II  **Special part**

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

1. General
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3. Savannahs (trees and grasses)
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[IMAGE]

Savannah with Acacia xanthophloea (background) and parched grass cover (Zonobiome II) in Serengeti National Park, Tanzania, at the beginning of the summer rainy season (photo: Breckle)

1 **General**

Tropical zonobiome II, characterized by a 12-month thermal growing season, is frost-free like ZB I in the lowlands, but already exhibits a noticeable annual variation in temperature. Heavy cenital rains fall during the warm, mostly perhumid season, and the cooler season is arid. The hygric climate of ZB II is characterized by a pronounced hygric seasonality with a rainy and a dry season, whereby the length of the hygric growing season, i.e. the number of humid and arid months, determines the hygric character of the respective savannah landscape. Accordingly, ZB II can be divided into semihumid (7-9 humid months) rainfed moist forests and moist savannahs, semiarid (4-6 humid months) rainfed dry forests and dry savannahs, and arid (1-3 humid months) rainfed thorn forests and thorn savannahs (► Fig. D-52).

In the Americas, this zonobiome climatically occupies a large area south of the Amazon basin, plus smaller areas as far north as above the 20th parallel in Central America and partly extrazonal in Venezuela. In Africa, ZB II covers vast areas on both sides of the equator. South of the equator, on the plateau of the Zambezi, sometimes severe frost damage is observed in cold years, limiting the spread of ZB II to the south. The cold plateau around Johannesburg is already predominantly a grassland. In Asia, the main areas of distribution are India and SE Asia , whereas in Australia it is restricted to the northern part (► Fig. C-22 to ► Fig. C-27). Corresponding to the humido-arid climate of ZB II on the flat areas are the zonal soils. These store so much water during the rainy season that they do not dry out completely during the drought season. This is a prerequisite for the growth of the zonal deciduous forests, which, although they greatly reduce transpiration losses by shedding their leaves during the drought season, must also absorb a certain amount of water from the soil during the drought season. Even the leafless twigs and branches still lose so much water that the quantities of water stored in the trunk are not sufficient for the whole drought period.

2 **Climate, soils and zonal vegetation**

A special feature of ZB II is that the zonal open forest vegetation is absent in many places and replaced by the savannah vegetation type. The causes for this are of various kinds. However, a particularly important one is the presence of impermeable layers (laterite crusts and others) in the soil at various depths. Their presence is well known, but their exceptionally wide distribution was first demonstrated by Tinley (1982) on a 200 km profile by very accurate soil profile surveys in East Africa. He established the location of accumulation layers with pits 7 m deep. These impermeable crusts alter the water balance of the soil to such an extent that the formation of zonal forest vegetation is prevented (◘ Fig. E-1).

◘ Fig. E-1 Vegetation as a function of the position of the impermeable layer. Signatures ► Fig. E-1a. Further explanations on ► page xxxxf. and in the individual legends (modified after Tinley from Walter & Breckle 2004).

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| **Legend for Fig. E-1:****Fig. E-1a:** Sandy area with a high groundwater level above a continuous impermeable horizon; the soil is waterlogged. This results in the development of a wet grassland. On sandy, drained flat hights, a tree savannah develops; on higher plateaus with more root space, forest stands, which can draw water from deeper layers during drought. In depressions, groundwater emerges and a lake or swamp forms with reed vegetation at the edge.**Fig. E-1b:** Hilly sand deposits with interrupted, impermeable crust at different levels, which only comes to the surface on the slope. There water escapes, the wetted ground is covered with grassland. Savannah or forest grows on the hights, depending on the availability of water in the dry season. In depressions, a Vley (periodic water basin) or a lake forms with grassland at the edge and individual gallery-like rows of trees.**Fig. E-1c:** Above a continuous, slightly sloping impermeable layer (crust) the soil is permanently waterlogged, but drains downslope, where in a depression water seeps out, sometimes evaporates and forms calcareous crusts (calcrete). Where the groundwater reaches almost to the surface, grassland grows, only outstanding termite heaps can support woody plants. Where the groundwater is deeper, savannah or even forest may develop. Woody plants grow at springs and seepage horizons and reeds around the lake.**Fig. E-1d:** On the Cheringoma coastal plain, a continuous waterlogged layer also occurs, so that mostly only grassland can develop. Woody plants grow on mounds or termite heaps, and on larger heights the water conditions are still so good, even during the dry season, that an extrazonal edaphic evergreen forest can develop, changing at the edges into a deciduous forest. In the deeply incised valley (Dambo) a gallery forest grows above flowing groundwater.**Fig. E-1e:** In the Urema Valley of the Rift Valley, the crust runs at very different depths and is up to 1.5 m thick. Where it is deep, rainwater is stored in the rooted soil so that a deciduous forest can develop, while on strongly swelling alkaline gleyic soils the special woody formation with mopane (Colophospermum m*opane*) develops.**Fig. E-1f:** In the western Caprivi area as part of the northern Kalahari, deep but coarse-grained sands often occur with low water storage capacity. Then only a very open tree savannah grows; but if there is a impermeable layer at depth, zonal deciduous forest (with Baikiaea) can grow. If the crust is shallow, base-saturated black clay-rich soils form with deep drought cracks in the dry season; they support only grasslands with annual grasses in the wet season. On the somewhat elevated areas mopane savannah, on termite heaps also other woody plants are found.**Fig. E-1g:** In the coastal dunes in Mozambique, depending on the water availability of the dune sand, one finds a low forest or grassland with individual shrubs. The crust is not continuous, again favoring grassland; on termite piles individual woody plants and at the base palms. In deep gullies over impermeable clay grows a swamp forest.**Fig. E-1h:** In the beach area of the Tonga coast (S Mozambique), parallel sand ridges have formed due to sea retreat, with hardened layers of fine dust in between. According to the water supply, forest and savannah alternate here again. |

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| **Box E-1** The humido-arid tropical zonobiome |
| Zonobiome II, the humid-arid tropical zonobiome, is characterized by the sharp alternation of rainy and dry seasons. During a short dry season, deciduous forests often cover the entire area, while grasslands and thorn savannahs predominate during a longer dry season. |

The savannahs and grasslands are mostly not only climatic, but edaphic, i.e. conditioned by the soil, and can thus largely be regarded as pedobiomes. A detailed description of the conditions is given below.

