CHAPTER 4-4

ADAPTIVE STRATEGIES: PHENOLOGY, TRADEOFFS AND HABITATS

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	Cavalcanti Pôrto & Mota de Oliveira 2002
archegonia	**6.7 per perichaetium**
antheridia	**13.4 per perigonium**
Sematophyllum subpinnatum	Mota de Oliveira & Cavalcanti 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*, 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.

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 2), and once they develop, they inhibit the further development of the stem, at least for that season (Figure 3). Thus, vegetative growth, in acrocarpous taxa at least, may be strongly limited by time of gametangial production.

Figure 2. *Polytrichum piliferum* splash cups that effectively stop growth of the stem while they are functional. 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.

Figure 3. *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.

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 4). 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* is day neutral; *Diphyscium foliosum*, *Atrichum angustatum*, *Trichocolea tomentella*, and *Nowellia curvifolia* 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.

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 (2001a) 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.

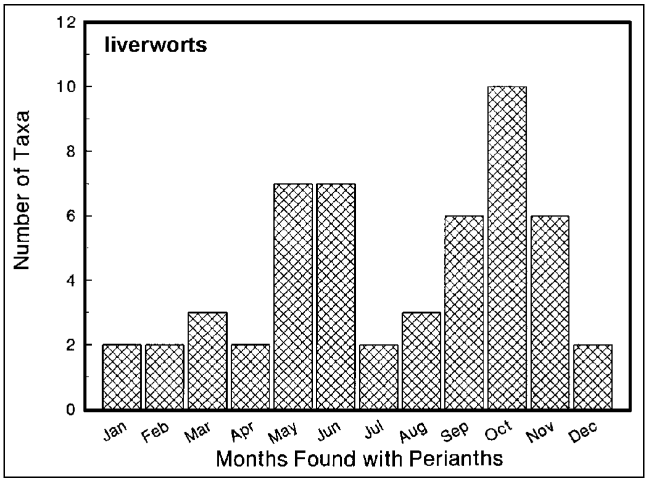

Figure 4. Numbers of taxa with perianths (leafy enclosure of liverwort archegonia) per month among the 30 taxa having perianths out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

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 5) 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 5. *Schistidium apocarpum* var. *confertum* growing on rock and exhibiting its typical abundant capsules. Photo by Michael Lüth.

Longton and Greene (1969) demonstrated a latitudinal difference in *Pleurozium schreberi* (Figure 6). 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 6. The red-stemmed moss, *Pleurozium schreberi*. Photo by Michael Lüth.

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.

Seasonal Differences among Habitats

It is the sum total of the timing of all the life cycle stages that can adapt a bryophyte for a better rate of survival. As the seasons change, so do the selection pressures. Hence, we find that sperm dispersal is timed to coincide with a rainy season and spore dispersal with dry air. But these timing events differ considerably among habitats.

Temperature, length of growing season, available moisture, and photoperiod all have effects on phenology. Studies on elevation can give us clues as to the effects of temperature, although gradients of these other variables exist as well. As already discussed, at low elevations of the Eastern Pyrenees, Spain, the life cycles follow a continuous progression of events with no dormant season (Lloret Maya 1987). By contrast, those living at higher elevations exhibit mature gametangia and accomplish fertilization in the first months of summer, with the sporophyte overwintering in a dormant state and maturing rapidly in early summer. If such differences exist in response to altitude, we might expect even greater differences among habitats of highly contrasting conditions. We shall examine the contrasts among the tropics, deserts, disturbed habitats, and wetlands as representatives of this spectrum.

Tropics

The rainy season is the primary governing factor in the phenology of many tropical mosses (Odu 1981). In four very different taxa of mosses (*Racopilum africanum*, *Fissidens glauculus*, *Thuidium gratum*, and *Stereophyllum* sp.), Odu found that gametangia develop at the onset of the rainy season (March/April), sporophytes develop later (October – December), and sporophyte maturation occurs at the end of the rainy season. In *F. glauculus* and *T. gratum*, sporophytes developed immediately after fertilization, and within one month in *R. africanum*, with all three producing mature capsules by the end of the rainy season (Odu 1982). Dispersal in these taxa begins at the end of the rainy season and continues into the dry season (November to April) (Odu 1981). This same seasonal pattern existed in the herbarium specimens Odu examined (Odu 1982). The rainy season is likewise the best season for development of juveniles and gametangia for *Octoblepharum albidum* (Figure 7; Cavalcanti Pôrto & Mota de Oliveira 2002). The importance of humidity for *O. albidum* is underscored by its development of sporophytes one month earlier at sites in western Nigeria, with constantly high humidity, than at sites with lower humidity (Egunyomi 1979). Thus, gametangial timing must be set so that capsule maturation is completed in time to take advantage of dispersal in the dry season. It appears that these tropical bryophytes differ from temperate bryophytes in that their rapid cycle permits them to disperse spores during the next dry season and germinate when the rainy season returns.

