

# CHAPTER 5-7

## ECOPHYSIOLOGY OF DEVELOPMENT: BROOD BODIES



Figure 1. *Tortula pagorum*, an acrocarpous moss with terminal gemmae. Photo by Michael Lüth.

### Definitions

Imura and Iwatsuki (1990) defined **propagules** as vegetative **diaspores** that have an apical cell and can grow directly into leafy shoots. However, most diaspores produce a protonema. **Gemmae**, by their definition, are vegetative diaspores that lack an apical cell and in which a protonema precedes development of a leafy shoot. While this is a clean separation, it is not always practical to determine the germination pattern, and multicellular gemmae may be construed as propagules. In the multilingual glossary for bryology (Magill 1990), **propagule** (Figure 3) is defined in a more practical way as a reduced bud, branch, or leaf serving in reproduction. This does not imply absence of a protonema, and indeed, there often is one. **Diaspore** is given as a synonym. **Gemmae** (Figure 2) are distinguished as uni- or multicellular, filamentous, globose, ellipsoidal, cylindrical, stellate, or discoid brood bodies, **relatively undifferentiated**, serving in vegetative reproduction. **Brood body** is the more inclusive category, including both

propagules and gemmae. These are genetically identical to their parents, thus producing clones (Laaka-Lindberg 2000). Bryophytes are the only group of plants with any sort of gametophytic brood body (Wyatt 1994).

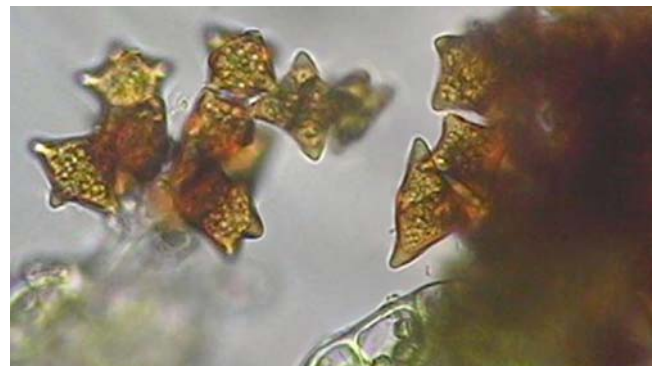


Figure 2. Leaf gemmae of *Lophozia bicrenata*, a leafy liverwort. Photo by Paul Davison, University of North Alabama.



Figure 3. Propagules. **Top:** *Leskeella nervosa* with bulbils at leaf bases. Photo by Michael Lüth. **Middle two:** *Platygyrium repens* with bulbils crowded at branch tips. **Bottom:** *Orthodicranum flagellare* with deciduous flagelliform branches. Photos by Janice Glime.

Imura (1994) recognized specialized vegetative reproductive structures in 186 species (15.7%) of Japanese mosses, including deciduous shoot apices, caducous branchlets, bulbils, flagella, rhizoidal tubers, gemmae, caducous leaves, and endogenous gemmae. He considered these to be adaptations to the dioicous habit (e.g. *Tortula pagorum*; Figure 1) and unstable habitat conditions.

The evolutionary pathway has capitalized on success of fragments by selecting more and more specialized

fragments. Mosses such as *Leskeella nervosa* (Figure 3), *Platygyrium repens* (Figure 3), *Bryum argenteum* (Figure 4), and *Orthodicranum flagellare* (Figure 3), to name a few, have special shoots that easily break off and disperse. This explains why *Bryum argenteum* is so common along paths in open areas such as cemeteries and roadsides. Each step of a boot carries tiny branches from the parent plants to a new location. To demonstrate its remarkable dispersal success, Clare and Terry (1960) prepared bare soil, then used a matchbook to "walk" on *Bryum argenteum* (Figure 4). They then "walked" on the bare soil with the same matchbook. As a control, they "walked" on a different part of the prepared soil with a different matchbook. True to its natural success, the *Bryum argenteum* (Figure 4) grew well where the matchbook had previously walked on the moss, but did not appear on the control area.



Figure 4. *Bryum argenteum* showing bulbous tips that break off easily to form new plants. Photos by Michael Lüth.