Lateritization occurs, on the one hand by slow dissolution of the silicic acid, by accumulation and solidification of round pisolite nodules, which can often consist largely of aluminium, iron and manganese oxides and can gradually be cemented into a hard crust; on the other hand, leaching processes and soil erosion play a major role (cf. the individual stages in ◘ Fig. E-2). What remains is an undulating concrete-hard surface on which hardly any plant growth is possible (◘ Fig. E-3).

The leaching over long periods of time results in another edaphic characteristic: The often very low nutrient content of the soils in the area of ZB II. The land surface in Africa, but also in Australia, in the Near East and especially the Brazilian plate in South America are parts of the Gondwana shield, i.e. the primeval mainland, which split into the corresponding continents many millions of years ago (in the Mesozoic). Since then, the land surface was never covered by the sea; the soils are ancient and their rejuvenation by marine sediments never took place. The rocks were constantly leached and eroded. Therefore, wherever young volcanic rocks are lacking, the weathering products forming the soil are severely depleted in nutrient elements important for plants (phosphorus, trace elements), so that no forest can develop (Campos Cerrados).

On large plateaus, the barely noticeable lower parts of the relief are flooded during the rainy season and the soils are waterlogged. Forest groves grow only on the somewhat higher non-flooded areas, while a tropical grassland develops on the wet areas (◘ Fig. E-4). A mosaic-like parkland is thus created with forest plots and grasslands that are ecologically not savannahs. This is because savannahs are understood to be an ecologically homogeneous plant community of scattered woody plants in the midst of a relatively dry grassland. However, many geographers take a broader view of savannahs.

Thus, in the ZB II one has to deal with three vegetation types:

1. With zonal deciduous forests
2. With relatively dry savannahs and
3. With the parklands wet in the rainy season.

Many laterite crusts are fossil, i.e. they were formed during the Pleistocene, the geological period characterized by several glaciation phases. These glaciations affected the Saharan desert zone (ZB III), not quite parallel in time, as pluvial periods with ± heavy rain, whereas in the tropical zone (ZB II), as recent pollen-analytical studies prove, they were dry periods extending into ZB I, which led to the formation of laterite crusts and relict savannahs still present today, even in the midst of evergreen rainforests.

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| **Box E-2** The Gondwana remnants in ZB II  |
| In Zonobiome II, peinobiomes are often developed on the old Gondwana shield areas: Biomes characterized by the severe nutrient depletion of the old soils.  |

Fig. E-2 Scheme of the individual stages and processes of lateritization in an alternating humid Savannah climate by leaching processes and formation of a concrete-hard laterite crust with soil erosion.

◘ Fig. E-3 Repeated drying of the B-horizon and erosion of the topsoil irreversibly hardens the iron oxide-rich layer (plinthite) to 'ironstone' (laterite) (modified after Schultz 1995, from Thomas 1974). The hard laterite crusts can 'cement' sinkholes and thus contribute to the formation of steps on mountain slopes (mesa formation).

◘ Fig. E-4 A broad plain in central Australia with imperceptible relief parts, covered with grassland and forest islands. It is flooded during the rainy season; waterlogged soils may then form. In the background the Olga Mountains, about 35 km away (photo: Breckle).

Species diversity in savannahs is much lower than in tropical rainforests. Some examples of neotropical areas are given in ◘ Table E-1.

Climatically, ZB II can be divided into two subzonobiomes according to the duration of the thermal and hygric growing season, namely a humid and a dry one. The corresponding climatic diagrams for India have been shown in ► Fig. D-73. It is not expedient to give certain climatic limit values for all continents; the conditions in each case are too different for this.

According to the climate, wet and dry zonal tropical deciduous forests are also distinguished. The zonal soils are probably still too little studied or the results often not generally valid to give general distinguishing characteristics for the moist and dry ones. Like those of ZB I, they belong to the group of red-colored ferrallitic soils, but SiO2 leaching does not go so far in these soils, which are wet only during the warm rainy season. While the ratio SiO2/Al2O3 is less than 1.3 in ZB I, it is 1.7 to 2 in ZB II. The sorptive power of zonal soils is also somewhat greater, that is, they retain ions important for plant nutrition better by adsorption due to a greater cation exchange capacity (CEC) and are therefore not quite as nutrient poor.

The most striking difference of the zonal vegetation of ZB II compared to ZB I is the leaf shedding, as a seasonal rhythm. It can be seen that in all climatic zones the tree species always develop the type of leaf structure that ensures the greatest production adapted to the respective climatic conditions. The leaf organs are always short-lived structures, because they age very rapidly, which means that they soon lose the ability to assimilate CO2, which is their main task. The reason for this is probably the accumulation of ballast material, which is supplied to the leaf dissolved in the transpiration stream, as well as of metabolic by-products (tannins, alkaloids, terpenes, etc.), which, however, almost always also have a defensive role against herbivores.

Even the evergreen trees of ZB I soon shed the old leaves when the young ones have become functional. Some species have been observed even in ZB I to be evergreen in good rainy years, but to lose their leaves before the leaf buds sprout when an unusual drought occurs, so the trees are bare for a short time. In ZB II, a long drought season is normal, while the rainy season is mostly very wet. Accordingly, the tree species only develop very drought-sensitive large and thin leaves at the beginning of the rainy season, for which they need less building material per leaf area unit than for the thick leathery leaves of the species of ZB I. Although the thin leaves assimilate CO2 only during the wet season, the saving of organic material makes the annual balance of production more favourable. For CO2 assimilation, i.e. the production of organic matter, the assimilation intensity is decisive in addition to the leaf area. The latter is higher for thin leaves.

