

CHAPTER 8-1

TROPICS: GENERAL ECOLOGY

JANICE M. GLIME AND S. ROBERT GRADSTEIN

TABLE OF CONTENTS

General Ecology.....	8-1-2
Water Relations.....	8-1-5
Light.....	8-1-8
Life and Growth Forms.....	8-1-9
Nutrient Relations.....	8-1-12
Productivity.....	8-1-13
Climate Effects.....	8-1-16
Reproductive Biology and Phenology.....	8-1-16
Life Cycle Strategies.....	8-1-17
Mosses.....	8-1-18
Antheridia and Archegonia.....	8-1-20
Monoicous vs Dioicous.....	8-1-20
Propagules and Regrowth.....	8-1-21
Propagule Forms.....	8-1-22
Fragments.....	8-1-25
Spore Size.....	8-1-26
Diaspore Banks.....	8-1-26
Prolonged Protonemal Stage.....	8-1-28
Liverworts.....	8-1-28
Monoicous vs Dioicous.....	8-1-28
Neoteny.....	8-1-29
Reduced Numbers of Antheridia and Archegonia.....	8-1-30
Short Life Cycles.....	8-1-30
Short Spore Longevity.....	8-1-31
Prolonged Protonemal Stage.....	8-1-31
Types of Gemmae.....	8-1-32
Diaspore Banks.....	8-1-36
Rheophilic Adaptations.....	8-1-36
Dispersal.....	8-1-37
Sampling.....	8-1-41
Braun-Blanquet Sampling Method.....	8-1-42
Drying Specimens.....	8-1-42
Summary.....	8-1-43
Acknowledgments.....	8-1-43
Literature Cited.....	8-1-43

CHAPTER 8-1

TROPICS: GENERAL ECOLOGY

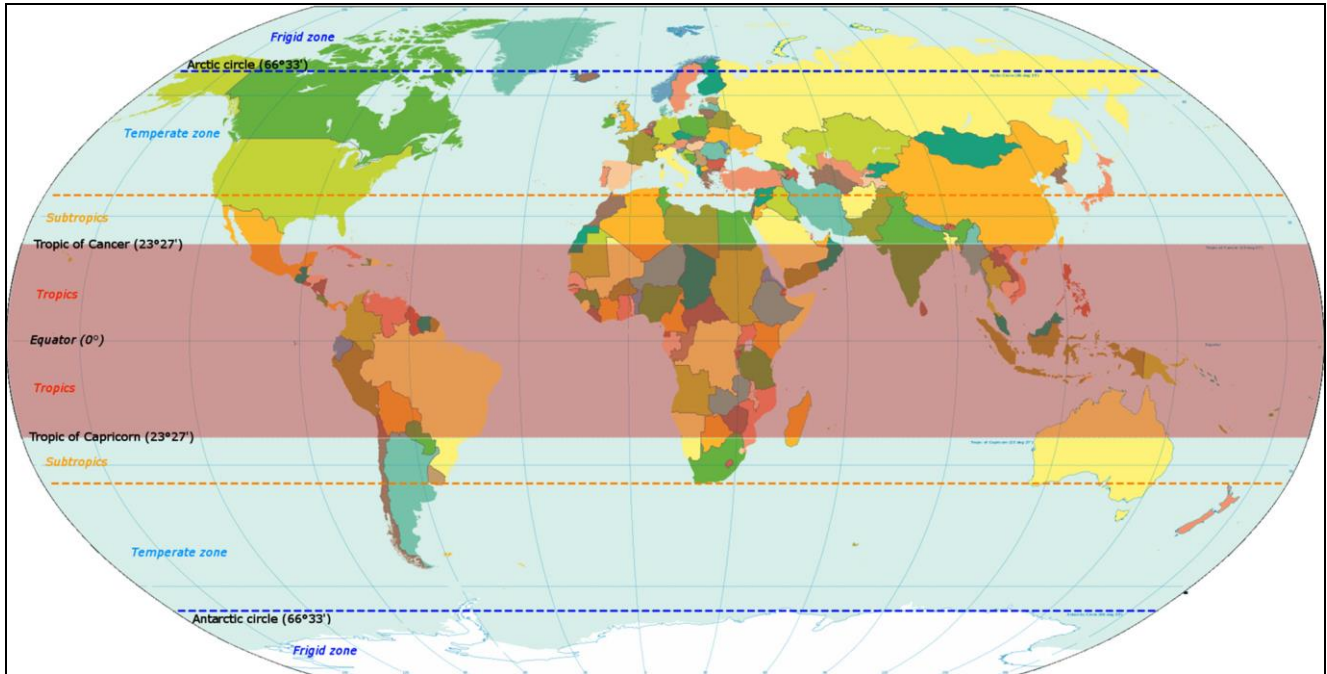


Figure 1. World map indicating tropics in pink band, subtropics in orange dotted line. Photo from KVDP, through Creative Commons.

General Ecology

Occupying the area between the Tropic of Cancer and the Tropic of Capricorn, the tropics comprise the most complex ecosystems of the world (Figure 1), extending 23°27' north and south of the Equator. The tropical land mass is nearly one-third of the land on the planet (Schuster 1988). Complex ecosystems provide multiple niches (Figure 2), and the tropics undoubtedly provide the highest number of niches anywhere with their multi-storied forests (Figure 3).



Figure 2. Tropical forest and waterfalls at Quebrada Cataguana, Honduras. Photo by Josiah Townsend, with permission.

Bryophytes in the tropics were largely ignored in early botanical studies. Resident botanists, lacking training by bryologists and preceding the development of taxonomic aids, largely ignored the bryophytes (Moreno 1992). Although bryophytes have been recorded from the tropics since the 18th century, tropical bryophyte ecology started to emerge only rather recently because keys to identify tropical bryophytes were long lacking. Early fieldwork in the tropics was done by foreign bryologists, *e.g.* Goebel (1888), Schiffner (1900), Fleischer (1904-1923) and Giesenhagen (1910) in Asia, and by Spruce (1884-1885) and Spruce and Wallace (1908) in tropical America. Spruce collected extensively in the Amazon regions and the Andes of Ecuador and Peru, and identified the liverworts himself, but gave his moss collections to William Mitten, who subsequently published them in *Musci Austro-Americani* (Mitten 1869).

Early studies on the ecology of tropical bryophytes has been summarized by Pócs (1982) and Richards (1984a). Some of the earliest studies were on **epiphyllous** (growing on leaves of other plants) bryophytes and will be discussed in the subchapter on epiphylls.

In Puerto Rico, Fulford *et al.* (1970, 1971) described liverwort communities in the elfin (cloud) forest (Figure 4). Griffin *et al.* (1974; Griffin 1979) reported on altimontane (Figure 5) bryophytes. Steere (1970) took advantage of the haploid condition of bryophytes to report on the effects of ionizing cesium radiation in Puerto Rico.

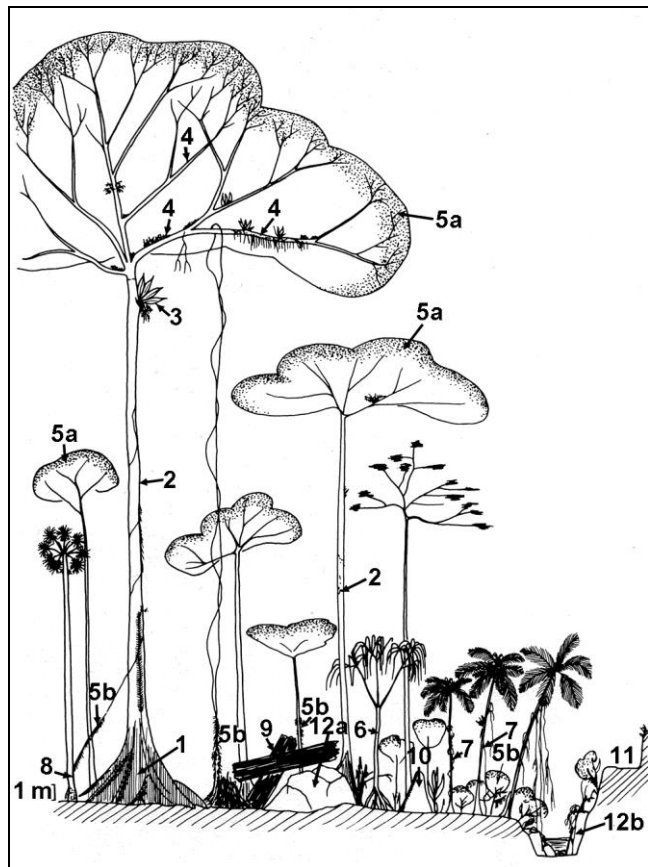


Figure 3. Microhabitats in tropical forests. **1:** Bases of large trees; **2:** upper parts of trunks; **3:** macro-epiphyte nests; **4:** bark of main branches; **5a:** terminal twigs and leaves; **5b:** bark of lianas, shrub branches, and thin trunks; **6:** *Pandanus* stems; **7:** tree fern stems; **8:** palm trunks and basal prop roots; **9:** rotting logs and decaying wood; **10:** soil surface and termite mounds; **11:** roadside banks and cuttings; **12a:** rocks and stones; **12b:** submerged or emergent rocks in streams. Image modified from Pócs 1982.



Figure 4. Elfin cloud forest fog, Luquillo Mountain, Puerto Rico, USA. Photo by Janice Glime.

Once the bryophytes were better known, bryologists began asking ecological questions (e.g. Frahm & Gradstein 1990). Based on the results of elevational transect analyses throughout the tropics, Frahm & Gradstein (1991) recognized five tropical rainforest belts using bryophytes as indicators: lowland rainforests (Figure 6-Figure 7), submontane rainforests (=premontane rainforest; Figure 8), lower montane rainforests (Figure 9), upper montane rainforests (Figure 10), subalpine rainforests (Figure 11).



Figure 5. Drakensberg, South Africa, altimontane region. Photo by Diriye Amey, through Creative Commons.



Figure 6. Lowland rainforest tree in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 7. Canopy in lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 8. Submontane rainforest, Peruvian Andes. Photo by Robbert Gradstein, with permission.



Figure 9. Lower montane forest in Colombia, rich in lignified vascular epiphytes. Photo by A. M. Cleef, courtesy of Robbert Gradstein.

To further complicate our ecological understanding, early differences in methodology made ecological comparisons nearly impossible, while poor understanding of the taxonomy gave that area of study priority and limited the kinds of ecological studies that were feasible. The earliest limited ecological studies have included the relationships among climate, mountain topography, vegetation zones (Pócs 1976), ecology, reproductive biology, and dispersal trends (Schuster 1988), biomass (Frahm 1990b), water relations, and CO₂ exchange (Zotz *et al.* 1997).



Figure 10. Upper montane forest, Pui-Pui Protection Forest, Peru. Photo by E. Lehr and R. von May, through Creative Commons.

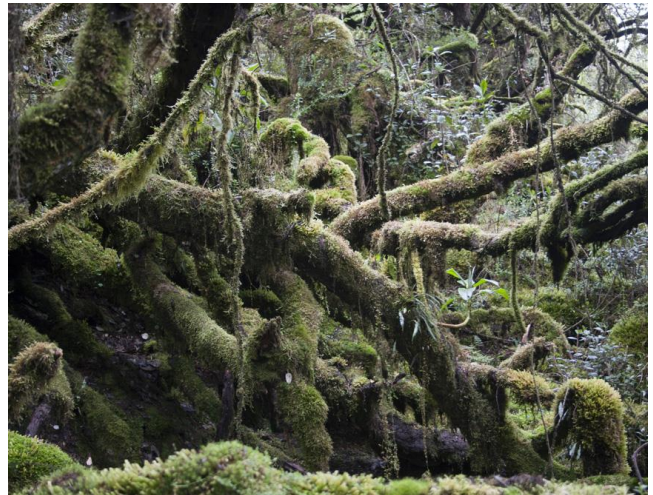


Figure 11. Subalpine dwarf mossy *Polylepis* forest in Ecuador. Photo by K. Romoleroux, courtesy of Robbert Gradstein.

Richards (1984a) provided a very useful overview of the ecology of tropical forest bryophytes, making it clear that studies at that time were limited and his coverage was superficial. One of the things that quickly becomes obvious is that most of the known ecological information relates to **epiphytes** (growing on other plants). This is because most of the tropical bryophytes are epiphytes, limited by low light levels and leaf burial on the forest floor.

In the Luquillo Mountains of Puerto Rico (Figure 12), three environmental factors cause contrasting communities of leafy liverworts (Bryant *et al.* 1973). Using area x area (**Q-mode**) analysis, they demonstrated that high-altitude liverwort communities contrast with those of low altitudes, shaded, moist habitats contrast with open, exposed habitats of all elevations, and disturbed low-elevation habitats contrast with less disturbed habitats of all elevations. **R-mode** analysis (species x species) produced nearly identical results to those of Q-mode.



Figure 12. Luquillo Mountains, Puerto Rico. Photo by Stan Shebs, through Creative Commons.

For recent species lists of tropical studies, see Gradstein *et al.* (2001) for tropical America, Churchill *et al.* (2010) on Bolivia, and many others. For additional older studies and reviews of tropical bryophyte species lists and ecology, see Delgadillo (1976) on Mexico; Lisboa (1976) on the Amazon; Egunyomi (1978) on distribution of pantropical *Octoblepharum albidum* (Figure 13) in Africa; Pócs (1982) on tropical forests; Gradstein *et al.* (1983) on Neotropical-African liverwort disjunction; Richards (1984a, b, 1988) on tropical forest ecology; Linares (1986) on the high Andes; Gradstein & Pócs (1989) on tropical rainforest bryophytes; Frahm & Gradstein (1990, 1991) on bryophytes as indicators of tropical rainforests; Frahm & Kürschner (1992) on tropical rainforests in general; Frangi & Lugo (1992) on biomass and nutrients in a Puerto Rico floodplain; Delgadillo (1993) on Neotropical-African disjunction; Miehe & Miehe (1994) on ecology in East Africa; Lösch *et al.* (1999) on Central African photosynthesis; Merwin & Nadkarni (2002) on tropical ecology, and others.



Figure 13. *Octoblepharum albidum*, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Niels Klazenga, with permission.

Water Relations

In general, tropical adaptations reflect moisture conditions, with light and other factors being secondary (Frahm 1990a). Hence, we find that lowland forests are dominated by **mats**, and montane and cloud forests by

welts (loosely interwoven, often ascending growth form). Thiers (1988) reported the leafy liverworts *Radula* (Figure 111), *Frullania* (Figure 14), and various **Lejeuneaceae** (Figure 130-Figure 131) to exhibit the mat growth form on their bark substrate; these taxa tend to lack dominance in the main axis. Where they form extensive mats on tree boles, they are able to trap water as it runs down the tree.



Figure 14. *Frullania* sp. from the Neotropics, demonstrating mat growth habit. Photo by Michael Lüth, with permission.

Studies on water relations seem to have been more common than other areas of tropical bryophyte ecology. Pócs (1980) studied the water interception and retention by bryophytic cover (biomass) in different types of tropical forest, forming the basis for all other studies on the subject. He found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates. Rainfall and epiphytes will be discussed in Chapter 8-3 of this volume.

When working on disturbance, Norris (1990) suggested four aspects of water relations that required consideration: hydration/dehydration frequency; hydration duration; dehydration duration; degree of water loss. We have since learned that rate of dehydration is important (Greenwood & Stark 2014). As Norris (1990) further surmised, these are all biomass-dependent functions, wherein large colonies typically maintain hydration longer than smaller colonies. Lateral branching of the colony allows lateral movement of capillary water. This spread of the water extends to clones that are in contact with each other. On the other hand, when tufts and cushions are separated, they contribute little to lateral spread of the water over the substrate.

Johnson and Kokila (1970) experimented with ten species of tropical mosses to determine their resistance to desiccation. These were exposed to relative humidities ranging 10-76% for four hours. After a recovery period of 24 hours, the researchers found the mosses could be divided into high and low resistance groups. Those species in the high resistance group occur in tropical forests with low humidity.

Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic bryophyte biomass in rainforest climates. As demonstrated by Larson (1981) mosses with a large surface area to weight ratio are able to absorb water very rapidly.

Thompson *et al.* (1994) calculated the bryophyte cover on a single tree of *Sloanea woollsii* (Figure 15-Figure 16) in a notophyll forest of southeast Queensland, Australia (subtropical), to be 66 sq m. Water collected by the bryophytes in a single rainfall event exceeded that of the maximum daily transpirational loss from the host tree. Hence, bryophytes can contribute significantly to the relative humidity of the forest through evaporation. This is also a typical role in the tropics.



Figure 15. *Sloanea woollsii*, a species known for a large cover of bryophytes. Photo by Peter Woodard, through public domain.



Figure 16. *Sloanea woollsii* forest, where many bryophytes grow. Photo by Pete the Poet, through Creative Commons.

Frey *et al.* (1990) recognized three principles of water conduction and storage by plants. In the wet season, it is necessary to drain off surplus water. In the dry season, storage and use of condensation of water vapor are important. Above 1700 m, structures that encourage condensation from water vapor aid in water capture. They felt that leaves with grooves could permit support as well as a means of draining off excess water, an adaptation that seems to reach its maximum in the cloud forest and subalpine zone. In the lowland forest, water sacs, mats, and smooth bark combine to preserve water during short dry periods.

Karger *et al.* (2012) considered air humidity to be one of the most difficult and time-consuming climatic measurements to obtain. Thus, they tested the use of bryophyte cover as a proxy, a suggestion proposed by van Reenen and Gradstein (1983), van Reenen (1987), and Frahm and Gradstein (1991). Using 26 study sites in tropical forests, these researchers considered the possibility of using bryophyte cover as a surrogate for relative humidity as a climatic measurement. They found only a weak correlation between bryophyte cover and relative humidity across all the sites. However, when the highland (1,800-3,500 m asl) data were separated from that of the lowland (<1,800 m asl) sites, relative air humidity had a significant and distinct relationship to bryophyte cover ($R^2 = 0.36-0.62$). Temperature, on the other hand, was related to bryophyte cover only in the lowlands ($R^2 = 0.36$). The researchers concluded that epiphytic bryophyte cover can be used as a proxy for air humidity if both temperature and altitude are considered, but cover might not be a good proxy across extensive elevational gradients or wide temperature differences.

Proctor (1990) has demonstrated the reasons for bryophyte distributions through the use of physiological experiments. Whereas many bryophytes tolerate drying, even down as low as 5% water by dry weight, their photosynthesis declines rapidly as water is lost. Regaining photosynthesis can be rapid or slow upon remoistening, depending on the species and the drying conditions. In the tropics, it is important to know that most bryophytes are shade plants, even when they grow in habitats with lots of sunlight, due to their low chlorophyll *a:b* ratios. This means that they become light-saturated at relatively low light levels and do not benefit when the canopy opens up, admitting more light. But it also means that photosynthesis does not occur at a high rate, so having moist conditions provides them with a longer period of photosynthetic activity.

Both moisture and light relationships can be seen easily within a single tree as well as between habitats. For example, when Sillett and coworkers (1995) compared bryophyte diversity in a cloud forest and pasture in Costa Rica, they found 127 species of bryophytes (50 mosses, 76 liverworts, 1 hornwort) in the crowns of just 6 *Ficus tuerckheimii* (Figure 17) trees in the lower montane wet forest. Of these, 109 species were on 3 intact forest trees and only 76 on 3 isolated trees, the isolated trees having more macrolichen cover. The isolated trees were more subject to drought conditions, with higher evaporation in the inner crowns and more exposure to sunlight. The higher moisture of the intact forest supported not only a greater bryophyte species richness and cover, but also a

greater frequency of **pendants, tall turfs, tails, and fans**. Furthermore, 52 species were found only on the intact forest trees, whereas only 18 were exclusive to the three isolated trees.



Figure 17. *Ficus tuerckheimii*, a strangler fig, substrate for significant bryophyte cover in Costa Rica. Photo by Dick Culbert, through Creative Commons.

Cardosa (2012) described the hydrological cycle and the implications of climate change, using data from a La Réunion cloud forest. As already noted, the bryophytes intercept both fog and rainfall over their entire surface. This ability is important in the hydrological cycle of their ecosystems. Using two liverwort species, *Mastigophora diclados* (Figure 18-Figure 19) and *Bazzania decrescens* (see Figure 20), they determined biomass, water storage capacity, atmospheric and cloud water interception, and photosynthetic response to desiccation. Compared to *M. diclados*, *B. decrescens* stored water at approximately double the mean and maximum per hectare while at the same time occupying less than half the bryophyte volume of *M. diclados*. On the other hand, *M. diclados* had a greater ability to intercept the atmospheric moisture. Both species showed a significant relationship between photosynthesis and water content, with both species losing photosynthetic capacity at both low and high water contents. If the clouds lift, as they are predicted to do by the global climate change models, these bryophytes will most likely not survive and their role in the water cycle will be lost.



Figure 18. *Mastigophora diclados* habitat. Photo by Claudine Ah-Peng, with permission.



Figure 19. *Mastigophora diclados*, a species that stores only half the water stored by *Bazzania decrescens*. Photo by Claudine Ah-Peng, with permission.



Figure 20. *Bazzania* sp. from the Neotropics. Photo by Michael Lüth, with permission.

In addition to decreasing diversity, tropical bryophyte productivity is already being impacted by global climate change (Zotz & Bader 2008; Jácome *et al.* 2011; Song *et al.* 2012; Pardow & Lakatos 2013). Jácome and coworkers

used transplanted communities to determine potential climate change effects on the ecology of these bryophyte species.

As a result of climate change, periods of drought are becoming longer and microclimatic conditions are drier (Pardow & Lakatos 2013). Unfortunately, few physiological studies are available on tropical bryophytes, and even less is known about community responses. Pardow and Lakatos, in the first pilot study for effects of climate change on bryophyte ecology in the tropics, used chlorophyll fluorescence to indicate recovery of bryophytes from a tropical lowland forest in French Guiana (Figure 21). They found that canopy species were well adapted to desiccation events, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after recovery from 9 days of desiccation at 43% relative humidity. Understory species were sensitive and could recover only if the relative humidity did not go below 75%. Water vapor, as one might find in fog, was sufficient to rehydrate and reactivate photosynthesis in all of these bryophytes.



Figure 21. Top of lowland rainforest canopy, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Additional discussions of water relations as they relate to habitat can be found in the following subchapters.

Light

Although moisture is the overriding factor in bryophyte distribution in most of the tropics, light is limiting near the forest floor in well-developed multi-story rainforests (Richards 1984a; Cornelissen & ter Steege 1989). Cornelissen and ter Steege demonstrated that true sun epiphytes increase in photosynthetic rates with

increasing light intensity, even when that intensity is very high and atmospheric humidity is low. Hosokawa *et al.* (1964) found that the vertical gradient of bryophyte and other cryptogamic species and growth forms is somewhat related to light and atmospheric humidity, with the lowermost canopy species being more limited by illumination and the uppermost occurrences of trunk species being limited by insufficient atmospheric humidity.

