CHAPTER 4-2

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

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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, with permission.

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 and examine how habitat and geography influence the timing.

Patterns

Stark (2002a) has compiled patterns of temperate zone phenology based on publications of a few bryophytes [***Pohlia*** (Figure 2) in UK, ***Ptychomitrium*** (Figure 3) in Japan, ***Grimmia laevigata*** (Figure 4) in Spain, ***Bryum argenteum*** (Figure 88) in UK, ***Polytrichum juniperinum*** (as ***P. alpestre***; Figure 5) in UK, ***Forsstroemia producta*** (Figure 6) 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)
3. Fertilization occurs in summer, lasting two weeks to several months.

Figure 2. ***Pohlia nutans*** with capsules, in a genus used to represent phenology of UK mosses. Photo by Bob Klips, with permission.

Figure 3. ***Ptychomitrium gardneri*** with capsules, in a genus used to represent phenology of Japanese mosses. Photo by Li Zhang, with permission.

Figure 4. ***Grimmia laevigata***, a species in a genus used to represent phenology of Spanish mosses. Photo by Sharon Pilkington, with permission.

Figure 5. ***Polytrichum juniperinum*** with antheridial splash cups, a species used to represent phenology of UK mosses. Photo by Ian Sutton, through Creative Commons.

Figure 6. ***Forsstroemia producta***, a species used to represent phenology of eastern USA mosses. Photo from Earth.com, with permission.

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 7) extends throughout the entire year (de Oliveira & Pôrto 2001). In the desert, both gametangial initiation and fertilization in ***Trichostomum sweetii*** occur in the autumn and winter (Stark & Castetter 1995).

Figure 7. Epiphytic moss ***Sematophyllum subpinnatum*** in Brazil. Photo by Michael Lüth, with permission.

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:

1. Fertilization in spring and summer with continuous development; spore dispersal anywhere from early summer to the following spring; suitable for a mild climate.
2. 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.
3. 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.
4. Fertilization in winter/spring with embryos forming first winter; dormancy in summer; sporophyte maturation second winter; known in several desert species.
5. Annual species, sporophyte development within two months; fertilization at various times of year – flexible.
6. 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, **Pleuroweisieae** in midyear, **Barbuleae** are bimodal, **Pottieae** 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_3 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 27; 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 8). Other taxa, adapted to full sun, may be more productive in summer. This is the case in ***Polytrichum juniperinum*** (as ***P. alpestre***; Figure 9), 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.

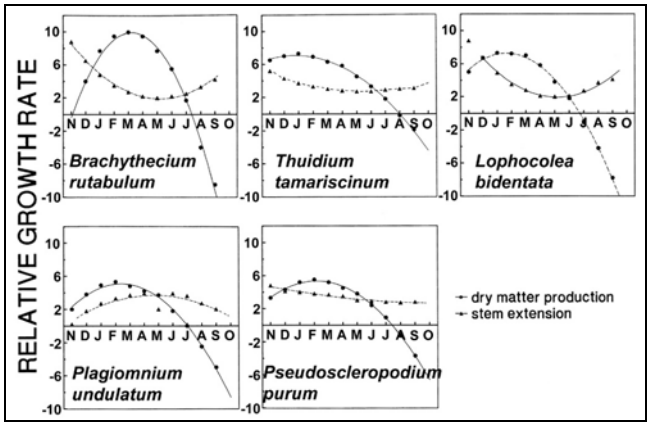

Figure 8. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime (1989).

Where winters are mild, growth may occur throughout the winter. In Japan Imura and Iwatsuki (1989) found that male plants of ***Trachycystis microphylla*** (Figure 10) 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.

Figure 9. ***Polytrichum juniperinum*** with yellowish calyptrae emerging. Photo by Janice Glime.

Figure 10. ***Trachycystis microphylla***, a species in which male and female plants elongate at different times. Photo by Li Zhang, with permission.

Epiphytes may take advantage of decreased desiccation and temperature in winter. Pitkin (1975) found the greatest growth of ***Hypnum cupressiforme*** (Figure 11), ***Platygyrium repens*** (Figure 12), ***Neckera pumila*** (Figure 13), ***Isothecium myosuroides*** (Figure 14), and ***Homalothecium sericeum*** (Figure 15) in November to January in Oxfordshire, UK, corresponding to highest rainfall and mean temperatures below 10ºC 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 ability to grow in winter when protection and moisture were available in the space between snow and tree trunk.

Figure 11. ***Hypnum cupressiforme*** in its epiphytic habitat. Photo by Dick Haaksma, with permission.

Figure 12. ***Platygyrium repens*** with bulbils, a species with most of the growth in November to January in Oxfordshire, UK. Photo by Claire Halpin, with permission.

Figure 13. Epiphytic habitat of ***Neckera pumila***. Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Isothecium myosuroides*** on tree at Swallow Falls, Wales. Photo by Janice Glime.

Figure 15. ***Homalothecium sericeum***, a species with most of the growth in November to January in Oxfordshire, UK. Photo by Kristian Peters, through Creative Commons.

Furness and Grime (1982) show strong seasonal effects of temperature that help to explain the phenology of some bryophytes (Figure 16). These results are consistent with peaks of growth in spring and autumn in British tall herb communities. 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 17) growth of rhizoids peaks at 12ºC, branches at 15ºC, and stems at 20ºC.

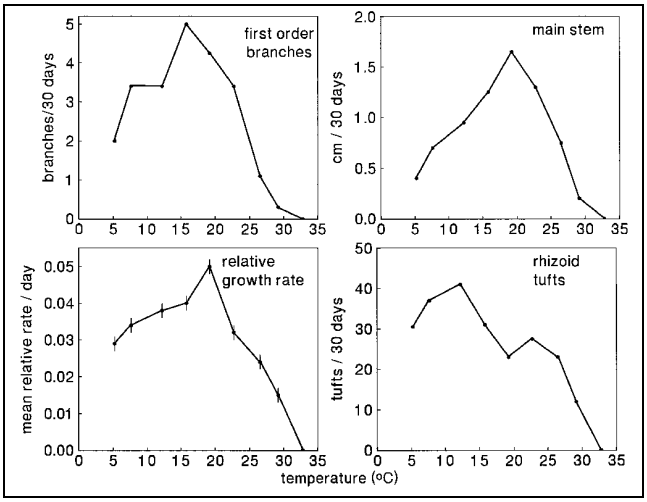

Figure 16. Effects of lab temperature on growth of branches, stems, and rhizoids of ***Brachythecium rutabulum*** (Figure 17) and relative growth rate among 9 growth temperatures under conditions of constant humidity. Redrawn from Furness & Grime 1982.

This difference in temperature, and thus timing of life processes, is consistent with observations on ***Fontinalis*** organs (Glime 1980, 1982, 1987b) and suggests that the bryophyte apportions its limited photosynthate to different activities at different times. This conserves energy and permits directing that energy into the needed structures. In ***Fontinalis***, we can presume that the timing is advantageous because the rhizoids (Figure 18) 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*** (Figure 19) 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 20). Timing of gametangial production must permit the gametes to be splashed from plant to plant without having these structures submersed where they will be carried away by the moving water in streams.

Figure 17. ***Brachythecium rutabulum***. Photo by Michael Lüth, with permission.

Figure 18. ***Fontinalis antipyretica*** wound rhizoids. Photo by Janice Glime.

Figure 19. ***Fontinalis antipyretica***; at least some members of ***Fontinalis*** have maximum growth and branching during the season of maximum runoff. Photo by Claire Halpin, with permission.

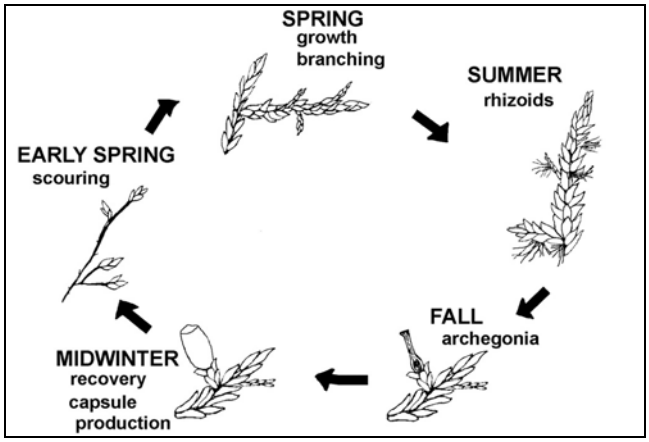

Figure 20. Phenological cycle of growth and reproduction in ***Fontinalis dalecarlica*** and ***F. novae-angliae***. Drawings by Janice Glime.