The water balance of the trees in ZB II is very balanced during the rainy season. This is because the diurnal variation of the transpiration curve runs parallel to the evaporation curve and hardly shows any midday depressions, which are always indicating a sign of incipient water shortage. The osmotic cell sap potentials of the leaves are also relatively low in the range of -0.7 to -1.9 MPa for all species. At the onset of drought, an increase in the sugar concentration in the cells of the leaves to six times is noticeable (by 0.2 MPa in absolute terms). Soon thereafter, yellowing or drying of the leaves occurs.

Frost damage has been observed on the southern border of ZB II in Africa in unfavourable years (Ernst & Walker 1973). Sprouting of annual shoots and unfolding of leaves occurs only after the onset of rain (◘ Fig. E-5). But it is noticeable that the flower buds of many tree species open before the first rains. Since the petals have only cuticular, extremely low transpiration, this is associated with a hardly noticeable greater loss of water; on the other hand, pollination of the flowers by insects is facilitated in the still leafless forest.

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| Table E-1 Floristic richness of some neotropical savannah areas (after Sarmiento 1996) |
| Region | Area (km2) | Species numbers | Total number of species |
| Grasses | Semi-shrubs and herbs | Trees and shrubs |
| Llanos in Colombia | 150 000 | 44 | 174 | 88 | 306 |
| Llanos in Venezuela | 250 000 | 43 | 312 | 200 | 555 |
| Cerrados in Brazil | 2 000 000 | 429 | 181 | 108 | 718 |

◘ Fig. E-5 Colophospermum mopane forest in northern Namibia greening at the beginning of the rainy season (large image). During this time, the trees also begin to flower (photos: Breckle).

The triggering factor for the onset of flowering is likely to be the maximum temperature, which occurs towards the end of the drought period but already before the onset of rain.

The most extensive ZB II forest stands are found in the sparsely populated parts of Africa south of the equator. These are the 'miombo' forests on the watershed between the Indian and Atlantic Oceans and on the Lunda threshold south of the Congo Basin, where there is no drinking water available for settlements during the drought season. At the dry frontier of ZB II, the occurrence of the ‘monkey bread’ or baobab tree (Adansonia digitata) is very striking; its misshapen bizarre trunk, which reaches a circumference of 20 m (◘ Fig. E-6), can store up to 120,000 liters of water. It can therefore be assumed that in a leafless state it survives the drought without absorbing water from the soil. Bottle treesbelonging to the same Bombacaceae family also occur in South America and Australia.

Medina (1968) determined soil respiration in Venezuela in a deciduous forest at 100 m asl (annual temperature 27.1°C, annual precipitation 1334 mm). It was three times more intense during the rainy season than during the drought season. It corresponded to an annually decomposed organic matter amount of on average 11,2 t•ha-1. The annual litterfall was8,2 t•ha-1. The difference could correspond to root respiration.

Some information on production can be found in Cannel (1982) (◘ Table E-2).

In Thailand, Ogawa et al. (1961) studied:

1. A sparse Dipterocarpaceous dry forest at an altitude of 300 m with light-standing trees about 20 m tall and a grass layer 20 to 30 cm high.
2. A moist mixed deciduous forest with trees 20 to 25 m tall and sparse grass growth.

The following values for phytomass t•ha-1 and primary production

(t•ha-1•a-1) were obtained:

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| Forest type | Phytomass | Production | (LAI) |
| 1 | 65,9 | 7,8 | 4,3 |
| 2 | 77,0 | 8,0 | 4,2 |

The deciduous forests are used by the population for shifting cultivation for three to five years at a time. After 10 to 20 years, a secondary forest grows on the abandoned areas. The trees do not seem to grow older than 100 years.

3 **Savannahs (trees and grasses)**

As mentioned, savannahs are tropical ecosystems in which woody species scattered in a tropical grassland compete with grasses (◘ Fig. E-7).

Grasses and woody species are two ecologically antagonistic plant types that are usually mutually exclusive (Huntley & Walker 1982). Only in the tropics with summer rains and on deep loamy sands are they in ecological balance with each other. The antagonism is caused by the difference of 1. The root system and 2. The water balance.

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| ◘ Table E-2 Quantitative comparison of two dry forests |
| 1 Light Miombo forest in Zaire (11°37'S, 27°29'E, 1244 m NN) |
| Tree species: Brachystegia, Pterocarpus, Marquesia and others |
| Soils: Latosols |
| BFI: 3.5 |
| Phytomasses above ground: 144.8 t•ha-1 (of which leaves 2.6 t•ha-1) |
| Phytomasses underground: 25.5 •ha-1 (estimated) |
| Net production: Litterfall 4 – 6 t•ha-1•a-1 |
| Wood production: Not determined |
| 2 Dry monsoon forest in India (24° 54'N, 83°E, 140-180 m NN) |
| Tree species: Anogeissus, Diospyros, Budenania, Pterocarpus and others |
| Soil: Reddish brown, lessivated sandy loam |
| Phytomass above ground: 66.3 t•ha-1 (of which leaves 4.7 t•ha-1) |
| Phytomass underground: 20,7 t•ha-1 (estimated)Annual net production:Trunks and branches: 4.4 t•ha-1•a-1Leaves: 4.75 t•ha-1•a-1Undergrowth: 0.35 t•ha-1•a-1Roots: (estimated) 3.4 t•ha-1•a-1 |

◘ Fig. E-6 Very large baobab (Adansonia digitata) east of Tsumeb (Namibia) (photo: Breckle) ► Fig. E-49.