Although high temperatures may be detrimental to some species, Barkman (1958) considered that these are probably not damaging to the bryophytes, but rather that direct solar radiation may be harmful. He cited examples of adaptive coloration exhibited by some bryophytes. Cornelissen and ter Steege (1989) found red to black pigmentation represented in many sun epiphytic species, including **Orthotrichaceae**, **Frullania** spp., and several members of holostipous **Lejeuneaceae**. The upper canopy species **Frullania apiculata** (Figure 22), **F. kunzei** (Figure 23), and **F. nodulosa** (Figure 24) are always dark red in these locations. By contrast, **F. mucronata** from zones 3 and 4 is dark olive green and **F. obcordata** (Figure 25), a generalist, is more strongly pigmented with red color in zones 5 and 6 than in zone 4. Krinsky (1968) described photochemical pathways that can be used by colored pigments that protect plants.



Figure 22. *Frullania apiculata* stem, SEM, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.



Figure 23. *Frullania kunzei*, a species that is dark red in sunny locations. Photo by Juan Larrain, with permission.

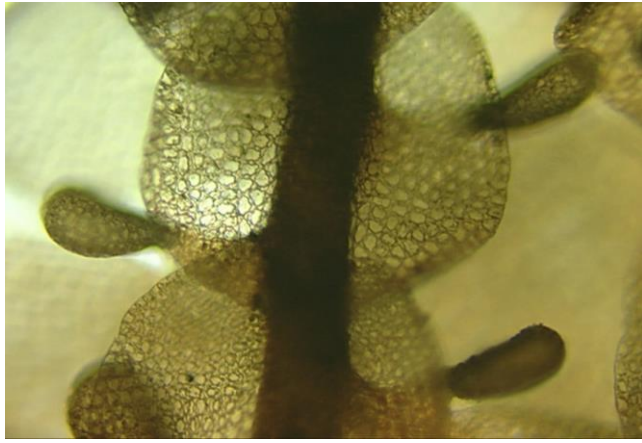


Figure 24. *Frullania nodulosa* stem ventral view, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.

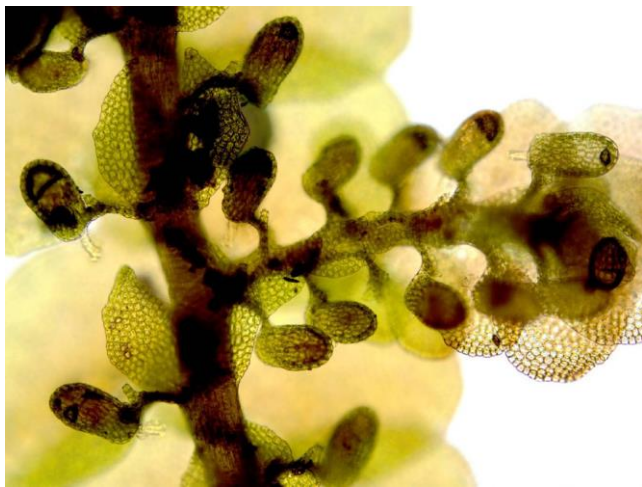


Figure 25. *Frullania obcordata*, a generalist species that is more strongly pigmented in tree zones that receive more light. Photo by Blanka Aguero, with permission.

Life and Growth Forms

Bryophyte life and growth forms reflect the habitat conditions, particularly that of available moisture. Life forms of tropical bryophytes were described in detail by Mägdefrau (1982). Aceby *et al.* (2003) found that 4-15-year-old fallows have a significantly decreased diversity of bryophyte families and mosses in Bolivia (Figure 26). Liverworts, on the other hand, have nearly as much diversity in the fallows as in the submontane rainforest. The life form is ~72% **smooth mat**, a much higher percentage than that found in the forest.

Pardow *et al.* (2012) used life forms as an indicator of high diversity in a tropical lowland cloud forest of the Guianas (Figure 27-Figure 28). These lowland cloud forests are hotspots of bryophyte diversity in tropical lowland areas compared to the common lowland rainforest, as shown in detail by Gradstein (2006) and Gehrig-Downie *et al.* (2011, 2013). The cloud forest benefits from the frequent early morning fog in the valleys. Pardow *et al.* compared the distribution of the functional groups of epiphytes across height zones in the lowland cloud forest and lowland rainforest and found a higher diversity of life forms of bryophytes in the cloud forest. In the cloud forest, **tail**, **weft**, and **pendants** are common, whereas in the

rainforest they are almost absent. The researchers suggested that identification of life forms could be used as a rapid method for identifying lowland cloud forests for conservation.



Figure 26. Bolivian old field at 600 m, surrounded by secondary forest with submontane rainforest in the background. Photo by Thorsten Krömer, courtesy of Robbert Gradstein.



Figure 27. Lowland cloud forest of French Guiana. Photo courtesy of Robbert Gradstein.



Figure 28. Canopy of lowland cloud forest in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

In our study (Li *et al.* 1989) of *Frullania* (Figure 14, Figure 22-Figure 25) in Papua New Guinea (Figure 29), moisture and elevation gradients were important in determining taxa assemblages. Although we suspected that light and temperature were likewise important, we had no data to test these directly. Pócs (1982) and Richards (1984a, b) and a review by Thiers (1988) likewise report that the most important influences on tropical rain forest liverwort (**Jungermanniales**) growth are relative humidity, rainfall, light, and temperature (Thiers 1988). Frahm (1990a) found compensation points for two mosses in controlled temperature regimes, relating these to the tropical temperature regimes. Within this group, growth habit and stem anatomy are often modified, but perhaps the most adaptive features are the development of both simple and complex saccate leaf lobules in liverworts such as *Frullania* (Figure 22-Figure 25), presumably for retention of water, and elongate, thin-walled leaf cells.



Figure 29. Papua New Guinea. Photo from eGuide Travel, through Creative Commons.

On the other hand, excess water can be a problem because it reduces diffusion of CO₂ and can encourage fungal growth (Frey *et al.* 1990). Trees in the tropics often have leaves with prolonged (**acuminate**) tips. This has been considered by some to be an adaptation that permits water to run off the leaf, thus reducing the colonization by fungi on leaves that are subjected to daily rains. **Pendent** bryophytes in rainforests have a somewhat similar adaptation, but the interpretation has been more debatable. For example, in north temperate forests, *Frullania* (Figure 30) is recognized as a liverwort that closely adheres to its bark substrate (**mats**). However, in the rainforest, several **pendent** species of *Frullania* (Figure 31) exist (Li *et al.* 1989). One interpretation of this is again the possibility of the water to be shed by running down the rope-like plant body. However, an alternate interpretation seems to be just the opposite. The **pendent** form is actually a response to the weight of water, first in weighing down taller plants with weak stems, and then in collecting the water at the tips of the branches where the dividing cells are. Thus, the tip of the moss, during the rainy season, may be bathed in water nearly all the time, giving it a nearly aquatic environment. This continual supply of water permits the cells to divide uninterrupted by periods of drought during the rainy season. Such bryophytes can be found not only in tropical and subtropical forests such as those of southern

Japan, but also in the rainforests of the Pacific Northwest in North America.



Figure 30. *Frullania bolanderi*, an adnate species in the North Temperate Zone. Photo by Janice Glime.



Figure 31. Pendent *Frullania* from the Neotropics. Photo by Michael Lüth, with permission.

Proctor (2002) found that the **pendent** mosses *Floribundaria floribunda* (Figure 32) and *Pilotrichella ampullacea* (Figure 33) hold large amounts of external capillary water. Nevertheless, both species are able to recover from 11 months of dry storage at 5°C (not a very likely temperature in lowland tropics, but possible at some higher elevations). Both require several days to recover, with *F. floribunda* taking somewhat longer. Short desiccation periods elicit rapid recovery, with *P. ampullacea* reaching a positive carbon balance after only 30-60 minutes following 20 hours of air drying. After six days, they require 2-5 hours, suggesting that they are adapted to the short periods of desiccation found in the humid tropical forests, but not to longer, frequent periods. *Floribundaria floribunda*, on the other hand, is best adapted for more shady and continuously moist forests.



Figure 32. *Floribundaria floribunda*, a species that holds large amounts of external capillary water. Photo from Taiwan Biodiversity website, through Creative Commons.



Figure 33. *Pilotrichella ampullacea*, a species that holds large amounts of external capillary water. Photo by Jan-Peter Frahm, with permission.

In the leafy liverworts, Thiers (1988) recognized stem characters such as growth habit (projecting, prostrate, rheophytic) and anatomical characters such as epidermal thickenings, stem reduction, and stem flattening (often present in **mats**) as conserving moisture during dry periods. The flattened stems, such as those in *Pteropsiella frondiformis* (Lepidoziaceae), do most of the photosynthesizing, and accompanied by reduced leaves, the reduced life form would most likely conserve water during dry periods. Other leaf modifications include development of simple and complex saccate leaf lobules [e.g. *Pleurozia* (Figure 34-Figure 35) and *Colura* (Figure 36-Figure 37)] and presence of elongate, thin-walled, hyaline cells in the leaf margins [e.g. *Cololejeunea marginata* (Figure 38), *C. cardiocarpa* (Figure 39)], all of which help to hold or absorb water.

Further descriptions of life forms and growth forms as they relate to habitat can be found in the following subchapters. For an introduction to the topic, see Volume 1, subchapter 4-5.



Figure 34. *Pleurozia purpurea*, a species with lobules. Photo by Matt von Konrat, through public domain.

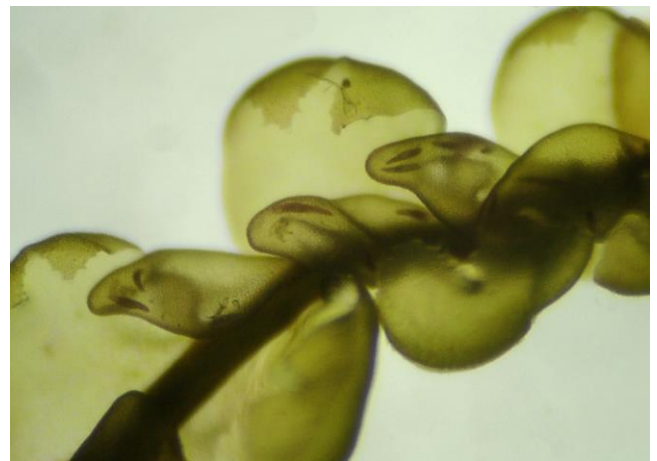


Figure 35. *Pleurozia purpurea* showing lobules with the protozoan *Blepharisma* living in them. Photo courtesy of Hess and Jan-Peter Frahm.



Figure 36. *Colura vitiensis* on leaf, Fiji Islands, a species with leaf lobules. Photo courtesy of Tamás Pócs.



Figure 37. *Colura* leaf showing lobule. Photo courtesy of Jan-Peter Frahm, with permission.



Figure 38. *Cololejeunea marginata*, a leafy liverwort species with thin-walled hyaline cells on the leaf margins. Photo by Jan-Peter Frahm, with permission.

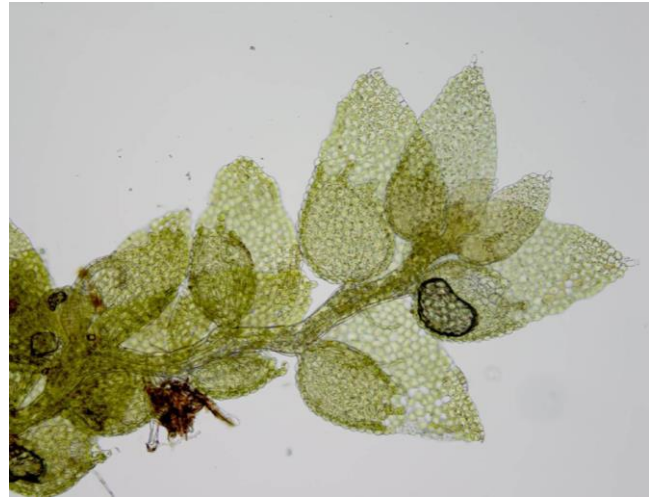


Figure 39. *Cololejeunea cardiocarpa*, a leafy liverwort species with thin-walled hyaline cells on the leaf margins; it also has lobules. Photo by Blanka Aguero, with permission.

Nutrient Relations

Nutrients are also affected by the rainy and dry seasons. Nutrient pulses occur as bryophytes dry and rewet. Damaged membranes leak nutrients and other substances such as sugars and polyols. Rainfall leaches these nutrients from the bryophytes, including their surfaces, and carries them to the forest floor (Lodge *et al.*). These pulses synchronize nutrient availability that maintains higher rates of nutrient mineralization, plant uptake, and forest productivity. It provides nutrients at the beginning of the growing seasons, a time at which they should be most beneficial to forest species. Thus the bryophytes serve as storage units that provide nutrients at the most critical time.

Coxson and coworkers (Coxson 1991; Coxson *et al.* 1992) noted the importance of wetting/drying cycles for the accumulation of sugars and polyols to more than 950 kg ha⁻¹ in the epiphytic bryophytes of the cloud forest canopy of Guadeloupe (French West Indies). These sugars can stimulate the growth of microbes and thus facilitate the breakdown of litter. These relationships suggest some of the importances of these wet to dry changes in nutrient release from the epiphytic bryophytes (and for some, probably ground-dwelling species as well) and their role in the forest dynamics.

Further support for these responses comes from differences between upper and lower canopy bryophytes. Coxson and coworkers (1992) found that the upper canopy leafy liverwort *Frullania atrata* (Figure 40) holds 17% of its dry weight as sugar and polyol reserves. [Note that the name *F. atrata* has been misapplied to a number of tropical *Frullania* specimens, so information regarding the species may actually belong to one of its look-alikes (pers. comm. Robert Gradstein).] By contrast the lower canopy moss *Phyllogonium fulgens* (Figure 41) holds these reserves as less than 6% of its dry weight. The upper canopy bryophytes seem better adapted at retaining these, with *F. atrata* releasing only 0.3 g m⁻² compared to 0.9 g m⁻² for *P. fulgens*. This relationship was supported by similar relationships of bryophytes under field conditions in the tropical montane cloud forest of Guadeloupe, French West Indies.

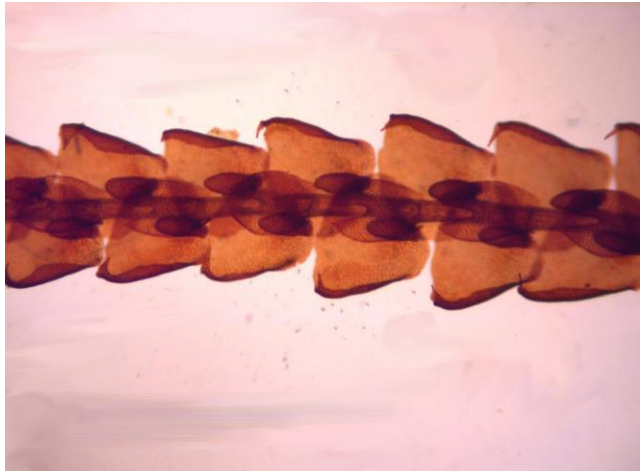


Figure 40. *Frullania atrata*, an upper canopy liverwort and a species that can hold 17% of its dry weight as sugar and polyol reserves. Photo by Juan Larrain, with permission.



Figure 41. *Phyllogonium fulgens*, a lower canopy moss in the Neotropics, where it holds less than 6% of its dry weight as sugar and polyol reserves. Photo by Michael Lüth, with permission.

Frangi and Lugo (1992) studied the biomass and nutrient accumulation in ten-year-old communities in a flood plain at the Luquillo Experimental Forest, Puerto Rico. They found a higher bryophyte cover on streambanks where flooding was frequent but of short duration. The cover decreased toward the longer-lasting flood plain, with the minimum cover occurring in depressions where water remained and became stagnant. They measured nutrient accumulations in ash-free biomass of bryophytes. These accumulations in kg ha^{-1} were 14.5 for N, 0.8 for P, 5.3 for K, 2.7 for Ca, 2.7 for Mg, 0.5 for Mn, 18.5 for Fe, and 22 for Al. These numbers were similar to those found in fine litter. Nevertheless, these values were low compared to that of other bryophyte communities. Both biomass and nutrients were greater in streambank slope communities and slopes of tree mounds than that in depressions that remained wet for a long time.

The bryophytes in these tropical flood plain communities appear to retain nutrients and serve as filters during flooding in these communities.

In the coastal forests of Kenya, some bryophytes specialize on acid or alkaline substrates (Wilding *et al.* 2016). For example, *Tortella tortuosa* (Figure 42) is strongly associated with calcareous substrates, whereas *Racomitrium lanuginosum* (Figure 43) only occurs on acid ground. These preferences most likely relate to their ability to obtain their needed nutrients, without getting them in excess.



Figure 42. *Tortella tortuosa*, a species of calcareous substrates. Photo by Michael Lüth, with permission.



Figure 43. *Racomitrium lanuginosum*, a species of acid substrates. Photo by Janice Glime.

Further discussion of nutrient relations of tropical bryophytes is in the subchapters on Epiphytes.

Productivity

Productivity studies, in particular, are difficult to compare because of differences in methodology. Moreover, few exist.

Pócs (1987) was among the early productivity researchers, examining the changes in biomass among bryophytes in the East African rainforests. As we might expect from temperate studies (Proctor 1982), physiological and experimental studies indicate that net productivity drops rapidly as temperatures rise above 25°C (Frahm 1990b). Add low light levels to the high temperatures and the bryophytes are hindered by high

respiration rates and low photosynthetic rates, resulting in low or negative net assimilation. Due to differences in precipitation, humidity, temperature, and desiccation (Frahm 1990a, b), it is generally true that biomass of epiphytic bryophytes in equatorial latitudes increases from the tropical lowlands to the treeline. Thus, high temperatures, combined with low light intensities, can account for the low diversity of bryophytes in the lowlands. Richards (1952) found data indicating that during the wet, and thus cloudy, season, the maximum temperatures in the ground layer are lower than those in the dry season when the sun shines a greater proportion of the time.

This raises the question of how the limited numbers of species in the lowlands survive. Frahm (1990b) suggested this could involve a specialized phytochrome system or more effective storage of the photosynthetic products. Perhaps more realistically, the relatively high nutrient supply that arrives through abundant precipitation could support a positive net photosynthesis. Another factor that could contribute is that the forest floor can have high CO₂ concentrations due to enhanced decomposition of leaves in a hot, moist environment, but increased CO₂ levels are most beneficial in high light levels.

Zotz *et al.* (1997) provided further information on the CO₂ and water relations for net photosynthesis. Using six tropical bryophytes, these researchers measured the daily changes in water status and net CO₂ exchange in a submontane tropical rainforest in Panama (Figure 44). Daily variation of water content was "pronounced." Both high and low water content limited carbon gain. Low light during rainstorms was less important in limiting CO₂ exchange compared to water content. More than half the carbon gain was lost at night to respiration.



Figure 44. Panamanian submontane and montane forests. Photo by S. B. Matherson, through Creative Commons.

In a more recent publication, Chen *et al.* (2016) examined photosynthetic properties of epiphytes in Southwest China. These adaptations include higher total chlorophyll concentrations, specific leaf area, and chlorophyll per unit leaf N (Chl/N), lower ratio of chlorophyll *a:b*, and greater photosynthetic nitrogen-use efficiency. Measurements, in $\mu\text{mol m}^{-2} \text{s}^{-1}$, showed means for light-saturated net photosynthetic rate (0.55), light saturation point (106.72), light compensation point (4.17) and dark respiration rate (0.25). They demonstrated

photosynthetic down-regulation under high light conditions for these low-light epiphytes. These trunk-dwelling epiphytes are adapted for high resource retention rather than high resource gain. This is accomplished by low respiration rates and low light compensation points in shady habitats.

Waite and Sack (2010) hypothesized that leaf trait values would "reflect the distinctive growth form and slow growth of mosses, but also that trait correlations would be analogous to those of tracheophytes." Using ten species from Hawaii (Figure 45), they quantified 35 physiological and morphological traits of cell, leaf, and canopy level of bryophytes growing on the ground, trunk, and canopy. These bryophytes had low leaf mass per area (A_{mass}) and low gas exchange rates. Perhaps not surprisingly, but in contrast to that of tracheophytes, the moss light-saturated photosynthetic rate per mass did not correlate with habitat irradiance. However, leaf area, cell size, cell wall thickness, and moss canopy density all correlated with microhabitat irradiance. Waite and Sack furthermore found that costa size, canopy height, and A_{mass} were coordinated traits linked with structural allocation.

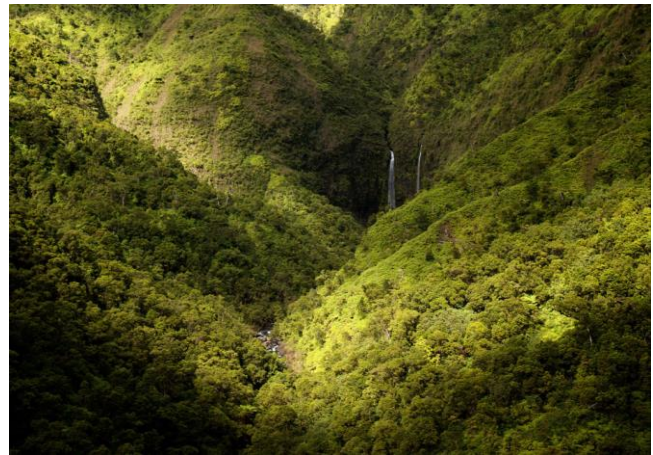


Figure 45. Hawaiian forest near Hanalei Bay, Kauai. Photo by Lukas, through Creative Commons.

Wagner *et al.* (2014) sought to explain the distribution of tropical bryophytes based on their physiological ecology. They noted the increase in bryophyte biomass with altitude in rain and cloud forests. They suggested that the low bryophyte abundance in the lowland rainforests is a result of the limitation of net carbon gain during fast drying and low light levels during daytime, coupled with the moist, warm nights. These moist, warm nights promote respiration and the daytime photosynthesis can be insufficient to balance the nighttime CO₂ loss. Wagner and coworkers concluded that the timing of hydration is crucial for net photosynthetic gain.

Datta Munshi (1974) studied seasonal changes in standing crop (chlorophyll) and annual net production of two moss communities at Varanasi, India. The mean bryomass in a perennial *Hydrogonium* (Figure 46) community was 95 g m⁻² and in the seasonal community of *Physcomitrium* (Figure 47) it was only 11 g m⁻². These values represent the first on non-epiphytic bryophytes in the tropics and were lower than those typical of bryophytes in temperate forests, being more like those in Arctic ecosystems.



Figure 46. *Hydrogonium ehrenbergii*, member of a perennial genus in the Indian tropics. Photo by Jan-Peter Frahm, with permission.



