TROPICAL RAIN FORESTS

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Summary

Tropical rain forests form Earth's most complex and species-rich ecosystem. Their immense diversity is due to the adaptability of their constituent plants and animals to survive periods of changing climate and geologic upheaval, expanding their ranges during periods of favorable climate, withdrawing to refuges when climates were adverse, and dispersing to other land areas at times when land bridges were temporarily available within their range of climatic tolerance. The first part of this article gives a brief characterization of present-day tropical rain forests, emphasizing their climatic requirements and geographical distribution, physiognomy, and floristic similarities from region to region. This is followed by a brief discussion of the criteria from which the former occurrence of tropical rain forests can be determined from the geological record.

The major part of the article is a synthesis of the evolution and geological history of tropical rain forests from the time of the initial radiation of the flowering plants (of which tropical rain forests are predominantly composed). After their initial establishment in the Late Cretaceous, they suffered substantially as a result of the bolide impact which wiped out the dinosaurs, but then expanded to remarkably high latitudes with warming "greenhouse" climates during the Paleocene and Early Eocene. Their

subsequent history was one of stepwise decline, paralleling global temperature trends, culminating with the climatic oscillations of the Ice Age, when during cool glacial periods, they became restricted to favorable refuges. Tropical rain forests have endured many upheavals since their first appearance possibly 100 million years ago, but are currently going through a crisis more devastating than any during their previous history due to forest destruction by humans. They contain an immense gene pool necessary to safeguard a long future for plant and animal life on this planet. Every effort should be made to preserve their biodiversity for perpetuity.

1. Introduction

Tropical rain forests (Figure 1) contain a greater diversity of plant and animal life than any other vegetation type. In the most species-rich forests, every second tree may be a different species, whereas in temperate forests, every second tree is likely to be an oak or a pine. The diversity of tropical rain forests is well illustrated by reference to Australia, where tropical rain forests cover a mere 0.5% of the continent, yet this tiny area includes 50% of the plant and animal species recorded from the whole continent. Because of the immense diversity of tropical rain forests and their constituent fauna, their intrinsic value is much greater than forests of temperate lands; they contain an immensely greater gene pool, necessary to safeguard a long future for plant and animal life on this planet. They also form a major source of hardwoods, of many plant and animal products, and also of chemical compounds which have been developed by plants as protection against attack by herbivores. They are also a major absorber of atmospheric CO_2, and thus help regulate global climate, providing a buffer to the deleterious effects of global warming. This chapter presents a brief outline of present-day tropical rain forests, and then presents an overview of the their geological history from the time of appearance of the flowering plants, with which they are overwhelmingly dominated, up to the present day.

Figure 1. Tropical lowland evergreen rain forest.

Although tropical rain forests were first encountered when the Romans extended their empire to India, they have become properly known to the Western world only for the last few hundred years, since the great voyages of discovery of the sixteenth and seventeenth centuries, and subsequent European colonial expansion. Indeed, the term *tropical rain forest* was coined only in 1898 (as *tropische Regenwald*) in Schimper's monumental book, translated into English in 1903 as *Plant Geography upon an Ecological Basis*. Subsequently, their ecology was described in a classic book by Richards first published in1952, and regional reviews have subsequently appeared. In the last few decades, research on tropical rain forests has continued at a faster rate than at any time previously, and this has led to a much better understanding of their taxonomy, ecology, dynamics, food webs, and nutrient cycles. This increased knowledge has come about at a time when tropical rain forests are fast disappearing following commercial timber extraction, and destruction for agricultural development and the expansion of the human population across the world. The prediction of Richards who stated in 1952 that "the whole of the tropical rain forest may disappear in the lifetime of those now living, except for a few inaccessible areas and small forest reserves," is now close to fulfillment. One fundamental aspect of tropical rain forest, which has mainly been the subject of speculation, is its long-term history, its origins, and its evolution. With a knowledge of the importance of tropical rain forest to global ecosystems over the time span of the last 100 million years, it becomes increasingly evident that the current phase of destruction of these magnificent forests may turn out to have far-reaching consequences with respect to global ecology. A first approximation of the pattern of the initial appearance, and subsequent evolution of tropical rain forests since the initial radiation of the flowering plants (with which they are overwhelmingly dominated) was published in 2000 by the author in the book *Origin and Evolution of Tropical Rain Forest*, of which this article forms an abridged summary. The reader is referred to this text for unreferenced details in this account.

