

CHAPTER 5-6

ECOPHYSIOLOGY OF DEVELOPMENT: FRAGMENTS



Figure 1. *Dicranum viride*, a moss that fragments regularly by a row of abscission cells across the upper half of the leaf. Note the broken leaf tips. Photo by Michael Lüth.

Fragmentation

Fragmentation may be random pieces that break due to abrasion, decay, or animal severance, or they may be programmed genetically by means of an abscission layer such as demonstrated in *Dicranum viride* (Figure 1). In certain habitats, fragmentation may be a regular phenomenon, accounting for nearly all the reproduction.

Even fossil evidence supports the importance of fragments in the dispersal and reproduction of bryophytes (Miller 1985). And buried fragments often retain viability, providing the source for the flora when a disturbance returns an area to previous conditions (Wasley 2004).

Yet, when we diagram life cycles, fragmentation is usually ignored, and certainly for many flowering plants it is unimportant. However, in bryophytes it is often the fragments that perpetuate the species. Likewise, Giordana and coworkers (1996) found that regeneration from the detached leaves was the major form of regeneration in

moss *Pleurochaete squarrosa* (Figure 2). Other bryophytes, such as *Hyophila crenulata*, share their successful regeneration from fragmentation with other means such as gemmae (Olarinmoye 1981).

Mishler and Newton (1988) contend that in perennial mosses reproduction and spreading is almost entirely by means other than spores. Many populations exist for which capsules are unknown, particularly for dioicous taxa (having males and females on separate plants; unisexual). Even when all individuals in the population can produce both sexes (monoicous; bisexual), water is needed at the right time for sperm and egg to meet, so success rate will vary with habitat and with weather in a given year. Newton and Mishler (1994) suggest that vegetative reproduction, including specialized propagules, can occur under more stressful conditions. Whereas spores germinate best on previously uncolonized substrates, vegetative

reproductive units can do well even in contact with existing colonies. However, they suggest that such vegetative units cannot travel as far as spores – tradeoffs again.



Figure 2. *Pleurochaete squarrosa*, a moss that relies on detached leaves for regeneration. Photo by Michael Lüth.

Some mosses even provide special means to accomplish fragmentation. *Dicranum viride* (Figure 1), *D. fragilifolium*, and *Tortella fragilis* (Figure 3) have a weakened area of cells that break easily, releasing the upper portion of the leaf. This is so typical that these species can be identified by their chopped off appearance. Other species have **caducous** leaves (leaves that normally detach).



Figure 3. Broken tips on leaves of *Tortella fragilis*. Photo by Michael Lüth.

The success of fragments within short range (Newton & Mishler 1994) is supported by experiments by Nehira and Nakagoshi (1987). They removed a community of bryophytes and found that the community became re-established within 1-2 years. Most of the growth occurred in spring and autumn despite little seasonal variation in propagule dispersal. Thallose liverworts and pleurocarpous mosses were able to regenerate more quickly than the acrocarpous mosses. Yet these same fragments may have been eaten or decayed before ever growing if the researchers had not removed the parent colony. Newton and Mishler (1994) found that at least for the dry habitat mosses they studied, the parent plants seemed to inhibit growth of the fragments, with growth commencing once they were separated.

Fragmentation is likely to determine success of the species in some environments. Miles and Longton (1990) found that *Funaria hygrometrica* reproduced and spread easily by spores, whereas *Atrichum undulatum* and *Bryum argenteum* were likely to experience failure before sporelings produced gametophores. On the other hand, these latter two species freely accomplished regeneration from shoot fragments. This ability of *Atrichum* to regenerate easily from leaf fragments permitted it to dominate the ground cover rapidly after the construction of a parking lot on the Michigan Technological University campus (Glime 1982). *Funaria hygrometrica*, on the other hand, apparently manages to arrive, presumably by spores, and colonize charred ground within a year after a fire, as occurred after the big Yellowstone fire (Glime pers. obs.).

Even on rocks, where one might expect a small spore and protonema to have more success than a large fragment, it seems that fragments dominate the reproductive success. Keever (1957) did find that spores germinated on granite, but colonization through fragmentation was more rapid. One such rock-dwelling (and bark-dwelling) species is *Orthodicranum montanum*. Chrobak and Sharp (1955) established that this species grew more successfully from the proximal (basal) half of broken leaves than from whole leaves or the distal portion of the leaf (Figure 4).