Figure 47. *Physcomitrium eurystomum* capsules; this genus is a member of seasonal community in the Indian tropics. Photo by Dick Haaksma, with permission.

Tropical forests generally have a larger biomass of epiphytic bryophytes than do temperate forests (Norris 1990). However, when trees are widely spaced or occur as lone trees, the greater penetration of wind can quickly desiccate the adhering bryophytes.

Overall, bryophytes comprised 40% of the epiphytic biomass in a Neotropical lower montane cloud forest at ca. 1600 m in Costa Rica (Nadkarni 1984) compared to 6% in the leeward rainforest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dyer 1980).

In an upper montane cloud forest at 3700 m in the Andes of Colombia (near the forest line), the bryophyte contribution to total epiphyte biomass was much higher, almost 70% (Hofstede *et al.* 1993) and total epiphytic biomass (including suspended soil) was a staggering 44 tons per hectare, the highest value ever reported.

Light is an important limiting factor for photosynthesis in the tropics. For three species of *Pogonatum*, chlorophyll content and chloroplast size differed with light intensities

where they predominated (Nasrullah-Boyce *et al.* 2011). For *P. cirratum* subsp. *macrophyllum* (Figure 48) and *P. subtortile*, the total chlorophyll and beta-carotene content are higher than that in *P. neesii* (Figure 49). The latter lives in the areas with much higher light intensities ($751 \pm 45 \text{ W m}^{-2}$), compared to 28 ± 4 and $230 \pm 39 \text{ W m}^{-2}$, respectively. The sun species, *P. neesii*, had a higher soluble protein content, likewise having a higher soluble protein to total chlorophyll ratio. *Pogonatum cirratum* subsp. *macrophyllum*, the species from the lowest light, had significantly larger chloroplasts as well as more grana and thylakoids per chloroplast than did the other two species. And the two species from the lowest light had more than double the numbers of starch grains. On the other hand, the leaf lamellae (vertical stack of cells on leaf; Figure 50) were shortest in the species receiving the lowest light levels. Nevertheless, the CO_2 assimilation rates were highest in *P. neesii* even when light intensities were low. Lamellae can provide more surface area for photosynthesis and capillary spaces to hold water longer. In low-light *P. cirratum* subsp. *macrophyllum*, these are rudimentary, whereas those of *P. subtortile* are 5-7 cells high.



Figure 48. *Pogonatum cirratum*, a species of low light and large chlorophyll. Photo by Li Zhang, with permission.



Figure 49. *Pogonatum neesii*, a species of higher light intensity and less chlorophyll than that in *P. cirratum* subsp. *macrophyllum*. Photo by Yang Jia-dong, through Creative Commons.

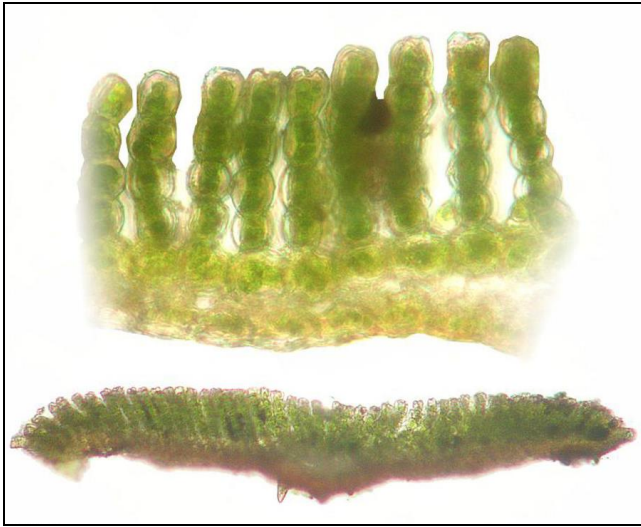


Figure 50. *Pogonatum* leaf cs showing leaf lamellae at two different magnifications. Photo by Michael Lüth, with permission.

Further discussions of productivity and biomass will be provided in the succeeding subchapters as they pertain to particular habitats.

Climate Effects

As noted above, moisture and temperature are important determinants of the types of bryophyte vegetation that survive. And precipitation events and cloud cover will diminish the light intensity. Among the early studies on the effects of these climate parameters on tropical bryophytes is a study by Biebel (1964, 1967). He examined temperature resistance of jungle mosses. Weber (1985) examined the effects of El Niño on bryophytes of the Galápagos. Furthermore, hurricanes can be devastating to epiphytes, ripping them from the trees or breaking branches and even toppling trees.

Rainy "seasons" are common in the tropics, punctuated by dry periods. If there are two periods in the year when the sun is overhead in the tropics, two wet seasons will occur (Richards 1952). If the two periods of overhead sun are close together, the two wet seasons will merge, but two maxima will still occur.

In the winters of many parts of the tropics, a dry season turns the area into near desert conditions. Akande (1984, 1985) attempted to understand the desiccation tolerance, or lack of it, among several tropical African bryophytes. Using the leafy liverwort *Mastigolejeunea florea* (now called *Spruceanthus floreus* according to Robbert Gradstein; see Figure 51) and the mosses *Calymperes palisotii* (Figure 52) and *Entodontopsis nitens*, he concluded that these mosses were more desiccation-tolerant than the liverwort. It is interesting that bryophytes maintained at 0% relative humidity for one week and one month at 28°C were able to resume respiration more quickly than those kept at 32 and 54% relative humidity. He considered this ability to recover from 0% humidity so easily to be a case of **anhydrobiosis** (living state without water).



Figure 51. *Spruceanthus planiusculus* in a genus where some of the tropical African species are less desiccation tolerant than mosses. Photo by Claudine Ah-Peng, courtesy of Robbert Gradstein.



Figure 52. *Calymperes palisotii* on bark, a species that seems to be capable of anhydrobiosis in tropical Africa. Photo by Scott Zona, with permission.

Reproductive Biology and Phenology

As discussed earlier, the timing of reproduction must coincide with conditions favorable for dispersal. For example, both *Sematophyllum subpinnatum* (Figure 53) and *Octoblepharum albidum* (Figure 13) in the tropical Brazilian lowland forest have considerably more juvenile, immature, and mature gametangia during the rainy season than during the dry season, and that corresponds with an increase in the number of fertilized eggs in the archegonia

(Oliveira & Pôrto 2001; Pôrto & Oliveira 2002). One must keep in mind that unlike the desert, the dry season is subject to occasional, but short, rainfall events. In contrast to gametes, spores benefit from dry air for dispersal, and these two species derived that advantage by beginning sporophyte development during the rainy season, but completing it during the dry season.



Figure 53. *Sematophyllum subpinnatum*, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Michael Lüth, with permission.

Despite our limited taxonomic knowledge, there have been several studies on the reproduction of tropical bryophytes. By their very nature, individual studies are limited to one or few species (e.g. Fatoba 1998). Nevertheless, Kürschner and Parolly (1998a, b), Kürschner *et al.* (1999), and Kürschner (2004) were able to review the life strategies and adaptations of bryophytes, noting that functional types are "important for the establishment, habitat maintenance, and dispersal of species," indicating relationships among site ecology, niche differentiation, and species evolution.

Bryophytes in tropical regions seem to have relatively fast population dynamics when compared to those of temperate species (Monge-Nájera 1989; Coley *et al.* 1993; Zartman 2004). This is often an adaptation to the ephemeral nature of many of their substrates.

Cerqueira *et al.* (2016) studied the seasonality of reproduction of epiphytic bryophytes in the flooded forests of the eastern Amazon. Of 54 species, 34 were fertile. They were unable to identify a pattern in the seven studied species when comparing those in dry vs rainy conditions. Two species, however, were associated with the seasonality. They concluded that some bryophytes may maintain constant fertility as an adaptation to these tropical forests.

Batista *et al.* (2018) found that in a humid forest in northeastern Brazil, with seasonal rainfall and dry season, the 76 bryophyte species were predominantly monoicous (67%) and exhibited reproductive traits that tolerated adverse conditions, permitting them to persist under the seasonal water availability of the forest. A total of 80% of the species had sporophytes, mostly among the monoicous species. Only 21% exhibited asexual reproduction,

including gemmae, regenerating fragments, and caducous leaves. Of these with asexual means, 75% were dioicous.

Life Cycle Strategies

Tropical forest substrata are usually rather temporary (Richards 1988), whether it be due to rapid decay, exfoliation, or soil erosion. In fact, Richards considers all substrata available to bryophytes in the tropics to be impermanent. Hence efficient short-distance dispersal is important. Epiphyllous species are frequently **colonists** with a short life span and production of numerous propagules. Species of *Fissidens* (Figure 71) and others that grow on termite mounds have a short-lived strategy. Richards (1988) carefully stated that the **perennial shuttle** with its relatively long life span and only moderate sexual or asexual reproduction is probably the commonest life strategy in the tropics, but that epiphylls are likely to be colonists because of the short duration of their substrate. **Fugitives** are rare, exceptions being the thallose liverwort *Riccia* (Figure 54) and the moss *Micromitrium* (Figure 55), as seen in West Africa.



Figure 54. *Riccia cavernosa*, a thallose liverwort; members of this genus are fugitives in West Africa. Photo by Des Callaghan, with permission.

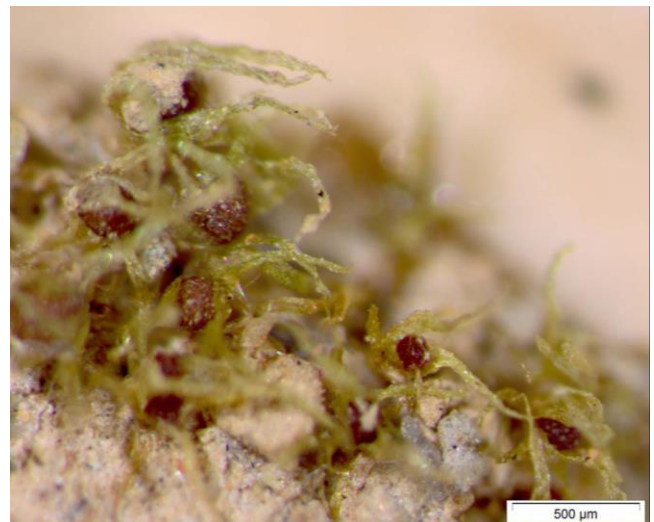


Figure 55. *Micromitrium tenerum*; members of *Micromitrium* are fugitives in West Africa. Photo by Amelia Merced, with permission.

Mosses

The earliest of the tropical reproductive studies I could locate were those of Odu (1979, 1981). Studies on the mosses *Racopilum* (Figure 56) and *Fissidens* (Figure 71), indicate the importance of temperature in early life stages, with germination occurring at 30°C and protonema growth at 25°C (Odu 1979). This temperature requirement coincides with the maturation and dispersal of spores in the dry season, favoring the establishment of new shoots.

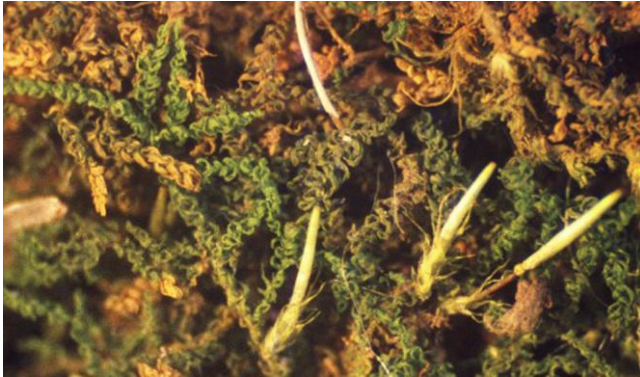


Figure 56. *Racopilum africanum*, a tropical species that relies on the rainy season for sexual reproduction. Photo by Jan-Peter Frahm, with permission.

Where seasons alternate between rainy and dry seasons, the rainy season is critical for completion of reproduction in species that rely on sexual reproduction. Odu (1981) demonstrated this for four species in southwest Nigeria, showing that release of spores was timed to take advantage of the dry season. The reproductive phenology of several tropical African mosses (*Racopilum africanum* (Figure 56), *Fissidens weirii* (see Figure 71; syn.=*F. glauculus*), *Pelekiium gratum* (Figure 57; syn.=*Thuidium gratum*), *Stereophyllum* sp. (Figure 58) illustrate this. Using populations in southwestern Nigeria, Odu found that gametangia develop at the onset of the rainy season (March-April), whereas the development of sporophytes occurs later, with capsule maturation occurring at the end of the same rainy season (October-December). This permits dispersal of spores during and after the dry season (November-April). Thus the entire reproductive cycle is completed within one year. A similar relationship occurred among four species in a savannah in southwestern Nigeria (Makinde & Odu 1994).



Figure 57. *Pelekiium gratum*, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Manju Nair, through Creative Commons.



Figure 58. *Stereophyllum radiculosum*, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Juan David Parra, through Creative Commons.

Both Olarinmoye (1974) and Egunyomi (1979a) determined that in studied bryophytes of west tropical Africa moisture is the regulatory factor for both growth and sporophyte production. Nevertheless, differences between species exist (Odu 1982). Odu found that *Fissidens weirii* (see Figure 71) and *Racopilum africanum* (Figure 56) have the shortest fertilization period, occurring in May. This fertilization period is earlier in *Pelekiium gratum* (Figure 57) and much later in *Octoblepharum albidum* (Figure 13; Figure 59) (July-September). Nevertheless, the sporophytes of all four species mature toward the end of the rainy season (October-November). Herbarium specimens of these mosses collected over an 11-year period support this pattern.

Maciel-Silva and Oliveira (2016) examined the seasonal relationships of *Octoblepharum albidum* (Figure 13; Figure 59) in Brazil. Among 100 sporophyte-bearing plants, representing ten populations, the development was clearly seasonal, relating principally to rainfall. The early stages (immature to post-meiotic) occurred primarily during the dry season. Dehiscence, on the other hand, occurred mostly during the rainy season. This seems to be the opposite of that found for the species in Africa.

Octoblepharum albidum (Figure 59) is an autoicous pantropical species. Thus, its handling of various climatic regimes can help us to understand adaptations of reproductive strategies. Maciel-Silva *et al.* (2013) compared reproductive traits of this species in two Atlantic rainforests and two coastal sites in northeastern Brazil. This species not only produces spores frequently (Figure 59), but also produces gemmae at the leaf tips (Figure 60). In the coastal sites, the shoots had higher numbers of sporophytes, male and female branches per shoot, male gametangia per sexual branch, and longer setae than in the forest sites. Numbers of female gametangia per sexual branch did not differ between the two habitats and the male-biased sex ratio was present at all sites. Longer shoots produced more sporophytes, protonemata, and/or buds than did shorter ones, compared to production of gemmae, but only in the forest sites. The researchers suggested that the longer setae could favor spore dispersal, aiding colonization in coastal sites.



Figure 59. *Octoblepharum albidum* with capsules, a pantropical species that adjusts its reproductive strategies based on habitat climate. Photo by John Bradford, with permission.



Figure 60. *Octoblepharum albidum* with gemmae on the leaf tips. Photo by Li Zhang, with permission.

Oliveira and Pôrto (2005) examined sporophyte production and population structure of two moss species in the Pottiaceae in Brazil. Both *Hyophila involuta* (Figure 61) and *Hyophiladelphus agrarius* (Figure 62) produce capsules in the Atlantic forest at Recife, Pernambuco, Brazil (see Figure 63). Both species had a significantly female-biased sex ratio. The ratio of sterile to fertile shoots was close to 1:1. *Hyophila involuta* had a mean shoot density of 19 cm⁻², whereas it was 27 for *Hyophiladelphus agrarius*. Furthermore, *H. involuta* had only 48% sporophyte production, whereas *H. agrarius* had 55%. Neither species seemed to change its sporophyte production based on any of the environmental parameters measured. The males and females do not clump by sex, favoring sporophyte production.



Figure 61. *Hyophila involuta* with capsules. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.



Figure 62. *Hyophiladelphus agrarius* with capsules. Photo by Fred Essig, with permission.



Figure 63. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemelk, through Creative Commons.

Antheridia and Archegonia

Pôrto and Oliveira (2002) did a more intensive study on the reproductive **phenology** (study of cyclic and seasonal natural phenomena) of *Octoblepharum albidum* (Figure 59) in the Atlantic Forest in Brazil. In this 2-year study, they found an average of 13.4 antheridia per **perigonium** (envelope of modified leaves surrounding antheridia) and 6.7 archegonia per **perichaetium** (ensheathing cluster of modified leaves surrounding archegonia). All stages of gametangia were much greater in the rainy season, with a concomitant increase in fertilized eggs in archegonia. The sporophytes began development during the rainy season and matured in the dry season, at which time spores were dispersed.

Even in the moss *Sematophyllum subpinnatum* (Figure 53), in which antheridia and archegonia initiate, mature, and achieve fertilization throughout the year, the frequency increases in the rainy season (Oliveira & Pôrto 2001). Sporophytes (see Figure 64) initiate primarily in June through September, indicating that the rainy season is the most favorable time for fertilization.



Figure 64. *Sematophyllum substrumosum* with capsules; capsules in *Sematophyllum subpinnatum* initiate in June through September in tropical Brazil, following fertilization in the rainy season. Photo by Michael Lüth, with permission.

Maciel-Silva and Valio (2011) found that in two different sites in the Brazilian rainforest, the phenology was somewhat different. Examination of eleven species of bryophytes indicates that the reproductive organs are active year-round. Female gametangia often mature before the onset of the rainy season. Male gametangia, however, tend to mature at the end of the dry season. Furthermore, at sea level, the highest production of immature male gametangia occurs at the start of the rainy season, whereas in the montane region, the highest production of immature male gametangia is at the end of the dry season. The researchers suggested that high temperatures could damage the development of male gametangia during the rainy season. Sporophytes dehisce before the rainy season begins, a time when spores can be dispersed farther by dry winds.

In summary, tropical gametangia mature primarily at the end of the dry season or beginning of the rainy season, most fertilizations occurs during the rainy season, and spore dispersal occurs during the dry season.

The pantropical moss *Sematophyllum subpinnatum* (Figure 53) is **autoicous** (having both sex organs on same plant but different branches) (Oliveira & Pôrto 2001). Sampling of two populations for two years in northeastern Brazil revealed that the average number of antheridia per perigonium ranges 9-20; archegonia per perichaetium ranges 3-26.

Monoicous vs Dioicous

As one might expect, **monoicous** (having both sexes on same plant) species have the highest levels of sporophyte production compared to **dioicous** (having sexes on separate plants) (Maciel-Silva *et al.* 2012a). Nevertheless, in the tropics, as elsewhere among mosses, the dioicous condition prevails in the tropical north Queensland, Australia, and most likely elsewhere in the tropics (Ramsay 1987).

Gradstein (1975, p. 29) found the highest level of sporophyte production in the autoicous *Acrolejeunea fertilis* (Figure 65) and *A. pycnoclada*, with 15% presence of sporophytes in 100 collections of each of the two species studied. In other *Acrolejeunea* species mature sporophytes were present in less than 10% of collections studied, and sporophytes were not seen in two dioicous species. In their study of fertilizations in 11 species from a Brazilian Atlantic rainforest, Maciel-Silva and coworkers found that female-biased sex ratios and low rates of fertilization are typically balanced by high production of reproductive structures at the beginning of the reproductive cycle.

These same 11 species expressed sexual organs continuously over the 15-month period of study (Maciel-Silva & Valio 2011). Nevertheless, male gametangia are typically mature by the end of the dry season, with fertilization occurring during the wettest months. Female gametangia, on the other hand, are receptive over the entire period, with many maturing before the rainy season begins. Male gametangia experience a high abortion rate and take longer to develop. This pattern of male gametangia taking longer to develop is typical of bryophytes in many parts of the world. Sporophytes subsequently develop during the dry season, dispersing their spores toward the end of the season. Although the patterns of gametangia and sporophyte development differ among the species, it does not differ between the sea level and montane sites.



Figure 65. *Acrolejeunea fertilis*, an autoicous species with good sporophyte production. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for non-commercial use.

In Mexico, two dioicous species of *Syntrichia* [*S. fragilis* (Figure 66), *S. amphidiacea* (Figure 67)] are abundant (Mishler 1988). Both produce sporophytes only in limited circumstances within their range. Nevertheless, they are just as abundant in areas where sporophytes are rare or absent. This suggests that they must rely heavily on asexual reproduction in these areas.



Figure 66. *Syntrichia fragilis* dry, an abundant dioicous species in Mexico, but seldom producing capsules. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 67. *Syntrichia amphidiacea* dry, with gemmae, an abundant dioicous species in Mexico, but seldom producing capsules. Photo by Claudio Delgadillo Moya, with permission.

Dwarf Males

The genus *Macromitrium* is well known not only for its two sizes of spores (see below), but also for its dwarf males. Having tiny males (<1 mm tall) permits the spores to germinate and the tiny plants to reach maturity on the female plants, often very close to the archegonia of the female. This does present a serious inbreeding probability, but the great advantage of having many more sperm be successful in reaching a female seems to outweigh the disadvantages, particularly for epiphytes (Ando 1977) where sperm dispersal is especially difficult.

Ramsay (1987) reported that at least 23 genera of mosses in tropical north Queensland, Australia, have dwarf males. Some are facultative (physiologically determined), being dwarf only when the spore germinates on a female plant. Others are obligate (genetically determined), always forming dwarf males from the male spore. Both types are present in among species of *Macromitrium* (Ramsay 1979; Une 1985).

Propagules and Regrowth

Some widespread tropical bryophytes do not produce capsules and spores, usually due to absence of the opposite sex, poor gamete dispersal, or unsuccessful development of the sporophyte. Olarinmoye (1986) examined survival strategies of the mosses *Hyophila crenulata* (see Figure 68), *Barbula lambarenensis* (see Figure 69-Figure 70), and *Fissidens asplenioides* (Figure 71) in Ibadan, Nigeria. He established that survival strategies during unfavorable periods of drought could be as spores (only in *Hyophila crenulata*), gemmae, and regrowth from the gametophores, as well as regrowth from rhizoids, shoot bases, apices, and the main stem. Rhizoids produce more regrowth than do shoot apices and main stems. He considered the production of spores in *H. crenulata* to give it a competitive advantage. Nevertheless, the gemma production and success of the other two species seems to more than compensate for lack of spores, as witnessed by their abundance and widespread distribution there.



Figure 68. *Hyophila involuta* (Pottiaceae) with capsules; *Hyophila crenulata* survives dry periods by spores, gemmae, and regrowth from any of its gametophore parts. Photo by Michael Lüth, with permission.



Figure 69. *Barbula horrinervis* (Pottiaceae) with bulbils in leaf axils; *B. lambarenensis* survives dry periods by gemmae that serve the same function as bulbils. Photo by Michael Lüth, with permission.



Figure 70. *Barbula tenuirostris* (Pottiaceae) showing broken leaves that could regenerate; *B. lambarenensis* uses such fragments to regrow following drying out. Photo by Michael Lüth, with permission.



