

# CHAPTER 4-2

## ADAPTIVE STRATEGIES: PHENOLOGY, IT'S ALL IN THE TIMING



Figure 1. *Atrichum undulatum*, emergent from the snow, has already formed capsules, but must time the release of spores for a time favorable for their dispersal and germination. Photo by Michael Lüth.

### Timing the Stages – Environmental Cues

It's all in the timing! Life cycles are the acrobatics of the plant world, and failure to time things correctly is just as deadly as missing your partner when swinging on the high wires. Timing determines when to germinate, when to release sperm, when to develop the sporophyte, and when to release the spores. This timing must be closely attuned to the climate of the area where the organism is growing and is a major factor in limiting the distributions of many species. In 1984, Taylor and Hollensen contended that there is "rarely any attempt to correlate life changes with time of year." However, where this ecophysiological information is lacking, there is no shortage of studies on dates of phenological events, despite their absence in most bryological manuals. In fact, the sheer numbers of studies

are daunting and have caused the delay of this chapter. I will attempt to provide some of the implications of cause and effect through that available literature.

### Patterns

Stark (2002a) has compiled patterns of temperate zone phenology based on publications of a few bryophytes (*Pohlia* in UK, *Ptychomitrium* in Japan, *Grimmia laevigata* in Spain, *Bryum argenteum* in UK, *Polytrichum alpestre* in UK, *Forsstroemia producta* in eastern USA):

1. Antheridia initiate in autumn and winter, maturing the next spring and summer (duration several months)
2. Archegonia initiate and mature in the same spring and summer (duration several weeks)

- Fertilization occurs in summer, lasting two weeks to several months.

This pattern most likely works well for the many bryophytes that live in areas where they rely on spring rains for fertilization. But notable exceptions exist to these examples with their strongly temperate bias. For example, in Brazil the period of fertilization for *Sematophyllum subpinnatum* (Figure 2) extends throughout the entire year (Moto de Oliveira & Cavalcanti Pôrto 2001). In the desert, both gametangial initiation and fertilization in *Trichostomum sweetii* occur in the autumn and winter (Stark & Castetter 1995).



Figure 2. Epiphytic moss *Sematophyllum subpinnatum* in Brazil. Photo by Michael Lüth.

The sporophyte is dependent on moisture for its own development, but it fares best if it is dry for spore dispersal. Stark (2002a) considered that six generalized patterns prevail for sporophyte maturation:

- Fertilization in spring and summer with continuous development; spore dispersal anywhere from early summer to the following spring; suitable for a mild climate.
- Fertilization in summer; embryos overwinter & sporophyte matures the following spring or summer; spore dispersal over extended period; typical of areas with harsh winter; two cohorts may be developing at the same time.
- Fertilization in summer (or spring) with continuous development to or just past meiosis; overwintering in meiotic/postmeiotic phase; spore dispersal winter-spring; known in south temperate of Northern Hemisphere.
- Fertilization in winter/spring with embryos forming first winter; dormancy in summer; sporophyte maturation second winter; known in several desert species.
- Annual species, sporophyte development within two months; fertilization at various times of year – flexible.
- No pattern; events throughout the year

Zander (1979) reported patterns with taxonomic affinities. He examined spore maturation times in the Pottiaceae and showed that differences tended to group by suprageneric taxa. The Trichostomoideae mature primarily in spring, Pleuroseisidae in midyear, Barbuleae are bimodal, Pottidae primarily spring, but also summer and winter, Cinclidotoideae spring and summer, and Leptodontieae poorly known but mainly spring. He attributed the patterns to regional climate and the stress-tolerant nature of these taxa. He further considered that their **ruderal** (waste areas) habitat subjected them to

competition from annual tracheophytes that forced them to take advantage of snowmelt water. He further concluded that spores of nearly all mid-latitude Pottiaceae taxa of variable, dry, lowland habitats mature in winter, spring, or early summer. Yet these taxa typically take 9 to 12 months for their sporophytes to mature. Perhaps this strategy permits the spores to germinate immediately while there is still available water, space, and light. Those species that occur in seepage areas or near waterfalls have summer or autumn maturation times instead, again suggesting that water is a driving force in sporophyte maturation times for the other taxa. Zander also found that non-endemic dioicous taxa in the Pottiaceae retain mature capsules slightly longer (mean 6.77 months) than do monoicous taxa (mean 5.55 months).

## Growth

Growth is generally controlled by a combination of factors (light, temperature, nutrients, water), but in bryophytes, available water generally is the most important (Zehr 1979). Once moisture is available, the temperature must be sufficiently warm for the water to be in liquid form. Since bryophytes are C<sub>3</sub> plants, most function best at temperatures less than 25°C, so growth may cease during summer.

In temperate climates, growth generally seems to occur in spring and autumn, ceasing or at least diminishing in summer (Al-Mufti *et al.* 1977). For example, *Atrichum undulatum* (Figure 1) exhibits this type of growth in South Wales (Figure 6; Benson-Evans & Brough 1966). For other species, growth is predominately in spring, and autumn seems to be a time for elongation without biomass production (Rincon & Grime 1989; Figure 3). Other taxa, adapted to full sun, may be more productive in summer. This is the case in *Polytrichum alpestre*, which grows in June and July (Longton 1979). Interestingly, dry weight continues to increase until September, despite the greater increase in photorespiration with rising temperature, a topic that will be discussed in more detail in the chapters on photosynthesis and productivity.

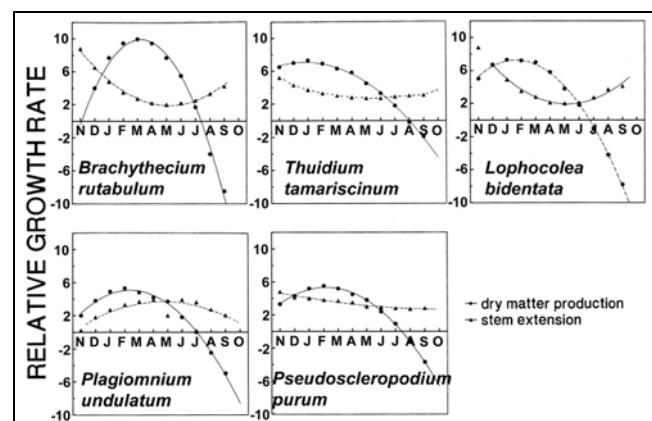


Figure 3. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime (1989).

Where winters are mild, growth may occur throughout the winter. In Japan Imura and Iwatsuki (1989) found that male plants of *Trachycystis microphylla* elongate most rapidly from October until January, but interestingly, the female plants begin their rapid elongation in January and

continue until June. In cases where this makes male plants taller than females during sperm dispersal stages, this could be an advantage for facilitating splash of sperm onto an archegonial inflorescence.

Epiphytes may take advantage of decreased desiccation and temperature in winter. Pitkin (1975) found the greatest growth of *Hypnum cupressiforme*, *Platygyrium repens*, *Neckera pumila*, *Isoetecium myosuroides*, and *Homalothecium sericeum* in November to January in Oxfordshire, UK, corresponding to the highest rainfall and mean temperatures below 10°C at 15:00 hours. Trynoski and Glime (1982) suggested that the appearance of more bryophytes on the south side of trees at breast height in the Keweenaw Peninsula of Michigan, USA, could indicate they were able to grow in winter when protection and moisture were available in the space between snow and tree trunk.

Furness and Grime (1982) show strong seasonal effects of temperature that help to explain some of the phenology of bryophytes (Figure 4). These results are consistent with peaks of growth in spring and autumn in British tall herb communities where they live. But they also show that different parts of the bryophyte can grow at different times and be favored by different temperatures. In *Brachythecium rutabulum* (Figure 4) growth of rhizoids peaks at 12°C, branches at 15°C, and stems at 20°C.

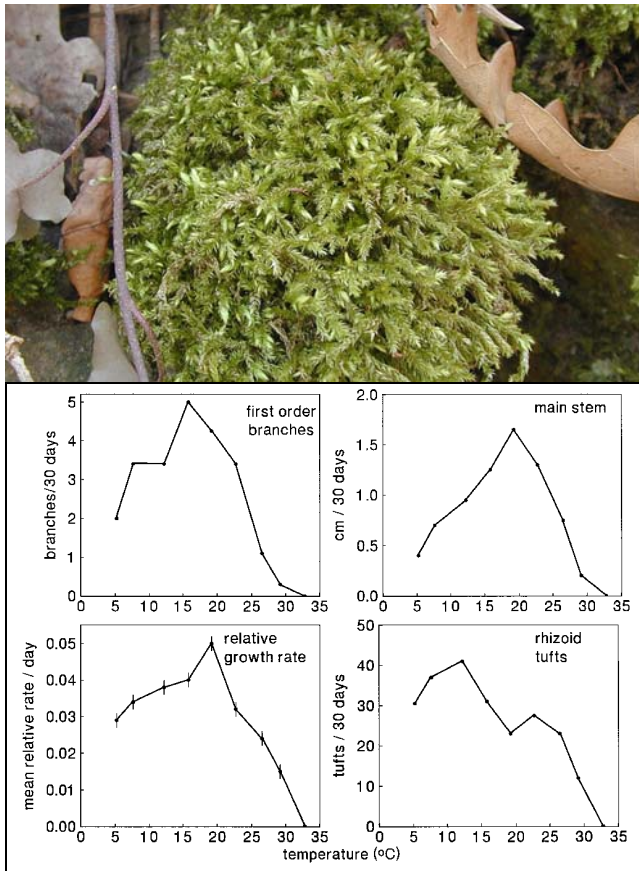


Figure 4. **Upper:** *Brachythecium rutabulum*. Photo by Michael Lüth. **Lower:** Effects of lab temperature on growth of branches, stems, and rhizoids of *Brachythecium rutabulum* and relative growth rate among 9 growth temperatures under conditions of constant humidity. Redrawn from Furness & Grime (1982).

This difference in temperature, and thus timing, is consistent with observations on *Fontinalis* parts (Glime 1980, 1982, 1987b) and suggests that the bryophyte apportions its limited photosynthate to different activities at different times. In *Fontinalis*, we can presume that the timing is advantageous because the rhizoids develop best at temperatures that coincide with the season when the moss is most likely to be stranded above water during low water (summer) and is therefore not likely to be dislodged by the motion of the water. The plants are typically "glued" to the rocks by their covering of sticky algae at this time. Furthermore, in *Fontinalis* branching and growth follow the season of maximum runoff when fragments have been delivered to new substrata in the stream. Intact but damaged plants can also be replenished then (Glime *et al.* 1979; Glime 1980; Figure 5).

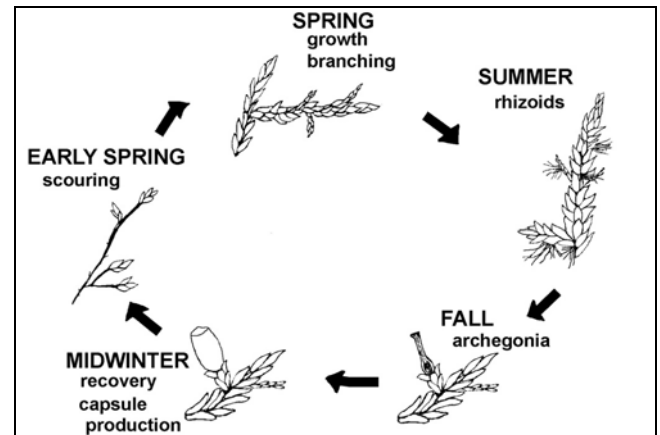


Figure 5. Phenological cycle of growth and reproduction in *Fontinalis dalecarlica* and *F. novae-angliae*. Drawings by Janice Glime.

Many bryophytes, such as *Eurhynchium praelongum*, are relatively dormant in winter, resuming growth in spring (April) and continuing through August, with the main peaks in May and September (Benson-Evans & Brough 1966). The common boreal forest feather moss *Pleurozium schreberi* grows little in winter, with growth from April to November (Longton & Greene 1969), but then one can't expect it to grow in the dim or absent light under snow.