## Brood Bodies

**Brood bodies** are a specialized means of asexual reproduction that permit plants to propagate and disperse, often when conditions are unfavorable in the present location. Perhaps this is why, among dioicous mosses, they are more common on upright mosses (Figure 5), where there is some hope of falling away from the parent plant, rather than landing within a mat that keeps them where they started. Herben (1994) claims that reproductive processes, including brood bodies, are crucial for between-habitat dispersal. Those mosses in the British flora that inhabit small patches and unstable habitats are more likely to have vegetative brood bodies. But shoot density also can determine the number of brood bodies. Kimmerer (1991a) found that low-density populations of *Tetraphis pellucida* (Figure 6) were more likely to reproduce asexually by

gemmae, whereas greater density increased incidence of sexual reproduction and subsequent spores. She (1991b) found that most gemmae landed within 10 cm of the colony, whereas spores travelled as far as 2 m. [Brodie (1951) considered that *T. pellucida* was too delicate to benefit much from splashing by raindrops, perhaps accounting for the much shorter dispersal distance compared to that of sperm in *Polytrichum* of up to 60 cm.] The asexual strategy permits mosses to colonize an area rapidly by gemmae, then move on by spores when space is saturated. Kimmerer (1991a) felt this was of particular importance in unstable environments such as rotting stumps where *T. pellucida* commonly occurs. On the other hand, ability to "move" by gemmae provides an opportunity to seek a mate when stranded in a single-sex clone.



Figure 5. *Bryum gemmilucens* showing axillary propagules. Photo by Michael Lüth.



Figure 6. *Tetraxis pellucida* with terminal gemmae cups, the only moss with gemmae splash cups. Upper photo by Janice Glime, lower by Paul Davison, University of North Alabama.

Chrobak and Sharp (1955) showed that scales from the deciduous flagelliform branches of *Orthodicranum flagellare* were more likely to form protonemata than whole leaves or their proximal or distal halves (Figure 7).

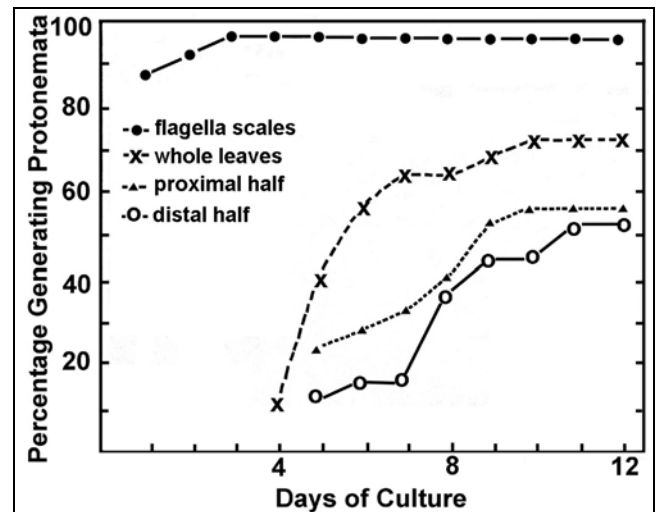


Figure 7. Success of producing protonemata from various leaf parts of *Orthodicranum flagellare* compared to that of the scales on the flagelliform brood branches. Redrawn from Chrobak & Sharp (1955).

Even in the *Sphagnum*-dominated peatlands, dispersal by gemmae is an advantage in regeneration. While *Sphagnum* must wait for recolonization by spores that often have poor success on the acid peatland substrate with its low nutrient quality, *Aulacomnium palustre* (Figure 8) can colonize rapidly from gemmae that have survived the disturbance (Li & Vitt 1994). Furthermore, perhaps again due to the more advanced state of the propagula, *A. palustre* had a much wider tolerance range for nutrient concentrations, being the only species not inhibited by N inputs. *Sphagnum angustifolium*, *S. magellanicum*, and *Polytrichum strictum* all had poor regenerative ability.



Figure 8. *Aulacomnium palustre* showing special extension of the stem with gemmae. Photo by Zen Iwatsuki.

It is reasonable then, that certain habitat conditions might favor the **apogamous** (condition of producing sporophytes without union of gametes) or **aposporous** (producing gametophyte from sporophyte tissue without meiosis) reproduction of bryophytes. Chopra (1988) was able to increase apogamy by reducing water or light levels and by raising the sugar concentrations in the growth medium. Likewise, low hormone concentrations favored apogamy. Not surprisingly, this plasticity was correlated

with a high chromosome number (suggesting polyploidy) and genetic variation. Apospory, on the other hand, was favored by the opposite conditions: suitable temperature and light, sufficient humidity, and lack of sugar in the medium. It was furthermore stimulated by wounding and the removal of apical dominance.

