CHAPTER 4-4

ADAPTIVE STRATEGIES: PHENOLOGY TRADEOFFS

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Figure 1. ***Hylocomium splendens*** with sporophytes and young shoot showing new growth of an unexpanded branch to their right. Photo by Janice Glime.

Tradeoffs

Just when you think you have solved all the problems, you discover that the solution has created a new problem. So it is with life, and so it is with optimizing the events in the life of a plant. Large spores give the plant a better start, small ones travel farther. Lots of spores give more chances for landing at a suitable time on a suitable spot, but their survival chances are lower. But what sorts of numbers are we talking about?

Finding this information is not easy, as few papers are written expressly for the purpose of comparing these numbers. We need a concerted effort to put together a representative list. A few are shown in Table 1.

In an organism where the male gamete must disperse without a very specific carrier and the female is stationary, we assume that more males are needed to service the females because many males will be unsuccessful. Rydgren and Økland (2003) stated that we still do not know if bryophytes exhibit reproductive costs (energy costs). Meager evidence suggests they do.

Table 1. Comparison of numbers of reproductive parts of bryophytes. This table is in no way representative.

Octoblepharum albidum	Pôrto & de Oliveira 2002
archegonia	6.7 per perichaetium
antheridia	13.4 per perigonium
Sematophyllum subpinnatum	de Oliveira & Pôrto 2001
archegonia	3-26 per perichaetium
antheridia	8-20 per perigonium
Sphagnum	Sundberg 2002
sporophytes	0.64-20 per dm^2
spores	16,000,000 per m^2
Trichostomum perligulatum	Stark & Castetter 1995
archegonia	2
antheridia	6
Cyathodium bischlerianum	Salazar Allen 2001
archegonia	1-2 per involucre
Plagiochila adianthoides	Johnson 1929
antheridia	22 per spike
sperm	25,000 per antheridium

Rydgren and Økland (2003) compared non-sporophyte-producing and sporophyte-producing sub-population of ***Hylocomium splendens*** (Figure 1) for five years. They found that indeed the plants with sporophytes had less size development of daughter segments, a lower branching frequency, and fewer new annual segments than those individuals with no sporophytes. This reduced development occurs primarily during the time when the capsule expands and spores are produced, suggesting that there is a significant cost for reproduction – a tradeoff.

However, if all the gametangia are accounted for, rather than individuals, this may not be the case. Stark and coworkers (2001), in examining the desert moss ***Syntrichia caninervis*** (Figure 2), found that when male and female expressing individuals were controlled for **inflorescence** (reproductive organ group) number, there were no significant differences in biomass between the sexes. Surprisingly, among those that were not expressing sexual traits, there was lower biomass, shorter total stem length, fewer branches, and shorter **ramets** (individual member of clone) than in sex-expressing males and females, and there were fewer ramets than there were sex-expressing female individuals. A threshold size seems to be necessary for sexual expression, accounting at least in part for size differences. In fact, for ***Syntrichia caninervis*** in this study, all individuals weighing more than 2.0 mg evidenced sexual expression. This biomass requirement supports the concept that more energy is needed for sexual expression, likewise supporting the expectation of a tradeoff between growth and reproduction.

Figure 2. ***Syntrichia caninervis***. Photo by John Game, through Flickr Creative Commons.

Tradeoffs with Spore Production

To understand the seasons of sexual reproduction, one needs to understand the tradeoffs within the growth cycle as well. First, there needs to be a sufficient energy supply for either a sexual or an asexual event, and while the formation of sex organs does not seem to produce as much biomass, it is a developmental stage that is costly in energy. Second, the production of gametangia may interfere directly with further growth. In acrocarpous mosses, the gametangia are terminal on the main stem (Figure 3), and once they develop, they inhibit the further development of the stem, at least for that season (Figure 4). Thus, vegetative growth, in acrocarpous taxa at least, may be strongly limited by time of gametangial production.

Figure 3. ***Polytrichum piliferum*** splash cups that effectively stop growth of the stem while they are functional. Photo by Janice Glime.