In contrast, Mishler and Oliver (1991) found that **innovations** (new shoots; in acrocarpous mosses, a new branch) in the drought-tolerant *Syntrichia ruralis* (in the mountains of southern New Mexico, USA) appeared in midwinter, lengthening slowly throughout spring, but growing rapidly in late summer and completing growth by winter. Likewise, the chlorophyll concentration was higher in late summer and winter than it was in early summer, but there was no regular pattern of chlorophyll *a/b* ratios.

Other species in these temperate climates lack seasonal growth peaks. Benson-Evans and Brough (1966) found that *Funaria hygrometrica* initiated new leafy shoots continuously throughout the year in South Wales, reaching their maximum height of about 5 mm in 10 weeks (Figure 6). This results in numerous shoots that can quickly colonize bare ground.

*Sphagnum* most likely is controlled primarily by water availability, not by temperature. Lindholm (1990) demonstrated that the hummock species *S. fuscum* could grow at most normal temperatures above 0°C, but that

moisture was the primary determinant in that range. Li (1991) found that 30-35°C was optimum for growth of the hummock-dwelling *Sphagnum papillosum* and *S. magellanicum* when adequate water was available.

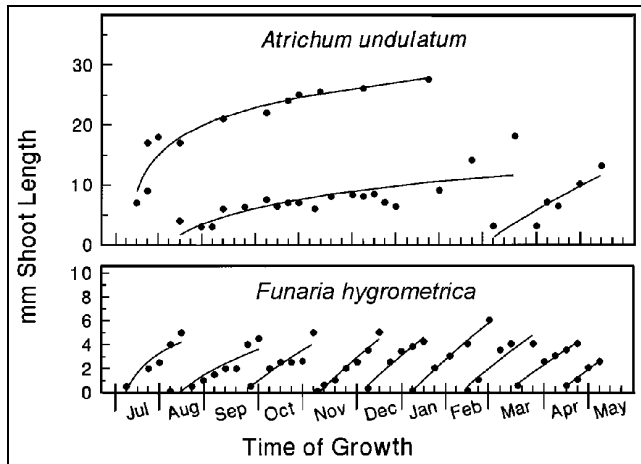


Figure 6. Contrast in vegetative growth periods for two bryophyte species in South Wales. *Atrichum undulatum* becomes dormant in late summer and begins growth again in January. The three curves follow three different sets of plants. In *Funaria hygrometrica*, growth can begin from new plants in any month of the year and is relatively continuous. Redrawn from Benson-Evans and Brough (1966).

Growth in most bryophytes is limited by water availability, with light, nutrients, and temperature playing lesser roles. Most grow best at temperatures below 25°C and go dormant above that. This puts most of their growth in temperate zones in spring and autumn, while permitting winter growth in warmer climates and summer growth in Polar Regions. Growth in mass can precede growth in length, and this may even be a general rule.

## Asexual Reproduction

The large number of propagule possibilities has already been discussed in the chapter on development. But what controls this production? In some species, these are so ever-present that they are used as taxonomic characters (*Plagiothecium*, *Pohlia* spp.). In fact, they may be more common than we supposed, as noted by researchers on *Orthotrichum* (BFNA 2007; Figure 8). But such propagula require energy to produce and thus we should expect some seasonal differences that avoid other large-energy-requiring events. It is well known that *Marchantia polymorpha* does not produce gemmae cups while it is producing sexual reproductive structures. This is demonstrated by the suppression of gemmae cup development during long-day conditions when archegoniophore development is occurring, but the addition of high sucrose concentrations can permit their development (Terui 1981). *Tetraphis pellucida* likewise does not have gemmae and female gametangia or sporophytes at the same time. Thus, we can in many cases surmise their phenology as those seasons when sexual reproduction is not occurring.

In liverworts, it appears that many taxa lack any seasonal absence of gemmae (Schuster 1988; Duckett & Renzaglia 1993), especially in the tropics (Schuster 1988). *Lophozia silvicola* had gemmae throughout the sampling

period of May to October in southern Finland, but their peak months were July through September (Figure 7; Laaka-Lindberg & Heino 2001).

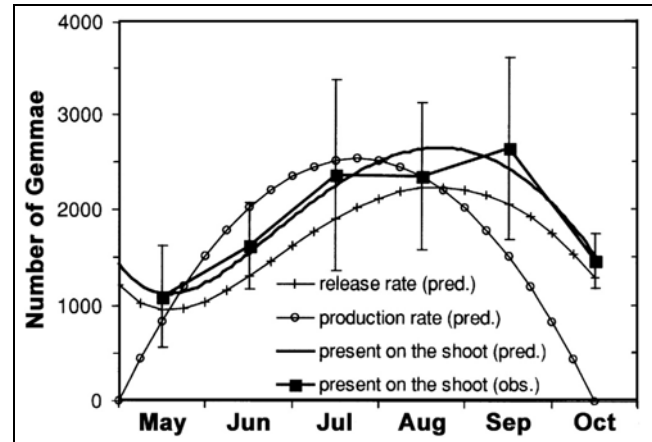


Figure 7. Model predictions (pred.) and observed behavior of gemmae from five colonies of *Lophozia silvicola* in southern Finland in 1997-1999. Redrawn from Laaka-Lindberg & Heino (2001).

Laaka-Lindberg and Heino (2001) suggested that there is a seasonal dormancy in gemmae of *Lophozia silvicola*. They modelled the effects of having two types of gemmae, dormant and non-dormant. Only the dormant gemmae could be expected to survive winter. This model fit well with data for southern Finland for this species and provided a mechanism for replacement of shoots lost to winter mortality. Success would be greatest if more dormant gemmae were produced at the end of the growing season.



Figure 8. Gemmae (dark spots on leaves) on *Orthotrichum obtusifolium*. Photo by Michael Lüth.

Response to light intensity in some taxa suggests that at least some liverwort gemma production should be seasonal. Kumra and Chopra (1989) found that maximum gemma cup production in *Marchantia palmata* occurred at continuous light at 4500 lux. However, this is an unlikely combination in nature, with full sun at ~70,000 lux and 24-hour light occurring only in Polar Regions.

Laaka-Lindberg (2000) considered that gemmae most likely follow the same seasonal trends as vegetative growth. She reasoned that since gemmae are produced by mitotic cell divisions, albeit in specialized cells, they would be susceptible to the same environmental regulation of growth as normal gametophytic tissue. Since growth often is arrested during sexual reproduction, this is a reasonable possibility.

In west tropical Africa, two species of the moss genus *Calymperes* exhibit distinct seasonal production of gemmae (Odu & Owotomo 1982). Reese (1984) found a striking seasonality in *Syrrhopodon texanus*, another member of the same family, with gemmae production increasing in August and peaking in September in the Gulf coastal plain. This follows the high rainfall season in July, which could be favorable to gemma production and establishment.

Aside from balancing the energy needs of sexual reproduction, the asexual structures generally do not have to wait for the right season, thus providing the plant with a more reliable means of reproduction.

## Gametangia

Timing of gametangial production might well be the most important timing function a **cryptogam** (any plant with an independent gametophyte) could have. With only one cell layer of protection during development, gametes begin their existence in peril. Once released, the sperm have virtually no protection and must reach the egg in a film of water before effects of sun and winds render their required watery milieu non-existent. Furthermore, it is likely that they are susceptible to UV damage, lacking even a cell wall for protection. Gamete availability itself typically lasts only 1-2 weeks (Crum 2001), and even less in some species. Hence, mechanisms that position this development at a time most likely for success are essential for this step to reach fruition.

The timing mechanisms available to bryophytes have been studied extensively in, of course, the lab rat moss, *Physcomitrella patens*. Hohe *et al.* (2002) have determined that temperature, light intensity, and day length all impact the number of sporophytes produced, and thus by inference we must conclude also impact the success of the gametes. In this moss, the highest number of sporophytes resulted when the mosses were cultured at 15°C, 8:16 light:dark cycle at 20  $\mu\text{mol}/\text{m}^2/\text{s}$ . Culture at 25°C or at 16-hour days drastically reduced the number of sporophytes, indicating that this species is adapted to reproducing under the conditions of spring in the temperate zone. As might be expected, growth diminished under conditions that favored reproduction. Hohe and coworkers even identified a MADS-box gene, PpMADS-S, that produced 2-3 times as much RNA under conditions that favored sporophyte development, suggesting its role in that development.

Laboratory experiments do not necessarily represent the real world. Day-night temperature differences may be critical, and certainly water is important. Maturation of reproduction must be timed to coincide with a season suitable for sperm transfer. For example, Odu (1981) showed that in four tropical African mosses, gametangia develop at the beginning of the rainy season. Sporophytes mature to coincide with the dry season.

Signals for timing of gametangial production are most likely a mix of direct responses to rainfall and other moisture sources and other cues, such as day length, that are generally good predictors of later environmental conditions. For example, we see in *Sphagnum* that success of sporophyte production was positively related to the precipitation the previous summer and that summer droughts had a negative influence on gametangial formation (Sundberg 2002). Even after fertilization,

however, drought has a negative effect on the sporophyte by drying it too soon before the spores are mature.

In Scandinavia, this favorable season for gamete release appears to be spring (Arnell 1875), most likely taking advantage of "spring showers." Arnell (in Crum 2001) found that 15% of the taxa released gametes in January-March, 52% April-June (20% in May), 25% July-September, and 8% October-December. However, some taxa do not have a "season." Leitgeb (1868) found that *Fontinalis antipyretica* formed antheridia from spring until autumn [although I found that archegonia matured in autumn and that numbers were greatest under short (6-hour) photoperiods (Glime 1984)].

In milder climates, such as California, USA, late autumn or winter months can provide the best season for successful fertilization. *Fossombronina longiseta* has mature archegonia and antheridia there in November and December (Haupt 1929b).

In Japan, Deguchi and Yananose (1989) found that *Pogonatum neesii* initiated its antheridia in early November, with maturity occurring in mid April. By late July they were all dead. Archegonia, on the other hand, matured only in early May.

Then there are bet hedgers. *Dicranum majus* (Figure 9) in central Norway can form gametangia in late autumn or early spring, permitting fertilization in June and July (Sagmo Solli *et al.* 1998). It appears that this species has not fine-tuned its gametangial timing; mature antheridia are present all summer and autumn, but archegonia are available only in June and July.



Figure 9. Immature sporophytes of *Dicranum majus*. Photo by Michael Lüth.

The initiation and maturation of sex organs of one sex before those of the other in a population may be a common phenomenon. Longton and Schuster (1983) contend that initiation of antheridia several months before archegonia in dioicous taxa results in their maturation at the same time. In the cases of *Atrichum rhystophyllum* (Figure 10) and *Pogonatum inflexum* in Japan, Imura (1994) found that shoot production of male plants preceded that of females by about four months. Likewise, antheridia production preceded that of archegonia, but antheridia took longer to develop. In the functionally dioicous *Pleurozium schreberi* in Great Britain, perigonia (♂) begin development in August whereas perichaetia (♀) first occur in October (Longton & Greene 1969). Both overwinter and fertilization occurs in April-May. This results in maturation of the sporophyte by October with spores being shed January-April. Fertilization is delayed in more

northern areas such as Scandinavia. On the other hand, Greene (1960) found that in *Mnium hornum* antheridia mature about one month before the archegonia, perhaps insuring that sperm will be available when proper conditions for fertilization occur.

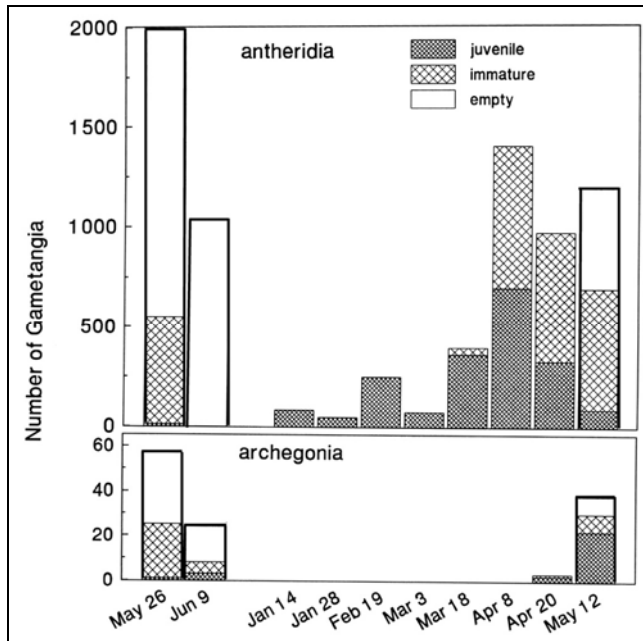


Figure 10. Maturation dates of antheridia and archegonia of *Atrichum rhystophyllum* at Miyajima Island, Japan, during 1987-1988. Samples included 1-10 individuals. Based on table by Imura (1994).