Figure 7. *Octoblepharum albidum* on tree bark in Florida, USA. Photo by Janice Glime.

Initiation of archegonia and antheridia in some tropical taxa may occur throughout the year, as it does with *Sematophyllum subpinnatum*, nevertheless increasing in frequency during the rainy season (Mota de Oliveira & Cavalcanti Pôrto 2001). Although the most favorable season for fertilization is during the rainy season, it likewise can occur throughout the year in that species. Sporophyte development of *S. subpinnatum* usually begins later in the rainy season, reflecting the higher fertilization rates during that season.

Deserts and Dry Habitats

Contrasting with mosses controlled by the rainy season, mosses of the Nigerian savannah have much shorter sexual cycles, as noted by Makinde and Odu (1994) for four mosses, *Archidium ohioense*, *Bryum coronatum*, *Fissidens minutifolius*, and *Trachycarpidium tisserantii*. Their entire sexual cycle, from production of gametangia to dehiscence of capsules, occurs during the rainy season. Protonemata and gametophytes develop in March-April; capsules mature and spores are dispersed in September-October. Nevertheless, spore discharge is somewhat difficult in the **cleistocarpous** *A. ohioense* and *T. tisserantii* compared to the other two species. (Cleistocarpous capsules have no operculum and must break apart without aid of lines of dehiscence to expel their spores.) Makinde and Odu suggest that this short maturation period may be advantageous in their savannah habitat.

In the Mojave Desert, Nevada, USA, where rainfall is rare and unpredictable, Stark (2001a) found that *Grimmia orbicularis* (Figure 9) and *Syntrichia inermis* (Figure 8) had a quite different dispersal strategy from the Nigerian savannah mosses. *Grimmia orbicularis*, a rock-dwelling species, retains operculate capsules for three months before its 3-week dispersal period. The entire clone, however, may disperse spores over a period as long as six months. *Syntrichia inermis*, a soil-dwelling species, retains operculate capsules for eleven months, then disperses spores for up to 2.5 years, the clone dispersal lasting up to 3 years! Stark concluded that the steeply inclined rock surfaces, supporting short, broad, inclined capsules, account for the more rapid rate of operculum shedding in *Grimmia orbicularis*.

Syntrichia inermis took an incredibly long time for antheridia to mature. Whereas the archegonia matured and became receptive in the same year, antheridia took one to several years to develop (Stark 2001a)! Despite this long maturation time in which desiccation was a common state, the abortion rate was only 3-4% for either gametangium type. Not surprisingly, more than 90% of the plants were morphologically bisexual. And unlike their temperate and northern counterparts, their growth was in the winter, albeit only 1.4 mm per year. To take advantage of this cooler and more moist season, fertilization occurred in winter, and despite the frequent desiccation, 50% of the perichaetia bore embryos. These embryos remained dormant from spring until fall, resuming their growth once more in the cooler days of winter when the seta and capsule developed. Spore dispersal, however, was delayed until late summer and early fall.

This species sets several bryophyte records through its phenological strategies to survive in the desert (Stark 1997). Considering the importance of reproductive development during the unpredictable and rare rainy periods, it is not surprising that it has the lowest known rates of stem elongation. It also has the longest known period required for antheridial maturation, and its sporophytes endure 18 or more months of dormancy during their development. Growth is greatly sacrificed to complete reproduction, presumably permitting the spores to remain dormant for long periods of time and to disperse over a wide range.

Growth in winter is most likely typical in the desert. A close relative, *Syntrichia ruralis*, grew, in this case by **innovations** (new shoots), in midwinter (Mishler & Oliver 1991). Female gametangia likewise were initiated in midwinter, causing cessation of growth in that innovation – a definite tradeoff. These female gametangia remained on the plants 6-9 months, during which no male gametangia were evident, and, of course, no sporophytes. But growth and structural development do not tell the whole story. In this species, the chlorophyll to dry weight ratio was higher in the late summer and winter than it was in early summer. One must pause to wonder what circumstance permitted the higher late summer values.

Figure 8. *Syntrichia inermis* with capsules in various stages of dispersal. Photo by Michael Lüth.

Figure 9. Rock-dwelling *Grimmia orbicularis*. Photos by Michael Lüth.

