# II Special part

**Part D - ZB I: Zonobiome of the evergreen tropical rainforest or of the equatorial humid diurnal climate**

**Part E - ZB II: Zonobiome of savannahs, tropical deciduous forests and grasslands of the tropical summer rainfall area**

**Part F - ZB III: Zonobiome of hot deserts or subtropical arid climate**

**Part G - ZB IV: Zonobiome of hardwoods or of the Mediterranean winter rain-fed areas**

**Part H - ZB V: Zonobiome of the laurel forests or of the warm temperate humid climate**

**Part I - ZB VI: Zonobiome of deciduous broadleaf forests or of the temperate nemoral climate**

**Part J - ZB VII: Zonobiome of steppes and cold deserts or of the arid temperate climate**

**Part K - ZB VIII: Zonobiome of the taiga or of the cold temperate boreal climate**

**Part L - ZB IX: Zonobiome of the tundra or of the arctic climate**

[IMAGE]

Rafflesia arnoldii in the tropical rainforest of Borneo (zonobiome I) attracts flies as pollinators, growing as parasite on liana roots (photo: Rafiqpoor)

[IMAGE]

Tropical rainforest (zonobiome I) on the slope of the Ambohitsitondroina Mountains on the Masoala Peninsula in NE Madagascar (photo: E. Fischer)

[IMAGE]

Submontane tropical rainforest (zonobiome I) in the morning fog in the Sierra de Tilarán in Costa Rica (photo: Breckle)

**II Special part**

**Part D - ZB I: Zonobiome of the evergreen tropical rainforest or of the equatorial humid diurnal climate**

1 **Typical formation of the climate in ZB I**

2 **Soils and pedobiomes**

3 **Vegetation**

4 **Divergent vegetation types in ZB I around the equator**

5 **Orobiome I - tropical mountains with diurnal climate**

6 **The biogeocenes of the ZB I as ecosystems**

7 **Fauna and food chains in ZB I**

8 **The human being in the ZB I**

9 **Zonoecotone I/II - Semi-evergreen forest**

10 **Literature**

Dipterocarpaceous tree giants with their enormous heights of over 60 m in the evergreen rainforests of SE Asia (Zonobiome I), e.g. in Borneo, Saba, tower above the irregular canopy of the forests (photo: Rafiqpoor)

1 **Typical features of the climate in ZB I**

The entire tropics are generally radiation surplus areas of the earth because of the equally favorable radiation conditions in the area between the tropics. They give off energy to the high latitudes through atmospheric circulation. Nevertheless, there are radiative climatic differences between the humid and dry tropics. The latter, especially the extensive desert regions (e.g. the Sahara) at the transition to the subtropics, have a negative radiation balance because of the maximum nocturnal radiation emission. Despite these differences, the uniform irradiation conditions the tropics to be primarily the Earth's heat belts. They are an area of **thermal** uniformity with 12 thermal vegetation months (◘ Fig. D-1 A) and a zone without noticeable temperature seasons at all elevations from sea level to the summit regions of the high mountains (Lauer 1975, Breckle 2004).

The clearly pronounced diurnal variation in temperature is the result of the greater temperature contrasts between day and night (diurnal climate). The decrease in temperature with altitude is continuous from the warm tropics of the lowlands to the cold tropics of the high mountains.

One can contrast the thermal tropics with the hygric tropics, since the seasons can be divided by rainy and dry seasons of different length and intensity and from year-round humidity to year-round aridity. As rainfall amounts and temporal duration decrease from the interior to the marginal tropics, humid tropics can be distinguished from the arid tropics (◘ Fig. D-1, B) (Lauer 1975, 1999).

In Zonobiome I, the monthly mean temperature often varies by only 2-3 K. But the diurnal fluctuations of temperature can reach over 9 K on sunny days (diurnal climate); on cloudy days they are insignificant at only 2 K. Accordingly, the humidity changes only slightly (◘ Fig. D-2). Frost never occurs, only in the high mountains, but even there a tropical diurnal climate prevails year in, year out.

Bogor (Buitenzorg) on Java, for example, has a distinctly permanently humid rainforest climate. The monthly average temperature there varies only between 24.3 °C (February) and 25.3 °C (October), the average annual precipitation is 4,370 mm, the rainiest month has 450 mm of rain, the less rainiest 230 mm. A month with less than 100 mm of rain is already considered relatively dry in this rainy zonobiome and is an exception. Only on the Malay Peninsula and in Indonesia are larger areas found that are wet all year round; in the Amazon Basin it is only a sub-area along the Rio Negro, and in Central America it is a few small, rain-facing mountain areas. In the Congo Basin, two periods of lower rainfall are mostly noticeable (◘ Fig. D-3).

In southern India, too, there are always one or two drier periods per year. Bogor (Buitenzorg) on Java has a distinctly permanently humid rainforest climate (► Fig. A-52).

Fig. D-1 The hygrothermal character of the climate of the tropics, using Africa as an example: thermal uniformity (A), hygric differentiation (B).

|  |
| --- |
| Box D-1 The tropics as areas with diurnal climates |
| Zonobiome I (the tropical rainforest) has a distinct diurnal climate: The diurnal amplitudes of the air temperature are considerably larger than the annual amplitudes of the monthly mean values. |

◘ Fig. D-2 Diurnal variation of weather factors in Bogor (Java) during the rainy season (compare sunny 12th February, when humidity dropped to almost 50%, with hazy 14th February). Figures for rain indicate absolute rainfall amounts in mm (data after Stocker, modified after Walter 1990).

◘ Fig. D-3 Climate diagrams of stations in the tropical rainforest region: Congo, Amazon Basin and New Guinea.

The rains fall mostly in the afternoon as short, heavy downpours, in the evening hours the sun shines again. Its radiation, when it is at its zenith, is very strong. As a result, leaves directly exposed to the radiation (e.g. in the crowncanopy) heat up by several degrees (up to 10 K) above the already very high air temperature. Therefore, high water vapour saturation deficits occur at the leaf surface even in vapour-saturated air (◘ Fig. D-4). Excess temperatures of 10 to 15 K have been measured on unshaded *Coffea leaves* on clear days in Kenya. Clear days are not so rare even in permanently humid Bogor (Buitenzorg) (► Fig. D-2). When this occurs, humidity drops to nearly 50% and temperature rises above 30 °C, increasing the saturation deficit to nearly 6 kPa with leaves overheated by 10 K, meaning that leaves are exposed to extreme dryness for hours at a time even in the wettest tropics. In contrast, humans, who have their own body temperature, constantly experience the air as muggy.

Researchers who worked in the jungle for years emphasize that even in the perhumid area on Borneo there are always weeks without rain, which means a dry period for the jungle trees. The long-term monthly rainfall averages do not indicate this. This is equally true for Amazonia.

It is therefore understandable that the leaves have high resistance to transpiration and also a very thick cuticle. They are leathery, but not completely xeromorphic (compare the gum tree Ficus elastica, Philodendron, Anthurium and others); they can strongly limit their transpiration when stomata are closed and permanently maintain a high hydrature of the plasma. They are often lauriphyllous, but not sclerophyllous. The cell sap concentration is usually only 1.0 to 1.5 MPa, and it is significant that some of these species, as houseplants, tolerate well the dry air in heated living rooms.

◘ Fig. D-4 Curves of saturation deficits in mm Hg at the leaf surface by overheating of 5 K and 10 K, respectively, as a function of air temperature in watervapor-saturated air.

Conditions are different for the species that grow in the forest shade. Inside the rainforest, the microclimate is much more balanced, especially on the ground, which receives almost no direct sunlight. Here, temperature fluctuations almost cease, and the air is constantly saturated with water vapor. With the high humidity, even with the slight nightly cooling, dew regularly falls on the treetops. It drips off and wets the leaves of the lower layers. Important for the forest plants are the light conditions. The irregular contour of the canopy and the highly reflective, leathery leaves allow light to penetrate deep into the forest interior, but at ground level the average intensity is very low. However, the brief sunspots on the ground play an important role in the light yield. Depending on the structure of the forest, on average 0.5 to 2% of the daylight (as in our deciduous forests), and more rarely only 0.1%, reaches the herb and ground layer. If the numerous gaps in the stand, which cause a very heterogeneous structure, are included, i.e. if the light yield is integrated over a larger area, values well above 2% are obtained; on average, more than just 2% of the light reaches the ground. This is due to the very non-uniform structure of the stands. However, the individual plant sometimes receives less than 1% of the light. Some of the very tender herbs have bluish reflecting undersides.

2 **Soils and pedobiomes**

If we disregard the young volcanic soils and the alluvions, the soils of the rainforest areas are mostly very old. They often go back to the Tertiary. Weathering penetrates several meters into the depth of siliceous rocks. A leaching of the bases and the silicic acid takes place; what remains are the sesquioxides (Al2O3, Fe2O3), i.e. a lateritization occurs and red-brown to yellow-red loams (ferrallitic soils or latosols) without visible division into horizons are formed. If we compare the great diversity of soil types, we find that about  of the soils in the tropics belong to the oxisols and ultisols; these are soils with only very moderate to very low fertility. About 7% of the tropical soils are alluvial terraces rich in quartz sand or other highly weathered, leached surfaces (psammente or spodosols) with extreme nutrient poverty. Only on about 20% of the tropical soils can arable farming be practiced with current methods; these are the younger volcanic soils (alfisols) and the rich alluvial areas in large river plains (fluvente, aquepte).

The decay of the litter is very rapid. The wood is destroyed by termites, which are not noticeable in the jungle because their burrows are underground. Usually, under a very thin layer of litter and dark humus (1 to 3 cm), the reddish-brown soil immediately appears. The typical soils are found on slightly sloping ground, because on flat surfaces, waterlogging with siltation easily becomes noticeable with the large amounts of rain. The soils are generally very poor in nutrients and acidic (pH = 4.5 to 5.5). This seems to contradict the outwardly lush vegetation. But almost all the nutrients needed by the forest are contained in the above-ground phytomass, almost nothing in the soil. Annually, some of the biomass dies, is rapidly mineralized, and the released nutrients can be immediately reabsorbed by the roots (always via mycorrhiza). Therefore, despite the high rainfall, there is almost no loss of nutrients through leaching. This is shown by the fact that the water in the streams of these areas has an electrical conductivity almost equal to that of distilled water. At most, it is slightly brown in colour due to humus brine (colloidal dispersion).

Nutrients are even reabsorbed before the mineralisation of the litter. In the lowland rainforest near Manaus on the Amazon, the suction roots of the trees on very poor sandy soils have a mycorrhiza at a depth of only 2 to 15 cm. Through the fungal hyphae, this is directly connected to the litter layer; through the fungi, the trees can receive nutrients in organic form directly from the litter (short-circuited cycle), similar to saprophytic flowering plants. This prevents leaching of nutrients by rain and thus loss from the ecosystem. The amount of leaves falling daily ranges from 4.5 to 12.6 g of dry matter per m2. The leaf turnover ranges between 0.9 and 2.2 years.

As a result of the rapid circulation of substances, the primeval forest may persist for thousands of years on the same soil. But as soon as it is cleared and all the wood is burned or removed, there is a heavy leaching of the entire nutrient capital suddenly mineralized by the fire. Only a small part is adsorbed by the soil colloids and can be utilized by cultivated plants for only a few years.

After abandoning the crops, as is the case with shifting cultivation, a secondary forest grows up, which, however, by no means reaches the lushness and diversity of the primeval forest. After the forest has been cleared again in shifting cultivation, nutrients are again lost through leaching until, after repeated use, only bracken (Pteridium) or Gleichenia species are able to thrive. If these areas are burnt down, they often become grassed over by alang-alang grass (Imperata) or other undemanding species that are of no value for grazing.

On completely degraded areas, virgin forest can re-emerge when soil erosion removes the entire soil down to the bedrock, which then weathers and a new primary succession begins, which of course requires considerable time and corresponding diaspores inputs from the surrounding area. If, on the other hand, the parent rock is very poor in nutrients from the outset, for example if it is weathered poor sandstones or alluvial sands, the nutrients are only sufficient for the establishment of very poor tree or heath stands or light savannahs. These are pedobiomes, specifically peinobiomes (deficient or nutrient-poor soils), which can cover very wide areas. They grow on podsol soils with 20 cm thick raw humus (pH = 2.8) and bleaching horizons or even on peat soils. These are known from Thailand and Indomalaya, as well as from Guyana (Humiria bush, Eperua forest) and the Amazon lowlands in the Rio Negro basin, which carries 'black water' (rich in humic acid colloids). They are also reported in Africa for the Congo Basin and the heaths on Mafia Island off the coast of Tanzania. However, peat soils have been most extensively studied in NW Borneo. Extensive (14,600 km2) domed forest raised bogs (helobiomes) with Shorea alba and others are found there, starting just beyond the mangrove boundary, with peat deposits up to 15 m thick (pH around 4.0). Heath forests (Agathis, Dacrydium, and others) on raw humus soils with Vaccinium as well as Rhododendron also occur there. The total area of tropical podsol soils is estimated at seven million hectares.

At the other extreme are the tropical calcareous soils, or lithobiomes, which are associated with very striking relief forms and have been described from Jamaica and Cuba. In the humid tropical climate lime is readily dissolved. Clints or grikes (karren)are formed, the softer limestone disappears, and only the hardest parts remain as razor-sharp ridges (◘ Fig. D-5). The whole area karsts and is dissected into a network of ridges (the remains of the former plateau surface) by sinkholes, which form as collapse funnels, are round and sometimes up to 150 m deep. If the erosion goes even further, as in Cuba, then only single, unconnected towers or cone karst mountains with almost vertical walls remain, like the 'Mogotes' (“organ” mountains or cockpit karst) in Cuba or the 'Moros' in N Venezuela. The soil of the sinkholes is filled with bauxitic red earth, on which a moist evergreen forest develops. The limestone ridges, on the other hand, form a very heterogeneous site, depending on whether alkaline soil (pH = 7.7) can accumulate in individual depressions or not. Therefore, one usually finds a very interesting flora with representatives from rain forest to cactus desert. In the mentioned areas the climate is characterised by little over 1000 mm rainfall. In NW Madagascar lush tropical rainforests are common outside the karst areas. On the karst landscape itself, the vegetation cover is sparsely developed with mostly deciduous tree species (► Fig. D-5).