## Tubers

Tubers are defined very differently in mosses and liverworts. In liverworts, they are extensions from the growing apex, growing downward gravitropically, and serving as perennating structures during conditions unfavorable for growth. In mosses, they are gemmae formed on the rhizoids (Figure 9).



Figure 9. *Bryum radiculosum* rhizoids with tubers. Photo by Michael Lüth.

A number of moss species form tubers on their rhizoids (Arts 1987a; Table 1). Risse (1987) described these rhizoidal gemmae in 82 species of European mosses. They serve as asexual means of reproduction, although one must question just how they get dispersed. Perhaps earthworms and other forms of disturbance accomplish the task. However, in their study of plant diaspores from earthworm guts, van Tooren and During (1988) found few bryophytes that regenerated from tubers so obtained, although bryophytes emerged frequently from some samples by other means. They interpreted this as a low survival rate of vegetative diaspores in the earthworm digestive tract. Risse (1987) reported that mites disperse protonemal gemmae in *Schistostega pennata*.

These tubers are densely packed with lipid droplets or starch grains (Duckett & Pressel 2003). In *Phaeoceros laevis* (hornwort), tuber cells deposit protein into the cell vacuoles as the cells differentiate, forming abundant starch in their plastids and lipid droplets in the cytoplasm (Ligrone & Lopes 1989). Such rich storage contents suggest that they should germinate rapidly and produce new plants quickly, using their abundant food reserves. Using *Haplodontium notarisii*, Arts (1988a) showed that this moss did just that, germinating in two weeks, and several weeks later producing numerous upright gametophores to form a colony.

Such tubers provide a diaspore bank that can help to revegetate disturbed ground (During *et al.* 1987) and benefit from extended longevity. Arts (1989) has demonstrated that even in a state of desiccation in a

herbarium, such tubers can survive and germinate after 10 years. Such a strategy is common among colonist species (During *et al.* 1987; Arts 1990a; Table 1), and seems to be confined among the mosses to acrocarpous species. This colonist connection suggests that perhaps they do not have to arrive, but are already there, much like buried seeds awaiting the day they once more arrive at the surface and receive light. During (1995) suggests that such colonist populations are maintained completely through occasional recruitment. He suggests that within extant populations there must be a density-dependent tuber mortality to regulate the population.

Table 1. Examples of bryophytes with tubers reported in the literature.

Species	Reference
<i>Conocephalum conicum</i>	Paton 1993
<i>Fissidens beckettii</i>	Arts 1998
<i>Fissidens cristatus</i>	Arts 1986a
<i>Ditrichum difficile</i>	Arts 1998
<i>Ditrichum lineare</i>	Matsui <i>et al.</i> 1985
<i>Ditrichum heteromallum</i>	Risse 1985b
<i>Ditrichum heteromallum</i>	Deguchi & Matsui 1986
<i>Bryum barnesii</i>	Wilczek & Demaret 1980
<i>Bryum bicolor</i>	El-Saadawi & Zanaty 1990
<i>Bryum bicolor</i>	Risse 1993
<i>Bryum cruegeri</i>	Whitehouse 1978
<i>Bryum dunense</i>	Cortini Pedrotti & Aleffi 2001
<i>Bryum veronense</i>	Cortini Pedrotti & Aleffi 2001
<i>Funaria hygrometrica</i>	El-Saadawi & Zanaty 1990
<i>Archidium alternifolium</i>	Arts 1990b
<i>Archidium globiferum</i>	Arts 1998
<i>Barbula cylindrica</i>	Ellis & Smith 1983
<i>Barbula tophacea</i>	Side 1983
<i>(Didymodon tophaceus)</i>	
<i>Didymodon nicholsonii</i>	Arts 1987b
<i>Chrysoblastella chilensis</i>	Matteri 1984
<i>Pottia bryoides</i>	Arts 1987c
<i>Pottia intermedia</i>	Risse 1985a
<i>Pottia lanceolata</i>	Arts 1987c
<i>Pottia truncata</i>	Arts 1987c
<i>Pseudocrossidium revolutum</i>	Arts 1988b
<i>Scopelophila cataractae</i>	Arts 1988b
<i>Haplodontium notarisii</i>	Arts 1988a
<i>Pleuridium acuminatum</i>	Arts & Risse 1988
<i>Pleuridium ecklonii</i>	Arts 1998
<i>Pleuridium nervosum</i>	Arts 1998
<i>Pohlia lutescens</i>	Hart & Whitehouse 1978
<i>Pohlia molanodon</i>	Arts 1986b
<i>Leptobryum pyriforme</i>	Imura <i>et al.</i> 1992
<i>Discelium nudum</i>	Side & Whitehouse 1987
<i>Cynodontium bruntonii</i>	Arts 1990a
<i>Campylopus pyriformis</i>	Arts 1986c
<i>Atrichum tenellum</i>	Arts 1987d
<i>Atrichum crispum</i>	Arts 1987d