Figure 71. *Fissidens asplenioides*, a species that survives following drought through regrowth from various plant parts. Photo by Jan-Peter Frahm, with permission.

Propagule Forms

Tropical moss gemmae do not seem to have the same limited number of forms as do liverwort gemmae. Odu (1987) found a "great multiplicity of forms" among the gemmae in tropical West African mosses. These occur in a variety of locations, including leaf and leaf axils, and sometimes occur in more than one type of location. Odu concluded that gemmae are of "immense ecological importance" to the tropical mosses. This is facilitated in **Calymperaceae** (Figure 52) by rapid germination – within 1-2 days after becoming dislodged from the leaves. In **Bryaceae**, asexual propagules are often produced as multicellular rhizoidal tubers (Figure 72). In addition to these, there may be gemmae in leaf axils and on rhizoids. As in **Calymperaceae**, gemma germination is rapid, within 2-3 days. In southern Nigeria, some species of **Pottiaceae** (Figure 68-Figure 70) have few male plants and hence rely on gemmae.



Figure 72. *Bryum dichotomum* rhizoidal tuber, a common means of reproduction in West Tropical Africa. Photo by Des Callaghan, with permission.

Calymperes (Figure 52) is one of the prominent gemmiferous mosses in the tropics. When examining *C. afzelii* (Figure 73) and *C. erosum* (Figure 74) Odu and Owotomo (1982) found that the shoots are **dimorphic** (having two forms). That is, the first leaves to develop do not produce gemmae. Later leaves are gemmiferous (Figure 74), and these alternate in coordination with the dry and rainy seasons.

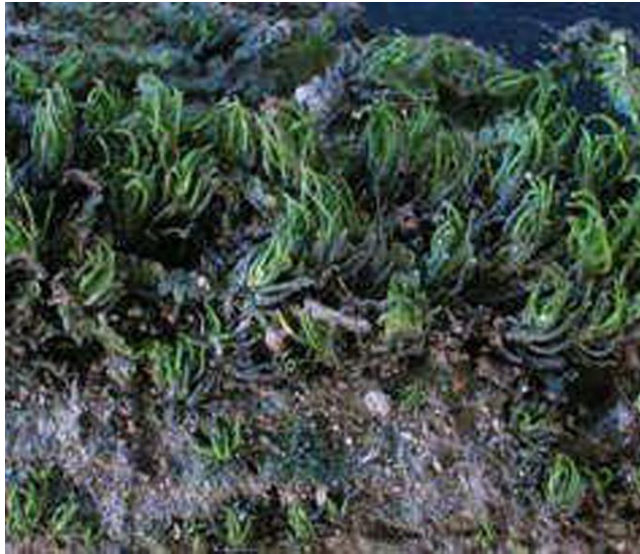


Figure 73. *Calymperes afzelii*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.



Figure 74. *Calymperes erosum* with gemmae; this species does not produce gemmae on its first shoots. Photo by Li Zhang, with permission.

Egunyomi (1984) surveyed the asexual **diaspores** (propagule; any structure that functions in plant dispersal) of mosses in Nigeria. He recognized two major categories: caducous shoots and gemmae. Species with one or more of these asexual diaspores comprise 15% of the Nigerian moss flora. He considered this means of reproduction to be especially important for mosses that do not produce sporophytes in all or part of their range. Seven of these species are sexually sterile.

The miniature **caducous** (can break away from the stem) shoots are often found with rhizoids (Egunyomi (1984). Species with this type of diaspore include *Trachycarpidium tisseranti* (see Figure 75), *Archidium* sp. (Figure 76), *Bryum argenteum* (Figure 77), *B. coronatum* (Figure 78), *Bryum nitens*, and *Campylopus* (Figure 79) species. The latter two are strongly caducous.

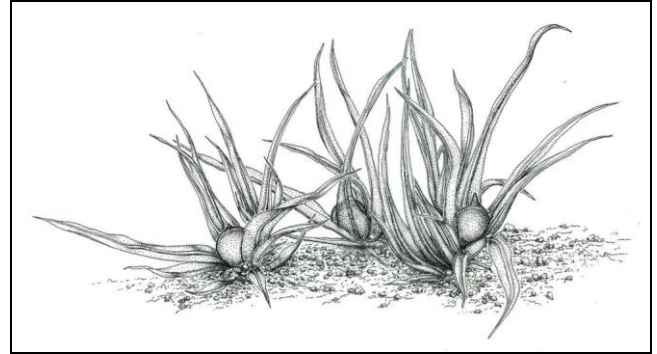


Figure 75. *Trachycarpidium brisbanicum*; *Trachycarpidium tisseranti* has caducous shoots that aid its dispersal in tropical Africa. Drawing by Rod Seppelt, with permission.



Figure 76. *Archidium alternifolium*, a species with caducous shoots. Photo by Jan-Peter Frahm, with permission.



Figure 77. *Bryum argenteum*, a species with caducous shoots. Photo by Tushar Wankhede, through Creative Commons.



Figure 78. *Bryum coronatum*, a species with caducous shoots. Photo by Michael Lüth, with permission.



Figure 79. *Campylopus subulatus* with broken tips that become dispersal units. Photo by David T. Holyoak, with permission.

The second type is the **gemma** (Egunyomi 1984). In some, these are **uniserial** (having only one cell layer) and produced from protonemata in leaf axils. This type includes *Splachnobryum gracile* (see Figure 80), *Jaegerina scariosa* (Figure 81), *Henicodium geniculatum* (Figure 82), and *Bryum argenteum* (Figure 77). Production of rhizoidal gemmae in *Splachnobryum gracile* and *B. argenteum* seems to be related to the high humidity where they were collected. Another type of gemma is borne on **excurrent** (extending beyond leaf tip) **costae** (leaf rib) and is **clavate** (club-shaped, like a baseball bat). Species with these include *Calymperes erosum* (Figure 74), *C. afzelii* (Figure 73), *C. palisotii* (Figure 52), and *C. rabenhorstii*. *Calymperopsis martinicensis* produces filamentous gemmae that occur in splash cups at the shoot apex. In *Octoblepharum albidum* (Figure 13), the gemmae occur at leaf apices and along the margins. Multiseriate gemmae occur in *Semibarbula lambareneis* and *Hyophila crenulata* (see Figure 61). *Gemmabryum apiculatum* (see Figure 83-Figure 85), and *Anoetangium spathulatum* (see Figure 86) produce **tubers** (Figure 85). These tubers are present on rhizoids in the soil and can germinate when the soil is disturbed. This can occur when wet season rains first disturb the soil. Tubers are able to remain viable 9-12 months after collection.



Figure 80. *Splachnobryum obtusum*; *Splachnobryum gracile* produces rhizoidal gemmae in the tropics. Photo from British Bryological Society, with permission.



Figure 81. *Jaegerina scariosa*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo courtesy of Lucas Matheus da Rocha.



Figure 82. *Henicodium geniculatum*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.



Figure 83. *Gemmabryum dichotomum*; *Gemmabryum apiculatum* is a species with both bulbils and tubers. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

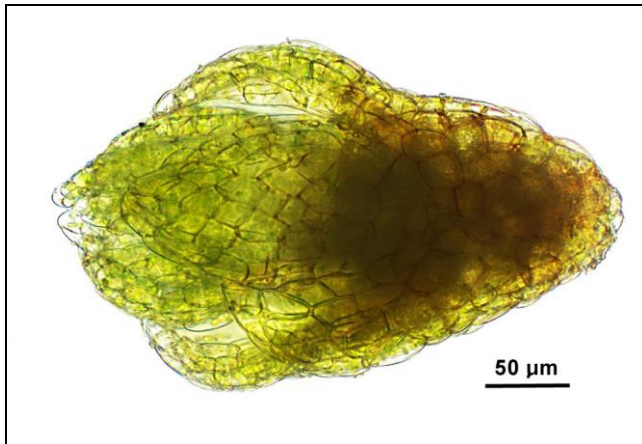


Figure 84. *Gemmabryum dichotomum* bulbil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

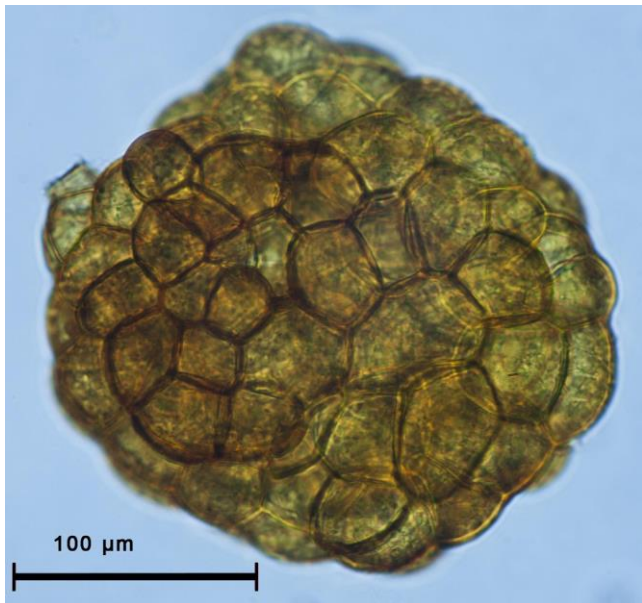


Figure 85. *Gemmabryum apiculatum* tuber. Photo by Jan Janssens, with permission.



Figure 86. *Anoctangium aestivum*; *Anoctangium spathulatum* produces tubers in the tropics. Photo by Hermann Schachner, through Creative Commons.

In Australia, Ramsay (1987) reported a variety of asexual reproductive types from the tropical north Queensland mosses. These include plantlets on leaf tips (*Octoblepharum albidum*), fragile leaf apices (*Groutiella tomentosa*), gemmae on leaf surfaces (*Macromitrium brevicaulis*, *Syrrhopodon* sp., *Calymperes tenerum*, *Clastobryella*), gemmae on leafless stem apices (*Trachyloma diversinerve*), or axillary toward stem apex (*Trachyloma wattsii*), Flagellate julaceous shoots (*Taxithelium wattsii*, *Wijkia extenuata*); shedding of whole leaves (*Arthrocnemum* sp.).

Fragments

In many cases throughout the world, fragments of bryophytes are important in producing new colonies [see, for example, *Octoblepharum albidum* (Figure 13) Egunyomi *et al.* 1980]. Nadkarni *et al.* (2000) tested the interception and retention of bryophyte fragments on branches in a tropical montane cloud forest in Costa Rica. They found that for canopy-dwelling tracheophytes, establishment of bryophytes frequently occurs first. Most fragments don't succeed in becoming established, but about 1% do adhere and become established when dropped from above. On the other hand, 24% were retained among undisturbed bryophytic epiphytes during the 6-month study and 5% were retained on stripped branches.

One of the more uncommon means of dispersal is through specialized branches that can break off easily. In the epiphytic, dioicous *Meteoriopsis undulata* (Figure 87), a recent addition to the Australian Wet Tropics flora, Meagher and Cairns (2016) found flagellate branches that break off when dry. Sexual reproduction is unknown in *M. undulata*. *Floribundaria walkeri* (Figure 88) is a relatively uncommon species in these Wet Tropics and also has flagellate branches. But in this case, the branches are not specialized, but rather are extensions of normal branches.

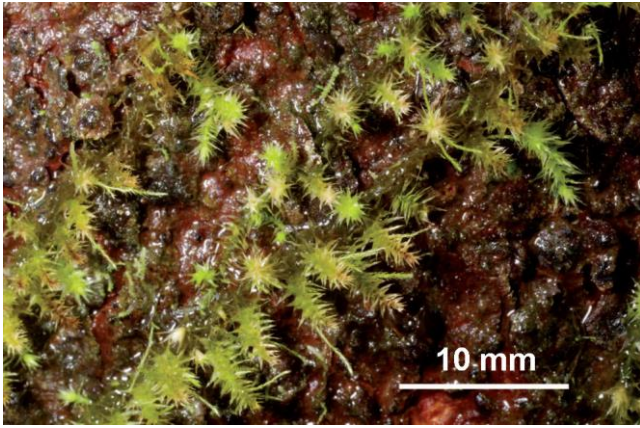


Figure 87. *Meteorioipsis undulata* on tree trunk in North Queensland, showing flagelliform branches. Photo from Meagher & Cairns 2016, with permission.



Figure 88. *Floribundaria walkeri*, a species that produces flagelliform ends on its branches. Photo by Manju Nair, through Creative Commons.

Spore Size

Richards (1984a) found that sun epiphytic mosses usually have larger spores than do shade epiphytes. This would provide a better energy source for establishment of sun mosses, whereas shade mosses would more opportunity for dispersal. Spore size seemed to be unimportant among liverworts, but van Zanten and Gradstein (1988) determined that some shade liverwort epiphytes had spores with much less drought resistance, failing germination after only a few days of desiccation. This lack of drought resistance greatly limits dispersal range.

Diaspore Banks

Diaspore (structure that functions in plant dispersal; propagule) banks provide temporary refuge for spores, gemmae, and sometimes fragments, particularly in habitats that are frequently dry (During & Moyo 1999).

Egunyomi (1979b) tested longevity of spores from Nigeria by keeping them at room temperature and humidity for 1-3.5 years. Subsequent germination ranged from 0 to 92%. Fifteen of 21 species had no germination after that time. Only four species [*Weisiopsis nigeriana*, *Microcampylopus nanus* (see Figure 89), *Mittenothamnium overlaetii* (see Figure 90), *Weissia*

papillosa (see Figure 91)] had at least 50% germination after two years. *Calymperes erosum* (Figure 74) survived at least 1 year with 71% germination. *Microcampylopus nanus* and *Weissia papillosa* had 75 and 76% survival, respectively, of alternate wetting and air drying every 24 hours for four weeks following two years of desiccation. None of the four species with 50% germination listed above survived 4 weeks at -2° following 2 years of desiccation. All four species had at least 43% survival for 4 weeks at 8°C following 2 years of desiccation, with *Microcampylopus nanus* having 80% and *Weissia papillosa* having 81%. Continuous submersion in water was as detrimental as freezing, with none of the four species surviving up to 3 weeks and the highest survival after one week was only 31% (*Weissia papillosa*). Egunyomi suggested that the submersion led to deterioration of the spores due to fungal attack.



Figure 89. *Microcampylopus laevigatus*; *M. nana* can germinate from spores after two years of storage. Photo by Jan-Peter Frahm, with permission.



Figure 90. *Mittenothamnium reptans* from the Neotropics; *M. overlaetii* can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.



Figure 91. *Weissia rutilans* with capsules; *Weissia papillosa* can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.

Zander and During (1999) noted that diaspore banks often harbor the small species with a short life cycle that make them difficult to find above ground. They found *Uleobryum occultum* (Figure 92) (new to Africa, a moss species formerly known only from Brazil and Australia) and *Bryocephospora aethiopica* (Figure 93) (new to Zimbabwe). They also described a new species of the moss family Pottiaceae – *Neophoenix matoposensis* (Figure 94) from the diaspore bank of an experimental fire plot in Zimbabwe.



Figure 92. *Uleobryum occultum*, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.



Figure 93. *Bryocephospora aethiopica* with capsules, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.



Figure 94. *Neophoenix matoposensis*, a new species discovered from a diaspore bank in Zimbabwe. Image modified from drawing by Patricia Eckel in Zander & During 1999.

Maciel-Silva *et al.* (2012b) examined the properties of diaspore species in diaspore banks in the tropical rainforests. They compared species from the Atlantic rain forest (montane and sea level) in Brazil. Of the species identified, 68 were from bark, 55 from decaying wood, and 22 from soil. These species numbers differed little between sites. Mosses predominated, and monoicous species were more numerous than dioicous species. There was little pH effect on shoot emergence. The extant vegetation was well represented, with gemmae and spores making a high contribution. The researchers postulated that the diaspore banks contribute to fast establishment of species after disturbance of the tropical rainforests, as well as contributing to succession there. This is particularly true for species that produce lots of gemmae or monoicous mosses with a large commitment to sexual reproduction.

Bisang *et al.* (2003) germinated diaspores from Malaysian soil. Many of the germinated plants could not be identified and lived only a short time. Two moss species germinated from stem fragments – *Isopterygium* (Figure 95) and possibly *Ectropothecium* (Figure 96). The diaspore origin of the third identifiable moss, *Calymperes* (Figure 52), could not be determined.



Figure 95. *Isopterygium tenerum*; the genus *Isopterygium* was among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Scott Zona, with online permission.



Figure 96. *Ectropothecium* sp., a genus tentatively identified among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Niels Klazenga, with permission.

Diaspore banks can be especially important after a major disturbance such as a fire (During 1998, 2007). In his study in southern Zimbabwe, During found emergence of 2 hornworts, 10 liverworts, and 22 mosses from surface soil samples of the savannah Matopos Sandveld Fire Plots. Annual burning did not seem to harm the diaspores hidden in the soil.

Conditions are not good for sexual reproduction in the tropics. Even if the plant has successful fertilization, sporophyte maturation and dispersal might not be successful. For example, in *Bryum coronatum* (Figure 78), sporophytes are common in Nigeria (Egunyomi 1982). Nevertheless, Egunyomi found 42% of the capsules remained undehisced even in the dry season. Furthermore, 41% of the setae had no capsules. On the other hand, spore germination was successful 65-88% of the time, but the protonemata exhibited abnormal growth. Egunyomi suggested that the numerous axillary propagules were important in dispersal in this species.

Prolonged Protonemal Stage

One adaptation to the short growth period is to prolong the duration of the protonema. As Gradstein and Wilson (2009) put it, this can be interpreted as a short-cut in the life cycle that permits rapid maturation and reproduction,

both providing benefits in unstable, impermanent habitats. In this extreme, it is known as **neoteny**. The most extreme of these are in bryophytes that produce capsules directly on the protonema. The thalloid type occurs only among epiphyllous bryophytes. In the tropics, the epiphytic moss *Ephemeropsis* (Figure 97-Figure 98) produces persistent thalloid protonemata.



Figure 97. *Ephemeropsis trentepohlioides* with capsules and neotenous gametophyte. Photo by David Tng, with permission.



Figure 98. *Ephemeropsis tjobodensis* protonematal mat on palm in Fiji. Photo by Tamás Pócs, with permission.

Liverworts

Liverworts in general produce gemmae more commonly than do mosses. And many of them are more sensitive to desiccation and low humidity. This leads to some differences in their adaptations to living in the tropics.

Monoicous vs Dioicous

Schuster (1988) surmised that sexuality of liverworts shifts to **monoicous** (both sexes on same plant) in the tropics, with *Plagiochila* (Figure 99) being a notable exception as entirely **dioicous** (sexes on separate plants). Schuster considers the ability of monoicous taxa to easily achieve fertilization to be an advantage on impermanent substrata such as leaf surfaces, twigs, and even tree trunks.



Figure 99. *Plagiochila* sp., a dioicous tropical leafy liverwort. Photo by Lin Kyan, with permission.

Neoteny

The monoicous property is further enhanced by multiple examples of **neoteny** (ability of juvenile plants to reproduce, e.g. species of *Cololejeunea* (Figure 100-Figure 102), a condition known for liverworts only in the tropics (Schuster 1988; Gradstein *et al.* 2006). Gradstein and Wilson (2009) note that botanists have interpreted neoteny as a short-cut in the life cycle because it permits rapid maturation and reproduction, an advantage in unstable, impermanent habitats. This is especially important for those species, like *Cololejeunea* species, that live on such temporary substrata as leaves (Schuster 1988; Gradstein *et al.* 2006). The high level of reproduction, especially sexual reproduction, coupled with the high diversity of niches in tropical forests, has resulted in a large number of liverwort taxa. In some cases, the leafy liverwort gametophyte is replaced by a large and persistent protonema (Figure 102) (Gradstein & Wilson 2009).

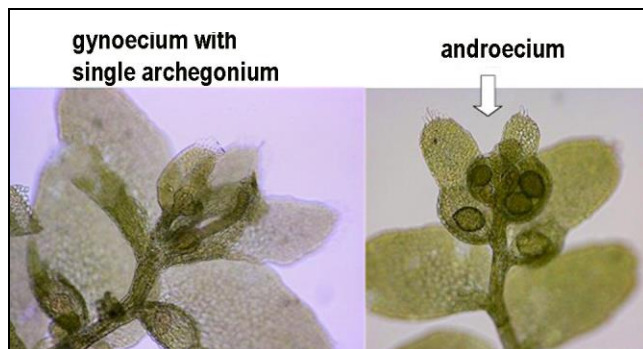


Figure 100. *Cololejeunea cardiocarpa* archegonium and antheridia exhibiting neoteny. Photo by Paul Davison, with permission.

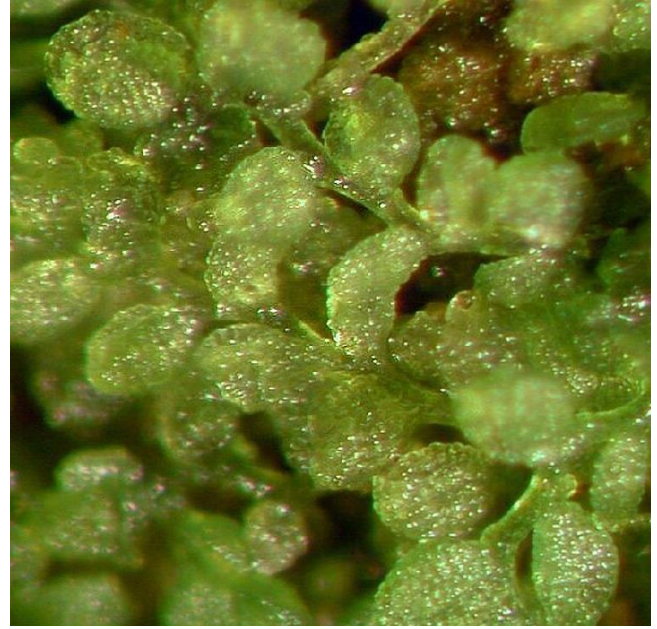


Figure 101. *Cololejeunea minutissima*; members of *Cololejeunea* exhibit neoteny in the tropics. Photo by Michael Lüth, with permission.