We will come back to the halobiomes (mangroves) later.

◘ Fig. D-5 Impressive karst landscape with clint (karren) formation on Jurassic limestones at the NW tip of Madagascar with an annual precipitation of >2000 mm. Forest vegetation grows in sinkholes with soils (Photo: E. Fischer).

3 **Vegetation**

3.1 **Structure of the tree layer, flowering periodicity**

The most striking feature of the tropical rainforest is the large number of wood species that make up the tree layer (Homeier et al. 2010). One often finds over 100 up to 300 species per hectare with a BHD of >10 cm (Valencia & Balslev 1994). But there are also forests with only a few tree species: Indomalaya is often dominated by Dipterocarpaceae and in Trinidad the upper tree layer is formed by Mora excelsa (Fabaceae). The floristic differences between the forests of South America, Africa and Asia are very large (◘ Fig. D-6). The forest types are correspondingly diverse; but we can discuss only those features that are more or less common to all. Palm trees are almost entirely absent from the African rainforests, but are common in the Central and South American ones (especially on wet sites). The tree layer reaches a height of 50 to 55 m, occasionally 60 m.

◘ Fig. D-6 Number of flowering plant families in each continental region (number in each region) and percent similarity (number among major regions), excluding cosmopolitan plant families (modified from Terborgh 1991).

Sometimes one distinguishes three tree layers, an upper, middle and lower one; but mostly a stratification is not recognizable. The upper tree layer is not closed; there are individual giants that protrude above the other trees. Only the middle or lower layer forms a dense canopy of leaves; in this case, for lack of light, the lower trunk space is quite free, so that locomotion is easily possible. But the structure of the forest varies greatly in detail; one must be cautious in making generalizations. Examples of profiles of the stand structure will illustrate this (◘ Fig. D-7, ◘ Fig. D-8, ◘ Fig. D-9).

In terms of tree shape, the trunks are generally slender and thin-barked, the crowns set high and are relatively small and irregular in outline, corresponding to the dense stand. The age of the trees is difficult to determine, as annual rings are usually absent. Estimates based on increment measurements gave 200 to 250 years for the thick old trees. The root depth is greater than assumed. 21 to 47% of the roots are in the upper 10 cm, most of the rest below that to 30 cm depth, but 5 to 6% go as deep as 1.3 to 2.5 m (Hüttel 1975).

The root mass was determined to be 23 to 25 t●ha-1 (49 t●ha-1 according to another method). The large tree giants achieve their stability through powerful board roots (◘ Fig. D-10), which can reach up to 9 m up the trunk in the shape of a pillar and run radially outwards from the base of the trunk with only a small thickness; many roots grow vertically into the soil from their base (Vareschi 1980), which can become stilt roots (◘ Fig. D-11) when the soil is washed out.

◘ **Fig. D-7** Rainforest profile through the Shasha Protected Forest (Nigeria). The strip of forest shown is 61 m long and 7.6 m wide. All trees taller than 4.6 m are plotted. The letters indicate different tree species (data after Richards, from Walter 1973).

◘ Fig. D-8 Schematic profile through dipterocarpaceous rainforest on Borneo, length 33 m, width 10 m, herbs absent (after Walter 1973).

◘ Fig. D-9 Schematic profile through tropical montane rainforest in the Sierra de Tilaran (Costa Rica) (from Sprenger & Breckle 1997).

◘ Fig. D-10 The development of board roots in the world's tropical rainforests is an important strategy for the large rainforest trees: they provide stability (photo: E. Fischer, Makokou-Ipassa rainforest, Gabon).

◘ Fig. D-11 From the trunk base of some rainforest trees arise many roots growing vertically into the soil, which can become stilt roots when the soil is washed out (photo: Breckle, rainforest in Rancho Grande, Venezuela).

The leaves of trees are larger the more humid and warmer the climate, but the leaves exposed to the light are always much smaller in one and the same tree species. In the East African rainforest, for example, a ratio of 8:1 (largest leaf 48×19 cm, smallest 16 × 7 cm) occurs in Myrianthus arboreus, and even 28:1 (largest leaf 162×38 cm, smallest 22×10 cm) in Anthocleista orientalis. Both are trees of the lower tree layer. However, in Elaeagia auriculata in the mountain forest of Costa Rica, a species that always has very large leaves, the differences are smaller.

Bud protection is not necessary for trees of the rainforest. The young leaf plants are sometimes enclosed by hairs, mucilage or juicy scales or by specially formed stipules. Although the growing conditions are permanently favourable, the growth of the shoots takes place in stages. The sprouting branch ends often show the appearance of shaking leaves (nodding foliage) (◘ Fig. D-12). During the rapid extension growth, no supporting tissue is formed at first, so that the young shoots droop downwards with the leaves; they are white or bright red in colour initially and only turn green later when they become stronger. Rapid differentiation of the leaf tip leads to the formation of a drip tip in some species (◘ Fig. D-13). It is found in 90% of the species in the understory in Ghana. Experiments in the forest showed that leaves with drip tips were dry within 20 minutes after rain, but those without still remained wet after 90 minutes (Longman & Jenik 1974).

A special problem is the periodicity of the development and growth of plants in the ever-humid tropics without annual variation of temperature. That a periodicity of shoot growth can be observed, has already been mentioned. Many trees have growth rings in their wood, usually several per year, which are therefore not annual growth rings. A similar thing is true of the rhythmicity of flowering. With the always uniform external conditions, periodic phenomena are usually not confined to a particular season.

In Malaysia, in wet weather, the old leaves are said to fall off after the young ones sprout, and in dry weather, they fall before. In this way, deciduous wood species have arisen in the climate zone with a drought. A tree may even be leafless for a short time. Then it can be observed in individuals of the same species that leafy and non-leafy trees stand side by side. In others, even the branches of one and the same tree behave differently, i.e. they do not sprout at the same time. The same applies to the flowering period. Different individuals of the same species or different branches of the same tree flower at different times (◘ Fig. D-14).

◘ Fig. D-12 The process of 'shaking leaves' is the distinctive feature of some rainforest trees (photo: Breckle).

◘ Fig. D-13 Some rainforest trees form drip tips in their leaves. This causes the leaves to dry more quickly after a rain event (photo: Breckle).

In all these cases, therefore, it is an autonomous periodicity which is not linked to the twelve-month period. Periods of two to four months, of nine months, but also of 32 months occur. As a consequence, there is no general flowering period in the rainforest. There are always only individual trees in flower and their blossom is only slightly noticeable in the prevailing greenery, however beautiful and large the blossoms may be. European species of trees (beech, oak, poplar, apple, pear, almond) have been planted in tropical mountains without seasons. The general experience was that at first they retained their annual periodicity of leaf fall, budding, and flowering. Over time, disturbances in inflorescence development occurred, the individual branches reacted differently, and finally one could see all seasons on a tree, i.e. leafless, sprouting, flowering and fruiting branches.

◘ Fig. D-14 Seasonality is extinguished on a coffee tree with flowers, green non-ripe and red ripe fruits (photo: http://bit-Do/brNss).

Central European species are mostly long-day plants, i.e. they only flower when exposed to long days (>14 h sunlight), as in summer in the temperate zone. Therefore, they generally do not flower in the tropics, but lower temperatures may substitute for long-day: Primula veris grows only vegetatively in Indomalaya at 1,400 m altitude, and flowers and fruits abundantly at 2,400 m altitude.

Fragaria species do not flower at low altitudes in the tropics, but form many stolons; in the mountains they only flower and fruit, while stolon formation is suppressed (for example in Sri Lanka) (Zeller 1973).

Pyrethrum plantations are found in Kenya at altitudes of 1,500 to 2,500 m, where the flowers are harvested that do not develop at lower altitudes. However, the endogenous rhythmicity of these plants immediately adapts to the climatic rhythmicity as soon as one is present, for example even in the humid tropics with only a short, slightly drier season, which, by the way, is the case in many areas, so that a ‘seasonal generator’ is usually present after all. In the case of the mango tree, which is cultivated everywhere in the tropics, the individual light sprouting branches in the otherwise very dark crown are particularly striking (◘ Fig. D-15). However, as soon as there is a distinct dry season, the sprouting and flowering of all branches and trees adapt to it. The teak or djatti tree (Tectona grandis) never becomes bare in West Java, which is always moist, while in East Java it sheds all its leaves during the dry season. But even in the humid tropics there are species, such as the dove orchid (Dendrobium crumenatum), which blooms in a larger area on one and the same day. It does form the buds, but for them to unfold, a sudden cooling as a signal is necessary for synchronization, for example, after particularly strong thunderstorms. The coffee tree also opens buds only after a short drought. Bamboo species often develop reproductive organs only after a drought year, then they all flower synchronously and die afterwards. In the very uniform climate just certain species are very sensitive to small deviations in the weather.

|  |
| --- |
| Box D-2 Day length in the tropics |
| The tropics differ from the temperate latitudes in that the days are constantly short, with twelve hours of daylight. |

◘ Fig. D-15 The new shoots of the mango tree in a mango plantation in the vicinity of Guayaquil, Ecuador, are conspicuous by their bright red colouring from afar (photo: Rafiqpoor).

A common phenomenon in tropical tree species is Cauliflory, i.e. the formation of inflorescences on old wood, for example on the trunk (◘ Fig. D-16). It is found in about 1,000 tropical species. It occurs in lower storey tree species and often in those that are chiropterogamous or chiropterochorous, that is, in which bats or flying foxes are the pollinators of the flowers or the dispersers of the seeds. They are particularly comfortable flying to cauliflorous flowers and fruits. Cauliflory also occurs in the carob tree (Ceratonia siliqua) and the Judas tree (Cercis griffithii), which are now widespread in the Mediterranean.

3.2 **Mosaic structure of the habitats**

A difficult question to study is the regeneration of virgin forest stands. When a giant tree falls, a large gap forms in the forest. If a large branch falls, there is a smaller gap. In these gaps, fast-growing species of the secondary forest (balsa = Ochroma lagopus and Cecropia in Central and S America, Musanga and Schizolobium in Africa, Macaranga in Malaya) often develop first. Ochroma forms annual shoots 5.5 m long with light wood, Musanga 3.8 m and Cedrela 6.7 m long. These trees are then gradually displaced again over time by the species of the upper tree layer (◘ Fig. D-17).

It has been found that among the tree species of the primeval forest there is often a lack of its own offspring, and from this it has been concluded that the primeval forest is composed in a mosaic fashion, that is to say that each tree species is replaced by another during regeneration and can only take the same place again after several generations. The cause can be very different. Often, however, it is due to herbivore or parasite pressure in close proximity to the parent tree. The seeds, seedlings or saplings are then exposed to a higher feeding pressure near the parent tree than at a greater distance; conversely, the number of seeds naturally decreases at a greater distance. It is therefore not uncommon for a maximum of the best establishment of seedlings to form at a certain distance (◘ Fig. D-18). However, other factors often also play a role; generalized, this can be characterized by the degree of disturbance.

This is explained in ◘ Fig. D-19, extrapolated also to animal communities that react differently. However, it must be emphasized that other processes also play a role beyond this. The model is therefore not valid for all tropical forests. However, the underlying dynamics of dispersal and establishment usually result in the individual species changing their place almost completely from generation to generation in a complex mosaic.

Something similar has been observed in meadows of temperate latitudes, in undisturbed primary forests of the taiga and in primeval forests in eastern Poland.

|  |
| --- |
| Box D-3 The regeneration of trees in tropical rainforests |
| In tropical forests, rotation or cyclic rejuvenation and regeneration of tree species occurs. |

◘ Fig. D-16 Cauliflory is one of the special features especially of the trees of the humid tropics. Here the flowers grow on the old stems of the trees (photos: a Ixora cauliflora, New Caledonia, Breckle; b Cola spp., Cameroon, Rafiqpoor; c: Cacao, Ivory Coast, Barthlott; d: Bignoniaceae, Madagascar, E. Fischer).

◘ Fig. D-17 The formation of a 'gap' (top) and competitive growth until the gap is closed (bottom) (after Tomlinson & Zimmermann 1976).

◘ Fig. D-18 The spatial occurrence of young growth often follows the Janzen hypothesis; it describes the interplay of disturbance (e.g. herbivory) and seed set as a function of distance from the parent tree. At intermediate distance, the best establishment is often observed, ultimately leading to a change of place of the species from generation to generation.

|  |
| --- |
| Box D-4 The mosaic structure of plant communities |
| The cyclical change of species and heterogeneous mosaic formation is a generally valid principle for all species-rich, original plant communities in a dynamic equilibrium. This explains why none of the species achieves absolute dominance in competition, but species-rich mixed stands are the rule in the long term. |

◘ Fig. D-19 High biodiversity in plant and animal communities have different maxima depending on resource availability or maximum plant growth and disturbance frequency. Subsequently, different patterns of lines of equal species density (isotaxes) emerge. Species density in plants depends on the frequency or intensity of disturbance in the stand (Janzen hypothesis 1978) or on a certain maximum growth rate and resource availability (Tilman's hypothesis 1982), summarized in the hypothesis of Huston (1980). Animals, including arthropods have their greatest species richness in disturbed habitats, especially when resource availability is high (modified from Begon et al. 1996).