Figure 4. ***Polytrichum ohioense*** male stems with new growth extended from the splash cups. When the antheridia are developing, further growth of this apex is arrested. Photo by Janice Glime.

Pleurocarpous mosses, on the other hand, develop gametangia on lateral branches and these do not interfere with the growth of the main stems. This difference is further complicated by the fact that most (all?) pleurocarpous mosses are perennial, whereas many of the acrocarpous mosses are annual. Furthermore, one might suppose, the annuals are much more likely to produce capsules (and by implication, gametangia) to permit them to overwinter as spores, whereas many perennials persist by vegetative means only. But, we have very little direct field evidence to support or refute this supposition.

It might be interesting to compare seasons of vegetative growth vs gametangial season in acrocarpous vs pleurocarpous mosses and annuals vs perennials, but data on gametangia are scarce. Among the mosses in Conard's 1947 study, only 15 of the 232 taxa collected had gametangia.

Based on Conard's survey, it appears that peaks in gametangial production in liverworts occur during late spring and again in fall, at least among the 60 Iowa taxa (Figure 5). This is consistent with the report by Zehr (1979) that photoperiod is the dominant factor in gametangial formation in four of the five taxa he studied: ***Lophocolea heterophylla*** (Figure 6) is day neutral; ***Diphyscium foliosum*** (Figure 7), ***Atrichum angustatum***

(Figure 8), ***Trichocolea tomentella*** (Figure 9), and ***Nowellia curvifolia*** (Figure 10) are long-day plants. However, Zehr's sample size is small and Conard's samples may have been biased, since they were subject to seasons favorable for collecting (and collectors), and collectors may be selective in what they collect and keep, favoring plants with capsules over those without.

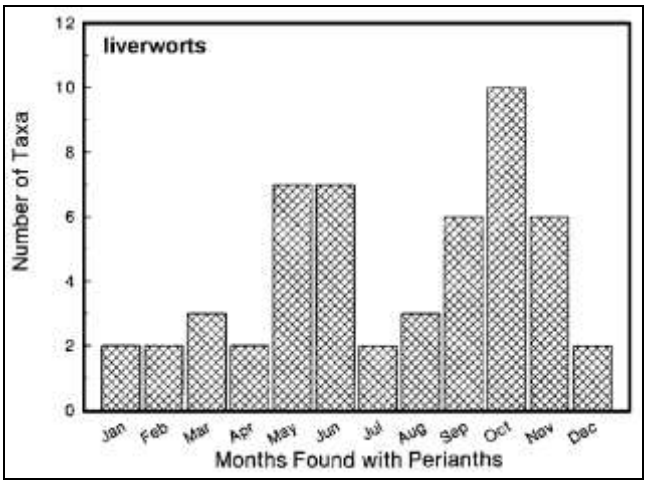

Figure 5. Numbers of taxa with perianths (leafy enclosure of liverwort archegonia) per month among the 30 taxa having perianths out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Figure 6. ***Lophocolea heterophylla***, a day-neutral liverwort, on log. Photo by Janice Glime.

Figure 7. ***Diphyscium foliosum*** females, a long-day species. Photo by David Holyoak, with permission.

Figure 8. ***Atrichum angustatum***, a long-day moss. Photo by Bob Klips, with permission.

Figure 9. ***Trichocolea tomentella*** from Europe, a long-day liverwort. Photo by Michael Lüth, with permission.

Figure 10. ***Nowellia curvifolia***, a long-day liverwort, on a log. Photo by Jan-Peter Frahm, with permission.

It seems that the co-occurrence of fertilization and spore release is relatively common among bryophytes, as seen in the studies of Grimme (1903), Arnell (1905), Lackner (1939), Jendralski (1955), Greene (1960), and van der Wijk (1960). Based on his British experience, Greene (1960) stated that even before a **cohort** (group of individuals with same starting point) of capsules has dehisced, new gametangia are developing. To him, it was "clear" that when sporophytes develop slowly, fertilization may be effected before the previous generation of spores has been released. Likewise, David Wagner (pers. comm.) finds spore and sperm dispersal during the same season in the Northwestern United States. Stark (2001) points out that we have few definitive studies on the duration of spore

dispersal and that in some cases this may last an entire year, as it does with most desert bryophytes.