## Development

There are more developmental pathways for propagules than there are kinds of propagules. Even within the same genus, Ligrone and coworkers (1996) found differences in the origins of the gemmae. In *Tortula latifolia*, gemmae develop on the upper leaf surface from single initial cells of both the lamina and the costa, whereas in *T. papillosa* they develop only on the costa (Figure 10). In both cases the old wall and cuticle of the cell initial rupture and a new, highly extensible wall replaces it.

Subsequent divisions of this gemma **primordium** produce a 6-8-celled gemma. Mucilage develops around these gemmae and eventually the plasmodesmatal connections are severed, leaving only the mucilage to connect the gemmae to the leaf. Multiple gemmae may form in this way from the same initial and remain in a chain until the leaf becomes fully hydrated. Despite their disconnection from the parent leaf, these gemmae accumulate lipids, indicating that they are functionally photosynthetic.

Lipids are commonly stored in brood bodies of mosses, including *Aloina aloides* var. *ambigua*, *Ceratodon purpureus*, *Ephemerum serratum*, *Leptodictyum riparium*, *Weissia controversa* (Goode *et al.* 1993), and *Splachnum ampullaceum* (Mallón *et al.* 2006). Due to the hydrophobic properties of lipids, large amounts can be stored, permitting these brood bodies to survive when the protonema or plant is damaged by desiccation. Such lipids are most common in long-lived propagules.

Some gemmae can even produce more gemmae. In *Hyophila crenulata*, the still-attached gemmae can germinate to produce more gemmae (Olarinmoye 1981).



Figure 10. **Upper:** *Tortula latifolia* showing gemmae on costa and lamina. **Lower:** *Tortula papillosa* showing gemmae restricted to costa. Photos by Michael Lüth.

## Hormonal Effects

Stange (1983) suggested that gemmae require auxin transport from the parent plant, based on disruption of gemma differentiation in *Riella helicophylla* when treated with an auxin antagonist. However, when ethylene and

IAA are applied together, the combination has positive, additive effects on cell elongation (Stange & Osborne 1988). On the other hand, gemmae generally fail to germinate while still on the parent thallus. Botanists have assumed that this is due to an inhibitory substance diffused from the parent. That inhibition can carry over to germination in the vicinity of the parent as well. Schneider and Sharp (1962) found that when gemmae of *Tetraphis pellucida* were grown on culture media that had previously had mature plants, the germination was inhibited. This suggests some sort of hormone leakage, but probably not the gaseous ethylene.

Rawat and Chopra (1976) found that secondary protonemata of *Bryum klinggraeffii* produce a diffusible substance when gemmae are produced. This induces gemma production on young protonemata that have not yet reached the critical size. Such a mechanism could insure maximum gemma production and greater survival if the initial stimulus for gemma production was indeed an unfavorable environment. Contrasting with the auxin requirement suggested by Stange (1983) for *Riella helicophylla*, external auxins inhibit production of gemma cups in *Marchantia palmata* (Kumra & Chopra 1989).

Since gemmae are such diverse structures, arising from protonemata, thallus, apical branches, leaf axils, and leaves, one might expect a variety of environmental and hormonal controls over their production. For example, in *Philonotis*, elongation of the propagules occurs on older, basal parts of the stem. Naming the hormones would be pure speculation, but we know that IAA moves basipetally, hence accumulating downward. We also know that more ethylene is likely to be produced in the older part of the stem, and there is less air movement, resulting in more accumulation. Perhaps it is some interaction of these two hormones that results in the basal propagules, but why in some taxa and not others? Bulbils are apical in some taxa, such as *Platygyrium repens* (Figure 3), and gemmae cups are apical in *Tetraphis pellucida* (Figure 6).

