

MAGYAR AFRIKA TÁRSASÁG
AFRICAN-HUNGARIAN UNION



AHU MAGYAR AFRIKA-TUDÁS TÁR
AHU HUNGARIAN AFRICA-KNOWLEDGE DATABASE

PÓCS, Tamás – GRADSTEIN, S. R.

Bryophytes

Eredeti közlés /Original publication:

in: LIETH, H. ed.: *Tropical Rain Forest Ecosystems*, Amsterdam, Elsevier,
311–325. old

Elektronikus újraközlés/Electronic republication:

AHU MAGYAR AFRIKA-TUDÁS TÁR – 000.003.180

Dátum/Date: 2018. szeptember / September.

filename: Pocs_etal_1989_TropRainForestBryophytes

Ezt az információt közlésre előkészítette

/This information prepared for publication by:

B. WALLNER, Erika és/and BIERNACZKY, Szilárd

Hivatkozás erre a dokumentumra/Cite this document:

PÓCS, Tamás – GRADSTEIN, S. R.: Bryophytes, *AHU MATT*, 2018, pp.
1–18. old., No. 000.003.180, <http://afrikatudastar.hu>

Eredeti forrás megtalálható/The original source is available:

Közkönyvtárakban / In public libraries

Kulcsszavak/Key words

magyar Afrika-kutatás,

African studies in Hungary,

AZ ELSŐ MAGYAR, SZABAD FELHASZNÁLÁSÚ, ELEKTRONIKUS,
ÁGAZATI SZAKMAI KÖNYV-, TANULMÁNY-, CIKK-
DOKUMENTUM- és ADAT-TÁR/THE FIRST HUNGARIAN FREE

ELECTRONIC SECTORAL PROFESSIONAL DATABASE FOR BOOKS,
STUDIES, COMMUNICATIONS, DOCUMENTS AND INFORMATIONS

* magyar és idegen – angol, francia, német, orosz, spanyol, olasz és szükség szerint más – nyelveken készült publikációk elektronikus könyvtára/
writings in Hungarian and foreign – English, French, German, Russian, Spanish, Italian and other – languages

* az adattárban elhelyezett tartalmak szabad megközelítésűek, de olvasásuk vagy letöltésük regisztrációhoz kötött/the materials in the database are free but access or downloading are subject to registration

* Az Afrikai Magyar Egyesület non-profit civil szervezet, amely az oktatók, kutatók, diákok és érdeklődők számára hozta létre ezt az elektronikus adattári szolgáltatását, amelynek célja kettős, mindenekelőtt sokoldalú és gazdag anyagú ismeretekkel elősegíteni a magyar afrikaisztikai kutatásokat, illetve ismeret-igényt, másrészt feltárni az afrikai témájú hazai publikációs tevékenységet teljes dimenziójában a kezdetektől máig./The African-Hungarian Union is a non-profit organisation that has created this electronic database for lecturers, researchers, students and for those interested. The purpose of this database is twofold; on the one hand, we want to enrich the research of Hungarian Africa studies with versatile and plentiful information, on the other hand, we are planning to discover Hungarian publications with African themes in its entirety from the beginning until the present day.

BRYOPHYTES

S.R. GRADSTEIN and T. POCS

INTRODUCTION

Tropical rain forests (including montane forests) probably harbour more bryophyte species than any other of the world's major ecosystems. Our rough estimate, based on recent catalogues and taking into account the discrepancy between published and accepted names (Touw, 1974), would arrive at about 1500 to 2000 species of mosses and a similar number of liverworts, hence totalling about 25 to 30% of all bryophytes. The number of synonyms among names of tropical bryophyte species is very high, as taxonomists have pointed out repeatedly. For example, Edwards (1980) could recognize only 6 instead of 93 described species in West African *Calymperes* and Bischler (1984) found 9 good species and 60 synonyms in New World *Marchantia*.

Why are there so many unnecessary names in tropical bryophytes? Reasons may be their relatively large areas of distribution, the serious lack of floras, keys and monographs, and ignorance of the variation patterns and phenotypic plasticity of the species. Mostly they were described by people who were not familiar with the species in the field. In Pterobryaceae and other tropical mosses, for example, male plants are often smaller than females. This type of sexual dimorphism is rare in temperate bryophytes and, when not properly understood, may lead to the description of different species (Argent, 1979). In tropical liverworts, habitat-induced plant size variation and leaf character modifications have often led to the unnecessary description of new taxa (Van Reenen, 1982; among others).

How well has the tropical rain forest been explored for bryophytes? As compared to angio-

sperms (Prance, 1977), the inventory has certainly been less detailed for bryophytes, but a precise answer to the question cannot be given at this stage. However, some useful information can be obtained from Geissler and Greene's (1982) world review of the extent of bryological exploration. It appears that in Malesia bryophyte exploration has been more intensive in the western than in the eastern portion of the area — possibly with the exception of Papua New Guinea where much recent fieldwork was done — and that very little is known about the bryoflora of the rain-forest remnants of northern Australia. As to tropical America, the better explored areas include the Caribbean and portions of the northern Andes, while vast other areas including large parts of the Amazon Basin remain virtually unexplored. In tropical Africa, a good deal of collecting has been done (Greene and Harrington, 1979; Pócs, 1982), and probably this continent is now bryologically better known than other tropical regions, at least for liverworts. This seems to be true for angiosperms as well (Prance, 1977). Nevertheless, also in Africa much basic collecting remains to be done, as Richards (1984b) has recently pointed out.

TROPICAL RAIN FORESTS OF AMERICA, ASIA AND AFRICA — A BRYOGEOGRAPHICAL COMPARISON

About 90% of the bryophytes of the tropical rain forest belong to only 15 families: Calymperaceae, Dicranaceae, Fissidentaceae, Hookeriaceae, Hyphaceae, Meteoriaceae, Neckeraceae, Orthotrichaceae, Pterobryaceae and Sematophyllaceae (mosses); Frullaniaceae, Lejeuneaceae, Lepodiziacae, Plachigiaceae and Radulaceae (Liver-

worts). Yet, characteristic assemblages of bryophytes may be found in each of the three main regions America, Asia, Africa, as the following abbreviated survey indicates.

The American rain forest is characterized by the almost exclusive presence of Pilotrichaceae (mainly Caribbean), Phyllogoniaceae, the Hookeriaceae genera *Crossomitrium*, *Hypnella* and *Lepidopilum*, *Porotrichodendron* (Lembophyllaceae), *Chorisodontium* (Dicranaceae), *Phyllo-drepanium* (Phyllo-drepaniaceae), and, among the liverworts, the robust thalloid Monocleales (also southern temperate) and a large number of Lejeuneaceae genera: *Brachiolejeunea*, *Bryopteris*, *Cyclolejeunea*, *Odontolejeunea*, *Omphalanthus*, *Symbiezidium*, etc. (Grolle, 1969). The richness in *Ceratolejeunea* and *Octoblepharum* species in lowland forests is also notable.

The Asiatic tropical rain forest holds a bryoflora quite different from that of tropical America. Very characteristic are the robust Dawsoniaceae, Hypnodendraceae, Spiridentaceae and Garovaglioidae. The region furthermore holds the centres of evolution for *Mitthyridium* (Calymperaceae), *Dicranoloma* and *Braunfelsia* (Dicranaceae), *Macrothamnium* (Hylocomiaceae), *Cyathophorella* (Hypopterygiaceae), *Aerobryum* (Metesoriaceae), *Homaliiodendron* (Neckeraceae), several Pterobryoideae (*Pterobryella*, *Symphysodontella*, *Trachyloma*), *Acroporium*, *Trismegistia* and *Mastopoma* (Sematophyllaceae) and Trachypodaceae. Among the liverworts *Podomitrium*, *Psiloclada*, *Wettsteinia*, and Treubiales — all four groups also in Australasia and presumably of southern temperate origin — and the Lejeuneaceae *Spruceanthus*, *Stenolejeunea* and *Tuyamaella* are characteristic. The peculiar neotenic epiphylls *Ephemeropsis* and *Metzgeriopsis* are also typical Asiatic rain-forest elements.

