Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 6 March 2017 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?

TABLE OF CONTENTS

CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?

Figure 1. ***Hylocomium splendens*** emergent from the winter snow. Timing of reproduction must be such that sperm do not mature on a warm day in winter, only to be frozen by ensuing sub-freezing temperatures. Photo by Michael Lüth, with permission.

Phenology, defined by Stark (2002) as "the study of the timing of growth and reproductive events," is also used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season. Classical studies in Europe have included branching architecture, timing of vegetative growth, gametangial initiation times, fertilization times, duration of sporophyte development, and time of spore liberation (Stark 2002). To these we can add nutritional status, population dynamics, fitness measures, spore dispersal patterns, interplay of sexual and asexual reproduction, **sexual dimorphism** (sexes look different), structural development, dormancy, and desiccation tolerance. Studying phenology permits us to understand interplay of plants with a constantly changing environment.

In the temperate forest, trees lose leaves in autumn, bloom and leaf out in spring, and store **photosynthate** (product of photosynthesis) in summer. These canopy phenological events have profound impact on smaller plants growing beneath them. Spring flowers bloom before leaves emerge on trees, taking advantage of a nearly full complement of sunlight. A few shade-tolerant species grow more slowly and take advantage of the tree canopy to protect them from bright light of summer. Other species use fungal partners to connect them with trees, taking advantage of canopy photosynthate that permits them to survive in low light. As these ground cover taxa enlarge through summer, bryophytes are impacted by light-depriving leaves of larger neighbors.

Bryophytes also must cope not only with a changing light and moisture regime resulting from the direct effect of changing seasons, but also with microclimatic changes resulting from changes in the tracheophytes around them. Their C_3 photosynthetic pathway (CO_2 is immediately put into photosynthesis, forming 3-C compound) permits them to take advantage of early light and moisture at snowmelt (Figure 1) when low temperatures prevent even other C_3 plants from having effective photosynthesis.

Bryophytes are limited in their occupancy of deciduous forests by the phenological event of leaf fall that fully blocks the light essential for their photosynthesis. Most forest bryophytes are perennials, yet, unlike their tracheophyte counterparts, most are unable to avoid the changing seasons by storing energy underground and losing their photosynthetic parts. As C_3 plants, they are able to photosynthesize at low temperatures as soon as the snow is gone, but they are likely to find the hot temperatures of summer to be detrimental. Furthermore, they require water to transfer their swimming sperm, rarely having an animal vector to carry these for them. Based on these constraints, we should expect that bryophytic phenological responses differ somewhat from those of their lignified vascular companions as the bryophytes take advantage of or avoid the changes provided by these companions.

One need only examine a few bryophyte floras to recognize that phenological events for mosses are poorly documented. Almost any flowering plant flora will include flowering dates, but bryophyte floras from Japan (Noguchi 1987-1994), the Nordic (Nyholm 1986, 1898, 1993), Michigan (Crum 2004), and the tropics (Gradstein *et al*. 2001) all fail to mention any season for any life cycle event, even the season of spore dispersal. Crum and Anderson (1981) occasionally include the season of spore ripening for the Eastern United States, but never any information on seasons for other events. In treating the genus ***Sphagnum***, for which both authors are world-renowned systematists, not a single species of the 42 described includes any phenological information. Conard (1947), in reporting the phenology of Iowa bryophytes, was able to find dates in the literature for presence of antheridia or archegonia for only 15 taxa out of 292. He was more successful in finding documentation of capsule production dates, locating it for all but 28 of the taxa that fruit in Iowa.

As the young field of bryophyte ecology began taking shape in the early 1970's, Longton (1974) suggested that the International Association of Bryologists and the British Bryological Society (Longton 1982) embark upon bryophyte phenology as a project. Perhaps because of British national pride, or because of the large number of good bryologists among the British society's mostly amateur membership, such a project had appeal to the BBS. It was a way for many people to contribute important information that could only be gained by such a wide undertaking. Through consorted efforts, they could define not only the phenology of a wide array of species, but could look at differences in patterns throughout the British Isles, comparing inland species with coastal, mountain and moor with valley and field.

Developing Consistency in Reporting

For comparisons among various studies and localities, a consistent way of examining and describing life cycle stages is necessary. Again, the British were the leaders, with a publication by Greene (1960) elucidating the stages. The British faithfully followed this nomenclature in making their reports. Slight modifications and refinements have made this system workable around the world.