For tropical forests, attempts have been made to explain the 'rotation' of species by the herbivore hypothesis of Janzen (1978). Only in the vicinity of old trees will there be a sufficient number of seeds, fruits and young plants at certain times, so that there the reproduction of herbivores, the extensive occurrence of parasites, the inhibition by mycorrhizal fungi or other factors can considerably limit the density of young growth. In the case of palms, it has been observed that the falling of leaves up to 10 m long and weighing many kilograms slays and crushes many young plants. These processes result in a reduction in the density of individuals of the seedlings and saplings, which is particularly severe in the vicinity of the old tree. Only at a certain distance from the old tree does a density maximum then form under certain circumstances. This has indeed been found on many occasions.

For somewhat species-poorer montane tropical oak forests in Costa Rica, Kapelle (1995) has carried out detailed investigations of the succession sequences. From the transects in ◘ Fig. D-20, on the one hand, the great heterogeneity of the stands with their only very indistinct stratification, the uneven upper canopy layer, but also the 'clumping' of certain species (► Fig. D-20) can be seen, which then grow up in the further course, in addition to many smaller or larger gaps in the stand ('gaps'). The number of stems per hectare (from 3 cm BHD) decreases only slightly at the beginning. The thinning process during late succession is a sign of particularly strong competition, during which some stems become dominant, out-competing the others.

◘ **Fig. D-20** Profile diagrams of three transects of tropical subalpine oak forest from the Cordillera de Talamanca (Costa Rica), comparing different aged secondary forest phases and primary forest structure (after Kapelle 1995).

3.3 **Herb layer**

About 70% of all species found in the rainforest are phanerophytes, i.e. trees. They are also absolutely dominant in terms of mass. The shrub and herb layers are difficult to separate, because herbs can grow several metres high, such as bananas, heliconias (◘ Fig. D-21), scitaminas and others. Undergrowth is often absent even in relatively good light conditions at ground level, perhaps due to competition for nitrogen or other nutrients from tree roots near the surface. Low herbs must make do with little light. They can withstand this even as houseplants under very low light (Aspidistra, Chlorophytum, Saintpaulia = Usambara Violet).

Curious is the frequent occurrence of velvety dull leaves or variegation, with white or red patches or metallic shimmer.

At high humidities, guttation plays a major role, accordingly the hydrature of the plasma is very high (cell sap concentration only 0.4 to 0.8 MPa). In the ferns with less efficient pathways, the cell sap concentration is 0.8 to 1.2 MPa. Heterotrophic flowering plants, saprophytes or parasites occur but play only an insignificant role. There are certainly many different synusia depending on light and water conditions, but corresponding investigations of the linkage of the subsystems are hardly available yet. Typical synusia of different types are the groups and life forms mentioned below.

3.4 Lianas

In the dense tropical jungle, the battle of the autotrophic plants is above all about light. The higher a tree is, the more light its leaves receive, the higher the production of organic matter can be. But to reach to the light in the tree layer, a trunk must first be formed over the course of many years, which requires a substantial investment of organic matter. The lianas and epiphytes arrive at the favorable enjoyment of light in a simpler way. The former do not form a rigid stem, but use the trees as a support for their rapidly growing flexible shoots (◘ Fig. D-22).

The epiphytes, on the other hand, relocate their germination site from the beginning to the upper branches of the trees, which serve them only as a support (◘ Fig. D-23).

The attachment of the lianas to the supporting trees takes place in various ways: In the **splay climbers** (◘ Fig. D-24), it is splaying branches that grow into the branch system, with slippage prevented by thorns or spines, for example, in the climbing palm Calamus (Rotang), Smilax, or the *Rubus* lianas. The **root climbers** (◘ Fig. D-25) form roots that adhere to the cracks in the bark or encircle the trunk (many Araceae).

◘ Fig. D-21 The various Heliconia species (a) can form the herbaceous layer of rainforests in the Amazon basin of Ecuador (photo: Rafiqpoor) and the *Musa* species(b) (photo: Breckle) in Asia together with other herbaceous plants.

The climbers (◘ Fig. D-26), also called petiole climbers, develop small corkscrew-like coiled holding organs with which they wrap around the branches of the host plant (the climbing aid). The climbing aid for the climbers must not exceed a diameter of 8 mm, otherwise the wrapping is no longer possible. The bindweed (◘ Fig. D-27) has rapidly growing, twining branch tips with very long internodes or tendrils on which the leaves initially remain undeveloped. To grow, the lianas need light. They therefore develop in the clearings of the forest and grow upwards at the same time as the trees; in the process they reach the canopy in time.

The tropical lianas, unlike those of the outer tropics, are long-lived. Their axial organs possess secondary thickness growth; but since they must remain flexible to follow the movements of the supporting trees, no compact woody body is formed, but a woody part fissured into individual strands by parenchyma tissue and broad medullary rays (anomalous thickness growth). The vessels are very large on the cross-section, therefore easily visible to the naked eye. They have no transverse walls, so that the crown of the liana can be supplied with sufficient water regardless of the small diameter of the flexible stem. When the leaves serving as support die and rot, the lianas nevertheless remain attached to the canopy of other trees, and the liana stems hang down freely like ropes. Often they slip off partially and then lie with the lower end in loops on the ground. The shoot tip, however, works its way back up. If this is repeated several times, the liana stem can reach a great length. In the case of Calamus (► Fig. D-24), a total length of 240 m was measured!

◘ Fig. D-22 Lianas in the tropical rainforest of Arroyo Blanco, Dominican Republic (photo: Breckle).

◘ Fig. D-23 Numerous bromeliads growing epiphytically on trees in a mountain rainforest on the eastern slope of the Andes of Ecuador (photo: Breckle).

Fig. D-24 Calamus lianas belong to the 'scrambling lianas'. The specimen here is growing through a stand in the rainforest of Cameroon (photo: Rafiqpoor).

Large clearcuts are particularly favourable for liana development. Lianas are therefore much more numerous in secondary forests than in pristine virgin forests, where they cover more of the forest edges. 90% of all liana species are restricted to the tropics; in Central America, 8% of all species are lianas. The fact that lianas are mainly restricted to the humid tropics is probably related to water recharge. In dry climates, strong suction stresses (deep water potentials) develop in the leaves, causing the long water filaments necessary for water conduction to break by overcoming cohesion in the wide vessels. Even in temperate climates, woody lianas are most common only in moist riparian forests. Here there are only a few woody lianas: The root-climbing ivy (Hedera helix), spreading and climbing woodland vines (Clematis vitalba) and grapevines (Vitis silvestris), and the twining Lonicera species. The blackberry species (Rubus spec.) do not rise high above the ground in Europe, whereas in New Zealand they grow as thick as an arm and reach the tops of trees.

3.5 **Epiphytes, hemi-epiphytes and** strangler

For the tropical rainforests, the epiphytic ferns and flowering plants are considered particularly characteristic. But this is true only for those forests where wetting water (mist, fog) is often available; high humidity is therefore not sufficient. There are many types with interesting adaptations (► Fig. D-23). In Liberia 153 species have been ecologically studied (Johannsson 1974).

Germination high up on the branches of the trees can take advantage of the favorable light conditions, but the more difficult is the water supply; it lacks the permanent water reservoir of the soil, from which water is absorbed. The epiphytic site can be compared to a rocky site. In fact, epiphytes can usually grow just as well on rocks if they have favorable light conditions. Water uptake in general is possible for epiphytes only during rain. Therefore, wetting frequency is more important to them than absolute rainfall. The frequency of rainfall is greater on mountain slopes, where ascending air masses cause upslope rains, than in the lowlands; for this reason montane forests are usually richer in epiphytes, especially the cloud forest, where it drips constantly from the leaves (◘ Fig. D-28).

In order to be able to survive longer intervals between rain showers, the epiphytes must either endure temporary desiccation without undergoing damage - this is the case with many epiphytic poikilohydric ferns, or they must store water in their funnels (bromeliads), or like the succulents of the dry regions; a number of cacti, for example, have switched to the epiphytic way of life (Rhipsalis, Phyllocactus, Cereus species) (◘ Fig. D-29). Like the succulents, the epiphytes release water very economically. Leaf tubers as water reservoirs are possessed by many orchids, woody tubers by some Ericaceae, succulent leaves have developed by most orchids, but also by Bromeliaceae, Peperomia, and others. Special devices for the rapid absorption of water during wetting by rain are the aerial roots of the orchids with the velamen absorbing the water, and the sucking scales of the Bromeliaceae, which take up the water from the funnels formed by the bases of the leaves, which collect the rainwater, or hold it capillary through the dense scaling of the leaves and then suck it up.

◘ Fig. D-25 Araceae as root climbers in a rainforest in Ecuador (photos: Rafiqpoor).

◘ Fig. D-26 Flagellaria from New Caledonia is a good example of the rank climbers (photo: Breckle).

◘ Fig. D-27 The bindweed wraps itself around the host tree and climbs upwards to reach the light. In central European forests, as shown here, Hedera helix can take over this task (photo: Breckle).

◘ Fig. D-28 The cloud forests (a) in the montane altitudinal zone of the tropical mountains are rich in epiphytic flowering plants (b). In these forests, although the amount of precipitation is somewhat lower compared to cloud forests, the always high humidity constantly provides the epiphytes with sufficient water (photos: Rafiqpoor, Mt. Kinabalu).

◘ Fig. D-29 Examples of some epiphyte types from the tropical cloud and fog forests: a: Guzmannia spec. (Bromeliaceae) (photos: Rafiqpoor); b: Epiphyllum phyllanthus (Cactaceae); c: Rhipsalis aff. crispata; Schlumbergera orsichiana (Cactaceae), d: Rhipsalis pilocarpa (Cactaceae) (photos: Barthlott).

The roots are in the epiphytic Bromeliaceae only adhesive organs (◘ Fig. D-30) and are completely absent in Tillandsia usneoides, which is reminiscent of bearded lichens, as well as other Tillandsias etc.,. Special hollow organs, partly inhabited by ants, are formed by Myrmecodia, Hydnophytum, and Dischidia species. Ferns that cannot tolerate desiccation can form their own soil by accumulating falling litter and detritus between the funnel-shaped leaves (Asplenium nidus) or with the help of overlapping special niche leaves (Platycerium) (◘ Fig. D-31). A humus-rich, water-containing soil is thus formed into which the roots grow. But this can also be observed in many other species.

◘ Fig. D-30 a: Usnea barbata (yellowish) together with a bromeliad species on a tree in the cloud forests of the lower Charazani Valley (Bolivia) (photo: Rafiqpoor); b: Another tree is completely overgrown with Tillandsia usneoides (photo: Breckle).

◘ Fig. D-31 Dead organic material has accumulated in the funnel of Asplenium nidus on a tree trunk in the rainforest of Ecuador. This provides the epiphytic plant with the necessary nutrients and also retains rainwater (photo: Rafiqpoor).

◘ Fig. D-32 Different techniques for recording epiphytes in the canopies of tropical rainforests. a and b in Gabon (photos: Szarzynski); c in Mt. Kinabalu Malaysia (photo: Rafiqpoor) and d in Venezuela (photo: Barthlott).

In a forest densely populated by epiphytes, the epiphytic humus can amount to several tons per hectare. In this way, a new biotope is created high above the ground, which can even be considered as an almost closed ecosystem. It is only now that attempts are being made to supplement the previous rather destructive (helicopters, balloon nets, etc.) or inadequate methods ('canopy walk ways', climbing techniques, etc.) in the exploration of this ecosystem by using new techniques (◘ Fig. D-32).

Nitrogen and nutrients are supplied to the canopy by dripping water and dust. Ants can settle and build their nests. They drag in seeds that germinate and grow into flowering plants. Such 'flower gardens’ or ‘ant gardens' (◘ Fig. D-33) are described from South America. They also harbour a special fauna and microflora; mosquito larvae, aquatic insects and protists live in the funnels of the Bromeliaceae, which often reach considerable dimensions (phytotelmae). In addition, there is an enormous diversity of insect species.

◘ Fig. D-33 On the rainforest trees in the Amazon lowlands of Ecuador, ant gardens represent small ecosystems (photo: Rafiqpoor).

It should be mentioned that the insectivore Nepenthes (pitcher plant) (◘ Fig. D-34) can also grow epiphytically, as can various Utricularia species. Epiphytes are dispersed by spores (ferns), by dusty seeds (orchids) or by diaspores with membranous appendages for wind dispersal, or by berry fruits (Cacteae, Bromeliaceae) that are eaten by birds, so that the seeds with the excrement easily reach tree branches far away. Many epiphytes can survive a prolonged dry period, for example orchids, some moving in completely, or densely scaled tillandsias, poikilohydric ferns and others. They also occur in dry tropical forests. Coutinho (1982) found diurnal acid metabolism (CAM) in some epiphytes in Brazil, that is, the uptake of CO2 at night when the stomata are open and the binding as organic acid (usually malate). The latter is then degraded during the day and assimilated immediately with the stomata closed. This is a process by which water loss by transpiration during the day is avoided, and is frequently found in succulents of arid regions. Medina already examined the Bromeliaceae in this respect in 1974.

Mosses and Hymenophyllaceae (skin ferns) require permanent wetness and are therefore the typical epiphytes of the páramo, as are the epiphyllous species.

Hemi-epiphytes occupy an intermediate position between lianas and epiphytes. Many Araceae germinate on the ground and then grow upwards as lianas (► Fig. D-25), usually as root climbers. In time, the lower part of the stem dies, and they are then epiphytes, but they can remain connected to the soil by aerial roots.

More interesting are the strangler trees, of which the many strangler figs (Ficus species) are the best known. However, there are such strangler trees in many different families, for example the Clusia species (Guttiferae) in South America, Metrosideros (Myrtaceae) in New Zealand, Hawaii and others more. These species germinate as epiphytes in a branch fork and initially form only a small shoot, but a long root that grows rapidly down the trunk of the supporting tree, entwining it in a net-like manner.

Fig. D-34 The Nepenthes species on Mount Kinabalu (a, photo: Rafiqpoor) live both terrestrially and epiphytically in the rainforests at different altitudes. An endemic Nepenthes species (b:) Nepenthes viellardii, (photo: Breckle) also occurs in New Caledonia, partly growing on extreme sites such as heavy metal soils.