1. The grasses have a very finely branched intensive root system that roots very densely through a small soil volume. It is particularly suitable for fine sandy soils with sufficient water capacity in summer rainfall areas where the soil contains a lot of water during the growing season. The woody species, on the other hand, have an extensive root system. The coarse roots reach very far horizontally as well as in depth and root through a large soil volume, but not so densely. This root system is particularly effective in stony soils where water is irregularly distributed, not only in summer rainfall areas but also in winter rainfall areas when water percolates and must be absorbed by the roots from greater soil depths in summer. Therefore, in winter rainfall areas, grasses do not play a role.
2. With regard to the water balance, the typical grasses are characterised by the fact that they transpire very strongly when the water supply is favourable, have an intensive photosynthesis and produce a lot of organic mass in a short time. When water shortage occurs after the end of the rainy season, transpiration is not slowed down, but continues until the leaves and usually the whole above-ground parts dry up. Only the root system and the shoot vegetation tips remain alive, and their meristematic tissue, protected by many sheaths of dry leaf sheaths, is capable of surviving a long dry season. The soil can almost dry out. Only after the first rains does new growth begin.

Woody plants, on the other hand, which have a large shoot system with many leaves, have a balanced water balance. At the first signs of water shortage, the stomata are closed and thus transpiration is greatly reduced. If the water deficiency worsens, leaf shedding takes place. During the dry season, only the axial framework with the buds remains. Although these are well protected against water loss, measurements have shown that even leafless twigs have a very low but measurable water release over the course of hours. The water reserves in the wood are not sufficient to compensate for water losses during a prolonged dry period, which means that the woody plants are dependent on absorbing a certain, albeit very small, amount of water even during the dry period. They dry out and die when the soil no longer contains absorbable water.

If one takes these differences into account, one can understand the ecological balance in the savannah. As an example, consider the conditions in SW Africa with gradually increasing summer precipitation in an area with balanced relief and fine sandy soils that absorb all rainwater and store most of it (◘ Fig. E-8). This is zonoecotone II/III, that is, the transitional area between ZB II and the deserts with summer rains. Climatic savannahs occur here with precipitation of 500 mm to 300 mm per year and a drought period of about eight months.

◘ Fig. E-7 Kigelia *africana* savannah(Bignoniaceae) in Kenya. The grass layer withers after the rainy season. One has the impression that the tree cover becomes denser on the slopes of the hills, but it is always the same savannah (photo: Breckle).

If the annual precipitation is only 100 mm (◘ Fig. E-8a), the water will not penetrate very deeply into the soil. In the soaked soil layers, the small horst grasses take root, consume all the stored water and then dry up after the rainy season; only the root system with the shoot vegetation tips (apical meristem) remains alive. Woody plants cannot survive because there is no water in the soil that can be absorbed by the plants during the drought (semi-desert). When rainfall is 200 mm, conditions are similar (◘ Fig. E-8b); the soil is more deeply soaked, and the horst grasses are larger, but they also consume all the water (grassland). Only when rainfall increases to 300 mm (◘ Fig. E-8c) will the grasses leave some water in the soil at the end of the rainy season; this small amount of water is not enough to keep the grass layer green, but it allows small woody plants to survive the drought period; a shrub savannah forms. If the annual precipitation is 400 mm (◘ Fig. E-8d), then the amounts of water remaining in the soil at the end of the summer rainy season are greater, so that individual trees establish themselves and a tree savannah results.

◘ Fig. E-8 Schematic representation of the transition from grassland (a and b) to shrub savannah (c) and tree savannah (d). Explanation in the text.

But even in this, the grasses are still the superior partner. It depends on them how much water is left for the woody plants, and this proportion can vary greatly from year to year.

Only when precipitation is so high that the tree crowns move together and, by shading the grass layer, prevent it from fully developing, does the competitive relationship reverse. In the savannah forests or rain-green tropical dry woodlands, the woody plants then become the determining competitive partner, and the grasses have to adapt to the light conditions on the ground.

However, this unstable competitive balance in the savannah is very easily disturbed when humans intervene through grazing. The grasses are eaten away, thus the water losses through their transpiration cease, more water remains in the soil after the rainy season and this benefits the woody plants (mostly *Acacia* species), which develop luxuriantly and fruit abundantly. Some species additionally form root shoots. The tree seedlings do not suffer from the competition of the grass roots; the tree seeds are spread with the excrement of the cattle that eat the pods and the mostly thorny shrubs grow so densely that scrub encroachment occurs, i.e. the pasture becomes worthless.

Scrub encroachment is a serious threat in all areas that are not rationally grazed. That is why thorn scrub is now more widespread as a substitute community than climatic savannah (thorn savannah), for example also in the arid parts of India, in N Venezuela and on the offshore islands (Curacao, Dominican Republic and others) (◘ Fig. E-9). If the area is more densely populated and the woody plants are used as firewood or for thorny enclosure of the cattle crest against predators, an anthropogenic desert with all the signs of desertification usually develops, covered with annual grasses only during the rainy season. During the dry season the cattle starve, having only the straw-like remains of the grasses as poor fodder. Such conditions prevail, for example, in Sudan, but also in N Kenya.

On stony soils the woody plants are absolutely superior to the grasses; grasses are almost entirely absent. With decreasing rainfall, woody plants become smaller and move further apart, because each shrub requires more root space, and the roots run shallow; for only the upper layers of soil are moistened.

Only a few small dwarf shrubs with xerophilous adaptations (dwarf shrub semi-desert) remain at the boundary with ZB III.

Special conditions prevail on two-storey soils (see below), as for example in Namibia, where a bush savannah then still grows with an annual precipitation of only 185 mm (◘ Fig. E-10).

◘ Fig. E-9 Cactus forest with Opuntia moniliformis and Neobootia paniculata near Jimani, Dominican Republic (photo: Breckle).