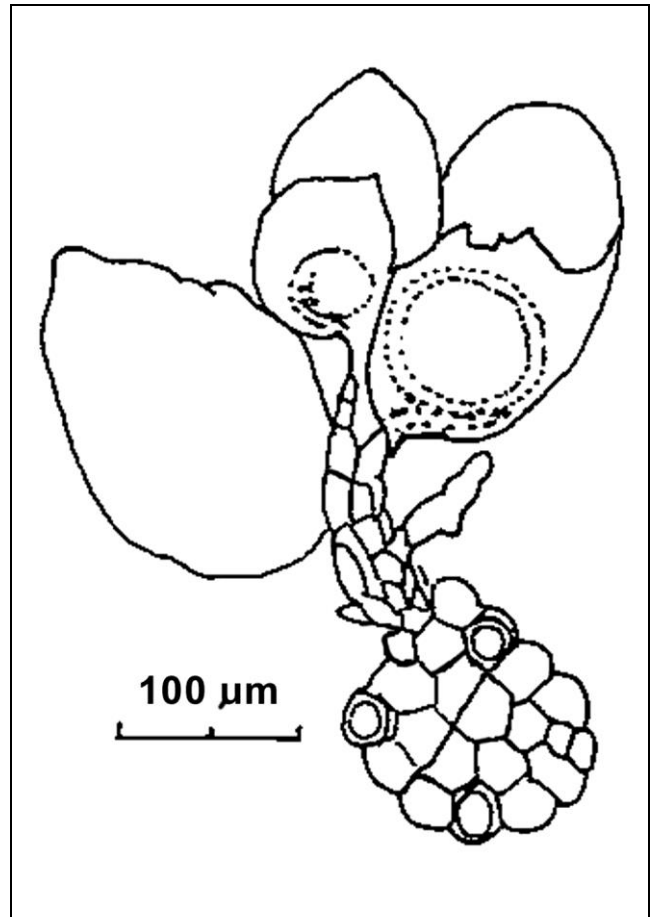


Figure 102. *Cololejeunea borhidiana* dwarf male, an extreme case of neoteny. Image by Tamás Pócs, slightly modified, with permission.

Reduced Numbers of Antheridia and Archegonia

Many temperate liverwort taxa produce numerous antheridia (5-16) and archegonia (12-25) (Schuster 1988). This is wasteful since only one archegonium on a branch can successfully produce a sporophyte. In tropical liverworts, these numbers are reduced to a more typical 1-4 archegonia and 1-2 antheridia per set of bracts (Figure 100). Furthermore, the size of gametangial branches is reduced (Figure 102) in many tropical taxa. Since gametes are typically released during the wet season, the danger of their drying out without achieving fertilization is reduced.

One rather unusual tropical leafy liverwort is *Colura irrorata* (Figure 103), a **rheophilous** (thrives in running water) member of **Lejeuneaceae** that grows part of the year submerged in torrential water (Figure 103). It was long known only from the banks of the Rio Topo in the Pastaza province of Ecuador (Thiers 1988) where it was discovered by Richard Spruce in 1857. It was long considered extinct until it was rediscovered there by Gradstein *et al.* (2004). A second locality of the rare species, in the same type of habitat, was recently found several hundreds of km further to the south in Ecuador (Gradstein & Benitez 2014). The species is more robust and has a more complex structure than other members of the **Lejeuneaceae**, but its most outstanding feature is its reproduction. Thiers (1988) estimated that a 2-cm section of stem could produce as many as 1600 **gynocia** (archegonia and surrounding bracts, *i.e.* female reproductive structures).



Figure 103. *Colura irrorata*, a species that produces up to 800 gynocia per cm. Photo by Lou Jost, through Robbert Gradstein.

Short Life Cycles

These tropical liverworts enjoy short life cycles (spore to spore), with epiphyllous species completing a full cycle in one year and those on other substrata in 2-3 years (Schuster 1988; Piippo 1992). This is enhanced by green spores (Figure 104) that are able to germinate immediately, and that predominantly germinate within the capsule (Schuster 1988). Despite these indicators that long-distance dispersals are unlikely, there is ample evidence that at least some of them are successful.

One example of the spore germination for a common tropical species is that of the leafy liverwort *Frullania ericoides* (Figure 104-Figure 105) (Silva-e-Costa *et al.*

2017). This species is **endosporic** (spores divide within spore wall), producing a globular protonema within the spore wall. By the fourth week, the protonema breaks through the spore wall and produces tightly concave primordial leaves. This germination occurs at 1/4, 1/2, full, and 1 1/2 strength Knop's nutrient solution, but fails to occur at double strength solution. This suggests nutrient requirements for successful germination are relatively low (compared to that of tracheophytes) and that nutrient-rich substrates would be detrimental to these liverworts.

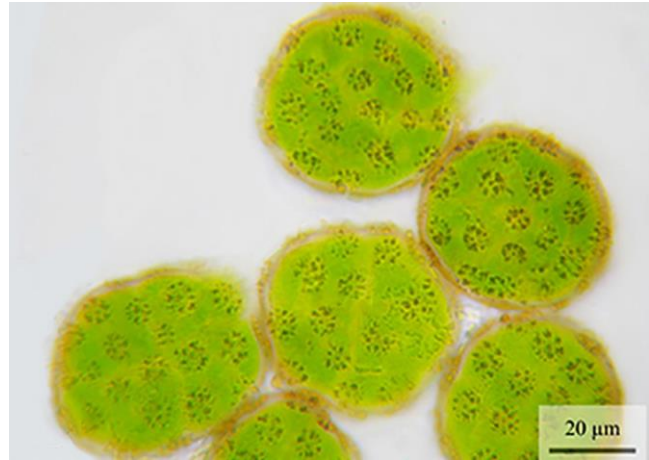


Figure 104. *Frullania ericoides* endospores, demonstrating their green color and germination within the spore. Photo from da Costa Silva-e-Costa *et al.* 2017, through Creative Commons.

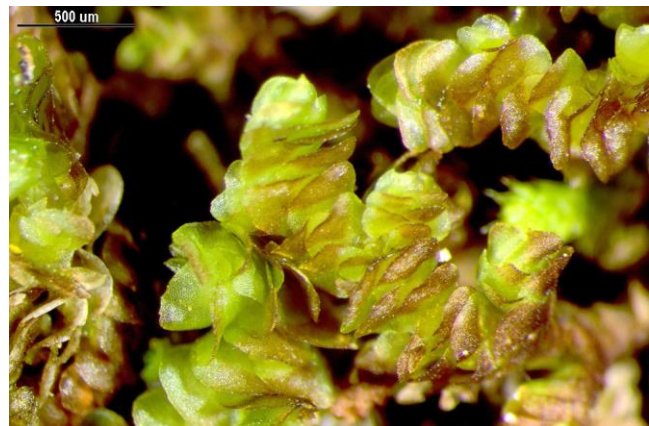


Figure 105. *Frullania ericoides*, a common tropical leafy liverwort. Photo by Blanka Aguero, with permission.

Alfayate *et al.* (2013) examined the spores of four pleurocarpous mosses in the Canary Islands, islands with a subtropical climate. They found that two of these were **isosporic** (all spores same size), but *Leucodon canariensis* (Figure 106) had two size classes of spores: medium-sized 1-celled spores and large multicellular spores. Furthermore, *Cryptoleptodon longisetus* (see Figure 107-Figure 108) has two sizes of spores, small spores and medium-sized spores. Spores germinate within the capsules in three of these species: *Leucodon canariensis*, *Cryptoleptodon longisetus*, and *Neckera intermedia* (Figure 109). *Neckera cephalonica* (Figure 110) spores do not germinate in the capsule. The perine wall of the spores of these species is papillose, an uncommon character for spores. The spores contain abundant lipid-like structures and chloroplasts with well-developed thylakoids.



Figure 106. *Leucodon canariense*, a species with two spore sizes: medium-sized 1-celled spores and large multicellular spores. Photo from BBS website, with permission from Barry Stewart.



Figure 107. *Cryptoleptodon* sp. in its habitat in India. Photo by Michael Lüth, with permission.

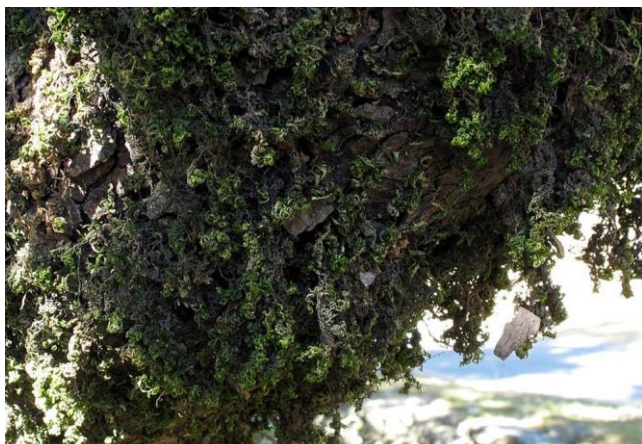


Figure 108. *Cryptoleptodon* sp. *Cryptoleptodon longisetus* is a species with two sizes of spores. Photo by Michael Lüth, with permission.



Figure 109. *Neckera intermedia*, a species with spores that germinate in the capsule. Photo by Jan-Peter Frahm, with permission.



Figure 110. *Neckera cephalonica*, a species with spores that do not germinate in the capsule. Photo by Jan-Peter Frahm, with permission.

Short Spore Longevity

Tropical liverwort spores have a short longevity and are unable to survive desiccation (Schuster 1988). Rather, they have several adaptations for rapid germination. They are typically **endosporic** (germinating and beginning development within spore wall; Figure 104), spores germinate within the capsule, and spores have elastic walls to facilitate development.

Prolonged Protonemal Stage

Several liverworts have remarkably prolonged protonemal stages, as in *Radula yanoella* (Figure 111) from the Amazonian rainforest (Thiers 1988; Gradstein & Wilson 2009). This species has since been found in French Guyana, Ecuador, and Costa Rica (Gradstein & Ilkiu-Borges 2009). In *Protocephalozia ephemeroides* (Figure 112) and *Cololejeunea metzgeriopsis* (Figure 113-Figure 114; syn.=*Metzgeriopsis pusilla*), the protonemal stage

replaces the leafy gametophyte except in association with the reproductive structures (Gradstein *et al.* 2006). *Metzgeriopsis pusilla* was formerly considered the only species in its genus, but has since been placed in *Cololejeunea* as *C. metzgeriopsis* (Gradstein & Wilson 2009). It lives in humid montane forests of tropical southeast Asia, growing as an epiphyll on living leaves. Its thallus is unistratose with minute, leafy sexual branches arising from the margins. *Protocephalozia ephemeroides* is a very rare liverwort, known only from two localities in southern Venezuela, near the border with Brazil, where it was collected by Richard Spruce. There it was growing on moist earth in shade and on little mounds "thrown up by mud worms." Thiers (1988) suggests that the normally short-lived liverwort protonemal stage has been lost in these taxa, replaced by a long one, because of the always abundant moisture. The protonemal stage of most bryophytes is typically subject to damage from rapid drying. This protonema can be thalloid, as in the liverworts *Cololejeunea metzgeriopsis* (Figure 114) and *Radula yanoella* (Figure 111), or filamentous, as in the leafy liverwort *Protocephalozia* (Figure 112) (Gradstein & Wilson 2009).

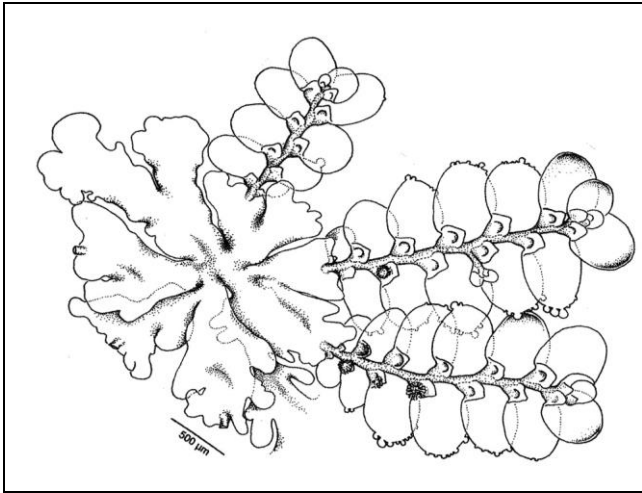


Figure 111. *Radula yanoella*, a leafy liverwort with a remarkably prolonged thalloid protonema. Drawing courtesy of Robert Gradstein, from Gradstein and Ilkiu-Borges 2009.

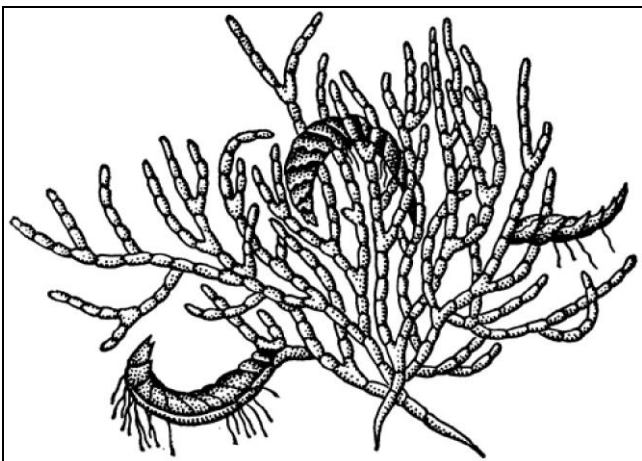


Figure 112. *Protocephalozia ephemeroides* with protonema and male gametophores. Image from Plantlife.ru, with implied online permission.

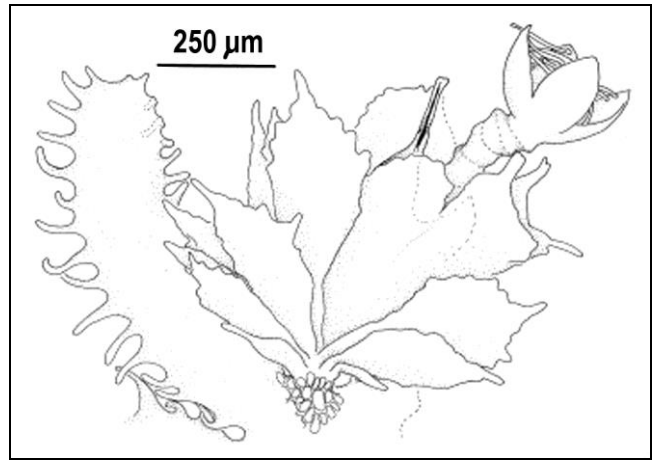


Figure 113. *Cololejeunea metzgeriopsis* plant with female organ. Drawing modified from Gradstein *et al.* 2006, with permission.

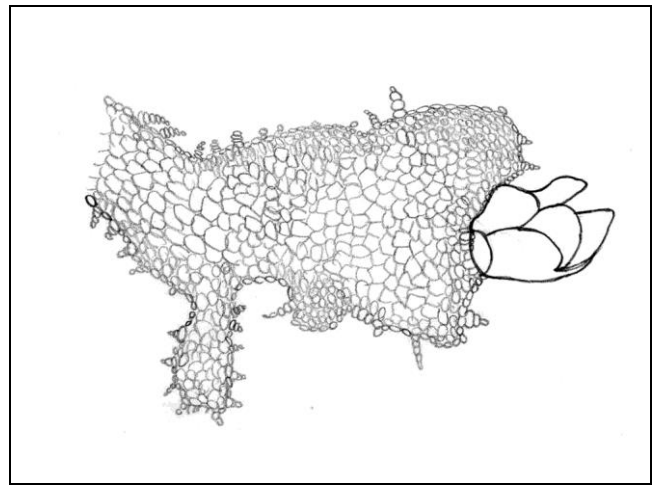


Figure 114. *Cololejeunea metzgeriopsis* protonema. Drawing by Zofie Juřičková, through Creative Commons.

Types of Gemmae

Even gemmae differ between the tropics and temperate zones (Schuster 1988). In temperate zones, the commonest types of gemmae are 1-2 cells and occur in branching chains (Figure 115). As such, they are easily dispersed, much like spores. These small gemmae occur in the **Jungermanniales** [*e.g.* **Cephaloziaceae** (Figure 116), **Calypogeiaceae** (Figure 117-Figure 118), **Scapaniaceae** (Figure 119-Figure 121), **Lophoziaceae** (Figure 122-Figure 124), **Cephaloziellaceae** (Figure 125-Figure 126)]. A single shoot can produce thousands of gemmae in a single growing season. This type of gemma is not so common in the tropics, where the more common **Porellales** (including **Lejeuneaceae**; Figure 127-Figure 128) have large gemmae. Instead, many tropical species tend to have discoid and single-layered gemmae, permitting easy dispersal to "considerable distances." The number of types is more limited, including discoid gemmae (Figure 128) and **caducous** (deciduous) branches (Figure 129). Even fragmenting branches are rare in the tropics. Gemmae are in general less common and less important among sexually reproducing tropical liverworts, even though many liverworts may produce both gemmae and sexual organs.



Figure 115. *Nowellia curvifolia* leaf gemmae, demonstrating the branching chains of 1-2-celled gemmae. Photo by Paul Davison, with permission.

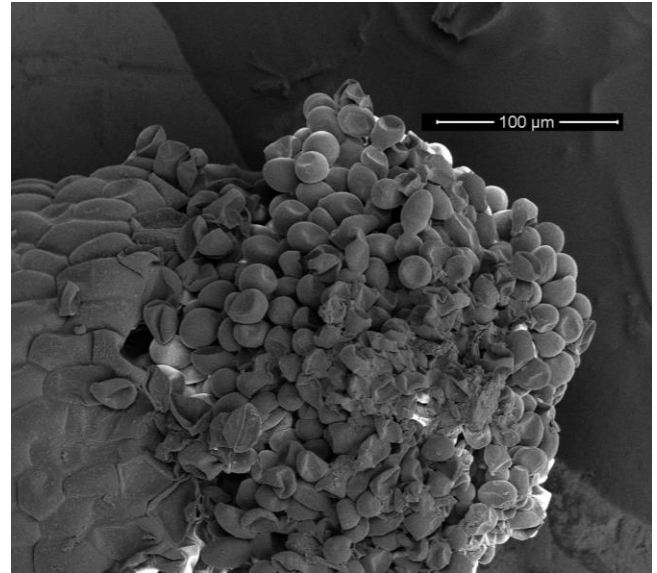


Figure 118. SEM of *Calypogeia muelleriana* leaf with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 116. *Odontoschisma longiflorum* (Cephaloziaceae) from the Neotropics, showing the small, branched chains of gemmae. Photo by Michael Lüth, with permission.

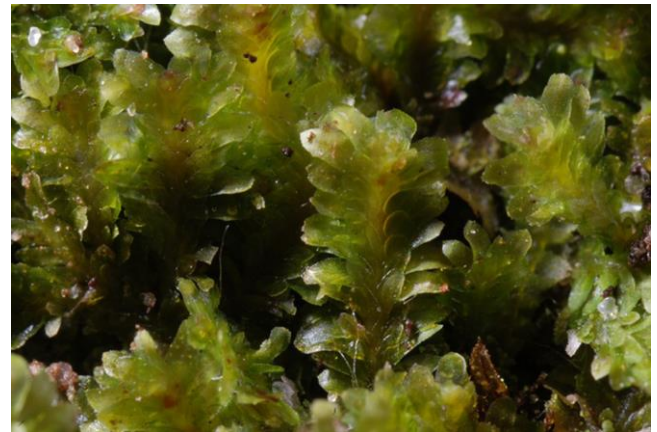


Figure 119. *Diplophyllum albicans* (Scapaniaceae), a species with worldwide distribution that includes the tropics. Photo by J. C. Schou, with permission.



Figure 117. *Calypogeia muelleriana*, with clusters of gemmae. Photo by David T. Holyoak, with permission.

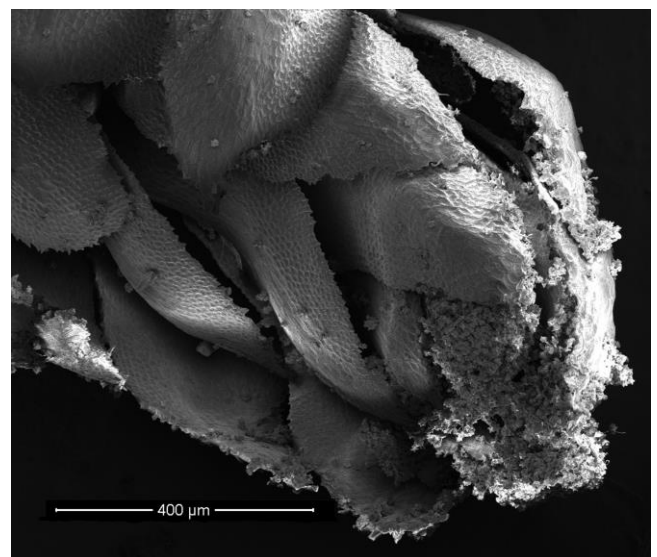


Figure 120. SEM of *Diplophyllum albicans* leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

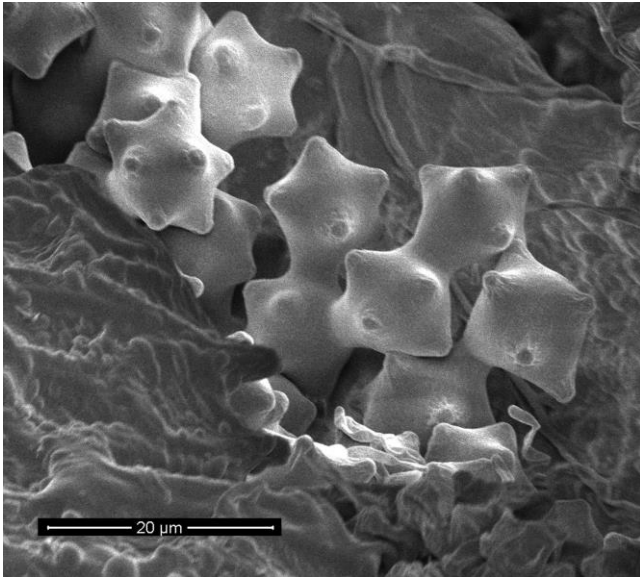


Figure 121. SEM of *Diplophyllum albicans* gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

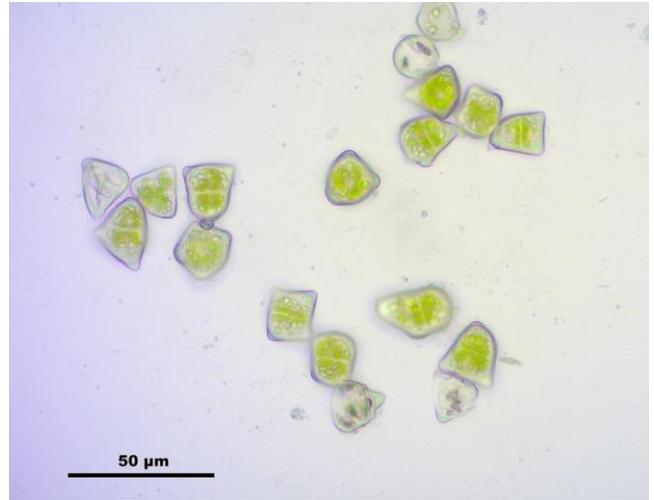


Figure 124. *Lophozia ventricosa* gemmae. Photo by Hermann Schachner, through Creative Commons.



Figure 122. *Lophozia ventricosa*, a widespread species that occurs in the Neotropics. Photo by Hermann Schachner, through Creative Commons.



Figure 125. *Cephaloziella bicuspidata* (Cephaloziellaceae). Photo by Botany Website, UBC, with permission.