To characterize the African rain forest bryologically is more difficult as it has fewer elements of its own, which concurs with the overall relative poverty of the flora of this continent (Richards, 1973). Typical African rain-forest elements are *Leucoloma* (Dicranaceae), some Cryphaeaceae, Rutenbergiaceae, certain Fabroniaceae (especially *Rhizofabronia*), the Pterobryaceous genera *Hildenbrandtiella* and *Renauldia*, and the liverwort *Spruceella*. The species richness in *Fissidens*, both in the lowlands and in the mountains, also is notable.

More striking are the various bryophyte links

between the African rain forest and the two other regions. With tropical America it shares the richness in species of *Pilotrichella*, *Schlotheimia* and *Zygodon*, as well as the presence of *Jaegerina*, *Leptoscyphus*, *Marchesia*, *Mittenothamnium*, *Porotamnium*, *Porotrichum* and *Squamidium*, which are lacking in Asia. At the species level, numerous examples of Afro-American links have recently become known (Gradstein et al., 1984a; Buck and Griffin, 1984). Characteristic Afro-Asiatic links are *Chaetomitrium*, *Cyathophorella*, *Ectropothecium*, *Leucophanes* and *Macrohymenium* among the mosses, and *Mastigophora*, *Ptychanthus*, and Schistochilaceae (also southern pan-temperate but lacking in tropical America) in liverworts. Among epiphylls, *Cololejeunea* is much richer in species in the palaeotropics than in the neotropics. Numerous bryophyte species with an Afro-Asiatic distribution area are known (Pócs, 1976).

Summing up, it appears that tropical Asia holds the most diversified rain-forest bryoflora in terms of generic and familial diversity, with a great number of moss groups restricted to that region. Rain forests of tropical America hold fewer unique moss groups but have a somewhat more diversified liverwort flora, especially regarding Lejeuneaceae. In montane rain forests of this continent, liverwort cover values may exceed those for mosses by far (Fig. 16.4). The African rain forest, finally, has few bryophyte groups of its own and holds a bryogeographical position somewhat intermediate between Asia and America.

ALTITUDINAL DIVERSIFICATION

A characteristic feature of the lowland tropical rain forest is the increase in abundance and species richness of bryophytes with increasing elevation up to the forest limit (Fig. 16.1). At family level about 60% are chiefly montane whereas less than 5% (Pilotrichaceae, Calymperaceae, Leucobryaceae) are predominantly lowland groups. In terms of biomass, montane forests may yield at least ten times more bryophyte weight than lowland forests (see below: bryophyte habitats).

It is generally assumed that climatic factors, especially the more favourable moisture conditions in the mountains, due to clouds and fog, and the prevailing lower temperatures, are responsible for

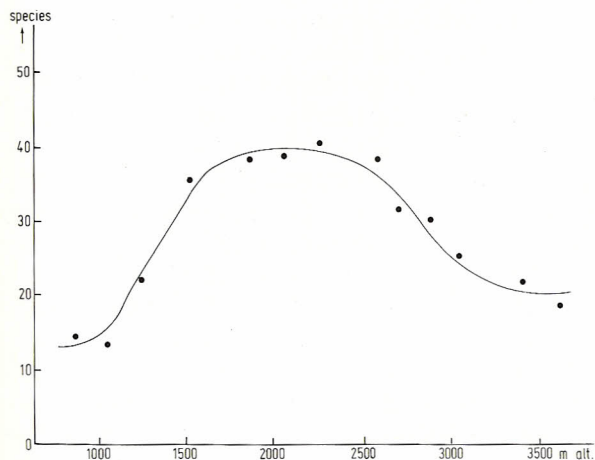


Fig. 16.1. Bryophyte species richness in relation to altitude in rain forests of the Sierra Nevada de Santa Marta, Colombia. Data taken in forest plots, 0 to 3 m above ground level. Epiphylls excluded. (After Van Reenen and Gradstein, 1983, and unpubl.)

the higher bryophyte diversity in the montane forests. The importance of the temperature factor has recently been emphasized by Richards (1984, p. 1238): "The increase in the abundance and species-richness of bryophyte vegetation with increasing elevation suggests that it may be high temperature which is unfavourable for the development of a rich and varied bryophyte flora. It is interesting that, though the bryophytes of the montane forest at El Yunque, Puerto Rico, were tolerant of very cold conditions..., most of them could not survive temperatures above 35°C (Biebl, 1964). The lack of tolerance of high temperatures might be because of high rates of respiration and because bryophytes are unable to maintain sufficiently high values of net assimilation at high temperatures and relatively low light intensity."

Laboratory measurements of assimilation and respiration rates under varying temperatures and light intensities in selected montane rain-forest bryophytes by Frahm (1987), show that these plants are not able to photosynthesize under tropical lowland rain-forest conditions (high temperatures together with low light intensity). Apparently these species are ecophysiologically not well adapted to life in lowland rain forests. It should be interesting to investigate lowland species in a similar manner.

Parallel to an elevational increase, species rich-

ness increases with latitude. A cursory inventory of a Vietnamese evergreen rain forest near sea level (Cuc Phuong National Park) yielded over 125 bryophyte species within a radius of not more than 4 km (Pócs, unpubl.). This type of forest lacks prolonged dry periods, and has a misty, cool winter monsoon instead. In temperate lowland forests bryophyte species richness may also be higher than in the equatorial lowland forest (Richards, 1984).

The bryoflora of the lowland rain forest is largely made up of members of pantropical families, such as Calymperaceae, Hookeriaceae and Lejeuneaceae. The montane bryoflora is much more heterogeneous and contains a mixture of tropical elements and cool-adapted elements of southern or northern temperate origins (Schuster, 1983). In the tropical Andes, for example, the Laurasian *Scapania portoricensis* and the Gondwanalandic *Lepicolea pruinosa* are very conspicuous components of the bryophyte layer of high montane cloud forests (Gradstein et al., 1977). Parallels are found among the dominant trees of these forests, viz. *Quercus* and *Weinmannia* spp. Presumably these groups could migrate into the cold Tropics since the upheaval of the Andes in the late Tertiary (Van der Hammen and Van Dommelen, 1973; Griffin et al., 1982).

The *Nothofagus*-dominated montane rain forests of New Guinea hold a characteristic mixture of Malesian elements and of putatively Gondwanalandic elements such as Dawsoniaceae, Hypnendraceae and Schistochilaceae. The Gondwanalandic groups are often quite abundant and may determine the aspect of the bryophyte vegetation of these forests. Presumably they migrated northwards to New Guinea during the Tertiary step-by-step overland or via short-range aerial dispersal by way of mountain hopping, at times when the island was still evolving and attached to the Australian landmass (Van Zanten and Pócs, 1981).

SPECIES RANGES

In the early 19th century there was a common belief that in many cases bryophyte species distribution was world-wide. Influenced by the evolution theory, the idea that bryophytes are normally restricted to single continents or smaller

regions became more widely accepted and initially resulted in an enormous increase in the number of described species. Recent monographic studies show that this "geographic species concept" was ill-founded and gradually the true ranges of species are now becoming known.

For brevity, this short review of species ranges will focus mainly on the endemic and on the transoceanic rain-forest species. It should be pointed out that the species concept in tropical bryophytes is still mainly morphological-anatomical. Genetic and chemical information is becoming increasingly important in the systematics and biogeography of temperate bryophytes (Szwejkowski, 1982; Mues et al., 1984), but in tropical bryology these fields remain largely unexplored. A first attempt to apply these modern techniques to the problem of species definition in rain-forest bryophytes is the paper by De Vries et al. (1983) on genetic variability and population dispersal in two species of *Racopilum* from the Philippines.