◘ Fig. D-35 a: Area consisting of a single fig tree that looks like a forest (photo: Barthlott). b: Schematic representation (after Barthlott's lecture "Vegetation of the Earth") of the development of a strangler tree (red) from the initial phase to the extinction of the host tree (green) and its complete replacement by the epiphyte (full red), which then continues its life in place of the host tree.

Only when the root has reached the ground does the shoot grow up; at the same time the roots thicken more and more, forms interconnections (anastomoses) and prevent the secondary growth of thickness of the bearing tree, that is, the tree is strangled; it then dies and its wood decays. The strangler's root network closes to form a true trunk that supports a broad crown (◘ Fig. D-35b). Such tree like structures can reach huge dimensions, and it is not obvious that they began their existence as epiphytes. The developmental strategy of the strangler from germination to complete strangulation of the host tree is shown in a diagram (► Fig. D-35b). Palms without secondary thickening growth are not strangled and remain alive longer until eventually the strangler crown shades their leaves too much. In temperate latitudes, only ivy (Hedera) is known to strangle (► Fig. D-27).

3.6 **Epiphyllic plants**

Epiphyllic plants grow on the surface of leaves of other plants. These are microscopic algae (Cyanophyceae and other bacteria; Azotobacter, which can bind N, green algae), yeasts and fungi, lichens and mosses, (especially liverworts, but also other mosses), then Selaginella, even small seed plants growing on leaves occur (◘ Fig. D-36).

Epiphylls occur mainly in the particularly humid tropical rainforest. The illumination, the wettability of the leaves and their longevity are fundamental for the colonization of the leaves by epiphylls. The leaves suffer additional light loss as a result. However, some epiphylls even may grow into the leaf tissue.

◘ Fig. D-36 a: Coating of epiphylls on a large leaf of Cyclanthus, composed of various blue-green algae, green algae, mosses and lichens, Hymenophyllaceae, Selaginella and even a B*egonia*; in primary forest (Reserva Biol. San Ramón, Costa Rica) (photo: Breckle); b: Part of a leaf with the epiphyllous liverwort Aphanolejeunea in Gisakura, Nyungwe National Park, Rwanda (photo: E. Fischer).

3.7 **Biodiversity**

Central European forests usually have only five to ten tree species, of which one or two are dominant, i.e. they account for more than 90% of the stems. Corresponding temperate forests in North America or East Asia are not quite so species-poor, but there are still only 15 to 40 tree species per hectare. In the tropics, the number of species is incomparably greater. On the island of Barro Colorado in Panama, about 1,400 higher plants occur in a 15 km2 research reserve, including 365 tree species. In the mountain rainforest in the Biological Reserve north of San Ramón in Costa Rica, there are 94 tree species per hectare alone (breath height diameter, DBH 10 cm and larger), belonging to very different families (Wattenberg & Breckle 1995), and in Ecuador's Yasuni National Park about 300 tree species with >10 cm BHD per ha (Valencia & Balslev 1994), these are still the 'diversity records' today. Over a third of these species are represented by only a single stem, meaning that the minimum area for recording the species assemblage is thus much higher than 1 ha (◘ Fig. D-37); it cannot be determined. Also from other places, for example in Peru (Yanamono area), almost 300 tree species have been described from one hectare. There, 63% of the species are represented by only one stem per hectare. However, the species assemblage of larger areas is still hardly known, as it requires years of effort to identify all species.

The tendency for the number of species per area to increase towards the equator applies not only to higher plants or trees, but also to reptiles, amphibians and birds, insects, etc. (exceptions: salamanders and aphids). For birds, MacArthur (1972) has shown the great difference in species numbers on a map of North and Central America (◘ Fig. D-38). Thus, tiny Costa Rica has more breeding land-bird species than the USA and Canada combined, although the land mass is only a small fraction (◘ Fig. D-39).

The greater structural diversity of tropical rainforests, the closer interconnectedness and tighter network with many more different food sources, the year-round activity of the organisms, their closer intermingling, narrower niches and specialization and the huge variety of mutual interdependencies (symbioses) that are possible as a result is one possible explanation for the higher diversity.

An important fact is the close functional interconnectedness of very many organisms. The temporal restriction of the flowering times of Heliconia species throughout the year can be taken as a relatively simple example (◘ Fig. D-40). Thus, for the various hummingbird species (◘ Fig. D-41), a food source is almost always available. However, this close web of relationships between several heliconias and several hummingbirds requires sufficiently large areas. If these are isolated too much, then at one point the network of relationships breaks down with far-reaching consequences for the other hummingbirds and in turn for other *Heliconia*.

|  |
| --- |
| Box D-5 Diversity of tropical rainforests |
| In the tropics, up to c.300 different tree species with a BHD of ≥10 cm per hectare occur; in the whole of Europe, north of the Alps to the Urals, a total of barely 50 tree species are native. |

Fig. D-37 Increasing species number of tree species (≥10 cm DBH) with study area in montane rainforest in the Sierra de Tilaran (Costa Rica). There is no minimum area. When the area is increased from 1 to 2 ha, 30 new tree species are added: dashed red line, and for the tropical rainforest in Central Africa (brown area), SE Asia (green area) and S America (blue area) (modified after Wattenberg & Breckle 1995, partly after Terborgh 1991).

During **glacial** periods, rainforest areas were sometimes drier than today, deserts wetter: pluvial periods. In earlier epochs, the extent of the **Amazonian** rainforests was probably severely restricted and probably fragmented into retreat areas. The present-day rainfall distribution is given by the map in ◘ Fig. D-42. It must be assumed that areas that now receive more than 3,000 mm of annual precipitation also received sufficient rainfall (more than 2,000 mm) to maintain closed tropical forests about 15,000 years ago.

These areas coincide quite well with certain retreat areas where both bird life, butterfly fauna, lizards, but also flowering plants are particularly rich in endemic species (◘ Fig. D-43). From this evidence, it can be concluded that the rainforests alternately shrank and expanded again, and that the foci of species richness and endemism correspond to sites that were permanently covered by rainforest. In between, large areas were probably covered with drier, seasonal rainforest. However, these changes occurred very slowly, whereas today's anthropogenic destruction is occurring at such a rapid speed, that organisms cannot adapt.

◘ Fig. D-38 The number of breeding bird species in northern America in grid areas of 0.31 million km2. Despite the tiny area, more landbird species breed in Costa Rica than in the USA and Canada combined, cf. with ►Fig. D-39 below (after Terborgh 1991, from MacArthur 1972).

◘ Fig. D-39 The north-south gradient of landbird species in northern America (dot symbol) and, in comparison, the land area along latitudes to the equator (modified after Reichholf 1990).

In the African forests, for example in Upper Guinea, Cameroon/Gabon and in Eastern Zaire, endemism-rich retreats have also been identified. Only there have forests rich in tree species become known, in which up to 140 tree species per hectare occur, while in all other regions in Africa the number is always below 100, in Nigeria for example, only 23.

The vegetation history of the Malayan rainforests is somewhat different. There, during the Pleistocene, a large part of the shelf sea was covered with rainforest. Presumably, the perhumid rainforests above sea level today have been preserved, which would explain their extreme species richness (with up to 180 tree species per ha) and the lack of geographic-geological evidence of earlier seasonal climates. Mt. Kinabalu in North Borneo has as many fern species as the entire African continent.

|  |
| --- |
| Box D-6 The functional networks and diversity of life forms |
| The preservation of the functional network with the immense diversity of tropical life forms requires much larger protected areas than in temperate latitudes. |

◘ Fig. D-40 The flowering times of heliconias in the rainforest in Costa Rica are distributed throughout the year and are similar in the individual years. They ensure a constant supply of nectar to the hummingbirds (modified after Terborgh 1991).

◘ Fig. D-41 Hummingbird moving its wings so fast that it appears to hover almost still in front of the nectar plant (photo: Barthlott).

◘ Fig. D-42 The present-day distribution of annual precipitation in tropical South America. Areas with more than 3000 mm per year probably also received sufficient rainfall 15,000 years ago (at least more than 2000 mm) so that closed rainforests survived there (modified after Simpson & Haffer 1978).

◘ Fig. D-43 The distribution of former rainforest refugia (c. 10,000 years ago) and present-day endemism in butterflies and birds (modified after Brown & Ab′Saber 1978).

4 **Different types of vegetation in zonobiome I around the equator**

For zonobiome I, climate diagrams with a perhumid diurnal climate are typical (► Fig. D-3), which has two equinoxial rainfall maxima coinciding with the zenith position of the sun around noon. However, such a climate is not present everywhere in the equatorial zone. Areas with humid monsoon winds (Guinea, India, Southeast Asia) show only a particularly pronounced rainfall maximum in summer, but a short dry season or even drought is noticeable (tendency to ZB II). The vegetation still consists of rainforests, but leaf fall and flowering are clearly bound to a certain season. One speaks of seasonal rainforests. On the Gold Coast (around Ghana), which is not hit by the monsoon, it still exist two rainfall maxima with droughts in between, similar to East Africa, where the monsoon winds are dry and the rain falls in the time of the wind change, distinguishing a major and a minor rainy season. In Somalia, the rainfall decreases so much that in some cases no humid season can be seen on the climatic diagram and the vegetation becomes desert-like: It is a zonoecotone I/rIII.

The trade winds also change the character of the climate, especially on the eastern sides of the continents. The SE-trade wind is humid and produces a rainforest climate in southeastern Brazil, eastern Madagascar, and northeastern Australia from the equator to beyond 20° S, with only one rainfall maximum. In contrast, the NE-trade wind in the south of the Caribbean Sea brings rain only to the mountains during wind jams at obstacles like mountains. As a result, Venezuela, with its many mountain ridges, has very diverse climates and vegetation (◘ Fig. D-44). The situation is similar in mountainous Costa Rica.

Venezuela is located between the equator and 12° N. All altitudes are present from sea level to the glaciated Pico Bolivar (5,007 m). The northern half of the country is under the influence of the strong trade winds from November to March; it rains in the lowlands only during the windless seven summer months, with rising air masses and frequent thunderstorms. Only in the south of the country, in the Amazon basin, does no month have less than 200 mm of rain. Annual rainfall varies from 150 mm on the island of La Orchila to over 3,500 mm in the south. In the mountains, on the windward side, rainfall increases rapidly up to the condensation level and decreases again above it. At the same time, temperatures decrease on average by 0.57 K per 100 m increase in altitude. The interior valleys, which lie in the rain shadow, are very dry (◘ Fig. D-45). The change in vegetation from north to south with increasing rainfall amounts as well as the elevational beltbelts are shown schematically in ◘ Fig. D-46.

In the driest parts, a semi-desert with cacti dominates (◘ Fig. D-47). The succulents store so much water that they easily survive a dry period of half a year or longer. If the rainfall increases slightly, thornbushes and ground bromeliads take hold. Impenetrable thickets develop, which correspond to the Caatinga in the dry area of NE-Brazil or the dry formations of the dry valleys of Ecuador. If the rainfall reaches 500 mm per year, the briars with umbrella crowns (Prosopis, Acacia) predominate. They are joined by Bursera, Guaiacum, Capparis and Croton species, as well as Agave, Fourcroya and others.

Peireskia guamacho (◘ Fig. D-48), the tree-shaped Cactaceae, which still has true leaves and is probably close to the ancestral form of the cacti, also occurs in the Caatinga. During the dry season these woody plants are leafless. The cactaceous semi-desert and the thorn bush are only used as goat pasture.

◘ Fig. D-44 Climate diagrams along a north-south profile through Venezuela (after Walter & Medina 1971). 1 offshore island, 2 coastal station, 3 typical trade wind climate (rainy season 7 months), 4 ever humid climate in the Amazon basin.

◘ Fig. D-45 North-south sequence of vegetation formations in Venezuela, arranged climatically according to climatic diagrams in ► Fig. D-44. a: Sand desert vegetation on the north coast of Venezuela with Melochia, Suriana, Jatropha, Sporobolus and many other species, among others; b: Semi-desert north of Mérida with columnar cacti and numerous tillandsias; c: Wet savannah with numerous palms in the Sierra d'Avila near Caracas; d: Tropical rainforest in Rancho Grande with epiphytes, lianas, stilt-root palms, Araceae, Melastomataceae and very many other species (photos: Breckle).

◘ Fig. D-46 Schematic representation of the vegetation zones in Venezuela from north to south, showing the annual precipitation in mm and the altitude levels as well as the mean annual temperature in °C (left).

◘ Fig. D-47 Cactus thornbush semi-desert with *Cereus* species on the wind-exposed slope of the coastal cordillera of Venezuela (photo: Breckle).

◘ Fig. D-48 Peireskia guamacho (Cactaceae) has the shape of a deciduous tree (a) with splendid flowers (b); its trunk, however, resembles cacti (photos: Barthlott).

If the rainfall increases further, the number of different tree species increases and true deciduous forests begin, which are very rich in species. The tree layer becomes 10 to 20 m high, only the Bombacaceae (Ceíba) and Malvaceae (◘ Fig. D-49), with thick trunks serving as water reservoirs, and the beautifully flowering Erythrina or Tabebuia species (◘ Fig. D-50) rise above this. During the dry season, such a forest looks much like a deciduous forest in winter in temperate latitudes. However, some tree species already begin to flower during this season. A distinction is made between, among others, dry tropical deciduous forests and moist ones with a precipitation level of up to 2,000 mm. The latter reach a height of over 25 m and contain forestry valuable woods, such as Swietenia (mahogany), Cedrela and many other species.

◘ Fig. D-49 a: Adansonia fony (Malvaceae), SW-Madagascar, b: Cavanillesia arborea (Malvaceae) in Bahia State, Brazil, are two examples of trees that store water in their bottle-like trunks (photos: Barthlott).

◘ Fig. D-50 Tabebuia a yellow-flowered species from the seasonal tropical forests of Ecuador, flowering in the dry season when the tree is still leafless (photo: Breckle).