Most researchers seem to recommend observing every two weeks to elucidate the phenology (Stark 1984). In general, the life cycle stages are arrested while the plants are dry, so it is possible to collect specimens periodically, then examine them later at one's convenience. The ability of bryophytes to continue their life cycle upon rehydration makes it possible to identify the stages after rehydration and even to photograph them. Nevertheless, one should exercise caution if high resolution is needed in defining dates because the ability to retain water may permit the bryophytes to continue development for a period of time. Mosses kept in plastic bags may continue growth for a month, elongating abnormally in the lower light of their new location. Dry mosses may shed the operculum prematurely, since drying itself is needed in most taxa to constrict the capsule and force the operculum off, occurring sooner in the dry lab than it would in nature with nightly dew to re-supply moisture.

When reviewing a series of dry collections, Stark (1984) recommends soaking the stems for a few minutes and removing the leaves on the upper 10-15 mm of the main stem, but not from the branches. This can be done with microforceps by holding the tip and pulling the leaves downward toward the base, being careful not to injure the gametangia in the process. Once leaves are removed, one can carefully remove a group of gametangia near the apex and place it in a drop of water on a slide. In **pleurocarpous** mosses (Figure 1), gametangia occur on side shoots, rather than at the stem apex where they occur in **acrocarpous** mosses (Figure 5). You can shorten the process by pressing the gametangia off with the side of a probe. In either case, use a cover slip and examine them with the compound microscope. Data should be recorded using one of the published systems of naming stages.

System of Naming

Fortunately for the British, and for bryologists everywhere, systems for scoring the developmental stages already existed. Greene made the "most significant" contribution to phenology (Stark 2002) when he suggested 20 stages (Figure 2), centering on the reproductive phases only, and omitting any presentation of the spore and protonema. He even recommended a method for preparing figures to illustrate the monthly changes (Figure 3).

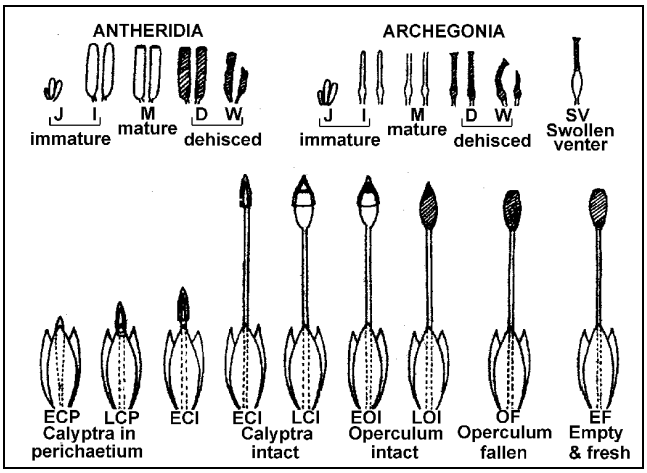


Figure 2. Maturation stages as represented by Greene (1960). **J** = juvenile, **I** = immature, **M** = mature, **D** = dehisced, **W** = withered archegonia or antheridia, **SV** = swollen venter, **ECP** = early calyptra in perichaetium, **LCP** = late calyptra in perichaetium, **ECI** = early calyptra intact, **LCI** = late calyptra intact, **EOI** = early operculum intact, **LOI** = late operculum intact, **OF** = operculum fallen, **EF** = empty and fresh.

