

CHAPTER 5-7

ECOPHYSIOLOGY OF DEVELOPMENT: BROOD BODIES

TABLE OF CONTENTS

Introduction	5-7-2
Definitions.....	5-7-2
Brood Bodies.....	5-7-4
Tubers	5-7-6
Development	5-7-7
Hormonal Effects	5-7-9
Auxins.....	5-7-9
Cytokinins.....	5-7-10
Environmental Effects.....	5-7-11
Temperature	5-7-11
Light.....	5-7-11
Water Relations.....	5-7-13
Gender.....	5-7-13
Nutrients and Inhibitors	5-7-14
Dormancy.....	5-7-14
Germination Time	5-7-15
Tradeoffs	5-7-15
Ecological Function	5-7-16
Summary	5-7-16
Acknowledgments.....	5-7-16
Literature Cited	5-7-17

CHAPTER 5-7

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Figure 1. *Syntrichia laevipila* (= *Tortula pagorum*), an acrocarpous moss with terminal gemmae. Photo by Michael Lüth, with permission.

Introduction

Ecology is a field of interconnections. Hence, writing any chapter brings with it many choices about where to include information. This chapter is in part redundant with the chapters on dispersal because an understanding of propagules was necessary to complete the dispersal story. That chapter emphasized travelling about and the environmental factors that influenced the success of that travel. This chapter emphasizes the physiology, but for clarity there is considerable overlap in what one must understand. The chapter is written to be independent so that one can read it without having to read the earlier chapter in order for it to make sense.

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 (Figure 2, Figure 37). 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-Figure 4) 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. In other words, they are specialized structures. **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).

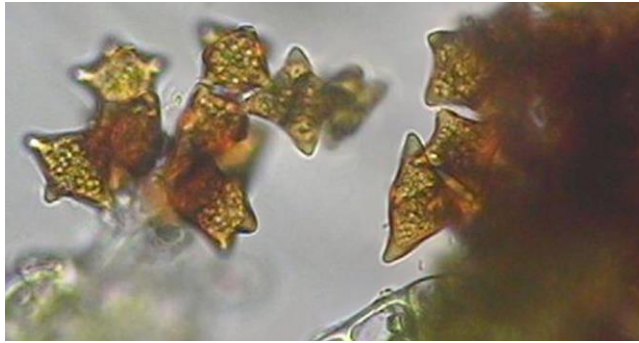


Figure 2. Leaf gemmae of *Lophozia bicrenata*, a leafy liverwort. Photo by Paul Davison, University of North Alabama, with permission.



Figure 3. *Leskeella nervosa* with bulbils at leaf bases. Photo by Michael Lüth, with permission.



Figure 4. *Bryum gemmilucens* showing axillary propagules. Photo by Michael Lüth, with permission.

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 5), *Dicranum flagellare* (Figure 6), and *Bryum argenteum* (Figure 7-Figure 8), 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 7-Figure 8). 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* grew well where the matchbook had previously walked on the moss, but did not appear on the control area.

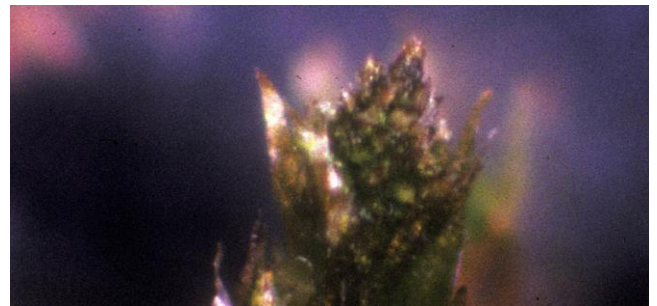
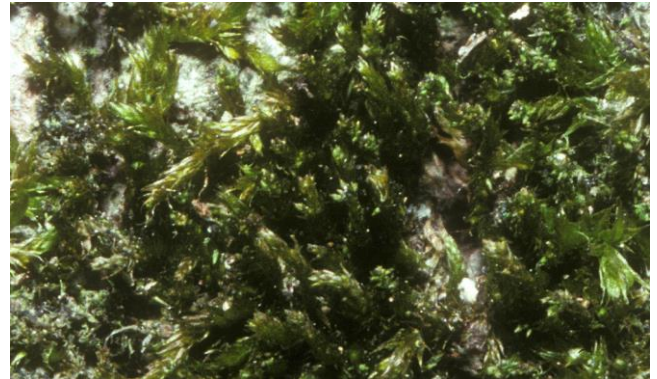


Figure 5. *Platygyrium repens* with bulbils crowded at branch tips. Photos by Janice Glime.