Endemism

Distribution areas in bryophytes, as well as other spore plants, are usually larger than in seed plants, and endemism therefore is comparatively rare. The geologically young Galapagos Islands have an endemism of about 50% among native phanerogams, whereas in ferns and bryophytes only c. 10% of the species are considered endemic (Gradstein and Weber, 1982). It is generally assumed that the relatively slow process of evolution at the morphological level, in addition to the obvious advantage of the possession of wind-carried diaspores for long-distance dispersal, are main reasons why endemism in bryophytes is rare (Van Zanten and Pócs, 1981).

In the Tropics, rates of endemism are probably higher in the mountains than in lowland areas (Schuster, 1983). Especially isolated mountains, such as the African massifs, may act as "biotic islands", enhancing speciation. The African genus *Renauldia*, for instance, has several species of apparently very restricted distribution, including *R. lycopodioides* known only from montane forest of the Usambara Mts. in Tanzania and *R. dusenii*, which is restricted to Mt. Cameroun. They are very conspicuous, robust epiphytes, which could hardly be overlooked. In tropical America, along the

Andean chain, the montane rain forest is less discontinuous and most species tend to spread almost continuously from Bolivia to Mexico, as for example the pendulous *Phyllogonium* species (Lin, 1983).

Endemism is also somewhat more pronounced in island regions than on the continent. In the Neotropical genus *Pilotrichum*, 50% of the species are restricted to rain forests of the Caribbean Islands (Crosby, 1969). Some are found only in the Greater Antilles, others are confined to the Lesser Antilles, but none of the species are restricted to one single island. During (1977) found good examples of island endemism at the infraspecific level in Indo-Pacific Garovaglioideae. His study shows that speciation can only be dealt with when large amounts of material are available for variation analysis. In many groups of rain-forest bryophytes, collections sufficient for that purpose are still wanting.

Probably the highest rates of endemism among rain-forest bryophytes are found in New Guinea, New Caledonia and Madagascar. According to Inoue (1982), 47 out of 59 species of *Plagiochila* from New Guinea are endemic. More than 65% of the species of Frullaniaceae are endemic to New Caledonia (Hattori, 1984) and Madagascar holds speciation centres for the epiphyllous *Colura* and *Diplasiolejeunea* and for the moss genus *Leucoloma*. The Madagascar flora holds close links to the flora of the old crystalline mountain massifs of Tanzania, however, and Pócs (1975) could record several examples of putative Madagascar endemics from the adjacent African mainland.

Rates of endemism are very low among tropical lowland bryophytes. For instance, members of the Calymperaceae are widespread in lowland rain-forest formations of America, Africa and Asia, and are usually epiphytic though sometimes found on the ground. They are usually dioecious, hence have unisexual spores, but in addition produce numerous gemmae from leaf tips, which may enhance dispersal over short distances. Reese (1978) reviewed the American species of the genus *Syrrophodon* and found only 4 endemics among 35 species (*S. theriotii* from Costa Rica, *S. steyermarkii* from Venezuela and *S. annotinus* and *S. rupestris* from limited areas in the Amazon Basin). Most other species proved to be rather wide-ranging, occurring throughout large parts of South America and

often penetrating into Central America and the West Indies.

Even larger distribution areas are seen in West African *Calymperes*. According to Edwards (1980), 50% of the species are Afro-American. One species proved to be pantropical, although an exhaustive comparison with Asiatic collections was not made.

Transoceanic ranges

Transoceanic ranges, as in *Calymperes* (see above), have been the subject of several papers (Pócs, 1976; Frahm, 1982; Buck and Griffin, 1984; Gradstein et al., 1984a) and appear to be more common among rain-forest bryophytes than previously believed. Most transoceanic species dwell in the warmer lowland and submontane regions, which is in clear contrast to the endemics. They seem to be rare in the montane forests, but are again more common in the tropical alpine zone where temperate, peregrine taxa abound (Van Zanten and Pócs, 1981). A reason for the higher ratio of transoceanic species in the tropical lowlands may be the younger age and greater isolation of upland regions; but, in addition, it may be assumed that lower speciation rates in the lowlands enhanced wider ranges.

Among liverworts, the greater part of the transoceanic species are members of the family Lejeuneaceae, whereas among mosses *Fissidens asplenioides*, *Floribundaria floribunda* and *Neckeropsis disticha* are characteristic and well-known examples.

There are different approaches to explain these intercontinental disjunctions. Some authors underline the importance of the geological events, especially plate tectonics, and step-by-step dispersal overland or short-range air dispersal. Others advocate the possibility of long-range air dispersal, using the floras of young oceanic islands as proof. The subject has been discussed at length by Van Zanten and Pócs (1981). For the long-range dispersal hypothesis, experimental studies by Van Zanten (1978, 1984) and Van Zanten and Gradstein (1987) are particularly relevant. Van Zanten tested spore survival following exposure to conditions simulating those experienced during long-distance transport. For New Zealand mosses, he demonstrated that wide-ranging species in general

have more resistant spores than endemic species. He furthermore established that spores of tropical moss species, especially those of the lowland rain forests, are less resistant to drought than temperate species (see also Egunyomi, 1978), but survive wet-freezing at -30°C . These results may imply that tropical mosses could migrate over longer distances via typhoons or heavy showers. Tests on tropical liverworts yielded comparable results, although in general spores were less viable under extreme conditions (Van Zanten and Gradstein, 1987).

In addition to good spore resistance several other conditions may determine successful long-range dispersal, such as: (1) whether or not spores are small and bisexual and plants monoecious; and (2) whether or not migrating species are able to compete successfully with autochthonous species after arrival in suitable habitats. Furthermore, spores should have good opportunities for take-off.

Competitive vigour: transoceanic species meeting this requirement would include the common, "weedy" ones, which may grow in primary as well as secondary habitats. Examples are *Cololejeunea cardiocarpa*, *Lophocolea martiana*, *Octoblepharum albidum* and *Rhizogonium spiniforme*. However, other weedy rain-forest species are presumably not transoceanic, such as the Neotropical *Frullania brasiliensis*, *Groutiella mucronifolia*, *Leptolejeunea elliptica*, *Meteoriopsis remotifolia* and *Plagiochila guilleminiana*. They may be "chance endemics" (Van Zanten, 1978), if their spores are apt for long-range dispersal.

Sexuality and spore size: although one would assume that bisexuality prevails in the transoceanic species, this is not true for mosses, where most transoceanic species are dioecious (Van Zanten and Pócs, 1981). However, in Neotropical liverworts about 2/3 of the transoceanic species are monoecious. Almost all of them are members of the family Lejeuneaceae and, except for *Rectolejeunea brittoniae*, no dioecious transoceanic taxa are known in this family. This would suggest that sex distribution, sometimes considered of little value as a taxonomic character in this family, is of considerable biogeographic significance in Lejeuneaceae. In the rain-forest genus *Stictolejeunea*, for instance, *S. balfourii* is pantropical and monoecious whereas *S. squamata* is Neotropical and dioeci-

ous (Gradstein, 1985). The genus consists of only three species and the third one, *S. iwatsukii*, is endemic to Japan (Fig. 16.2). Known from the three continents among different names, *S. balfourii* is a highly skiophilous element of sheltered habitats in lowland rain forests, where it grows close to the ground on tree bases and roots. These locations can hardly be considered as suitable for long-range dispersal, as against forest margins and tree crowns, where many other transoceanic rain-forest species grow (Gradstein et al., 1984a). In the case of *Stictolejeunea balfourii*, one might therefore assume that the species is very old and became widespread by the ancient migration of land masses, but such explanations remain purely speculative.

Spore-size data for Neotropical transoceanic liverworts (Gradstein et al., 1984) indicate that dioecious species usually have small spores ($< 25 \mu\text{m}$ in diameter), hence by their size well-suited for air transport. In the Lejeuneaceae, however, spores are larger and multicellular ($40\text{--}60 \mu\text{m}$ in diameter). This would suggest that in Lejeuneaceae the disadvantage of having large spores is compensated by bisexuality, which would increase their chances for successful establishment after transoceanic spore migration.