2. Present-day Tropical Rain Forests

Tropical rain forests can be found today in each of the three land areas which occur within the tropical zone (Figure 2), and prior to the destructive effects of humans during the past century, as a result of which much of the rain forest has now been destroyed, occupied about one-third of the tropical land surface. Neotropical rain forests, in Central and South America, are the most extensive, where about half of the global total are found, followed by southeast Asia, with about a third, and Africa, with a fifth. They are chiefly found over much, but not all of the areas astride the equator between 5° N and S, between the northern and southern subtropical high pressure zones, where convectional rain occurs more or less throughout the year. Subsidiary areas of tropical rain forest occur along eastern coastlines, which lie within the path of moist trade winds, and where orographic uplift creates winter moisture.

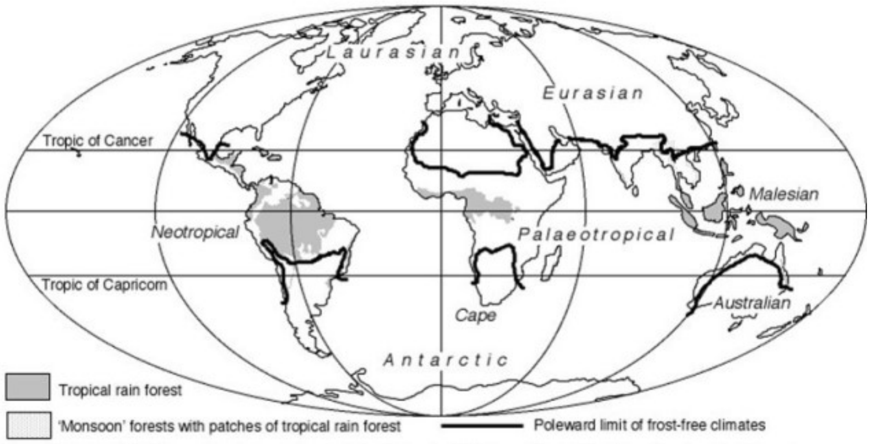

Figure 2. Global distribution of tropical rain forests (after Richards P.W. (1952, second edition, 1996). *The Tropical Rain Forest.* Cambridge University Press. 450 pp.), in relation to frost-free climates. Floristic regions mentioned in the text are shown in italics. This and all subsequent world maps use Mollweides equal area projection (from Morley R.J. [2000.] *Origin and Evolution of Tropical Rain Forests*, 362 pp. London: Wiley; with permission of J. Wiley and Sons).

Tropical rain forests are evergreen to partly evergreen, and occur in areas typically receiving more than 2000 mm of rain annually, with not more than four consecutive months with less than 100 mm of precipitation in two years out of three, with the coldest mean monthly temperatures not falling below 18°C. They are characterized by small annual temperature variations and are essentially frost free. It is the virtual absence of frosts that differentiate tropical rain forests from other types of rain forests. A very large number of flowering plant families are limited in their distribution by the occurrence of frosts. Such families have been termed *megathermal*, and those that prefer abundant moisture are wholly restricted to tropical rain forests. Today, it is a essentially a coincidence of the present global climate regime that areas which are subject to a rain forest climate and are essentially free of frosts also more or less coincide with the tropical zone (Figure 2). This, however, has not been the case throughout geological time; during some periods, frosts must have occurred within the tropical zone, forcing tropical rain forests to refuges along the equatorial belt during cold glacial maxima, but during periods of warmer, "greenhouse" climate during the Tertiary and Cretaceous, much of the midlatitudes would have been frost free. The "tropics" are strictly defined by their insolation regime. From the point of view of the distribution of tropical rain forest, the insolation regime is secondary to the absence of frosts, and therefore, from a geological point of view the term *megathermal rain forest* is a more appropriate term.