When differences in initiation time occur, we can presume that different stimuli are needed to initiate the development. This is discussed briefly in the development chapter on gametogenesis, but it appears we know little about the signals for initiation when they differ for the two gametangial types. One such signal is light intensity. In *Riccia discolor*, female clones developed gametangia maximally at 3500 lux continuous light at pH 5.5 (Gupta *et al.* 1991). However, male plants failed to produce antheridia at pH 3.5 or 5.5 at any light intensity in the experiment.

The longer development time for antheridia is common. For example, in Australia *Dicranoloma menziesii* and *D. platycaulon* initiate their antheridia during winter and archegonia in the spring (Milne 2001). However, the archegonia mature in two months, whereas antheridia require 5-6 months. By contrast, a third species, *D. billardiarei*, that is **sympatric** (occurring in the same geographic area) with these two initiates its antheridia during late spring-summer and its archegonia in autumn. The result is that *D. menziesii* has fertilization in late summer, *D. platycaulon* in mid autumn, and *D. billardiarei* in early winter. This separation of fertilization time permits these sympatric species to co-exist without the danger of interbreeding that could soon diminish the species distinctions. The sporophyte development is slow, requiring 18-24 months in *D. billardiarei* and *D. platycaulon*, but only 12 months in *D. menziesii*.

Initiation of antheridia before archegonia may extend to monoicous taxa as well. Van der Wijk (1960) reported that 14 out of 18 mosses from the Netherlands initiated

antheridia before archegonia; three of these 14 taxa were monoicous. The remaining 4 initiated archegonia in the same month as antheridia; one of these was monoicous. In his study, it was typical for antheridia to be initiated in the autumn with archegonia initiated the following spring. In *Entodon cladorrhizans*, a monoicous perennial, antheridia likewise initiate well before archegonia (Stark 1983).

Antheridia generally require longer to develop than archegonia. Therefore, male and female gametangia must time their development so that they both mature at the same time, and that maturity occurs at a time when water is available for fertilization. That fertilization period typically is less than one month. For many parts of the temperate zone, this means spring is the best season, with autumn being a second possibility, provided early frost is not a danger to the gametes or the embryo. In dry climates and the tropics, winter is usually the best season because of greater moisture.

### Protandry and Protogyny

With the advent of the monoicous condition, bryophytes faced the problem of inbreeding. The solution to this is to have a mechanism to prevent that event. When there is no carrier organism involved, this can be accomplished in two ways. There can be some self-incompatibility mechanism involved, or the two types of gametangia can mature at different times.

Towle (1905) found protogynous timing in *Atrichum undulatum*, Egunyomi (1979) in *Octoblepharum albidum*. Longton and Schuster (1983) summarize several studies that indicate that **protandry** (maturation of antheridia before archegonia on same plant) and **protogyny** (maturation of archegonia before antheridia on same plant) are common among monoicous bryophytes, as in *Funaria hygrometrica* and *Atrichum undulatum* (Figure 11). [*Atrichum undulatum* is functionally dioicous, at least in Michigan, USA, *i.e.*, it does not produce male and female gametangia on the same plant at the same time, but it can, at least in some populations, produce antheridia the first year and archegonia the next (Crum 1976)]. This is similar to the sequential hermaphroditism seen in some animals such as the blue-headed wrasse. Interestingly, Crum (1976) reports that in North America *F. hygrometrica* produces **perigonia** first (housing antheridia), then **perichaetia** (housing archegonia), making them **protandrous**, but Benson-Evans and Brough (1966) report the same species in Great Britain as **protogynous** (having females mature first).

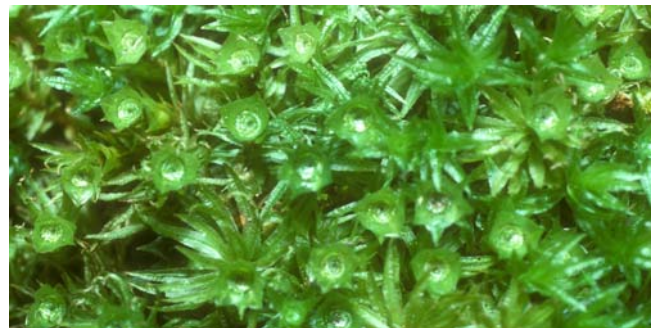


Figure 11. Male plants with splash cups on *Atrichum undulatum*. Photo by Janice Glime.

Even in the dioicous perennial moss *Forsstroemia trichomitria*, gametangial maturation is protogynous (Stark 1985). On the other hand, Greene (1960) was surprised to find that in perennial moss *Brachythecium rutabulum* the intermixed archegonia and antheridia also had intermixed developmental stages for both gametangia, and that they both appeared to be produced year-round. But in *Bryum argenteum*, although archegonia and antheridia are produced at the same time in Reading, England, in north Wales antheridia typically begin development in November and archegonia in the following April (Miles *et al.* 1989).

Some monoicous mosses may benefit, or at least survive, with self-fertilization. In the Chihuahuan Desert, on *Trichostomum perligulatum* each branch produces an average of 2 archegonia and 3 perigonia containing 6 antheridia, being at first protogynous, but then synchronous, and finally only male. Stark and Castetter (1995) found that fertilization among the gametangia on a single stem in this species appeared to be common.

## Habitat Differences for Gametangia

### Desert

The advantages of seasons vary among habitats. In dry habitats such as the desert, it is often easier to eke out a tiny bit of water in the winter than in the summer when the little rain that does fall evaporates almost before it lands. Although they found no antheridia, Mishler and Oliver (1991) found fresh female gametangia on *Syntrichia ruralis* in the dry mountains of southern New Mexico, USA, from December to June or even August. Despite the long period of archegonia presence, and perhaps attesting to the difficulty of accomplishing fertilization in an arid environment, they could find no capsules (or antheridia). Stark (2001a, 2002c) suggests that bryophytes of the Mojave Desert, USA (*Syntrichia inermis*, *S. caninervis*, and *Grimmia orbicularis*; Figure 12), contrast sharply with those of other climatic regions, with phenological events tied almost solely to local rainfall events, hence being highly variable. Spore dispersal occurs over a long period and may last more than one year. This long dispersal period may partially compensate for the very high rate of sporophyte abortion in these mosses following a summer rainfall that apparently uses up too many resources in repairing the cells (Stark 2001b).



Figure 12. Mojave Desert where *Syntrichia inermis* survives under shrubs and may be dormant for long periods. Photo by Lloyd Stark.

When maturation of gametangia is an autumn event, it forces the young embryo to survive the winter. Haupt (1929b) found that the liverwort *Fossombronina longiseta* in California, USA, had gametangia in the "best" condition in November and December, perhaps relating to the wetter weather in winter. The overriding importance of water is evidenced by *Octoblepharum albidum* in Nigeria, where immature antheridia and archegonia are most abundant during July, the wettest month (Egunyomi 1979).

Herrnstadt and Kidron (2005) examined reproduction in *Bryum dunense* in three different habitats in the Negev Desert. Despite differences in exposure, including exposed site, under shrub canopy, and partially shaded at foot of north-facing dune slope, all three populations initiated their gametangial development prior to the first winter precipitation. This suggests that the species are attuned to their environment by a signal such as declining day length or temperature. This prepared them for dispersal of both bulbils and sperm as soon as water was available.

### Aquatic

For the aquatic *Fontinalis*, Glime (1984, 1987a) found that on Isle Royale and in the Keweenaw Peninsula of Michigan, USA, several species produced gametangia in September prior to resumption of growth. In this genus, autumn production of gametangia might be a means to facilitate movement of sperm in small puddles of water and on moist but not submerged mosses, reducing loss of sperm downstream due to strong currents. Once winter begins, these species of *Fontinalis* are completely submersed and this permits the development of the sporophyte in a fully hydrated state. *Fontinalis* species respond to photoperiod, having peak gametangia maturity in autumn and producing capsules in February. Temperatures soon become too warm in summer for aquatic bryophytes that generally remain hydrated, even when stranded above water. The easiest season for many of them to disperse sperm is autumn as water levels rise and dispersal is facilitated. Temperatures are cool enough for photosynthetic activity and the plant is almost guaranteed of remaining cool and hydrated following fertilization.

## Sporophyte Maturation

Degree of maturity of sporophytes may be reported in various ways, and the system of Greene (1960; see previous subchapter on phenology) seeks to straighten out these ambiguities. Some authors report the season for spores, which we may assume is the OF (operculum fallen) stage of Greene. Conard (1947), in his phenological study on Iowa herbarium specimens, considered the "perfect capsule" stage to include some opercula shed and others in place. The spike stage of Conard corresponds to the ECI (early calyptra intact) stage of Greene.

### Energy Needs

Sporophytes require tremendous energy to mature. Stark and Stephenson (1983) have demonstrated the compensation for insufficient energy in the pleurocarpous *Entodon cladorrhizans* (Figure 13) through abortion of sporophytes, much like the abortion of fruits in *Asclepias*. But it would seem that the best way to provide sufficient energy would be to optimize time of development of the sporophyte. To this end, we will examine the timing of capsule production in several examples.

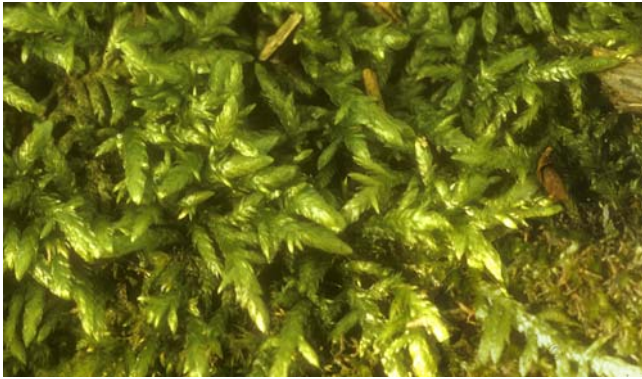


Figure 13. Gametophytes of the monoicous perennial *Entodon cladorrhizans*. Photo by Janice Glime.

A common way to optimize energy is to avoid having two means of propagation at the same time. Thus, *Tetraphis pellucida* produces capsules in spring, whereas gemmae with gemmae cups are produced after spores are shed. In *Atrichum undulatum*, spores are shed in March in Vermont (Figure 1), and new archegonia are present by early May (Towle 1905). As already noted, the antheridia were present earlier (mid April), but they do not compete for sporophyte energy in this dioicous species.

### Optimizing Dispersal Time

Often, maturation of capsules is timed to take advantage of dry weather for dispersal. For example, in Nigerian populations of *Octoblepharum albidum*, capsules develop quickly from August to early December, when spore liberation begins, coinciding with the dry season (Egunyomi 1979). But natural phenomena are rarely so predictable. The difficulty in drawing generalizations about behavior based on either habitat or climate is exemplified by comparing *Pylaisiella polyantha* (Figure 14) to *Hypnum cupressiforme* var. *resupinatum* (Greene 1960), two species that have somewhat similar gross vegetative morphologies. Although both taxa are found on the bark of deciduous trees in the same areas in the British Isles, *H. c.* var. *resupinatum* begins its sexual cycle like *P. polyantha*, with a swollen venter in July-August, but instead of the sporophyte requiring a year (or more), as in *P. polyantha*, it soon completes its capsule development and loses its spores beginning in January. Although *P. polyantha* is monoicous and *H. c.* var. *resupinatum* is dioicous, it is difficult to imagine how this could affect development of the sporophyte. Similar differences occur in *Ulotia* in Great Britain (Jones 1946). *Ulotia crispata* var. *intermedia* matures in July-August, var. *crispata* in spring, and *U. bruchii* in winter, suggesting that season of dehiscence may not be critical for these taxa in this particular location.