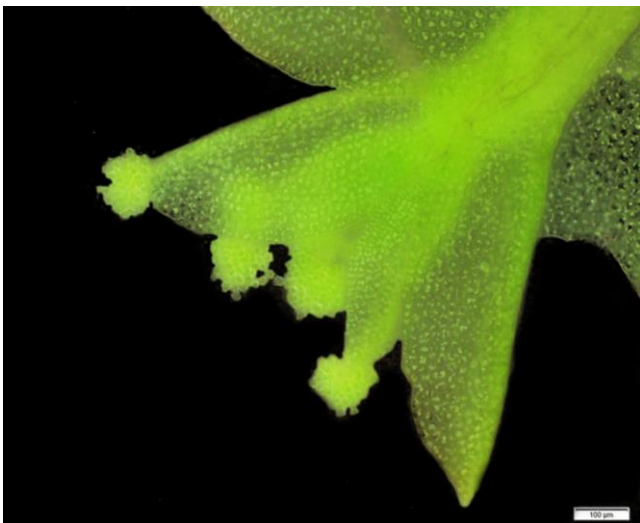


Figure 123. *Lophozia ventricosa* with gemmae on the leaf tips, a species found in the Neotropics. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

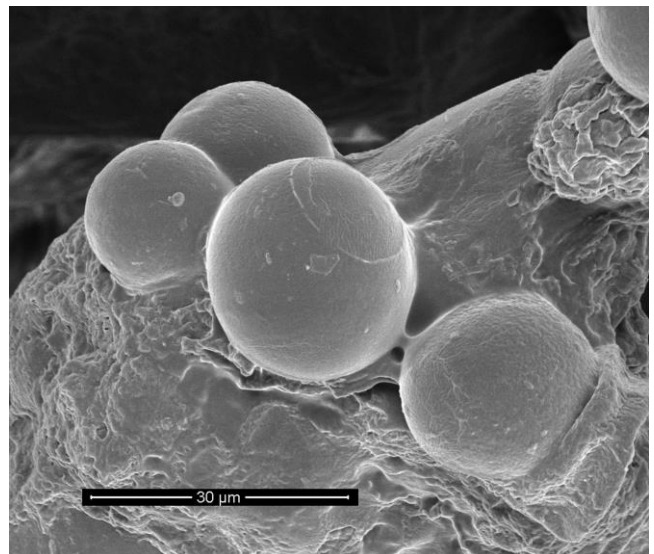


Figure 126. SEM of *Cephaloziella bicuspidata* gemmae, demonstrating the small gemma size of the Cephaloziellaceae. Photo courtesy of Jeff Duckett and Silvia Pressel.

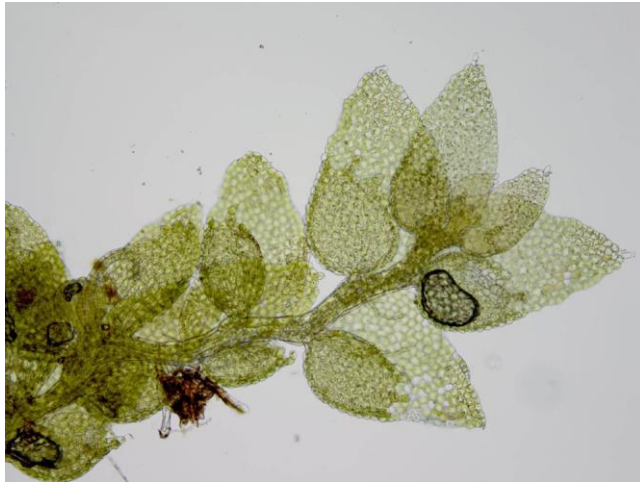


Figure 127. *Cololejeunea cardiocarpa* (Lejeuneaceae), a leafy liverwort that occurs in the tropics and has large gemmae. Photo by Blanka Aguero, with permission.

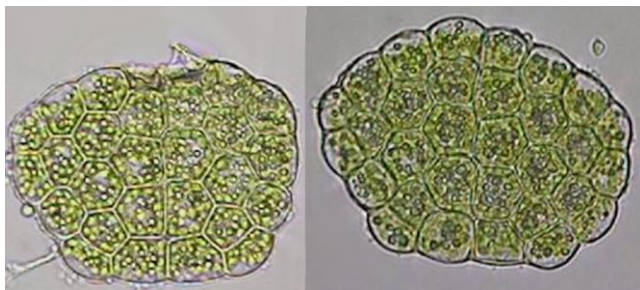


Figure 128. *Cololejeunea cardiocarpa* gemmae, showing the large gemma size typical of the Lejeuneaceae. Photo by Paul Davison, with permission.



Figure 129. *Prionolejeunea saccatiloba* showing small, caducous branch that can fall off for asexual reproduction. Photo by Michaela Sonnleitner, with permission.

Another anomaly among tropical liverworts is that gemmae and sexual organs can be produced at the same time, as in many species of *Cololejeunea* (Figure 127-Figure 128, Figure 130-Figure 131) (Schuster 1988). By contrast, in temperate regions many species of **Lophoziaceae** and **Scapaniaceae** (Figure 132) may

produce gemmae and sex organs at the same time. Their gemmae are typically produced in response to submarginal growth conditions that would often suppress production of sex organs.



Figure 130. *Cololejeunea minutissima*; many species in this large genus produce gemmae and sexual organs at the same time. Photo by David T. Holyoak, with permission.



Figure 131. *Cololejeunea truncatifolia* from Uganda; many species in this genus produce gemmae and sexual organs at the same time. Photo by Martin Wigginton, with permission.



Figure 132. A temperate one *Scapania nemorea* with gemmae. Some temperate populations of *Scapania* can at times produce sexual structures and gemmae at the same time. Photo by Dick Haaksma, with permission.

Van Zanten and Gradstein (1987) found that spores of endemic liverwort species had less resistance to drying and freezing than did the transoceanic species of Colombian liverworts. When subjected to intercontinental transport on the wing tips of a jet airplane, spores of 60 out of 61 species became inviable, presumably due to high UV levels

at jet stream levels. Only spores of two species growing at high elevation (ca. 4000 m) were able to germinate after the flight. Probably they were well-adapted to UV radiation. On the other hand, van Zanten and Gradstein found that wet freezing permitted survival. They suggested that liverworts from high altitudes had a "good possibility" for aerial long-distance dispersal through hurricanes and tropical storms.

Diaspore Banks

Bisang *et al.* (2003) cultured diaspores from three Malaysian mountain rainforests. They found that more liverworts than mosses germinated in the samples, especially those from lower altitudes. Samples from higher elevations produced twice the species diversity compared to those from lower elevations. They were able to identify the liverworts *Calypogeia arguta* (Figure 133), *C. fusca*, *Lepidozia wallichiana* (Figure 134), and *Zoopsis liukuensis* (Figure 135), all common taxa in the collection area. The diaspore origin of the liverworts could not be determined.



Figure 133. *Calypogeia arguta*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jan-Peter Frahm, with permission.

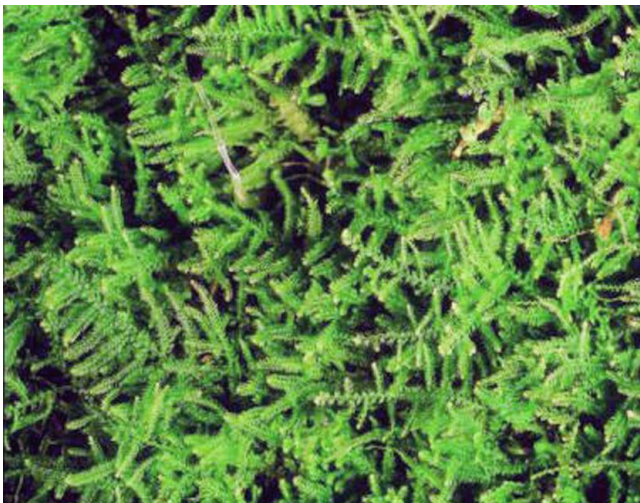


Figure 134. *Lepidozia wallichiana*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jiadong Yang, through Creative Commons.

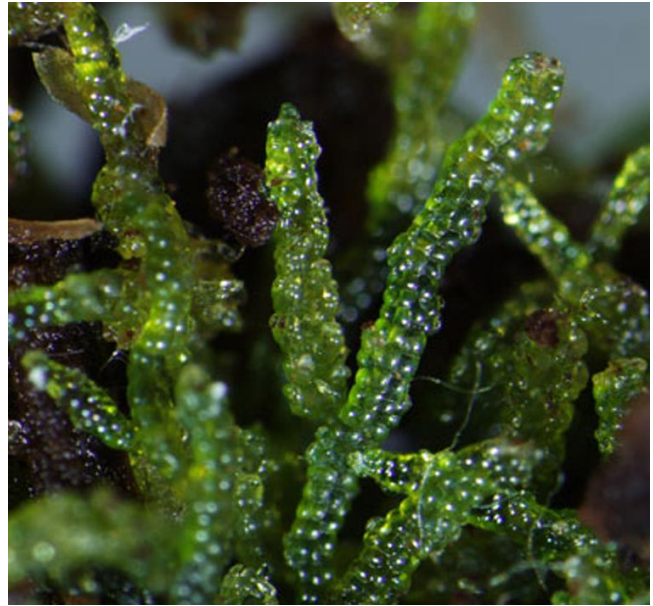


Figure 135. *Zoopsis liukuensis*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Rui-Liang Zhu, with permission.

Rheophilic Adaptations

River banks present problems unique to that habitat. The leafy liverwort *Cololejeunea stotleriana* (Figure 136) from Ecuador presents a highly specialized morphology and represents adaptations to that habitat (Figure 137) where little study has occurred (Gradstein *et al.* 2011). This species is both rheophilous and epiphyllous. Its adaptations include a robust stem, flatness, triangular lobules, large rhizoid fields not produced near each leaf base, super fertility, and clustered gynoecia. It was growing with the rare mosses *Fissidens hydropogon* (Figure 138) and *Lepidopilum caviusculum* (Figure 139).



Figure 136. *Cololejeunea stotleriana* on a fern frond. Photo by F. Werner, courtesy of Robert Gradstein.



Figure 137. Habitat of the rheophilous *Cololejeunea stotleriana*, *Fissidens hydropogon*, and *Lepidopilum caviusculum*. Photo by F. Werner, courtesy of Robbert Gradstein.



Figure 138. Herbarium specimen of *Fissidens hydropogon*, a rare rheophilic moss from Ecuador. Photo from Alchetron.com, through Creative Commons.



Figure 139. Herbarium specimen of *Lepidopilum caviusculum*, a rare rheophilic moss from Ecuador. Photo from the Natural History Museum, London, through Creative Commons.

Dispersal

Norhazrina *et al.* (2016) considered bryophytes to be very good dispersers, especially in contrast to flowering plants. This superior dispersal of bryophytes may lead to similar species richness patterns among the tropical regions, although tropical Africa has significantly fewer species than tropical America and tropical Asia. They found a slight but significantly higher beta diversity within tropical regions than among them. For many locations, oceans act as a barrier to "routine" dispersal, causing large-scale floristic patterns.

Suitable dispersal differs among regions and habitats. The tropics is in some places remote, separated from propagule sources by a wide expanse of ocean, and in others a mountain-valley topography likewise provides an expanse of unsuitable habitats. Thus, in discussing an area as expansive as the tropics, dispersal considerations are important for both biogeography and ecology.

With no experimental evidence but with vast ecological experience in the tropics and other regions, Richards (1988) ventured to apply his experience to hypothesize about dispersal of bryophytes in the tropics. First, he noted the impermanent nature of tropical substrates and suggested that these conditions would require efficient short-distance dispersal. He furthermore noted that each microhabitat has a distinct synusia of bryophytes that are characterized by particular life forms and life strategies. The swampy or oft-flooded sites are usually richer in species than sites that are well drained. The undergrowth probably has less effective wind dispersal than does the canopy.

For various asexual diaspores, splash is probably important (Richards 1988). For example, *Calymperopsis* species in Africa, as noted above, have their gemmae in splash cups. And discoid *Lejeuneaceae* (Figure 130-Figure 131) gemmae are probably dispersed by splashing rainfall. Richards also considered it likely that birds disperse fragments, particularly of *Meteoriaceae* (Figure 32-Figure 33), when they gather the mosses for nest building.

Baas-Becking (1934) introduced the concept that "everything is everywhere" for small things that can be dispersed by wind. The tropics seem like a good place to test this concept for bryophytes. Shaw *et al.* (2005) considered global patterns of moss diversity, patterns that must to some degree reflect dispersal patterns. Based on 86 globally distributed taxonomic checklists, they concluded that mosses are not more species-rich in the tropics than elsewhere. On the other hand, analysis of only North, Central, and South American samples demonstrate that a latitudinal gradient is apparent. Molecular diversity suggests that moss diversity is highest in the Southern Hemisphere, thus lowest in the Northern Hemisphere. The tropics are intermediate. These differences, however, are small, and essentially all moss lineages are represented in all three latitudinal zones. Hence, their data support the "everything is everywhere" hypothesis (Baas-Becking 1934) that is evident among many organisms with small

propagules. (See Chapter 4-8 for more information on the topic of "everything is everywhere.")

But liverworts seem to exhibit a somewhat different pattern, more closely mimicking the distribution patterns of the tracheophytes (Schuster 1969). Schuster cites as evidence their patterns of endemism and disjunction, as well as their having highly specific, restricted ranges. He cites further support from the high number of species of liverworts in the Arctic. Nevertheless, some taxa, especially the **monoicous** (both sexes on same plant) ones, seem to have wide spore dispersal, as suggested by their presence on islands in the Mid-Atlantic and Indian Ocean ridges. Interpretation is complicated by our inability to distinguish between ancient "overland" dispersal and more recent dispersal by spores. But in 1969, tropical liverworts were poorly known. Can we still support Schuster's (1969) distributional conclusions today?

Based on analysis of a large, world-wide data set of species distributions, Wang *et al.* (2016) found a clearcut latitudinal diversity gradient in liverworts and hornworts. The highest species richness was found in the tropics, which they explained by the explosive diversification of some of the most speciose liverwort lineages, such as **Lejeuneaceae** (Figure 36-Figure 39, Figure 65, Figure 101-Figure 103, Figure 113-Figure 114, Figure 127-Figure 131, Figure 136), **Plagiochilaceae** (Figure 99), and **Frullaniaceae** (Figure 14, Figure 105) in the humid tropical forests. But they also noted that there is much evidence to suggest that dispersal is not limiting, and that long-distance dispersal is common among bryophytes. In fact, bryophytes exhibit a much lower global turnover of **beta diversity** (ratio between regional and local species diversity) than do flowering plants and maintain relatively constant levels of **alpha diversity** (local species richness) on a gradient of geographical isolation (Patiño *et al.* 2015).

New ideas are emerging suggesting that islands, including tropical islands, are sources of diversity instead of the previously thought evolutionary dead ends and diversity sinks (Patiño *et al.* 2015). The dead end concept was based on "perceived low levels of genetic diversity, poor interspecific competitive and defensive ability, and loss of dispersal capacities." But bryophytes do not fit well into this model. They have high dispersal capabilities compared to most tracheophytes, and when genetic diversity was examined, it proved to be higher in island populations than in continental populations. Patiño and coworkers suggest that rather than being evolutionary dead ends for such organisms as bryophytes, islands become sources of diversity for bryophytes that subsequently disperse to continents. They also found that species richness of islands correlates by habitat diversity, not by size or age of the islands or distance to the continent, hence is not driven by dispersal.

Karlin *et al.* (2012) examined genetic diversity on the remote Hawaiian Islands in the Neotropics. Because of this remoteness, the popular opinion was that long-distance dispersal to the islands was rare. In

their investigation into the population genetic diversity, the researchers concluded that the peat moss *Sphagnum palustre* (Figure 140) most likely arrived with a single dispersal event. This species lacks sporophytes on the Hawaiian Islands and most likely lacks sexual reproduction. Further evidence to support a single dispersal event is that all samples share a rare genetic trait. They concluded that the original Hawaiian dispersal event was from vegetative propagation.



Figure 140. *Sphagnum palustre*, a species that apparently arrived on the Hawaiian Islands as a single dispersal event. Photo by Bernd Haynold, through Creative Commons.

Bryophytes exhibit a high capacity for transoceanic dispersal (Lewis *et al.* 2014) when compared to flowering plants (Patiño *et al.* 2014). This thinking is further supported by the low levels of competition among bryophytes compared to that among flowering plants (Rydin *et al.* 2009). This low competition suggests that the niche preemption hypothesis (Whittaker & Fernández-Palacios 2007) does not apply to bryophytes and thus makes it easier for them to succeed when they arrive on an island or subsequently on a new continent. The clonal nature of bryophytes (Cronberg *et al.* 2006; Hutsemékers *et al.* 2010, 2013; Karlin *et al.* 2011; Patiño *et al.* 2013), and their ability to disperse viable fragments means that the minimum population size is quite small (Bengtsson & Cronberg 2009) and further enables them to succeed when they colonize. Thus, as indicated by a compilation of data, island populations of bryophytes are not necessarily genetically depauperate (Fernández-Mazuecos & Vargas 2011; Laenen *et al.* 2011; Désamoré *et al.* 2012; García-Verdugo *et al.* 2015). Even seed plants can have a larger genetic diversity on islands than in associated continents (Désamoré *et al.* 2012). Based on these studies, and particularly that of Patiño *et al.* (2015), it is likely that the Macaronesian archipelagos, including the tropical portion, have provided a stepping stone for trans-continental bryophyte immigration to other tropical regions in new continental locations. Hence, islands may help to explain the **pantropical** (distribution covers tropical regions of both hemispheres) distribution of many bryophytes.

Another possibility, potentially as an additional scenario rather than a preferred one, is that islands can serve as refugia during times when the continent becomes uninhabitable. Such seems to be the case for the leafy

liverwort *Radula lindenberiana* (Figure 141) in Macaronesia (Laenen *et al.* 2011). It appears that a number of European plants, including *R. lindenberiana*, share a Macaronesian common ancestor and that these species may have back-colonized Europe. The widespread (including tropical Africa and tropical America) aquatic moss *Platyhypnidium riparioides* (Figure 142-Figure 143) likewise supports the concept that oceanic islands serve as major sources of biodiversity for recolonization of continents following glaciation (Hutsemékers *et al.* 2011). The lack of morphological diversity among the bryophytes, but presence of high genetic diversity, reflects the simple structure of the bryophytes.



Figure 141. *Radula lindenberiana*, a species that seems to have used Macaronesia as a refugium. Photo by Dick Haaksma, with permission.



Figure 142. *Platyhypnidium riparioides* in its usual habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 143. *Platyhypnidium riparioides*, a species that exhibits some genetic variation along its river course, using mostly fragments as dispersal units. Photo by Hermann Schachner, through Creative Commons.

For the moss *Platyhypnidium riparioides* (Figure 142-Figure 143), Hutsemékers *et al.* (2013) found that some genetic variation occurs along the river basin and indicates that this widespread aquatic moss has weaker dispersal than that expected for pollen or wind-dispersed seeds. Rather, it appears that fragments are more important than spores for local dispersal of this moss, thus explaining the low levels of genetic diversity.

Even the dispersal-limited dung moss *Tetraplodon* (Figure 144) has **amphitropical** (distributed on both sides of the tropics) and bipolar (distributed in cold temperate regions) disjunctions that seem to require long-distance dispersal (Lewis *et al.* 2014). Lewis and coworkers suggested that the disjunct distribution in the Western Hemisphere may have been accomplished through stepwise migration along the Neotropical Andes. But *Tetraplodon* is typically dispersed by flies that provide only short dispersal ranges. Furthermore, experiments indicate that the spores of *Tetraplodon* cannot survive long-distance dispersal by wind. The researchers suggest that instead, birds might provide the dispersal vector necessary to account for the widespread but disjunctive distribution of the species in South America.



Figure 144. *Tetraplodon mnioides*, an amphitropical moss, with the toad *Nannophryne variegata* in South America. Photo by Filipe Osorio, with permission.

In examining bryophytes on oceanic islands, Patiño *et al.* (2013) concluded that even bryophytes exhibit an island syndrome. They exhibit genetic drift, indicating relatively slow migration rates between the oceanic islands and continents. This suggests that the ocean does impede migration. This period of isolation seems to lead to an increase in production of specialized asexual diaspores and a decrease in sporophyte production on the oceanic islands.

To demonstrate the relatively large number of Afro-American distributions in bryophytes, Gradstein (2013) examined records of liverworts in tropical regions of both Old World and New World tropics. Based on the disjunctions of 74 liverworts in 13 genera with Afro-American ranges, he estimated that about 5% of the

Neotropical and 8% of the African liverwort species had Afro-American disjunct distributions. This number is doubled when pantropical species are included. Gradstein cited spore dispersal experiments and molecular-phylogenetic studies to conclude that for the majority of these genera, long-distance dispersal was the reason for the disjunction.

Ah-Peng *et al.* (2010) demonstrated the high bryophyte diversity on the small, oceanic La Reunion Island. In only 2512 km², 776 taxa are known. This island is near East Africa and Madagascar. The high diversity is fostered by its subtropical climate, a high altitudinal range (to 3070 m asl), and high rainfall.

Much of our understanding of long-range dispersal comes from van Zanten (1978; van Zanten & Pócs 1981; van Zanten and Gradstein 1987). In their laboratory experiments using 86 Colombian liverwort species, van Zanten & Gradstein (1987) found that spores of transoceanic species were more durable than those of endemic species. Survival was also greater in wet air-currents at high altitudes than in dry air currents. When they placed the spores on airplane wing tips during flights at jet stream elevation from Amsterdam to Los Angeles and back, however, only two species, the endemic *Marchantia chenopoda* (Figure 145) and the transoceanic *Gymnocoleopsis cylindriciformis*, could survive. All others were dead, probably due to exposure to UV radiation. Presumably *G. multiflora* spores survive because this species grows in the high Andes above 4000 m, where UV radiation is high. Van Zanten and Pócs (1981) concluded that tropical lowland moss species are much less drought tolerant than are temperate species. These tropical species are, however, resistant to wet-freezing and can be dispersed over short distances by rain showers and typhoons. They concluded that north-south dispersal across the equator was the most difficult and occurred rarely, if at all.



Figure 145. *Marchantia chenopoda* archegoniophores, a species whose spores can survive flight on the wings of a jet plane. Photo by Janice Glime.

Dispersal by wind is considered limited in forests, except in the canopy (Richards 1988). Some species, such as African moss species of *Syrrhopodon* (Figure 146) subsect. *Calymperopsis*, produce gemmae in splash cups similar to those of the moss *Tetraphis pellucida* (Figure 147). Although experimental dispersal studies are lacking for tropical species, but Richards suggests that the discoid

gemmae (Figure 128) of many of the **Lejeuneaceae** (Figure 130-Figure 131) are probably dispersed by splashing rain. Hanging mosses get dispersed by birds through dropped fragments when they are collected for nest making.