Two determining factors must be kept in balance to maintain a life cycle: the energy requirements and the growing conditions. For dispersal of sperm, clearly water is needed, and energy must be available leading up to sperm maturation. Spore dispersal is most often favored by dry weather, which as already pointed out, can alternate effectively with wet weather in spring. Spore dispersal itself is a mechanical process and presumably requires no energy. Spore maturation does, but dispersal can wait, being effected in most cases when the capsule dries out, forcing the operculum off. This process likewise might be presumed to require no energy. Therefore, energy requirements may be sufficiently spread over time so that the processes of gametangial maturation and spore/capsule maturation do not compete enough to be detrimental. Once these demands are met, it is beneficial for spores that lack dormancy to be dispersed when good growing conditions are close at hand. The alternating wet and dry conditions of spring would seem to be ideal for this. It remains for us to demonstrate that in fact this is so, since we know virtually nothing about spore germination and protonema development in nature for most species.

Geographic Differences

Both latitude and altitude create different climatic conditions. Inland conditions can be quite different from coastal conditions. The wide range of temperature and moisture created by these geographic conditions imposes strong selection pressures on the genes controlling the phenology of the organisms living there.

Some bryophytes seem to ignore winter, as does ***Schistidium apocarpum*** var. ***confertum*** (Figure 11) in the eastern Pyrenees (Lloret Maya 1987). This species, despite living above 1800 meters elevation, is not affected by winter conditions. However, other taxa in these mountains have mature gametangia and fertilization early in the summer with dormant winter sporophyte development followed by rapid maturation of the sporophyte in the first months of summer. At the same time, species living at lower elevations exhibit a continuous progression of stages with no dormancy. Only ***Schistidium apocarpum*** var. ***confertum*** behaves this way at high altitudes.

Figure 11. ***Schistidium apocarpum*** var. ***confertum*** growing on rock and exhibiting its typical abundant capsules. Photo by Michael Lüth, with permission.

Longton and Greene (1969) demonstrated a latitudinal difference in ***Pleurozium schreberi*** (Figure 12). In Great Britain, perigonial development begins in August. Antheridial development apparently is dormant in an immature stage through the winter. Archegonia are first evidenced by perichaetial development in October, but the archegonia likewise overwinter in an immature stage. In spring, both gametangia develop rapidly and fertilization ensues in April and May. The young sporophytes begin to emerge in May, but seta elongation is delayed until August. By October the operculum is in its mature stage, but spores are retained until January, with dispersal occurring January through April – a 9-12 month cycle. Thus, even in this maritime climate, winter is unsuitable for most developmental activities, although presumably winter growth is possible. In France, Finland, and North America, vegetative growth is arrested during the winter, resuming for the period of April to November.

Figure 12. The red-stemmed moss, ***Pleurozium schreberi***. Photo by Michael Lüth, with permission.

Measuring winter growth under the snow is difficult. One cannot remove the snow to measure the growth because that would alter the conditions, affecting subsequent measurements. Ideally, one could measure length or biomass just before the first snowfall and just after spring melt, but that is not as easy as it may seem. The first snowfall may only provide temporary cover, followed by a warm period. One cannot be there every day to ensure measurement on the one day that lies just before the permanent winter cover. And spring is not as easy to determine as it might seem. In many habitats, bryophytes are covered with water for a short period of time during and just after snowmelt. Furthermore, the snow may leave, but the air remain cold, or temperatures might rapidly climb to a balmy spring day when there is no more change of state from solid ice to liquid or gas as the snow melts. Predicting and being there and knowing that the patch you measure has just come out from the snow would require being a psychic.