With this amount of rainfall, pure grassland would be expected on deep sandy soil; however, the soil profile shows sandstone of the Fish River Formation overlain by a 10 to 20 cm layer of sand, which is either finely bedded with small fissures or coarsely bedded with larger cracks. The upper sand layer does not retain all the rainwater, some seeps into the crevices of the sandstone. The grasses make use of the water in the sand layer, while the roots of the shrubs penetrate the deeper sandstone and consume the water contained in the cracks. The water supply in the crevices of the fine layered sandstone is only enough for the small *Rhigozum* bush. Roots in the cracksof the large-banked sandstone allow the larger *Catophractes* shrubto thrive (◘ Fig. E-11). Thus, the distribution of shrubs reflects the structure of the sandstone and is similarly found where the covering sand layer is absent. Competition exists between the shrubs. In larger crevices both species may germinate, but in time the larger one displaces the smaller, of which only the dead remains. There is no competition between grasses and the woody species in this case.

◘ Fig. E-10 Line profile (1 m wide) through a typical vegetation plot at Voigtsgrund (SW Africa). Grasses droughty during the dry season. Below, plant cover in plain view (without grasses). Ca = Catophractes, Rh = Rhigozum († dead).

**◘ Fig. E-11** *Catophractes alexandri* savannahin Namibia. Shrubs grow in the small crevices of the sandstones of the Fish Formation, and even trees in the larger ones (photo: N. Derber).

In ZE II/III, zonal savannahs occur instead of deciduous forests when annual precipitation is too low for the latter. In ZB II, on the other hand, where despite sufficiently high precipitation the soil contains too little water during the drought period for a forest to survive, zonal savannahs spread. On the other hand, too much water during the rainy season, i.e. waterlogging, also precludes the growth of woody plants. A pure grassland then forms, which can dry out during the drought season and which is typical of parklands. In ► Fig. E-1 **a-h** we have explained this. Some examples are given to show how the crust formed in the soil at different depths affects the vegetation mosaic. The effect of the crust can only be determined and studied in more detail by working in the field during heavy rains to observe runoff and water infiltration into the soil and relate it to the vegetation type in question (although areas are often difficult to access during the rainy season).

The ► Fig. E-1**e** is a slightly hilly area of the northern Kalahari with deep sand. Adherent water at field capacity is relatively low, so that much of the rainwater percolates and the adherent water is only sufficient for savannah vegetation. But in places laterite crusts prevent water from percolating. Depending on the depth of the crust, dense woody vegetation or dry forest may develop over the moist sand. If the crust is shallow in a depression, the soil above it is waterlogged, and only grassland grows.

On ► Fig. E-1**f**, there is a continuous laterite crust in the sandy soil, which forms a depression on the left, above which seepage water flowing in laterally also collects. The soil is well aerated and moist at depth, so that the zonal deciduous forest finds favourable conditions; in the middle is a depression with grassland that is flooded during the rainy season, on the right on somewhat higher relief parts with clayey, base-saturated soils, the grassland is interspersed with some woody species adapted to heavy soils (mopane, Balanites, flute *Acacia*) (◘ Fig. E-12).

► Figure E-1**b** shows the vegetation structure again in a low-water-holding sandy area with a savannah in which the woody plants dry down to the ground during the drought and sprout again from the stem base or as root shoots in the rainy season. Where laterite crusts lie at different depths, depending on the water conditions, a grove or a savannah forest develops on the elevations or, in the lowlands, a shallow small lake (Vley) with swamp vegetation that can dry out during the drought. Some trees may also occur over laterally draining excess water at the edge of the crust. One can thus see how, depending on the position of the crusts, forest and savannah alternate or, in the case of waterlogged soils, parklands develop.

◘ Fig. E-12 Acacia drepanolobium scrub (flute *Acacia*) with galls (ant nests) over heavy soils in the grass savannahs of northern Kenya (photo: Breckle).

In contrast to ► Fig. E-1**f**, the continuous crust in ► Fig. E-1**a** is the same depth everywhere and the overlying soil is waterlogged and covered with grassland in the rainy season; only on small elevations is the soil better drained and supports a tree savannah (left) or, in the case of larger root space, a woody plant. On the far right is a depression with an open water table; a reed bed is developing at the edge of the water basin.

The hardened layer of the B-horizon is not infrequently exposed on slopes by erosion. It leads to the formation of mesas. At the edge of these mountains, step formation leads to steep slopes, as shown in the development in ► Fig. E-3.

There are other factors that promote savannah vegetation, such as fire (◘ Fig. E-13), the large game herds (◘ Fig. E-14), and the various interventions of humans with their livestock. For example, in Pendjari National Park in Benin, West Africa, park management sets small-scale controlled fires annually at the beginning of the dry season to prevent the accumulation of larger dry masses. These fires are considered 'cool' and once out of “topkill height” do not kill trees and shrubs and prevent uncontrollable large-scale 'hot' fires (► Fig. E-13).

◘ Fig. E-13 Fire in the savannah in Pendjari National Park in Benin, West Africa (photo: A. Erpenbach).

Fire has been effective in the climatic region of ZB II as a natural factor long before the appearance of man. Thunderstorms usually usher in the rainy season; since there is a lot of dry grass around this time, lightning can easily start a fire. The frequency of such fires is proved by the many pyrophytes, that is, species of wood which are resistant to the action of fire. The tree or shrub species often have a thick bark which is only charred and protects the cambium, or the shrubs have dormant buds above the root collar in the ground which sprout when the above-ground shoot parts burn. Many species have underground storage organs that can lignify (Lignotuber, ► fig. E-54) and allow rapid regeneration.

**◘ Fig. E-14** Big game herds in the Ngorongoro Crater National Park (Tanzania) in the grass savannah area (photo: Breckle).

Grass fires were already set up by primitive man in prehistoric times to protect himself and his places of settlement from the danger of surprising fires caused by lightning. For with the high growth of grasses in the wetter zones, fires spread with great speed and violence. Today, burning during the dry season has become a common bad habit to facilitate the hunting of big game, or to destroy vermin (snakes, etc.). After a grass burn, the grasses sprout earlier, which is initially favorable for grazing.

The grass fires can only invade dry forests with grass understory, but they also push back the wet forest at the edge, causing a sharp borderline. Above all, however, they prevent the forest from reclaiming lost terrain as well as the cleared and subsequently grassed areas.