EPIPHYTISM AND GROWTH FORMS

A characteristic feature of the tropical rain forest is the enormous development and diversification of epiphytism (see Benzing, Ch. 7, Johansson, Ch. 9, and Wallace, Ch. 13). Very important in this respect is the constantly high atmospheric humidity in the lower levels of the forest.

Among the 15 main bryophyte families of the tropical rain forest, 14 are predominantly epiphytic; the Fissidentaceae are the exception. Epiphytic bryophytes are sometimes classified as microepiphytes, as opposed to the vascular macroepiphytes (Tixier, 1966). In a phylogenetic sense, most of them are on the branch tips of bryophyte evolution (Vitt, 1984, p. 717, fig. 34) and presumably co-evolved with the rain forest since the late Cretaceous. Their evolution parallels that of the main macroepiphytic groups of the rain forest, such as the Orchidaceae and Bromeliaceae.

Most epiphytic bryophytes inhabit the trunks, branches and twigs of trees, but some, the epiphylls, have adapted to growth on living leaves. Various structural adaptations, aimed at survival in the hazardous epiphytic environment, are seen among epiphytic bryophytes:

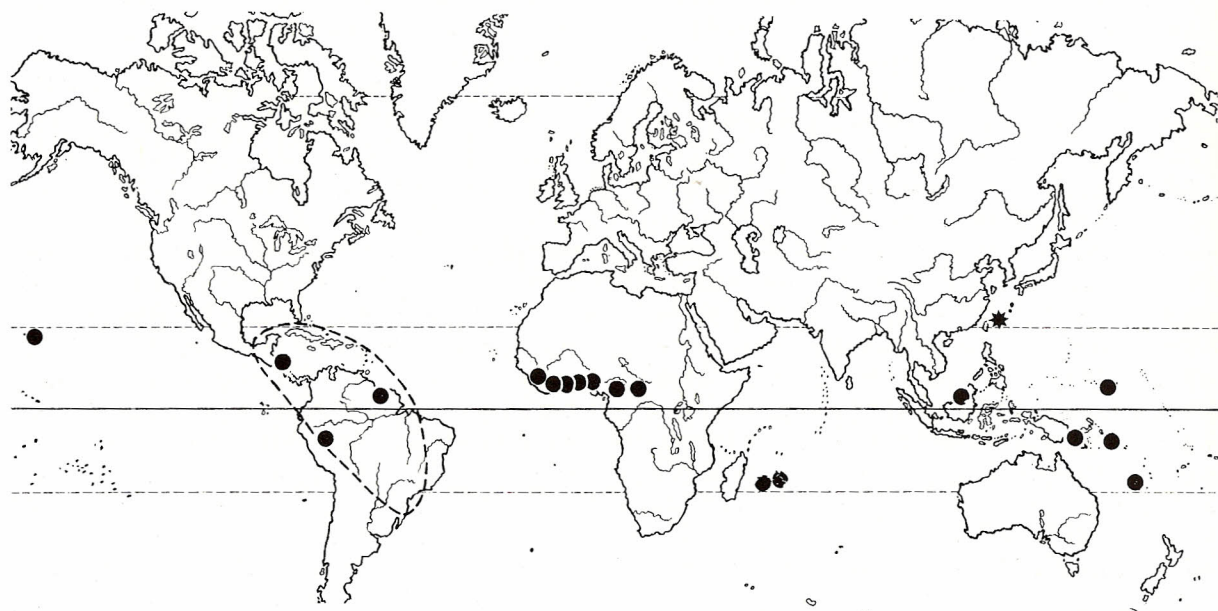


Fig. 16.2. The distribution of *Stictolejeunea* (Lejeuneaceae). Dots: *S. balfourii*, star: *S. iwatsukii*, Gradstein, 1984.)

(1) Development of green, multicellular spores containing endosporous protonema which may germinate within the spore wall before or upon spore release from the capsule. Examples are Dicnemonaceae and Lejeuneaceae (Nehira, 1983).

(2) Sexual dimorphism and development of phyllodioecy in various mosses, possibly enhancing gene flow.

(3) Development of numerous devices for asexual reproduction, monoecious condition, and retention of juvenile characters in the adult stage (neoteny) in response to ephemeral environments such as fine twigs and living leaves (Schuster, 1984; Richards, 1984a). Examples are found especially in Lejeuneaceae.

(4) Development of rhizoid discs for anchoring and adhesion on smooth surfaces, especially in epiphylls (Winkler, 1967).

(5) Development of devices for absorption and retention of atmospheric water, such as the water sacs (lobules) in Frullaniaceae and Lejeuneaceae and hyaline leaf margins in epiphylls. Particularly sophisticated are the water sacs of *Colura*, which possess a complicated closing apparatus at the entrance of the sac (Jovet-Ast, 1953). Water retention is probably also enhanced by the hyaline cells of the leaves in many Calymperaceae (Richards, 1984a).

(6) Occurrence of cushion-form growth types which promote humus and water accumulation. These growth forms are characteristic for the branching system of rather open, montane forests, where nutrients and water are available in limited amounts for the epiphytes (Pócs, 1982).

Attempts to classify the different ecological adaptations of rain-forest bryophytes have resulted in the recognition of a considerable number of growth forms (Fig. 16.3). Several of these growth forms occur almost exclusively in the tropical rain forest, including the feather type, the bracket type and the hanging, pendulous type (Fig. 16.6d). Only very few representatives of these three types are known from temperate forests, — *Leucodon sciurioides* and *Neckera pennata* in Europe, *Leucodon pendulus* in the East Siberian taiga and *Leucodon immersus* and *Pseudoleskiella laxiramea* in the South Caspian lowland forest (Frey and Probst, 1974).

In contrast to growth forms, which are static morphological features each with presumed adap-

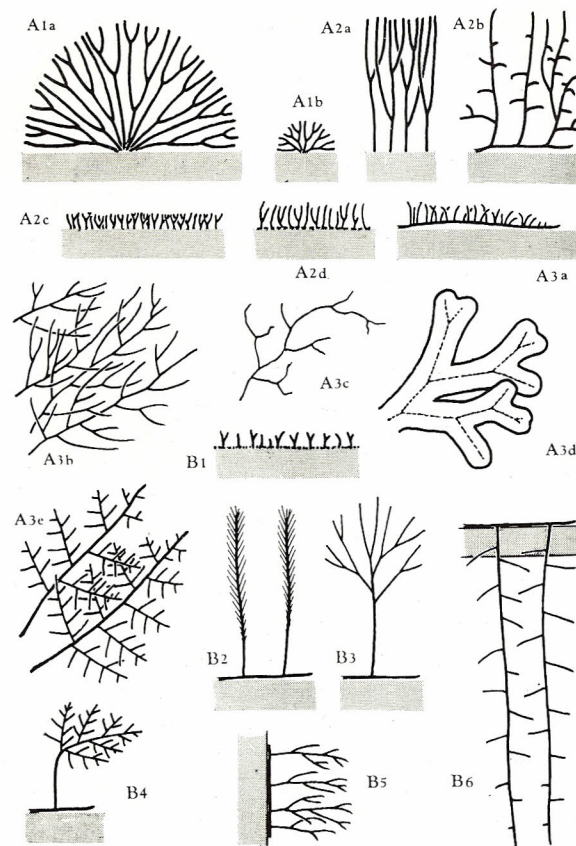


Fig. 16.3. Classification of growth forms of tropical forest bryophytes (from Richards, 1984). A1 a: large cushions; A1 b: small cushions; A2 a: tall turfs; A2 b: tall turfs with divergent and creeping branches; A2 c: short turfs; A2 d: open turfs; A3 a: rough mats; A3 b: smooth mats; A3 c: thread-like forms; A3 d: thallose mats; A3 e: wefts; B1: protonematal bryophytes; B2: unbranched dendroid forms; B3: branched not dorsiventral dendroid forms; B4: feather forms; B5: bracket mosses; B6: hanging bryophytes.

tations to the environment, the life strategy system elaborated for bryophytes by During (1979) reflects a dynamic approach which mirrors ecologically relevant life-history characteristics of the bryophytes. Six different bryophyte life strategies were established for temperate bryophytes, based on ways of sexual and a-sexual reproduction, size and number of spores, annual production, standing crop and life expectancy. Their correlation with growth forms was also established. Evidently, life strategies should be a workable tool for a better understanding of the ecology of tropical rain-forest bryophytes, but no comprehensive attempts have been made as yet to study these in the tropics.

