Kemball *et al.* 1992), while other plants are able to translocate resources through rhizomes and roots (Landa *et al*. 1992). This permits the ramets to take advantage of flashes of sunlight called **sunflecks**, and horizontal growth that permits such advantages has been termed **foraging** (Bates 1998). Ramets furthermore may have seasonal advantages as different parts become exposed to light at different times of the year. Even nutrient and moisture advantages may accrue if part of the plant receives sunlight while another part extends into moister or more nutrient-rich soil. Even in simpler plants like lycopods (*Diphasiastrum flabelliforme*), Lau and Young (1988) demonstrated that ramets that had been severed from their connecting ramets experienced 50% more mortality than unsevered ramets. Those ramets connected to shaded ramets were able to maintain higher water potentials, giving them the ability to take advantage of the sun in one ramet while maintaining high water potential through that supplied by another ramet.

In bryophytes, as in tracheophytes, we can expect advantages to the clonal habit. Living where their parents have lived increases the probability that the habitat is suitable, thus reducing wastage of propagules. A greater area of soil and atmospheric water is contacted by a clone, in some cases permitting a greater nutrient capture and the opportunity to provide needed water and nutrients to the growing tip. However, the ability to transport hormones, nutrients, and photosynthate is known for so few examples of bryophytes that we cannot generalize these benefits. In some tracheophytes, leaves on different parts of the plant and within the clone differ in morphology, permitting different environmental conditions to favor them. Such differentiation may be possible on rhizomatous taxa such as ***Climacium***, and some leafy liverworts exhibit different leaf morphologies on the same branch (*e.g.* ***Lophocolea heterophylla***, Figure 5), but no systematic investigation has explored this as a possible clonal advantage.

Figure 5. Heteromorphic leaves of ***Lophocolea heterophylla***. Compare the two leaves indicated by arrows. Photo by Janice Glime.

If indeed clonal transport such as that demonstrated in tracheophytes is possible in most bryophytes, nutrients could move internally from favorably placed ramets to those in less favorable positions in a patchy environment, benefitting the bryophytes in a competitive environment (Bates 1998). Bergamini and Peintinger (2002) likewise compared the bryophytes to tracheophytes, suggesting that their overall morphological responses to the differences in light levels approximated that of tracheophytes with stolons – a "spacer and branching strategy." But does this ability to share with less favorably placed ramets only work for bryophytes with internal conduction? Eckstein and Karlsson (1999) tested this hypothesis by comparing the movement of nitrogen in ***Polytrichum commune***, with well-developed internal conduction, with that of ***Hylocomium splendens***, with predominantly external conduction. Indeed, the labelled nitrogen pool in ***Hylocomium splendens*** moved from older segments to younger segments. In ***Polytrichum commune***, it disappeared from younger segments in autumn, presumably going to underground storage organs. Both of these examples support the hypothesis that ramets can provide sources of translocatable substances from one part of the clone to another, but we have few studies to permit us to assess the extent of this phenomenon among bryophytes, nor does this explicitly demonstrate the transfer from one ramet to another less favorably positioned. And could gametophytes such as those in Figure 6 transfer substances from one gametophore to another through the protonema?

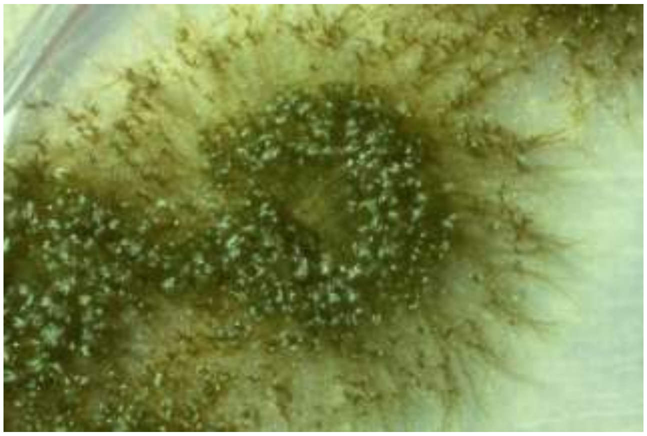

Figure 6. Circular growth pattern of gametophores developing from a single spore of ***Funaria hygrometrica***. Photo by Janice Glime.

There need be no internal conduction to foster other types of advantages, however. For example, ***Sphagnum magellanicum*** is able to keep its neighbors moist through its efficient external conduction, and cushion mosses like ***Leucobryum*** (Figure 7) conserve moisture by growing in dense clones.

Implications for Reproduction

Perhaps there is a division of labor that provides a reproductive advantage among ramets of a clone that is independent of type of translocation. Stark *et al.* (2001) found that in the desert moss ***Syntrichia caninervis*** more mature ramets with larger size were more likely to reproduce than the smaller ramets, suggesting a division of labor that permitted smaller plants to conserve energy until they achieved a greater size. While this may be simply a function of age, it would permit the colony to have multiple reproductive strategies simultaneously, with larger ones reproducing sexually and smaller ones using only fragments or vegetative propagules.

Figure 7. Cushion of ***Leucobryum glaucum***. Photo by Janice Glime.

Many of the modes of reproduction of bryophytes result in clonal growth. Rarely does one see just a single bryophyte stem. Rather, clumps, cushions, tufts, mats, any number of growth forms, suggest that these are all siblings of an original single parent. In fact, even if only a single spore lands on the rock or soil, many plants arise, at least in mosses. The spore produces a protonema that branches, and in the case of the filamentous protonemata, the numerous branches can give rise to numerous upright gametophores. Knoop (1984) identifies two types of gametophore origin: ***Funaria*** type (Figure 6), developing gametophores on the caulonema only in a circular fashion around the spore; ***Polytrichum*** type, developing few gametophores near the germinated spore or even from the spore cell itself (Sood & Chopra 1973, Nehlsen 1979). Both result in several to many gametophores.

In ***Sphagnum*** a single spore produces a small thalloid protonema that gives rise to only one gametophore, thus resulting in populations when more than one spore germinates, and making one uncertain in any given clump of ***Sphagnum*** whether the clump is a clone derived from apical branching or a population derived from separate spores. However, if one considers that the branching of the **capitulum** contributes to a major portion of the mat growth, then, again, clonal behavior is at work. Furthermore, spores are likely to land on their own parents or siblings or cousins of the parent, and thus not be far removed from clonal relatedness.

Even gemmae can form circular arrangements of gametophores, as reported by Chopra and Rawat (1977) for ***Bryum***, or other arrangements of numerous gametophores, as in ***Physcomitrium sphaericum*** (Figure 8; Yoshida & Yamamoto 1982). Since these have arisen from one parent, they likewise produce clones. In ***Bryum bicolor***, numerous tubers and gemmae are produced early in the growth of the gametophore, permitting it to build up a large clone (Joenje & During 1977).