Many bryophytes, such as ***Eurhynchium praelongum*** (Figure 21), 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*** (Figure 22) 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.

Figure 21. ***Eurhynchium praelongum*** Bicton Common England. Photo by Janice Glime.

Figure 22. ***Pleurozium schreberi***, a moss that spends its winter under snow and resumes growth when the snow melts. Photo by Janice Glime.

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; Figure 23) 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.

Figure 23. ***Syntrichia ruralis*** benefitting from the rain. Photo courtesy of Peggy Edwards.

Other species in these temperate climates lack seasonal growth peaks. Benson-Evans and Brough (1966) found that ***Funaria hygrometrica*** (Figure 54) initiated new leafy shoots continuously throughout the year in South Wales, reaching their maximum height of about 5 mm in 10 weeks (Figure 27). 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*** (Figure 24) could grow at most normal temperatures above 0ºC, but that moisture was the primary determinant in that range. Li (1991) found that 30-35ºC was optimum for growth of the hummock-dwelling ***Sphagnum papillosum*** (Figure 25) and ***S. divinum*** (Figure 26) when adequate water was available.

Figure 24. ***Sphagnum fuscum***, a hummock species that grows well at most temperatures above 0ºC, but that is water limited. Photo by Martina Poeltl, through Creative Commons.

Figure 25. ***Sphagnum papillosum***, a hummock species with optimum growth at 30-35ºC. Photo from Botany Website, UBC, with permission.

Figure 26. ***Sphagnum divinum***, a hummock species with optimum growth at 30-35ºC. Photo by Kjell Ivar Flatberg, through Creative Commons.

In South Wales, ***Atrichum undulatum*** (Figure 1) becomes dormant in late summer and begins growth again in January (Figure 27). Benson-Evans & Brough 1966). Different clones of this species can have different growth periods. In ***Funaria hygrometrica*** (Figure 54), growth can begin from new plants in any month of the year and is relatively continuous (Figure 27).

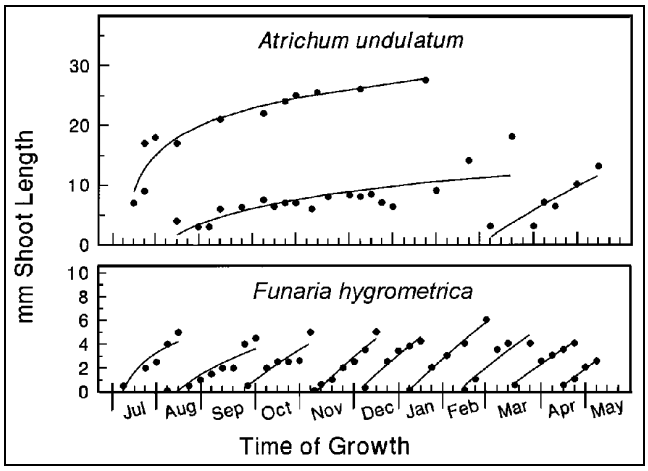

Figure 27. Contrast in vegetative growth periods for two bryophyte species in South Wales. ***Atrichum undulatum*** (Figure 1) becomes dormant in late summer and begins growth again in January. The three curves follow three different sets of plants. In ***Funaria hygrometrica***, growth can begin from new plants in any month of the year and is relatively continuous. Redrawn from Benson-Evans and Brough (1966).

The leafy liverwort ***Lophozia silvicola*** (Figure 28) seemed to exhibit no change in shoot density during the growing season (Laaka-Lindberg 1999). Measurements on liverworts are rare, and for the many very small species, very difficult.

Figure 28. ***Lophozia silvicola*** with gemmae, a species that does not seem to change shoot density during the growing season. Photo by Štěpán Koval, with permission.

One factor that may play a role in seasonal changes in growth is chlorophyll concentration. Valanne (1984) felt chlorophyll concentrations did not change seasonally. On the other hand, Raeymaekers and Glime (1986) found that

chlorophyll concentrations in ***Pleurozium schreberi*** (Figure 22) were slightly higher in summer than in early spring or late autumn. This is not surprising as the plants are shielded from light by snow in winter, thus being unable to replace chlorophyll. The heat and drought of summer can likewise reduce the ability to replace damaged chlorophyll. Habitats can affect the seasonal changes in chlorophyll content of bryophytes. For example, the forest species ***Brachythecium rutabulum*** (Figure 17) has seasonal chlorophyll changes (Kershaw & Webber 1986), increasing as the summer progresses and the light penetration decreases. Epiphytic bryophytes likewise respond to the decreasing light penetration through the canopy (Miyata & Hosokawa 1961). For the aquatic moss ***Fontinalis*** (Figure 29), both light intensity and temperature may play a role in the observed seasonality of chlorophyll content (Bastardo 1980).

Figure 29. ***Fontinalis antipyretica***, a moss that grows in cooler weather. Photo by Andrew Spink, with permission.

Growth in most bryophytes is limited by water availability, with light, nutrients, and temperature playing lesser roles. Most grow best at temperatures below 25ºC 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. Chlorophyll concentrations respond to changes in light intensity – a seasonal phenomenon.

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*** (Figure 30-Figure 31), ***Pohlia*** spp. (Figure 32)]. In fact, they may be more common than we supposed, as noted by researchers on ***Orthotrichum*** (BFNA 2007; Figure 33). 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*** (Figure 34) does not produce gemma cups while it is producing sexual reproductive structures. This is demonstrated by the suppression of gemma 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 (Figure 35) and female gametangia or sporophytes (Figure 36) at the same time. Thus, we can in many cases surmise their phenology as those seasons when sexual reproduction is not occurring.

Figure 30. ***Plagiothecium cavifolium***, a species with brood bodies year-round. Photo by Bob Klips, with permission.

Figure 31. ***Plagiothecium cavifolium*** with axillary brood bodies that are present year-round. Photo by Bob Klips, with permission.

Figure 32. ***Pohlia annotina*** with bulbils that remain throughout the life cycle. Photo by Hermann Schachner, through Creative Commons.

Figure 33. Gemmae (dark spots on leaves) that are present throughout the life cycle on ***Orthotrichum obtusifolium***. Photo by Michael Lüth, with permission.

Figure 34. ***Marchantia polymorpha*** with gemmae cups and antheridiophores present on different plants. Photo by Claire Halpin, with permission.

Figure 35. ***Tetraphis pellucida*** with gemmae cups, a stage that does not co-occur with sexual structures. Photo by Stefan Gey, through Creative Commons.

Figure 36. ***Tetraphis pellucida*** with capsules, a stage in which gemmae cups do not form. Photo by Bob Klips, with permission. Note spent gemmae cups on left, topping plants with no sporophytes.

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*** (Figure 28) had gemmae throughout the sampling period of May to October in southern Finland, but their peak months were July through September (Figure 37; Laaka-Lindberg 1999; Laaka-Lindberg & Heino 2001).

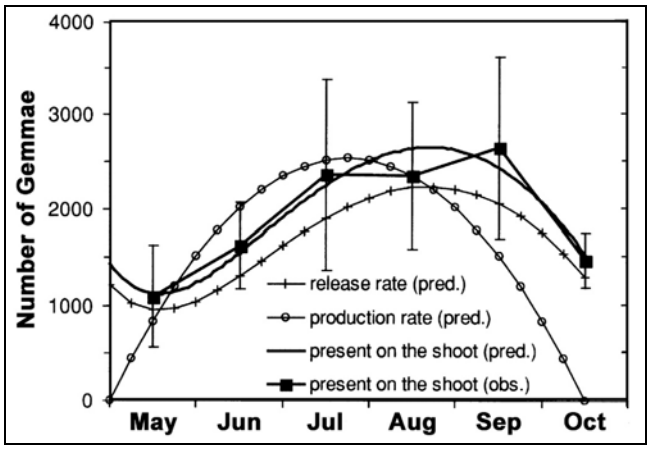

Figure 37. Model predictions (pred.) and observed behavior of gemmae from five colonies of ***Lophozia silvicola*** in southern Finland in 1997-1999. Redrawn from Laaka-Lindberg & Heino (2001).