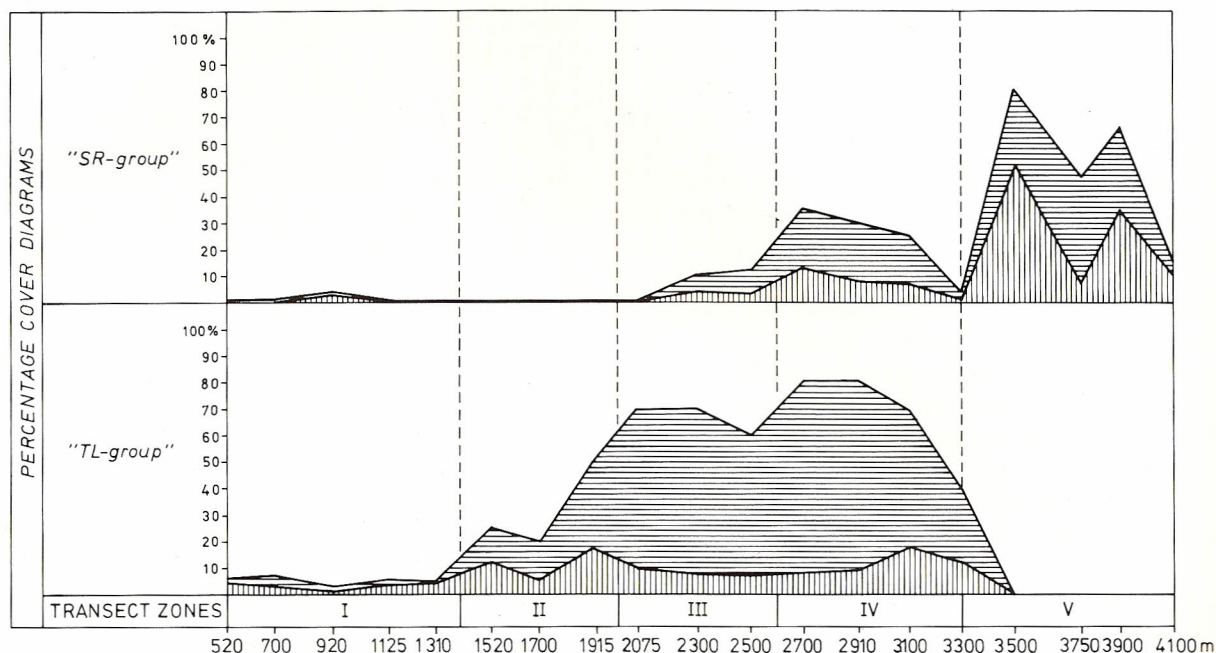


Fig. 16.4. Bryophyte cover values in relation to altitude in the Sierra Nevada de Santa Marta, Colombia (after Van Reenen and Gradstein, 1983). Zone I: lowland rain forest; zone II: submontane rain forest; zone III: lower montane rain forest; zone IV: upper montane rain forest (condensation zone); zone V: paramo. TL group: epiphytes; SR group: terrestrial and saxicolous species. Vertical lines: mosses; horizontal lines: liverworts.

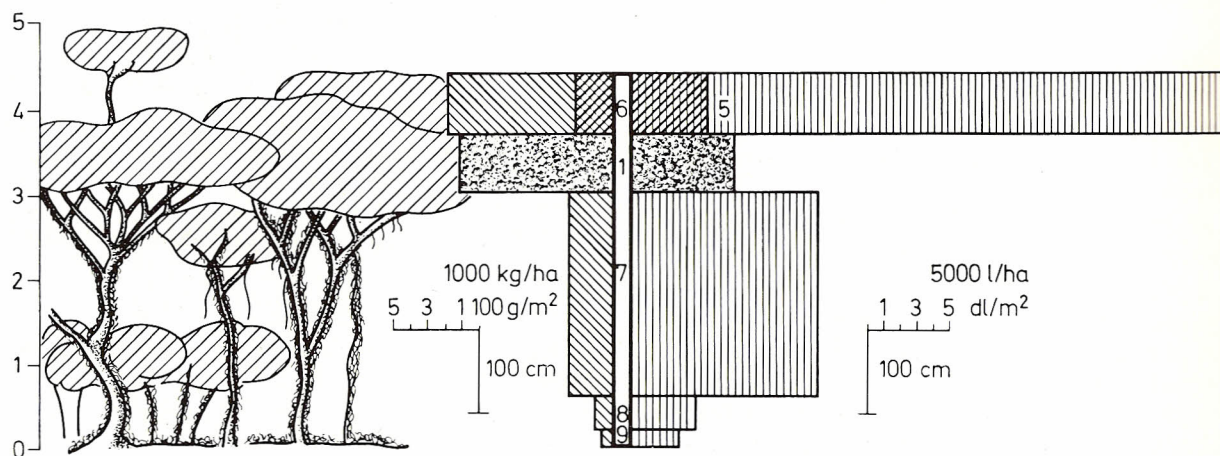
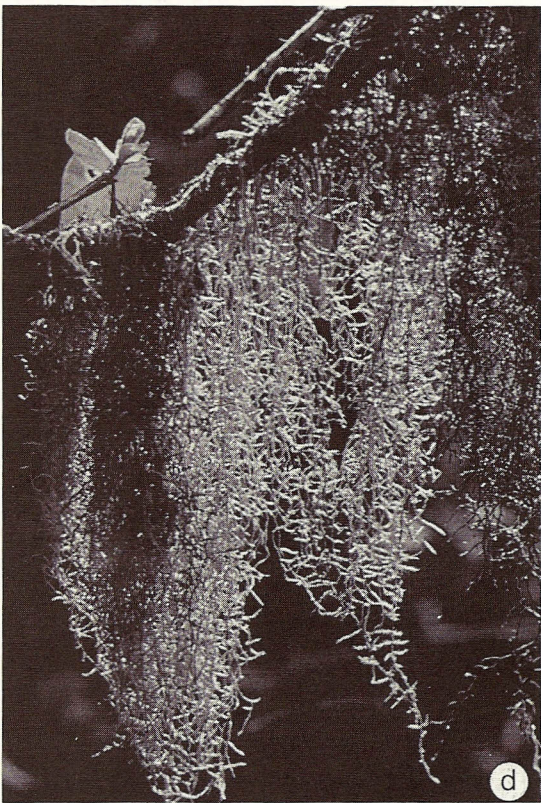


Fig. 16.5. The biomass and water interception of epiphytes and phorophyte leaves in a mossy elfin forest in Tanzania, Uluguru Mts. at 2140 m alt. (after Pócs, 1980). On the left side the dry weight of different layers in 1000 kg ha^{-1} . On the right side the water interception capacity in 1 ha^{-1} according to the different layers, as: 1, Leaves of phorophyte trees forming the canopy; 5, humus and detritus among the canopy epiphytes (the darker part); 6, canopy microepiphytes including small orchids; 7, microepiphytes (bryophytes and filmy ferns) on the trunk; 8, microepiphytes (bryophytes) on the roots; 9, bryophyte cover on the ground.