Density Effects

Colony density has varying effects on moss success. In ectohydric mosses, it is more likely that density will favor success and increase growth (During 1990; Økland & Økland 1996). But in ***Sphagnum*** (Clymo 1970) and ***Rhytidiadelphus triquetrus*** (Bates 1988) density is detrimental to both branching and growth. Shoot mortality can increase, as in **Polytrichaceae** (Watson 1979), or decrease, as in ***Tetraphis pellucida*** (Kimmerer 1991), with density. Almost nothing is known of density effects on liverworts; Laaka-Lindberg (1999) showed that density had no effect on gemma production.

Figure 8. Clone of *Physcomitrium sphaericum*. Photo by Michael Lüth, with permission.

On the other hand, Kimmerer (1991), found that density was an important factor in asexual vs sexual expression in the acrocarpous ***Tetraphis pellucida*** (Figure 9). Gemmae were common in low-density colonies and the sex ratio was female-biased. High-density colonies, on the other hand, were more likely to have sexual reproduction and a greater proportion of males. She pointed out the advantage of this plastic strategy in unstable environments such as the rotting stump habitat of ***Tetraphis pellucida***, permitting the plants to expand by gemmae when the colony was not dense.

Figure 9. ***Tetraphis pellucida***. **Upper:** Uncrowded plants with gemmae on tips. **Lower:** Dense patch of plants with sporophytes. Photos by Michael Lüth, with permission.

Tradeoffs

Traditional life history theory holds that "maximizing reproductive value at each age is equivalent to maximizing fitness" (DeRidder & Dhondt 1992). However, in bryophytes, as in many species of seed plants, there is a negative correlation between sexual reproduction and asexual reproduction (Caswell 1985). On the other hand, in the clonal insectivorous flowering plant ***Drosera intermedia***, DeRidder (1990) found only limited evidence of a tradeoff between the two types of reproduction. DeRidder and Dhondt (1992) suggest that traditional theory may apply to the clonal ***D. intermedia***, whereas in many clonal species, it is an inappropriate theory because it was based on organisms (vertebrates) with only one mode of reproduction.

Ramets of one taxon, all from the same spore, seemingly competing for space and resources, seems like a maladaptive thing to do. However, the old safety in numbers adage may apply here. Multiple stems are less likely to dry out than a single plant. The colony can acquire a cushion shape as the middle members grow better due to moisture held by their neighbors. The edge members are slowed because if they too grow like the middle members, they are left with no protection from drought on the outer side. Hence, the adventurous stem that grows a bit taller is soon stopped by lack of moisture, and those on the edge are slowed the most because they lack a similar tall plant on the outside to protect them. For tracheophytes, Price and Hutchings (1992) also consider design constraints that limit vascular connections between some ramets, a consequence that should not be a problem for the ectohydric bryophytes. Could this, however, reduce the advantages for **endohydric** bryophytes, *i.e.* those relying significantly on internal conduction?

Perhaps one of the greatest benefits to ramets from a single spore of monoicous bryophyte taxa is availability of the opposite sex. Since in many cases, the male and female gametangia don't mature at exactly the same time on the same individual, gametangia of a neighbor are more likely to be receptive than other gametangia on the same plant. Such an opportunity is not so important to the tracheophytes because of their dependence on external pollinators that can readily visit nearby clumps of a different clone. Nevertheless, for the bryophytes, concomitant with the advantages of having nearby sexual partners are the tradeoffs in disadvantages of marrying your twin, in particular the loss of genetic diversity.

Like the tracheophytes, bryophytes must pay a price for the clonal habit. The advantage of being able to respond rapidly to environmental change is unlikely for the slow-growing bryophytes. Reduced recruitment from spores will make the clonal bryophytes vulnerable to permanent changes in the environment, and the connectedness makes the entire clone vulnerable to disturbance (*cf.* tracheophytes, Callaghan *et al.* 1992). The longevity of the clump in habitats like the Arctic make the probability of frost heave damage an eventuality in some habitats. Mosses seem less likely than tracheophytes to reap benefits from having only part of the clone disturbed. If part of a cushion is removed, the entire cushion is likely to dry out, whereas an intact cushion is able to keep its interior moist under most circumstances. In most cases, spread by spores in less clonal species may be a better strategy, particularly for those that require fresh soil in open, disturbed areas. Thus, as their habitat changes, they have the means to move on to other suitable areas.

The trade-offs and benefits of clonal growth, contributing to increased bryophyte density, are hard to assess. The overwhelming presence of clonal growth suggests that it has its advantages for bryophytes, perhaps almost completely in the greater moisture retention.

r & K Strategies

Life cycles are basic to the survival of a species. Those that are annuals must usually survive the winter as spores. Those that are perennial must have other ways to survive the cold of winter. Still others may live where it is a dry season, not winter, that must be reckoned with. These differences in seasonal stresses are generally met by differences in life strategies.

Ramensky (1938) described three types of outcomes to the differences in life strategies as **violents** (aggressive species), **patients** (tolerant species), and **explerents** (non-competitive species that fill the spaces between others). Rabotnov (1975) added **pioneers** (species able to colonize substrata that are not yet suitable for other species). Meanwhile, MacArthur and Wilson (1967) introduced the concept of **r and K selection** as the extremes of a life cycle strategy continuum, and the western world seemingly ignored Ramensky and Rabotnov, generally only using the term "pioneer" among these. Although r and K strategies were largely described to fit animal concepts, many of the ideas can be applied as well to plants.

The **r-selected species** are characterized by a rapid growth rate, early reproduction, numerous, small offspring (spores or seeds in plants), and a high resource uptake; the **r** can be compared to the **r** (intrinsic growth rate) in the **logistic population model**. The **r strategist** is likely to be a short-stayer, adapted to disturbed or **ruderal** (field & wasteland) habitats where it is necessary to arrive quickly and mature before the habitat changes. By contrast, the **K-selected species** is characterized by slow growth rate, late reproduction, few, large offspring, and efficient use of resources; the **K strategist** optimizes for a high population density at the environment's carrying capacity (*cf.* the logistic model). The K strategist is likely to grow where the habitat is more stable, and it can be a long-stayer, eventually reaching considerable size (or cover). The K strategist is more likely to depend on asexual reproduction such as rhizomes and perennial habit whereas the r strategist is more likely to rely on seeds or spores and an annual habit with good dispersal.