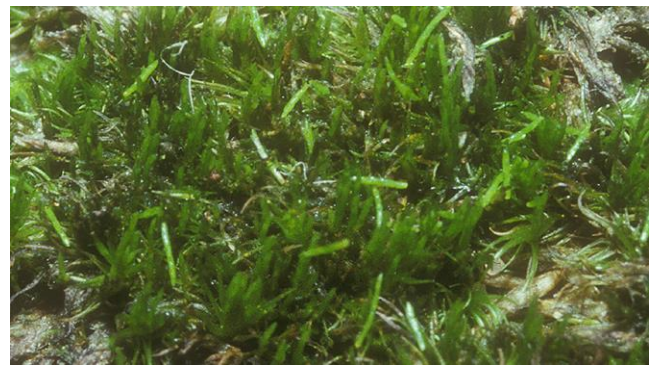


Figure 6. *Dicranum flagellare* with deciduous flagelliform branches. Photo by Janice Glime.



Figure 7. *Bryum argenteum* showing bulbous tips that break off easily to form new plants. Photo by Michael Lüth.



Figure 8. *Bryum argenteum* showing bulbous tips that break off easily to form new plants. Photo by Michael Lüth, with permission.

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. *Syntrichia laevipila*, Figure 1) and unstable habitat conditions.

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 4), 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 9) 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.

Chrobak and Sharp (1955) showed that scales from the deciduous flagelliform branches of *Dicranum flagellare* (Figure 6) were more likely to form protonemata than whole leaves or their proximal or distal halves (Figure 10).



Figure 9. *Tetraphis pellucida* with terminal gemma cups, the only moss with gemma splash cups. Upper photo by Janice Glime, lower by Paul Davison, University of North Alabama, with permission.

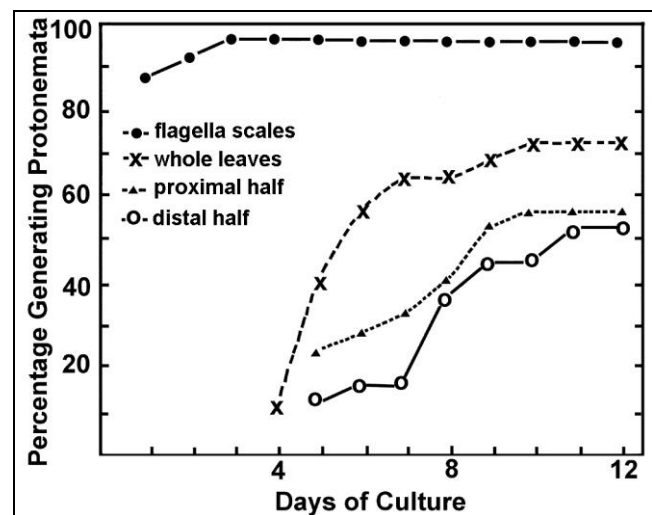


Figure 10. Success of producing protonemata from various leaf parts of *Dicranum flagellare* compared to that of the scales on the flagelliform brood branches. Redrawn from Chrobak & Sharp (1955).

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 11) 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* (Figure 12), *S.*

magellanicum (Figure 13), and *Polytrichum strictum* (Figure 14) all had poor regenerative ability.

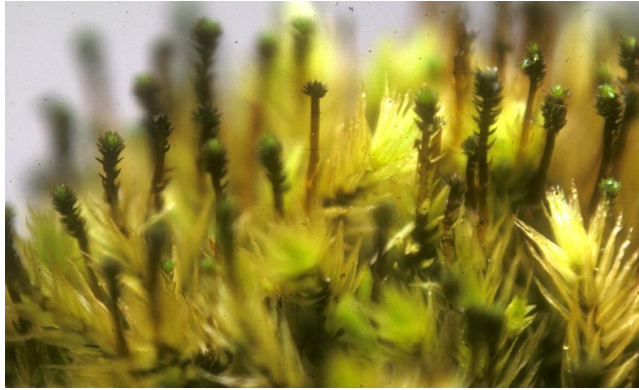


Figure 11. *Aulacomnium palustre* showing special extension of the stem with gemmae. Photo by Zen Iwatsuki, with permission.