Fig. 16.6. (a) Lowland rain forest in Vietnam with bryophyte-covered buttressed tree bases; (b) epiphyllous liverworts (mostly *Radula acuminata*) on leaves of shrubs in Vietnamese lowland rain forest; (c) ramicolous *Plagiochila floridana* in the lower layer of a montane rain forest in Cuba; (d) hanging *Zelometeorium patulum* in submontane forests of the Galapagos Islands. (Photographs by the authors.)

BRYOPHYTES



BRYOPHYTE HABITATS

Lowland rain forests

The bryophytes of lowland and lower submontane rain forests — which are ranging up to 1500 m near the Equator and up to 600 m near the northern and southern boundaries of the Tropics — may be divided into two groups, separated spatially by the morphological inversion surface of the forest (Hallé et al., 1978). This surface runs practically at the lower surface of the closed canopy of the B layer (below the emergents), joining the lower branches. According to Richards (1983) this imaginary plane, which is undulating from place to place, separates the exposed “euphotic” zone from the shaded region below it, called “oligophotic” zone. Sun epiphytes are characteristic for the euphotic zone, whereas shade epiphytes and terrestrial species are mainly in the oligophotic zone.

Euphotic habitats

Main habitats in the euphotic zone are the twigs and main branches of the canopy. Twigs in the canopy are inhabited only in the most humid types of lowland rain forest. A dense, rain-absorbing bryophyte vegetation may develop in full light, consisting of feathery or hanging mosses and liverworts or tiny species adherent to the twigs. These species are not easily detected due to the inaccessibility of the canopy, and their geographical distribution is therefore poorly known. Examples are *Mastigolejeunea turgida* and *Pycnolejeunea contigua* in West Africa (Jones and Harrington, 1983). In drier types of forest, if not mist-affected, this vegetation cannot develop, as the habitat is too much exposed to temporary droughts.

The inner part of the canopy, where the main branches are, is more protected against direct irradiation and desiccation than the outer part but still receives a considerable amount of light. Usually a rich bryophyte vegetation of dense, mat- or cushion-forming, more or less drought-tolerant species develops here, belonging, for instance, to

the genera *Frullania* and *Macromitrium*. Under very humid conditions pendulous bryophytes are present and epiphyllous lichens and liverworts establish themselves on the inner crown leaves.

Oligophotic habitats

The oligophotic zone includes tree trunks, small trees and shrubs, living leaves, decaying wood and the ground surface. The upper part of tree trunks is inhabited by shade-tolerant and more or less drought-tolerant species, which usually cover the bark only partly and not in large masses. Patches of crustose lichens, small turfs of mosses (such as *Orthotrichaceae*) and appressed mats of liverworts (mainly *Lejeuneaceae*) are common here. This habitat is also characterized by the occurrence of bracket mosses, including several *Pterobryaceae* (Pócs, 1982).

Tree bases offer the most shady habitats in tropical rain forests (Fig. 16.6a). Due to the steadily high degree of humidity, bryophyte diversity reaches peak values here, both in cover and in species richness (Richards, 1954). Mat-, weft- and turf-forming mosses, and to a lesser extent liverworts, form an almost continuous, often thick carpet, which is usually intermixed with creeping *Hymenophyllaceae*. Perhaps the most typical bryophyte growth form here is the feather type which may occur in great masses. The upper limit of this moss carpet is called the “moss line” (Richards, 1984a) which in ever-wet rain forests may be 5 to 8 m up the trunk. In less humid, seasonal rain forests this moss line may be as low as 50 cm above the ground. Above the moss line, air humidity values are more variable and may sink to 60% during dry periods (Pócs, 1974), causing the scantiness of the bryophyte vegetation at higher trunk levels.

Narrow stems of small trees and branches of shrubs in this zone are inhabited by ramicolous bryophytes which usually include other species than the bark-inhabiting corticolous group (Pócs, 1982). Many dendroid, feather or bracket-type mosses and liverworts, belonging to *Neckeraceae*, *Hookeriaceae*, *Pterobryaceae*, *Plagiochilaceae* and *Lejeuneaceae*, are specialists of this habitat.

Fig. 16.7. (a) Large cushions of *Dicranoloma billardieri* and *Lepidozia cupressina* in the montane mossy forests on Mt. Kilimanjaro, at 2700 m alt.; (b) epizoic *Daltonia angustifolia* in the montane mossy forests of New Guinea. (Photographs by the authors.)



The upper surface of the living, evergreen leaves in this zone are often covered by epiphylls (Fig. 16.6b). The majority of the obligatory epiphyllous bryophyte species are liverworts of the family Lejeuneaceae. They show interesting adaptations to their habitat (see above). In a sufficiently humid and not too shady environment, large amounts of epiphyllous bryophytes may develop during the 2 to 4 years' life-span of an evergreen leaf, which eventually becomes fully covered. Species diversity increases with leaf age, and a well-developed epiphyllous community may consist of 8 to 15 (seldomly up to 30) species on one leaf (Pócs, 1978).

Epiphyllous communities are a special feature of tropical rain forests and only very rarely have they been recorded outside the tropical belt (Richards, 1984a). Presence of well-developed epiphyllous communities always indicates high atmospheric humidity. It has been shown that the epiphyllous community promotes nitrogen uptake by the host plant through the leaf surface, probably due to blue-green algae living in the community (Harrelson, 1969; Edmisten, 1970). On the other hand, extensive epiphyllous growth can be harmful for the host, because too dense a cover may presumably prohibit leaf assimilation and can promote fungal infection (Thorold, 1952). Epiphylls in general seem to behave as epiphytes, not taking nutrients from the host leaves nor causing mechanical damage, although some exceptions were noted (Winkler, 1967; Berrie and Eze, 1975).

Decaying logs, stumps and branches on the forest floor are also important bryophyte habitats. They may be fully covered by mats of species belonging to Hookeriaceae, Hypnaceae, Lepidoziaceae, Lophocoleaceae, Sematophyllaceae, as well as by cushions of *Leucobryum*. The floor of the lowland rain forest is very poor in bryophytes, probably due to the smothering effect of leaves covering the ground (Richards, 1954). Terrestrial species are mainly found on exposed patches of disturbed soil, such as road cuts and termite mounds, and include many species of *Fissidens*.

There are several other special bryophyte habitats in rain forests, such as palm, bamboo and tree-fern stems, each of which may be inhabited by characteristic bryophyte communities. For a discussion we refer to Pócs (1982).

Montane rain forests

Montane rain forests — ranging from 1500 to 3000 or 4000 m near the Equator, but lower in elevation at increasing latitudes, on islands and in coastal regions — are cooler and wetter than lowland rain forests. Mean annual temperatures are usually between 20 and 10°C, decreasing gradually with altitude and latitude. Frosts are very rare. Annual rainfall is usually over 2000 mm and, in addition, clouds and mist precipitation may supply extra liquid water to the forest. These climatic conditions are more or less even throughout the year, and are thus favourable for bryophyte growth.

While the montane rain forest is structurally simpler than the lowland forest and woody species diversity is lower, the epiphytic vegetation including the bryophyte component is perplexingly more diversified, both in terms of species richness and of biomass. Van Reenen and Gradstein (1983) measured the total bryophyte cover in rain-forest plots along an altitudinal gradient in the Andes of Colombia, and found epiphytic bryophyte cover values in the montane forests up to ten times higher than in the lowland forests (Fig. 16.4). Bryomass measurements taken from selected rain-forest trees along an altitudinal gradient in Peru yielded similar results (Frahm, 1987). Van Reenen and Gradstein found highest cover values in the condensation zones where cloud formation was maximal. These cloud forests are usually called "mossy forests" and include the mossy dwarf forests or elfin forests, which develop near the forest line and on exposed mountain ridges, as well as in summit areas of low tropical islands. Not only tree stems but often all branches, canopy twigs and shrubs in mossy forests are covered by a bryophytic "fur" often much thicker than the branches themselves (Fig. 16.7a). The bryophyte biomass of a Tanzanian elfin forest (Fig. 16.5) can be as much as 11 000 kg ha⁻¹ dry weight as compared to 1773 kg in lower submontane rain forest in the same area (Pócs, 1982), 355 kg in an oak forest in Atlantic Europe (Schnock, 1972) and 41 kg in a continental European oak forest (Simon, 1974).