Thus K strategists tend to be competitors; r strategists tend to be opportunists but not competitors. An r strategist is the more likely one to succeed on unstable, disturbed environments (sometimes a pioneer, sometimes an explerent), whereas the K strategist is the more likely one to succeed in more stable and predictable habitats (the patient or tolerant species and sometimes the violents or aggressive species).

Grime (1977) considered the **r strategist** to be **ruderal** (of field or wasteland) species that took advantage of disturbed habitats (Figure 10). The **K strategists** he considered to be the **stress tolerators** that were able to survive dry or cold periods as whole plants, the **perennial stayers**. Between those two he placed the competitors.

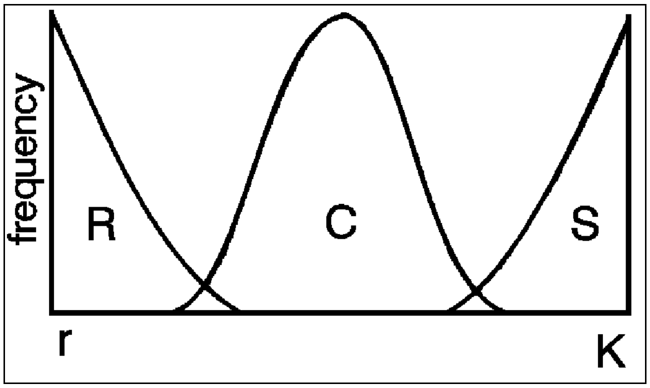

Figure 10. Frequency of ruderal (R), competitive (C), and stress-tolerant (S) species along an r-K continuum. Redrawn from Grime (1977).

Bet Hedgers

But between these two extremes are lots of possibilities for having some of the characteristics of each. Few species can meet all the criteria of either, and trade-offs abound to permit the organisms to meet the demands of their particular habitats. Plants that seem to have both good sexual reproduction and a means of vegetative reproduction are **bet hedgers**. Like the people to whom we refer as bet hedgers, these plants are "unwilling" to put "all their eggs in one basket." They use two strategies simultaneously so that they do not lose entirely. The price they pay is that they likewise never win entirely – at the ends of the spectrum, there is either an r strategist or a K strategist that is better adapted to the circumstances.

Production of gemmae among sexually capable species is one example of bet hedging. In the dry interior of North America, ***Syrrhopodon texanus*** (Figure 11) exhibits seasonal production of gemmae, arising in August (33% of specimens) and climaxing in September (50% of specimens) (Reese 1984). In this species, rarity of males makes this bet hedging a desirable strategy, although sporophyte-bearing females invariably occur when males are present.

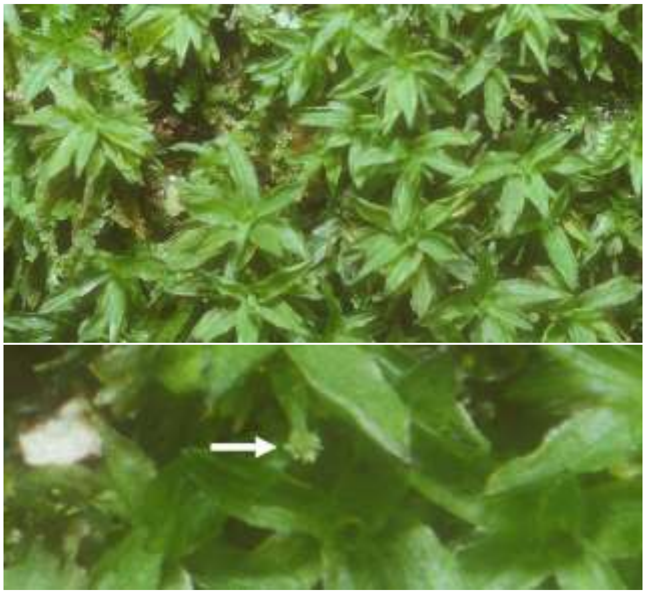

Figure 11. Gametophytes of ***Syrrhopodon texanus***. **Arrow** in lower picture indicates gemmae at leaf tip. Photo by Janice Glime.

Dedifferentiation Issues

It is somewhat difficult to consider bryophyte r and K strategists in the same way as that of seed plants. These two strategies rely heavily on three characteristics of the plant life cycle: arrival and persistence, establishment and growth to maturity in a developing community, and time taken for the species to reach critical life stages (During 1992). Bryophytes are problematic because they do not follow a consistent pathway from spore (propagule) → juvenile → immature individual → reproductive individual. They can revert, growing from a fragment into an adult, or growing from a broken tissue of a fragment into a protonema → juvenile → immature individual → reproductive individual. Bryophytes are able to **dedifferentiate** – return a cell to its embryonic (undifferentiated) state

Compared to most tracheophytes, most bryophytes would appear to be r strategists, utilizing many small progeny (spores) that travel great distances and having short life cycles, permitting them to move on to new locations easily. This may help to account for the widespread distribution of many bryophytes relative to that of seed plants. However, when compared to phanerogams, most bryophytes do not meet the requirement for rapid growth.

Since most species will fall between the two extremes of r and K, the first thing one must realize when trying to determine the r or K status of a species is that ascribing r or K must be done in the context of comparison. Thus, within bryophytes, both ends of the continuum exist, while most species have a mix of characters.

Although bryophytes typically produce large numbers of small spores, many taxa also can increase in numbers by stolons, rhizomes, and branching, qualifying them as K strategists, or long-term stayers. For example, Hedenäs and co-workers (1989) found that the invading moss ***Orthodontium lineare*** in Sweden had a high spore output, but that colonies had a clumped pattern that indicated strong neighborhood effects that permitted spread within a locality. Thus, within the bryophytes, as in tracheophytes, species can be divided into r and K strategists, but they are unlikely to meet all criteria of either, and many trade-offs exist (Stearns 1989). Instead, it appears that many of them are bet-hedgers, being prepared to take advantage of whatever comes along instead of being prepared with a single strategy.

To succeed, they must balance their energy expenditure between sexual reproduction and vegetative growth in a way that best permits them to survive. These strategies must of course be coordinated with their entire physiology and the methods by which each developmental stage is signalled.

The r Strategist

Like typical r strategists, bryophyte r strategists rely heavily on massive numbers, typically 50,000 per capsule, of small spores (10-15 µm) to get to a new location (Schofield 1985). For example, ***Funaria hygrometrica*** can arrive quickly on disturbed sites such as soil charred by fire or agricultural land. But should this be true in predictably disturbed sites such as flood plains? In flood plains one finds members of Archidiidae (Figure 12), a subclass of large-spored mosses, with spores usually 50-150 µm, large enough to be seen without a lens (Schofield 1985). Here it would appear to be advantageous to stay put by producing large, long-lived spores (Söderström 1994). It is likely that this stay-put strategy is available to many mosses and liverworts through spore longevity in soil banks.