2.1. Distribution and Characterization

Tropical rain forest occurs in a number vegetation types, or formations, of different physiognomy, depending primarily upon their physical habitat. The tropical lowland evergreen rain forest formation occurs in areas of permanently moist climate on well-drained zonal soils, whereas along the ecotone relating to decreasing moisture availability, this is replaced by the tropical semi-evergreen rain forest formation, and subsequently by monsoonal forests, deciduous woodland and savanna. With increasing latitude, tropical rain forests grade into warm temperate and cool temperate rain forests, whereas along the altitudinal ecotone, they grade into the lower montane and upper montane rain forest formations, and tropicalpine vegetation. There are also distinctive formations associated with edaphic settings, such as freshwater swamp forest on permanently wet sites, peat swamp forests on oligotrophic peats and mangrove and beach forest along coasts. See Chapters ***Temperate Forest***, ***Freshwater Systems***, and related contributions of Earth´s biomes chapters.

The tropical lowland evergreen rain forest formation is the richest, and most luxuriant of all plant communities, and occurs in areas which experience a wet tropical climate without dry seasons. It is this vegetation type with respect to which frequently exaggerated descriptions have been made by early explorers and writers, and is often referred to as "jungle," mainly through popular writings, although this word actually refers to seral vegetation in North India. These are also the forests which are currently being most extensively exploited for their rich timber resources.

Figure 3. Inside tropical lowland evergreen rain forest.
Note absence of branching and lack of ground flora.

Tropical lowland rain forest is physiognomically similar in each of the three continental areas where it proliferates, although floristically, there may be hardly any similarities between these areas, and thus it provides us with one of the classic examples of convergent evolution. It is typically dense, evergreen forest, with trees reaching 50–70 m in height, and is often devoid of ground flora (Figure 3). The tree component is typically very diverse, and gregarious dominants are generally uncommon. Tropical rain forest is popularly regarded as being multilayered, with tree crowns forming distinct strata, but in practice, such layers are rarely well defined. For instance, in Equador, no clear vertical discontinuity of structure could be discerned at any level and strata could be delimited only arbitrarily. Tree crowns are rarely stratified in tropical rain forest because they are composed of a very large number of species, each maturing at different heights and reacting differently to light and other factors. Boles are usually straight, often with smooth or dimpled bark and buttresses are common. Cauliflory and ramiflory are frequent. Leaves and leaflets are generally coriaceous, and of mesophyll size, with pinnate leaves being common. Leaf margins are typically entire, frequently with drip tips irrespective of leaf organization (Figure 4). Lianes and woody climbers are common which often bear peltate leaves. Epiphytes are also common and diverse. All other rain forest formations differ from tropical evergreen lowland rain forest in having lower species diversities, fewer life forms, and simpler structure.

Figure 4. Leaves with pronounced drip tips, Bogor Indonesia.

The single most distinctive feature of tropical lowland evergreen rain forest is its very high diversity. A complete enumeration of all synusiae on a 0.1 ha plot from Costa Rica revealed the presence of 233 species in 2171 specimens, but currently the richest communities occur on the eastern flanks of the Andes, in Peru and Equador, where around 300 tree species have been determined on a single 1-ha plot. Very high diversities have also been recorded from southeast Asian localities, whereas diversities of African forests tend to be much lower, for instance, the palm flora of the tiny island of Singapore is richer than that of the whole of the African continent.