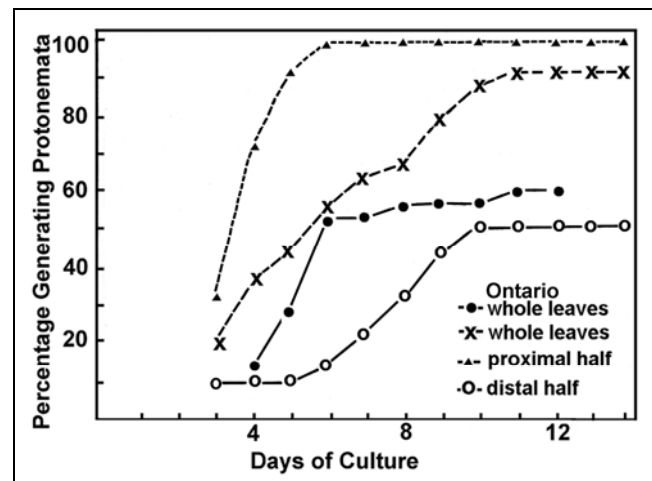


Figure 4. Success of producing protonemata from various leaf parts of *Orthodicranum montanum* from Michigan, USA, and Ontario, Canada. Redrawn from Chrobak & Sharp (1955).

Arctic and Alpine

In the Arctic, fragments on the ice are common, and are easily moved around over the smooth surface, permitting rapid transport over considerable distances. Miller and Howe Ambrose (1976) found more than 4000 viable moss fragments per cubic meter of snow on a summer snowbed on Bathurst Island in the Canadian high Arctic. These regenerated by protonemata, shoots, or rhizoids, or simply resuming growth. Liverworts, however, did not fare as well, with only one fragment producing new growth. They surmised that such moss fragments may be "routine" in Arctic climates.

Mogensen (1986) found that *Platydictya* was dispersed in Greenland primarily by vegetative propagules and Bonde (1959) found viable *Polytrichum piliferum* fragments among the wind-blown debris of a Colorado glacier. Lindsog and Eriksen (1995) found that the fragments of

mosses, in particular, that were on the glacier reflected accurately the composition of the surrounding vegetation.

The importance of fragments may reach its climax in the Antarctic. In colonizing a new Antarctic volcanic island, fragments of *Campylopus* (Figure 5), *Marchantia*, and *Bryum* species seemed to be the most important means of arrival (Smith 1984).



Figure 5. *Campylopus pilifer* showing fragments formed by tips of plants. Photo by Michael Lüth.

McDaniel and Miller (2000) demonstrated the importance of fragments in alpine areas of the Adirondack Mountains of New York, USA, and suggested that fragments dispersed in winter might be a significant means of establishing new populations following spring snowmelt. It would certainly be much easier for fragments to glide across a snow pack than to travel amid ground vegetation.

Streams and other Aquatic Habitats

In flowing streams, sporophytes seem rare, and asexual propagules seem to be unimportant. However, significant dispersal can occur from fragments during spring runoff, and entire clumps as well as branches and smaller fragments become impinged on rocks and roots in the stream. The larger surface area of fragments makes it more likely that they will become lodged than will the small spores and asexual propagules. Glime *et al.* (1979) demonstrated that for *Fontinalis duriaei* these actually do become established in nature, occasionally even achieving upstream movement (by feet of bears?).

For aquatic mosses and liverworts, fragmentation may be the only means of reproduction for many years before appropriate conditions exist for completing sexual reproduction. In dioicous mosses such as *Fontinalis*, sexual reproduction seems to be so infrequent as to be totally ineffective as a means of providing dispersal units (spores), whereas fragments are numerous during times of ice melt and high water (Figure 6; Conboy & Glime 1971, Glime *et al.* 1979, Glime & Knoop 1986). Even when spores are produced in this genus, the spore faces numerous challenges in becoming located where its subsequent protonema will neither be washed away nor desiccated, and sufficient light will be available for development. Since there is no documentation of the occurrence of any protonema of any *Fontinalis* species in the field, we can only conjecture about the success of reproduction by spores in this genus.