Figure 12. *Sphagnum angustifolium*, a species that does not regenerate well. Photo by Michael Lüth, with permission.



Figure 13. *Sphagnum magellanicum*, a species that has poor regenerative ability. Photo by Michael Lüth, with permission.



Figure 14. *Polytrichum strictum*, a species with poor regenerative ability. Photo by Des Callaghan, with permission.

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.

In the leafy liverwort *Odontoschisma denudatum* (Figure 15-Figure 16), gemmae are produced in branched chains on the leaf margins (Duckett & Ligrone 1995). The initial cells of these gemmae are distinguished by forming a protrusion that contains a large central nucleus, small vacuoles, starch-free chloroplasts, and scattered cytoplasmic lipid droplets. Unlike other leaf cells, they lack oil bodies. However, as the gemmiferous filaments develop, oil bodies arise. These are closely associated with the cytoplasmic lipid bodies. These bodies swell rapidly, quickly reaching their final diameter. As the gemmae mature, the walls become dense and may account for their extreme water repellence. This repellant surface could permit them to be dispersed on the surface of a water film or in the air.



Figure 15. *Odontoschisma denudatum*, a species with apical gemmae. Photo by Michael Lüth, with permission.

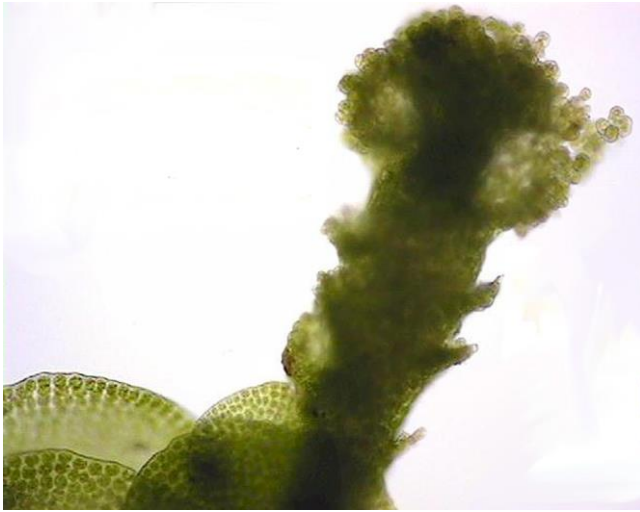


Figure 16. *Odontoschisma denudatum* showing apical gemmae. Photo by Paul Davison, with permission.

The germination and development of gemmae in the tropical moss *Calymperes* have been described (Egunyomi & Olarinmoye 1983; Duckett & Ligrone 1991).

Tubers

Tubers are defined very differently in mosses and liverworts (Magill 1990). 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 17).



Figure 17. *Bryum radiculosum* rhizoids with tubers. Photo by Michael Lüth, with permission.

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* (Figure 18).



Figure 18. *Schistostega pennata* showing pinched off gemmae on the protonema. Photo by Irene Bisang, with permission.

These tubers are densely packed with lipid droplets or starch grains (Duckett & Pressel 2003). In *Phaeoceros laevis* (hornwort; Figure 19), 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 notarissii* (Figure 20), 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.



Figure 19. *Phaeoceros laevis* with sporophytes. Photo by Bob Klips, with permission.



Figure 20. *Haplodontium notarisii*, a moss that stores dense starch in its tubers, permitting them to germinate and grow rapidly. Photo by Jan-Peter Frahm, with permission.

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.

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* (Figure 21), gemmae develop on the upper leaf surface from single initial cells of both the lamina and the costa, whereas in *Syntrichia* (= *Tortula papillosa*) (Figure 22) they develop only on the costa. 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.