Figure 12. A floodplain moss, ***Archidium alternifolium***. Photo by Michael Lüth, with permission.

The K Strategist

Our understanding of perennial stayers (K strategy) is limited by our ability to determine the age of an individual. To age a moss or liverwort is somewhat difficult because among the perennial ones, the bottoms typically die as the tops continue to grow. However, many mosses carry their own age markers (Hagerup 1935), as described in more detail in another chapter, much as trees can be aged by terminal bud scars while they are young. ***Polytrichum*** males can be aged by counting the number of splash cups along the stem, because a new year of growth will come from the cup in the following spring. Ulychna (1963) found ***Polytrichum commune*** with a mean age of 3-5 years, but dead parts in the hummocks ranged 15-17 years. Brunkman (1936) found ***Hylocomium splendens*** (Figure 13) up to 30 years old by counting the successive sets of branches that form like stair steps, each from a point near the apex of the old, but it is unlikely that the oldest parts were still live and functioning. Because most bryophytes do not require their lower parts to keep the upper parts of the plant alive, they could theoretically grow indefinitely in a location due to the growth of the tips. Such a phenomenon is approached in ***Sphagnum***, which will continue to grow as long as the habitat remains suitable.

Figure 13. ***Hylocomium splendens*** showing stairstep branching used for aging the moss. Photo by Janice Glime.

Spores, however, are not the only stage in which r and K strategies might be applied. One could also expect that there would exist a trade-off between numbers of male and female gametangia. Just as some trees, such as maples (*Acer*) can adjust the number of male and female flowers based on tree crowding, one might look for regulation of numbers of male and female gametangia. In their studies of tropical bryophytes, Cavalcanti Pôrto and Moto de Oliveira (Moto de Oliveira & Cavalcanti Pôrto 2001; Cavalcanti Pôrto & Moto de Oliveira 2002) found that development of gametangia was responsive to rainfall. In the moss ***Sematophyllum subpinnatum***, the number of antheridia per perigonium was 8-20 while the number of archegonia per perichaetium was 3-26. For ***Octoblepharum albidum*** (Figure 14) mean number of antheridia per perigonium was 13.4 and of archegonia per perichaetium 6.7. Could moisture regime change these ratios?

Figure 14. ***Octoblepharum albidum***. Photo by Michael Lüth, with permission.

Just how do the r and K strategies of bryophyte gametangia line up? Fuselier and McLetchie (2004) considered this problem in ***Marchantia inflexa***. They found that females had a greater growth rate, but males had more asexual reproduction. Males were also more likely to be present in a high light regime (55% shade), where they began sexual development earlier; males in low light produced no sexual structures (McLetchie *et al.* 2002). Fuselier and McLetchie (2004) postulated that eventually, the greater female growth rate would result in a population of all females as they overgrew males. However, under a disturbance regime, more males would be successful. They found a female bias in sex expression, with many genetically male plants failing to express sexual traits.

The r and K strategies are at best a continuum. Individual species often do not meet the criteria completely. Evolution is imperfect and time is required to drive it toward perfection. Furthermore, the model predictions work only if the environment perfectly matches with the set of bryophyte characters predicted. In the Antarctic, extreme conditions would seem to test this r and K continuum to its limits. And there the imperfections of these predictions are evident. The disturbed nature of this volcanic habitat favors r-selected taxa that must arrive from considerable distances (Convey & Smith 1993). However, the difficulty of spreading during the short, cold growing season favors certain short-lived taxa with large spores. Five of the species that are widespread in the Antarctic have large numbers of small spores and are most likely long-distance colonists. Even the longer-lived taxa seem to defy the r & K model predictions, having a large investment in sexual reproduction.

Life Cycle Strategies

To combat all the insults of the environment that might be encountered in a global array of habitats and climates, a variety of strategies exist among both plants and animals. For bryophytes, the predominant controlling factor is available moisture, but we must consider that temperature is also a major contributor to the timing of life cycle events.

As we consider the life cycle strategies of bryophytes, we must keep in mind that they potentially expose all of their alleles to expression and selection through a considerable portion of their lives – as 1*n* gametophytes. All the variety in strategies discussed above come into play in permitting these tiny organisms to occupy the widest array of conditions of any group of plants. For the greatest number of species to survive across the greatest number of habitats, some have adapted to be **opportunists**, constantly moving from place to place, while at the other extreme are **perennial stayers**, finding a suitable place and remaining there for a long time. But because an individual bryophyte must stay in one place, it must have a life cycle that permits it to survive the onslaught of environmental fluctuations during the entire time it develops from protonema to leafy plant to fertilization to sporophyte to dispersal of spores.

The environment thus provides the major selection pressure on the life cycle strategies. Recognizing the instability of the environment, Stearns (1976) classified the environment into three main types (examples are mine):

1. having **long cyclic fluctuations**, with a period much longer than that of the generation time of the organism (*e.g.* fires)
2. having **short cyclic fluctuations**, with a period that is as long as or shorter than the generation time of the organism (*e.g.* seasons)
    a. cycle highly predictable
    b. start of cycle unpredictable
    c. start of cycle predictable, but conditions of growing season unknown
    d. start of cycle predictable, but conditions only partly known
3. having **random fluctuations**, *i.e.* not predictable (*e.g.* flash floods)

To survive in a fluctuating environment, the life cycle must prepare the bryophyte for the fluctuations. This means that at times it is advantageous to "run for your life" to other locations (produce spores), whereas under other, more favorable conditions it is best to sit still and keep your family together (reproduce vegetatively).

During (1979) has examined in detail the life cycle strategies of bryophytes in dealing with environmental conditions. In finding that most tracheophyte life cycle strategy systems either did not apply or were incomplete for the bryophytes, he devised a system of six strategies. He considered that bryophytes utilize three major trade-offs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) *vs* survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort (for tolerants only) (During 1992). In addition, there is a usually tradeoff between sexual and asexual reproduction (Schofield 1981, During 1992). These considerations resulted in his organization of strategies based on life span, spore number and size, and reproductive effort (Table 1 and figures from During 1992; table slightly modified):

Table 1. Spore and life span characteristics of the various life cycle strategies for bryophytes as defined by During (1979).