Figure 6. Fragments of *Fontinalis dalecarlica* caught in ice of a stream. Fragmentation appears to be its primary form of dispersal and new establishment. Photo by Janice Glime.

Dedifferentiation

Dedifferentiation is the process involved in the return of a cell to its embryonic state. It is necessary before a mature cell can form into a different kind of cell, or into a protonema, permitting the development of new plants from fragments. In bryophytes, virtually all cells seem to have the ability to undergo dedifferentiation once they have been isolated from the intact plant (Giles 1971). This is not the case for cells such as xylem elements of tracheophytes, which no longer have protoplasm and hence are non-living.

Moss fragments seem to retain their polarity, resulting in protonemata at the apical end and rhizoids at the basal end, but inverting them causes the base to act as the apex and vice versa (Westerdijk 1907), suggesting a gravimetric response by some growth factor. Mosses tend to have more regenerative ability at the base of the gametophyte than at the apex. Their sporophytes, however, are strongly polar in regeneration (von Wettstein 1924). Liverworts, on the other hand, seem to be much more strongly polar, and new growth is nearly restricted to the apical end of the gametophytes, but the sporophyte seems to lack polarity (Giles 1971). This strong polarity of the liverwort gametophyte regeneration, however, decreases with tissue age (Kreh 1909).

Earliest known reports on regeneration from bryophyte fragments come from Necker in 1774 (Giles 1971). Kreh (1909) showed that for liverworts, every part of the plant except the antheridia could regenerate. Nevertheless, few reports of liverwort regeneration from fragments are known. In mosses, even the seta will regenerate into a protonema, forming diploid gametophytes (von Wettstein 1924).

It is common for the nuclei to increase in size in dedifferentiating cells (Giles 1971). The dedifferentiation process involves a sort of "budding" of the chloroplasts and mitochondria, producing more of these organelles. At the same time, nucleolar volume increases only in regenerating cells. We now understand that the nucleolus is not an organelle in its own right, but rather that it is the site of extensive protein synthesis, hence staining more densely. This is an indication of building activity in the regenerating cell.

In *Campylopus pyriformis* fragments, it is the chloronema that gives rise to buds, with no caulonema forming. By contrast, and unlike the growth from a spore, the caulonema of *Plagiomnium affine* grows nearest the plant fragment and the chloronema is the farthest and youngest tissue (Sironval 1947; Bopp 1959a,b; Giles 1971). The ensuing buds develop, therefore, nearest the leaf fragment from the caulonema. Up to 100 secondary protonemata may originate from the dedifferentiated leaf cells of a single leaf in this species.

Establishment

It appears that fragments may survive better in water than spores, thus providing an additional means of long-distance dispersal. Dalen and Söderström (1999) tested five species of mostly terrestrial mosses and found that in all five taxa, regeneration frequency of fragments was lower than that of spores, but that fragments survived as well in water as they did dry, whereas spores did not.

Light quality and intensity may be influential in success of fragments. Dagar and coworkers (1980) found that for the thallose liverwort *Riccia discolor* regeneration is best in diffused light. Red light can induce regeneration; far-red inhibits it (Giles & von Maltzahn 1967, 1968). There is evidence the red/far-red system may affect the "budding" or division of the chloroplasts (Hahn & Miller 1966), and its reversibility suggests that phytochrome may be active during the process. Little else seems to be known about light effects specifically on fragments, so these phenomena may be restricted to certain taxa or habitats.

When dispersal occurs over long distances, it is quite likely that only one gender will arrive, making its survival dependent on asexual means. As discussed elsewhere, fragments seem to provide the easiest means by which bryophytes can be propagated for gardens, so one should expect that nature makes widespread use of this ability as well. When a plant is damaged, the damaged surface will often produce protonemata and/or rhizoids (LaRue 1942) and subsequently develop a new leafy gametophore. In other cases, the new plant may develop directly with no protonemal intermediary, as in the leafy liverwort *Scapania undulata* (Figure 7) that developed from a leaf fragment (Figure 8; Glime 1970).



Figure 7. *Scapania undulata* growing in its streamside, wet habitat. Photo by Michael Lüth.