For many bryophytes, those early days following snowmelt are the best time all year for growing as they take advantage of the open canopy and warm but not hot temperatures. But we know next to nothing about the ability of bryophytes to grow under the snow. Could they get enough light through thin layers of snow and enough moisture from partial melt to photosynthesize at times in the winter? Is there a possibility they begin their spring productivity two weeks before they are uncovered? And what about the epiphytes that rest within that funnel of air between the snow and the bark? Are they warm enough

and humid enough to continue photosynthesis throughout most of the winter? Trynoski and Glime (1982) suggest they might, based on finding more bryophytes and bryophyte biomass on the south side of the tree at breast height in Keweenaw County, Michigan, USA.

Longevity Tradeoffs

In 2009, Bryonetters asked "How long do mosses live?" In 2014, Bryonetter Wang Zhe asked about the **longevity** (length of life span) of bryophytes. There is no satisfactory answer to this question. True, some have very short life cycles, emerging from spores as flood waters recede and completing an annual life cycle within a few months. Others, like ***Sphagnum***, may live hundreds of years, dying at the bottom and growing at the top. Others challenge our definition of death, regaining photosynthesis after a long desiccation dormancy.

Thus, the first problem is to determine if the bryophyte is alive. In an organism that thrives on fragmentation, we are confounded by the possibility that a cell or cells remain alive and can under the appropriate conditions begin new growth, often to produce a new plant, a condition known as **totipotency**. In other cases, tissues may remain dormant for years, only to resume growth when getting the light and water they vitally need.

Guy Brassard responded to this query on Bryonet: "This is interesting in a rather odd way. Some years ago, when I was at Memorial University, I found a piece of ***Hylocomium splendens*** (Figure 1) that I had dried between the pages of a book some 20 years earlier. I put it on a damp paper in a Petri dish on a window ledge without hoping for anything to happen. But, much to my surprise, after about 2 or 3 weeks a NEW BUD appeared on the stem and proceeded to grow into a new branch. So there must have still been some live germ-plasm in the stem of that dried old specimen. If such a tiny piece could remain 'alive' for two decades inside the pages of a book (no water and essentially no light), this means that the time span for air-dried bryophytes retaining live tissue could be much longer (50? 100? years), and that most herbarium specimens are still 'alive' as well!"

This year I watched my moss garden emerge from under the snow after a long and especially cold winter. I was shocked to see that most of the mosses were brown and appeared to be dead. I resisted the temptation to replace them and watched. It took about a month, but green appeared, and most of the clumps now look fully green after a mild, bryophyte-favorable summer. How DO we recognize a dead bryophyte?

The second problem is to determine the age of the bryophyte. As already noted, some mosses have natural annual markers. ***Hylocomium splendens*** (Figure 1) is named stair-step moss because each year it produces a new primary branch. These stack up like stairs and can be used to determine the age of the moss. ***Polytrichum*** species have small sections of reduced leaves that mark the end of one year's growth and the beginning of the next (Figure 13). Male ***Polytrichum*** plants mark each year of growth with the antheridial splash cup (Figure 14-Figure 15). Petraglia (2007) reported ***Polytrichastrum sexangulare*** (Figure 16) in the Italian Alps as having shoots 9 years in age, with soil humidity apparently influencing longevity (Alessandro Petraglia, Bryonet 25 February 2009). On the other hand, ***Polytrichastrum formosum*** (Figure 17) in a Dutch forest has an estimated age of 80-100 years, based on the size of the **genets** (free-living individuals that develop from original zygotes, parthenogenetic gametes, or spores and that produce branches vegetatively during growth) (van der Velde *et al.* 2001). Other genera [*e.g.* ***Bryum*** *s.l.* (Figure 18), ***Schistidium*** (Figure 19), ***Zygodon*** (Figure 20)] have indentations (Rod Seppelt, Bryonet 25 February 2009) similar to those of female ***Polytrichum***. But does every plant produce sexual structures every year? How many years pass before the first sexual organs occur on the perennials? Do two rainy seasons cause two growth increments? Do drought interruptions cause growth increments?

Figure 13. ***Polytrichum commune*** showing growth interruptions (**arrow**). Photo by Michael Lüth, with permission.