Laaka-Lindberg (1999) found that gemmae of ***Lophozia silvicola*** (Figure 28) was highest in early spring, declining rapidly as the end of the growing season approached. Laaka-Lindberg and Heino (2001) suggested that there is a seasonal dormancy in gemmae of ***L. 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.

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 emarginata*** (Figure 38) 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.

Figure 38. ***Marchantia emarginata*** with gemmae. Photo by 楊玉鳳, through Creative Commons.

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*** (Figure 39) exhibit distinct seasonal production of gemmae (Odu & Owotomo 1982). Reese (1984) found a striking seasonality in ***Syrrhopodon texanus*** (Figure 40), 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.

Figure 39. ***Calymperes tenerum*** with gemmae in a genus where at least some gemma production is seasonal. Photo by Damon Tighe, through Creative Commons.

Figure 40. ***Syrrhopodon texanus***, a moss with seasonal gemma production that peaks in September in the Gulf coast, USA. Photo by Janice Glime.

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*** (Figure 41). 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 μmol/m^2/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.

Figure 41. ***Physcomitrella patens*** with capsules; growth diminishes while capsules are maturing. Photo by Michael Lüth, with permission.

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*** (Figure 42) 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.

Figure 42. ***Sphagnum palustre*** with capsules. Photo by Andrew Hodgson, with permission.

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*** (Figure 29) 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. ***Fossombronia longiseta*** (Figure 43) has mature archegonia and antheridia there in November and December (Haupt 1929b).

Figure 43. ***Fossombronia longiseta***, a species that has successful fertilization in November and December in California, USA. Photo by D. L. Bowls, through Creative Commons.

In Japan, Deguchi and Yananose (1989) found that ***Pogonatum neesii*** (Figure 44) 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.

Figure 44. ***Pogonatum neesii*** with capsules, a species that initiates antheridia in early November in Japan, with them maturing in mid April. Photo by Siddarth Machado, through Creative Commons.

Then there are bet hedgers. ***Dicranum majus*** (Figure 45) 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 45. Immature sporophytes of ***Dicranum majus***. Photo by Michael Lüth, with permission.

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*** and ***Pogonatum inflexum*** (Figure 46) in Japan, Imura (1994) found that shoot production of male plants preceded that of females by about four months (Figure 47). Likewise, antheridia production preceded that of archegonia, but antheridia took longer to develop. Similar differences occur in ***Atrichum androgynum*** (Figure 46), with antheridia beginning development in spring after the sporophytes reach maturity (Biggs and Gibson 2006). Archegonia begin development one month later. Development of the sporophyte takes 12 months, with spores being released in the spring. In four species of ***Ptychomitrium*** (Figure 3) in Japan, Deguchi and Takeda (1986) found that antheridia typically required 9 months whereas archegonia required only 1 month to develop, with both maturing in the June rainy season.

Figure 46. ***Pogonatum inflexum***, a species in which production of male shoots precedes that of female shoots by four months in Japan. Photo by Harum Koh, through Creative Commons.

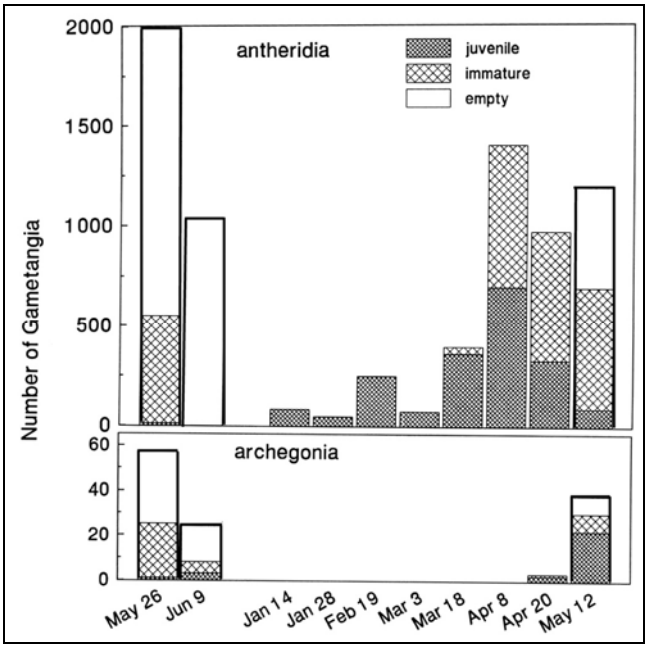

Figure 47. Maturation dates of antheridia and archegonia of ***Atrichum rhystophyllum*** at Miyajima Island, Japan, during 1987-1988. Samples included 1-10 individuals. Based on table by Imura (1994).

In the functionally dioicous ***Pleurozium schreberi*** (Figure 22) 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*** (Figure 48) antheridia mature about one month before the archegonia, perhaps insuring that sperm will be available when proper conditions for fertilization occur.

Figure 48. ***Mnium hornum*** from Europe. Photo by Michael Lüth, with permission.

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*** (Figure 49), female clones developed gametangia maximally at 3500 lux continuous light at *p*H 5.5 (Gupta *et al*. 1991). However, male plants failed to produce antheridia at *p*H 3.5 or 5.5 at any light intensity in the experiment.

Figure 49, ***Riccia discolor***, a species in which light intensity signals time to develop female clones. Photo by Jan Ševčik, through Creative Commons.

The longer development time for antheridia is common. For example, in Australia ***Dicranoloma menziesii*** (Figure 50) and ***D. platycaulon*** **(**Figure 51**)** 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. billardierei*** (Figure 52), 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. billardierei*** 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. billardierei*** and ***D. platycaulon***, but only 12 months in ***D. menziesii***.

Figure 50. ***Dicranoloma menziesii***, a species that initiates antheridia in winter and archegonia in spring. Photo by John Walter, through Creative Commons.

Figure 51. ***Dicranoloma platycaulon***, a species that initiates antheridia in winter and archegonia in spring. Photo by Emily Roberts, through Creative Commons.

Figure 52. ***Dicranoloma billardierei, a species that*** initiates its antheridia during late spring-summer and its archegonia in autumn. Photo by Michael Lüth, with permission.

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*** (Figure 56), 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*** (Figure 53), Egunyomi (1979) in ***Octoblepharum albidum*** (Figure 102). 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*** (Figure 54) and ***Atrichum undulatum*** (Figure 53). [***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).

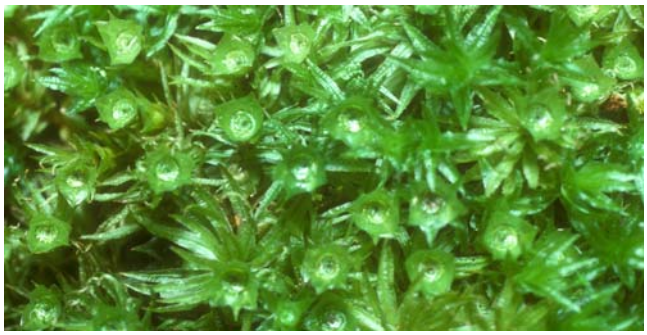

Figure 53. Male plants with splash cups on ***Atrichum undulatum***. Photo by Janice Glime.

Figure 54. ***Funaria hygrometrica*** with young sporophytes in Europe. Photo by Michael Lüth, with permission.

Even in the dioicous perennial moss ***Forsstroemia trichomitria*** (Figure 55), gametangial maturation is protogynous (Stark 1985). On the other hand, Greene (1960) was surprised to find that in perennial moss ***Brachythecium rutabulum*** (Figure 17) 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*** (Figure 88), 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).

Figure 55. ***Forsstroemia trichomitria*** with capsules, a species that develops female organs first. Photo by Jennifer Doubt, through Creative Commons.

Some monoicous mosses may benefit, or at least survive, with self-fertilization. In the Chihuahuan Desert, on ***Trichostomum planifolium*** 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.

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 56) through abortion of sporophytes, much like the abortion of fruits in *Asclepias* (milkweed). 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 56. 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*** (Figure 35-Figure 36) produces capsules in spring (Figure 36), whereas gemmae with gemma cups (Figure 35) are produced after spores are shed. In ***Atrichum undulatum*** (Figure 1), 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*** (Figure 102), 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 ***Pylaisia polyantha*** (Figure 57) to ***Hypnum cupressiforme*** var. ***resupinatum*** (Figure 58) (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 ***Ulota*** in Great Britain (Jones 1946). ***Ulota intermedia*** (Figure 59) capsules mature in July-August, ***U. crispa*** (Figure 60) in spring, and ***U. bruchii*** (Figure 61) in winter, suggesting that season of dehiscence may not be critical for these taxa in this particular location.