It is the parent plant that determines which of these will develop – chloronema, caulonema, or rhizoids. Knoop (1984) tells us that small explants result in reversion to an

early developmental stage wherein single leaf cells behave like spores and form chloronemata. On the other hand, large fragments revert back only to caulonemata, or go directly to buds and gametophore plants. Furthermore, apical leaves regenerate more easily than basal leaves (Gay 1971). It is puzzling that in *Plagiomnium undulatum*, basal leaves regenerate only from the lamina, whereas apical ones regenerate only from the costa (Schröder *et al.* 1970).

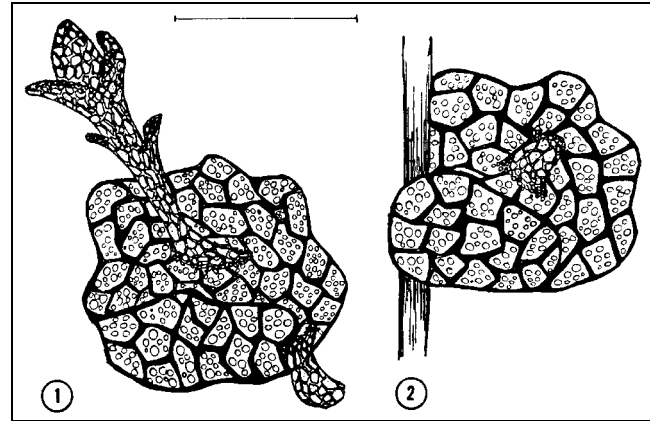


Figure 8. *Scapania undulata*, a leafy liverwort known to reproduce from fragments. 1: Young plant growing from detached leaf. 2: Bud of young plant growing on leaf still attached to living stem. Drawings by Flora Mace.

Mishler and Newton (1988) demonstrated that fragments can require conditions opposite to those required for spores. In their study, *Syntrichia princeps* fragments were slightly more successful when they experienced periodic drying, whereas the spores required continuously hydrated conditions. With such requirements, it is easy to understand why fragments are more successful on rocks and sand than are spores. Mishler and Newton attribute this success to the ability of fragments to produce a protonemal mat and new shoots much more rapidly than could spores. Furthermore, as mentioned earlier, the existing plants exhibited a much stronger inhibitory effect on the spores than on the fragments.

On the other hand, both spores and fragments can be inhibited by the presence of mature plants (Mishler & Newton 1988). *Dicranum* seemed to be more inhibitory than *Syntrichia princeps*, perhaps relating to the dry habitat of the latter. They considered that at least some of this inhibition was due to chemical exudates.

In an aquatic habitat, Florschütz and coworkers (1972) found that fragments of *Fissidens crassipes* (Figure 9) produced caulonemata, this time on moist bricks. This ability permitted them to spread rapidly in response to a rise in water temperature.

Regeneration often occurs from small leaf fragments that have begun to decay. This could be an indication that an inhibitor has been lost, or some colonizing microorganism could be providing a hormonal signal that starts the development. When growing *Leucolejeunea clypeata* on Ca-free media, Geldreich (1948) discovered that only contaminated leaves of Ca-deficient plants produced regenerants. It was only mature or old and necrotic leaves that regenerated, and these Ca-deficient leaves had oil bodies that were characteristic of old, senescent leaves. Since the contaminating microorganisms were typical of soil flora, and regenerants of this species

are known in nature (Fulford 1947), perhaps the microorganisms do indeed play a role in providing the necessary stimulus.



Figure 9. *Fissidens crassipes* growing on rock. Photo by Michael Lüth.

Liverworts rarely regenerate from fragments. Occasionally a leaf may produce a new plant, as for example that of *Scapania undulata*, an aquatic leafy liverwort mentioned earlier (Glime 1970). Could it be that liverworts dry out too rapidly and cells lose their viability before new plants can arise? Would this explain the accomplishment of this aquatic species?

Growth Regulators

Like all other developmental processes, hormones and other growth regulators influence the developmental pathway of fragments. Patidar and coworkers (1987) found that 0.03 ppm gibberellin can stimulate regeneration in the thallose liverwort *Targionia hypophylla* (Figure 10). Concentration is of course important; at 0.1 ppm gibberellin is inhibitory to *T. hypophylla*.



Figure 10. *Targionia hypophylla*. Photo by Michael Lüth.

