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BRYOPHYTE DIVERSITY OF THE TROPICAL RAINFOREST

BY

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INTRODUCTION

Tropical forests make up about half of the world's closed forests, yet are rapidly being destroyed. By the end of the 1970s, the Food and Agriculture Organization (FAO) of the United Nations estimated that about 46 per cent of the tropical forests were already gone and the remainder were disappearing at a rate of over 2 per cent per year, either by clear-cutting or by shifting cultivation. The conclusion was that all tropical rainforests would be destroyed by the middle of the next century, while the seasonal forests, occurring in regions with more pronounced fluctuations in rainfall and usually more suitable for human inhabitation, would already have disappeared long before.

Tropical forests, because of their complexity and variety of microhabitats, usually harbour a rich diversity of bryophytes (mosses, liverworts). Even though they are often small and inconspicuous, especially in the lowland forest, they may play a significant role in the forest ecosystem. Thick bryophyte mats on trees capture rain water, especially in the montane forest, and help to keep humidity in the forest high. They serve as a substrate for the establishment of vascular epiphytes, especially orchids, and offer shelter to a great variety of invertebrates and micro-organisms. Bryophytes are also valuable as sensitive pollution monitors and are sources of unique chemical compounds, some of which show significant antibiotic or other pharmacologically interesting activity (Asakawa, 1990).

Most of the bryophytes of the tropical rain forest are epiphytes. Trees, treelets, shrubs, saplings, and woody lianas are colonized by the epiphytes and some species grow on living leaves. Subtle differences in water supply, nutrients, light, and inclination of the substrate affect the ability of the bryophytes to establish themselves and therefore tree bases, trunks, ascending branches, and twigs often have different species.

Altitudinal diversification

The bryophyte diversity of the tropical rain forest varies considerably with altitude, both in structure and in floristic composition. At lower altitudes, below 1500 m, the

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forest canopy is usually complex and very high and may often reach up to 50-60 m. Woody species are numerous and include many different trees and lianas. Bryophyte cover is poor and mostly restricted to the canopy. A terrestrial layer is absent due to the presence of a thick layer of dead fallen leaves covering the forest floor. Lejeuneaceae (Hepaticae) are the most important bryophyte family of the lowlands rain forest; about 30 per cent of all the bryophyte species are members of this family. Many of them are "foliicolous" and inhabit the surface of living evergreen leaves. Foliicolous growth is a very characteristic feature of the bryophyte flora of lowland rain forests. Above 2000 m these foliicolous taxa become rare. On a single leaf an average number of 3-15 species of bryophytes may be found, with a maximum of about 30.

Montane rain forests, ranging from about 1500 to 3000 or 4000 m on high tropical mountains (at lower elevations on tropical islands), are structurally simpler than the lowland forest. The forest canopy is lower, woody species diversity is much reduced, and growth of epiphytic bryophytes is much more luxuriant. Moreover, the forest floor may be covered with dense bryophyte carpets. The well-developed terrestrial bryophyte layer of the montane rain forest, as compared to its virtual absence in lowland rain forest, is perhaps one of the most striking differences between the two forest types. The lower temperatures and higher light levels in the montane forest and the availability of plentiful water due to frequent clouds and fog favour the accumulation of dead organic material on the ground and the abundant growth of the apiphytic and terrestrial bryophytes. Tree trunks and branches may be covered with a dense fur of bryophytes, up to 15 or 20 cm thick and made up of different growth forms, including "pendant" ones (Meteoriaceae, Frullaniaceae, etc.). Such pendant taxa thrive only in such perhumid environments and are entirely lacking in the lowland rain forest. Probably the most speciose bryophyte genus of montane rain forests is the liverwort genus *Plagiochila*, which is represented here by hundreds of species. Unfortunately, the taxonomy of this genus is still chaotic and the species are usually difficult to identify, especially in tropical America. Lejeuneaceae are much less abundant than in the lowland forest and make up only 25% or less of the montane forest flora.

The large masses of epiphytic bryophytes in the montane rain forest are known to function as captors of large amounts of rain water. Pócs (1980) estimated that the interception of rainfall by bryophytes in upper montane rain forest of Tanzania with a very dense canopy totalled over 50 percent of the annual precipitation. In forests with a more open canopy interception by bryophytes is lower, however. The efficacy of rain fall interception by the bryophytes is thus dependent on the structure of the canopy of these forests.

Species richness

Our understanding of the species richness of the bryophyte flora of the rain forest is still fragmentary. Complete inventories are very scarce. Most studies only deal with part of the flora, leaving "difficult" groups such as the tiny Lejeuneaceae unidentified.

Moreover, attention is usually restricted to the lower part of the forest whilst the higher portions of the trunks and the canopy branches are neglected due to their inaccessibility. Sampling of felled trees or fallen branches is useful to obtain information on the flora of the tree crowns, but some species may be missed due to the rapid desiccation and decay of the fallen tree.

One of the most complete inventories of the bryophyte flora of a piece of lowland rain forest is the study by Montfoort and Ek (1990) in French Guiana. Using special mountaineering techniques for access into the canopy, 28 mature standing trees (belonging to 22 species) in a humid, virgin forest were sampled from the bases of the trunks up to the highest canopy twigs. In total, 154 species were identified: 66 mosses, 88 liverworts (including 71 Lejeuneaceae). These numbers are the highest thus far recorded in tropical lowland forest. The total number of species would undoubtedly have been even higher if lianas, shrubs, rotten logs, and other substrates in the understorey were included in the study. A dryer type of Guyanan lowland rain forest inventoried by Cornelissen and Ter Steege (1989), using the same sampling technique, yielded only about half the number of species (26 mosses, 53 liverworts). The lower figure is probably explained by the lesser humidity of the forest and by the fact that foliicolous bryophytes were not taken into account; moreover, fewer host trees (11) belonging to only two different species of Leguminosae were inventoried.