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

Species	Reference
<i>Archidium alternifolium</i>	Arts 1990b
<i>Archidium globiferum</i>	Arts 1998
<i>Atrichum crispum</i>	Arts 1987d
<i>Atrichum tenellum</i>	Arts 1987d
<i>Barbula cylindrica</i>	Ellis & Smith 1983
<i>Didymodon tophaceus</i>	Side 1983
<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>Campylopus pyriformis</i>	Arts 1986c
<i>Chrysoblastella chilensis</i>	Matteri 1984
<i>Conocephalum conicum</i>	Paton 1993
<i>Cynodontium bruntonii</i>	Arts 1990a
<i>Didymodon nicholsonii</i>	Arts 1987b
<i>Discelium nudum</i>	Side & Whitehouse 1987
<i>Ditrichum difficile</i>	Arts 1998
<i>Ditrichum heteromallum</i>	Deguchi & Matsui 1986
<i>Ditrichum heteromallum</i>	Risse 1985b
<i>Ditrichum lineare</i>	Matsui <i>et al.</i> 1985
<i>Fissidens beckettii</i>	Arts 1998
<i>Fissidens cristatus</i>	Arts 1986a
<i>Funaria hygrometrica</i>	El-Saadawi & Zanaty 1990
<i>Haplodontium notarisii</i>	Arts 1988a
<i>Leptobryum pyriforme</i>	Imura <i>et al.</i> 1992
<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>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



Figure 21. *Tortula latifolia* showing gemmae on costa and lamina. Photo by Michael Lüth, with permission.



Figure 22. *Syntrichia* (=Tortula) *papillosa* showing gemmae restricted to costa. Photos by Michael Lüth, with permission.

Lipids are commonly stored in brood bodies of mosses, including *Aloina aloides* var. *ambigua* (Figure 23), *Pohlia annotina* (Figure 24), *Ephemerum serratum* (Figure 25), *Leptodictyum riparium* (Figure 26), *Weissia controversa* (Figure 27) (Goode *et al.* 1993), and *Splachnum ampullaceum* (Figure 28) (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.



Figure 23. *Aloina aloides*, a species with brood bodies that store lipids that help them survive desiccation. Photo from Proyecto Musgo, through Creative Commons.



Figure 24. *Pohlia annotina* with bulbils, a species that stores lipids in its brood bodies, permitting them to survive desiccation. Photo by Dick Haaksma, with permission.



Figure 25. *Ephemerum serratum* with capsules. This species produces brood bodies that store lipids, a protection against desiccation. Photo by Michael Lüth, with permission.



Figure 26. *Leptodictyum riparium*, a species that produces brood bodies that store lipids and survive when the moss dies from disturbance or desiccation. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.



Figure 27. *Weissia controversa* with capsules. This species stores lipids in its brood bodies, permitting them to survive when the plants die of desiccation or disturbance. Photo by Michael Lüth, with permission.



Figure 28. *Splachnum ampullaceum* with capsules. This species stores lipids in its brood bodies, permitting them to survive desiccation. Photo by Michael Lüth, with permission.

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

Hormonal Effects

Hormones control every stage of development, but their role in gemma production and germination is not clear, or at the very least, differs among species.

Rawat and Chopra (1976) found that secondary protonemata of *Bryum klinggraeffii* (Figure 29) 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. The biggest advantage may be that it creates a colony that can reduce water loss.



Figure 29. *Bryum klinggraeffii*, a species in which protonemata produce a diffusible substance that stimulates gemma production on young protonemata. Photo by Des Callaghan, with permission.

Auxins

Stange (1971, 1977, 1983) suggested that gemmae require **auxin** transport from the parent plant, based on disruption of gemma differentiation in *Riella helicophylla* (Figure 30) when treated with an auxin antagonist. Contrasting with the auxin requirement suggested by

Stange (1983) for *Riella helicophylla* gemmae, external auxins inhibit production of gemma cups in *Marchantia palmata* (Kumra & Chopra 1989). In *Lunularia cruciata* (Figure 31), auxins produced in the apical buds of the thalli inhibit the germination of the gemmae on the thallus (LaRue & Narayanaswami 1957).