Figure 146. *Syrrhopodon albovaginatus*; some species of this genus produce gemmae in cups in the tropics. Photo from Natural History Museum, London, through Creative Commons.



Figure 147. *Tetraphis pellucida* with gemmae cup and discoid gemmae – similar to those of African species of *Syrrhopodon*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Dispersal adaptations reflect moisture relationships. The secretion of sticky mucilage (Thiers 1988) can aid in the attachment to vertical surfaces and prevent being washed away during rainstorms. Gemmae and the precocious development of spores permit more rapid development and thus greater chance for establishment. The prolongation of the protonemal stage may also aid in insuring attachment, whereas the **neotenus life cycle** (see under Liverworts above) permits early maturity, providing greater likelihood of completion of the life cycle before host leaves are shed during the rainy season.

I must re-emphasize the strategies of the **Lejeuneaceae** (Figure 36-Figure 39, Figure 130-Figure 131), a large pantropical family of considerable importance among the liverworts. This family has many monoicous species, and many species have intercontinental ranges, but all have large, multicellular spores – an atypical character for taxa with transoceanic distributions (Gradstein *et al.*

1983; Gradstein & Pócs 1989). Nevertheless, the multicellular large spores should permit the species to become established more easily once they arrive because of greater food reserves to permit a quick start. And the monoicous character facilitates sexual reproduction.

Although I have discussed the flying fox in volume 1, a discussion of dispersal in the tropics cannot be complete without the recalling this unique mechanism for some bryophytes in the Wet Tropics of northeastern Australia. Parsons *et al.* (2007) found that the spectacled flying fox *Pteropus conspicillatus* (Figure 148) spreads bryophyte fragments in its feces (Figure 149). When the researchers cultured the feces, they found that the fragments were viable (Figure 150). Not only were there bryophyte fragments, but also live invertebrates and other organisms.

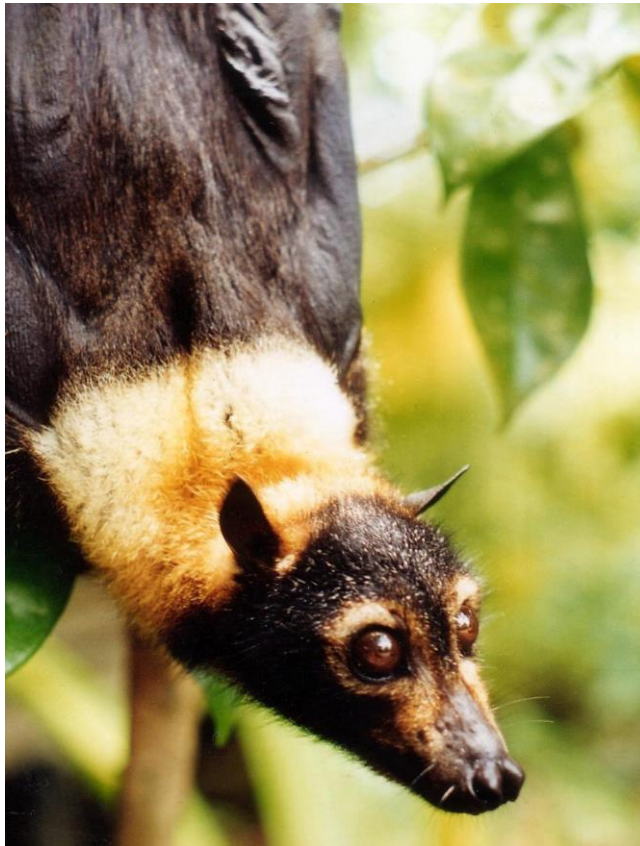


Figure 148. Spectacled flying fox (*Pteropus conspicillatus*), a possible disperser of bryophytes in the Wet Tropics of Australia. Photo courtesy of Jennifer Parsons.



Figure 149. Bat splat (feces) of the spectacled flying fox. Photo by Jennifer Parsons, with permission.



Figure 150. *Racopilum* sp. from flying fox splat. Photo courtesy of Andi Cairns.

Sampling

Sampling in the tropics can present problems that are less important elsewhere – such difficulties as canopy height and excessive moisture. Mountainous areas may be remote, with some available only by foot paths. Tall trees make small branches of the canopy almost impossible to sample; methods to overcome this obstacle are in the subchapter on epiphytes. Several researchers have addressed the problems unique to bryological collecting in the tropics (Mori & Holm-Nielson 1981; Edwards 1986; Delgadillo 1987; O'Shea 1989; see Frahm *et al.* 2003 for a comprehensive review).

One important consideration when collecting in tropical countries is that researchers there are often struggling with inadequate herbarium materials, particularly ones that can be used for checking their own collections. Duplicate specimens should always be provided to an accessible herbarium in the country – one that has a curator and can loan specimens. And of course one should be aware of local collection laws, obtain proper collecting permits, and determine in advance what restrictions there might be by customs and plant control in both the country of collection and in the receiving country.

Delgadillo (1987) and Frahm *et al.* (2003) detail many things to consider before departing for the tropical country, behavior during the visit, and how to treat specimens from another country upon return home. He suggests researching the geography, customs, and language of the country and contacting one or more resident bryologists for suggestions on places to stay and places to sample. Obtain collecting permits in advance for each country you plan to visit. Be sure you have health insurance to cover you in the places you will visit. Follow the routines of the local herbaria and institutions you visit and take their advice on food, roads, and other items of local knowledge. Remember that appointment times are not as rigid in some countries, so be patient, especially with local natives who might help you. Be sure you provide the local herbaria or national herbarium with a set of identified specimens. If possible, use their herbarium specimens in their herbarium so you don't have to borrow from their typically small number of specimens. To get both loans and your own specimens back to your own country, use registered mail.

Be sure you understand the quarantine regulations in both countries. Avoid travelling in the field alone; taking a local student along can benefit both of you. Carry a first-aid kit and a letter of introduction from the local university or herbarium in case it is needed to satisfy local authorities. Upon returning home, return loaned specimens as soon as possible, being sure to meet quarantine requirements. Send a set of duplicate specimens from your own identified collections for any species you have not already deposited in a herbarium in the country visited.

Braun-Blanquet Sampling Method

While sampling may be more difficult in a tropical jungle, methods used elsewhere often work well. A common method of sampling vegetation, particularly in Europe, is the **Braun-Blanquet method**. This method uses a cover-abundance scale to describe the vegetation. These levels are divided into cover classes, typically using 5-7 categories:

- | | |
|---|--------|
| 1 | <1 |
| 2 | 1-5 |
| 3 | 5-10 |
| 4 | 10-25 |
| 5 | 25-50 |
| 6 | 50-75 |
| 7 | 75-100 |

The levels are estimated through the use of **relevés**. This system has been applied originally to tracheophytes, but many bryologists have adapted it for a more efficient means of quantitative sampling. Poore (1955) criticized the system, but Moore (1962) countered those criticisms, stating that Poore had misapplied the method. Damgaard (2014) determined that despite its bias to over-estimate abundance, the Braun-Blanquet method gave results comparable to those of other methods of estimating plant cover. It has the added advantage of providing comparisons to the many studies that have used it, permitting data comparisons over time.

Wikum and Shanholtzer (1978) noted that most methods of measuring vegetation density are time-consuming and costly. The Braun-Blanquet method requires only about one-third to one-fifth the amount of field time, giving comparable results. I am unaware of any studies comparing the Braun-Blanquet system with other cover estimates for bryophytes, but it has been used in tropical studies and provides a relatively rapid method that is helpful when time is often quite limited.

A discussion of the unique methods for sampling epiphytes is in the subchapters on epiphytes and epiphylls in this chapter.

Drying Specimens

Because of periods of daily rain, there isn't enough time for anything to get dry, and that includes your clothes and your bryophytes. And both damp clothing and bryophytes can soon become a garden for molds. Molds make the bryophytes difficult to identify, and certainly make them unsightly, not to mention a health hazard. They introduce molds to the herbarium, and their spores can cause allergic reactions and asthma. They will also make it more difficult to get the bryophytes through plant protection agencies when you enter another country.

Frahm and Gradstein (1986) note these difficulties in the tropics, making several suggestions to overcome them.

One method that is used is to place the bryophytes in paper bags on a dry floor of a tent with open flaps (Frahm & Gradstein 1986). The opening is covered with mosquito netting to permit air movement. But during the rainy season, the dry periods are often insufficient for the bryophytes to dry. Some bryologists have resorted to putting a professional plant dryer in the back of a truck, using butane to provide the heat. But this method is not practical when only foot paths are available to the campsite. And most budgets can't afford such equipment. A less expensive approach is to suspend the bryophytes near a campfire, but the fire might get too hot and thus requires close watching. It can heat the bryophytes too much and thus damage them, particularly for those who might later want to use them for chemical analysis.

Frahm and Gradstein (1986) suggest an inexpensive, lightweight apparatus for drying bryophytes (Figure 151). It is constructed of L-shaped aluminum pieces with a frame that supports a wire mesh. Nylon should not be used because of its flammability. The heat source is two kerosene camping stoves (see also Croat 1979). The structure should then be surrounded with cotton cloth, as shown in the inset, again avoiding the more flammable nylon. The frames are about 1 m high, but the level of the screen can be adjusted to change the heat level. The apparatus should be monitored until you learn how much flame you need to avoid toasting the bryophytes or causing a forest fire. Once the ideal flame size is determined, the apparatus can be left unguarded overnight.

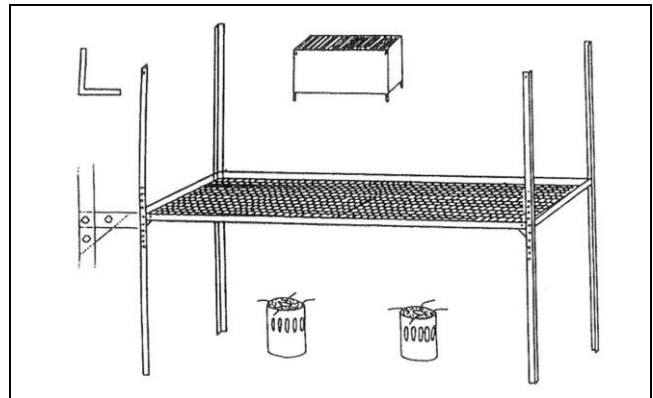


Figure 151. Light-weight drying apparatus for bryophytes in the field. From Frahm & Gradstein 1986.

Greene (1986) used chicken wire instead of wire screening. He suggested a method for keeping the specimens dry once getting them that way. They should immediately be put into large, heavy-duty plastic bags with silica gel to absorb moisture and sealed. [The plastic bags can be sealed by folding in the top corners, then folding down the top several times and fastening it with several large paper clips. – JG.] The specimens themselves can be kept in paper bags or packets. Greene transported the silica gel containers to the site in cotton bags. When they were needed, the silica gel containers were put into paper specimen bags and heated along with the specimens so that they were dry and ready when the specimens were stored.

Summary

Bryophytes in the tropics undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. Because of their sponge-like behavior, they can maintain moisture and nutrients for other members of the ecosystem. Nutrients can be released slowly, providing nutrients to the forest floor at critical times.

The primary environmental drivers determining the types of bryophyte communities are moisture, temperature, and light intensity. Life and growth forms differ among the habitats, with such forms as **pendants**, **fans**, and **tails** in moist habitats and **mats** and short acrocarpous mosses in dry conditions. Likewise, productivity differs with habitat, with dense growths in wet cloud forests and little biomass on the rainforest floor where there is little light penetration. Furthermore, growth periods and reproduction coincide with rainy periods, whereas the bryophytes are typically dormant in dry seasons.

Moss reproduction varies with habitat, but antheridia and archegonia are typically produced during the rainy season. **Monoicous** species have the most sexual reproduction. Many species lack sexual reproduction and spread through gemmae and regrowth. Sun species typically have larger spores than do shade species. Protonemal development is often prolonged.

Some liverworts and a few mosses may exhibit **neoteny**. Liverworts often have shortened life cycles, fewer antheridia and archegonia, longer spore lives, longer protonemal stages, and few types of gemmae in the tropics. Both mosses and liverworts can survive as spores, vegetative propagules, or fragments in diaspore banks, but liverwort spores typically have short longevity in the tropics. Liverworts have a limited number of propagule types, whereas the mosses have many.

Dispersal is mostly by wind and occurs in most cases in the dry season. Long distance dispersal is often important between mountains, and some species exhibit disjunct distributions between Africa and the Neotropics.

Rheophilic species probably have similar adaptations to the stream habitat, but few tropical studies have occurred.

Sampling brings special problems of getting mosses dry in the cloud forest or in the rainy season, often necessitating drying racks and a heat source. Investigators need to gain permission and should leave a set of herbarium specimens with a notable herbarium in the host country.

the chapter. Without his input this chapter would be far less complete. Tatiany Oliveira da Silva provided a critical reading for clarity, provided additional references, and shared her knowledge of the Amazon. Andi Cairns helped me add information on the Australian tropics to the appropriate subchapters and reviewed those chapters for the November 2019 version.

Literature Cited

- Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Ah-Peng, C., Bardat, J., Stamenoff, P., Hedderson, T. A., and Strasberg, D. 2010. Bryophytes of the island of La Réunion: Diversity, endemism and conservation. *Cryptog. Bryol.* 31: 241-270.
- Akande, A. O. 1984. Anhydrobiosis in corticolous bryophytes. *Trop. Ecol.* 25: 255-259.
- Akande, A. O. 1985. Osmotic potential – A factor for resistance to water stress in some Nigerian species of corticolous bryophytes. *Trop. Ecol.* 26: 80-84.
- Alfayate, C., Ron, E., Estébanez, B., and Pérez-Batista, M. Á. 2013. Mature spores of four pleurocarpous mosses in the Canary Islands: Ultrastructure and early germination stages. *Bryologist* 116: 97-112.
- Ando, H. 1977. Topics of the sexuality of bryophytes. *J. Jap. Bot. Soc.* 2: 30-32.
- Baas Beeking, L. G. M. 1934. *Geobiologie of inleiding tot de milieukunde*. W. P. Van Stockum & Zoon, The Hague, The Netherlands.
- Barkman, J. J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. van Gorcum, Assen, 628 pp.
- Batista, W. V. S. M., Pôrto, K. C., and Santos, N. D. 2018. Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil. *Acta Bot. Brasil.* 32: 303-313.
- Bengtsson, B. O. and Cronberg, N. 2009. The effective size of bryophyte populations. *J. Theor. Biol.* 258: 121-126.
- Biebl, R. 1964. Temperaturreistenz tropischer Pflanzen auf Puerto Rico. [Temperature resistance of tropical plants in Puerto Rico.]. *Protoplasma* 59: 133-156.
- Biebel, R. 1967. Temperaturreistenz tropischer Urwaldmoose. [Temperature resistance of tropical jungle moss.]. *Flora* 157: 25-30.
- Bisang, I., Piippo, S., and Hedenäs, L. 2003. Bryophyte diaspore bank in three Malaysian mountain rainforests. *J. Bryol.* 25: 68-70.
- Bryant, E. H., Crandall-Stotler, B., and Stotler, R. E. 1973. A factor analysis of the distribution of some Puerto Rican liverworts. *Can. J. Bot.* 51: 1545-1554.
- Cardoso, A. W. 2012. *Bryophytes in the hydrological cycle and climate change implications: A case study of La Réunion cloud forest*. Ph. D. dissertation, University of Cape Town, S. Afr.
- Cerqueira, G. R., Ilkiu-Borges, A. L., and Ferreira, L. V. 2016. Seasonality of reproduction of epiphytic bryophytes in flooded forests from the Caxiuanã National Forest, Eastern Amazon. *An. Acad. Brasil. Ciên.* 88: 903-910.
- Chen, X., Liu, W. Y., Song, L., Li, S., Wu, C. S., and Lu, H. Z. 2016. Adaptation of epiphytic bryophytes in the understorey

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make an early version of this chapter reliable. Her helpful discussions kept me going on this part of the world I know so little about. My co-author, Robbert Gradstein, has been very helpful in discussions, obtaining images and references, and in providing a critical review of

- attributing to the correlations and trade-offs between functional traits. *J. Bryol.* 38: 110-117.
- Churchill, S. P., Sanjines A., N. N., and Aldana M., C. 2010. Catálogo de las briofitas de Bolivia: Diversidad, distribución y ecología. Missouri Botanical Garden, 340 pp.
- Coley, P. D., Kursar, T. A., and Machado, J.-L. 1993. Colonization of tropical rain forest leaves by epiphylls: Effects of site and host plant leaf lifetime. *Ecology* 74: 619-623.
- Cornelissen, J. H. C. and Steege, H. ter. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- Coxson, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.
- Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). *Biotropica* 24: 121-133.
- Croat, T. B. 1979. Use of a portable propane gas oven for field drying plants. *Taxon* 28: 573-580.
- Cronberg, N., Rydgren, K., and Økland, R. H. 2006. Clonal structure and genet-level sex ratios suggest different roles of vegetative and sexual reproduction in the clonal moss *Hylocomium splendens*. *Ecography* 29: 95-103.
- Damgaard, C. 2014. Estimating mean plant cover from different types of cover data: A coherent statistical framework. *Ecosphere* 5(2): 1-7.
- Datta Munshi, J. 1974. Seasonal changes in standing crop and annual net production of two moss communities at Varanasi. *Trop. Ecol.* 15: 28-38.
- Delgadillo M., C. 1976. Estudio botánico y ecológico de la región de Río Uxpanapa, Veracruz. No. 3. Los Musgos. Publ. Inst. Invest. Recurs. Bioticos 1: 19-28.
- Delgadillo M., C. 1987. Additional recommendations for bryologists visiting the tropics. *Taxon* 36: 289-291.
- Delgadillo M., C. 1993. The Neotropical-African disjunction. *Bryologist* 96: 604-615.
- Désamuré, A., Laenen, B., Carine, M. A., Gonzalez-Mancebo, J. M., Molina, R. J., and Vanderpoorten, A. 2012. Inverted patterns of genetic diversity in continental and island populations of the heather *Erica scoparia s.l.* *J. Biogeogr.* 39: 574-584.
- During, H. J. 1998. De diasporeenvoorraad in de bodem van een savanne in Zimbabwe. [The diaspore bank in the bottom of a savannah in Zimbabwe.]. *Bauxbaumiella* 45: 12-13.
- During, H. J. 2007. Episodic bryophytes in the diaspore bank of a Zimbabwean savanna. *Lindbergia* 32: 55-61.
- During, H. J. and Moyo, C. 1999. The diaspore bank of bryophytes in a Zimbabwean savanna. *Hausknechtia Beiheft (Riclef Grolle-Festschrift)* 9: 111-114.
- Edwards, S. R. 1986. Bryophyte collecting and plant photography. *Univ. Hull Dept. Geogr. Misc. Ser.* 30: 65-72; 102-108.
- Egunyomi, A. 1978. The distribution of pantropical moss, *Octoblepharum albidum* Hedw. in Africa with special reference to Nigeria. *Rev. Bryol. Lichénol.* 44: 141-148.
- Egunyomi, A. 1979a. Autecology of *Octoblepharum albidum* Hedw. in Western Nigeria II. Phenology and water relations. *Nova Hedw.* 31: 377-389.
- Egunyomi, A. 1979b. The viability of spores of some tropical moss species after long-time storage and their survival changes in nature. *J. Hattori Bot. Lab.* 45: 167-171.
- Egunyomi, A. 1982. Dispersal mechanisms of *Bryum coronatum* in Nigeria. *Lindbergia* 8: 89-92.
- Egunyomi, A. 1984. A survey of asexual reproductive diaspores in the Nigerian moss flora. *J. Hattori Bot. Lab.* 56: 115-121.
- Egunyomi, A., Harrington, H. J., and Olarinmoye, S. O. 1980. Studies on regeneration from the leaves of *O. albidum* Hedw. (Musci). *Cryptog. Bryol. Lichénol.* 1: 73-84.
- Fatoba, P. O. 1998. Reproductive phenology of three selected tropical African mosses in South Western Nigeria. *Niger. J. Bot.* 11: 25-33.
- Fernández-Mazuecos, M. and Vargas, P. 2011. Genetically depauperate in the continent but rich in oceanic islands: *Cistus monspeliensis* (Cistaceae) in the Canary Islands. *PLoS One* 6: e17172.
- Fleischer M. 1904-1923. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java), 5 vols. Brill, Leiden.
- Frahm, J.-P. 1990a. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedw.* 51: 151-164.
- Frahm, J.-P. 1990b. Bryophyte phytomass in tropical ecosystems. *Bot. J. Linnean Soc.* 104: 22-33.
- Frahm, J.-P. and Gradstein, S. R. 1986. An apparatus for drying bryophytes in the field. *Bryol. Times* 38: 5.
- Frahm, J.-P. and Gradstein, S. R. 1990. Ecology of tropical bryophytes: A bibliography. *Trop. Bryol.* 3: 75-77.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Frahm, J.-P. and Kürschner, H. 1992. Moose tropischer Regenwälder. [Moss of tropical rainforests.]. *Spektr. Wissen.* 10: 58-67.
- Frahm, J.-P., Pócs, T., O'shea, B., Koponen, T., Piipo, S., Enroth, J., Rao, P., and Fang, Y. 2003. Manual of Tropical Bryology. *Trop. Bryol.* 23: 1-196.
- Frangi, J. L. and Lugo, A. E. 1992. Biomass and nutrient accumulation in ten year old bryophyte communities inside a flood plain in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 24: 106-112.
- Frey, W., Gossow, R., and Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord-Borneo). *Nova Hedw.* 51(1-2): 87-119.
- Fulford, M., Crandall, B., and Stotler, R. 1970. The ecology of an elfin forest in Puerto Rico, 11. The leafy Hepaticae of Pico del Oeste. *J. Arnold Arbor.* 51: 56-69.
- Fulford, M., Crandall, B., and Stotler, R. 1971. The ecology of an elfin forest in Puerto Rico. Part 15. A study of the leafy hepatic flora of the Luquillo Mountains. *J. Arnold Arbor.* 52: 435-458.
- García-Verdugo, C., Sajeva, M., Mantia, T. La, Harrouni, C., Msanda, F., and Caujapé-Castells, J. 2015. Do island plant populations really have lower genetic variation than mainland populations? Effects of selection and distribution range on genetic diversity estimates. *Molec. Ecol.* 24: 726-741.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2011. Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. *Biotropica* 43: 591-596.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *J. Bryol.* 35: 243-254.