	Spores		
Potential life span (yrs)	**Numerous very light <20 µm**	**Few large >20 µm**	**Repro effort**
<1	Fugitives	Annual shuttle	High
Few	Colonists		Variable
	Ephemeral	Short-lived shuttle	
	Colonists	Long-lived shuttle	
	Pioneers		
Many	Perennial stayers	Dominants	Low
	Competitive		
	Stress-tolerant		

The system of During has attributes that work as well for higher plants, and Frey and Hensen (1995) have proposed a modified system based on this one to be used for all plants. (Now how often do you see those tracheophyte folks copying a bryophyte idea?! Kudos to During!) They have expanded upon the original six strategies proposed by During to include nine: annual shuttle species, fugitives, kryptophytes, short-lived shuttle species, colonists, perennial colonists, perennial shuttle species, perennial stayers, and perennial stayers with diaspore years. Hürschner and Frey (2012) included geophytes and perennial shuttle species to the bryophyte list.

Fugitives (Figure 15), **colonists** (Figure 16), **annual shuttle species** (Figure 17), and **short-lived shuttle species** (Figure 18) are **r strategists** and all succeed in disturbed environments. The fugitive strategy is relatively rare, with ***Funaria hygrometrica*** being one of the few examples (During 1992). That many species require disturbance and therefore are relatively rare in any specific locality is usually overlooked in trying to conserve rare taxa. The very disturbance they need to persist is often prevented in an effort to maintain them! Noble and Slatyer (1979) attribute success following disturbance to plant strategies related to three factors: method of arrival (fugitives, colonists, annual shuttle species) or persistence at disturbed site (short-lived shuttle species); ability to become established and reach maturity in disturbed site; time needed to reach critical life cycle stage. These criteria are not intended to include those of taxa adapted to continuously disturbed or catastrophically disturbed habitats, but rather to those recurring events such as fire, flood, or treefall. The **perennial** bryophytes are **K strategists** (Figure 19, Figure 20) of stable habitats.

During (1992) added the category of **dominant** to accommodate taxa with large spores and long life expectancy, such as some ***Sphagnum*** species. It is a rare combination among bryophytes, whereas it is relatively common among trees. Other categories will surely be added as we gain understanding of tropical ecology and the adaptive strategies of bryophytes there (During 1992). One such category could develop based on **neoteny**, where juvenile characters are retained in adults, a condition that occurs among some species of ephemeral habitats such as living on leaves in the tropics (During 1992). In some taxa, such as ***Buxbaumia***, neoteny permits the species to avoid some life cycle stages, in this case the leafy gametophyte! La Farge-England (1996) has suggested the category of **protonema mosses** to encompass these few taxa (see chapter on life forms and growth forms). Others, such as ***Dicranum*** and ***Fissidens*** species, have **dwarf males** that develop on leaves of female plants, facilitating the transfer of sperm to the egg, a kind of male neoteny. (See chapters on sexuality and on the development chapter on gametogenesis for further discussion of dwarf males.)

Diaspore Banks

Disturbed habitats, whether the product of predictable natural phenomena or unpredictable events such as human intervention or volcanic eruptions, benefit from the bank of spores and asexual **diaspores** (any structures that become detached from parent plant and give rise to new individuals) stored in the soil out of reach of sun and sometimes even water. Major disturbances can bring these propagules to the surface where they can break dormancy and become established. We need only look at a recently disturbed bank in a forest, sloping deforested hillside, or crumbling streambank to recognize the importance of bryophytes in colonizing and often maintaining the surface integrity. Yet, as Ross-Davis and Frego (2004) pointed out, while these regeneration processes "may be critical to conservation of severely disturbed communities..., they are poorly understood." In an attempt to quantify this importance they sampled two grids in managed Acadian forests of New Brunswick, Canada. They identified 51 taxa in the aerial diaspore rain and buried diaspore banks. Of these, 36 represented species in the existing community of the Acadian forest. The composition of aerial diaspores was more similar to the existing community than to that of buried ones.

Tradeoffs

For bryophytes, the system of success strategies is complicated by the ability to reproduce from fragments, and in many cases the production of asexual propagules on the protonemata as well as on the leafy plant, leading During to his 1992 revision. One must keep in mind that bryophytes may be among the best dispersers in the world. Therefore, large spore size, as opposed to small ones with worldwide dispersal potential, may be a tradeoff of great magnitude. While many of these small spores will not survive the long distance travel due to UV radiation and other atmospheric hazards (see dispersal chapter later), many will survive significant local travel, with a few travelling for hundreds of kilometers.

Once the spores arrive, different attributes become important. The spore must have sufficient energy to survive until favorable conditions arise, and it must get the new protonema off to a good start with enough energy to survive in some very harsh environments. This has resulted in a correlation of spore germination patterns with habitat (Nehira 1987). Epiphytic and saxicolous species of both mosses and liverworts tend to have **endosporic** germination (*i.e.*, early development of several mitotic divisions within the spore wall; Figure 21), permitting them to be multicellular when they emerge from the protection of the spore. This would suggest that these species carry sufficient nutrients with them to supply their initial developmental nutrient needs. On nutrient-poor, **xeric** (dry) substrates such as rock and bark, internal development could insure protection during early, critical stages of development. However, most mosses have **exosporic** germination (first mitotic division occurs outside spore after rupture of spore wall).

Life Cycle Strategies

based on During (1979, 1992)

Fugitives

Fugitives – *species that live in unpredictable environments*

example: ***Funaria hygrometrica***
short life span; ephemeral or annual
high sexual reproductive effort; large percent of plant devoted to spore production
low age of first reproduction (first year)
spores small (<20 µm), very persistent and long-lived
no asexual reproduction
innovations absent
open turfs
rare in phanerogams (mustards?) and bryophytes; found among bacteria, algae, fungi

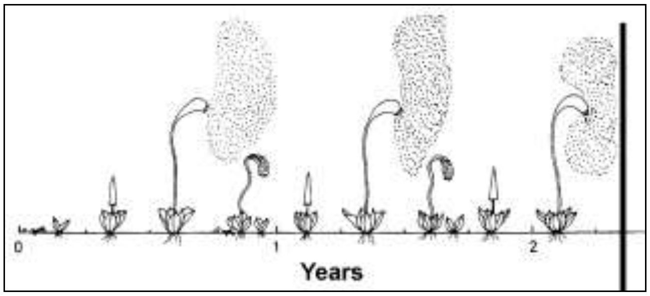

Figure 15. **Fugitive** strategy. From During (1979).