The deciduous forests are sometimes cleared for the plantation of coffee crops under shade trees. Sugar cane, maize, pineapple and many other crops can also be grown here. Cattle pastures can be established after sowing Panicum maximum. The forests are poor in lianas, but epiphytes (drought-resistant ferns, cacti, Bromeliaceae and orchids) are common.

In even rainier areas with an even shorter dry season, the semi-evergreen forest occurs, in which only the lower shrub and tree layer consists of evergreen species. Finally, with even more rain, the tropical evergreen rainforest commences (Vareschi 1980).

A peculiarity of Venezuela is that in the area of the llanos of the Orinoco basin, which extend far into Colombia, instead of the deciduous forests suddenly appears a grassland with interspersed small forest stands or individual small trees. It is savannah or pure grassland. Climatically it is an area of deciduous forests. The grass that is now pasture is burned regularly, but here fire cannot be the primary cause of the absence of forests, rather it is the soil. We shall return to the special soil conditions in this area. Not due to the climatic, but also due to the edaphic (pedobiome) conditions or due to the relief it exist also still the following vegetation formations in Venezuela: the mangroves, on the sea coast and in the estuaries, the beach and dune vegetation, the freshwater swamps and the aquatic plant communities as well as the floodplain forests and the vegetation of dry shallow rocky soils.

Deciduous forests are an extrazonal occurrence in Venezuela, due to the dry trade winds, and are discussed in more detail in the context of ZB II.

The orobiomes must also be treated separately, since the elevationalbelts of the orobiome have certain peculiarities. Very diverse is also the equatorial mountainous East Africa.

5 **Orobiome I - tropical mountains with diurnal climate**

5.1 **Forest belt**

In many tropical areas, mountains or volcanoes rise from the lowland rainforests (◘ Fig. D-51).

The tropical orobiomes are the particular habitats where the main mass of the population lives, especially in the Latin American Andean countries (Mexico, Venezuela, Colombia, Ecuador, Peru, Bolivia), finding a favorable livelihood due to the diversity of habitats along the elevational belts. The climates of the tropical orobiomes (high mountains) are characterized by an altitudinal gradient of temperature and precipitation. They are associated with an altitudinal gradient of vegetation. The thermal altitude gradient is 0.5-0.7K/100 m. The gradient of heat with elevation is not only of climatological but also of vegetation-geographical and economic relevance, because it results in a vertical division of the zones of life both for plants and animals and for man and his economic activity. Since temperatures start from a high level at sea level (27 °C on average), the vertical extent of the habitat in the orobiomes of the tropical zonobiomes is very extensive. The mean altitudes between 1,000-3,000 m also correspond to the most favourable temperature interval between 24-12 °C for the human organism.

◘ Fig. D-51 The extinct volcano Mt. Kinabalu in Saba (a) and the Antisana (Eastern Cordillera Ecuador, b) are two good examples of mountains (orobiomes) rising from the rainforests of the tropical lowlands. On these mountains, all elevational belts of climate and vegetation are formed according to physical specifications (photos: Rafiqpoor).

It is therefore not surprising that in Latin America some of the mega-cities (Mexico City, Mérida, Bogotá, Quito, La Paz) have developed in the mountains. Beyond the forest and tree line, i.e. in the subnival elevation range between 4,000 and 5,000 m, there is hardly any snow cover that lasts more than a day. Here, frosts are also tied to the rhythm of the diurnal periods (nocturnal cooling, daily warming).

The thermo-isopleth diagram of Quito shows (◘ Fig. D-52) that the elevational areas within the tropics must be classified climatologically as tropical, since the isotherm of the seasons persists up to the summits of the high mountains. The annual variation in temperature is only 0.4 K at the inner tropical station of Quito at 2,850 m altitude. Towards the tropics, this fluctuation increases successively, and the annual fluctuation also gradually becomes noticeable (Mexico City: daily fluctuation = 16 K, annual fluctuation = 13.5 K). Lauer (1995) has illustrated the structure of the tropical orobiomes in a diagram for South America (◘ Fig. D-53).

Precipitation also has a characteristic vertical distribution in tropical orobiomes, where a continuous thermal decrease with elevation is contrasted by a mostly discontinuous gradient of precipitation. Although the absolute water vapour content of the air decreases exponentially with altitude during convective processes, the multiple attainment of levels of complete water vapour saturation (100% relative humidity) also leads to the formation of multiple condensation levels with corresponding precipitation events at different elevational belts of the tropical mountains (Lauer 1975).

◘ Fig. D-52 The thermoisopleth diagram of Quito (modified after Troll 1943).

◘ Fig. D-53 Three-dimensional arrangement of the tropics according to climatic criteria (modified after Lauer 1995).

◘ Figure D-54 shows a synthetic picture of the elevational belts of climate and vegetation on the eastern slope of the Eastern Cordillera of Ecuador, with a level of maximum precipitation at about 1,500 m NN (◘ Fig. D-55) and a second, but somewhat weak, level of condensation in the area of fog forests at 3,200-3,800 m NN. In the cloud forest area at about 1,500 m, epiphytic plants reach their maximum abundance and diversity (◘ Fig. D-56). In the tierra fría, where the second condensation level as the so-called ceja de la montaña (eyebrow of the forest, ► Fig. D 27) allows the formation of fog forests, the branches and twigs of the trees are covered with epiphytic mosses and lichens (◘ Fig. D-57). The forest here appears more humid than in the cloud forest further down, because here fine droplets of water float in the water-vapour-saturated fog atmosphere and only precipitate when they come into contact with objects. The plants comb the moisture out of the water-saturated fog (► Fig. D-55). Passing through the dripping wet fog, clothes become wet without rain. Above the timberline, the equatorial orobiome contains **páramo**, an exceedingly exotic-looking vegetation formation of grasses (Poaceae), espeletias (Asteraceae) (◘ Fig. D-58), bromeliads (Puya), etc. In the nival belt, glaciers occur, but with short tongues, as the year-round constant frost line is quickly reached here (◘ Fig. D-59).

The mountains thus often have very different altitudes. If the trade wind meets a mountain ridge at right angles to the direction of the wind, the cooling of the air masses forced to rise causes condensation, i.e. cloud formation and upslope rain. As the strength of the trade wind diminishes in the late evening, the nights and early mornings are clear; during the rest of the time the cloud cover is at a certain height, so that this altitudinal beltbelt is shrouded in fog during the day. In addition to the rising rains, condensation of the fog droplets on the branches of the trees and the lack of transpiration are present here because the atmosphere is saturated with water vapor (► Fig. D-57).

The extremely humid and, due to the altitude, also cooler climate causes the development of the hygrophilous, tropical Páramo, which is characteristic of all tropical mountains exposed to the winds. The succession of altitudes is determined by the increasing precipitation level, while the decreasing temperature only becomes clearly noticeable above 2,000 m NN.

◘ Fig. D-54 Scheme of the three-dimensional arrangement of the elevational beltbelts of climate and vegetation on the humid eastern slope of the Eastern Cordillera of Ecuador (modified after Lauer 1995).

◘ Fig. D-55 Formation of the first condensation level at about 1,500 m NN in the altitudinal belt of tropical mountain rainforests on the western slope of the Western Cordillera of Ecuador above Machala (photo: Rafiqpoor).

◘ Fig. D-56 Abundance and frequency of epiphytic flowering plants are highest in cloud forests in the area of the first condensation level (►Fig. D-55). The picture shows an epiphyte survey in Gabon (photo: Barthlott).

◘ Fig. D-57 In the tropical fog forests, the branches and twigs of the trees are covered with mosses and lichens. Fine water droplets float in the air and are combed out by the plants when touched (Mount Kinabalu, Saba, Borneo) (photo: Rafiqpoor).

◘ Fig. D-58 Exotic crested-leaf plants (*Espeletia*) grow in a sea of grass in the altitudinal zone of the Páramo in the Andes (here Páramo del Angel in Ecuador) (photo: Rafiqpoor).

◘ Fig. D-59 Glaciers exist in the nival altitudinal zone of the humid tropics, but they form only short tongues, as here on Cotopaxi volcano (5,600 m NN) in Ecuador (photo: Breckle).

In N Venezuela, the following altitudinal sequence occurs:

|  |
| --- |
| Firn surfaces (glaciers)*-------------------Climatic snow line--------------------* Cold desertAndine (alpine) level (Páramos) *------------------------------Potential timber line----------------------------* High montane forests with many *Podocarpus*Cloud forestsSemi evergreen forestsDeciduous forestsThornbushCactus semi-desert |

The cool cloud forest, which is always dripping wet, differs from the hot tropical rain forest in the large number of tree ferns and epiphytic mosses that hang down from all the branches, as well as in the Hymenophyllaceae (filmy ferns) that cover all the branches and trunks. In the high montane forest, which is often above the cloud cover and not so humid, the epiphytic lichens are more predominant.

Due to the upslope rains, precipitation on the mountain slopes, as far as they are not in the lee, increases with altitude. Any dry season that may occur in the lowlands becomes shorter or disappears with altitude. The montane forests are therefore particularly luxuriant and rich in epiphytes, which are frequently wetted. As the slopes in the tropics are usually very steep, the soils are well drained, and the marshiness of the lowlands is absent. The decrease in temperature is at first scarcely noticeable. Eventually the cloud level is reached to which the Páramos are attached with maximum moisture. The more humid the air at the foot of the mountains, the lower is the cloud cover; in a climate with rainy season and dry season, the position of the clouds is higher in the dry season. Cloud forests may occur between 1,000 and 2,500 m and even higher and may have different temperature conditions, which causes floristic differences. The height of the tree layer also decreases upwards in the mountains.

More upwards in the fog forests only wind-formed, low trees occur. With increasing altitude, the number of heat-loving epiphytic flowering plants also decreases, but that of ferns, lycopodia and above all Hymenophyllaceae and mosses increases. The ground is often covered with a bright green carpet of Selaginella species. In many tropical mountains, the wettest elevational beltbelt is characterized by palms (S-America) or dense stands of bamboo (E-Africa). Soils change with altitude: The red loams of the lower belt change to more yellowish or brown ones; at the same time a gauze horizon forms and the clay content decreases. Still higher, a slight podsolization becomes noticeable and finally true podsols with raw humus and bleaching horizon develop (◘ Fig. D-60); in the perhumid cloud level, gley soils can be found.

◘ Fig. D-60 Mountain podsol under a dense grass layer of Calamagrostis effusa (Poaceae) over Cangahua in the Páramo de Papallacta, Eastern Cordillera Ecuador (photo: Rafiqpoor).

5.2 **Forest line**

Above the cloud level (mostly above 2,500 to 3,000 m) precipitation decreases rapidly. If the forest extends even higher up the slope, the foliage of the trees becomes smaller and more xeromorphic. In Venezuela, conifers occur, namely Podocarpus species, which have no needles but hard, narrow, leaf-like structures. The mosses are replaced by bearded lichens (Usnea barbata, Parmeliaceae). Finally, the forest line is reached, which changes into a scrub zone and is lower in the tropics than in the subtropics. From the Andes of Venezuela, an altitude of 3,100 to 3,250 m a.s.l. is recorded, from Costa Rica 3,200 to 3,300 m (◘ Fig. D-61); in Venezuela, shrublands sheltered by rocks are still found at 3,600 m a.s.l.; in N Ecuador, the forest boundary is about 4,100 m (Lauer et al. 2001), in S Ecuador it is slightly lower (about 3500 m).

◘ Fig. D-61 Oak forest at 2,500 m a.s.l. north of Cerro de la Muerte (Central Costa Rica) with small *Puya* bogsin the middle. Oaks dominate, with some other tree species also admixed. However, the forest line is about 800 m higher (photo: Breckle).

The shrub zone is narrow, but the shrubs also become lower further up (◘ Fig. D-62); in Costa Rica, Escallonia, Weinmannia, Myrrhodendron (shrubby Apiaceae), etc., are then replaced by bamboo (Chusquea species) as a sign of anthropogenic encroachment.

Fig. D-62 The elevationalbelt of the scrub Páramo in Ecuador lies between 3,700-4,100 m and is composed of various species of the genera Bacharis, Loricarya, Chuquiraga, Ribes etc.. They are accompanied by horst grasses (Calamagrostis effusa, Festuca subulifolia, etc.) (photo: Rafiqpoor).

From the central Cordillera in Costa Rica (Sierra de Talamanca), which rises to almost 3,800 m (at Chirripó), very detailed studies of montane forests are available from Kapelle (1995). In most cases, oak species (◘ Fig. D-63) and bamboo (Chusquea) dominate, so that characterization according to dominant species is possible. Species diversity decreases with increasing elevation; for the woody species, this also results in a considerable change in importance, with the Rubiaceae, for example, decreasing from 2,000 m with 31 species to two species at 3,200 m (◘ Table D-1).

The question of which factors are decisive for the tree line in the tropics is difficult to answer. The precipitation decreasing again from a certain height upwards made it seem possible that it is a drought limit. On the other hand, it could also be a frost line, because frosts can already occur at this altitude. However, studies in Venezuela (Walter & Medina 1969) and Ecuador (Lauer et al. 2001, Bendix & Rafiqpoor 2006), as well as worldwide, (Körner 2012) make it likely that the soil temperature is of decisive importance, although a wide variety of factors always interact in such phenomena. The diurnal climate in the equatorial zone means that temperature fluctuations penetrate very little deep into the soil. When the soil is shaded, the temperature at a depth of about 30 cm is constant throughout the year (Walter & Medina 1969, Körner 2007) and equal to the mean annual air temperature calculated by meteorologists on the basis of their measurements. With a few pricks of the spade and a thermometer, it is thus possible to determine the annual temperature at any point in the tropics in a few minutes (Lauer 1982, Lauer et al. 2001).