Few studies seem to have centered specifically on growth regulators of fragments, yet many in vitro studies are actually studies of fragments, particularly those of pleurocarpous mosses. Presumably, the same growth regulation applies to fragments as to the intact plants covered earlier. Yet, literature on the wound response seems to be lacking, as is literature on the remarkable ability of some fragments to persist under extremely stressful conditions. For example, we have grown *Fontinalis flaccida* from specimens dried for three months under herbarium conditions (ca. 30% relative humidity). In

another case, *Fontinalis novae-angliae* that had been boiled for about 12 hours daily for two weeks developed new leaves on one portion of the remaining stem when it was returned to its native stream (Glime & Carr 1974). And what permits a partially decayed stem to suddenly spring forth a new plant after it has been uncovered from many years of burial (Daring *et al.* 1987)?

Animal Dispersal

Dispersal by animals is scarcely known in the bryophytes. Yet, we must suppose that the various activities of animals contribute to bryophyte movement. Various aquatic insects, especially Trichoptera (caddis flies), use mosses or liverworts in their cases, so the insect will carry the bits around wherever it goes. When drift carries the insect downstream, the moss goes too, and if the insect crawls upstream in the quiet interface at the bottom, the moss comes along. Lacewings (*Nodita pavidia*) carry viable bryophytes (and lichens) on their backs as camouflage (Slocum & Lawrey 1976).

Bears, beaver, and other animals can get mosses tangled around among their toes and carry them for miles. Birds carry them off to build nests. I have even concluded that the turtle in my garden room was responsible for the distribution of *Conocephalum conicum* (Figure 11) all over the room from the single spot where it had been planted. When the turtle died, the spread of the liverwort stopped. In a field experiment, I found fragments of tagged *Fontinalis duriaei* upstream from their initial location, a movement that could only have been effected by animals such as bears or humans.



Figure 11. *Conocephalum conicum* showing evidence of herbivory (arrows) that could lead to dispersal of fragments. Photo by Janice Glime.

Others may spread bryophytes as they eat them (Slack 1936, Mutch & Pritchard 1984), particularly if they only digest the surface organisms and return the moss fragments with their feces. Suren and Winterbourn (1991) found that 14 aquatic invertebrate taxa had bryophyte fragments in their guts, and two tipulid larvae regularly consumed bryophytes. I tested the hypothesis that rainbow trout, known to strike at anything, could serve as dispersal agents by eating the aquatic *Fontinalis duriaei*. However, the fish could not be tempted to strike at or eat the moss, even when it housed numerous aquatic insects. Finally, we force fed the fish. The moss was delivered back as feces in a neat, cylindrical package with bright green moss. At last it

seemed we had demonstrated a potential upstream dispersal mechanism! But, alas, we were surprised the following day to find that the moss had lost all its color (Figure 12), even though it was maintained in a gallon jar of its own stream water at a cool temperature. It does not appear that rainbow trout are likely dispersal vectors after all!

I have watched larvae of the Rhyphidae dipteran eat wet, dirty (most likely with diatoms) mosses and observed fragments of green moss come out the other end, clean. These fragments would be ideal propagules, although not dispersed very far, but I did not culture them to see if they met the same fate as the trout package.

Further discussion of bryophyte fragment dispersal is in the adaptations subchapter on dispersal.



Figure 12. Feces of rainbow trout consisting primarily of *Fontinalis duriaei* as a result of force-feeding. Photo by Janice Glime.

Summary

Fragmentation results from random breakage or from genetically programmed cleavage areas on leaves, buds, or stems. For perennial mosses, especially pleurocarpous mosses, it is typically the primary means of spreading. Arctic/alpine and aquatic habitats may rely primarily on this type of reproduction. Fragments are more likely to become established than spores and survive better in water than do spores. Their establishment can be inhibited by the presence of mature plants, but they have a greater competitive ability than spores.

Regeneration from mature cells requires **dedifferentiation** and may begin as protonemata, rhizoids, or both. Light quality and intensity may play a role in early development. Little is known about growth regulation, but gibberellin can stimulate regeneration in at least some bryophytes. Dispersal can be accomplished by wind, water, and animals, sometimes because the animal transports the bryophyte for use in a nest or house.

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Literature Cited

Bonde, E. K. 1969. Plant disseminules in wind-blown debris from a glacier in Colorado. *Arct. Alp. Res* 1: 135-139.