## Environmental Effects

For any plant system to be effective, it must be tuned to its environment. Propagules are no exception, being finely tuned to kick in when conditions favor their growth and development. In *Hyophila crenulata*, gemmae production is enhanced by moisture, and during flooding numerous protonemal gemmae develop. This strategy greatly increases the chances for success of this species in flooded areas such as gutters and drainage areas.

Whitehouse (1980) found that *Schistostega pennata*, *Eucladium verticillatum*, *Gyroweisia tenuis*, and *Didymodon trifarius* all produce protonemal gemmae at low light intensities, but not at higher ones. These species can all grow in rock crevices, and such a mechanism might permit them to "try again" by dispersing if they germinate in a crevice that is too dark to complete the life cycle. A similar low-light response causes many protonemata to produce aerial shoots that break off and presumably serve as propagules (Whitehouse 1980). Similarly, in *Marchantia palmata*, maximum production of gemmae cups is attained when the plants receive continuous light at 4500 lux (Kumra & Chopra 1989). Full sunlight is about 70,000 lux. In *Marchantia nepalensis*, having only 50-100

lux inhibits the production of gemmae cups (Chopra & Sood 1970).

Otto and Halbsguth (1976) found that rhizoid induction on gemmae of *Marchantia polymorpha* was dependent on wavelength of light. The most effective wavelength was 350 nm, whereas no rhizoids were produced at less than 550 or more than 670 nm. They attributed this response to phytochrome and showed that an application of  $10^{-4}$  M IAA for one hour had the same effect as the red-far red reversibility known for phytochrome.

Environmental effects might likewise play a role in the adaptive location of brood bodies. In *Hyophila crenulata*, gemmae occur on the protonema and are sensitive to humidity, with greater humidity causing greater gemmae production (Olarinmoye 1981). Flooding results in abundant basal protonematal gemmae. In its habitats of gutters, drainage areas, and other periodically flooded areas, these abundant gemmae facilitate spreading. The location of gemmae on protonemata provides them with the longest conditions of sufficient humidity.

In Arctic populations of *Tetraphis pellucida*, gemmae (Figure 11) have a broad range of germination conditions similar to those of the spores (Forman 1964). The broad 18-30°C range for gemma production sharply contrasts to sporophyte maturation requirements of -0.2 to 7.3°C, or 0-5°C in dark cultures. Such low temperature requirements account for the capsule maturation in spring. Gemmae seem to be able to persist as well as spores in cold conditions, and certainly better than some, as for example gemmae of *Aulacomnium heterostichum* (Figure 12), which germinated after two years of storage in a freezer (Imura *et al.* 1991).



Figure 11. *Tetraphis pellucida* gemma showing germination and development of rhizoid. Photo with permission from Biology 321 Course Website, [www.botany.ubc.ca/bryophyte/LAB6b.htm](http://www.botany.ubc.ca/bryophyte/LAB6b.htm).

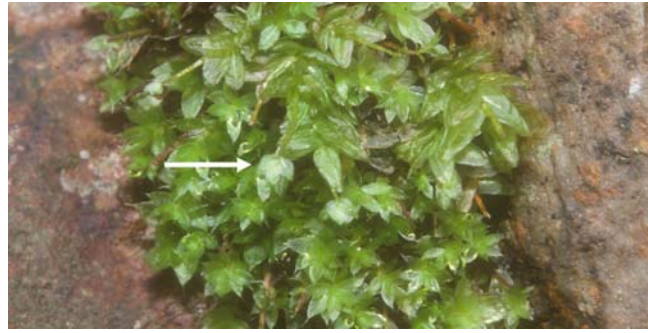


Figure 12. *Aulacomnium heterostichum* showing terminal gemmae (arrow). Photo by Janice Glime.

It appears that gender can also play a role in timing of gemmae production. This is expected, since the energy required by production of antheridia and sperm is considerably less than that needed for the development of the sporophyte following fertilization. Thus, we might expect a delay in gemma production in females of a species, providing a longer span of energy to be diverted to the young sporophyte. Fuselier and McLetchie (2002) addressed this relationship in the dioicous *Marchantia inflexa*. In a low-light environment, the onset of gemma production and plant size early in development were under sex-specific selection. Furthermore, females paid a higher price for plasticity in the onset of gemma production under high light. Selection for asexual fitness shifted the offspring toward monomorphism rather than sexual dimorphism. However, there were negative tradeoffs between the asexual and sexual fitness, at least in females, under some light conditions. Fuselier and McLetchie suggest that the opposing selection forces of these two reproductive strategies (sexual and asexual) might explain the persistence of sexual dimorphism of mature plants, while selection favored immature plants in which gender was indistinguishable.