Colonists

Colonists (sensu stricto) – *species that live where habitat start is unpredictable, but lasts several years; secondary succession*

bryophyte examples: ***Bryum bicolor***, ***Bryum argenteum***, ***Ceratodon***, ***Marchantia***
short life span; (annual-) pauciennial-pluriennial
sporophyte late, somewhat rare in many; first sexual reproduction at least after 1 and usually 2-3 years
high reproductive effort
spores < 20 µm, persistent
innovations present
asexual in early life; first asexual reproduction in a few months
usually short turf
old field species like *Solidago*

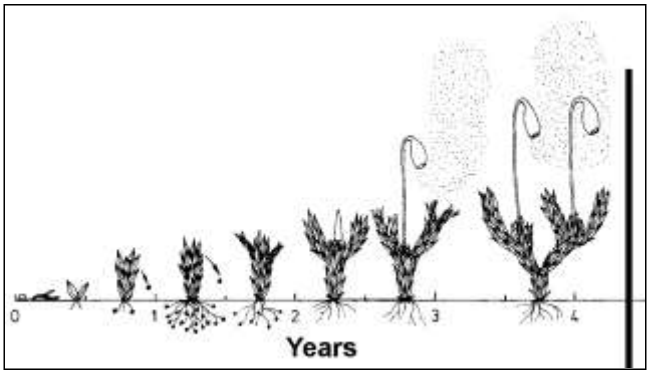

Figure 16. **Colonist** (*sensu stricto*) life cycle strategy. From During (1979).

Colonists

Colonists (ephemerals) – *gap-dependent species*

bryophyte example: ***Bryum erythrocarpum***
short life span; (annual-) pauciennial-pluriennial
first sexual reproduction in a few months
sexual reproduction rare
spores < 20 µm, persistent, numerous
high asexual reproductive effort by subterranean tubers on rhizoids
river flood plains, low areas submerged in spring, cultivated fields
usually short turf

Colonists (pioneers) – *species that live where habitat start is unpredictable and habitat lasts at least several years after disturbance; make habitat suitable for perennial stayers (Rabotnov 1975)*

bryophyte examples: ***Grimmia***, ***Schistidium***
long life span
slow growth
perennial
high reproductive effort
first sexual reproduction in a few years???
sexual reproduction low
asexual reproduction high
spores < 20 µm, persistent
river flood plains, low areas submerged in spring, cultivated fields
usually short turf

Shuttles

Annual Shuttle – *species that require small disturbances that last 1-2 years; survive severe stress periods*

bryophyte examples: ***Ephemerum***, ***Physcomitrium***, ***Fossombronia***
short life span; (ephemeral-) annual-pauciennial
sexual reproduction effort high and frequent
age of first reproduction < 1 year
spores large, 25-50 (-200) µm
survive by spores
capsules often immersed (short or no setae) (Longton 1988)
specialized asexual reproductive structures absent
innovations rare
open turf or thalloid mat
agricultural weeds, hoof prints, steep stream banks, dung
disturbed habitat species like *Brassica*

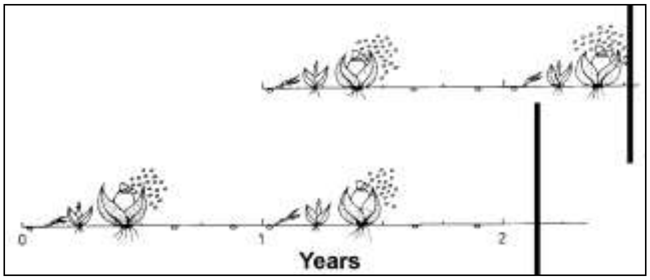

Figure 17. **Annual shuttle** life cycle strategy. From During (1979).

Short-lived Shuttle – *species that don't avoid periods of severe stress; habitat lasts 2-3 years*

bryophyte examples: ***Hennediella heimii***, ***Splachnum***, ***Tetraplodon***
life span several years, pauci-pleuriennial
sexual reproductive effort high; sporophytes more or less frequent
overall reproductive effort medium
ages of first reproduction 2-3 years
spores large, 25-50 (-100) µm
asexual reproduction rare
innovations present
short turf or thalloid mat

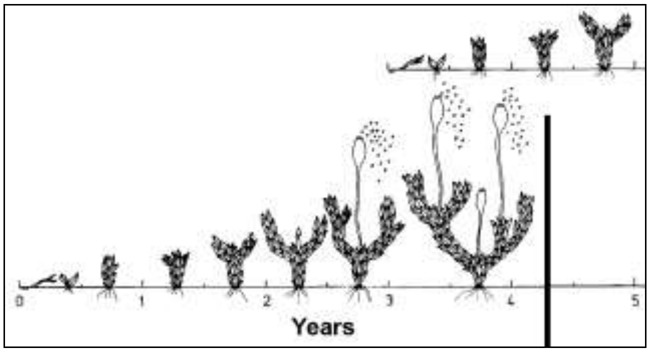

Figure 18. **Short-lived shuttle** life cycle strategy. From During (1979).

Perennial (Long-lived) Shuttle – *species that require stable environments, such as epiphytes, where end of habitat is predictable*

bryophyte examples: ***Orthotrichum***, **Marchantiales**
long life span; pluriennial, perennial
sexual reproduction effort moderate (During 1979) or low (During 1992)
age of first sexual reproduction high (>5yrs)
spores large (25-200 µm)
spore life span short
asexual reproduction effort moderate
innovations present
age of first asexual reproduction variable
cushion, rough mat, smooth mat, tuft
tracheophytes include bromeliads, *Betula*, *Populus*

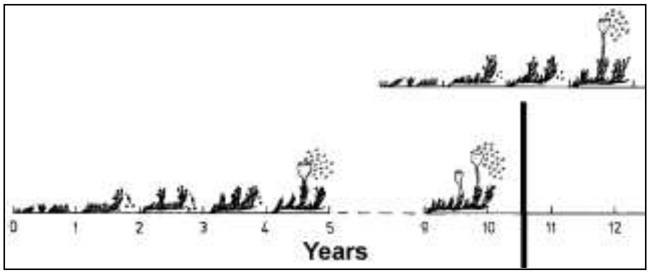

Figure 19. **Perennial long-lived shuttle** life cycle strategy. From During (1979).