- Bopp, M. 1959a. Neue Gesichtspunkte zum Problem der Protonema differenzierung. *Rev. Bryol.* 28: 137-163.
- Bopp, M. 1959b. Neue Gesichtspunkte zum Problem der Protonemadifferenzierung. *Rev. Bryol. Lichenol.* 28: 319-325.
- Chrobak, B. and Sharp, A. J. 1955. A preliminary comparative study of asexual reproduction in *Dicranum flagellare* and *Dicranum montanum*. *J. Hattori Bot. Lab* 28: 122-128.
- Conboy, D. A. and Glime, J. M. 1971. Effects of drift abrasives on *Fontinalis novae-angliae* Sull. *Castanea* 36: 111-114.
- Dagar, J. C., Ahlawat, A. S., and Singh, V. P. 1980. Effect of light quality on the growth and photosynthetic pigments of *Riccia discolor* L. et L. *Cryptog. Bryol. Lichénol.* 1: 305-309.
- Dalen, L. and Söderström, L. 1999. Survival ability of moss diaspores in water – An experimental study. *Lindbergia* 24: 49-58.
- During, H. J., Bruges, M., Cros, R. M., and Lloret, F. 1987. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. *Lindbergia* 13: 137-149.
- Florschütz, P. A., Gradstein, S. R., and Rubers, W. V. 1972. The spreading of *Fissidens crassipes* Wils. (Musci) in the Netherlands. *Acta. Bot. Neerl.* 21: 174-179.
- Fulford, M. 1947. *Leucolejeunea cyypeata* – its habit and structure. *Bryologist* 50: 97-112.
- Gay, L. 1971. Correlative systems controlling regeneration on gametophytes of *Polytrichum juniperinum* Willd. *Z. Pflanzenphysiol.* 66: 1-11.
- Geldreich, E. E. Jr. 1948. Some effects of calcium deficiency on the vegetative plant of *Leucolejeunea clypeata*. *Bryologist* 51: 218-229.
- Giles, K. L. 1971. Dedifferentiation and regeneration in bryophytes: A selective review. *N. Zeal. J. Bot.* 9: 689-694.
- Giles, K. L. and Maltzahn, K. E. von. 1967. Interaction of red, far-red and blue light in cellular regeneration of leaves of *Mnium affine*. *Bryologist* 70: 312-315.
- Giles, K. L. and Maltzahn, K. E. von. 1968. Spectrophotometric identification of phytochrome in two species of *Mnium*. *Can. J. Bot* 46: 305-306.
- Giordana, S., Alfano, F., Esposito, A., Spagnuolo, V., Basile, A., and Castaldo Cobianchi, R. 1996. Regeneration from detached leaves of *Pleurochaete squarrosa* (Brid.) Lindb. in culture and in the wild. *J. Bryol.* 19: 219-227.
- Glime, J. M. 1970. An observation on the vegetative reproduction of *Scapania undulata*. *Bryologist* 73: 624-625.
- Glime, J. M. 1982. New mosses by a new road at Michigan Technological University. *Mich. Bot.* 21: 58.
- Glime, J. M. and Carr, R. E. 1974. Temperature survival of *Fontinalis novae-angliae* Sull. *Bryologist* 77: 17-22.
- Glime, J. M. and Knoop, B. C. 1986. Spore germination and protonemal development of *Fontinalis squamosa*. *J. Hattori Bot. Lab.* 61: 487-497.
- Glime, J. M., Nissila, P. D., Trynoski, S. E., and Fornwall, M. D. 1979. A model for attachment of aquatic mosses. *J. Bryol.* 10: 313-320.
- Hahn, L. W. and Miller, J. H. 1966. Light dependence of chloroplast replication and starch metabolism in the moss *Polytrichum commune*. *Physiol. Plant.* 19: 134-141.
- Keever, C. 1957. Establishment of *Grimmia laevigata* on bare granite. *Ecology* 38: 422-429.
- Knoop, B. 1984. Development in bryophytes. In: Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, pp. 143-176.