Pócs (1980) established that montane rain-forest bryophytes are very effective rainfall interceptors. Comparative measurements in Tanzania showed

that rainfall interception in the elfin forest was about 2.5 times higher than in the submontane rain forest. Total interception in the elfin forest was over 50% of the annual rainfall, due largely to the dense carpet of bryophytes in the canopy layer which made up about 80% of the total canopy biomass (Fig. 16.5). The liverworts *Bazzania* and *Plagiochila* (Fig. 16.6c), as well as *Frullania*, *Lepidozia* and *Trichocolea* proved to be the most effective rain interceptors.

After interception part of the rainwater re-evaporates and another part is retained by the epiphyte. The surplus rainwater slowly drips down, keeping the environment moist even in periods when there is no rain or mist. Apparently, suitable conditions are thus created for terrestrial bryophyte growth. The continuous supply of humus provided by the epiphytic bryophytes, and the relatively small size of the leaves of trees at these altitudes, are other factors which are favourable for terrestrial growth (Pócs, 1980).

The richness of the bryophytic ground cover of the mossy montane rain forest as opposed to its virtual absence in lowland rain forest is perhaps one of the most striking differences between the two forest types (Fig. 16.4). Also characteristic is the diminution of substrate preference of individual species in mossy forest. Thus, epiphytic species may establish themselves on the ground or on fallen logs, whereas terrestrial species may be found on the trees (Van Reenen and Gradstein, 1983). Some species invade unusual substrates, such as the moss *Daltonia angustifolia*, which in New Guinean mossy forest may colonize the back of slow-moving weevils (Fig. 16.7b). The ability of this moss to mature rapidly, its growth on a soft substrate (such as bark) and its ramicolous habit on very small branches, are presumably attributes that allow its epizoid growth (Gressitt et al., 1968; Gradstein et al., 1984b).

In terms of bryophyte habitat diversification, montane rain forests are only partly similar to lowland forests. The simpler forest stratification, the lower canopy height and the more favourable moisture conditions allow the moss line to go up higher and even reach the canopy (Fig. 16.7a), (Richards, 1984). The oligophotic zone is strongly reduced or absent and the entire tree trunk may be covered by the community of the tree base. Feathery, dendroid, large cushion and pendulous

growth forms are much more common than in the lowland forests, and often dominant. Horizontal branches of small trees and shrubs are the usual substrates of the pendulous *Meteoriaceae* (Fig. 16.6d), *Phyllogoniaceae*, *Frullania* and *Taxilejeunea*. Epiphyllous communities occur in the montane rain forest up to about 3000 m (Pócs, 1982). The upper limit of their existence seems to be determined by the occurrence of night frosts.

ACKNOWLEDGEMENTS

We are grateful to Dr. P.W. Richards and G.B.A. van Reenen for their comments on the manuscript.

Preparation of this chapter was made possible through a grant of the Netherlands Organization for the Advancement of Pure Research to S.R.G.

REFERENCES

- Argent, G.C.G., 1979. The systematics of tropical mosses. In: G.C.S. Clarke and J.G. Duckett (Editors), *Bryophyte Systematics*. Academic Press, London, pp. 185–193.
- Berrie, G.K. and Eze, J.M.O., 1975. The relationship between an epiphyllous liverwort and host leaves. *Ann. Bot.*, 39: 953–963.
- Biebl, R., 1964. Temperaturrestistenz tropischer Pflanzen auf Puerto Rico. *Protoplasma*, 59: 133–156.
- Bischler, H., 1984. *Marchantia* L. The New World Species. *Bryophyt. Bibl.*, 26: 1–228.
- Buck, W.R. and Griffin, D., 1984. *Trachyphyllum*, a moss genus new to South America with notes on African–South American bryogeography. *J. Nat. Hist.*, 18: 63–69.
- Crosby, M.R., 1969. Distribution patterns of West Indian mosses. *Ann. Mo. Bot. Gard.*, 56: 409–416.
- De Vries, A., Van Zanten, B.O. and Van Dijk, H., 1983. Genetic variability within and between populations of two species of *Racopilum* (Racopilaceae, Bryopsida). *Lindbergia*, 9: 73–80.
- During, H.J., 1977. A taxonomical revision of the Garovaglioidae (Pterobryaceae, Musci). *Bryophyt. Bibl.*, 12: 1–244.
- During, H.J., 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia*, 5: 2–18.
- Edmisten, J., 1970. Preliminary studies of the nitrogen budget of a tropical rain forest. In: H.T. Odum (Editor), *A Tropical Rain Forest, a Study of Irradiation and Ecology at El Verde, Puerto Rico*. U.S. Atomic Energy Commission, Washington, D.C., pp. 211–215.
- Edwards, S.R., 1980. A revision of West Tropical African Calymperaceae I. *J. Bryol.*, 11: 49–93.
- Egunyomi, A., 1978. The viability of spores of some tropical moss species after long-time storage and their survival chances in nature. *J. Hattori Bot. Lab.*, 45: 167–171.