Perennial Stayers

Perennial stayers (competitive) – *forest floor*

bryophyte examples: ***Brachythecium rutabulum***
long life span
perennials
rapid growth
sexual and asexual reproduction low or nearly absent
age of first reproduction several years
spores <20 µm
spore longevity variable
wefts, dendroids, mats, large cushions

Perennial stayers (stress-tolerant) – *fens, bogs, desert*

bryophyte examples: ***Sphagnum***, ***Syntrichia ruralis***
long life span; perennials
slow growth
sexual and asexual reproduction low or nearly absent
age of first reproduction several years
spores <20 µm
spore longevity variable
growth form plasticity
in deserts include acrocarpous taxa with long setae
tracheophytes include ericaceous shrubs

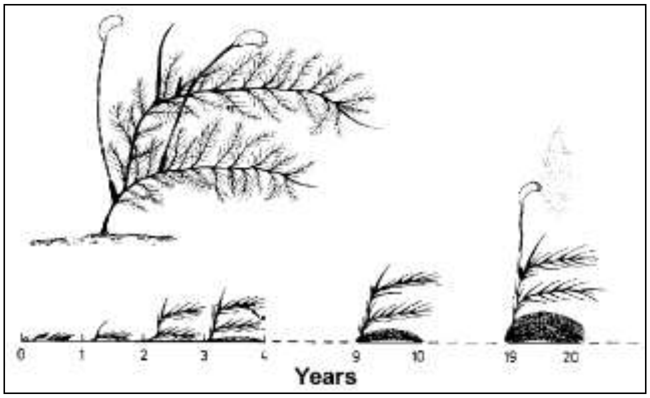

Figure 20. **Perennial stayer** life cycle strategy. From During (1979).

Dominants – bogs

bryophyte example: some ***Sphagnum***
long life span; perennial
sexual reproduction effort low
spores large (>20 µm)
asexual reproduction effort low
turf

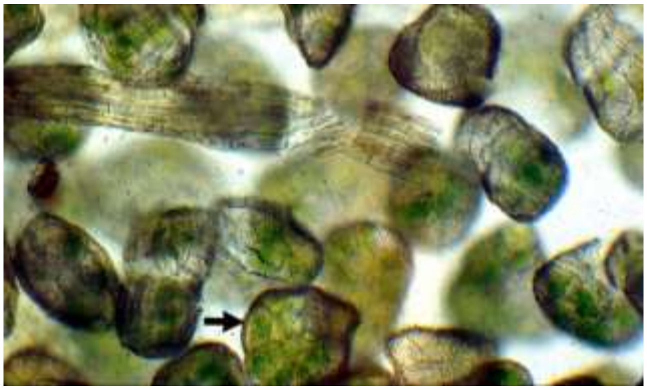

Figure 21. Endosporic development (**arrow**) in spores of the hornwort ***Dendroceros tubercularis***. Photo courtesy of Karen Renzaglia.

But spores are not the only way to travel. Fragments and propagules can carry the species to a new location, although the generally much larger size would usually limit distance considerably. Moss balls (see chapter on life form) along lake shores and on glaciers and snow banks serve as means of dispersing large units, including multiple plants. Landslides, rock movement in streams, trampling, and vehicle tires can carry fragments for some distance. For those producing asexual propagules, sexual reproduction and asexual propagules are usually not produced at the same time. Thus, investment in specialized asexual structures is indeed a trade-off. Taxa with annual life cycles, surviving unfavorable conditions as spores, rarely produce such specialized structures, investing their energy instead in the production of spores (During 1992).

We know little about the energy costs of producing spores and other propagules, and in particular know nothing of the effect of spore production on mortality (During 1992). There is evidence, however, that development of sporophytes slows the growth of the gametophytic plant in ***Scorpidium scorpioides*** (A. M. Kooijman & H. J. During, unpubl. data) and ***Plagiothecium undulatum*** (Figure 22; Hofman 1991), as well as in ***Dicranum polysetum*** mentioned earlier (Bisang & Ehrlén 2002). This tradeoff may be a general rule, as discussed in the chapter on sporophyte development.

Figure 22. ***Dicranum polysetum*** exhibiting its multiple setae per stem. Photo by Janice Glime.

Some characteristics of the life strategies may be interrelated. For example, Hedderson (1995) found that in the Pottiales the probability of producing capsules decreased with increased life expectancy and was negatively associated with asexual propagules. As discussed in the chapter on asexual propagules (brood bodies), these compete for energy with the production of capsules and generally do not occur simultaneously. It therefore follows that dioicous taxa in this group have more asexual propagules, corresponding with their lower likelihood of having sexual reproduction. Unlike sporophytes, asexual propagules were positively associated with life expectancy. On the other hand, size accounts for only a small, but statistically significant, proportion of the variation in life history traits in the Funariales, Polytrichales, and Pottiales (Hedderson & Longton 1996). Rather, characteristics related to water relationships were most important, accounting for 40-50% of the variation. It is interesting that the ability to take in and retain water coincides with monoicous taxa that are short-lived and produce few large spores, whereas those at the opposite end of the endo-ectohydric gradient have opposite characters. Spore number and spore size are strongly related to family, with most of the variation occurring among genera. Variation among species is moderate. Hedderson and Longton suggested the possibility of coevolution of water relations and life history in these orders.

Longton (1997) used the concept of life history strategies to predict character relationships. Colonists, fugitives, and shuttle species exhibit an earlier age for first reproduction as the longevity decreases. These strategies are accompanied by greater monoicy and reproductive effort (Longton 1997, 1998). Such species tend to have more plastic phenotypes and experience greater success at establishment by spores. Dioicous moss colonists, on the other hand, are more likely to produce asexual propagules, whereas such propagules are widespread among liverworts.

Generation Time

Generation time is one of the contributors to life cycle strategy, but we have no comprehensive study by which to label this function for bryophyte species in general. In order to meet the IUCN red list criteria, bryophytes mus be put into generation time categories. This is important because environmental changes may take longer to affect numbers of those species with a long life cycle than for those with a short one. Tomas Hallingbäck (Bryonet 9 January 2014) reports that in Sweden they have used templates of 10, 20, 50, and 100 years as the intervals for three generations. Since hard data are generally not available, the Swedes agreed upon approximate generation lengths and **life spans** and classified their species based on the potential life span of the gametophyte:

- 'short' (colonists s. str., fugitives) = 3 generations = 10 (*e.g.* ***Microbryum*** spp.)
- 'medium' (pioneer colonists, short-lived shuttle) = 3 generations = 20 years (*e. g.* a typical epiphyte like a ***Syntrichia***)
- 'long' (long-lived shuttle – perennial stayers) = 3 generations = 50 years (*e.g.* ***Hylocomium splendens***).
- For species rarely found with sporophytes, a generation time of 25 years was recommended

Habitat Studies

Occasionally a habitat study will describe the growth forms or life forms that dominate there. But quantitative studies to describe these are rare. However, a few examples from tropical habitats can serve to provide an understanding of their usefulness in giving a mental picture of the bryophyte cover in places we have never visited.