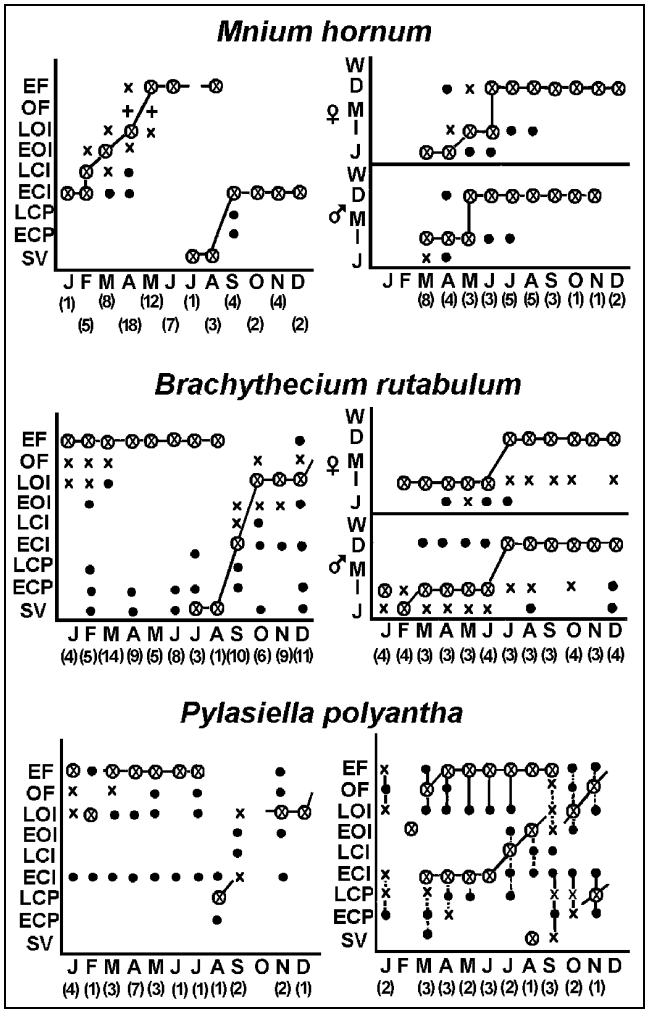
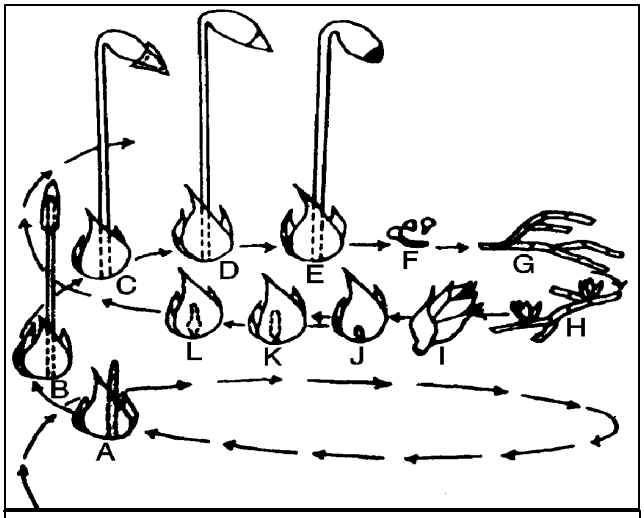


Figure 3. Sample figure given by Greene (1960) to illustrate the gametangial and capsular cycles of three species of moss. **Numbers in parentheses** indicate number of collections in which the majority state occurred. The **circled x** represents the state that was clearly the most abundant, **x** alone represents other stages that occurred as majority states in some collections, and a **solid circle** indicates present but never abundant. As in the previous figure, **SV** = swollen venter, **ECP** = early calyptra in perichaetium, **LCP** = late calyptra in perichaetium, **ECI** = early calyptra intact, **LCI** = late calyptra intact, **EOI** = early operculum intact, **LOI** = late operculum intact, **OF** = operculum fallen, **EF** = empty and fresh; **J** = juvenile, **I** = immature, **M** = mature, **D** = dehisced, and **W** = withered archegonia or antheridia.

Shortly thereafter, Forman (1965) developed a somewhat easier system by which researchers could make consistent descriptions related to phenological events. He decided that no two stages should be named separately unless they were morphologically distinct. Furthermore, the stages should be relatively easy to recognize without the use of a microscope. He defined the life cycle in 12 stages (Figure 4) for the purpose of describing the phenology and other events more precisely and in a standard fashion.

Forman (1965) decided that stages need not be delimited if they did not require any change in environmental conditions. For example, early and late stages of seta elongation are not separated because they occur as a continuous process independent of any environmental trigger. On the other hand, growth of the



A. **Embryonic calyptra**. (This corresponds with the development of the embryo following fertilization.) This stage commences with fertilization and terminates with the rupture of the gametophytic calyptra from the tissue beneath. The seta is not visible under the expanded neck cells of the archegonium.

B. **Seta with calyptra**. (This corresponds with the growth of the sporophyte from the embryo.) This stage commences when the seta becomes visible and terminates at the beginning of capsule expansion at the tip of the seta. A few plants lose their calyptras during this stage, but it is doubtful that these can eventually produce spores.