Figure 57. Dehisced sporophytes and seta spikes representing two cohorts present at the same time in ***Pylaisia polyantha***. Photo by Michael Lüth, with permission.

Figure 58. ***Hypnum cupressiforme*** var. ***resupinatum***, an epiphyte in the British Isles that begins sporophyte development in July-August and disperses spores in January. Photo by Claire Halpin, with permission.

Figure 59. ***Ulota intermedia*** with capsules that mature in July-August in Great Britain. Photo by Michael, through Creative Commons.

Figure 60. ***Ulota crispa*** growing epiphytically. ***Ulota intermedia*** and ***U. crispa*** have different capsule maturation dates in summer vs spring, respectively. Photo by Janice Glime.

Figure 61. ***Ulota bruchii***, a species where capsules mature in winter. Photo by Michael Lüth, with permission.

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 and ter Horst 1983; During 1986; van Zanten & Gradstein 1988; van Zanten 1992; During 1997; Frahm 2002).

In ***Sphagnum*** (Figure 42), 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*** (Figure 62), 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, ***Marchantia chenopoda*** (Figure 63), sporophytes mature earlier, in late spring to early summer (Moyá 1992), suggesting that temperature may be a signal.

Figure 62. ***Marchantia polymorpha*** with young and older archegoniophores. Photo by Claire Halpin, with permission.

Figure 63. ***Marchantia chenopoda*** females, Maraquez Mountain, Puerto Rico, 5 January 1991; in the tropics the sporophytes mature in late spring to early summer. Photo by Janice Glime.

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 64). Capsules matured mostly May - June or October - November (Figure 64). 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.

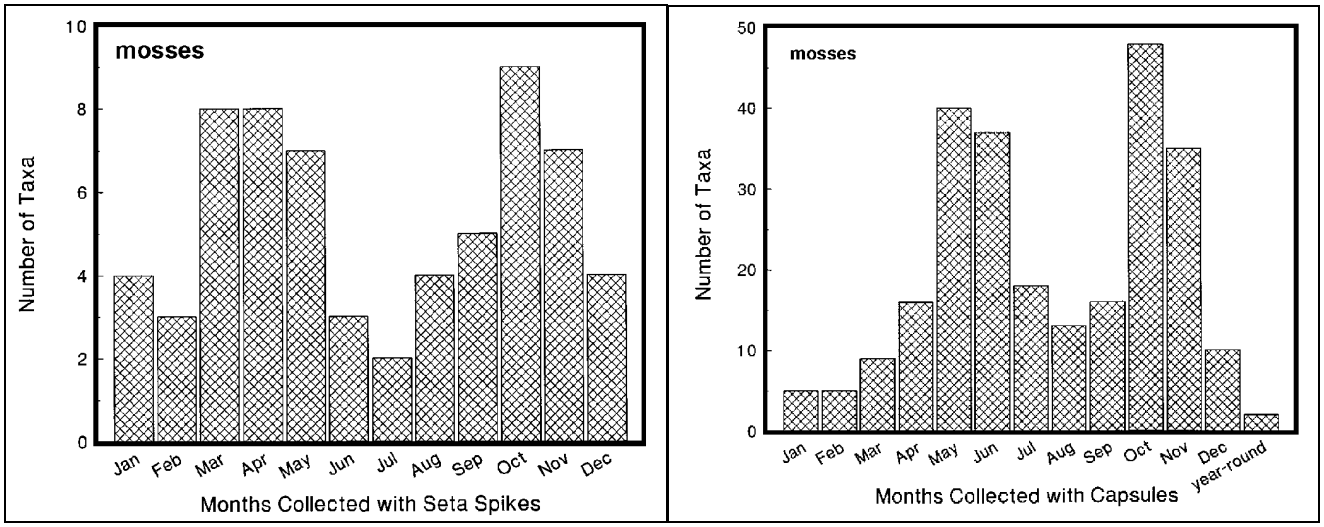

Figure 64. **Left:** Numbers of moss taxa with young setae ("spikes") per month among the 33 taxa that had spikes. **Right:** Numbers of taxa per month with capsules. Study based on 232 species of Iowa mosses in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Lackner (1939) showed capsule and spore maturation times of 182 species in East Prussia. Capsules are present mostly from May to September, contrasting with the summer low reported by Conard (1947) for Iowa, USA. 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 65 and indicate that 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 65).

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 capusule	(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)

Anomodon viticulosus
Atrichum undulatum
Barbula unguiculata
Brachythecium albicans
B. populeum
B. rutabulum
B. velutinum
Bryum argenteum
Buxbauhmia aphylla
Climacium dendroides
Dicranella rufuscens
Dicranella sp.
Didymodon fallax
Discelium nudum
Entodon sp.
Eurhynchium hians
E. striatum
Fissidens bryoides
F. taxifolius
Hedwigia ciliata
Homalia trichomanoides
Homalothecium lutescens
Hylocomium splendens
Hypnum cupressiforme
Leucodon sciuroides
Phascum cuspidatum
Pogonatum urnigerum
Racomitrium heterostichum
Rhizomnium punctatum
Rhynchostegium murale
Rhytidiadelphus squarrosus
R. triquetrus
Schistidium apocarpum
Tetraphis pellucida
Thamnium alopecurum

(b)

Amblystegium serpens
A. subtile
Aulacomnium palustre
Bartramia ithyphylla
Bryum caespiticium
B. pallens
B. warneum
Calliergon cordifolium
Calliergonella cuspidatum
Ceratodon purpureus
Cratoneuron filicinum
Dicranum scoparium
Distichium capillaceum
Encalypta vulgaris
Helodium blandowii
Herzogiella striatella
Homalothecium nitens
Hygrohypnum luridum
Leptobryum pyriforme
Leptodictyum riparium
Mnium hornum
M. marginatum
Physcomitrium pyriforme
Plagiomnium affine
P. cuspidatum
P. medium
P. rostratum
P. undulatum
Plagiothecium cavifolium
P. curvifolium
P. nemorale
Pohlia nutans
Polytrichum commune
P. formosum
P. juniperinum
P. piliferum
Sanionia uncinata
Splachnum ampullaceum
Syntrichia ruralis
Syntrichia subulata
Tortula muralis
Warnstorfia fluitans

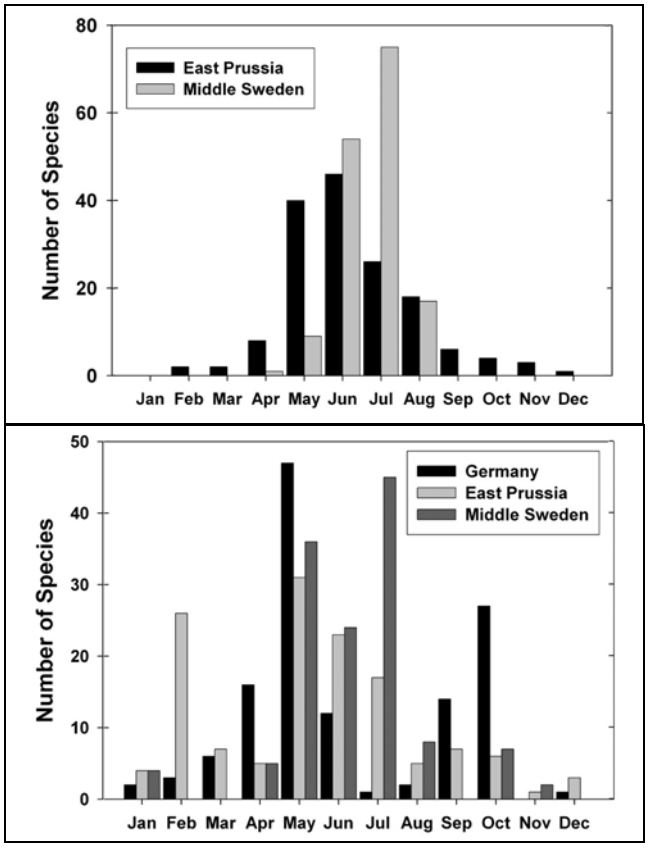

Figure 65. **Top:** Months of capsule appearance in two locations in Europe. **Bottom:** Months of spore ripening in three countries in Europe. Redrawn from Lackner (1939).