One pattern that seems to emerge is that in many terrestrial bryophytes spore dispersal may be timed for alternating moist and dry conditions. If moss spores do indeed depend on flexes of peristome teeth, then a season in which moisture conditions change from wet to dry frequently would be advantageous. Liverworts seem to be largely timed for the same benefit (Schuster 1966). On the other hand, perhaps the important timing is not dispersal as much as it is germination. Spore germination requires water, and if spores are to germinate immediately before being consumed or losing viability, a season of alternating

wet and dry could be an advantage. While this latter explanation may have merit for some taxa, it seems that many bryophyte spores are viable for long periods in quite adverse conditions (van Zanten & Pocs 1981; During & ter Horst 1983; During 1986; van Zanten & Gradstein 1988; van Zanten 1992; During 1997; Frahm 2002).



Figure 14. Dehiscent sporophytes and seta spikes representing two cohorts present at the same time in *Pylaisiella polyantha*. Photo by Michael Lüth.

In *Sphagnum*, if the capsule dries too soon, the spores are not mature and are forced out of the capsule before they are mature (Sundberg 2002). It appeared to be an advantage for these taxa to mature and have early spore dispersal in the drought-sensitive lawn species to avoid the risk of premature drying of the sporophyte during the summer droughts.

In *Marchantia polymorpha*, we have already seen that long days are important for development of the archegoniophore, causing it to reach its maximum height by mid summer when sporangia are mature and warm, dry conditions most likely optimize dispersal of the mature spores (Terui 1981). Thus, this liverwort has to time its gametophyte to carry out the function known for the sporophyte stalk of a moss, necessitating the expression of the trait in the gametophyte instead of the sporophyte generation. In its more tropical relative, *M. chenopoda*, sporophytes mature earlier, in late spring to early summer (Moyá 1992), suggesting that temperature may be a signal.

### Spring and Autumn Dispersal

The best overall picture of temperate zone sporophyte phenology seems to be that of Conard (1947) for Iowa, USA, bryophytes. He used herbarium specimens from the State University of Iowa and Grinnell College to determine the number of collections with sporophytes each month. Like gametangia, sporophytes exhibited two seasons of abundance. "Spikes," or setae with no capsule development, were present mostly in March - May and October - November (Figure 15). Capsules matured mostly May - June or October - November (Figure 15). However, these data lack details of timing, and as noted already, could possibly represent development that continued after the collecting date, and could have contained considerable collecting bias.

Lackner (1939) showed capsule and spore maturation times of 182 species in East Prussia (now part of Poland and Russia). The capsules are present mostly from May to September, contrasting with the summer low reported by Conard (1947) for Iowa. However, when these taxa are

separated into those that do not delay capsule development and those that do, it is the ones that delay development that mature mostly in summer (Table 1; Hughes 1990); the others disperse spores mostly in spring (February - April). Previous work by Arnell (1875), as presented by Lackner (1939), on the beginning of capsule appearances for two locations in Europe are shown in Figure 16 and indicate that the capsules began to form primarily from April to August in those locations. In these same areas and in Germany, Lackner shows spores ripening mostly in May through July, with other peaks (for East Prussia) in February and October (Figure 16).

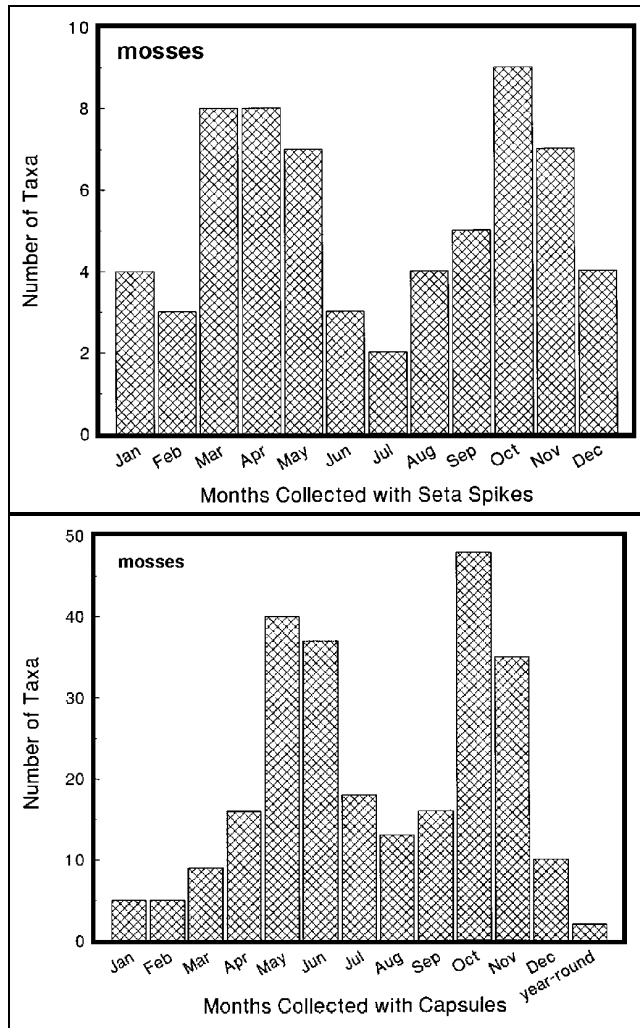


Figure 15. **Upper:** Numbers of moss taxa with young setae ("spikes") per month among the 33 taxa that had spikes. **Lower:** Numbers of taxa with capsules per month. Study based on 232 species of Iowa mosses in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Liverworts seem neglected in most areas of ecological research. Nevertheless, Conard (1947) included them in his phenological study (Figure 17). Like the mosses, the months with the greatest number of mature capsules were April - June and September - October. In a recent study, Bray (pers. comm.) found that the liverwort *Fossombronia foveolata* produces capsules in both spring and autumn on the same individuals, drying out in the summer and surviving by producing a dense terminal bud that seems to be protected by its dark, red-brown color. *Fossombronia*

typically lives in places where it gets submerged part of the year and dried out another part, so it is not surprising that it has a life cycle much like some of the moss ephemerals.

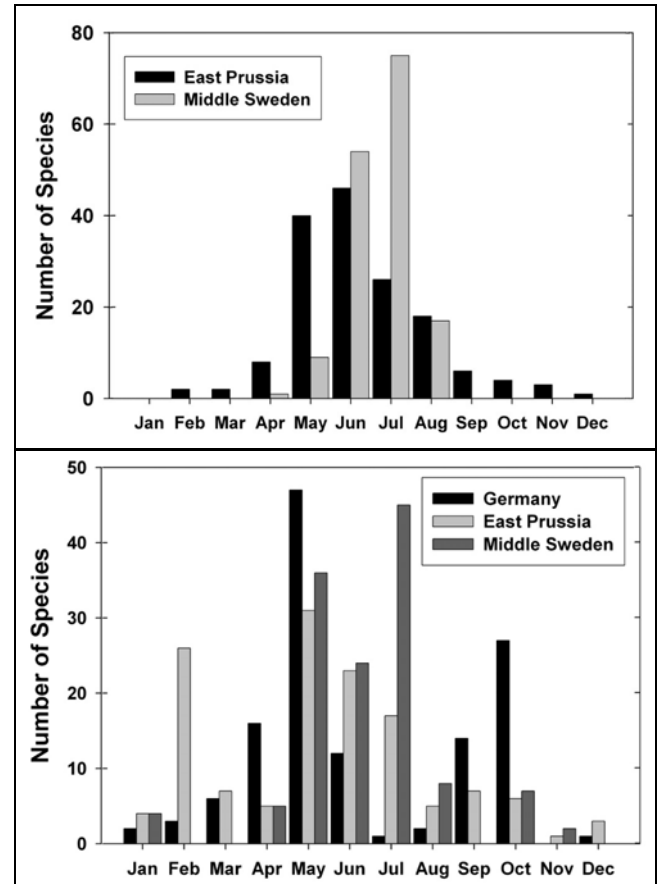


Figure 16. **Upper:** Months of capsule appearance in two locations in Europe. **Lower:** Months of spore ripening in three countries in Europe. Redrawn from Lackner (1939).

In the mild climate of California, USA, the thallose liverwort *Asterella californica* occurs on moist banks and canyon walls, where its growth occurs autumn to spring and its capsules mature in April (Haupt 1929a). It dries out in summer and survives from tips of branches.

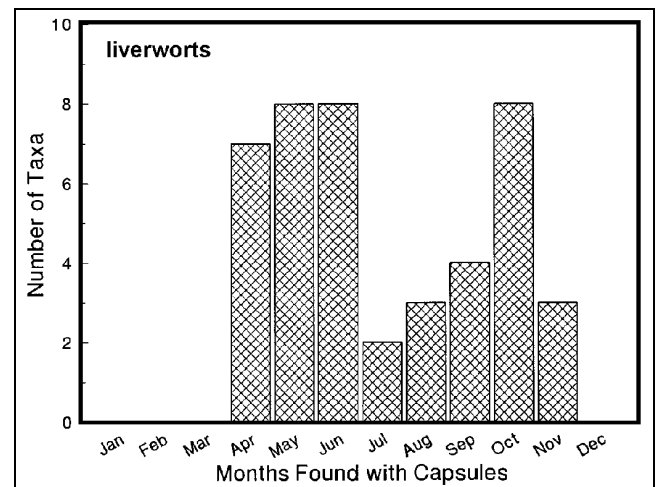


Figure 17. Numbers of taxa with capsules per month among the 30 taxa having capsules out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Table 1. Phenology of (a) 35 species in which capsule formation is not delayed and (b) 42 species in which there is a lengthy delay. Table based on Lackner (1939) and modified from Hughes (1990).

		Number of species making response in each calendar month																	Total number of species				
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	
Fertilization	(a)			1	4	12	11	6	1														35
	(b)		1	1	2	11	13	9	4	1													42
Swelling of capsule	(a)							4	16	8	6	1											35
	(b)													4	17	14	7						42
Spore shedding	(a)									1	3	1	12	10	5	2	1						35
	(b)															1	11	13	13	0	4		42
(a)		<i>Hedwigia ciliata</i>				<i>A. subtile</i>				<i>Physcomitrium pyriforme</i>													
		<i>Homalia trichomanoides</i>				<i>Aulacomnium palustre</i>				<i>Plagiomnium affine</i>													
<i>Anomodon viticulosus</i>		<i>Homalothecium lutescens</i>				<i>Bartramia ithyphylla</i>				<i>P. cuspidatum</i>													
<i>Atrichum undulatum</i>		<i>Hylocomium splendens</i>				<i>Bryum caespitium</i>				<i>P. medium</i>													
<i>Barbula unguiculata</i>		<i>Hypnum cupressiforme</i>				<i>B. pallens</i>				<i>P. rostratum</i>													
<i>Brachythecium albicans</i>		<i>Leucodon sciuroides</i>				<i>B. warneum</i>				<i>P. undulatum</i>													
<i>B. populeum</i>		<i>Phascum cuspidatum</i>				<i>Calliergon cordifolium</i>				<i>Plagiothecium cavifolium</i>													
<i>B. rutabulum</i>		<i>Pogonatum urnigerum</i>				<i>Calliergonella cuspidatum</i>				<i>P. curvifolium</i>													
<i>B. velutinum</i>		<i>Racomitrium heterostichum</i>				<i>Ceratodon purpureus</i>				<i>P. nemorale</i>													
<i>Bryum argenteum</i>		<i>Rhizomnium punctatum</i>				<i>Cratoneuron filicinum</i>				<i>Pohlia nutans</i>													
<i>Buxbaumia aphylla</i>		<i>Rhynchosstegium murale</i>				<i>Dicranum scoparium</i>				<i>Polytrichum commune</i>													
<i>Climacium dendroides</i>		<i>Rhytidiadelphus squarrosus</i>				<i>Distichium capillaceum</i>				<i>P. formosum</i>													
<i>Dicranella rufescens</i>		<i>R. triquetrus</i>				<i>Encalypta vulgaris</i>				<i>P. juniperinum</i>													
<i>Dicranella</i> sp.		<i>Schistidium apocarpum</i>				<i>Helodium blandowii</i>				<i>P. piliferum</i>													
<i>Didymodon fallax</i>		<i>Tetraphis pellucida</i>				<i>Herzogiella striatella</i>				<i>Sanionia uncinata</i>													
<i>Diselium nudum</i>		<i>Thamnum alopecurum</i>				<i>Homalothecium nitens</i>				<i>Splachnum ampullaceum</i>													
<i>Entodon</i> sp.						<i>Hygrohypnum luridum</i>				<i>Syntrichia ruralis</i>													
<i>Eurhynchium hians</i>						<i>Leptobryum pyriforme</i>				<i>Syntrichia subulata</i>													
<i>E. striatum</i>						<i>Leptodictyum riparium</i>				<i>Tortula muralis</i>													
<i>Fissidens bryoides</i>						<i>Mnium hornum</i>				<i>Warnstorfia fluitans</i>													
<i>F. taxifolius</i>						<i>M. marginatum</i>																	
(b)		<i>Amblystegium serpens</i>																					

## Development Time

Sporophyte maturation can be a slow process, thus crossing multiple seasons. Grimme (1903) reported that in Germany he found the minimum time for sporophyte development to be that of *Atrichum tenellum* (4 months) and the maximum to be for *Grimmia ovata* (24 months). Crum (2001) reports *Polytrichum* to require 13 months and *Dicranum* 17 months. Many other variations occur, attesting to the fact that these sporophytes must withstand a wide range of conditions during their development, yet maintain a timing that is suitable for spore dispersal.