In dense forests, the temperature is already also constant just below the surface. It is decisive for the root system. Körner (2007) mentions about 6.5 °C as an almost world-wide value for the temperature limit at tree lines. Although we do not know the temperature minima for the root growth of tropical trees, it is known that the enzymes that are decisive for the metabolic processes taking place in roots have a temperature minimum in tropical species that is far above 0 °C; tropical species can therefore already 'catch cold' at temperatures above freezing point and slowly die. Ceíba seedlings only grow at temperatures above 15 °C. If we assume that at the roots of trees at the tree line the temperature minimum is 6 to 8 °C, this would just correspond to the soil temperature in Venezuela at the tree line. The latter is formed by typical tropical species, holarctic species being completely absent. If our assumption is correct, this would also explain the higher position of the tree line in the subtropics. There an annual variation of temperature already occurs, so that during the summer season the soil warms up considerably above the annual temperature, and the tree species can take advantage of this favourable season, which is lacking in the diurnal climate.

◘ Fig. D-63 Schematic mountain profile of the upper belts with montane-subalpine tropical oak forest in the area of Chirripó National Park (Costa Rica) on both mountain flanks (modified after Kapelle 1995).

◘ Table D-1 The plant families with woody species, arranged according to their number of species (indicated in parentheses), from five different elevations of montane oak forests of the Sierra de Talamanca in Costa Rica (after Kappelle 1995).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 2000 m | 2300 m | 2600 m | 2900 m | 3200 m |
| Rubiaceae (31) | Lauraceae (20) | Ericaceae (14) | Ericaceae (9) | Asteraceae (11) |
| Lauraceae (27) | Melastomataceae (14) | Melastomataceae (11) | Rosaceae (9) | Ericaceae (9) |
| Melastomataceae (27) | Asteraceae (12) | Myrsinaceae (11) | Poaceae (8) | Rosaceae (6) |
| Asteraceae (15) | Myrsinaceae (12) | Loranthaceae(9) | Asteraceae (6) | Clusiaceae (5) |
| Myrsinaceae (14) | Araliaceae (11) | Poaceae (9) | Clusiaceae (6) | Poaceae (5) |
| Araliaceae (11) | Ericaceae (11) | Araliaceae (8) | Cunoniaceae (6) | Cunoniaceae (3) |
| Solanaceae (11) | Rubiaceae (10) | Asteraceae (8) | Loranthaceae (6) | Scrophulariaceae (3) |
| Ericaceae (10) | Solanaceae (10) | Lauraceae (8) | Araliaceae (5) | Clethraceae (2) |
| Euphorbiaceae (9) | Rosaceae (9) | Rosaceae (8) | Lauraceae (5) | Lauraceae (2) |
| Piperaceae (9) | Fagaceae (6) | Solanaceae (8) | Myrsinaceae (5) | Loranthaceae (2) |
| Rosaceae (9) | Poaceae (5) | Cunoniaceae (7) | Solanaceae (5) | Melastomataceae (2) |
| Loranthaceae (7) | Celastraceae (5) | Rubiaceae (7) | Caprifoliaceae (4) | Rubiaceae (2) |
| Myrtaceae (7) | Cunoniaceae (5) | Aquifoliaceae (4) | Aquifoliaceae (3) |  |
| Poaceae (7) | Loranthaceae (5) | Caprifoliaceae (4) | Fagaceae (3) |  |
| Clusiaceae (6) | Aquifoliaceae (4) | Chloranthaceae (4) | Melastomataceae (3) |  |
| Moraceae (6) | Acanthaceae (3) | Fagaceae (4) | Rubiaceae (3) |  |
| Celastraceae (5) | Caprifoliaceae(3) | Myrtaceae (4) | Clethraceae (2) |  |
| Cyatheaceae (5) | Chloranthaceae (3) | Celastraceae(3) | Myrtaceae (2) |  |
| Fagaceae (5) | Clusiaceae (3) | Clethraceae (3) | Polygalaceae (2) |  |
| Smilacaceae (5) | Cyathaeceae (3) | Clusiaceae (3) | Rhamnaceae (2) |  |
| Urticaceae (5) | Myrtaceae (3) | Loganiaceae (3) | Rutaceae (2) |  |
| Cunoniaceae (4) | Onagraceae (3) | Rutaceae (3) | Scrophulariaceae (2) |  |
| Flacourtiaceae (4) | Rhamnaceae (3) | Symplocaceae(3) | Symplocaceae (2) |  |
| Mimosaceae (4) | Rutaceae (3) |  |  |  |
| Theaceae (4) | Theaceae (3) |  |  |  |
| 14 families (3) | 11 families (2) | 14 families (2) |  |  |
| 17 families (2) | 35 families (1) | 23 families (1) | 25 families (1) | 22 families (1) |
| 26 families (1) |
| 82 families | 71 families | 60 families | 48 families | 34 families |
| 349 Species | 226 Species | 197 Species | 125 Species | 74 Species |

5.3 **Andine (alpine) belt**

The Andean elevational zone of the humid tropics is called the **Páramo.** It is almost permanently humid and foggy, inhospitable and cold. In the inner tropics of Ecuador, the elevational belt of the páramo follows above the upper timberline in about 3,500-3,700 m. Year-round low temperatures with high interdiurnal variability, night frosts, constant cloud cover, frequent fog, occasional short snowfalls and reduced evapotranspiration are the climatic-ecological characteristics of the páramo. On the frequent foggy days, the temperature level does not increase significantly. This results in a balanced day/night difference of air and soil temperature mostly excluding night frost up to about 4,200 m a.s.l.. On such days there is practically no evaporation. During a 14-day period of bad weather from 12-25 November 1988, only 1.8 mm of evaporation was recorded in the Páramo de Papallacta (Ecuador) at 4,200 m using a Piche tube (◘ Table D-2).

The altitudinal distribution of the Páramo de Papallacta (Eastern Cordillera of Ecuador) is shown in ◘ Table D-3. The páramo spreads in the humid Eastern Cordillera of Ecuador above the present forest line from 3,700 m following the Ceja forest, consisting mainly of Tournefortia, Miconia, Senecio, Vallea, Podocarpus, ferns, and numerous epiphytic mosses and lichens. The grass páramo between 3,700-4,100 m consists mainly of Festuca subulifolia and Calamagrostis *intermedia* (◘ Fig. D-64e) and is interspersed with small forest islands of Polylepis, Gynoxys, Escallona, Hesperomelis, etc. Lauer et al. (2001) suggest that the entire Graspáramo may once have been completely covered with a dense, medium-high forest, and only after settlement and anthropogenic deforestation with fire-clearing has it been cleared and converted to open landscape. The potential forest line is marked at 4,100 m by the Polylepis-Gynoxys groves (◘ Fig. D-64f) (Keßler 2002).

Above this, between 4,100-4,200, a belt of shrub-grass páramo begins, up to about 100 m wide, dominated by Loricarya ilinissae, Diplostephium rupestre, and Chuquiraga jussieui, together with Festuca subulifolia (◘ Fig. D-64c). Between 4,200-4,600 m, the altitudinal belt of cushion páramo is formed. Here the surface is almost completely covered with cushion-forming Xenophyllum humile, Plantago rígida, Azorella compacta, and Huperzia crassa, interspersed with small shrubs of Diplostephium rupestre and Gentiana sedifolia, etc. (◘ Fig. D-64d). This stage eventually becomes more patchy in the upper part due to the action of daily frost change (◘ Fig. D-64a). Finally, the 'super-páramo' belt is dominated by frost-patterned soils (patterned grounds) with single specimens of Werneria crassa and Azorella compacta (◘ Fig. D-64b), very sharply demarcated upwards against the nival belt, which has almost no higher plants because of the continuous frost in the diurnal climate. The elevational belts are asymmetrically structured on the two sides of the mountains because of different hygric endowments (east side humid, west side dry).

In the Páramos of Venezuela, there is very little rain during the trade wind season (November to March). One can experience a whole week of cloudless skies in January. The cloud cover is lower. The hourly temperature values for days during the rainy season or during the dry season reflect the lack of radiation, or strong radiation (February 10) or strong radiation at night (February 12) (◘ Fig. D-65). The coldest day of 1967 almost immediately followed the warmest. During the dry season, the air at 3,600 m usually warms to 10 °C during the day, while it freezes at night. The plants, of course, are exposed to much more extremes than the thermometer in the hut. But this constant change of frost does not harm the plants, just at this time of the year is the main flowering. About this time also the upper layers of soil, in which the páramo plants are rooted, warm up during the day above the annual temperature. Rocky sites seem to be more favorable than wet soils. The annual temperature was determined by measurements in the soil: at an elevation of 3,600 m 5.0 °C (corresponding to the meteorological data), at 3,950 m 3.9 °C, at 4,250 m 2.0 °C and in the firn snow at 4,765 m -1.5 to -3.5 °C.

◘ Table D-2 Measurements of evaporation using a Piche tube in the Páramo de Papallacta (Ecuador) at 4,100 m a.s.l. between 12-25 November 1988 (data from Lauer et al. 2001).

|  |  |  |
| --- | --- | --- |
| Date | Evaporation [mm] | Weather situation |
| 12-19 Nov 1988 | 1.4 | Cloudy, fog |
| 19-20 Nov. 1988 | 0.0 | Rain, fog |
| 20-22 Nov. 1988 | 0.3 | Rain, fog |
| 22-25 Nov. 1988 | 0.1 | Rain, fog |
| Total | 1.8 mm in 14 days |

As the temperature decreases, the plants are forced to root shallower and shallower. Thus, the plant cover becomes more and more open until finally a vegetationless stage develops below the firn and snow zone. This belt of cold desert with frost-sheltered and -patterned soils (◘ Fig. D-66) due to permanent frost-change days is characteristic of the tropical mountains. The altitudinal limit of occurrence of vascular plants in tropical mountains is much sharper than in temperate mountains. In Bolivia, it is almost exactly 5,200 m, e.g. at the Chacaltaya. At higher latitudes (e.g. in the Alps) plants can take advantage of the most favorable season for growth even in the nival belt in places not covered by snow. The soil of the páramos is moist even during the dry season, so that the vegetation does not suffer from drought and has a hygromorphic appearance. In Colombia, in addition to páramos with a dry season, permanently wet soils with cushion plants, dwarf bamboo, grasses and mosses have also been studied.

The flora of the páramos in S-America, Africa and Indonesia is very different and each area has its own peculiarities. However, it is striking that besides the plants pressed to the ground, there are also tall plants, mostly Compositae (Asteraceae), with a proper trunk and crested large leaves that have a thick white hair felt. In the Andes these are *Espeletia* (27 species) (◘ Fig. D-67a,b), in the equatorial African regions the tree *Senecio* species (◘ Fig. D-67c), in Indonesia Anaphalis species. In addition to the crested tree form, the woolly candle forms of Lupinus (◘ Fig. D-67g), Lobelia (◘ Fig. D-67h), and *Puya* species (◘ Fig. D-67d,e,f) should also be mentioned as special life forms. The many Helichrysum species on Kilimanjaro, Mt Kenya or Mt Elgon, which occur up to over 4,400 m, are also very heavily hairy. That this pubescence (◘ Fig. D-67f) serves as thermal insulation and thus as protection against sudden extreme fluctuations in leaf temperature seems probable. On radiating days at these elevations, the passage of a cloud always results in a fall in temperature. The upper limit of vegetation, which is usually very sharp, is at about 4,400 to 4,600 m and is likely to coincide with an annual temperature of about +1 °C. At this elevation frost occurs once a day.

◘ Table D-3 Altitudinal belts of climate and vegetation in the Páramo de Papallacta, Eastern Cordillera of Ecuador (after data from Lauer et al. 2001).

|  |  |  |
| --- | --- | --- |
| Elevation a.s.l.[m] | Climate | Vegetation |
| Elevational belt | Temperature [°C] |
| >4800 | Tierra nevada | < 0° | Glacier region |
| 4800 | Tierrasubnevada | 1° | Frost debris belt(Super Páramo)single Werneria *crassa* cushions |
| 4600 |  | 2°Thirdfog level | Cushion plant páramowith Distichia muscoides, Xenophyllum humile, Plantago rigida, Azorella compacta, Gentiana sedifolia |
| 4200 | Tierrahelada | 5° | Dwarf shrub páramowith Loricaria ilinissaepotential forest boundary |
| 4100 | 6° | Genuine páramowith Polylepis forest islands dominated by Polylepis pauta, P. incana, Gynoxis acostae, G. halii, Escallonia myrtilloides, Hesperomeles heterophylla, Plantago rigida present forest boundary |
| 3700 |  | 7,5° | "Ceja de la montaña"with Miconia salicifolia |
| 3500 | Tierra fría II | Secondfog level | Fog forestsof Tournefortia fuliginosa, Miconia latifolia, M. bracteolata, Senecio onae, Vallea stipularis with ferns, and many epiphytic mosses and lichens |
| 3100 | Tierra fría I | 10° | High-altitude evergreen forestswith numerous Miconia species |
| 21001000 | Tierratemplada | 16°Firstcloud level22° | Evergreen mountain forestswith Geonoma, Prestoea, Nectandra, Cestrum, Solanum, Boehmeria, and numerous epiphytic flowering plants (orchids, bromeliads) |

◘ Fig. D-64 Images of elevational belts of vegetation in the Páramo de Papallacta, Eastern Cordillera Ecuador. a: A double cushion of Xenophyllum and Azorella surrounded with frost-patterned soils; b: Single cushion plants in superpáramo with mainly frost-patterned soil forms; c: Scrub páramo with Loricarya, Diplostephium and single Gynoxys shrubs; d: Cushion páramo with Xenophyllum, Azorella and Lycopodium; e: Calamagrostis grass páramo, f: Grass páramo with Polylepis forest islands (photos: Rafiqpoor).

◘ Fig. D-65 Diurnal variation of temperature at the meteorological hut (Páramo belt at 3600 m NN in Venezuela) on 26 June as well as 27 July during the rainy season (variation only 1.6 and 2.0 °C, respectively) and on 10 February (hottest day) as well as on 12 February (coldest day) during the dry season with a variation of 17.0 and 17.5 °C, respectively, a t-maximum of 14.5 and a t-minimum of -7.5 °C.