C. **Capsule green with calyptra**. (This corresponds with meiosis.) This stage ends either with the shedding of the calyptra or with the urn of the capsule beginning to turn brown. Meiotic divisions may occur from the latter portion of capsule expansion through the darkening of the operculum, depending upon the species.

D. **Capsule operculate and post-meiotic**. (This corresponds with spore maturation.) Since species appear differently in this stage, both green capsules without a calyptra and capsules at least partly brown with or without a calyptra are included here. This stage terminates with the dehiscence of the operculum.

E. **Capsule de-operculate**. (This corresponds with spore dispersal at the beginning.) This stage includes capsules containing spores, empty capsules in the year of maturation, and empty capsules from a previous year.

F. **Spore wall bulging**. (This corresponds with spore germination.) This stage terminates with the appearance of the cross wall of the first cell division.

G. **Protonema**. (This corresponds with growth of the protonema.) This stage begins with the two-celled structure as it emerges from the spore and terminates with the initiation of buds.

H. **Bud on protonema**. (This corresponds with the initiation of the leafy shoot.) This stage terminates with the beginning of rapid stem elongation.

I. **Juvenile stem**. (This corresponds with growth of the leafy shoot.) This stage terminates upon cessation of stem elongation and development. In practice two criteria have been used to identify this stage, namely, smaller leaves at the shoot tip plus a lighter green color in these leaves (indicating new growth). These two criteria may not be apparent in all species, in which case additional criteria should be found.

J. **Juvenile gametangium**. (This corresponds with the initiation of a sex organ.) Antheridia and archegonia are indistinguishable from each other at this stage. This stage ends when the sex can be determined.

K. **Antheridium**. (This corresponds with growth of the sex organ and differentiation of microgametes, *i.e.* sperm.)

L. **Archegonium**. (This corresponds with growth of the sex organ and differentiation of megagametes, *i.e.* eggs.) The presence of differentiated perichaetial leaves in some species will identify this stage from k.

Figure 4. Life cycle stages based on Forman (1965).

embryo within the perichaetium is likely to differ from growth of the seta because the developmental environment changes substantially once the seta emerges from the protective leaves. Forman conveniently chose the embryonic calyptra as the first stage (of course there is no beginning or end to a cycle), placing the protonema to gametophore stages (including production of gametangia) last, perhaps because these "later" stages are the most difficult and least likely stages to be observed.

Figure 5. ***Bryum pallescens*** showing terminal seta and capsule of an acrocarpous moss. Note that the capsule is protruding from last year's gametophyte while the growth for the current year is tall. Photos by Michael Lüth, with permission.

Stark (1984), in encouraging North Americans to join in collecting phenological data, recommended a modification of the systems of Longton (1979) and Greene (1960) for describing gametangia. It adds clarity and distinguishes between young, mature, and ruptured gametangia, distinctions that are important in taxa that have gametangial development interrupted by winter or a dry season:

1 = unruptured and less than 1/2 full length
2 = unruptured and more than 1/2 their full length
3 = green or hyaline with apices ruptured
4 = brown with apices ruptured
A = abortive; brown and unruptured

Stark later (2002) developed a system of fourteen events, but this system requires a 400x lens to distinguish the beginnings of gametangia before the gender is distinguishable, and while it provides more information, such requirements as determining that the theca contains fewer than half the spores makes the system rather impractical.

Imura (1994) reduced the number of stages to five in his study of ***Pogonatum inflexum***, but provided us with a graphical way of representing the sequence of events that is easy to produce and useful in understanding phenological relationships across multiple years (Figure 6). The degree of detail needed depends on the purpose, and certainly the representation by Imura serves a useful purpose to see the progression and overlap of events between years.

While the stages of the life cycle are similar for all bryophytes, the timing differs. This chapter will examine the major events and factors that control their timing. As demonstrated by Imura (Figure 6), these events include gametophyte growth, production of gametangia, fertilization, production of sporophytes, and dispersal of spores, as well as events that are more difficult to examine in the field – spore germination and development of gametophore buds.