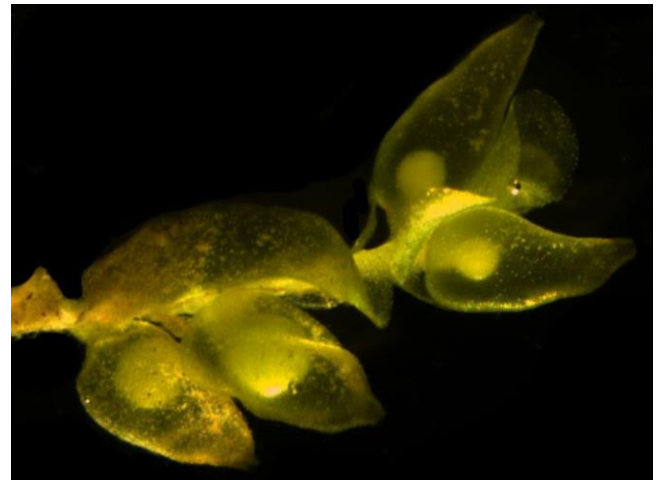


Figure 30. *Riella helicophylla*, a liverwort that seems to require external auxins for gemma differentiation. Photo from NACICCA, through Creative Commons.



Figure 31. *Lunularia cruciata* showing ungerminated gemmae on the thallus. Photo by Martin Hutten, with permission.

However, when ethylene and IAA are applied together in cultures of *Riella helicophylla* (Figure 30), the combination has positive, additive effects on cell elongation of gemmae (Stange & Osborne 1988). On the other hand, gemmae generally fail to germinate while still on the parent thallus of *Marchantia* (Figure 44-Figure 45) species, suggesting that these two genera might, like roots and stems of tracheophytes, respond differently to the same hormones. Botanists have assumed that the inhibition of gemmae on the parent thallus 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* (Figure 32) were grown on culture media that previously had had mature plants, the germination was inhibited. This suggests some sort of hormone leakage, but probably not the gaseous ethylene.



Figure 32. *Tetraphis pellucida* with gemmae, a species where the gemmae are inhibited by the parents. Photo by Michael Lüth, with permission.

Marchantia polymorpha (Figure 44) exhibits apical dominance, resulting from polarity (Binns & Maravolo 1972). This can be attributed to the behavior of auxins. Binns and Maravolo found evidence that there is an endogenous, basipetal auxin gradient that is vital to normal growth. Interestingly, cytokinins can destroy the polarity by causing the auxin-synthesizing capacity to increase.

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. 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 gemma cups are apical in *Tetraphis pellucida* (Figure 32).

Cytokinins

We know that cytokinins are needed to stimulate bud production on protonemata, so early researchers experimented with cytokinin effects on gemma production on the protonema. Logic would suggest that if cytokinins stimulate buds, they might inhibit protonemal gemma production.

Rahbar and Chopra (1982) found that the usual substances did not induce buds in the moss *Hyophila involuta* (Figure 33). In fact, when the protonemata were grown on basal Knop's medium, auxins, gibberellic acid, abscisic acid, chelates, vitamin B₁₂, activated charcoal, coconut milk, and altered hydration, pH, temperature, and light intensity and duration all failed to induce buds. Rather, they found that added cytokinins could initiate multicellular protonemal gemmae. Chopra and Dhingra-Babbar (1984) found similar responses in the moss *Trematodon breviculax*. Demonstrating the complexity of the bryophyte developmental system, Rahbar and Chopra (1982) demonstrated that for bud induction *H. involuta* required the interaction of IAA with kinetin or DMAAP.



Figure 33. *Hyophila involuta*, a moss in which cytokinins can induce gemma production. Photo by Niels Klazenga, with permission.

Mehta (1990) further explored the role of kinetin on *H. involuta* (Figure 33) and was able to isolate a protonemal diffusate from those protonemata that had gemmae. These protonemata served as "nurse protonemata" by promoting the growth of nearby protonemata. He found that kinetin (10^{-5} - 10^{-8} M) plus the protonemal diffusate acted synergistically on gemma formation. ABA (abscisic acid, 10^{-5} - 10^{-7} M), on the other hand, was inhibitory, resulting in no gemma formation.

Unlike *Hyophila involuta* (Figure 33) in Knop's plus Nitsch's medium, *Ptychostomum* (= *Bryum*) *capillare* (Figure 34) produced gemmae in both solid and liquid Nitsch's basal medium (Sarla & Chopra 1989). When the medium was supplemented with kinetin or 2iP (bryokinins), the protonemata produced gemmae, whereas the cytokinin 6-benzylaminopurine (BAP) caused the formation of buds instead, while the 2iP inhibited the growth of the protonemata. Gemmae on media with kinetin or BAP regenerated, producing secondary protonemata, but these failed to produce gemmae or buds in response to kinetin. Hence, not all cytokinins are created equal – they may cause opposite responses.