It is particularly strange, however, that in the Andes of Venezuela, even in the middle of the alpine belt at an altitude of about 4,200 m, i.e. at an annual temperature of 2 °C, small stands of trees of the Rosaceae Polylepis occur. They are always attached to steep boulder slopes in east or west exposure, irradiated by the sun in the morning or afternoon, respectively. The rooting depth of Polylepis can reach 1.5 m.

The explanation for this occurrence of trees 1,000 m above the present timberline is that block piles have particularly favourable temperature conditions. When insolation occurs, the layer of air near the ground above the block pile heats up very strongly; the cold air in the block pile is specifically heavier and should flow out in the lower part of the block pile, whereby the warm air in the upper part should be sucked in. This explanation is supported by the fact that the lower part of the block dump is not forested and is often completely bare.

◘ **Fig. D-66** Combice (**a**, **b**), striped soils (**c**), cellular soils or miniature polygons (**d**), and soil buds or clay patches (**e**) as small frost pattern soil forms in the subnival altitudinal zone of tropical mountains, using examples from the Andes in Bolivia (photos: Rafiqpoor).

◘ Fig. D-67 Convergent life forms in different páramos. a: Espeletia hartwegiana in the Páramo de Mucubaji, Venezuela (photo: Breckle), b: Espeletia hartwegiana in the Páramo del Angel, Ecuador (photo: Rafiqpoor); c: Senecio keniodendron in the afroalpine belt of Mt. Kenya in the Teleki Valley (photo: Breckle); d: Anaphalis triplinervis representing the páramo of Java (photo: BotGart Berlin-Dahlem: http://bit.ly/2maGin1); e, f: Puya clava-hercules in the Páramo del Angel, Ecuador (photos: Rafiqpoor). g: Lupinus humilis in the Páramo de Pichincha, Ecuador (photos: Rafiqpoor); h: Lobelia deckenii ssp. kenyensis (photo: Breckle). All pictures (except d) at about 4,200 m a.s.l.

Accurate temperature measurements at block piles of Mexican mountains have shown the same phenomenon. Numerous such high-altitude *Polylepis* forestplotsare also found in Ecuador. They are now also discussed in connection with long-lasting historical fire clearing events (see above and Keßler 2002).

◘ Fig. D-68 Huperzia saururus (Lycopodium crassum) (a), shimmering red from a distance, in the elevational belt of the cushion páramo (b) in Papallacta is one of the dominant life forms in the humid páramos of the Eastern Cordillera of Ecuador (photos: Rafiqpoor).

Somewhat less humid is the elevational sequence at the African volcanoes (Mt. Elgon, Mt. Kenya, Kilimanjaro), which rise from a humid savannah zone. Soil temperatures at the timberline (with Hagenia, Podocarpus species) are similar to Venezuela. Erica arborea plays a major role in the lower alpine belt, with crested *Senecio* (► Fig. D-67) and candle *Lobelia* above. Interspersed, however, are bogs with waterlogged soils, on which Cyperaceae, Alchemilla or Lachemilla species, Gentianaceae and the southern hemispherically widespread thickish Huperzia saururus (*Lycopodium crassum*) (Lycopodiaceae) occur (◘ Fig. D-68).

6 **The biogeocoenes of the zonobiome I as ecosystems**

The tropical evergreen rainforest is one of the most complicated plant communities. The individual biogeocoenes are still largely unknown, probably they cannot be plausibly delimited at all. The difficulty of dividing them into ecosystems is thus extraordinarily great.

The luxuriance of the vegetation and its high biodiversity tempt one to assume a very large primary production. The first estimates were 100 t●ha-1●a-1 (dry weight), but they were much too high. It must be borne in mind that the phytomass in the tropical jungle is characterized by a very high water content (75 to 90% for herbaceous parts). The green leaves can assimilate CO2 all year round, but the respiration losses at night are also particularly high due to the high temperature. The phytomass of wood and leaves is two to three times higher in tropical forests, but the costs of maintaining this mass, the respiration losses, are four times higher in the wood and six times higher in the leaves. Tropical forests are forced to greater metabolic turnover at the high temperatures, so relatively less can be invested in the production of wood.

Of very great importance for the matter production of a biogeocoene is the leaf area index (LAI), i.e. the ratio of the total leaf area of a stand to the soil surface covered by the stand. It was very low in the Ivory Coast. But this experimental plot cannot be considered representative. Although the gross production is very high, 75% of the organic matter produced is lost again through respiration, whereas in the central European beech forest only 43% of the gross production is lost.

We therefore understand that the annual primary production of the tropical virgin forest in this case was not higher than that of a well-managed beech forest in Central Europe:

Tropical virgin forest 13.4 t●ha-1●a-1

Beech forest 13.5 t●ha-1●a-1

Timber yields in forest plantations in the tropics reach 13 t●ha-1, which is only about twice as high as in a good European beech forest, which is also due to the twice as long vegetation period. A forest studied in Thailand with 2,700 mm rainfall and an annual temperature of 27.2 °C has an aboveground phytomass of 325 t●ha-1, which should correspond to a total phytomass of 360 t●ha-1. It still increased by 5.3 t●ha-1 per year during the three years of observation. They were: LAI = 12.3.

|  |
| --- |
| Box D-7 Turnover rates in tropical forests |
| Tropical forests have high turnover rates due to the permanently high temperatures. However, the very high productivity is more than compensated by particularly high respiration losses. |

One must distinguish three phases in virgin forests, which form a small-scale mosaic: A juvenile phase with stand regeneration and positive phytomass increase, an optimal phase with maximum phytomass remaining unchanged, and an aging phase with decreasing phytomass. The Ivory Coast stand was probably a light juvenile phase. But all three phases usually occur mixed as a mosaic.

According to the available data, the following mean values can be given for the optimum phase of a lush tropical rainforest in ZB I:

Total phytomass 350 to 450 t●ha-1 and, with a leaf area index of 12 to 15, a gross production of up to 120 to 150 t●ha-1 per year, which would correspond to a primary production of 30 to 35 t●ha-1, with 10 to 12 t●ha-1 on litterfall.

Soil respiration is approximately equal to the amount of litter, but a substantial part of the primary production is probably already mineralized above ground (standing dead trees, epiphytes). Litter returns 106 kg●ha-1 of nitrogen annually to the soil in the Amazon, but only 2.2 kg●ha-1 of phosphorus. The depletion of secondary forests is likely to be mainly a phosphorus problem, especially since P is rapidly bound to Fe and Al in the soil and is then no longer available to plants. Nitrogen is also steadily supplied from the atmosphere during the frequent heavy thunderstorms.

7 **Fauna and food chains in the zonobiome I**

Only a few remarks can be made here. The organismic diversity and also the gaps in knowledge are still very large. The interrelations of organisms in the tropical rainforest are very close, and the resulting sensitivity to interventions has already been pointed out.

There are now many generally understandable books and extensive literature, also with comprehensive overviews of the tropical rainforest and its fauna. In each case, the close interconnection of the organisms is emphasized. A few examples of general works should be mentioned (Terborgh 1991, Richards 1996, Scholz 2003, Germanwatch 2004, Reichholf 2011, etc.).

For the animal world, as well as for many plants, it is characteristic that the canopy space is an important action space. More than half of the mammals live in the treetops and have a prehensile tail; very large is the number of birds, again with a focus of activity in the canopy area. The number of species can only be roughly estimated so far and especially the number of invertebrates above and below ground is actually unknown so far, as well as the functional relationships.

We know the most about bird species, e.g. their functional guilds in bird communities. As an example in comparison with a region from the temperate latitudes of the USA (ZB VI), such an overview of the guilds is given in ◘ Table D-4. It becomes clear that the number of species on the one hand, and the number of guilds on the other hand, is considerably larger in the tropics. In temperate latitudes some guilds are completely absent. It is also easy to see that seed and fruit dispersal or destruction by birds is of great importance for the regeneration and thus future structure of the forest.

Furthermore, termites and ants are of particular importance for ecosystem processes; they do turn over quite a bit of biomass, but their zoomass , despite their diversity, is not large.

Typical canopy animals in the Neotropics are the sloths (Cholopus, Bradypus), whose lifestyle has been studied in detail (Montgomery et al. 1975). The total zoomass of the animals was 23 kg●ha-1, and the leaf mass eaten annually was 53 kg●ha-1; this represents 0.63% of leaf production. The excrement decomposes slowly and provides a reserve of nutrients in the soil.

Leafcutter ants (Atta) (► Fig. C-11) exert a particularly strong influence through selective infestation (Haines 1975). They increase light enjoyment in the stand by up to 7%. They haul their material from tree species in the secondary forest up to 180 m to the 10-m-diameter underground nest, where they establish fungal gardens on the cut leaves. The cut leaf area can reach 4,000 m2.The mushrooms provide the food for the ants. So, they are perfect states with 'microbiological agriculture'. The number of other ant species living there on a single tree not infrequently exceeds the number of all ant species in a temperate country in central Europe (Wilson 1988).

8 **Man in the zonobiome I**

The tropical rainforest on poor soils is hostile to settlement and is mostly avoided by humans. It is often the refuge of native tribes. In Africa these are the pygmies, in Latin America the original Indian tribes. In Southeast Asia, too, remnants of the original inhabitants still live. In contrast, the former primeval forest areas on nutrient-rich, young volcanic soils are now densely populated cultivated land (Java, Central America and others). Only there is reasonably sustainable agriculture possible. On all poorer soils, clearing leads to catastrophic nutrient losses. The 'ecological disadvantage of the tropics' (Weischet 1980) is particularly evident here. Cleared areas are worthless after a few years and fall victim to erosion or cover themselves with worthless Gleichenia or *Imperata* thickets.

Yet today there are good reasons to realistically assess the economic value of tropical rainforests. Even without the completely inestimable genetic resources of an incredible biodiversity that has not yet been clearly recognized, the tropical rainforest is always worth much more than the wood standing on it, as the simple calculation in ◘ Table D-5 shows. What an appalling overexploitation deforestation represents is clear from these figures. At the same time, the loss of biodiversity cannot be calculated; the enormous abundance and value of possible secondary constituents in such calculations is not taken into account.

Deforestation has accelerated at an incredible rate in recent decades. Costa Rica should be cited as an example: The forest area there has decreased alarmingly in just a few decades (between 1940 and 1987) (◘ Fig. D-69). It was not until after 1987 that the forested area increased again due to effective conservation measures and an increase in environmental awareness among the population (FONAFIO 2012: http://bit.ly/2vnPtau).

Today in Costa Rica, although 21% of the country's land is under protection (national parks, reserves, etc.), the pressure on these areas is great, since hardly any other forest with larger wood reserves is available. In the Dominican Republic on Hispaniola, the primary forest area has fallen from over 70% to less than 6% in half a century, and in Haiti on Hispaniola everything has been deforested.

The forecasts for the preservation of the rainforests foresee dire things. Of the approximately six million square kilometres of humid tropical forests that still exist today, all will have been cleared by 2040 according to current deforestation rates; according to other forecasts, this catastrophic state will occur as early as 2025, as the rate of deforestation will increase even further due to overpopulation and impoverishment (◘ Fig. D-70). This is not just a regional or national problem, but a global one. Even if in the USA or in Central Europe, too, almost all native and primary forests and prairies have been destroyed and replaced by monotonous forests or maize fields, the endowment of the landscapes and the climate are so favourable there that it is possible to establish an efficient agriculture and forestry industry and to hope for a largely sustainable use. In the tropics this is quite different (► Box D-8). It is worse, rather than better.

New data by FAO on all tropical rainforests indicate a total area of 13.4 million km2 . The net loss of forest area for the three rainforest regions was 54,000 km2 annually between 2000 and 2010. Of this, the Amazon Basin accounted for 36,000 km2, Southeast Asia 10,000 km2 and the Congo Basin 7,000 km2.

Global Forest Watch (GFW) has calculated that in 2018, about 120,000 km2 of forest were lost in the tropics, including 36,000 km2 of humid tropical rainforests, namely primary forests, i.e. the largely untouched forests. In 2019, the area of lost primary rainforests increased to 37,700 km2, according to GFW. A total of 121,500 km2 of forest was lost in the tropics this year. So again, it is worse, rather than better.

Table D-4 The bird communities of a temperate forest (Congaree floodplain, USA) and of a tropical rainforest (Peru), broken down by guilds (functional units) (from Terborgh 1993).

|  |  |  |
| --- | --- | --- |
| Bird community guild | Number of species in the tropical rainforest Peru | Species count in midlatitude Congaree floodplain USA |
| Scavenger | 2 | 1 |
| Mammalian predator | 7 | 1 |
| Bird predator | 4 | 1 |
| Other birds of prey | 7 | 1 |
| Owls | 5 | 2 |
| Nightjar | 1 | 0 |
| Terrestrial seed eaters | 5 | 2 |
| Arboreal seed eaters | 8 | 0 |
| Terrestrial fruit eaters | 3 | 0 |
| Arboreal fructivores | 18 | 1 |
| Nectarivore | 8 | 1 |
| Terrestrial insectivores | 10 | 2 |
| Woodpeckers | 8 | 5 |
| Leaf-scanning insectivores | 9 | 1 |
| Leaf peepers | 19 | 15 |
| Failures undertaking insectivores | 27 | 3 |
| Insectivores hunting in the airspace | 4 | 1 |
| Ants following insectivores | 6 | 0 |
| Dead leaf scavenging insectivores | 7 | 0 |
| Climbing insectivores | 7 | 0 |
| Fruit eaters, predators | 6 | 2 |
| Tree-dwelling substrate-feeding fruit and insectivores | 12 | 1 |
| Tree-dwelling, foraging fruit and insectivores | 13 | 0 |
| Fruit, insect and nectar eaters | 11 | 0 |
| Total | 197 | 40 |

**Table D-5** Wood value of marketable logs per hectare on an experimental area in Amazonia (rainforest of Misana on the Rio Nanay in Peru) in the case of irreversible one-time deforestation and compared with the annual yield and market value of fruits, raw rubber, resins and other continuously usable products per year (Peters et al. 1989, Reichholf 1990)**.**

|  |  |  |
| --- | --- | --- |
|  | Unique wood value | Ongoing use (per year!) |
| Number of species | 27 | 12 |
| Wood volume (m3) | 94 | - |
| Wood value ($) | 1001 | - |
| kg Raw products | - | 160 |
| Number of fruits | - | 5500 |
| Market value ($) |  | 698 |

◘ Fig. D-69 Decline in percent forest cover in Costa Rica by 1987 as a result of deforestation and regrowth of forested areas by 2010 as a result of conservation measures in recent years (data from FONAFIFO 2012; http://bit.ly/2vnPtau).

|  |
| --- |
| Box D-8 Protecting tropical rainforests |
| The close coupling with the global cycle, the unique, incredibly high biodiversity with its corresponding irreplaceable genetic resources, the sensitive soils, the irreversible damage to landscapes when deforestation occurs, all call for an immediate, global effort to save the rainforests. |

Fig. D-70 The humid tropical rainforest is constantly losing area. The straight line shows the prognosis for constant deforestation, i.e. for a constant annual area cleared from 1990 onwards. The other two curves are based on projections by various organizations and take into account the still increasing demand (after Terborgh 1991).