In addition to defining developmental stages, Greene (1960) suggested a scheme based on time required for development (examples from Benson-Evans & Brough 1966):

### categories of sporophyte development

6 months	–no resting stage (ex. <i>Atrichum undulatum</i> )
10 months	–short winter resting stage (ex. <i>Mnium hornum</i> , <i>Eurhynchium praelongum</i> )
14-18 months	–resting stage in winter, often persisting partly into next growing season (ex. <i>Funaria hygrometrica</i> )

At least in the temperate zone, the spring and autumn maturation times may follow a long development, as found in *Polytrichum* – 7-16 months in Scandinavia, 9-20 months

in Sweden (Arnell 1905), and *Forsstroemia trichomitria* – 17 months (Stark 1984), or 15 months for *P. alpestre* in the Antarctic (Longton 1972). In others, such as *Mnium hornum*, the seta emerges in the autumn, remaining in that state throughout the winter, and continues development in early spring (Greene 1960). In Great Britain, this species has lost its opercula by early May.

The capsule cycle of the epiphytic *Pylaisiella polyantha* requires so much time for development that two generations of capsules are present at the same time, not only in Great Britain, but in many locations in both Europe and North America (Greene 1960). The venter is swollen in July to August, and the calyptra is retained for an entire year, falling in the next July. Capsule development continues, with the operculum falling early in the following year. In Great Britain, this species has lost its opercula by early May

## Winter Dispersal

Winter is a good time for capsule maturation to occur in mild climates where that is the moist season. In Great Britain, *Brachythecium rutabulum* has lost its opercula by early May (Greene 1960). It continues development from its early calyptra stage in September on to an intact operculum with the operculum falling December to February. By March the capsules are empty. If it were to follow that timing in the Keweenaw Peninsula of Michigan, USA, its capsules would be imbedded in snow at the time

of dispersal. In Japan, the thallose liverwort *Mannia fragrans* has mature spores in early winter (Furuki 1992).

Lackner (1939) found that *Orthotrichum* species were notable exceptions to the spring and summer dispersals of bryophytes in his study. This epiphytic/saxicolous genus typically produced capsules in the winter months. Perhaps winter is good for mosses if they can avoid being covered by snow, although early frost causes mortality in young capsules of the soil-dwelling *Buxbaumia aphylla* (Hancock & Brassard 1974; Figure 18).

Winter may also favor aquatic bryophytes, but for somewhat different reasons because the problems are quite different. Dispersal by air would seem to be nearly impossible when the environment is continuously moist or submersed. And, in fact, we have no direct evidence of the success of the spores of such submersed taxa as *Fontinalis*. Nevertheless, *F. novae-angliae* and *F. dalecarlica* produce capsules in winter, at least in New Hampshire, USA, with abrasion apparently serving as the primary means of opening the capsule (pers. obs.). The subsequent dispersal of the spores is pure conjecture, but since the peristome teeth are generally not exposed to air, one might suppose that water is the only available agent. It is interesting that the aquatic liverwort *Scapania undulata* likewise produces its capsules in winter (Grainger 1947).



Figure 18. Young sporophytes of *Buxbaumia aphylla* in Michigan, USA. Photo by Janice Glime.

### Elevation Effects

For those bryophytes not adapted for development during winter conditions, elevation provides evidence of the importance of temperature. For thirteen taxa growing at four elevations in the Eastern Pyrenees, Girona, Spain, those living at higher elevations have dormant sporophytes in the winter, completing their development early in the summer (Lloret 1987). Those that live at lower elevations have continuous development. Only one species among these, *Schistidium apocarpum* var. *confertum*, is able to continue development at locations above 1800 meters.

One of the factors that can affect success of a sporophyte is the weather during development of pre-winter stages, as shown by the high mortality due to early frost in young sporophytes of *Buxbaumia aphylla* in Newfoundland (Hancock & Brassard 1974). In this species, young capsules are formed in the autumn and remain green over the winter, maturing the following spring. By summer, little evidence of the capsule remains, although their thick setae are sometimes still present.

Fortunately, mosses are adaptable in their physiological responses, often resulting in physiological races in different parts of the world. Longton (1979), in comparing *Polytrichum alpestre* populations at the more northern Churchill, Manitoba, Canada, site to those at Pinawa, Manitoba, found that the initiation of the LCP (late calyptra in perichaetium) stage began earlier in the autumn and that shift to the OI (operculum intact) stage occurred later in the spring at Churchill (Figure 19). However, the sporophyte development proceeded more quickly at Churchill during the growing season, surpassing that of the mosses at the Pinawa site, and compensating for the longer dormancy.

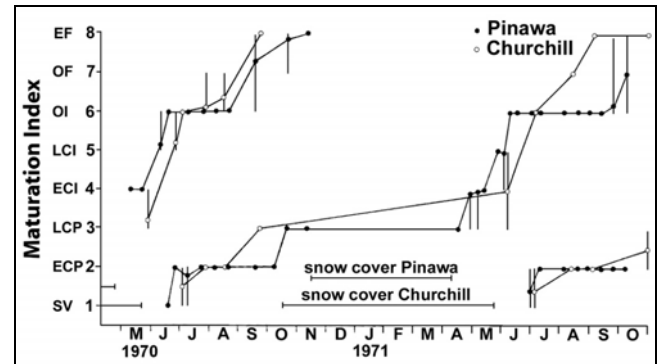


Figure 19. Comparison of sporophyte development of *Polytrichum alpestre* in Pinawa and Churchill, Manitoba, Canada. Points represent the maturity indices with vertical bars indicating the range of stages present. Based on Longton (1979).

### Spores and Protonemata

Spore dispersal is most advantageous if the air is dry and breezy, permitting the spores to travel long distances before becoming lodged within the minute crevices of the soil or other substrate. In fact, dryness usually initiates the shedding of the operculum, as illustrated by Johnsen (1969) for *Orthotrichum anomalum*. On the other hand, to mature, the capsule must have energy available, so these two factors must be included in the dispersal strategy to determine the season of dispersal. It may be this need for energy, then a dry season, followed by a suitable moist season, that some mosses disperse their spores in winter, e.g. *Anomobryum julaceum* and *Bryum argenteum* (Figure 20) (Pedersen & Hedenäs 2002) and the liverwort *Mannia fragrans* in Japan (Furuki 1992). In the seasonally dry interior of North America, *Syrrhopodon texanus* has optimal spore release in October to March, followed by rain that peaks in July, then decreases rapidly to a low in November (Reese 1984). As we have already seen, one way to accommodate these needs for energy and the right moisture conditions is for the capsule to persist in a mature state, operculum intact, for months to years before initiating dispersal.

Using herbarium specimens, Nishimura (1993) determined the dates of dispersal for mosses from the Hiruzen Highlands on the island of Honshu, Japan (Figure 21). He found 34 species that disperse spores in late autumn to early spring (late November to early April), 12 in late spring to summer (May to August), and 5 in autumn (September to November). *Bryum argenteum* dispersed in both spring and autumn. *Sematophyllum subhumile* subsp. *japonicum* was the only species that had no definite season

of dispersal. Although herbarium specimens can introduce error because opercula tend to come off more easily under the dry conditions of the herbarium, the 551 specimens used in this study give us a general picture of events.



Figure 20. Capsules on *Bryum argenteum*. Photo by Michael Lüth.

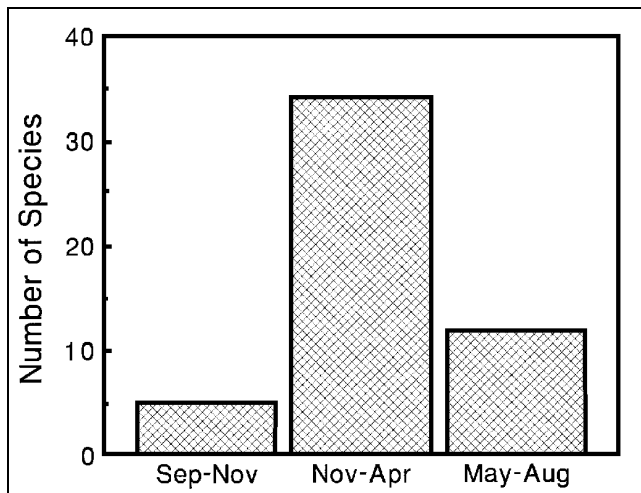


Figure 21. Seasons of dispersal in 51 species of mosses from the Hiruzen Highlands, Honshu, Japan. From data of Nishimura (1993).

Egunyomi (1979) found that capsules of *Octoblepharum albidum* in Nigeria matured just in time for spores to be liberated during the dry season. Stark (2001a.) finds that most desert bryophytes release spores year-round, an advantage in a dry climate where rainfall is rare and not seasonal. On the other hand, spores in *Pleurozium schreberi* in Britain are shed January-April when it is cool and relatively moist (Longton & Greene 1969). In a later study in Great Britain, Longton and Miles (1982) found that five mosses had fertilization in the period of April to July, but that sporophyte maturation time varied considerably. Spore liberation took place from six to twelve months later, spanning a variety of climatic conditions.

To determine the availability of spores, Fenton and Bergeron (2006) studied the spore dispersal of *Sphagnum* species in a black spruce (*Picea mariana*) forest in Québec, Canada. Using spore traps, they determined the phenology of spore dispersal (Figure 22) for two years. Dispersal at these locations began in July, rose in mid August, and ended mid to late September, with peak dispersal near the

beginning of September. The earlier dispersal than that of the study in Japan (Nishimura 1993) may be the result of the higher latitude.

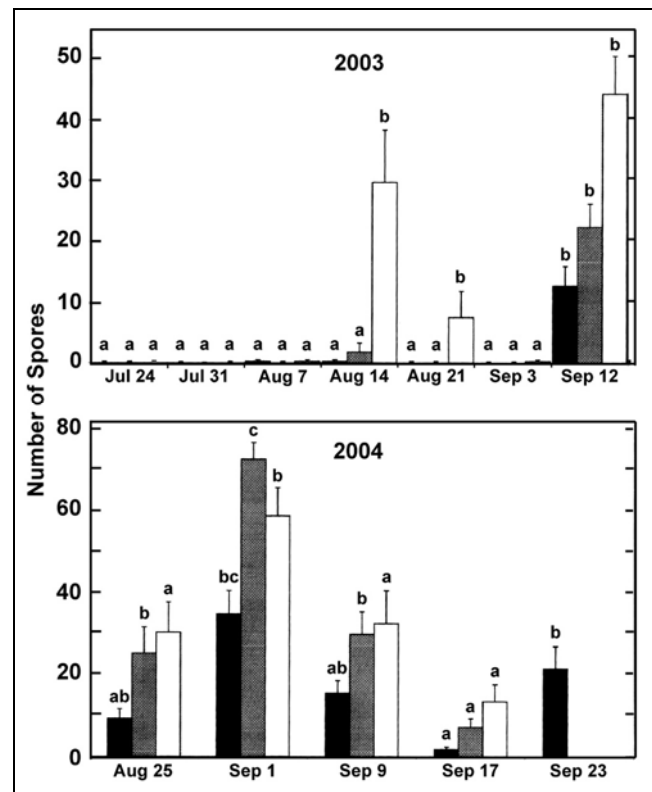


Figure 22. Number of spores collected in 20 spore traps at each of three sites in Québec, Canada. Vertical bars represent standard error. Different letters indicate those values that are significantly different within a site. Redrawn from Fenton & Bergeron (2006).