Figure 34. *Bryum capillare*, a moss that responds differently to different cytokinins, in some cases producing protonemal gemmae whereas in others they are inhibited. Photo by David T. Holyoak, with permission.

More recent work by Ahmed and Lee (2010) demonstrated that production of protonemal gemmae can vary with the concentration of IAA and kinetin in the moss *Palustriella* (= *Cratoneuron*) *decipiens* (Figure 35-Figure

36). In this species, kinetin influenced both gemma formation and gametophyte regeneration. Only low concentrations of IAA and kinetin (10^{-8}M) caused production of green, oval, mostly intercalary gemmae. Higher concentrations resulted in brown gemmae.



Figure 35. *Palustriella decipiens*. Photo by Michael Lüth, with permission.

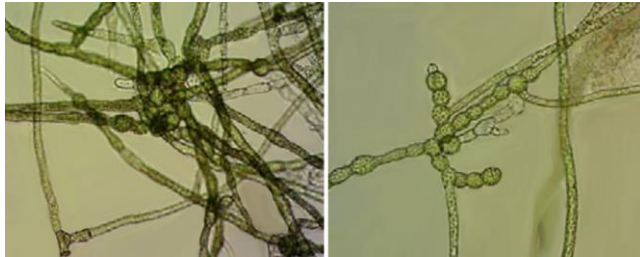


Figure 36. Effects of 10^{-8}M IAA (left) and 10^{-8}M kinetin (right) on gemma formation on protonemata of *Palustriella decipiens*. Photos modified from Ahmed & Lee 2010.

But the role of cytokinin not only interacts to control production of gemmae, in *Marchantia polymorpha* (Figure 44) it inhibits the germination of the gemmae (Binns & Maravolo 1972). Could production of exogenous cytokinins be the factor that prevents germination of gemmae on the parent thallus?

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.

Temperature

For plants living outside the tropical regions, cold can inhibit growth and freezing may actually kill the tissues. Therefore, it is reasonable to expect that those species that survive have developed means to sense temperature conditions in both the production and germination of gemmae and to maximize these when conditions are best suited to continued growth.

In Arctic populations of *Tetraphis pellucida* (Figure 32), gemmae (Figure 37) have a broad range of germination conditions similar to those of the spores (Forman 1964). The broad $18\text{--}30^\circ\text{C}$ range for gemma

production sharply contrasts to sporophyte maturation requirements of -0.2 to 7.3°C , or $0\text{--}5^\circ\text{C}$ in dark cultures. Such low temperature requirements account for the capsule maturation in spring. Gemmae, as for example gemmae of *Aulacomnium heterostichum* (Figure 38), which germinated after two years of storage in a freezer, seem to be able to persist as well as spores in cold conditions, and certainly better than some (Imura *et al.* 1991).

Light

Chopra and Rawat (1977) found that the response to temperature can be light dependent. In *Bryum klinggraeffii* (Figure 29) the initiation of secondary protonemata is correlated with protonemal age and growth. Although the gemmae of *B. klinggraeffii* are formed at or above 20°C in both light and dark, at $10\text{--}15^\circ\text{C}$ in the light this species forms larger, lobed green structures and stunted gametophores. The addition of 1.0 ppm kinetin causes moruloid buds to differentiate on the protonemata, but at lower concentrations of kinetin, these protonemata produce gemma-like structures. This 1ppm concentration even inhibits previously formed gemmae from developing into gametophores, instead resulting in stunted gametophores. But in a sister species, *Bryum coronatum* (Figure 39), temperatures of 30°C in both light and dark induce the formation of protonemal gemmae that resemble the rhizoidal gemmae. In *Leptobryum pyriforme* (Figure 49), the gemmae develop on both the protonemata and gametophores in the dark. The short story is that for these species low temperatures and sufficient light results in energy being shifted to the development of gametophores. The conditions that favor gemma formation do not favor bud formation.