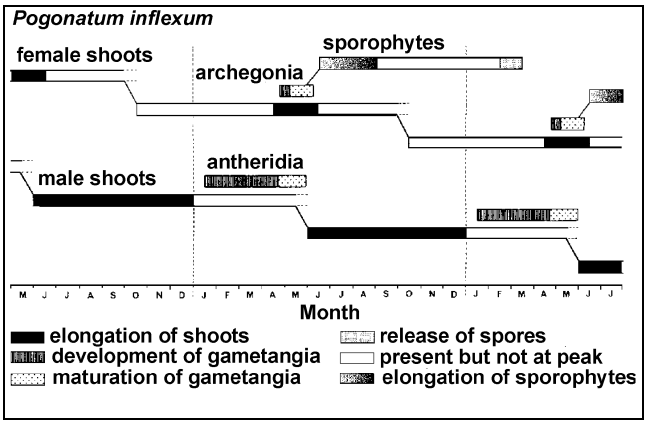


Figure 6. Annual sequence of events for ***Pogonatum inflexum*** on Miyajima Island, Japan. Redrawn from Imura (1994).

Summary

Phenology is defined by Stark (2002) as "the study of the timing of growth and reproductive events." The term is likewise used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season.

The life cycle of a bryophyte 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**.

Acknowledgments

I appreciate the helpful comments of Heather Smith in giving me a student's perspective on this chapter. Linda Luster checked the literature citations, proofread, and checked for needed glossary entries.

Literature Cited

Conard, H. S. 1947. Phenology of mosses in Iowa. Iowa Acad. Sci. Proc. 53: 141-146.

Crum, H. 2004. Mosses of the Great Lakes Forest, Fourth edition. The University of Michigan Herbarium, Ann Arbor, 592 pp.

Crum, H. A. and Anderson, L. E. 1981. Mosses of Eastern North America. Columbia Univ. Press, New York, 2 Vol.

Forman, R. T. T. 1965. A system for studying moss phenology. Bryologist 68: 289-300.

Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001. Guide to the Bryophytes of Tropical America. Mem. N. Y. Bot. Gard. 86: 1-577.

Greene, S. W. 1960. The maturation cycle, or the stages of development of gametangia and capsules in mosses. Trans. Brit. Bryol. Soc. 3: 736-745.

Imura, S. 1994. Phenological study in two dioecious mosses, *Atrichum rhystophyllum* (C. Mull.) Par. and *Pogonatum inflexum* (Lindb.) Lac. J. Hattori Bot. Lab. 76: 105-114.

Longton, R. E. 1974. Biology of widely distributed bryophytes: A possible project for the International Association of Bryologists. Taxon 23: 213-214.

Longton, R. E. 1979. Studies on growth, reproduction and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. Bryologist 82: 325-367.

Longton, R. E. 1982. A B.B.S. project on reproductive biology of selected British mosses. Bull. Brit. Bryol. 39: 30-32.

Noguchi, A. 1987. Illustrated Moss Flora of Japan. Part 1. Hattori Botanical Laboratory, Nichinan, 242 pp.

Noguchi, A. 1988. Illustrated Moss Flora of Japan, Part 2. Hattori Botanical Laboratory, Nichinan, 491 pp.

Noguchi, A. 1989. Illustrated Moss Flora of Japan, Part 3. Hattori Botanical Laboratory, Nichinan, pp. 493-742.

Noguchi, A. 1991. Illustrated Moss Flora of Japan, Part 4. Hattori Botanical Laboratory, Nichinan, pp. 743-1012.

Noguchi, A. 1994. Illustrated Moss Flora of Japan, Part 5. Hattori Botanical Laboratory, Nichinan, pp. 1013-1253.

Nyholm, E. 1986. Illustrated Flora of Nordic Mosses, Fasc. 1. Fissidentaceae – Seligeriaceae. The Nordic Bryological Society, Lund, pp. 1-72.

Nyholm, E. 1989. Illustrated Flora of Nordic Mosses, Fasc. 2. Pottiaceae – Splachnaceae – Schistostegaceae. The Nordic Bryological Society, Lund, pp. 75-141.

Nyholm, E. 1993. Illustrated Flora of Nordic Mosses, Fasc. 3. Bryaceae – Rhodobryaceae – Mniaceae – Cinclidiaceae – Plagiomniaceae. The Nordic Bryological Society, Lund, pp. 145-244.

Stark, L. R. 1984. Introducing phenology. Evansia 1: 25-27.

Stark, L. R. 2002. Phenology and its repercussions on the reproductive ecology of mosses. Bryologist 105: 204-218.