One control of gemmae survival under conditions of cold or dehydration lies in their ability to maintain dormancy. We know that *Marchantia* gemmae are unable to germinate while remaining on the parent plant, a condition in which we assume the parent to be responsible for inhibiting the germination and thus attaining gemma dormancy. But some dormancy seems to be under environmental control in ways that protect the young gemmalings from unfavorable environmental conditions. For example, the leafy liverwort *Lophozia silvicola* produces gemmae that are able to grow and replace dead shoots of the parent colonies. But these gemmae can be deposited throughout the growing season, some of them arriving upon favorable substrata when winter is imminent. Laaka-Lindberg and Heino (2001) propose that some gemmae are destined to become non-germinating gemmae, entering a "season-specific" dormancy. They suggest that only the dormant gemmae are able to survive winter.

Mallón *et al.* (2006) experimented with vegetative propagules in the dung moss *Splachnum ampullaceum* and suggested that ABA might be important in the ability of the protonema to produce brood cells and survive desiccation. This added production of brood cells would also permit the colony to spread, perhaps accounting for the very dense populations that are typical (Figure 13).

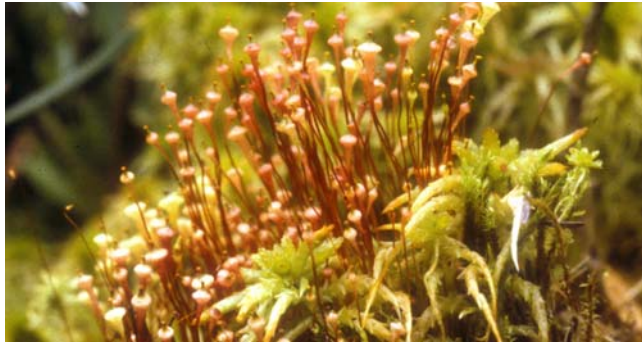


Figure 13. *Splachnum ampullaceum* growing on dung in a cow pasture. Photo by Janice Glime.

We know that sucrose can cause germination of gemmae in *Marchantia nepalensis*, suggesting that a photosynthetic response is needed to provide a continuous energy supply (Chopra & Sood 1970). This is supported by the increased germination with increased light intensity.

One factor we know to be important in any cell growth is calcium. Grotha (1983) found evidence in *Riella helicophylla* suggesting that the distal lobe of the gemma and the non-dividing cells of the rhizoid initials of the gemma have zones that facilitate  $\text{Ca}^{+2}$  absorption.

Other plants can have an effect on the success of gemmalings. This is manifest not only in competition for light, but in chemical warfare as well. The epiphytic leafy liverwort *Radula flaccida* is affected by leachates and extracts of the supporting tree upon which it grows (Olarinmoye 1982). Although these seem to have no effect on the germination of the gemmae, they are important in the later establishment of the gemmalings, affecting cell length, leaf size, and rhizoid development. These effects seem to be dependent on the species of tree leaf involved and could account for differences in the colonization success on different species of trees.

## Dormancy

Dormancy is an adaptive strategy of utmost importance to organisms inhabiting unpredictable environments. Laaka-Lindberg (2000) considered it a way to spread the risk and enhance survival by making more effective use of resources. By remaining dormant when conditions are less favorable, resources are not lost to competition (Rees 1996; Hyatt & Evans 1998). Dormancy has been viewed by some as an alternative to dispersal, creating a facultative response in patchy environments where some patches are suitable and others are not (Cohen & Levin 1991; McPeck & Kalisz 1998). It is also a way to survive over winter in the leafy liverwort *Lophozia silvicola*, with summer-produced gemmae germinating immediately and late-season gemmae becoming dormant for the winter (Laaka-Lindberg 2000).