Figure 37. *Tetraphis pellucida* gemma showing germination and development of rhizoid. Photo with permission from Biology 321 Course Website at the University of British Columbia, Canada, with permission.

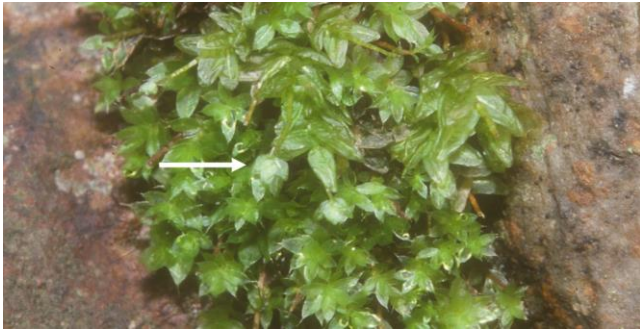


Figure 38. *Aulacomnium heterostichum* showing terminal gemmae (arrow). Photo by Janice Glime.



Figure 39. *Bryum coronatum*, a moss that produces protonemal gemmae when the temperatures reach 30°C. Photo by Michael Lüth, with permission.

Whitehouse (1980) found that *Schistostega pennata* (Figure 18), *Eucladium verticillatum* (Figure 40), *Gyroweisia tenuis* (Figure 41), and *Saelania glaucescens* (as *Didymodon trifarius*; Figure 42) 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 gemma 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 gemma cups (Chopra & Sood 1970).



Figure 40. *Eucladium verticillatum* (Whorled Tufa-moss) with mite. This moss responds to low light intensities by producing protonemal gemmae. Photo by Barry Stewart, with permission.

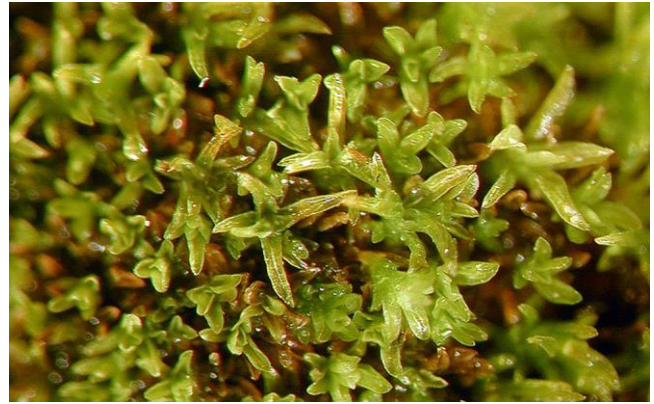


Figure 41. *Gyroweisia tenuis*, a moss in which the protonemata produce protonemal gemmae in low light. Photo by Michael Lüth, with permission.



Figure 42. *Saelania glaucescens*, a moss that responds to low light by producing protonemal gemmae. Photo by Michael Lüth, with permission.

Hence, we might surmise that photoperiod plays a role in gemma production. Lockwood (1975), working with the leafy liverwort *Cephalozia media*, found that the magnitude of the normal reproductive response could be significantly stimulated or inhibited by low concentrations of certain amino acids or kinetin. Certain metabolites (10^{-6} M arginine, cysteine, tryptophan plus kinetin) could overcome photoperiodic control of the reproductive response. Generally, organic compounds which stimulated asexual reproductivity under short photoperiod inhibited sexual reproductivity under long photoperiod.

Germination of gemmae and other propagula is likewise affected by light. In *Philonotis hastata* (Figure 43), the greatest germination rate for brood branches was around 750 lux, with percentage germinating decreasing in both directions from that figure (Egunyumi 1981). Such a low optimum would permit these propagula to germinate in the presence of tracheophyte ground flora where light is often minimal. In *P. hastata*, elongation of the propagules occurs on older, basal parts of the stem, and these are the most mature, becoming partially detached. However, both young and old brood branches will form new plants from any part. These are able to germinate in both low and high light, but in high light they typically fail to complete development of gametophores.



Figure 43. *Philonotis hastata*. This wet habitat moss has its greatest gemma germination at around 750 lux. Photo by Jan-Peter Frahm, with permission.

Otto and Halbsguth (1976) found that rhizoid induction on gemmae of *Marchantia polymorpha* (Figure 44) 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.