Figure 14. ***Polytrichum commune*** male innovations, starting a new year of growth from the splash cup. Photo by James K. Lindsey, with permission.

Figure 15. ***Polytrichum juniperinum*** splash cups with new growth. Photo by Li Zhang, with permission.

Figure 16. ***Polytrichastrum sexangulare*** from southern Europe. Photo by Michael Lüth, with permission.

Figure 17. ***Polytrichastrum formosum***. Photo by David Holyoak, with permission.

Figure 18. ***Rosulabryum*** (=***Bryum***) ***billarderi*** showing three years of growth. Photo by Jan-Peter Frahm, with permission.

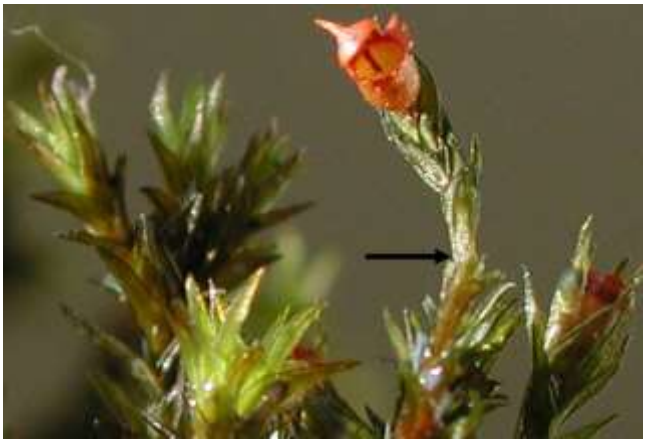

Figure 19. ***Schistidium rivularis*** showing growth increment (**arrow**). Photo courtesy of Betsy St. Pierre.

Figure 20. ***Zygodon dentatus*** showing growth increments (**arrows**). Photo by Michael Lüth, with permission.

Although this also seemed like a simple question, the answer is often not so simple. As Heinjo During and Martha Nungesser (Bryonet 25 February 2009) pointed out, a single **ramet** (stem/branch) may behave as an **annual** (living only one year), but the **genet** may exist for decades. This seems to be the case for ***Crossidium crassinerve*** (Figure 21) in the Mojave Desert, USA (Stark & Delgadillo 2003). The problem of genets seems to be further complicated by more extensive sexual reproduction than we often imagine, with males and females arising from one clone and reproducing within a distance of centimeters to several meters, as in ***Polytrichastrum formosum*** (Figure 17) (van der Velde *et al*. 2001).

Figure 21. ***Crossidium crassinerve***, a moss with annual ramets but perennial genets, from Europe. Photo by Michael Lüth, with permission.

As already noted, in ***Sphagnum***, some plants may be 100's of years old, but these plants keep dying at the bottom and growing at the top, so one must determine what portion of the plant is still alive before answering any question about its longevity. Yet, Dick Andrus (Bryonet 25 February 2009) found ***Sphagnum magellanicum*** (Figure 22) measuring 80 cm in Tierra del Fuego and reminded us of Clymo's opinion that ***Sphagnum*** from a meter or so down could be a 1000 years old. Despite looking old, new plants could be grown from fragments down a meter or more from the surface.

Figure 22. ***Sphagnum magellanicum***, a species that Clymo estimated could grow to be 1000 years old. Photo by Michael Lüth, with permission.

In the presumably annual ***Crossidium crassinerve*** (Figure 21), all is not what it seems to be. Stark and Delgadillo (2003) estimated that some of the stems were as much as 70 years old. Even the older portions were able to produce buds and protonemata in culture.

In the Antarctic, being frozen may suspend biological activity of bryophytes for even thousands of years (Miller 2014; Roads *et al*. 2014; Zimmer 2014). The moss ***Chorisodontium aciphyllum*** (Figure 23) was removed from a core sample of Antarctic permafrost (Roads *et al*. 2014). Samples from depths of 30, 110, 121, and 138 cm grew, suggesting that they had been preserved in permafrost that was subsequently overrun by a glacier. The stems removed from 110 cm showed evidence of growth *in situ* in ff days. Protonemata arose on rhizoids at the base of the core in 22 days. This older part of the core was estimated to be 1153-1697 years old.