As in mosses, Conard (1947) found that the months with the greatest number of mature liverwort capsules were April - June and September - October (Figure 66). Bray (pers. comm.) found that ***Fossombronia foveolata*** (Figure 67) 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.

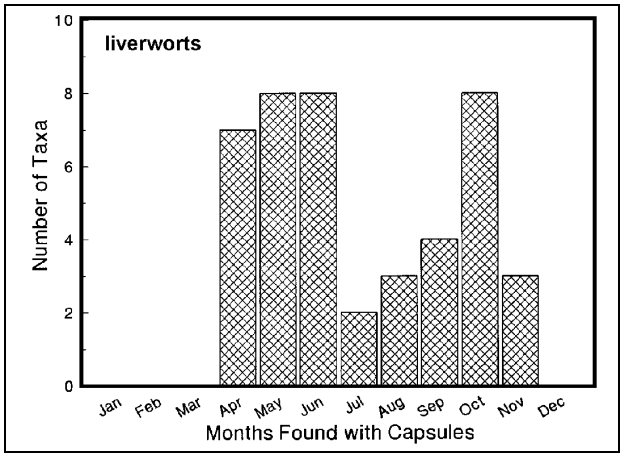

Figure 66. Numbers of liverwort taxa with capsules per month among 30 taxa with capsules out of 60 Iowa liverwort taxa (including Anthocerotopsida) in herbaria. Based on Conard 1947.

Figure 67. ***Fossombronia foveolata*** with capsules, a species that produces capsules in both spring and fall. Photo by Sharon Pilkington, with permission.

In the mild climate of California, USA, the thallose liverwort ***Asterella californica*** (Figure 68) 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 68. ***Asterella californica*** mature females with capsules ready to emerge. Photo by Peter J. Bryant, with permission.

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; Figure 69-Figure 70) and the maximum to be for ***Grimmia ovalis*** (24 months; Figure 71). Crum (2001) reports ***Polytrichum*** (Figure 72) to require 13 months and ***Dicranum*** (Figure 45) 17 months. These times differ with geographic location and may depend on such factors as length of growing season, temperature, and water availability. 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 (Figure 74).

Figure 69. ***Atrichum androgynum***, a perennial species with a rapid sporophyte development. Photo by Niels Klazenga, through Creative Commons.

Figure 70. ***Atrichum tenellum*** capsules that are able to develop in 4 months. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Grimmia ovalis*** with both immature and spent capsules that take 24 months to develop. Photo from Earth.com, with permission.

At least in the temperate zone, the spring and autumn maturation times may follow a long development, as found in ***Polytrichum*** (Figure 9, Figure 72) – 7-16 months in Scandinavia, 9-20 months in Sweden (Arnell 1905), and ***Forsstroemia trichomitria*** (Figure 55) – 17 months (Stark 1984), or 15 months for ***P. juniperinum*** (Figure 9, Figure 72) in the Antarctic (Longton 1972). In others, such as ***Mnium hornum*** (Figure 48, Figure 73), the seta emerges (Figure 73) 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.

Figure 72. ***Polytrichum juniperinum*** capsules with calyptra, a species in which capsules take 15 months to develop in the Antarctic; maturation time depends on location. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 73. ***Mnium hornum*** with young sporophytes that are able to overwinter before completing development. Photo by Bob Klips, with permission .

categories of sporophyte development

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

Figure 74. Scheme for representing sporophyte development. Based on Greene 1960; examples from Benson-Evans & Brough 1966.

The capsule cycle of the epiphytic ***Pylaisia polyantha*** (Figure 57) 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*** (Figure 17) 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*** (Figure 75-Figure 76) has mature spores in early winter (Furuki 1992).

Figure 75. ***Mannia fragrans*** with emerging sporophytes. Photo by Samuel Brinker, through Creative Commons.

Figure 76. ***Mannia fragrans*** with nearly mature sporophytes, with mature spores in Japan occurring in winter. Photo by Botanical Wanderer, through Creative Commons.

Lackner (1939) found that ***Orthotrichum*** (Figure 86) 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*** (Figure 77-Figure 78) (Hancock & Brassard 1974). The result is that survival depends on the rapid maturation of the sporophyte in the autumn, permitting the capsules to be dormant during the winter.

Figure 77. Immature sporophytes of ***Buxbaumia aphylla*** in Michigan, USA. Photo by Janice Glime.

Figure 78. ***Buxbaumia aphylla*** mature capsules with one that has been damaged. Photo by Bernd Haynold, through Creative Commons.

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. dalecarlica*** (Figure 79-Figure 80) and ***F. novae-angliae*** (Figure 81) produce capsules in autumn and mature them 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*** (Figure 82-Figure 83) likewise produces its capsules in winter (Grainger 1947).

Figure 79. ***Fontinalis dalecarlica*** with developing capsules in late autumn. Photo by Janice Glime.

Figure 80. ***Fontinalis dalecarlica*** capsules that mature in winter in New Hampshire, USA. Photo by Janice Glime.

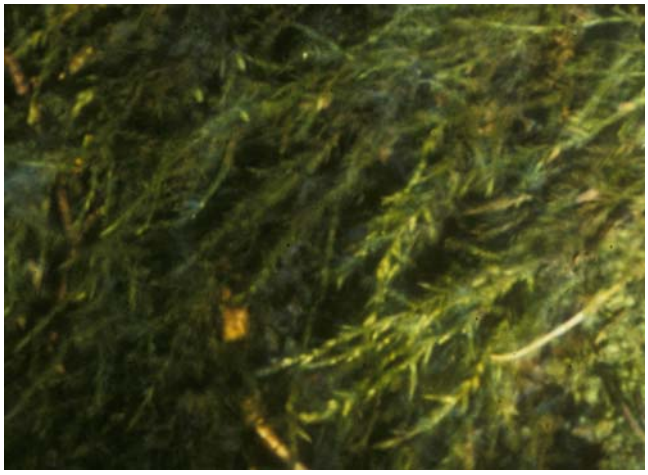

Figure 81. ***Fontinalis novae-angliae*** with young capsules in late autumn. Photo by Janice Glime.

Figure 82. ***Scapania undulata*** with its capsule in winter. Photo by Malcolm Storey <DiscoverLife>, with online permission.

Figure 83. ***Scapania undulata*** with dehiscing capsules. Photo by Malcolm Storey <DiscoverLife>, with online permission.

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 confertum*** (Figure 84), is able to continue development at locations above 1800 meters.

Figure 84. ***Schistidium confertum*** with capsules, a species that is able to continue its development at elevations above 1800 m. Photo by Gordon Rothero, with permission.

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*** (Figure 77-Figure 78) 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 juniperinum*** (as ***P. alpestre***; Figure 9, Figure 72) 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 85). 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.

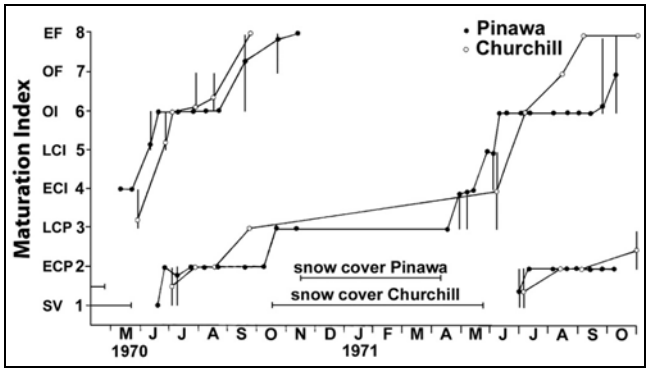

Figure 85. Comparison of sporophyte development of ***Polytrichum juniperinum*** in Pinawa and Churchill, Manitoba, Canada. Points represent the maturity indices with vertical bars indicating the range of stages present. Based on Longton (1979).

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*** (Figure 86). 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*** (Figure 87) and ***Bryum argenteum*** (Figure 88) (Pedersen & Hedenäs 2002) and the liverwort ***Mannia fragrans*** (Figure 75-Figure 76) in Japan (Furuki 1992). In the seasonally dry interior of North America, ***Syrrhopodon texanus*** (Figure 40) 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.

Figure 86. ***Orthotrichum anomalum*** with capsules. Photo by Claire Halpin, with permission.

Figure 87. ***Anomobryum julaceum*** with dry capsules that disperse spores in winter. Photo by David T. Holyoak, with permission.