In northern Venezuela, fire also plays an important role in the equilibrium between Byrsonima crassifolia (with very low density) and the perennial C4 grasses Trachypogon vestitus and Axonopus canescens, in addition to water supply and nutrient distributions (► Fig. E-26). However, there is also a very unstable equilibrium between the two grasses, which Inchausti (1995) investigated by transplanting experiments. Only under absolute protection does Axonopus gradually replace Trachypogon.

A very essential factor for savannahs is grazing by large game (Anderson et al. 1973) (◘ Fig. E-15). Young tree growth is destroyed by browsing and trampling. Elephants are particularly hostile to forests. They tear out trees or debark the trunks. Elephant tracks clear the forest and allow grass fires to enter the forest. One elephant can destroy an average of four trees per day. Tree losses in miombo woodlands reach up to 12.5% per year. Elephant numbers are increasing rapidly in protected areas. Lake Albert's Murchison Park (in Uganda) is being deforested by elephants over time. In the Serengeti (in Tanzania), on the other hand, there seems to be a balance between game damage and vegetation regeneration (◘ Fig. E-16).

It is striking that in Africa, which is rich in game, many woody plants of the savannahs are thorny (◘ Fig. E-17; ◘ Fig. E-18), whereas this is much less the case in South America and Australia, which are poor in game. This speaks for a selection of species protected from wild browsing.

An indirect impact on vegetation comes from game trails, which easily initiate furrow erosion. This is especially true for hippos, which climb up the riverbanks from the water at night to graze on the grasslands.

Erosion furrows can drain a wet grassy area, which in turn allows woody plants to encroach. A summary of these multiple impacts of big game can be found in Cumming (1982). Even greater is the impact of humans, both livestock producers and arable farmers.

Grazing on the savannahs north of the equator began at least 7,000 years ago. Forests are only present in small remnants in this area; a large part of the savannahs is therefore likely to be secondary in nature (Hopkins 1974).

In summary, the following savannah types are distinguished according to their genesis:

1. Fossil savannahs formed under formerly different conditions in the area of ZB I
2. Climatic savannahs in the area of ZE II/III with annual precipitation below 500 mm
3. Edaphic savannahs, that is, ZB II savannahs conditioned by soil properties:
4. On soils whose water balance is less favourable than it should be according to the amount of rainfall due to crusty accumulation horizons (laterite crusts, clay layers, compacted silt or sand layers).
5. On soils that are primarily so poor in nutrients that forests cannot grow on them.
6. Within parklands with wet soils during the rainy season as a special type of palm savannah.
7. Secondary savannahs as a result of fires, impact of big game and the various interventions of man.

What type of savannah it is in each individual case cannot be determined by eye, but requires a detailed investigation.

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| **Box E-3** Human interventions against forests  |
| All interventions, such as fire, grazing, clearing in the context of shifting cultivation or firewood extraction are directed against the forest.  |

◘ Fig. E-15 The volcanic areas in East Africa are blessed with fertile soils. Here, a savannah landscape with a high species richness of big game can be found (photo: E. Fischer).

◘ **Fig. E-16** Acacia savannah in Maasai land of the Serengeti in Tanzania (photo: Breckle).

◘ Fig. E-17 Inselberg and thornbush savannah in Olduvai Gorge, Tanzania, west of Ngorongoro, the valley of prehistoric man with numerous Pleistocene fossil sites of hominids (photo: Breckle).

◘ Fig. E-18 Thorn and succulent bush savannah with arboreal euphorbias on the slope of Ngorongoro Crater (photo: Breckle).

**4 Park** landscapes

In the case of very flat terrain, park landscapes usually form in the ZB II. This landscape is conditioned by differences in relief that are hardly noticeable in the terrain and which are not perceived during the drought period. During heavy rainfalls in summer, all deeper parts of the relief are flooded, because it takes months for the water to drain away. These biotopes are occupied by grasslands; the soils are grey, while on the higher non-flooded parts, where the woody plants grow, the soils are deep, red sandy loams. The river system here begins on the watershed with barely sunken strips covered with grass, which unite below and gradually change into incised stream and river beds as the gradient becomes steeper (easily seen from the plane).

A special formation is the termite savannah, which is understood to mean wide grass-covered depressions from which broad, abandoned termite heaps protrude as islands, which are not flooded and which can therefore be covered with tree growth. It is therefore a mosaic of two different communities (◘ Fig. E-19), i.e. not an actual savannah. However, this depends entirely on the particular termite species and its species-specific burrows. In N Australia, savannahs with numerous small columnar burrows are found. Massive tower-shaped structures in the Catophractes savannah in Namibia and Uganda remain for decades (◘ Fig. E-20).

◘ Fig. E-19 Dry bush with young baobab trees, briars and Sansevieria in the understory in the Serengeti, Tanzania (photo: Breckle).

◘ Fig. E-20 "Termite savannah", intermittently flooded grassland with tree growth on old termite piles west of Georgetown, Murchison Falls, Uganda (photo: E. Fischer).

◘ Fig. E-21 Polygonal dry cracks of the clay layer in an Amphi-Biom, in the dry valley of the Rio Chota in Ecuador (photo: Rafiqpoor).

The deeper depressions with black clays referred to as 'Mbuga' are a special Amphi-Biom with alternating wet soils and a hard iron concretion layer at 50 cm depth. Because potential evaporation far exceeds the 1,000 mm rainfall, the clay soil dries to a depth of 50 cm in August to December and is divided into polygons by deep crevices (◘ Fig. E-21). Such biotopes are unsuitable for tree species. Trees only grow where the groundwater table is always below 3 m. The laterite crust is also located at this depth and the roots of the trees reach just as deep.