Figure 23. ***Chorisodontium aciphyllum*** in Antarctica. Photo from Polar Institute, through Creative Commons.

LaFarge *et al*. (2013) found bryophytes emerging from the edge of the Arctic glacier on Ellesmere Island. The radiocarbon dating suggested they had been entombed by the ice during the Little Ice Age (1550-1850) AD. As these often blackened bryophytes emerged, some developed green stem tips or new lateral branches.

Tamás Pócs (Bryonet 18 September 2014) described longevity indicators in cushion-forming bryophytes like ***Leucobryum*** (Figure 24-Figure 26), **Dicranaceae** (Figure 27-Figure 29), and **Calymperaceae** (Figure 30) when living in seasonal climates. By examining the cushion in section, one can observe yearly layers, much like the annual rings of a tree trunk.

Figure 24. ***Leucobryum glaucum*** cushions. Photo by James K. Lindsey, with permission.

Figure 25. ***Leucobryum*** section showing layers. Photo by Lucas. Origin unknown.

Figure 26. ***Leucobryum glaucum*** clump section showing close view of growth layers. Photo by Walter Obermayer, with permission.

Figure 27. ***Campylopus introflexus*** (**Dicranaceae**) cushion. Photo by Michael Lüth, with permission.

Figure 28. ***Campylopus introflexus*** (**Dicranaceae**) growth increments exposed by eroding sand. Photo by Robin Stevenson, with permission.

Figure 29. ***Campylopus introflexus*** (**Dicranaceae**) indicating growth increments that form layers. Photo by Robin Stevenson, with permission.

Figure 30. ***Syrrhopodon involutus*** (**Calymperaceae**) showing layers. Photo by Jan-Peter Frahm, with permission.

How do you determine the age of an individual ***Sphagnum*** (Figure 31) that can give rise to all populations on the Hawaiian Islands (see Karlin *et al*. 2012)? How do we deal with mosses like ***Pleurozium schreberi*** (Figure 12) that spread horizontally, dying (?) at the base while continuing growth at the tips? Do we start over in aging them when a branch breaks off, becoming an independent plant?

Figure 31. ***Sphagnum fuscum*** showing two heads that share a base. Photo by J. C. Schou, with permission.

Richard Zander (Bryonet 18 September 2014) suggested that perhaps it is the diploid (sporophyte) stage that we should measure because it is important in repairing gene damage. He referred to the gametophyte as mostly immortal but genetically degrading.

New methods are making more accurate age determinations possible. Robinson *et al*. (2007) has used ANSTO to make rapid and accurate age determinations from small amounts of material. This technique uses a radiocarbon analysis to determine growth rates based on samples from different portions (5 cm segments) of the plants. They have indicated changes in the growth rates of ***Bryoerythrophyllum recurvirostre*** (Figure 32) in the Antarctic.

Figure 32. ***Bryoerythrophyllum recurvirostrum*** from southern Europe, a species with documented changes in growth rate. Photo by Michael Lüth, with permission.

There surely are tradeoffs between longevity and new plants, but such tradeoffs have not really been investigated. We have evidence that spores of at least some bryophytes, for example ***Dicranum scoparium*** (Figure 33), are unable to germinate when subjected to water extracts of their parents or other members of the same species (Mishler & Newton 1988; Newton & Mishler 1994). Hence, there is a tradeoff between asexual reproduction by ramets and sexual reproduction producing new clones. But which is best for the species? For evolution, sexual reproduction is usually best because it permits selection against plants with the weaker genomes. But the established genome is obviously adapted to that particular microenvironment.

Figure 33. ***Dicranum scoparium*** in Michigan, USA, showing what is most likely clonal growth because the adults inhibit the germination of spores. Photo by Janice Glime.

Control of Phenological Events

As implied by the above timing of life cycle stages, phenological events must have internal controls that are called into play by external phenomena. For example, ***Funaria hygrometrica*** (Figure 34) is under an intricate set of controls that determine where and when it germinates (Hoffman 1966). If it germinates where it is dark, it cannot complete its life cycle.