Although the time of spore dispersal is fairly well known, or at least available in herbaria, virtually nothing is known about the time of spore germination. Longton and Schuster (1983) comment that little is known about spore dormancy in liverworts and virtually nothing about the effect of day length on germination. This is due largely to the difficulty of locating this stage and, even if located, to identify even the genus, much less the species.

We can speculate on the importance of timing for spore establishment. Proctor (2000) pointed out that the need for water would limit the successful establishment of spores and their protonemata on rocks and bark to the lengthy wet season of autumn and winter in western Europe and whatever wet season elsewhere.

Even in taxa with persistent protonemata, such as *Buxbaumia*, where sexual organs are produced directly on the protonema, field knowledge is lacking. After an extensive study of *Buxbaumia aphylla* spanning three years, Hancock and Brassard (1974) were unable to determine if the protonema persisted for more than one season or if the gametangia were produced the same season.

In most taxa, it is probably not necessary to couple suitable germination and protonema development conditions with those of dispersal. Spore viability can last from less than an hour in some epiphyllous and epiphytic liverwort taxa (Longton & Schuster 1983) to 50 years in

other bryophytes (Sussman 1965), and probably longer in some taxa. Most spores probably have considerable longevity, as seen in several diaspore bank studies in the Netherlands (e.g. During 1986, 1990, During & ter Horst 1983, During *et al.* 1987). They even survive temperatures near absolute zero when dried and placed in vacuum tubes (Becquerel 1932). Van Zanten (1976) has shown that most taxa can survive desiccation for one year, with wet-frozen spores surviving better than dry-frozen ones. But for spores that fall near their parents and do not effect long-distance dispersal, immediate germination success will provide a better chance of establishing the next generation, particularly in overwintering annual taxa, by giving them an early start and a higher percentage of survival.

Protonemata can likewise survive considerable drying (Lipman 1936) and in some taxa such as *Grimmia* may even require a drought period before advancing to the next stage (During, pers. comm.). In fact, Johnsen (1969) found that in *Orthotrichum anomalum* watering during the dormant period (hot and dry) was detrimental. Thus it appears that germination should require more than just the right seasonal event, but rather a seasonal event coupled with the right environmental conditions to take things to the next stage. There seems to be no hope at present of generalizing about phenological events related to the protonemata based on any foundation in data.

### Duration of Stages

Longton (1997, 1998) found that those bryophytes that have shorter life spans become reproductively active at a younger age and tend to have greater phenological flexibility. This strategy necessarily implies that each stage is short. This is especially true for the colonists, fugitives, and annual shuttle species to be discussed later in the life strategies chapter. For those taxa that stay longer, the stages may be longer, often depending on habitat characteristics, particularly availability of water.

### Gametangia

One of the factors that is important in maintaining distinct species when more than one member of a genus cohabit a region is that their reproductive periods do not overlap or that their means of dispersing gametes are mutually exclusive. Among three Australian species of *Dicranoloma*, all three species studied required 5-6 months for antheridia to mature, but only 2 for archegonia (Milne 2001), the longer time for antheridial development being typical for most mosses. Yet the timing for these three taxa was such that their periods of fertilization were mutually exclusive.

In *Entodon cladorrhizans*, the fertilization period lasts five weeks in Pennsylvania, USA (Stark 1983). In the desert moss *Syntrichia inermis* (Figure 23), maturation of the antheridia takes one to several years due to the intervening dry periods that cause dormancy (Stark 1997). Table 2 provides additional examples of maturation times, ranging from less than one month for some archegonia and three months for some antheridia to nearly one year for others.

### Sporophytes

Ephemeral species have short-lived capsules that may last only a few weeks. Liverworts do likewise, with their deliquescent stalk soon withering away. Furthermore, the

valvate capsules of liverworts shed all the spores at one time, whereas in mosses peristome teeth operate to extend dispersal over a longer period, providing the mosses with more opportunities to disperse under conditions favorable for greater dispersal or germination success. *Sphagnum* likewise has short-lived stalks, in this case a deliquescent pseudopodium that develops from the gametophyte to extend the capsule away from the plant. It lacks teeth and disperses most of its spores in one explosive burst when the operculum is shed due to capsule drying and at least some of the time, internal gas expansion due to high temperatures.



Figure 23. *Syntrichia inermis* in its dry state beneath shrubs. Photo by Lloyd Stark.

But other mosses may have quite extensive periods of sporophyte development. In *Dicranoloma*, *D. billardierei* and *D. platycaulon* required 18-24 months while those of *D. mizensii* required only 12 (Milne 2001).

Mosses that depend on rainy periods may have very short periods for maturation of the sporophyte, attuned to dispersal at the end of the rainy season, as in *Racomitrium africanum*, *Fissidens glauculus*, *Thuidium gratum*, and *Stereophyllum* sp. from SW Nigeria (Odu 1981). These mosses required 12 months from onset of gametangia to capsule maturity and dispersal, but sporophyte development itself is complete at the end of the rainy season (October-December), following gametangial development at the onset of the rainy season (March/April). Spore dispersal occurs during the dry season (November-April). The entire process requires 12 months. Other desert mosses can have very long maturation periods spanning several years with long dormancy periods intervening.

The soil-dwelling *Syntrichia inermis*, in the Mojave Desert, USA, requires about 21 months for sporophyte development, while being dormant for 18 of those months (Stark 1997). Span of operculum detachment may last up to 2.5 years, and capsules of the same cohort may disperse spores over a period of three years (Stark 2001a). In the same desert, the rock-dwelling *Grimmia orbicularis* required only 3 months for its capsule to mature following meiosis, and its operculum dehiscence spanned only three weeks; spore release of the cohort lasted about six months (Stark 2001a).

The perennial moss *Entodon cladorrhizans* requires six to nine months for the sporophyte to mature (Stark 1983).

Table 2. Examples of times of initialization of gametangia, fertilization, and spore dispersal in bryophytes in the temperate zone.

	location	antheridia initialized	archegonia initialized	fertilization	spores dispersed	
<i>Atrichum undulatum</i>	UK	Jan-Feb	Apr-May	May-Jun	Jan-May	Miles <i>et al.</i> 1989
<i>Polytrichum alpestre</i>	UK	Sep-Oct	Mar-Apr	Jun	Jun-Jul	Miles <i>et al.</i> 1989
<i>Bryum argenteum</i>	UK	Oct-Nov	Apr-Jun	Apr-Jun?	Jan-May	Miles <i>et al.</i> 1989
<i>Grimmia pulvinata</i>	UK	most of yr	most of yr	most of yr	Apr-Jun	Miles <i>et al.</i> 1989
<i>Tortula muralis</i>	UK	anytime	anytime	anytime	Apr-Jun	Miles <i>et al.</i> 1989
<i>Pellia epiphylla</i>	UK	Jan-Jun	Jun	Jun	Mar-Jun	Clapham & Oldroyd 1936
<i>Cephalozia</i>	UK	Feb	Mar	May	?	Clapham & Oldroyd 1936
<i>Marchantia polymorpha</i>	UK	Mar-Apr	Mar-Apr	May	Aug	Clapham & Oldroyd 1936
<i>Aplozia</i>	UK	Apr	May	Jun	May	Clapham & Oldroyd 1936
<i>Conocephalum conicum</i>	UK	Apr-Jun	Jun-Jul	Jul	Mar-Apr	Clapham & Oldroyd 1936
<i>Conocephalum conicum</i>	MI, USA	Aug	Aug	Jun	Apr	Taylor & Hollensen 1984
<i>Diplophyllum</i>	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936
<i>Scapania</i>	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936

Zander (1979) did an exhaustive study in the Pottiaceae of the north temperate zone of Europe, Asia, and North America, comparing dioicous and monoicous taxa. The Pottiaceae typically require 12-13 months for sporophyte development (Krieger 1915), but Zander found that the phenology of the two sexual conditions differed, with dioicous taxa having mature capsules over a slightly longer period of time than did monoicous taxa. Non-endemic dioicous taxa have a mean span of mature capsules of 6.77 months, whereas the non-endemic monoicous ones have only a 5.55-month mean. Among the 86 dioicous taxa studied, 12 have mature capsules spanning nine or more months, whereas only 5 of the 82 monoicous taxa exhibit this duration. He reasoned that this afforded dioicous taxa a better chance for dispersal, perhaps in part compensating for the smaller likelihood of fertilization. This compensation concept was further supported by finding that the monoicous taxa did not have a significantly wider distribution. Since the ratio of monoicous to dioicous taxa in Pottiaceae is similar to that of bryophytes as a whole, this study might be a model of mature capsule duration in monoicous vs. dioicous taxa. It would be interesting to determine if capsule duration can indeed compensate for the reputedly greater percent of species producing capsules among the monoicous taxa than among the dioicous ones (Gemmell 1950, Longton & Schuster 1983).

### Winter Effects

In bryophytes, unlike the tracheophytes, embryos and gametangia are capable of surviving prolonged freezing of winter (Stark 1984). Continuous melt of snow during parts of the winter could facilitate fertilization of some bryophytes under the snow, but no broad-scale studies have examined this in areas where the phenomenon is likely, and while the gametangia might survive, one must question whether the sperm can swim and locate a female at near-freezing temperatures. Furthermore, while sperm can swim at speeds of 100-200  $\mu\text{m}$  per second (Richards 1978), they require a chemical attractant to find the archegonium (Muggoch & Walton 1942), and cold temperatures might reduce the effectiveness of such an attractant. Even so, we know that the aquatic liverwort *Scapania undulata* produces gametangia and accomplishes fertilization in winter (Grainger 1947).

On the other hand, Imura and Iwatsuki (1989) found that in *Trachycystis microphylla* in Japan, antheridia

production begins in January with sperm being released March to May. Archegonia production is delayed until March, but they are ready to accept sperm from April to July. The partitioning of energy among life cycle stages would appear to be complex in this species, with overlapping life cycle stages, since spores are released near the time of fertilization of the next generation. (Imagine sending one kid off to college while you are pregnant with the next!) Development of the sporophyte begins in May, and rapid sporophyte elongation occurs in October to November and again in February. Spores are released in April – apparently near the time sperm are released. One would think this delicate timing would require competing environmental conditions, wet for sperm and dry for spores. Since spring is a time of alternating sunshine and rain, these contrasting conditions are probably available.

One explanation for the success of overwintering antheridia as a strategy is that it may spread out the energy requirements over a longer period and give antheridia a chance to grow rapidly in spring, thus insuring that they precede the archegonia in maturity. Benson-Evans and Brough (1966) found that a cold period followed by warmer temperatures can induce more rapid maturation of sex organs if sufficient moisture is available, whereas low temperatures and drought retard development. In this case, the antheridia would receive the stimulation, but the archegonia, by delaying initiation until spring, would not. This advantage is consistent with the 10 out of 18 taxa examined by van der Wijk (1960) in which male gametangia overwintered; female gametangia in these were generally initiated in early spring. One must ask why it is the males that seem to overwinter, whereas females of the same species often delay initiating gametangia until spring. Is it because winter is in fact destructive, but male gametes are much more abundant than are female gametes and can therefore afford to sacrifice some in order to mature earlier? Is there some developmental reason why antheridia require a longer time to develop than do archegonia? Or is it a mechanism to increase protandry, thus ensuring at least some cross fertilization?

Despite the ability of gametangia to survive over winter, Arnell (1905) reported that most of the 33 German and Swedish taxa he studied had gametangial dehiscence in the summer, which suggests that fertilization must have occurred then as well. However, many parts of the world lack sufficient moisture in summer to ensure fertilization.