Figure 44. *Marchantia polymorpha* thallus with gemma cups. Photo by Michael Lüth, with permission.

Water Relations

No growth can occur in the absence of water, but water can also affect the production of gemmae as an adaptive strategy to take advantage of flooding. In *Bryoerythrophyllum campylocarpum* (= *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 compared to those on the stem or leaves.

In *Marchantia*, which is not typically a flood plain species, Kaul *et al.* (1962) found that gemmae did not produce rhizoids when grown in liquid culture, but did in solid media.

Gender

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* (Figure 45). 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.



Figure 45. *Marchantia inflexa*, a species where the sexes respond differently to light intensity. Photo by Scott Zona, through Creative Commons.

Mallón *et al.* (2006) experimented with vegetative propagules in the dung moss *Splachnum ampullaceum* (Figure 46) 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 46).

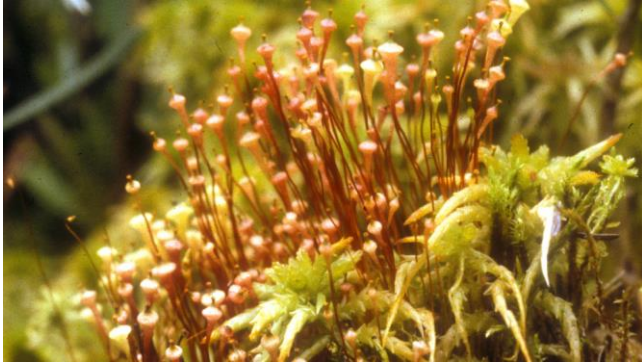


Figure 46. *Splachnum ampullaceum* growing on dung in a cow pasture. Photo by Janice Glime.

Nutrients and Inhibitors

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* (Figure 30) suggesting that the distal lobe of the gemma and the non-dividing cells of the rhizoid initials of the gemma have zones that facilitate 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 gemmaling, 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

One control of gemmae survival under conditions of cold or dehydration lies in their ability to maintain dormancy. We know that *Marchantia* gemmae (Figure 44) 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 ventricosa* var. *silvicola* (Figure 47) 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. This is a good "bet hedging" strategy that permits some gemmae to get an early start on the competition while the season is still favorable, but permits some gemmae to safely overwinter while some of the germinated gemmalings might not make it through.



Figure 47. *Lophozia ventricosa* with gemmae that can replace dead shoots. Photo by Jan-Peter Frahm, with permission.

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 ventricosa* var. *silvicola* (Figure 47), 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* (Figure 48) 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.



Figure 48. *Lunularia cruciata*, a liverwort where dormancy is induced by a variety of environmental conditions. Photo by David Holyoak, with permission.

This dormancy in *Lunularia cruciata* (Figure 48) 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 44). 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 gemma cups and vegetative plants of *Marchantia palmata*. The auxin IAA is likewise known to inhibit germination of gemmae of *Lunularia cruciata* (Figure 48) in the lab (LaRue & Narayanaswamy 1957).

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.

Germination Time

Germination times vary with type of propagule, size, age, and available water. And light seems to be required for most (all?). Propagula can germinate in 2-4 days in *Bryum* and *Syntrichia* (Llo Stark, pers. comm. 3 February 2015).

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* (Figure 39) 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* (Figure 32), one cannot find gemma cups and sporophytes on the same plant. Both need to occupy the same location at the shoot apex, making it physically impossible. But typically, even the population tends to have these at different times.

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 49), if the protonema is grown in water, gametophore production ceases while tubers and rhizoidal gemmae develop abundantly.



Figure 49. *Leptobryum pyriforme*, a prolific moss in disturbed areas. Photo by Michael Lüth, with permission.

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* (Figure 44), this response can be counter-acted by the application of high sucrose concentrations, thus inducing development of gemma 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 ventricosa* var. *silvicola* (Figure 47), shoots lacking gametangia produced three times as many gemmae as female shoots, and that males produced twice as many. In *Marchantia polymorpha* (Figure 44), the number of gemma 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* (Figure 49) and *Bryum rubens* (Figure 50) 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.



Figure 50. *Bryum rubens* showing red rhizoidal tubers in disturbed soil. Photo by Michael Lüth, with permission.

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.

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