Figure 88. Capsules on ***Bryum argenteum***. Photo by Michael Lüth, with permission.

Using herbarium specimens, Nishimura (1993) determined the dates of dispersal for mosses from the Hiruzen Highlands on the island of Honshu, Japan (Figure 90). 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*** (Figure 88) dispersed in both spring and autumn. ***Sematophyllum subhumile*** (Figure 89) 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 89. ***Sematophyllum subhumile*** with capsules, a species for which dispersal is not seasonal. Photo by Geoff Bryne, through Creative Commons.

Egunyomi (1979) found that capsules of ***Octoblepharum albidum*** (Figure 102) 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*** (Figure 22) 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.

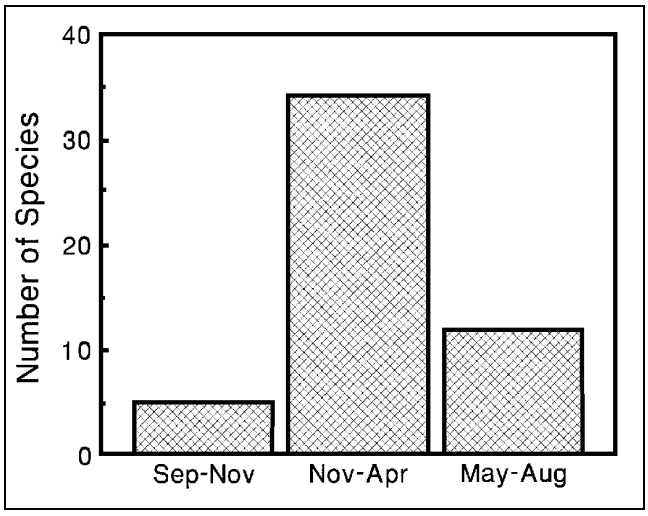

Figure 90. Seasons of dispersal in 51 species of mosses from the Hiruzen Highlands, Honshu, Japan. From data of Nishimura (1993).

To determine the availability of spores, Fenton and Bergeron (2006) studied the spore dispersal of ***Sphagnum*** (Figure 91) species in a black spruce (***Picea mariana***) forest (Figure 92) in Québec, Canada. Using spore traps, they determined the phenology of spore dispersal (Figure 93) 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 91. ***Sphagnum fallax*** with capsules that disperse spores in July-August in Québec, Canada. Photo by James K. Lindsey, with permission.

Figure 92. Spruce peatland, where spore dispersal in Ontario begins in July, rises in mid August, and ends mid to late September, with peak dispersal near the beginning of September. Photo by Richard Norby, Oak Ridge National Laboratory, with permission.

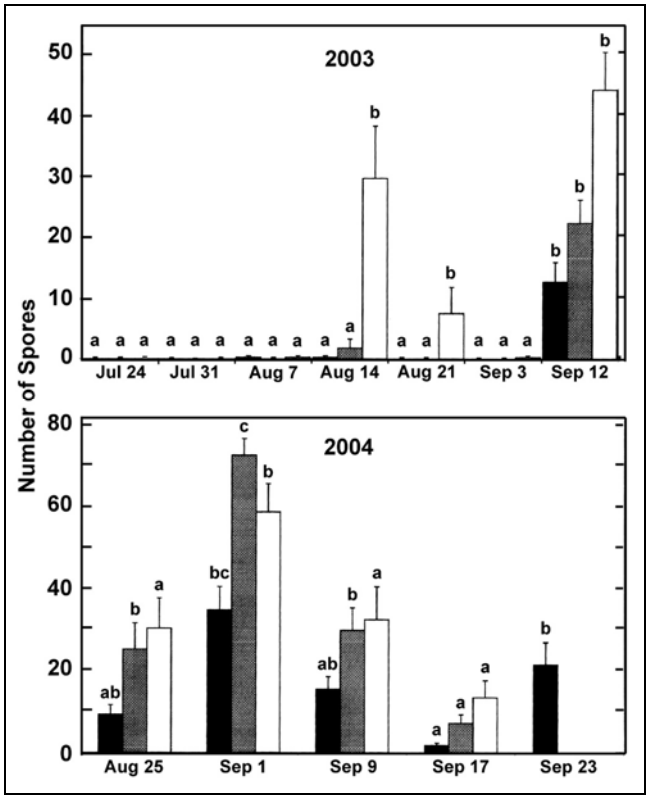

Figure 93. Number of spores collected in 20 spore traps at each of three sites in Québec, Canada. Vertical bars represent standard error. Different letters indicate those values that are significantly different within a site. Redrawn from Fenton & Bergeron (2006).

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, *e.g.* ***Buxbaumia***, where sexual organs are produced directly on the protonema, field knowledge is lacking. After extensive study of ***Buxbaumia aphylla*** (Figure 77-Figure 78) 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*** (Figure 4, Figure 71) may even require a drought period before advancing to the next stage (During, pers. comm.). In fact, Johnsen (1969) found that in ***Orthotrichum anomalum*** (Figure 86) 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*** (Figure 50-Figure 52), 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.

For ***Entodon cladorrhizans*** (Figure 56) growing in Pennsylvania, USA, the fertilization period lasts five weeks (Stark 1983). In the desert moss ***Syntrichia inermis*** (Figure 94), 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 (Figure 91) 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 94. ***Syntrichia inermis*** in its dry state beneath shrubs. Photo courtesy of Lloyd Stark.

But other mosses may have quite extensive periods of sporophyte development. In ***Dicranoloma***, ***D. billardierei*** (Figure 52) and ***D. platycaulon*** (Figure 51) required 18-24 months whereas those of ***D. menziesii*** (Figure 50) required only 12 (Milne 2001). ***Atrichum androgynum*** (Figure 46) likewise requires 12 months for sporophyte maturation (Biggs & Gibson 2006).

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	reference
Atrichum undulatum	UK	Jan-Feb	Apr-May	May-Jun	Jan-May	Miles *et al*. 1989
Polytrichum juniperinum (= *P. alpestre*)	UK	Sep-Oct	Mar-Apr	Jun	Jun-Jul	Miles *et al*. 1989
Bryum argenteum	UK	Oct-Nov	Apr-Jun	Apr-Jun?	Jan-May	Miles *et al*. 1989
Grimmia pulvinata	UK	most of yr	most of yr	most of yr	Apr-Jun	Miles *et al*. 1989
Tortula muralis	UK	anytime	anytime	anytime	Apr-Jun	Miles *et al*. 1989
Pellia epiphylla	UK	Jan-Jun	Jun	Jun	Mar-Jun	Clapham & Oldroyd 1936
Cephalozia	UK	Feb	Mar	May	?	Clapham & Oldroyd 1936
Marchantia polymorpha	UK	Mar-Apr	Mar-Apr	May	Aug	Clapham & Oldroyd 1936
Aplozia	UK	Apr	May	Jun	May	Clapham & Oldroyd 1936
Conocephalum conicum	UK	Apr-Jun	Jun-Jul	Jul	Mar-Apr	Clapham & Oldroyd 1936
Conocephalum conicum	MI, USA	Aug	Aug	Jun	Apr	Taylor & Hollensen 1984
Diplophyllum	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936
Scapania	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936

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 ***Racopilum africanum*** (Figure 95), ***Fissidens weirii***, ***Thuidium gratum***, and ***Stereophyllum*** sp. (Figure 101) 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*** (Figure 94), 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*** (Figure 97-Figure 98) 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).

Figure 95. ***Racopilum africanum*** with young sporophytes. In this species, gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo by Jan-Peter Frahm, with permission.

Figure 96. ***Stereophyllum radiculosum***, one of the mosses where gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo from Missouri Botanical Garden, with permission.

Figure 97. Rock-dwelling ***Grimmia orbicularis***. Photo by Michael Lüth, with permission.

The perennial moss ***Entodon cladorrhizans*** (Figure 56) requires six to nine months for the sporophyte to mature (Stark 1983).

Figure 98. Capsule of ***Grimmia orbicularis***. Photo by Michael Lüth, with permission.

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 μm 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*** (Figure

82-Figure 83) produces gametangia and accomplishes fertilization in winter (Grainger 1947).

On the other hand, Imura and Iwatsuki (1989) found that in ***Trachycystis microphylla*** (Figure 99) 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.

Figure 99. ***Trachycystis microphylla***. Photo by Li Zhang, with permission.

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*** (Figure 100) 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 ant thawing in autumn.