In contrast to the termite savannah, the palm savannah is a homogeneous plant community. As woody monocotyledons, palms have a tufted root system consisting of identical, barely branching roots that spread radially so that the palms stand alone in the grassland. They tolerate intermittent flooding. The soils of palm savannahs are likely to dry out less during drought than those of pure grasslands, but no studies are available on the competitive relationship between palms and grasses (► 'Palmares').

In very open savannahs, the trees stand far apart as isolated individual trees. Belsky & Canham (1994) compared this island biotope situation (idiotpe) with that of tree gaps in forests (◘ Fig. E-22). The area influenced by a treefall in the forest and its dynamics up to canopy closure and, on the other hand, the area dominated by the individual tree in the grassland and its development into a group of trees or tree-free grassland are compared as contrasting structural elements in ◘ Table E-3.

Fig. E-22 Comparing individual trees in the savannah and the tree-fall gap in the rainforest, there are remarkable parallels in the expression of the 'island biotope' or 'idiotope' (modified after Belsky & Canham 1994).

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| Table E-3 Comparison of some processes in forest gaps of a closed forest and in individual trees in grassland (after Belsky & Canham 1994). |
|  | Forest gap  | Isolated tree in the savannah |
| Origin | Mostly sudden (episodic storm event) | Slow (germination, seedling establishment) |
| Enlargement | Seldom due to falling branches or trunks of neighbouring trees | Gradually by enlarging the crown |
| Disappear | Mostly quickly due to overgrowth by neighbouring trees | Possibly very suddenly due to the death of the tree |
| Duration | Short (5-30 years) | Long (lifetime of the tree, usually well over 50 years) |
| Resource dynamics | Usually only short, additional release of nutrients | Mostly permanent preference by game and input from outside (detritus) |
| Secondary succession | Only in large gaps in the forest | Rarely identifiable |
| Ecological effect on the environment | Short range (5-20 m) | Longer range (50-100 m) |

5 **Examples of large savannah areas**

In South America, very extensive savannah-like vegetation types are common along the Orinoco, in central and eastern Brazil, and in the Chaco region.

Along the gradient from the perhumid tropical rainforest to the extremely dry tropical desert, the structure of the vegetation stocks changes fundamentally; the importance of the respective life forms is also very different. Ellenberg (1975) has summarized this in a general scheme (◘ Fig. E-23) that applies to the lowlands of the Andes but is in principle also transferable to other areas with similar gradients.

A few examples of large-scale savannahs are highlighted below.

5.1 **Llanos on the Orinoco**

The Llanos are located in Venezuela at 100 m asl in a basin landscape that was still a sea in the Tertiary. They occupy a width of 400 km on the left bank of the lower Orinoco and continue for another 1,000 km to Colombia. This basin was filled up by the rivers with the weathering products of the Andes. The climate of the central llanos around Calabozo (► Fig. E-44) is very typical of zonobiome II: Annual precipitation over 1,300 mm, rainy season seven months, drought season five months. Thus, a moist deciduous forest would be expected in this area. It is also present in typical formation, but only in the form of isolated very small groves - the "Matas". The deep llanos bordering the river and flooded during the rainy season are, as usual in ZB II, a pure grassland (trees only on the embankments as gallery forest: ◘ Fig. E-24). Otherwise, the area is covered by a grassland about 50 cm high with scattered small trees (Curatella, Byrsonima, Bowdichia), i.e. a typical savannah. Since this cannot be climatic (the precipitation is too high), only edaphic causes, i.e. soil conditions, come into question.

Fig. E-23 Formation structure and distribution of life forms in the lowlands of the Andean foreland along a climatic gradient (modified after Ellenberg 1975).

The often expressed assumption that it is an anthropogenic savannah created by fire from forest is the simplest, but also the most uncritical. The savannah existed before the arrival of the whites. The Indians had not used it for cropland or pasture. Fires always occur in grasslands by lightning. Certainly, the Indians will have set fire to the dry grass more often than not, but they could only do so because natural grasslands already existed. Fire helped shape the savannah by causing only fire-resistant woody species to grow in the grasslands and at the edge of the Matas, but it was not the primary cause of these vast grasslands. In the central llanos, it has been demonstrated that at a time when groundwater was still very high in the basin landscape, a laterite crust was formed that was cemented by iron hydroxide. It is referred to there as 'Arecife' (◘ Fig. E-25). It extends at variable but shallow depths (most commonly 30 to 80 cm deep) below the ground surface, rarely sinking below 150 cm, but also emerging at the surface or being eroded out.

◘ Fig. E-24 Example of gallery forests: Here from West Africa along a river in the savannah areas of Comoé National Park (Côte d'Ivoire) (photo: Barthlott).

The impermeability of the arecife to water is not true in this case; because during the summer rainy season 750 mm of rain falls in three months. These quantities cannot be absorbed by the soil above the arecife; there would therefore have to be a flooding of the flat surface, which is not the case. The red colouring of the soil also argues against prolonged waterlogging. On the other hand, a groundwater-rise under the arecife from -575 cm to -385 cm (► Fig. E-25), i.e., by almost 2 m, was observed at the end of the rainy season. Assuming a pore volume of the alluvial deposits of about 50%, this would mean that about 300 mm is retained by the soil above the arecife and 1,000 mm percolates through. On an arecife exposed by erosion on the river bank, it could be clearly seen that quite irregular passages lead through the hard crust at individual points.

◘ Fig. E-25 Scheme for interpreting water conditions in the llanos north of the Orinoco. Below the arecife, the changing groundwater table is accessible only to deep-rooted plants (modified after Walter 1990).