- Giesenhagen, K. 1910. Die Moostypen de Regenwalder. [The moss types of rainforests.]. Ann. Jard. Bot. Buitenz. suppl. 3, pt.2: 711-790.
- Goebel, K. 1888. Morphologische und biologische Studien. I. Uber epiphytische Farne und Muscineen. Ann. Jard. Bot. Buitenzorg 7: 1-73.
- Gradstein, S. R. 1975. Studies on Lejeuneaceae subfam. Ptychanthoideae III. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae). Bryophyt. Biblioth. 4: 1-162.
- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. Cryptog. Bryol. 27: 141-152.
- Gradstein, S. R. 2013. Afro-American hepatics revisited. Polish Bot. J. 58: 149-177.
- Gradstein S. R. and Benitez, A. 2014. A second locality for the critically endangered *Colura irrorata* (Lejeuneaceae) in the Ecuadorian Andes. J. Bryol. 36: 151-155.
- Gradstein, S. R. and Ilkiu-Borges, A. L. 2009. Guide to the Plants of Central French Guiana. Part 4. Liverworts and Hornworts. Mem. N. Y. Bot. Gard. 76(4): 140 pp.
- Gradstein, S. R. and P6cs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Wilson, R. 2009. Protonemal neoteny in bryophytes. In: Mohamed, H., Baki, B. B., Nasrullah-Boyce, A., and Lee, P. K. Y. (eds.). Bryology in the New Millennium. University of Malaya, Kuala Lumpur, pp. 1-11.
- Gradstein, S. R., P6cs, T., and Vana, J. 1983. Disjunct Hepaticae in tropical America and Africa. Acta Bot. Hung. 29: 127-171.
- Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001. Guide to the Bryophytes of Tropical America. Mem. N. Y. Bot. Gard. 86: 1-577.
- Gradstein, S. R., Reiner-Drehwald, M. E., and Jost, L. 2004. The systematic position and distribution of *Myriocolea irrorata* (Lejeuneaceae, Hepaticae), an endangered liverwort from the Ecuadorian Andes. J. Hattori Bot. Lab. 93: 235-248.
- Gradstein, S. R., Wilson, R., Ilkiu-Borges, A. L., and Heinrichs, J. 2006. Phylogenetic relationships and neotenic evolution of *Metzgeriopsis* (Lejeuneaceae) based on chloroplast DNA sequences and morphology. Bot. J. Linn. Soc. 151: 293-308.
- Gradstein, S. R., Ilkiu-Borges, A. L., and Vanderpoorten, A. 2011. Habitat specialization triggers the evolution of unusual morphologies – the case of *Cololejeunea stotleriana* sp. nov. from Ecuador. Bryologist 114: 9-22.
- Greene, S. W. 1986. Keeping them dry. Bryol. Times 38: 6.
- Greenwood, J. L. and Stark, L. R. 2014. The rate of drying determines the extent of desiccation tolerance in *Physcomitrella patens*. Funct. Plant Biol. 41: 460-467.
- Griffin, D. III. 1979. Briofitos y Liquenes de los paramos. pp. 79-87. In: Salgado-Laboarian, M. L. (ed.). El Medio Ambiente Paramo. M6rida, Venezuela. Centro de Estudios Avanzados, Ediciones CEA-IVIC, Caracas.
- Griffin, D. III, Breil, D. A., Morales-Zurcher, M. I., and Eakin, D. 1974. Observations on bryophyte community of the Poas Volcano, Costa Rica. Observaciones sobre la comunidad de Bri6fitas del Volcan Poas, Costa Rica. Misc. Bryol. Lichenol. 6: 174-175.
- Hofstede, R. G. M., Wolf, J. H. D., and Benzig, D. H. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forests. Selbyana 14: 37-45.
- Hosokawa, T., Odani, N., and Tagawa, H. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. Bryologist 67: 396-411.
- Hutsem6kers, V., Hardy, O. J., Mardulyn, P., Shaw, A. J., and Vanderpoorten, A. 2010. Macroecological patterns of genetic structure and diversity in the aquatic moss *Platyhypnidium riparioides*. New Phytol. 185: 852-864.
- Hutsem6kers, V., Sz6v6nyi, P., Shaw, A. J., Gonzalez-Mancebo, J. M., Munoz, J., and Vanderpoorten, A. 2011. Oceanic islands are not sinks of biodiversity in spore-producing plants. Proc. Natl. Acad. Sci. 108: 18989-18994.
- Hutsemekers, V., Hardy, O. J., and Vanderpoorten, A. 2013. Does water facilitate gene flow in spore-producing plants? Insights from the fine-scale genetic structure of the aquatic moss *Rhynchostegium riparioides* (Brachytheciaceae). Aquat. Bot. 108: 1-6.
- Ingram, S. W. and Nadkarni, N. M. 1993. Composition and distribution of epiphytic organic matter in a Neotropical cloud forest, Costa Rica. Biotropica 25:370-383.
- Jacome, J., Gradstein, S. R., and Kessler, M. 2011. Response of epiphytic bryophyte communities to simulated climate change in the Tropics. In: Tuba, Z., Slack, N., and Stark, L. (eds.). Bryophyte Ecology and Climate Change. Cambridge University Press, pp. 191-210.
- Johnson, A., and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. Bryologist 73: 682-686.
- Karger, D. N., Kluge, J., Abrahamczyk, S., Salazar, L., Homeier, J., Lehnert, M., Amoroso, V. B., and Kessler, M. 2012. Bryophyte cover of trees as proxy for air humidity in the tropics. Ecol. Indic. 20: 277-281.
- Karlin, E. F., Andrus, R. E., and Shaw, A. J. 2011. One haploid parent contributes 100% of the gene pool for a wide spread species in northwest North America. Molec. Ecol. 20: 753-767.
- Karlin, E. F., Hotchkiss, S. C., Boles, S. B., Sten6ojien, H. K., Hassel, K., Flatberg, K. I., and Shaw, A. J. 2012. High genetic diversity in a remote island population system: Sans sex. New Phytol. 193: 1088-1097.
- Krinsky, N. I. 1968. The protective function of carotenoid pigments. Photophysiology: Current Topics 3: 123-195.
- Kurschner, H. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. Turkish J. Bot. 28: 73-84.
- Kurschner, H. and Parolly, G. 1998a. Lebensstrategien stammepiphytischer moose in regenwaldern am andenostabhang und im Amazonas-Tiefeland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru]. Nova Hedw. 67: 1-22.
- Kurschner, H. and Parolly, G. 1998b. Lebensformen und adaptationen zur wasserleitung und wasserspeicherung in epiphytischen moosgesellschaften nord-Perus (Amazonastiefeland, cordillera oriental, cordillera central). [Life forms and adaptations to water conduction and water storing in epiphytic bryophyte communities in northern Peru (the Amazon lowlands, eastern and central cordillera).]. Nova Hedw. 67: 349-379.
- Kurschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. Nova Hedw. 69: 73-99.
- Laenen, B., D6samor6, A., Devos, N., Shaw, A. J., Gonzalez-Mancebo, J. M., Carine, M. A., and Vanderpoorten, A. 2011. Macaronesia: A source of hidden genetic diversity for post – glacial recolonization of western Europe in the leafy liverwort *Radula lindenbergiana*. J. Biogeogr. 38: 631-639.
- Larson, D. W. 1981. Differential wetting in some lichens and mosses: The role of morphology. Bryologist 84: 1-15.

- Lawton, R. and Dryer, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101-116.
- Lewis, L. R., Rozzi, R., and Goffinet, B. 2014. Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae). *J. Biogeogr.* 41: 2385-2395.
- Li, X., Glime, J. M., and Hattori, S. 1989. Ecological gradient analysis of the genus *Frullania* on Mt. Albert Edward, Papua New Guinea. *J. Hattori Bot. Lab.* 66: 359-369.
- Linares, E. L. 1986. Estudio taxonomico y ecologico de la brioflora en la franja alto andina de "El Tabalzo", Cundinamarca. [Taxonomic and ecological study of the bryoflora in the high Andean strip of "El Tabalzo," Cundinamarca.]. Ph.D. Thesis, Universidad Nacional de Colombia, Bogotá, 308 pp.
- Lisboa, R. C. L. 1976. Estudos sobre a vegetação des campinas amazonicas V. Briocologia de uma campina amazonica. *Acta Amazon.* [Studies on the vegetation of the Amazonian plains V. Bryoecology of an Amazonian plain. *Acta Amazon.*] 6: 171-191.
- Lösch, R., Mülders, P., Fischer, E., and Frahm, J.-P. 1994. Photosynthetic gas exchange of bryophytes from tropical lowland and mountain forests of eastern Central Africa. *Trop. Bryol.* 9: 169-186.
- Maciel-Silva, A. S. and Oliveira, M. P. 2016. How tropical moss sporophytes respond to seasonality: Examples from a semi-deciduous ecosystem in Brazil. *Cryptog. Bryol.* 37: 227-239.
- Maciel-Silva, A. S. and Valio, I. F. M. 2011. Reproductive phenology of bryophytes in tropical rain forests: The sexes never sleep. *Bryologist* 114: 708-719.
- Maciel-Silva, A. S., Valio, I. F. M., and Rydin, H. 2012a. Altitude affects the reproductive performance in monoicous and dioicous bryophytes: Examples from a Brazilian Atlantic rainforest. *AoB Plants* 2012, pls016,14 pp.
- Maciel-Silva, A. S., Válio, I. F. M., and Rydin, H. 2012b. Diaspore bank of bryophytes in tropical rain forests: The importance of breeding system, phylum and microhabitat. *Oecologia* 168: 321-333.
- Maciel-Silva, A. S., Coelho, M. L. P., and Pôrto, K. C. 2013. Reproductive traits in the tropical moss *Octoblepharum albidum* Hedw. differ between rainforest and coastal sites. *J. Bryol.* 35: 206-215.
- Mägdefrau, K. 1982. Life-forms in bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 45-58.
- Makinde, A. M. and Odu, E. A. 1994. Phenological studies of selected savanna mosses of south-western Nigeria. *Experientia* 50: 616-619.
- Meagher, D. and Cairns, A. 2016. *Meteoriopsis undulata* Hork. & Nog. (Bryophyta: Meteoriaceae) new to the Australian flora. *Telopea* 19: 37-44.
- Merwin, M. C. and Nadkarni, N. M. 2002. 100 years of tropical bryophyte and lichen ecology: A bibliographic guide to the literature from 1901-2000. *Trop. Bryol.* 21: 47-67.
- Miehe, G. and Miehe, S. 1994. East African bryophytes. XII. Bryophytes from Bale Mountains, SE Ethiopia. 1. Phytoecological introduction. *Fragm. Flor. Geobot.* 39: 165-219.
- Mishler, B. D. 1988. Reproductive ecology of bryophytes. In: Lovett Doust, J. and Lovett Doust, L. *Plant Reproductive Ecology: Patterns and Strategies*. Oxford University Press, Oxford, pp. 285-306.
- Mitten, W. 1869. Musci Austro-Americani. *J. Linn. Soc. Bot.* 12: 1-659.
- Monge-Nájera, J. 1989. The relationship of epiphyllous liverworts with leaf characteristics and light in Monte Verde, Costa Rica. *Cryptog. Bryol. Lichénol.* 10: 345-352.
- Moore, J. J. 1962. The Braun-Blanquet System: A reassessment. *J. Ecol.* 50: 761-769.
- Moreno, E. J. 1992. Revisión histórica de la briología en Venezuela. *Trop. Bryol.* 6: 139-146.
- Mori, S. A. and Holm-Nielson, L. B. 1981. Recommendations for botanists visiting Neotropical countries. *Taxon* 30: 87-89.
- Nadkarni, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249-256.
- Nadkarni, N. M., Cobb, A. R., and Solano, R. 2000. Interception and retention of macroscopic bryophyte fragments by branch substrates in a tropical cloud forest: An experimental and demographic approach. *Oecologia* 122: 60-65.
- Nasrullah-Boyce, A., Haji Mohamed, M. A., Lim, A. L., Barakbah, S. S., Yong, K. T., and Nor, D. M. 2011. Comparative morphological and photosynthetic studies on three Malaysian species of *Pogonatum* from habitats of varying light irradiances. *J. Bryol.* 33: 35-41.
- Norhazrina, N., Wang, J., Hagborg, A., Geffert, J. L., Mutke, J., Gradstein, S. R., Baselga, A., Vanderpoorten, A., and Patiño, J. 2016. Tropical bryophyte floras: A homogeneous assemblage of highly mobile species? Insights from their spatial patterns of beta diversity. *Bot. J. Linn. Soc.* 183: 16-24.
- Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. *J. Linn. Soc. Bot.* 104: 281-291.
- Odu, E. A. 1979. Spore germination in two tropical mosses: *Fissidens* sp. and *Racopilum* sp. *Ann. Bot. (London)* 44: 147-152.
- Odu, E. A. 1981. Reproductive phenology of some tropical African mosses. *Cryptog. Bryol. Lichénol.* 2: 91-99.
- Odu, E. A. 1982. Phenology of west tropical African mosses. *J. Hattori Bot. Lab.* 52: 283-285.
- Odu, E. A. 1987. On the gemmae of west tropical African mosses. *Symp. Biol. Hung.* 35: 215-225.
- Odu, E. A. and Owotomo, O. O. 1982. Periodic production of gemmiferous leaves in two west tropical African *Calymperes* species: *C. afzelii* Sw. and *C. erosum* C. Muell. *Bryologist* 85: 239-242.
- Olarinmoye, S. O. 1974. Ecology of epiphyllous liverworts: Growth in three natural habitats in Western Nigeria. *J. Bryol.* 8: 275-289.
- Olarinmoye, S. O. 1986. Aspects of survival strategies in three common mosses in Ibadan, Nigeria. *Cryptog. Bryol. Lichénol.* 7: 213-218.
- Oliveira, S. M. and Pôrto, K. C. 2001. Reproductive phenology of the moss *Sematophyllum subpinnatum* in a tropical lowland forest of north-eastern Brazil. *J. Bryol.* 23: 17-21.
- Oliveira, S. M. and Pôrto, K. C. 2005. Sporophyte production and population structure of two species of Pottiaceae in an Atlantic Forest remnant in Pernambuco, Brazil. *Cryptog. Bryol.* 26: 239-247.
- O'Shea, B. J. 1989. A guide to collecting bryophytes in the tropics. *British Bryological Society Special Volume No. 3*: 1-30. British Bryological Society, Cardiff.
- Pardow, A. and Lakatos, M. 2013. Desiccation tolerance and global change: Implications for tropical bryophytes in lowland forests. *Biotropica* 45: 27-36.
- Pardow, A., Gehrig-Downie, C., Gradstein, S. R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical

- lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Parsons, J. G., Cairns, A., Johnson, C. N., Robson, S. K., Shilton, L. A., and Westcott, D. A. 2007. Bryophyte dispersal by flying foxes: A novel discovery. *Oecologia* 152: 112-114.
- Patiño, J., Bisang, I., Hedenäs, L., Dirkse, G., Bjarnason, Á. H., Ah-Peng, C., and Vanderpoorten, A. 2013. Baker's law and the island syndromes in bryophytes. *J. Ecol.* 101: 1245-1255.
- Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K. A., Naranjo-Cigala, A., Sólomos, P., and Vanderpoorten, A. 2014. Differences in species-area relationships among the major lineages of land plants: A macroecological perspective. *Global Ecol. Biogeogr.* 23: 1275-1283.
- Patiño, J., Carine, M., Mardulyn, P., Devos, N., Mateo, R. G., González-Mancebo, J. M., Shaw, A. J., and Vanderpoorten, A. 2015. Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. *Syst. Biol.* 64: 579-589.
- Piippo, S. 1992. On the seasonal reproduction of *Plagiochila pluma* Steph. *Trop. Bryol.* 5: 7-9.
- Pócs, T. 1976. Correlations between the tropical African and Asian bryofloras, I. *J. Hattori Bot. Lab.* 41: 95-106.
- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Scient. Hung.* 26: 143-167.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 59-104.
- Pócs, T. 1987. Changes in the biomass and productivity of bryophytes in East African rainforests. XIV Internat. Bot. Congress Abstracts: 264.
- Poore, M. E. D. 1955. The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet System. *J. Ecol.* 43: 226-244.
- Pôrto, K. C. and Oliveira, S. M. 2002. Reproductive phenology of *Octoblepharum albidum* (Bryopsida, Leucobryaceae) in a tropical lowland forest of north-eastern Brazil. *J. Bryol.* 24: 291-294.
- Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In Smith, A. J. E. (ed.). *Bryophyte Ecology*, Chapman and Hall, London, pp. 333-382.
- Proctor, M. C. F. 1990. The physiological basis of bryophyte production. *Bot. J. Linn Soc.* 104: 61-77.
- Proctor, M. C. F. 2002. Ecophysiological measurements on two pendulous forest mosses from Uganda, *Pilotrichella ampullacea* and *Floribundaria floribunda*. *J. Bryol.* 24: 223-232.
- Ramsay, H. P. 1979. Anisospory and sexual dimorphism in Musci. In: Clark, G. C. E. and Duckett, J. G. (eds.). *Bryophyte Systematics*. Systematics Association Special Volume 14. Academic Press, London, pp. 281-316.
- Ramsay, H. P. 1987. Studies on the reproductive biology of some mosses from the Australian Wet Tropics. *Proc. Ecol. Soc. Austral.* 15: 273-279.
- Reenen, G. B. A. van. 1987. Altitudinal bryophyte zonation in the Andes of Colombia: A preliminary report. *Symp. Biol. Hung.* 35: 631-637.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Richards, P. W. 1952. *The Tropical Rain Forest, An Ecological Study*. University Press, Cambridge, 450 pp.
- Richards, P. W. 1984a. The ecology of tropical forest bryophytes. In: Schuster, R. M. (ed.). *New Manual of Bryology Vol. 2*. Hattori Botanical Laboratory, Miyazaki, Japan, pp. 1233-1270.
- Richards, P. W. 1984b. Introduction. In Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, pp. 1-8.
- Richards, P. W. 1988. Tropical forest bryophytes. *Synusiae and strategies*. *J. Hattori Bot. Lab.* 64: 1-4.
- Rydin, H., Goffinet, B., and Shaw, A. J. 2009. Population and community ecology of bryophytes. In: Shaw, A. J. and Goffinet, B. (eds.). *Bryophyte Biology*. 2nd ed. Cambridge University Press, Cambridge, pp. 393-444.
- Schiffner, V. 1900. *Die Hepaticae der Flora von Buitenzorg, Erster Band*. Brill, Leiden.
- Schuster, R. M. 1969. Problems of antipodal distribution in lower land plants. *Taxon* 18: 46-91.
- Schuster, R. M. 1988. Ecology, reproductive biology and dispersal of the Hepaticae in the Tropics. *J. Hattori Bot. Lab.* 64: 237-269.
- Shaw, A. J., Cox, C., and Goffinet, B. 2005. Global patterns of moss diversity: Taxonomic and molecular inferences. *Taxon* 54: 337-352.
- Sillett, S. C., Gradstein, S. R., and Griffin, D. III. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. *Bryologist* 98: 251-260.
- Silva-e-Costa, J. D. C., Luizi-Ponzo, A. P., Resende, C. F. D., and Peixoto, P. H. P. 2017. Spore germination, early development and some notes on the effects of in vitro culture medium on *Frullania ericoides* (Nees) Mont. (Frullaniaceae, Marchantiophyta). *Acta Bot. Brasil.* 31, available at <http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0102-33062017000100019>.
- Song, L., Liu, W. Y., and Nadkarni, N. M. 2012. Response of non-vascular epiphytes to simulated climate change in a montane moist evergreen broad-leaved forest in southwest China. *Biol. Conserv.* 152: 127-135.
- Spruce, R. 1884-1885. *Hepaticae Amazonicae et Andinae*. Transactions et Proceedings of the Botanical Society of Edinburgh 15: 1-588. [published in two parts, the first in 1884 as 15(1): 1-308, the second in 1885 as 15(2): 309-588].
- Spruce, R. (1908) *Notes of a botanist on the Amazon and the Andes*. MacMillan, London, UK.
- Spruce, R. and Wallace, A. R. 1908. *Notes of a botanist on the Amazon and Andes*. Macmillan & Co., London, 2 vols.
- Steere, W. C. 1970. Bryophyte studies on the irradiated and control sites in the rainforest at El Verde, Puerto Rico. In: Odum, H. T. (ed.). *A tropical rainforest: A study of irradiation and ecology at El Verde, Puerto Rico*. Atomic Energy Commission, Washington, D.C.
- Thiers, B. M. 1988. Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rainforest habitat. *J. Hattori Bot. Lab.* 64: 5-14.
- Thompson, S. L., Yates, D. J., and Bergstrom, D. M. 1994. Water holding capacity of epiphytic bryophytes in subtropical forests. *Austral. Bryol. News.* 31: 6.
- Une, K. 1985. Sexual dimorphism in the Japanese species of *Macromitrium* Brid. (Musci: Orthotrichaceae). *J. Hattori Bot. Lab.* 59: 487-513.

- Wagner, S., Bader, M. Y., and Zotz, G. 2014. Physiological ecology of tropical bryophytes. In: Hanson, D. T. and Rice, S. K. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Springer, Dordrecht, pp. 269-289.
- Waite, M. and Sack, L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytol.* 185: 156-172.
- Wang, J., Vanderpoorten, A., Hagborg, A., Goffinet, B., Laenen, B., and Patiño, J. 2016. Evidence for a latitudinal diversity gradient in liverworts and hornworts. *J. Biogeogr.* 44: 487-488.
- Weber, W. A. 1985. Effects on cryptogamic vegetation (lichens, mosses and hepatics). In: *El Niño en la Islas Galápagos: El evento de 1982-1983*. Fundación Charles Darwin para las Islas Galápagos. Quito, Ecuador, pp. 343-361.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, Oxford, 402 pp.
- Wikum, D. A. and Shanholtzer, G. F. 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. *Environ. Mgmt.* 2: 323-329.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Magombo, I. 2016. *Bryophytes of Kenya's Coastal Forests. A Guide to the Common Species*. Published by authors in electronic format, 66 pp.
- Zander, R. H. and During, H. J. 1999. *Neophoenix* (Pottiaceae), a new African moss species found through soil diaspore bank analysis. *Taxon* 48: 657-662.
- Zanten, B. O. van. 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. *J. Hattori Bot. Lab.* 44: 455-482.
- Zanten, B. O. van and Gradstein, S. R. 1987. Feasibility and long-distance transport in Colombian hepatics, preliminary report. *Symp. Biol. Hung* 35: 315-322.
- Zanten, B. O. van and Gradstein, S. R. 1988. Experimental dispersal geography of Neotropical liverworts. *Beih. Nova. Hedw.* 89: 41-94.
- Zanten, B. O. van and Pócs, T. 1981. Distribution and dispersal of bryophytes. *Adv. Bryol.* 1: 479-562.
- Zartman, C. E. 2004. *Habitat fragmentation and epiphyllous bryophytes in a central Amazonian forest*. Ph.D. thesis, Duke University, Durham, NC.
- Zotz, G. and Bader, M. Y. 2008. Epiphytic plants in a changing world – Global change effects on vascular and non-vascular epiphytes. *Progress in Botany* 70: 147-170.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rain forest in Panama. *Bot. Acta* 110: 9-17.