Figure 100. ***Bazzania trilobata***, a species that has the most essential oils in September and lowest in January. Photo by John Garrett, through Creative Commons.

Geographical Differences within Species

Earlier studies by Richards (1959) indicate that seasonal behavior of bryophytes may vary in different climatic regions. 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*** (Figure 88) 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*** (Figure 101), 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).

Figure 101. ***Lunularia cruciata***, a long-day plant in Wales but a short-day plant in Israel. Photo by David Holyoak, with permission.

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 confertum*** (Figure 84), however, lives at elevations above 1800 m but, like lowland taxa, has no dormant period in winter.

The example of ***Funaria hygrometrica*** (Figure 54), 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 bryophytes may have greater physiological variability than do tracheophytes, enabling individual species to occupy wider ranges of conditions than those of their tracheophyte counterparts. These adaptations permit bryophytes to conserve energy and to optimize it across time.

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 because the advantages of seasons vary 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*** (Figure 95), ***Fissidens glauculus***, ***Thuidium gratum***, and ***Stereophyllum*** sp. (Figure 96)], 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 102) (Pôrto & 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. Hence, archegonia mature during the rainy season and sporophytes begin developing while it is still rainy. 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 102. ***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*** (Figure 103), nevertheless increasing in frequency during the rainy season (de Oliveira & 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.

Figure 103. ***Sematophyllum subpinnatum***, a moss that produces antheridia and archegonia throughout the year, from the Neotropics. Photo by Michael Lüth, with permission.

Deserts and Dry Habitats

Growth in winter is most likely typical in the desert. Stark (2001a, 2002c) suggests that phenology of bryophytes of the Mojave Desert, USA (Figure 104), contrasts sharply with that of other climatic regions, such as Nigerian savannah mosses, with phenological events tied almost solely to local rainfall events, which are rare and unpredictable. One adaptation to this unpredictable environment is that spore dispersal occurs over a long period. ***Grimmia orbicularis*** (Figure 97-Figure 98), a rock-dwelling species, retains operculate capsules for three months before its 3-week dispersal period (Stark 2001a). The entire clone, however, may disperse spores over a period as long as six months and within the area may last more than one year. This long dispersal period may also 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). ***Syntrichia inermis*** (Figure 94, Figure 105), 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 (2001a) concluded that the steeply inclined rock surfaces, supporting short, broad, inclined capsules, account for the more rapid rate of operculum shedding in ***Grimmia orbicularis*** (Figure 98).

Figure 104. Mojave Desert where ***Syntrichia inermis*** survives under shrubs and may be dormant for long periods. Photo courtesy of Lloyd Stark.

But 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*** (Figure 105) 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.

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. Hence, we should expect the phenology of desert bryophytes to be different from that of bryophytes in most other habitats. Mojave Desert populations of ***Syntrichia inermis*** (Figure 105) took an incredibly long time for antheridia to mature (Stark 2001a). Whereas the archegonia matured and became receptive in the same year, antheridia took one to several years to develop! 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 (Stark 2001a); sporophytes endure 18 or more months of dormancy during their development (Stark 1997). Spore dispersal, however, was delayed until late summer and early fall.

Figure 105. ***Syntrichia inermis*** with capsules in various stages of dispersal. Photo by Michael Lüth, with permission.

Syntrichia inermis (Figure 105) 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. 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.

Syntrichia caninervis (Figure 107) also a resident of the Mojave desert, 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.

Herrnstadt and Kidron (2005) examined reproduction in ***Bryum dunense*** (Figure 106) in three different habitats in the Negev Desert, southern Israel. 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.

Figure 106. ***Bryum dunense***, a species in the Negev Desert, Israel, that initiates gametangia prior to the first winter precipitation. Photo by Dror Melamed, with permission.

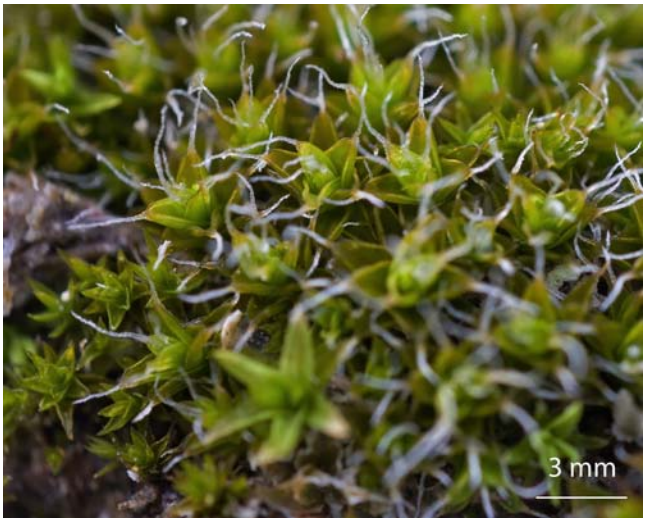

Figure 107. ***Syntrichia caninervis***. Photo from Proyecto Musgo, through Creative Commons.

In the dry mountains of southern New Mexico, USA, a close relative of several desert species, ***Syntrichia ruralis*** (Figure 108) 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 (December to June or even until August), 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.

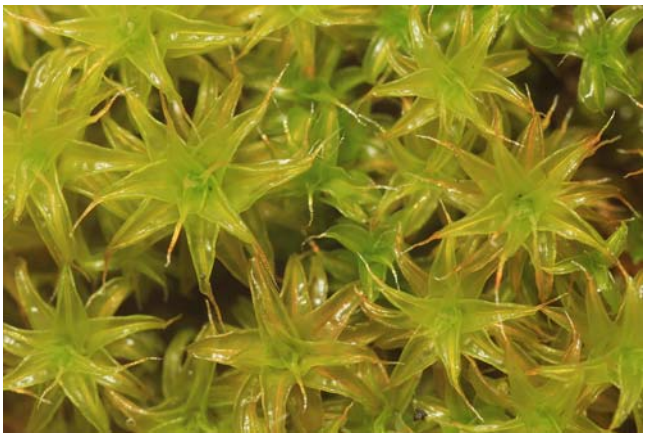

Figure 108. ***Syntrichia ruralis*** var. ***ruraliformis*** (Sand-hill Screw-moss). Photo by Barry Stewart, with permission.

When maturation of gametangia is an autumn event, it forces the young embryo to survive the winter. Haupt (1929b) found that the liverwort ***Fossombronia longiseta*** (Figure 43) 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*** (Figure 102) in Nigeria, where immature antheridia and archegonia are most abundant during July, the wettest month (Egunyomi 1979).

Moisture obviously is important in the regulation of season of growth. In the mountains of southern California, ***Asterella californica*** (Figure 109) grows on canyon sides and moist banks that become dry in summer. The liverwort dries out in summer (cf. Figure 110), surviving by terminal buds (Haupt 1929a). Bray (pers. comm.) found a similar survival mechanism in ***Fossombronia*** (Figure 111) in southern Illinois, permitting it to grow in fall through spring.

Figure 109. ***Asterella californica***, a liverwort that dries out in summer and survives by terminal buds. Photo by Peter J. Bryant, University of California, Irvine, with permission.

Figure 110. ***Asterella tenella*** with drying thallus and mature archegoniophore with open capsules. Photo by Janice Glime.

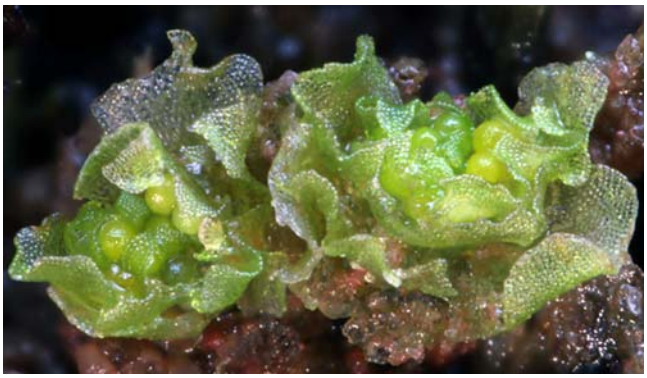

Figure 111. ***Fossombronia incurva***. Photo by Des Callaghan, with permission.

Trichostomum planifolium, 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.

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.