In the **Colombian cloud forest**, epiphytes are abundant due to the high moisture availability from the clouds and the infrequency of desiccation events. This type of climate supports growths of tall turfs and smooth mats as predominant growth forms on the trees (van Leerdam *et al*. 1990). On the other hand, the life strategies of bryophytes on trees on the **eastern Andean slopes** of northern Peru reflect the drier habitat. Colonists form short turfs of acrocarpous mosses, primarily in secondary forests suffering disturbance. In the **lowland** and **submontane forests**, perennial shuttle species and perennial stayers exercise low sexual reproductive effort and take advantage of the high humidity to accomplish high vegetative reproduction through both propagules and clonal growth (Kürschner & Parolly 1998a). ***Macromitrium*** (Figure 23) and ***Phyllogonium fulgens*** (Figure 25) have dwarf males resulting from small male spores compared to large female spores. (Dwarf males are discussed more thoroughly in the chapters on sexuality and gametogenesis.) ***Leptodontium viticulosoides*** (Figure 24) exhibits functional heterospory in which small spores are dispersed long distances and large ones only short distances. On the other hand, at high elevations **near timberline**, the perennial shuttle and perennial stayer species instead exercise a high sexual reproduction and produce numerous sporophytes. Similar altitudinal differences occur in Southeast Asia and Central Africa.

Figure 23. ***Macromitrium sulcatum***, member of a genus with small male spores and dwarf males. Photo by Manju Nair, through Creative Commons.

Bryophytes of the **tropical lowlands** have a very different character from these montane epiphytes, providing them with maximum water conservation in this much drier habitat. The mat life form encompasses species with water lobules, water sacs, and rhizoid discs (Kürschner & Parolly 1998b). This life form gives way to fans, wefts, dendroids, and pendants in the more humid **montane belt**. These forms serve as collectors to condense water vapor from the frequent fog and mist (**fog-stripping**; Figure 26). Deeply fissured or ciliate leaves and rill-like arrangement provide the fine wire-like surfaces needed for this water capture. The **tropical oreal** (high altitude) and **subandean belt** contrasts with this foggy area by having strongly contrasting diurnal conditions and supporting short-turf, tall-turf, and tail life forms with central strands, rhizoids, and rill-like leaf arrangements.

Figure 24. ***Leptodontium viticulosuides***, a species that has functional heterospory. Photo by Li Zhang, with permission.

Figure 25. Pendant ***Phyllogonium fulgens*** in Japan. Photo by Janice Glime.

Figure 26. "Fog-stripping" by thin leaves of ***Campylopus holomitrius*** in the mist from geothermal vents at Karapiti, New Zealand. Photo by Janice Glime.

Bryophytes of **arid habitats** are typically small and may include acrocarpous perennial stayers with small spores and long setae that aid in dispersal (Longton 1988). Annual shuttle species here are primarily ephemerals that avoid desiccation by going dormant as spores, develop rapidly to maturity following rain, and produce large spores in capsules that typically lack stalks and remain submersed among the perichaetial leaves; often these capsules lack peristomes and opercula and may be dispersed as whole capsules (see chapter on development of sporophytes). The perennial shuttle species are mostly thallose liverworts such as ***Riccia*** (Figure 27) that curl up and become dormant or survive as large spores. Fugitives may arrive, but generally are gone after 1-2 years, travelling to new sites as small spores.

Figure 27. ***Riccia sorocarpa***, showing curling leaves that facilitate survival of dry conditions. Photo from Botany website, UBC, with permission.

González-Mancebo and Hernández-García (1996) related life strategies to habitats along an altitudinal gradient in the Canary Islands. They found the following trends for the most abundant strategies:

higher elevations: colonists
rocks in driest forest: colonists, short-lived shuttle, long-lived shuttle
humid forest trees: long-lived shuttle, short-lived shuttle
humid forest soil: perennials
soil in shady, dry forest: perennials

These strategies seem to be determined by humidity conditions, substrate dynamics, and vegetation disturbance. Not surprisingly, the perennial life strategy had the lowest percentage of fertile species. The other strategies typically have approximately 70% fertility.

Summary

Bryophyte life strategies must be closely attuned to the water regime of their environment. They accomplish this fine tuning by using spores, fragments, and specialized asexual propagules during times when conditions are not suitable for the gametophyte. Furthermore, they attune their times of sexual reproduction to meet the availability of water. Secondary to the water schedule is the advent of disturbance for which some bryophytes are especially adapted (**opportunists**).

Bryophytes, especially mosses, are clonal organisms. All bryophytes are able to spread vegetatively through fragments and propagules. Perennial mosses also spread by branching (**ramets/genets**). Mosses, additionally, produce many upright gametophytes from the protonema developed from a single spore. Clones have the advantage of maintaining moisture, but have the disadvantage of being genetically identical. Bryophytes that grow horizontally have been considered **foragers** that are able to take advantage of a patchy environment to obtain nutrients, light from **sunflecks**, and even water in different parts of the plant. They are able, at least in some taxa, to transport these nutrients or the photosynthate to other parts of the plant. Sexual reproduction is favored when clones and clumps provide both sexes, and even in monoicous taxa the differences in maturation times among members of the clone become an advantage.

Density can work for and against bryophytes. At low densities, water loss is greater and sexual reproduction is less successful, favoring spread by spores at high densities. However, in some mosses, such as ***Polytrichum***, shoot mortality can increase with density, but in other taxa it can decrease.

There is a tradeoff between sexual reproduction and asexual reproduction, including branching and growth, as these events compete for energy.

Compared to tracheophytes, bryophytes are **r strategists**, but within the bryophytes there is an entire range from **r strategist** to **K strategist**. The **r strategists** rely on large numbers of small spores and a short life cycle (**opportunists**). **K strategists** rely on their clonal, perennial growth (**perennial stayers**) and often have only limited sexual reproduction or are strictly vegetative. But most bryophytes lie somewhere on the **bet hedger** line, producing spores sexually, but using fragments and asexual propagules during seasons when energy is not needed for sexual reproduction or spore production. Because of their ability to

dedifferentiate, bryophytes often spread by fragments of ordinary tissue.

Availability of water is the most important determinant of life cycle strategy. Endosporic development is more common on low water, low nutrient substrates like rock and bark. Disturbance is actually required for some species.

Bryophytes utilize three major tradeoffs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) *vs* survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort. **Diaspore banks** permit bryophytes to survive untenable periods of time in a dormant state and begin growth when suitable conditions return. **Endosporic development** permits some bryophytes to get a head start in particularly short-lived periods of adequate moisture, such as deserts, floodplains, and vertical substrates.

Acknowledgments

Jean Faubert caught some serious inconsistencies in the r-K selection text and made valuable suggestions to improve this subchapter.

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