The generic and specific makeup of tropical lowland evergreen rain forests vary greatly within each of the three centers of rain forest development. However, at the family level, the composition of the trees within lowland forests is remarkably similar, with Leguminosae, Annonaceae, Moraceae, Rubiaceae, Euphorbiaceae, Sapindaceae, Apocynaceae, Burseraceae, and Guttiferae being represented by considerable diversity in each region. The most important regional difference is the substitution of Dipterocarpaceae for Leguminosae as the most species-rich woody family in southeast Asian forests, where it is overwhelmingly dominant in terms of biomass. Australian rain forests are also distinctive and contain abundant representatives of families not widely seen in rain forests elsewhere, such as Elaeocarpaceae, Monimiaceae, and Proteaceae.

The occurrence of representatives of so many plant families within each of the three continental regions requires a historical explanation, since many of the representatives of these families have diaspore dispersal mechanisms which prohibit transoceanic dispersal. For instance, Myristicaceae bear seeds which can only germinate under the protection of the rain forest itself. Others have heavy seeds which are unlikely to be dispersed far from the parent tree. Obtaining an explanation for the distribution of such families remains one of the fundamental problems of tropical plant geography which is now beginning to be resolved from the fossil record.

Wolfe introduced in 1979 the term *paratropical rain forest* (para meaning close) for evergreen rain forests delimited by the 20–25°C mean annual temperature isotherms occurring at the latitudinal ecotone between tropical evergreen lowland and warm temperate rain forests. He envisaged that this ecotone includes forests which are the closest analogue to many early Tertiary tropical aspect vegetation types from the midlatitudes. Paratropical forests do not comprise a formation separate from lowland evergreen rain forests, but the term is a useful one for making reference to tropical rain forests close to the latitudinal ecotone.

3. Geological Evidence for Tropical Rain Forests

Many lines of evidence can be used to infer the former occurrence of tropical rain forest. This may be in the form of fossils of plant taxa which are found in present-day rain forests (using the nearest living relative approach), or in the form of physiognomic features which are characteristic of, or restricted to closed-canopy, megathermal vegetation, such as the dominance of mesophyll or megaphyll leaf classes, dominance of entire leaves and presence of drip tips. Faunal evidence may also be useful, especially vertebrate body size variations and habit. In addition to leaves, palaeobotanical records may be in the form of wood or seeds, or microfossils, such as pollen spores and cuticular fragments. In general, fossils which can be referred to extant taxa are more useful in younger deposits, whereas those suggesting physiognomy are particularly valuable in older deposits of Cretaceous and earliest Tertiary age, at which time few of the representatives of extant rain forests had evolved. A surprising new source of information is from geochemical fossils, such as the derivative compounds of resins which are produced by Dipterocarpaceae. In addition, the presence of temperature-sensitive marine fossils, such as larger foraminifera, corals, palaeosols, climatically sensitive lithologies and oxygen isotope data provide evidence for the former occurrence of rain forest climates. Even in the absence of data from specific localities, the former distribution of rain forests can be inferred from climate modeling, either through the use of computer simulations, or empirically.

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Biographical Sketch

Robert J. Morley was born in Suffolk, England, in 1949, and studied Geography at Hull University. He subsequently completed a Ph.D., also at Hull (awarded 1976), on the Quaternary history of tropical rain forests in Sumatra (Indonesia) and the Malay Peninsula. After completing his Ph.D., he joined a group of international geological consultants, to use palynology as a dating tool in petroleum exploration, and has subsequently spent 25 years as a stratigraphic palynologist, working mainly on Tertiary sediments from southeast Asia and Africa.

In 1990, he joined the overseas division of the British Geological Survey to establish a palynological laboratory for the Indonesian government in Jakarta, funded by the Overseas Development Administration, UK, and subsequently, in 1992, established the palynological consultancy *Palynova*, near Cambridge, UK, using palynology as a stratigraphic tool and providing training in palynology to scientists from developing countries.

He has had an interest in tropical rain forests throughout his professional career, and has recently fulfilled an ambition to establish the pattern of evolution of tropical rain forests, based on his observations as a stratigraphic palynologist, in his recent book *Origin and Evolution of Tropical Rain Forests*, published by Wiley (see Bibliography). He has produced over 50 publications, mainly on palynology from southeast Asia and west Africa.