It is generally assumed that the bryophyte flora of tropical lowland forests is much poorer in species than that of montane forests byt recent studied indicate that this may not always be true. Gradstein et al. (in prep.) found about 175 species of bryophytes in 4 ha of montane forest in Costa Rica, hence little more than in Guyanan lowland forest. Similar figures were obtained in rich montane forest of Colombia (Wolf, 1993). The main differences between the bryophyte floras of lowland and montane rain forest seem to be their very different taxonomic make-up and the much more luxuriant growth in the montane forest. As argued above, most previous studies in the rain forest suffered from neglect of the rich canopy flora. Indeed, Cornelissen and Gradstein (1990) found that in the lowland rain forest of Guyana about 50 per cent of the bryophyte species occurred only in the tree crowns and the upper portions of the trunks, over 10 m above ground level. In contrast, only 14 per cent of the species were exclusive to the understorey.

Dispersal and Distribution

Rain forests are dynamic communities and the substrates available to the bryophytes may be frequently disturbed by natural causes. Most trees do not live for more than 200-300 years and the life span of leaves in the understorey, which are the main habitat of the foliicolous species, is probably about 1.5-3 years. Tree falls or breakage of tree crowns by storms or lighting strikes are common in the forest and cause frequent habitat disturbance and succession in the forest community (Richards, 1984).

Because of the impermanence of the substrates, short-distance dispersal is important for the forest species, especially in the understorey. Here, asexually produced diaspores or "gemmae" are the most important dispersal agents. In the high canopy of the forest, however, where chances for diaspores to become airborne are more favorable, dispersal by spores is much more common. The different dispersal strategies of canopy and understorey species appear to be correlated with the size of their geographical ranges. Species of the understorey appear to be most frequently restricted to a single continent; those of the canopy, however, are more often wide-ranging and frequently occur in more than one continent. In the lowland rain forest of French Guiana, for example, the number of bryophyte species with intercontinental distributions is twice as high in the canopy than in the understorey (Montfoort and Ek, 1990).

How do we explain these wide, intercontinental distributions? Some authors underline the importance of the geological events, especially plate tectonics, others advocate the possibility of long-range air dispersal. Accepting the geological explanation one would have to assume that the intercontinental species are very old and evolved at least 80-90 million years ago, which is when Africa and South America began drifting apart. Such an old age seems very unlikely for a species, however, and it would thus seem that the geological explanation is more likely to operate at the level of genus or family.

For the long-range air dispersal hypothesis, one must assume that spores are able to survive the hazards of exposure to the harsh conditions (drought, low temperatures) high up in the atmosphere. This was tested experimentally for a large number of rain species by Van Zanten and Gradstein (1988). These authors found that spores of species restricted to one continent were indeed much less drought- and frost-resistant than those of wide-ranging, intercontinental species. Their experiments clearly supported the long-distance air dispersal hypothesis. A striking exception, however, was the liverwort *Stictolejeunea balfourii* which grows in strongly sheltered habitats in the understorey of the forest, on tree bases and roots close to the ground. The spores of this species lose their capacity of germination within a day of desiccation, yet the species is distributed widely throughout the tropics. As the species is obviously incapable of long-range dispersal, the very wide range of *Stictolejeunea balfourii* might only be explained by assuming that the species is a very ancient taxon which spread step-by-step during and after the Cretaceous, via the migrating land masses, and did not evolve during many millions of years. The species might thus be looked upon as a living fossil!

Conservation

The massive forest destruction in the tropics, noted earlier, has a deleterious effect on the bryophytes. Studies in various tropical regions indicate that the flora of secondary forests and plantations is usually much impoverished as compared with the virgin forest. A comparison between the epiphytic bryophyte floras of primary rain forest and planted forests on the slopes of Mt Kilimanjaro, Tanzania, showed that 90 per cent of the native forest species did not occur in the plantations and that only 5 per cent of the epiphytic biomass had remained (Gradstein, 1992). Species of the forest understorey are usually more seriously affected than those of the canopy, although some canopy species may also become rare or disappear after disturbance. Hyvönen et al. (1987) checked the occurrence of 43 rain forest mosses in disturbed and undisturbed habitats of Papua New Guinea and found that 29 species grew in both environments, whereas 14 did not occur outside the virgin forest. Those restricted to the virgin forest were usually shade epiphytes of the forest understorey.

Even though no species of bryophytes and lichens have as yet been reported as extinct, many species should be considered endangered and threatened with extinction when the forest vanishes. In order for these and other species to be preserved, habitat samples should be set aside in all life zones throughout the tropics. These forest reserves would probably not need to be very large for bryophytes, as preliminary data on species density in the rain forest suggest, but they should be large enough to ensure protection and rejuvenation of the forest and the host trees. The safeguarded areas may not only serve as refugia for the threatened species, but should also be laboratories for the study of the natural richness in bryophytes of the rain forest. Because of the speed at which forests are vanishing in the tropics, such studies are needed urgently.

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