Huneck *et al.* (1984) determined that essential oils in the temperate leafy liverwort *Bazzania trilobata* were highest in September and lowest in January, suggesting that perhaps these oils might be used for energy reserves during autumn and early winter. It is also possible that they offer a protective function to the cells during the period of freezing and thawing in autumn.

### Geographical Differences within Species

Earlier studies by Richards (1959) indicate that seasonal behavior of bryophytes may vary in different climatic regions. In particular, the basic developmental pattern of gametangia and sporophytes may differ. Furthermore, lack of proper environmental signals, such as not reaching the necessary temperature at the necessary photoperiod, or inability of the plant to interpret the signals can result in failure to produce gametangia or in failure of females to produce mature archegonia at a time when sperm are ready for release (Newton 1971, 1972, Longton 1972).

Even within a small geographic range, signals can come at a different time. For example, in North Wales, *Bryum argenteum* begins development of antheridia before winter, in November, whereas archegonia develop in April (Miles & Longton 1987). In Reading, UK, both gametangia develop at the same time.

Some taxa have adopted different physiological responses in different parts of the world, as, for example, *Lunularia cruciata*, which seems to function as a long-day plant in Wales and a short-day plant in Israel (Longton 1974), but in much of the British Isles it is the climate that prevents this liverwort from producing an archegoniophore and capsules (Benson-Evans & Hughes 1955).

Elevation has a strong effect on timing of the life cycle in the Eastern Pyrenees. Bryophytes at high elevations have arrested sporophyte development in the winter, with maturation occurring in the summer concurrent with the next fertilization. However, at lower elevations, there is a continuous progression of stages with no dormant period. *Schistidium apocarpum* var. *confertum*, however, lives at elevations above 1800 m but, like lowland taxa, has no dormant period in winter.

The example of *Funaria hygrometrica*, as studied by Hoffman (1966), exemplifies the sorts of controls that determine the selection pressures affecting the maturation cycle. In that moss, Hoffman found that gametophytes appeared in early spring, with sporophytes maturing in June, but that maturation dates were progressively later at higher elevations. High light intensities contributed to more rapid gametophyte development, while a longer photoperiod resulted in larger stems and leaves. Thus, physiological controls adapt the bryophytes to their particular conditions and may be important factors in selection as bryophytes spread around the world. Whereas morphological variation between species is limited by small size, it is possible that the bryophytes may have greater physiological variability than do the tracheophytes, enabling the individual species to occupy wider ranges of conditions than those of their tracheophyte counterparts. These adaptations permit the bryophytes to conserve energy and to optimize it across time.

### Summary

The life cycle of a moss can be described based on those stages that are observably different, are discontinuous, and require a change in environmental conditions. This definition presents us with the recognizable stages of embryonic calyptra, seta with calyptra, green capsule with calyptra, operculate post-meiotic capsule, de-operculate capsule, spore with bulging wall, protonema, protonema with bud, juvenile stem, antheridium, archegonium.

**Growth** requires sufficient moisture, nutrients, and light at a time when the temperature does not cause a high level of respiratory loss, below 25°C for most shade-adapted taxa. Growth usually ceases in hot summers when the temperature is too high and carbon loss would be greater than carbon gain, and in cold winters when there is no free water and bryophytes go dormant. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. There is a trade-off between growth and reproduction so that growth diminishes or ceases during reproduction.

**Gemmae** are more likely than other life cycle events to lack seasonal behavior, but their production may cease during sexual reproduction due to competition for energy.

**Antheridia** generally initiate before **archegonia** and require longer for development. Many will begin development, then become dormant during winter, resuming in spring to mature when archegonia, initiated in spring, are also mature. 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 for fertilization. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Cross-fertilization in monoicous bryophytes is supported by **protogyny** and **protandry** in many taxa. In dioicous taxa, the perigonia (housing antheridia) are typically initiated first and mature at about the same time as perichaetia (housing archegonia).

Desert bryophytes may have multiple periods of dormancy interrupting any of the developmental stages. Some take advantage of cooler temperatures and greater availability of water in winter to accomplish fertilization. Aquatic bryophytes such as *Fontinalis* may have fertilization in autumn when water levels are rising, ensuring water for development, then produce capsules in winter when spring runoff can aid dispersal.

Sporophyte maturation of most taxa is timed for dispersal during the dry season and may last from only a few days to several years. For most temperate zone bryophytes, spring and autumn seem to be the best time for dispersal. Elevation generally meant that events start later in the year, but higher light levels and in some cases longer days, along with innate adaptations, may cause stages to mature in less time than at lower elevations.

## Acknowledgments

Thank you to Jean Faubert for her suggestions to alter the discussion of gemmae on *Orthotrichum*.

## Literature Cited

- Al-Mufti, M. M., Sydes, C. L., Furness, S. B., Grime, J. P., and Band, S. R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-92.
- Arnell, H. W. 1875. The Skandinaviska Löfmossornas Kalendarium. Upsala Univ. Arsskr.
- Arnell, H. W. 1905. Phaenological observations on mosses. *Bryologist* 8: 41-44.
- Becquerel, P. 1932. La vie latente des spores des mousses aux basses températures. *C. R. Acad. Sci. (Paris)* 194: 1378-1380.
- Benson-Evans, K. and Brough, M. C. 1966. The maturation cycles of some mosses from Forest Ganol, Glamorgan. *Cardiff Nat. Soc. Trans.* 92: 4-23.
- Benson-Evans, K. and Hughes, J. G. 1955. The physiology of sexual reproduction in *Lunularia cruciata* (L.) Dum. *Trans. Brit. Bryol. Soc.* 2: 513-522.
- BFNA. 2007. Flora of North America North of Mexico. Volume 27. Bryophytes: Mosses, Part 1. Oxford University Press, New York.
- Clapham, P. M. and Oldroyd, M. 1936. A time-table for the life cycles of some of the liverworts in Yorkshire. *Naturalist* 1936: 253-259.
- Conard, H. S. 1947. Phenology of mosses in Iowa. *Iowa Acad. Sci. Proc.* 53: 141-146.
- Crum, H. 1976. Mosses of the Great Lakes forest, revised edition. *Univ. Mich.* 10: 1-404.
- Crum, H. 2001. Structural Diversity of Bryophytes. University of Michigan Herbarium, Ann Arbor, 379 pp.
- Deguchi, H. and Yananose, N. 1989. Development of sporophyte, calyptra and vaginula in *Pogonatum neesii* (C. Müll.) Dozy. *Proc. Bryol. Soc. Japan* 5: 209-214.
- Duckett, J. G. and Renzaglia, K. S. 1993. The reproductive biology of the liverwort *Blasia pusilla* L. *J. Bryol.* 17: 541-552.
- During, H. J. 1986. Longevity of spores of *Funaria hygrometrica* in chalk grassland soil. *Lindbergia* 12: 132-134.
- During, H. J. 1990. The bryophytes of calcareous grasslands. In Hillier, S. H., Walton, D. W. H., and Wells, D. A.: Calcareous grasslands - ecology and management, Proceedings of a Joint British Ecological Society/Nature Conservancy Council Symposium, University of Sheffield, Bluntisham Books, Huntingdon, UK, pp. 35-40.
- During, H. J. 1997. Bryophyte diaspore banks. *Adv. Bryol.* 6: 103-134.
- During, H. J. and ter Horst, B. 1983. The diaspore bank of bryophytes and ferns in a chalk grassland. *Lindbergia* 9: 57-64.
- During, H. J., Bragues, M., Cros, R. M., and Lloret, F. 1987. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. *Lindbergia* 13: 137-149.
- Egunyomi, A. 1979. Autecology of *Octoblepharum albidum* Hedw. in Western Nigeria II. Phenology and water relations. *Nov. Hedw.* 31: 377-387.
- Fenton, N. J. and Bergeron, Y. 2006. *Sphagnum* spore availability in boreal forests. *Bryologist* 109: 173-181.
- Forman, R. T. T. 1965. A system for studying moss phenology. *Bryologist* 68: 289-300.
- Frahm, J. P. 2002. Spores 18 years alive under water. *Bryonet-1*, 4 November 2002.
- Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes. I. An investigation of *Brachythecium rutabulum*. *J. Ecol.* 70: 513-523.
- Furuki, T. 1992. Ecological notes and distribution range of *Mannia fragrans* (Balbis) Frye et Clark in Japan. *Proc. Bryol. Soc. Japan* 5(10): 158-160.
- Gemmell, A. R. 1950. Studies in the Bryophyta: I. The influence of sexual mechanism on varietal production and distribution of British Musci. *N. Phytol.* 49: 64-71.
- Glime, J. M. 1980. Effects of temperature and flow on rhizoid production in *Fontinalis*. *Bryologist* 83: 477-485.
- Glime, J. M. 1982. Response of *Fontinalis hypnoides* to seasonal temperature variations. *J. Hattori Bot. Lab.* 53: 181-193.
- Glime, J. M. 1984. Physio-ecological factors relating to reproduction and phenology in *Fontinalis dalecarlica*. *Bryologist* 87: 17-23.
- Glime, J. M. 1987a. Phytogeographic implications of a *Fontinalis* (Bryopsida) growth model based on temperature and flow conditions for six species. *Mem. N. Y. Bot. Gard.* 45: 154-170.
- Glime, J. M. 1987b. Growth model for *Fontinalis duriaei* based on temperature and flow conditions. *J. Hattori Bot. Lab.* 62: 101-109.
- Glime, J. M., Nissila, P. D., Trynoski, S. E., and Fornwall, M. D. 1979. A model for attachment of aquatic mosses. *J. Bryol.* 10: 313-320.
- Grainger, J. 1947. Nutrition and flowering of water plants. *J. Ecol.* 35: 49-64.
- Gray, F. W. 1935. Pygmies again and again. *Bryologist* 38: 25-28.
- Greene, S. W. 1960. The maturation cycle, or the stages of development of gametangia and capsules in mosses. *Trans. Brit. Bryol. Soc.* 3: 736-745.
- Grimme, A. 1903. Über die Bluthzeit Feutscher Laubmoose und die Entwicklungsdauer ihrer Sporogone. *Hedwigia* 42: 1-75.
- Gupta, A., Sarla, and Chopra, R. N. 1991. In vitro studies on growth and gametangial formation in *Riccia discolor*: Effect of physical factors. *J. Hattori Bot. Lab.* 70: 107-117.
- Hancock, J. A. and Brassard, G. R. 1974. Phenology, sporophyte production, and life history of *Buxbaumia aphylla* in Newfoundland, Canada. *Bryologist* 77: 501-513.
- Haupt, A. W. 1929a. Studies in Californian Hepaticae. I. *Asterella californica*. *Bot. Gaz.* 87: 302-318.
- Haupt, A. W. 1929b. Studies in California Hepaticae. II. *Fossombronina longiseta*. *Bot. Gaz.* 88: 103-108.
- Herrnstadt, I. and Kidron, G. J. 2005. Reproductive strategies of *Bryum dunense* in three microhabitats in the Negev Desert. *Bryologist* 108: 101-109.
- Hoffman, G. R. 1966. Ecological studies of *Funaria hygrometrica* Hedw. in eastern Washington and northern Idaho. *Ecol. Monogr.* 36: 157-180.
- Hohe, A., Rensing, S. A., Mildner, M., Lang, D., and Reski, R. 2002. Day length and temperature strongly influence sexual reproduction and expression of a novel MADS-box gene in the moss *Physcomitrella patens*. *Plant Biol.* 4: 595-602.
- Hughes, J. G. 1990. Seasonal growth and development of sporophytes in wild populations of *Pogonatum* and *Polytrichum* species. *J. Bryol.* 16: 97-108.