Figure 34. ***Funaria hygrometrica*** with developing sporophyte. Photo by Michael Lüth, with permission.

On the other hand, it does germinate over a wide range of both temperature and light intensities (Hoffman 1966). It fails to germinate without light, but can be stimulated to do so by supplying a source of carbon, particularly sugars, suggesting that the importance of light is to provide energy needed to power the process.

Funaria hygrometrica (Figure 34) produces its gametophytes in early spring, produces capsules in the early summer, and sheds its spores in July-September Hoffman 1966). It fails to germinate on soil treated with nutrients, but succeeds on soil from burned areas. If it

germinates where nutrients are too rich, other plants will be able to grow more easily, so competing plants may shade it before it is able to reach maturity. Humic acids inhibit germination (Raeymaekers, unpub. data.), perhaps accounting for its short life after invasion of a new area.

While it grows well on soil previously heated to temperatures of 200-300°C (sufficient to destroy litter and associated humic acids), ***Funaria hygrometrica*** (Figure 34) fails to grow on soil previously heated to greater than 300°C. At these high temperatures, N and P are released; addition of these two nutrients to soil previously heated to 600°C permits the moss to grow. Since the moss grows in open areas, it does not benefit from nutrients leached from the canopy, so it is not surprising that addition of K, Ca, and Mg (important canopy leachates) failed to benefit it. The controls at other stages of the life cycle of ***Funaria hygrometrica*** are less well known, but we do know a considerable amount about the kinds of internal and external controls that are available to mosses, and thus an entire chapter will be devoted to that discussion.

Although we know little about field development of protonemata, we know much about their physiology from laboratory studies, as discussed in the chapter on development. From these, we can surmise the importance of certain environmental controls. Certainly water and light are needed for spore germination. Kinugawa and Nakao (1965) found that photoperiod was important for both germination and protonemal development in ***Bryum pseudo-triquetrum*** (Figure 35). Both processes required a minimum of 12 hours light, although they could be fooled into thinking they had sufficient light by interrupting a long dark period with only 2 minutes of light.

Figure 35. ***Bryum pseudotriquetrum*** with antheridia. Photo by David Holyoak, with permission.

Timing of phenological events that bring antheridia and archegonia in the population to maturity at the same time is crucial to reproductive success. Yet different controls seem to guide these two developmental pathways. Hence, as some taxa expand into new geographic areas with different timing of day length, uncoupling of appropriate temperature from appropriate day length, and changes in seasonal moisture regimes, it is not surprising that some fail to produce capsules despite the presence of both sexes. Clearly phenology is an area requiring further study and may help us understand the success of bryophytes through the widespread areas where we find them. While their morphology has remained relatively unchanged, it appears that their ability to take advantage of seasonal events by a wide variety of phenological strategies, even within a species, may have been evolving rapidly.

Summary

There is a **trade-off** between growth and reproduction so that growth diminishes or ceases during reproduction. Growth also usually ceases in a cold winter when there is no free water and in summer when the temperature is too high and carbon loss would be greater than carbon gain. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. Reproduction may be coupled with photoperiod, light intensity, and temperature, and these will most likely be coordinated to provide the reproductive bryophyte with the greatest possibility of sufficient water. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Phenological events must not only coordinate with favorable climatic conditions, but they must coordinate with what is occurring among the other occupants of the ecosystem. For example, the non-competitive ***Funaria hygrometrica*** must grow in early spring, produce capsules in summer, and shed spores starting in July, permitting it to complete its life cycle before the arrival of other plants that compete for light and alter the nutrient regime. Following a fire, it takes advantage of the low nutrients before weathering, microbes, and other plants alter the soil and make it too nutrient-rich. Signals for initiation of life cycle stages often include photoperiod, and the required day length may differ between males and females of a species. Antheridia typically take longer to mature than do archegonia, thus requiring different signals to initiate in order to insure maturity at the same time.

Acknowledgments

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