Epiphytes

Epiphytes live in a habitat that is frequently dry, but unlike the desert, water is also frequently available. This alternate wet-dry microclimate brings its own set of problems. There can be relatively long periods of time when it is unsuitable for sperm transfer. The epiphyte ***Forsstroemia trichomitria*** (Figure 112) produces five sets of reproductive structures per year. This may be an adaptation to increase the chances of having the right weather (rain) to accomplish fertilization. Fertilization occurs in late summer through autumn, about four months duration. Both types of gametangia are produced at the same time. The sporophytes require 17 months for maturation, enduring two winters.

Figure 112. ***Forsstroemia trichomitria***, an epiphytic moss that produces five sets of gametangia each growing season. Photo by Misha Ignatov, with permission.

Savannah

Contrasting with mosses controlled by the rainy season, as in the tropics, or those of dry periods that can last years, mosses of the dry habitat of Nigerian savannah have much shorter sexual cycles than those of the desert, as noted by Makinde and Odu (1994) for four mosses, ***Archidium ohioense*** (Figure 113), ***Bryum coronatum*** (Figure 114), ***Fissidens minutifolius*** (Figure 115), 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.

Figure 113. ***Archidium ohioense***. Photo by Li Zhang, with permission.

Figure 114. ***Bryum coronatum*** in India, a moss that completes its entire sexual cycle during the rainy season in the savannahs of Nigeria. Photo by Michael Lüth, with permission.

Figure 115. ***Fissidens minutulus***, a generic relative of ***F. minutifolius*** – one of the mosses that completes its entire sexual cycle in the rainy season in the savannahs of Georgia. Photo by Jan-Peter Frahm, with permission.

Polar and Alpine

Ayukawa *et al*. (2002) investigated ***Polytrichastrum ohioense*** (Figure 116-Figure 117) in the Yatsugatake Mountains of Japan. They found mature antheridia from late May to early August and mature archegonia from late June to mid July, permitting fertilization to occur from late June to mid July. This timing of gametangial maturity avoided the occasional temperatures below 0°C in May. The longer period of sperm maturity permits variability in time of egg maturation and suggests that the two types of gametangia respond to different triggers. Sporophytes began showing at the end of June, became dormant for the winter, and began growth again in May. Spores were dispersed from mid July to mid August. Hence the 13-month sporophyte maturation included a 6-month resting period in winter.

Figure 116. ***Polytrichastrum ohioense***, sowing females with light geen tops on left and males with unopened golden splash cups on right. Photo by Janice Glime.

Figure 117. ***Polytrichastrum ohioense*** with immature capsules. Photo by Li Zhang, with permission.

Antarctic populations of ***Polytrichum juniperinum*** (as *P. alpestre*; Figure 5, Figure 9, Figure 72) behave quite differently (Longton & Greene 1967). The antheridia begin development in March and overwinter (May-October) with no further development. Development resumes after

snowmelt and most of the antheridia mature in December-early January. Archegonia, on the other hand, do not begin development until the end of November, but still reach maturity at the same time as the antheridia. Sporophyte development was much longer, beginning with fertilization in December and January but not completing development until mid-March the following year.

Clarke and Greene (1970) found somewhat different timing adaptations in populations of ***Pohlia*** (Figure 2) in the Arctic and sub-Arctic. In these populations, maturation was somewhat faster than for the same species in Britain.

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*** (Figure 118) late summer to early spring; ***Tortula acaulon*** (Figure 119) November to May; ***Microbryum floerkeanum*** (Figure 120-Figure 121) October to April; ***Acaulon*** spores mature in late autumn to spring [***A. triquetrum*** (Figure 122), ***A. muticum*** (Figure 123)]. Michigan spring ephemerals include ***Pleuridium subulatum*** (Figure 124), ***Tortula truncata*** (formerly in ***Pottia***; Figure 125), and ***Physcomitrium pyriforme*** (Figure 126), whereas ***Ephemerum cohaerens*** (Figure 127) appears in both spring and autumn. ***Pottia davalliana*** (Figure 128) appears in the autumn, but sometimes can be found in summer.

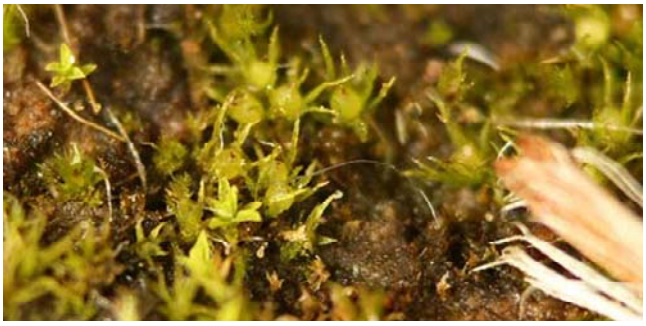

Figure 118. ***Ephemerum crassinervium***, an ephemeral moss that grows in the moisture from late summer to early spring. Photo by Bob Klips, with permission.

Figure 119. ***Tortula acaulon***, a species that is visible autumn through spring. Photo by David Holyoak, with permission.

Figure 120. ***Microbryum floerkeanum*** (inside red circle), an ephemeral that grows from October to April. Photo by Michael Lüth, with permission.

Figure 121. ***Microbryum floerkeanum***, an ephemeral that grows from October to April. Photos by Michael Lüth, with permission.

Figure 122. ***Acaulon triquetrum*** on sand; an ephemeral whose spores mature in late autumn to spring. Photo by Michael Lüth, with permission.

Figure 123. ***Acaulon muticum***, an ephemeral whose spores mature in late autumn to spring. Photo by Jan-Peter Frahm, with permission.

Figure 124. ***Pleuridium subulatum***, a moss of disturbed agricultural fields and roadsides. Photo by Michael Lüth, with permission.

Figure 125. ***Tortula truncata***, a Michigan, USA, spring ephemeral. Photo by Bob Klips, with permission.

Figure 126. ***Physcomitrium pyriforme***, a spring ephemeral in Michigan, USA, and elsewhere. Photo by Li Zhang, with permission.

Figure 127. ***Ephemerum cohaerens*** with perigonia, an ephemeral that appears in spring and again in autumn. Photo by Dick Haaksma, with permission.

It is not surprising that some ephemerals typically produce more than one generation of capsules in the same year. Gray (1935) found that ***Aphanorrhegma serratum*** (Figure 129) and ***Micromitrium tenerum*** (as ***Nanomitrium austinii***; Figure 130) 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.

Figure 128. ***Pottia davalliana***, an autumn ephemeral that sometimes also appears in summer. Photo by Michael Lüth, with permission.

Figure 129. ***Aphanorrhegma serratum***, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Bob Klips, with permission.

Figure 130. ***Micromitrium tenerum***, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Jan-Peter Frahm, with permission.

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 131-Figure 132), seem especially adapted for such strategies (Kürschner & Parolly 1999).

Figure 131. ***Riccia sorocarpa*** in European floodplain. Photos by Michael Lüth, with permission.

Figure 132. ***Riccia beyrichiana*** showing folded up lobes that can close up as the plant dries. Photo by Jan-Peter Frahm, with permission.

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*** (Figure 91) 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.

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*** (Figure 133) 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).

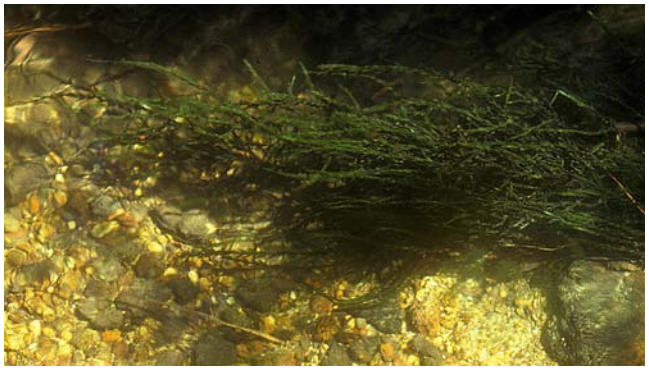

Figure 133. ***Fontinalis duriaei*** in Japan, a moss that begins its growth season in November. Photo by Janice Glime.

For populations of ***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.

But the big surprise came when we found abundant capsules on ***Fontinalis dalecarlica*** (Figure 79-Figure 80) (Glime 1984) and ***F. novae-angliae*** (Figure 134) (Glime 1987c) in February in New Hampshire, USA. 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 134. ***Fontinalis novae-angliae*** with capsules in February. Photo by Janice Glime

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 25ºC 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. Chlorophyll concentrations generally increase in response to decreasing light intensity, thus responding to seasonal changes.

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

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