Moisture obviously is important in the regulation of season of growth. In the mountains of southern California, *Asterella* (Figure 10) *californica* grows on canyon sides and moist banks that become dry in summer. The liverwort dries out in summer, surviving by terminal buds (Haupt 1929). Bray (pers. comm.) found a similar survival mechanism in *Fossombronia* (Figure 11) in southern Illinois, permitting it to grow in fall through spring.

One can learn a lot about what makes things work by stressing them to their limits. Deserts provide a good model for such stressful conditions. Stark (2002b) found that in the Mojave Desert, one population of *Syntrichia inermis* initiated sporophyte development in 1995, but that the cohort remained dormant until early 1998. By that time, approximately 66% of the sporophytes had aborted. The remaining viable sporophytes of this group were considerably shorter and had less biomass than the previous cohort. In the next two years, sexual reproduction failed completely, apparently due to reduced winter-spring rainfall. On the other hand, it appeared to be heavy summer rainfall in 1997 that caused the abortion of many of the 1995 sporophyte cohort, with sporophyte numbers increasing again following 1998 summer rains. Stark suggested that the abortion may have been the result of rapid drying and high temperatures while the sporophytes were hydrated, causing membrane damage.

Figure 10. *Asterella tenella* with drying thallus and mature archegoniophore with open capsules. Photo by Janice Glime.

Figure 11. *Fossombronia wondraczekii*. Photo by Jan-Peter Frahm.

Trichostomum perligulatum, a tiny **protogynous** (producing female organs before male organs) desert moss, has populations 20-50 years old (Stark & Castetter 1995). It solves the capsule drying problem by having fertilization in late fall with sporophytes maturing continuously until spring, when it disperses its spores. Completion of its entire sexual cycle during cooler months, coupled with extensive intra-stem fertilization, permits it to survive its desert habitat.

Syntrichia caninervis (Figure 8), another desert moss, exhibits a sex ratio of roughly 7.9 female to 1 male to 3.1 non-expressing individuals (Stark *et al.* 2001). This large ratio of female to male may help to compensate for the 63% loss of developing sporophytes observed during three years of study. However, there is also partial, if not complete, compensation of sexes by the greater number of reproductive units on males than on females.

Bryophytes in deserts are very dependent on the annual moisture cycle for their life cycle. In the Nigerian desert, sexual cycles are short, occurring completely within the rainy season. In the Mojave Desert in southwestern USA, there is no rainy season, and rainfall events are unpredictable. In that regime, bryophytes have very long sexual cycles, sometimes taking several years to develop antheridia, several years for capsules to mature, and six months to disperse all the spores. Growth is mostly in winter, fertilization is in winter, and dispersal of spores occurs in late summer and early autumn. Some dry habitat thallose liverworts become dormant in summer, surviving as terminal buds while the remaining thallus dies.

Disturbed Habitats – Ephemerals

The ephemerals, or short-lived taxa, face some of the same problems as desert bryophytes. They are very dependent on climatological events to coordinate their phenological events. They often grow in areas that experience flooding during part of the year. Although the sequence of most life cycle events is poorly known in ephemerals, Crum (1976) provides us with information on when to expect to see these plants (capsules) in Michigan. We can suppose that during the remainder of the year the moss exists either as spores or as dormant protonemata, but in some cases absence is really a measure of lack of collecting inconspicuous non-fruiting upright gametophyte plants. Because of their tiny stature and non-mossy look of their habitats, these taxa are often overlooked by visiting bryologists in a hurry to get as many taxa as possible, so their presence may be much greater than would appear from collection records, and their sporophytic stage is probably over-represented in collections. By targetting such habitats, Kucyniak (1946) found numerous new or rare species in Québec (Jean Faubert, pers. comm.)

Spring and autumn seem to favor ephemerals when more moisture is available than in summer in most habitats, with a number of species visible all winter (Crum 1976 for Michigan, USA): *Ephemerum crassinervium* late summer to early spring; *Phascum cuspidatum* November to May; *P. floerkeanum* October to April; *Acaulon* spores mature in late autumn to spring [*A. triquetrum* (Figure 12), *A. muticum*]. Michigan spring ephemerals include *Pleuridium subulatum* (Figure 13), *Physcomitrium pyriforme*, and *Pottia truncata*; *Ephemerum cohaerens* appears in both spring and autumn. *Pottia davalliana* appears in the autumn, but sometimes can be found in summer.

Figure 12. *Acaulon triquetrum* on sand. Photo by Michael Lüth.