Like spores, gemmae are typically under the control of light for germination, failing to germinate in the dark (Risse 1987). Schwabe (1972) reported that *Lunularia cruciata* could survive dormant for months in total darkness. In *L. cruciata*, long days induce dormancy. Nevertheless, it is a complex interaction of photoperiod, temperature, and phytochrome response that determines dormancy or germination. Furthermore, lunularic acid within the gemma cup promotes dormancy. The presence of other plants of their own or other species also provides

an inhibitory function, as discussed earlier. The ability of lunularic acid to inhibit algal and fungal growth and to delay seed germination in some species suggests it may be allelopathic not only to its own offspring, but to other groups of taxa as well, thus potentially making the environment more friendly toward the success of the gemmalings once conditions are suitable for them.

This dormancy in *L. cruciata* permits gemmae to remain dormant underground in soil banks (Schwabe 1972). However, it is not that simple. If they are wet, they will not survive more than 10 days without germinating, and their fat reserves are depleted in 15 days if they are unable to replace it through photosynthesis. Furthermore, once they have imbibed water and begun to germinate, in as few as 12 hours, they are sensitive to desiccation and will not survive if dried at that stage.

Many have observed the dormancy of gemmae while still in the cups on the thallus of *Marchantia polymorpha* (Figure 14). Yet, when these gemmae get splashed onto the soil or the thallus dies around them, they seem able to germinate immediately. Schwabe (1976) has shown that it is lunularic acid from the parent thallus, serving as an inhibitor, that is responsible for this dormancy. Kumra and Chopra (1989) have shown that application of exogenous auxins inhibit growth of both gemmae cups and vegetative plants of *Marchantia palmata*. The auxin IAA is likewise known to inhibit germination of gemmae of *Lunularia cruciata* in the lab (LaRue & Narayanaswamy 1957).

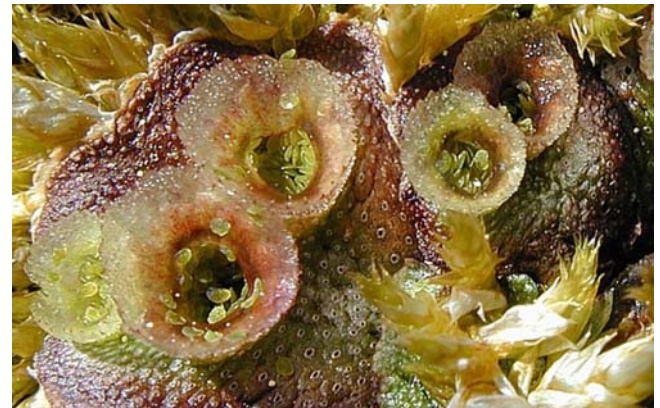


Figure 14. *Marchantia polymorpha* thallus with gemmae cups. Photo by Michael Lüth.

Lunularic acid occurs in the soluble fraction of the cell (as well as in association with the cell wall; Schwabe 1990). Therefore, inhibitors such as lunularic acid can be leached from the plant (Schwabe & Nachmony-Bascomb 1963), especially older parts of the thallus (Schwabe 1990), therefore potentially having an effect on neighbors of the same or even different species. Since leaching is likely to be greater during dry periods or immediately following them, this could cause a seasonal or weather-related response.

## Tradeoffs

There are tradeoffs in using energy to produce brood bodies instead of spores. Whereas spores require a prior fertilization, which requires abundant water for sperm to swim, spores disperse farther than brood bodies and are able to germinate maximally on previously uncolonized substrates; brood bodies do not require fertilization, hence

negating the need for excessive water, but can only disperse locally, yet, at least in some cases, are more successful amid other plants than are spores (Newton & Mishler 1994). Egunyomi (1978) found that the protonemata of gemmae grow faster, a factor likely to be true for most bryophytes, but that spores produce more gametophytes. However, one must be cautious in transferring these laboratory results to field generalizations. In the field, protonemata from spores may be less successful than gemmae just because they take longer to develop and therefore are more likely to encounter unfavorable conditions, including competition. In a later study on *Bryum coronatum* in Nigeria, Egunyomi (1982) found that vegetative propagules may succeed where capsules fail. In that species, 41% of the setae had no capsules and 42% of the capsules did not dehisce. The spore germination was 65-88%, but the protonemal growth was abnormal, suggesting that spreading by spores in nature might be rather limited. On the other hand, this species is likely to succeed in dispersal through its numerous axillary propagules.

But production of gemmae usually comes at a price. Sharing of energy can mean no one does well, so it is not surprising that sporophyte development does not coincide with gemma development. In *Tetraphis pellucida*, one cannot find gemmae cups and sporophytes on the same plant. Both need to occupy the same location at the shoot apex, making it physically impossible.