- Kreh, W. 1909. Über die Regeneration der Laubmoose. *Nova Acta Leopold* 90: 213-301.
- LaRue, C. D. 1942. The effect of wounding, of wound hormones and of growth hormones on rhizoid formation in mosses and liverworts. *Bryologist* 45: 35-39.
- Lindskog, A. and Eriksen, B. 1995. The identification of fossil plant fragments in glaciers. *Svensk Bot. Tidskr.* 89: 83-88.
- McDaniel, S. F. and Miller, N. G. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. *Bryologist* 103: 592-600.
- Miles, C. J. and Longton, R. E. 1990. The role of spores in reproduction in mosses. *J. Linn. Soc. Bot.* 104: 149-173.
- Miller, N. G. 1985. Fossil evidence of the dispersal and establishment of mosses as gametophyte fragments. *Monogr. Syst. Bot. Missouri Bot. Gard.* 11: 71-78.
- Miller, N. G. and Howe Ambrose, L. J. 1976. Growth in culture of wind-blown bryophyte gametophyte fragments from arctic Canada. *Bryologist* 79: 55-63.
- Mishler, B. D. and Newton, A. E. 1988. Influence of mature plants and desiccation on germination of spores and gametophytic fragments of *Tortula*. *J. Bryol.* 15: 327-342.
- Mogensen, G. S. 1986. Taxonomy and distribution of Greenland mosses. II. *Platydictya* Berk. (Musci: Amblystegiaceae [sic]). *Lindbergia* 12: 139-143.
- Mutch, R. A. and Pritchard, G. 1984. The life history of *Philocasca alba* (Trichoptera: Limnephilidae) in a Rocky Mountain stream. *Can. J. Zool.* 62: 1282-1288.
- Nehira, K. and Nakagoshi, N. 1987. Reproductive processes of bryophytes in an urban environment. *Symp. Biol. Hung.* 35: 269-278.
- Newton, A. E. and Mishler, B. D. 1994. The evolutionary significance of asexual reproduction in mosses. *J. Hattori Bot. Lab.* 76: 127-145.
- Olarinmoye, S. O. 1981. Regeneration and gemma development in *Hyophila crenulata* C. Muell. ex Dus. *Cryptog. Bryol. Lichénol.* 2: 457-460.
- Patidar, K. C., Jain, D., and Solanki, C. M. 1987. Effects of gibberellic acid on regeneration of *Targionia hypophylla* L. *Cryptogamie, Bryol. Lichenol.* 8: 151-155.
- Schröder, H., Muller-Stoll, W. R., and Erdtmann, J. 1970. Entstehung von Regeneraten an den Blättern von *Mnium undulatum* L. in Abhängigkeit von deren Insertion und vom Blattbezirk. *Biochem. Physiol. Pflanzen* 161: 542-559.
- Sironval, C. 1947. Expériences sur les stades de développement de la forme filamenteuse en culture de *Funaria hygrometrica* L. *Bull. Soc. Bot. Belg.* 29(1-2): 48-78.
- Slack, H. D. 1936. The food of caddis fly (Trichoptera) larvae. *J. Anim. Ecol.* 5: 105-115.
- Slocum, R. D. and Lawrey, J. D. 1976. Viability of the epizoic lichen flora carried and dispersed by green lacewing (*Nodita pavidia*) larvae. *Can. J. Bot.* 54: 1827-1831.
- Smith, R. I. L. 1984. Colonization by bryophytes following recent volcanic activity on an Antarctic island. *J. Hattori Bot. Lab.* 56: 53-63.
- Suren, A. M. and Winterbourn, M. J. 1991. Consumption of aquatic bryophytes by alpine stream invertebrates in New Zealand. *N. Zeal. J. Mar. Freshwat. Res.* 25: 331-343.
- Wasley, J. 2004. The Effect of Climate Change on Antarctic Terrestrial Flora. Ph. D. dissertation, University of Wollongong, Australian Digital Theses Program. Accessed on 26 April 2006 at <<http://www-library.uow.edu.au/adt-NWU/public/adt-NWU20050707.151516/>>.
- Westerdijk, J. 1907. Zur Regeneration der Laubmoose. *Rec. Trav. Bot. Neerl.* 3: 1-66.
- Wettstein, E. von. 1924. Morphologie und Physiologie des Formwechsels der Moose auf genetische Grundlagen. I. Z. induckt. Abstamm. Vererb. Lehre. 33: 1-236.