Figure 13. *Pleuridium subulatum*, a moss of disturbed agricultural fields and roadsides. Photo by Michael Lüth.

It is not surprising that some ephemerals typically produce more than one generation of capsules in the same year. Gray (1935) found that *Aphanorhegma serratum* and *Nanomitrium austinii* have life cycles as short as 62-65 days in Florida, producing two or more sets of capsules per year. Between these cycles the moss is often buried by floods and silt. Gray surmised that since he always found both mature and immature capsules, these mosses must continuously produce capsules when growing conditions are suitable. Younger plants seem to be produced at the edge of older clumps.

It appears that one strategy for these floodplain ephemerals is to produce some sort of survival structure. These may include very large spores, spores that remain in tetrads, and asexual structures that can remain in the mud for a prolonged period of time, then provide a good supply of energy to jumpstart the gametophyte plant when the mud becomes exposed to the sun. Members of the Marchantiopsida, especially members of the genus *Riccia* (Figure 14), seem especially adapted for such strategies (Kürschner & Parolly 1999).

Wetlands

One might expect that bryophytes growing in wetlands face few problems in dispersing their gametes and might instead time events so that capsules are not submersed or too humid. But Sundberg (2002) found that even in this "wet" habitat, rainfall of the previous summer had a strong effect on the number of capsules produced, suggesting that gametangia formation was improved under wetter conditions. In wetter peat pits, the amount of precipitation in spring of the same year seemed more important, suggesting that greater precipitation increased sperm dispersal and fertilization. Spore dispersal in *Sphagnum* is indeed facilitated by dry air, but summer droughts can cause premature drying, which negatively affects spore dispersal. At least some *Sphagnum* species grow best at higher temperatures, around 35°C (Li 1991), but it seems that growth might need to compete with spore production. All the species in Sundberg's study release their spores from the beginning of July to the end of August (summer in the North Temperate Zone), with up to a month difference in release times among the species present. Even in this wet habitat, there are dry seasons and wet seasons.

Figure 14. *Riccia beyrichiana* showing folded up lobes that can close up as the plant dries. Photo by Jan-Peter Frahm.

Aquatic

In aquatic habitats, winter may be the best growth period. Glime (1987b), found that in the Keweenaw Peninsula of Michigan, USA, where snow covers the ground about five months of the year, the lake and stream moss *Fontinalis duriaei* takes advantage of its C_3 metabolism and begins new growth in November, continuing through winter, then accelerating from February to June, with little subsequent growth until cooler weather returns. Laboratory data on temperature effects on growth of six *Fontinalis* species suggest this is a general trend in the genus (Glime 1984, 1987a, b, c).

But the big surprise came when we found abundant capsules on *Fontinalis dalecarlica* (Glime 1984) and *F. novae-angliae* (Figure 15; Glime 1987c) in February. These capsules were abraded by spring runoff and had disappeared by the time the snow had melted. No wonder most bryologists think the genus almost never has capsules! No one is looking in midwinter. It appears that archegonia mature in the short days of September and the capsules are most likely the product of that fertilization season.

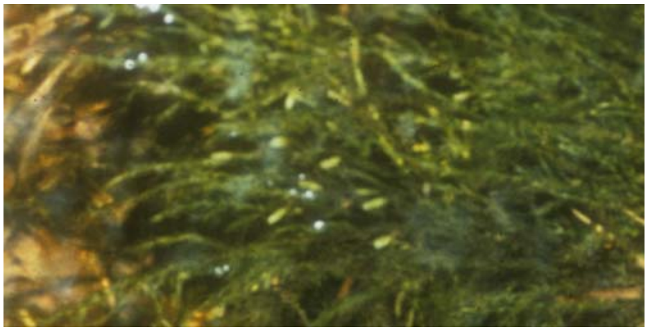

Figure 15. *Fontinalis novae-angliae* with capsules in February. Photo by Janice Glime.

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* 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.

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 16) 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.

Figure 16. *Funaria hygrometrica* with developing sporophyte. Photo by Michael Lüth.

While it grows well on soil previously heated to temperatures of 200-300°C (sufficient to destroy litter and associated humic acids), it 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*. 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.

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.

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.

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.

Acknowledgments

I appreciate the helpful comments of Heather Smith in giving me a student's perspective on this chapter. Linda

Luster checked the literature citations, proofread, and checked for needed glossary entries. KT McConnell suggested the minisummaries of some sections and made suggestions to improve the clarity. Jean Faubert made several useful suggestions for this chapter.

Acknowledgments

Jean Faubert helped me with the French reference by Kucyniak.

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