Risse (1987) found that among colonist species, propagation is almost entirely vegetative, giving little chance for new combinations of genes. Tubers are common among mosses of disturbed habitats. In *Leptobryum pyriforme* (Figure 15), if the protonema is grown in water, gametophore production ceases while tubers and rhizoidal gemmae develop abundantly.



Figure 15. *Leptobryum pyriforme*, a prolific moss in disturbed areas. Photo by Michael Lüth.

Hedderson (1995) demonstrated that in the Pottiales, production of sporophytes decreases with increasing life expectancy and is negatively associated with production of asexual brood bodies. Among the Funariales, Polytrichales, and Pottiales, dioicous taxa are more likely to produce asexual brood bodies, as are monoicous taxa for which gametangia are unknown. However, production of these brood bodies is positively associated with a longer

life expectancy, suggesting that at least the brood bodies do not deplete the plant of its energy supply.

Competition for resources and energy are likely to account for the suppression of gemma production during the production of sexual structures (Terui 1981). In *Marchantia polymorpha*, this response can be counteracted by the application of high sucrose concentrations, thus inducing development of gemmae cups.

Because of competing energy requirements, the two genders are likely to differ in their production of gemmae. Female plants require considerably more energy to produce archegonia and sporophytes than do male plants to simply produce antheridia. For example, Laaka-Lindberg (2001) found that in the leafy liverwort *Lophozia silvicola*, shoots lacking gametangia produced three times as many gemmae as female shoots, and that males produced twice as many. In *Marchantia polymorpha*, the number of gemmae cups produced by females was less than 1/6 that produced by their male counterparts (Voth 1941). Interestingly, when phosphate supplies decrease to stress levels, the number of cups on male plants decreases while the number on females increases, making them nearly equal!

## Ecological Function

Many types of asexual propagules comprise the propagule bank, available to colonize when disturbance brings them to the surface. In this way, taxa such as *Leptobryum pyriforme* and *Bryum rubens* readily colonize disturbed habitats and tip-up mounds (Risse 1987).

As Ross-Davis and Frego (2004) pointed out, our understanding of the role of bryophyte propagules in structuring communities is meager. To address this question, they examined the propagule rain and buried propagule banks of the mature mixed forests in southeastern New Brunswick, Canada. They found 51 taxa in the diaspore rain and buried propagule banks, but only 36 of these were present in the forest floor community. Differences in phenology were evident in the high seasonal variability within the aerial diaspore sources. Considering the hundreds of species available in the geographic region, these propagule sources are relatively limited, undoubtedly to nearby sources. The extant community was most similar to that of the aerial diaspores, suggesting that the buried diaspore bank was reminiscent of a different ecosystem and was ready if that set of conditions returned. Further discussion of brood bodies is in the adaptations subchapter on dispersal.

## Summary

Brood bodies include both gemmae and propagules (vegetative diaspores). Propagules can be defined as reduced buds, branches, or leaves that serve in reproduction. Gemmae are relatively undifferentiated vegetative reproductive structures and come in a variety of shapes and sizes. Brood bodies provide a safe mode to survive environmental disturbances such as desiccation, physical disturbance, and freezing. Colonist species rely almost entirely on brood bodies to invade newly disturbed habitats. Asexual means are important in colony spread of non-perennial taxa. Brood bodies are most common on dioicous (unisexual) species and compete for energy, thus typically not being

present during sporophyte production. As a result, they are often more common on males than on females.

Tubers of mosses occur on the rhizoids, but in liverworts they are extensions of the growing apex and grow toward the ground to serve as a perennating structure. In both cases they provide a diaspore bank that makes the species available when favorable conditions return.

Gemmae seem to require auxin (IAA) to develop and are inhibited from germination by the parent plant, presumably by lunularic acid in liverworts and probably by ABA in mosses. Production is affected by light intensity, wavelength, and moisture availability. These factors plus photoperiod and temperature are known to affect their germination and dormancy as well. Addition of sucrose enhances germination, suggesting the importance of photosynthesis to provide energy.

## Acknowledgments

Inspiration for this chapter evolved from discussions with Dr. Heinjo During and especially with Dr. Gert Steen Mogensen. Sanna Laaka-Lindberg kindly provided me with a copy of her thesis on asexual reproduction in hepatics. I appreciate the many suggestions from a student's perspective by Medora Burke-Scoll.

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