- Huneck, S., Jänicke, S., Meinunger, L., Snatzke, G., Connolly, J. D., and Asakawa, Y. 1984. Seasonal dependence of the essential oil from *Bazzania trilobata*. The stereochemistry and absolute configuration of (-)-5-hydroxycalamenene. *J. Hattori Bot. Lab.* 57: 337-342.
- Imura, S. 1994. Phenological study in two dioecious mosses, *Atrichum rhystophyllum* (C. Mull.) Par. and *Pogonatum inflexum* (Lindb.) Lac. *J. Hattori Bot. Lab.* 76: 105-114.
- Imura, S. and Iwatsuki, Z. 1989. Phenological study of *Trachycystis microphylla* (Dozy et Molk.) Lindb. (Mniaceae, Musci). *Hikobia* 10: 303-308.
- Johnsen, A. B. 1969. Phenological and environmental observations on stands of *Orthotrichum anomalum*. *Bryologist* 72: 397-403.
- Jones, E. W. 1946. The time of fruiting of *Ulota bruchii* Hornsch and *U. crispa* Brid. *Trans. Brit. Bryol. Soc.* 1: 20-22.
- Kinugawa, K. and Nakao, S. 1965. Note on spore germination and protonemal growth controlled by day length in *Bryum pseudo-triquetrum*. *Bot. Mag. Tokyo* 78: 194-197.
- Krieger, W. 1915. Über die Dauer der Sporogonentwicklung bei den Laubmoosen. *Hedwigia* 57: 154-199.
- Kumra, S. and Chopra, R. N. 1989. Studies on growth and gemma cup formation in *Marchantia palmata* Nees. *Beitr. Biol. Pflanzen* 64: 243-252.
- Laaka-Lindberg, S. 2000. Ecology of Asexual Reproduction in Hepatics. E-thesis, University of Helsinki, Finland, 28 pp.
- Laaka-Lindberg, S. and Heino, M. 2001. Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*. *Oikos* 94: 525-532.
- Lackner, L. 1939. Über die Jahresperiodizität in der Entwicklung der Laubmoose. *Planta* 29: 534-616.
- Leitgeb, H. 1868. Beiträge zur Entwicklungsgeschichte der Pflanzenorgane I. Entwicklung der Antheridien bei *Fontinalis antipyretica*. In: Hof, K. K. *Mathematisch-Naturwissenschaftlichen Classe* 58(1): 525-537.
- Li, Y. 1991. Ecological and Eco-physiological Studies of Two *Sphagnum* Species. Ph. D. Dissertation, Michigan Technological University, Houghton, 155 pp.
- Lindholm, T. 1990. Growth dynamics of the peat moss *Sphagnum fuscum* on hummocks on a raised bog in southern Finland. *Ann. Bot. Fenn.* 27: 67-78.
- Lipman, C. B. 1936. The tolerance of liquid air temperature by dry moss protonema. *Bull. Torrey Bot. Club* 63: 515-518.
- Lloret, F. 1987. Efecto de la altitud sobre la fenología de briofitos en el Pirineo oriental. [The effect of altitude in the phenology of bryophytes in the Eastern Pyrenees.]. *Anales Jard. Bot. Madrid* 43(2): 203-215.
- Longton, R. E. 1972. Reproduction of Antarctic mosses in the genera *Polytrichum* and *Psilopilum* with particular reference to temperature. *Brit. Antarct. Surv. Bull.* 27: 51-96.
- Longton, R. E. 1974. Biology of widely distributed bryophytes: A possible project for the International Association of Bryologists. *Taxon* 23: 213-214.
- Longton, R. E. 1979. Studies on growth, reproduction and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. *Bryologist* 82: 325-367.
- Longton, R. E. 1997. Reproductive biology and life-history strategies. *Adv. Bryol.* 6: 65-101.
- Longton, R. E. 1998. Reproductive biology and life-history strategies. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). *Bryology for the Twenty-first Century*. Maney Publishing and the British Bryological Society, UK, pp. 369-370.
- Longton, R. E. and Greene, S. W. 1969. The growth and reproductive cycle of *Pleurozium schreberi* (Brid.) Mitt. *Ann. Bot. New Ser.* 33: 83-105.
- Longton, R. E. and Miles, C. J. 1982. Studies on the reproductive biology of mosses. *J. Hattori Bot. Lab.* 52: 219-240.
- Longton, R. E. and Schuster, R. M. 1983. Reproductive biology. In Schuster, R. M. (ed.): *New Manual of Bryology*, Hattori Botanical Lab, Nichinan, Japan. Vol. 1, Pp. 386-462.
- Miles, C. J. and Longton, R. E. 1987. Life history of the moss, *Atrichum undulatum* (Hedw.) P. Beauv. *Symp. Biol. Hung.* 35: 193-207.
- Miles, C. J., Odu, E. A., and Longton, R. E. 1989. Phenological studies on British mosses. *J. Bryol.* 15: 607-621.
- Milne, J. 2001. Reproductive biology of three Australian species of *Dicranoloma* (Bryopsida, Dicranaceae): Sexual reproduction and phenology. *Bryologist* 104: 440-452.
- Mishler, B. D. and Oliver, M. J. 1991. Gametophytic phenology of *Tortula ruralis*, a desiccation-tolerant moss, in the Oregon Mountains of southern New Mexico. *Bryologist* 94: 143-153.
- Moto de Oliveira, S. and Cavalcanti Pôrto, K. 2001. Reproductive phenology of the moss *Sematophyllum subpinnatum* in a tropical lowland forest of north-eastern Brazil. *J. Bryol.* 23: 17-21.
- Moyá, M. T. 1992. Phenological observations and sex ratios in *Marchantia chenopoda* L. (Hepaticae: Marchantiaceae). *Trop. Bryol.* 6: 161-170.
- Muggoch, H. and Walton, J. 1942. On the dehiscence of the antheridium and the part played by surface tension in the dispersal of spermatocytes in Bryophyta. *Proc. Royal Soc. B130*: 448-461.
- Newton, M. E. 1971. A cytological distinction between male and female *Mnium undulatum*. *Trans. Brit. Bryol. Soc.* 6: 230-243.
- Newton, M. E. 1972. An investigation of photoperiod and temperature in relation to the life cycles of *Mnium hornum* Hedw. and *M. undulatum* Sw. (Musci) with reference to their histology. *Bot. J. Linn. Soc.* 65: 189-209.
- Nishimura, N. 1993. Bryophytes of the Hiruzen Highlands. 5. Preliminary observation for reproductive phenology of mosses. *Bull. Hiruzen Res. Inst., Okayama Univ. Sci.* 19: 139-146.
- Odu, E. A. 1981. Reproductive phenology of some tropical African mosses. *Cryptog. Bryol. Lichénol.* 2: 91-99.
- Odu, E. A. and Owotomo, O. O. 1982. Periodic production of gemmiferous leaves in two west tropical African *Calymperes* species: *C. afzelii* Sw. and *C. erosum* C. Muell. *Bryologist* 85: 239-242.
- Pedersen, N. and Hedenäs, L. 2002. Phylogenetic relationships between *Bryum* and supposedly closely related genera. *J. Bryol.* 24: 277-289.
- Pitkin, P. H. 1975. Variability and seasonality of the growth of some corticolous pleurocarpous mosses. *J. Bryol.* 8: 337-356.
- Proctor, M. C. F. 2000. Mosses and alternative adaptation to life on land. *New Phytol.* 148: 1-6.
- Pujos, J. 1992. Life history of *Sphagnum*. *J. Bryol.* 17: 93-105.
- Reese, W. D. 1984. Reproductivity, fertility and range of *Syrhopedon texanus* Sull. (Musci: Calymperaceae), a North American endemic. *Bryologist* 87: 217-222.
- Richards, P. W. 1959. Bryophyta. In: Turrill, W. B. *Vistas in Botany*. Pergamon Press, Oxford, England, pp. 387-420.

- Richards, P. W. 1978. The taxonomy of bryophytes. In Street, H. E. (ed.). *Essays in Plant Taxonomy*. London, pp. 177-209.
- Rincòn, E. and Grime, J. P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. *J. Ecol.* 77: 447-455.
- Sagmo Solli, I. M., Söderström, L., Bakken, S., Flatberg, K. I., and Pedersen, B. 1998. Reproductive phenology of *Dicranum majus* in central Norway. *J. Bryol.* 20: 311-321.
- Schuster, R. M. 1966. *The Hepaticae and Anthocerotae of North America*. Vol. 1. Columbia University Press, New York.
- Schuster, R. M. 1988. Ecology, reproductive biology and dispersal of Hepaticae in the tropics. *J. Hattori Bot. Lab.* 64: 237-269.
- Stark, L. R. 1983. Reproductive biology of *Entodon cladorrhizans* (Bryopsida, Entodontaceae). I. Reproductive cycle and frequency of fertilization. *Syst. Bot.* 8: 381-388.
- Stark, L. R. 1984. Introducing phenology. *Evansia* 1: 25-27.
- Stark, L. R. 1985. Phenology and species concepts: A case study. *Bryologist* 88: 190-198.
- Stark, L. R. 1997. Phenology and reproductive biology of *Syntrichia inermis* (Bryopsida, Pottiaceae) in the Mojave Desert. *Bryologist* 100: 13-27.
- Stark, L. R. 2001a. Spore liberation in *Grimmia orbicularis* and *Tortula inermis*: Two patterns from the Mojave desert. *J. Bryol.* 23: 83-90.
- Stark, L. R. 2001b. Widespread sporophyte abortion following summer rains in Mojave Desert populations of *Grimmia orbicularis*. *Bryologist*: 104: 105-125.
- Stark, L. R. 2002a. Phenology and its repercussions on the reproductive ecology of mosses. *Bryologist* 105: 204-218.
- Stark, L. R. 2002b. Skipped reproductive cycles and extensive sporophyte abortion in the desert moss *Tortula inermis* correspond to unusual rainfall patterns. *Can. J. Bot.* 80: 533-542.
- Stark, L. R. 2002c. Phenological Patterns in Desert Mosses. Accessed on 4 November 2002 at <http://www.unlv.edu/faculty/lstark/Phenology.html>
- Stark, L. R. and Castetter, R. C. 1995. Phenology of *Trichostomum perligulatum* (Pottiaceae, Bryopsida) in the Chihuahuan desert. *Bryologist* 98: 389-397.
- Stark, L. R. and Stephenson, A. G. 1983. Reproductive biology of *Entodon cladorrhizans* (Bryopsida, Entodontaceae). II. Resource-limited reproduction and sporophyte abortion. *Syst. Bot.* 8: 389-394.
- Sundberg, S. 2002. Sporophyte production and spore dispersal phenology in *Sphagnum*: The importance of summer moisture and patch characteristics. *Can. J. Bot.* 80: 543-556.
- Sussman, A. S. 1965. Longevity and resistance of the propagules of bryophytes and pteridophytes. In: Ruhland, W. (ed.). *Handbuch der Pflanzenphysiologie XV: Differenzierung und Entwicklung* 15(2): 1086-1093.
- Taylor, J. and Hollensen, R. H. 1984. Sexual reproductive cycle of the liverwort *Conocephalum conicum*. *Mich. Bot.* 23: 77-85.
- Terui, K. 1981. Growth and gemma-cup formation in relation to archegoniophore protrusion in *Marchantia polymorpha* L. *Ann. Rept. Fac. Ed. Iwate Univ.* 40: 19-28.
- Towle, P. M. 1905. Notes on the fruiting season of *Catharinea*. *Bryologist* 8: 44-45.
- Trynoski, S. E. and Glime, J. M. 1982. Direction and height of bryophytes on four species of northern trees. *Bryologist* 85: 281-300.
- Wijk, R. Van der 1960. De Periodiciteit in de Ontwikkeling der Bladmossen. *Buxbaumia* 14(3/4): 25-39.
- Zander, R. H. 1979. Patterns of sporophyte maturation dates in the Pottiaceae (Bryopsida). *Bryologist* 82: 538-558.
- Zanten, B. O. van 1976. Preliminary report on germination experiments designed to estimate the survival chances of moss spores during aerial trans-oceanic long-range dispersal in the Southern Hemisphere, with particular reference to New Zealand. *J. Hattori Bot. Lab.* 41: 133-140.
- Zanten, B. O. van 1992. Distribution of some vulnerable epiphytic bryophytes in the north of the province of Gröningen, The Netherlands. *Biol. Conserv.* 59: 205-209.
- Zanten, B. O. van and Gradstein, S. R. 1988. Experimental dispersal geography of neotropical liverworts. *Beih. Nova Hedw.* 90: 41-94.
- Zanten, B. O. van and Pocs, T. 1981. Distribution and dispersal of bryophytes. *Adv. Bryol.* 1: 479-562.
- Zehr, D. R. 1979. Phenology of selected bryophytes in southern Illinois. *Bryologist* 82: 29-36.