- Frahm, J.P., 1982. Grossdisjunktionen in Artarealen südamerikanischer und afrikanischer *Campylopus*-Arten. *Lindbergia*, 8: 45–52.
- Frahm, J.-P., 1987. Ökologische Studien an der epiphytische Moosvegetation in Regenwäldern NE-Perus. In: Ergebnisse der BRYOTROP Expedition nach Peru 1982. *Beih. Nova Hedwigia*, 88.
- Frey, W. and Probst, W., 1974. Hangeformen von *Pseudoleskeella laxiramea* (Schiffn.) Broth. und *Leucodon immersus* Lindb. (Musci) im südkaaspischen Waldgebiet (Iran). *Bot. Jahrb. Syst.*, 94: 267–282.
- Geissler, P. and Greene, S., 1982. Bryophyte taxonomy: methods, practices and floristic exploration. *Beih. Nov. Hedwigia*, 71: 1–558.
- Giesenhagen, K., 1910. Moostypen der Regenwälder. *Ann. Jard. Bot. Buitenzorg (Suppl.)*, 3: 711–790.
- Gradstein, S.R., 1985. A revision of the genus *Stictolejeunea* (Spruce) Schiffn. *Beih. Nov. Hedwigia*, 80: 209–232.
- Gradstein, S.R. and Weber, W.A., 1982. Bryogeography of the Galapagos Islands. *J. Hattori Bot. Lab.*, 52: 127–152.
- Gradstein, S.R., Cleef, A.M. and Fulford, M.H., 1977. Oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. *Proc. K. Ned. Akad. Wet., Ser. C*, 80: 377–420.
- Gradstein, S.R., Pócs, T. and Vána, J., 1984a. Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Hung.*, 29: 127–171.
- Gradstein, S.R., Vitt, D.H. and Anderson, R.S., 1984b. The epizoid occurrence of *Daltonia angustifolia* (Musci) in Papua New Guinea. *Cryptog. Bryol. Lichén.*, 5: 47–50.
- Greene, S.W. and Harrington, A., 1979. *The Bryological Literature of Africa*. Nature Conservation Research Council, Penicuik, 141 pp.
- Gressitt, J.L., Samuelson, G.A. and Vitt, D.H., 1968. Moss growing on living Papuan moss forest weevils. *Nature*, 217: 765–767.
- Griffin, D., Gradstein, S.R. and Aguirre, J., 1982. On a new antipodal element in the Neotropical páramos — *Dendrocryphaea latifolia* sp. nov. (Musci). *Acta Bot. Neerl.*, 31: 175–184.
- Grolle, R., 1969. Grossdisjunktionen in Artarealen Lateinamerikanischer Lebermoose. In: E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe and H. Sioli (Editors), *Biogeography and Ecology in South America*, Vol. 2. Junk, The Hague, pp. 562–582.
- Hallé, F., Oldeman, R.A.A. and Tomlinson, P.B., 1978. *Tropical Trees and Forests*. Springer, Berlin, 441 pp.
- Harrelson, M.A., 1969. *Nitrogen fixation in the epiphyllae*. Ph.D. Diss., Univ. of Georgia, Athens, Ga., 103 pp.
- Hattori, S., 1984. New Caledonian Frullaniaceae. *J. Hattori Bot. Lab.*, 57: 405–426.
- Inoue, H., 1982. Speciation and distribution of *Plagiochila* in Australasia and the Pacific. *J. Hattori Bot. Lab.*, 52: 45–56.
- Jones, E.W. and Harrington, A.J., 1983. The hepatics of Sierra Leone and Ghana. *Bull. Br. Mus. Nat. Hist. Bot.*, 11: 215–289.
- Jovet-Ast, S., 1953. Le genre *Colura*. *Rev. Bryol. Lichén.*, 22: 206–312.
- Lin, S.H., 1983. A taxonomic revision of Phyllogoniaceae (Bryopsida), Part. I. *J. Taiwan Mus.*, 36: 37–86.
- Mägdefrau, K., 1982. Life-forms of bryophytes. In: A.J.E. Smith (Editor), *Bryophyte Ecology*. Chapman and Hall, London, pp. 45–58.
- Mues, R., Hattori, S., Asakawa, Y. and Grolle, R., 1984. Biosystematic studies on *Frullania jackii* and *F. davurica*. *J. Hattori Bot. Lab.*, 56: 227–240.
- Nehira, K., 1983. Spore germination, protonema development and sporeling development. In: R.M. Schuster (Editor), *New Manual of Bryology*, Vol. 1. The Hattori Botanical Laboratory, Nichinan, pp. 343–385.
- Pócs, T., 1974. Bioclimatic studies in the Uluguru Mountains (Tanzania, East Africa) I. *Acta Bot. Hung.*, 20: 115–135.
- Pócs, T., 1975. Affinities between the bryoflora of East Africa and Madagascar. *Boissiera*, 24: 125–128.
- Pócs, T., 1976. Correlations between the tropical African and Asian bryofloras, I. *J. Hattori Bot. Lab.*, 41: 95–106.
- Pócs, T., 1978. Epiphyllous communities and their distribution in East Africa. *Bryophyt. Bibl.*, 13: 681–713.
- 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. Hung.*, 26: 143–167.
- Pócs, T., 1982. Tropical forest bryophytes. In: A.J.E. Smith (Editor), *Bryophyte Ecology*. Chapman and Hall, London, pp. 59–104.
- Prance, G.T., 1977. Floristic inventory of the Tropics: where do we stand? *Ann. Mo. Bot. Gard.*, 64: 659–684.
- Reese, W.D., 1978. The genus *Syrhodon* in the Americas II. The limbate species. *Bryologist*, 81: 189–225.
- Richards, P.W., 1954. Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio*, 6: 319–328.
- Richards, P.W., 1973. Africa, the “odd man out”. In: B.J. Meggers, E.S. Ayensu and W.D. Duckworth (Editors), *Tropical Forest Ecosystems in Africa and South America*. Smithsonian Institution, Washington, D.C., pp. 21–26.
- Richards, P.W., 1983. The three-dimensional structure of tropical rain forest. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Editors), *Tropical Rain Forest: Ecology and Management*. Blackwell, Oxford, pp. 3–24.
- Richards, P.W., 1984a. The ecology of tropical forest bryophytes. In: R.M. Schuster (Editor), *New Manual of Bryology*, Vol. 2. The Hattori Botanical Laboratory, Nichinan, pp. 1233–1270.
- Richards, P.W., 1984b. The bryologically underworked regions of the world, with special reference to West Africa. *J. Hattori Bot. Lab.*, 55: 165–172.
- Schnock, G., 1972. Evapotranspiration de la végétation épiphytisme de la base des troncs de chêne et d'érable champêtre. *Bull. Soc. R. Bot. Belg.*, 105: 143–150.
- Schuster, R.M., 1983. Phytogeography of the Bryophyta. In: R.M. Schuster (Editor), *New Manual of Bryology*, Vol. 1. The Hattori Botanical Laboratory, Nichinan, pp. 463–626.
- Schuster, R.M., 1984. Evolution, phylogeny and classification of the Hepaticae. In: R.M. Schuster (Editor), *New Manual of Bryology*, Vol. 2. The Hattori Botanical Laboratory, Nichinan, pp. 892–1070.
- Simon, T., 1974. Estimation of phytomass dry-weight of epiphytic mosses at Sikfókut (near Eger, N. Hungary). *Acta Bot. Hung.*, 21: 117–136.
- Szweykowski, J., 1982. Genetic differentiation of liverwort

- populations and its significance for bryotaxonomy and bryogeography. *J. Hattori Bot. Lab.*, 53: 21–28.
- Thorold, C.A., 1952. The epiphytes of *Theobroma cacao* in Nigeria in relation to the incidence of black pod disease (*Phytophthora palmivora*). *J. Ecol.*, 40: 125–142.
- Tixier, P., 1966. *Flore et végétation orophiles de l'Asie tropicale. Les épiphytes du flanc méridional du Massif Sud Annamitique*. Thesis, Univ. of Aix-Marseille, pp. 1–240.
- Touw, A., 1974. Some notes on taxonomic and floristic research on exotic mosses. *J. Hattori Bot. Lab.*, 38: 123–128.
- Van der Hammen, T. and Van Dommelen, H., 1973. Palynological record of the upheaval of the northern Andes. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 16: 1–24.
- Van Reenen, G.B.A., 1982. High Andean species of *Herbertus* S.F. Gray (Hepaticae). *Lindbergia*, 8: 110–120.
- Van Reenen, G.B.A. and Gradstein, S.R., 1983. 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.
- Van Zanten, B.O., 1978. Experimental studies on transoceanic long-range dispersal of moss spores in the Southern Hemisphere. *J. Hattori Bot. Lab.*, 44: 455–482.
- Van Zanten, B.O., 1984. Some considerations on the feasibility of long-distance transport in bryophytes. *Acta Bot. Neerl.*, 33: 231–232.
- Van Zanten, B.O. and Gradstein, S.R., 1987. Experimental dispersal geography of neotropical Liverworts. *Beih. Nova Hedwigia*, 89.
- Van Zanten, B.O. and Pócs, T., 1981. Distribution and dispersal of bryophytes. In: W. Schultze-Motel (Editor), *Advances in Bryology, Vol. 1*. Cramer, Vaduz, pp. 479–562.
- Vitt, D.H., 1984. Classification of the Bryopsida. In: R.M. Schuster (Editor), *New Manual of Bryology, Vol. 2*. The Hattori Botanical Laboratory, Nichinan, pp. 696–759.
- Winkler, S., 1967. Die epiphyllen Moose der Nebelwälder von El Salvador, C.A. *Rev. Bryol. Lichén.*, 35: 303–369.

ECOSYSTEMS OF THE WORLD 14B

TROPICAL RAIN FOREST ECOSYSTEMS

BIOGEOGRAPHICAL AND ECOLOGICAL STUDIES

Edited by

H. Lieth

*Fachbereich Biologie/Chemie
Universität Osnabrück
Postfach 4469
D-4500 Osnabrück (F.R.G.)*

and

M.J.A. Werger

*Department of Plant Ecology
State University of Utrecht
Lange Nieuwstraat 106
3512 PN Utrecht (The Netherlands)*

Dr. PÓCS TAMÁS
FELSŐTÁRKÁNY, Ady E. u. 67.
H-3324



ELSEVIER

Amsterdam—Oxford—New York—Tokyo 1989