Today, thousands of fires burn every night (► Fig. C-20). The smoke still inhibits the greenhouse effect. Slash-and-burn must not be allowed to continue. Natural fires almost do not occur in the rainforests in ZB I.

It is getting drier and drier in the Amazon in recent years, more and more fires are deliberately set in order to gain land, and more and more often these fires get out of control; whereby out of control fires also create new acreage for invading colonists, according to WWF. In September 2020 there were over 32,000 different sources of fire in the Brazilian Amazon alone.

Clearance and fire clearance on a large scale only know the value of the forest, which comes from its wood, not really its natural resources. Above all, its area as arable land. The year 2021 is not over yet, but one can extrapolate already a record deforestation. It is assumed that the deforestation rate is a third higher than the year before. This disaster entails: probably more than 200,000 fires by the end of the year 2021.

9 Zonoecotone **I/II - Semi-evergreen forest-thorn savannah**

The zonoecotone between ZB I with evergreen rainforest and ZB II of the tropical summer rainfall area with deciduous forests is the semi-evergreen tropical rainforest, i.e. a transition zone with diffuse mixing of the two vegetation types.

In small areas, this is also locally formed as a vegetation mosaic, sometimes a patchwork of the most diverse vegetation types, modified according to groundwater, soil structure, water and nutrient availability. On very poor sandy soils in Venezuela and Guyana, the periodically flooded Igapo forest grows as a pedobiome near the river. Higher up on sandy soils follows the caatinga, which becomes a low caatinga or even a puny 'bana' when sandy soils are thick, although rainfall is high (3,300 mm). However, the sandy soil has no nutrients and the water storage capacity during the dry season is very low. Viewed over a larger area, the following series can be identified with decreasing annual precipitation and increasing duration of the dry season in Venezuela (► Fig. D-45 and ► Fig. D-44, respectively):

**Evergreen rainforest - Semi-evergreen forest - Deciduous forest**

Within the equatorial climatic zone this series is seldom observed, such a gradation of rainfall as occurs in Venezuela being an exception. This series, however, can be generally observed as we move from the equator toward the tropics (of Cancer or Capricorn); for we thereby enter more and more into the tropical climatic zone of cenital summer rains, the absolute amount of rain constantly decreasing, the rainy season shortening, and the dry season lengthening. The difference with Venezuela is that in this the annual variation of temperature becomes gradually perceptible and more and more marked, the dry season being the cool season. However, since the latter is a dormant season for vegetation, temperature differences do not play a significant role for vegetation.

It has already been mentioned that in the very humid tropical area, when a short dry season occurs, the endogenous rhythmicity of the tree species adapts to the climatic rhythmicity. The general character of the forest does not change, but many tree species lose their leaves at about the same time, or sprout and flower at the same time. The vegetation thus exhibits a clearly synchronized seasonal aspect sequence (seasonal rainforest).

If the duration of the dry season increases further, the forest type changes: the uppermost tree layer is formed by deciduous tree species; in S America these are the large, thick-stemmed Bombacaceae and beautifully flowering Erythrina species (◘ Fig. D-71), while the lower layers still consist of many evergreen species. We therefore speak of the semi-evergreen tropical forest.

◘ Fig. D-71 A semi-evergreen tropical rainforest with *Erythrina* trees, conspicuous from afar by the red colour of its flowers. This forest is native to the leeward sides of the Ecuadorian coastal cordillera (photos: Rafiqpoor).

◘ Fig. D-72 Climate diagrams of Indian stations in the area of the evergreen, semi-evergreen, wet and dry monsoon forest.

If the precipitation decreases further and the dry season is prolonged even more, then all tree species shed their leaves, so that the forest is bare for a shorter or longer period of time, i.e. it is a moist or dry deciduous tropical forest. This sharp transition is realized from central Costa Rica to the northwest (Guanacaste) and in Ecuador at the Andean western slope near Loja in a very short distance.

The climate diagrams for corresponding forest types in India, where this transition can be observed particularly well in the area of monsoon rainfall in summer, are shown in ◘ Fig. D-72.

The question arises as to what determines the structure of the forest, the amount of precipitation or the duration of the dry season. The diagram ◘ Fig. D-73 shows that both factors are ecologically important. One must not consider either factor alone. From the course of the boundary lines (slope) one can see that for the moist forest types the duration of the drought period is more important, whereas for the dry types the amount of rainfall is more significant.

In Africa the above-mentioned series is not so clearly observable. Due to increased settlement and the practice of shifting cultivation, it is precisely the area of semi-evergreen forests and moist deciduous forests that has been largely cleared. These forests are easier to clear than the rainforests, because they could be burned down during the dry season in the past; however, the rainfall is still high enough that one can expect an annual crop yield when cultivating the land.

◘ Fig. D-73 The relationships between annual precipitation (y-axis, ordinate) and duration of drought in months (x-axis, abscissa) in India for different types of of forest vegetation. A evergreen and B semi-evergreen tropical rainforest, C monsoon forest (h wetter, a drier), D savannah (thorn bush forest), E desert (after Walter, from a work commissioned by UNESCO).

10 Literature

Begon, M., Mortimer, M. & Thompson, D.J. 1996. Population Ecology: A Unified Study of Animals and Plants. Third Ed. Blackwell Science Ltd., Oxford, UK, 247 p. ISBN 0-632-03478-5

Bendix, J. & Rafiqpoor, M.D. 2001: Studies on the Thermal Conditions of Soils at the Upper Tree Line in the Páramo of Papallacta (Eastern Cordillera of Ecuador). Erdkunde 7: 257-276

Breckle, S.–W. 2004: Flora, Vegetation und Ökologie der alpin-nivalen Stufe des Hindukusch (Afghanistan). In: Breckle, S.–W., Schweizer B., Fangmeier, A. (eds.): Proceed. 2nd Symposium AFW Schimper–Foundation: Results of worldwide ecological studies. Stuttgart–Hohenheim: 97–117

Brown, K.S.J. & Ab'Saber, A.N. 1978: Ice age refuges and evolution in the neotropics: correlation and paleoclimatological, geomorphological and pedological data with modern biological endemism. Paleoclimas (Sao Paulo) 5: 1-30

Coutinho, L.M. 1982: Ecological effect of fire in Brazilian Cerrado, 273-291. In: Huntley, B. J. & Walker, B.H. (eds.) s. there

Germanwatch 2014: Die Bedrohung der tropischen Regenwälder und der internationale Klimaschutz. Arbeitsblätter zum globalen Klimawandel. http://bit.ly/2eSyeXe

Haines, B. 1975: Impact of leaf-cutting ants on vegetation development at Barro Colorado Island. Ecol. Stud. 11: 99-111

Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R.T. et al. 2010: Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. Biotropica 42: 140–148

Hüttel, Cl. 1975: Root distribution and biomass in three Ivory Coast rain forests plots. Ecol. Stud. 11: 123-130

Janzen, D.H.1978: Seeding patterns of tropical trees. In: Tomlinson, P.B. & Zimmermann, M.H. (eds.): Tropical trees as living systems. Cambridge Univ. Press: 83–128

Johansson, D. 1974: Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suecica 59: 129 p.

Kapelle, M. 1990: Ecology of mature and recovering Talamancan montane Quercus forests, Costa Rica. Acad. Proefschrift, Amsterdam 270 p.

Keßler, M. 2002: The „*Polylepis*-Problem”: where do we stand? Ecotropica 8: 97–110

Körner, Ch. 2007: Alpine ecosystems. Encyclopedia of Life Sciences, John Wiley

Körner, Ch. 2012: Alpine treelines. Springer-Verlag, Basel

Lauer, W. 1975: Vom Wesen der Tropen. Klimaökologische Studien zum Inhalt und zur Abgrenzung eines irdischen Landschaftsgürtels. Abh. d. Akad. d. Wiss. u. d. Lit. Mainz, Math.-nat. Kl., Nr. 3

Lauer, W. 1982: Zur Ökoklimatologie der Kallawaya-Region (Bolivien). Erdkunde 36: 223-248.

Lauer, W. 1995: Die Tropen – Klimatische und landschaftsökologische Differenzierung. Rundgespräche der Kommission für Ökologie. Bay. Akad. der Wiss.: „Tropenforschung“, Bd. 10: 4360.

Lauer, W. 1999: Klimatologie. Das Geographische Seminar. Westermann Verlag Braunschweig

Lauer, W. Rafiqpoor, M.D. & Theisen, I. 2001: Physiogeographie, Vegetation und Syntaxonomie des Páramo de Papallacta (Ostkordillere Ecuador). Erdwissenschaftliche Forschung, Bd. 39, Franz Steiner Verlag, Stuttgart

Longman, K.A. & Jenik, J. 1974: Tropical forest and its environment (Ghana), Thetford, Norfolk, 196 p.

Macarthur, R.H. 1972: Geographical ecology: patterns in the distribution of species. Harper & Row, New York

Medina, E. 1974: Dark CO2-fixation, habitat preference and evolution within the Bromeliaceae. Evolution 28: 677–686

Montgomery, G.G. & Sunquist, M.E. 1975: Impact of sloths on neotropical forest. Energy and nutrient cycling. Ecol. Stud. 11: 69–98

Reichholf, J.H. 1990: Der unersetzbare Dschungel. Leben, Gefährdung und Rettung des tropischen Regenwaldes. BLV, München 207 S.

Reichholf, J.H. 2011: Der Tropische Regenwald: Die Ökobiologie des artenreichsten Naturraums der Erde. Fischer Taschenbuch Verlag, Frankfurt.

Richards, P.W. 1996: The tropical Rain Forest: An Ecological Study. Cambridge Uni. Press, 450 p.

Scholz, U. 2003: Die feuchten Tropen. Das Geographische Seminar. Braunschweig.

Simpson, B.B. & Haffer, J. 1978: Speciation patterns in the Amazonian forest biota. Ann. Rev. Ecol. Syst. 9: 497–518

Sprenger, A. & Breckle, S.-W. 1997: Ecological studies in a submontane rainforest in Costa Rica. Bielefelder Ökologische Beiträge 11 (Contributions to tropical ecology research in Costa Rica): 77-88

Terborgh, J. 1991: Lebensraum Regenwald, Zentrum biologischer Vielfalt. Spektrum Akad. Verl., Heidelberg 253 S.

Tomlinson, P.B. & Zimmermann, M.H. 1976: Tropical trees as living systems. Cambridge Univ. Press, UK

Troll, C. 1943: Thermische Klimatypen der Erde. In: Petermanns Mitteilungen 89: 81-89

Valencia, R. & Balslev, H. 1994: High tree alpha diversity in Amazonian Ecuador. Biodiversity and Conservation 3: 21–28

Vareschi, V. 1980: Vegetationsökologie der Tropen. Ulmer, Stuttgart, 253 S.

Walter, H. 1973: Die Vegetation der Erde, Bd. I: Tropische und subtropische Zonen. 3. Aufl., Fischer, Jena, Stuttgart, 743 S.

Walter, H. 1990: Vegetationszonen und Klima. 6. Aufl., Ulmer/Stuttgart 382 S.

Walter, H. & Medina, E. 1969: Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subaplinen Stufe in den Anden Venezuelas. Ber. Dt. Bot. Ges. 82: 275-281

Walter, H. & Medina, E. 1971: Caracterizacion climatica de Venezuela sobre la base de climadiagramas de estaciones particulares. Bol. Socied. Venez. de Cienc. Natur. 29: 211-240

Wattenberg, I. & Breckle, S.-W. 1995: Tree species diversity of a pre-montane rain forest in the Cordillera de Tilaran, Costa Rica. Ecotropica 1: 21-30

Weischet, W. 1980: Die ökologische Benachteiligung der Tropen. 2. Aufl., Teubner, Stuttgart

Wilson, E.O. 1988: Biodiversity. National Academy Press, Washington D.C. ISBN 0-309-03783-2

Zeller, O. 1973 Blührhythmik von Apfel und Birne im tropischen Hochland von Ceylon. Gartenbauwissenschaften 38: 322–342

[IMAGE]

Savannah landscape in Serengeti National Park (Zonobiom II), Tanzania, at the beginning of the summer rainy season (Photo: Breckle)

[IMAGE]

Rainfed dry savannahs with Acacia spec. in Pendjari National Park, Benin, W-Africa (Photo: A. Erpenbach)

[IMAGE]

The big old lion keeps a lookout. Large animal world in the savannah of Tanzania (Zonobiom II) in the Serengeti National Park (Photo: Breckle)