The grasses take root in the fine-grained soil above the arecife and consume about 300 mm of rainwater for their development. The woody plants, however, stand where their roots growing along the arecife surface, find a passage through the arecife and through this then reach the moist rock layers below. There, water is available to them in sufficient quantity. If the passages are very large or if they lie close together, a group of trees can grow above them; small forest stands, on the other hand, can only be found where the arecife is completely absent in places or lies very deep, so that the vegetation appropriate to the climate develops, i.e. a deciduous forest. One must thus regard this savannah as a stable, natural plant community in which the tree distribution reflects the arecife structure. This is supported by the following facts:

* 1. Where the arecife is superficial, the grass cover is absent, but scattered small trees at greater distances grow on it; in this case the roots must reach through the arecife into the soil below.
	2. Curatella remains green during the dry season, in contrast to the other behaviour of woody plants in the typical savannah, a sign that its water supply is good all year round. Transpiration measurements showed that a small tree transpires about 10 liters per day during the drought season; since the soil above the arecife is dry during this time, the water must come from the soil layers below the arecife. The same is true of the other species of wood.
	3. Where the groves ('Matas') grow, arecife is locally absent, allowing tree roots to penetrate deep into the soil unhindered.

The final proof could only be provided by root excavations on larger areas, which, however, are very difficult to carry out. Blasting the arecife with dynamite would have to lead to the spread of the woody plants. Slight depressions are interspersed in the savannahs of the llanos, into which the water drains after heavy downpours (1961: 38 mm in 20 minutes) and in which grey clays are deposited, so that the water in the depressions is about 30 cm deep during the rainy season. Towards the end of the drought period the grey soil dries out completely.

This alternating humidity is well tolerated by certain grasses (Leersia, Oryza, Paspalum and others), but not by the tree species, with the exception of the palms. The 'Palmares' are then formed, grasslands with the palm Copernicia tectorum, i.e. palm savannahs, also widespread in tropical Africa. These areas also often burn down, but palms withstand fire well (as do tree ferns) because they have no cambium to be damaged. The dead leaves of palms that surround the trunk burn, and the outer leading bundles char; this char layer acts as an insulator in later fires. The cone of vegetation surrounded by young leaves remains. If old leaves are completely missing from the trunk, it is a sign that the palm savannah has only recently burned down; if they enclose the trunk down to the ground, the palm has not yet been exposed to fire; if only the lower part of the trunk is bare, the palm has grown a number of years in height since the last fire.

Part of the water must run off the areas covered with palms; otherwise, the soils would dry out, since a rainfall of 1,300 to 1,500 mm is countered by a potential evaporation of 2,428 mm, i.e. the hydrological water balance is negative. When the soils are permanently wet, Mauritia *minor* palmoccurs. Black acidic peaty soils with some grasses, Rhynchospora, Jussieua, Eriocaulon and the insectivorous Drosera species (sundew) and others are formed. These areas, as well as the alternating wet grassland already mentioned, are also a particular form of helobiome and amphibiome.

Today, many of these areas are burned annually to improve pasture. This naturally synchronizes the growth of the different grass species. The periodic niching of biomass production is then particularly clear (◘ Fig. E-26).

Fig. E-26 The annual rhythm of green biomass of six dominant grass species of the Venezuelan llanos after the usual fire in March shows a close temporal mixing of the grass species (yellow grid: flowering time) (modified after Sarmiento 1996).

Further east, the llanos merge into a plain with sandy deposits of the Orinoco River, which used to bend north here and flow into the Caribbean Sea through the Unare lowlands.

The quartz sands, which are often quite white, are weathering products of the quartzitic sandstones of the Guiana mesas, which correspond to those of the Brazilian Shield and are likewise almost nutrient-free. Similar leached quartz soils also occur on other ancient Gondwana sites. The savannahs, some of them pure grasslands, are probably due to similar causes as the Campos Cerrados.

5.2 **Campos Cerrados**

These are savannah-like vegetation covering an area of two million square kilometres (= 23% of the total area of Brazil, Ruggiero et al. 2002) in central Brazil (Eiten 1982) (◘ Fig. E-27). The cover of the 4- to 9-m-high tree stand varies from 3% to 30%. The climate, with annual precipitation of 1,100 to 2,000 mm, is characterized by a five-month long drought. Rawitscher (1948) was the first to study the water balance of these savannahs and proved that the deep soil remains permanently moist even at a depth of 2 m, so that the deeper-rooted woody species always have sufficient water available, remain evergreen and transpire strongly even during the drought period. Only the grasses and shallow-rooted species dry out or drop their leaves during drought. The soils are weathered products of the granites and sandstones of the Brazilian Shield and are very low in nutrients, especially phosphorus, but also potassium, zinc and boron. Crops of cotton, maize and soya with various applications of fertiliser showed this to be the case. That it is not the water factor but nutrient poverty that prevents the formation of zonal deciduous forests is shown by the fact that near Sao Paulo a zonal semi-evergreen forest grows on basalt soils. The Campos Cerrados were regularly burned. The presence of many pyrophytes shows that fire was also a natural factor here since ancient times. Fires reduce the density of stands, but they are not the real cause of the lack of closed forest vegetation (Coutinho 1982).

◘ Fig. E-27 Campos Cerrados comprise large areas in Minas-Gereis, SE Brazil, with tree heights of 3-4m. They form a partly impenetrable bush formation (photo: Denis A.C. Conrado, https://pt.m.wikipedia.org/wiki/Ficheiro:Bonfim\_047.jpg).

5.3 **The Chaco area**

This is the westernmost part of ZB II in South America, a vast plain between the Brazilian Shield to the east and the pre-Andean mountain ranges to the west. The central part of this plain is only about 100 m above sea level. The plain extends from S Bolivia, most of Paraguay, and well into W Argentina for 1,500 km from north to south at an average width of 750 km (Hueck 1966).

During the heavy summer rains, large parts of the plain are flooded, especially in the eastern part (annual precipitation 900 to 1,200 mm). The temperature can rise above 40 °C, it is the heat center of S America. It is a park landscape with forest, wide periodically flooded grasslands, palm savannahs or swamps (◘ Fig. E-28). In the central part, dry savannahs occur in addition to parkland. The western part in Argentina is heavily scrubby, and salt pans with the halophytes Allenrolfea and Heterostachys also occur. The southern Chaco leads to the Pampa. The relief is very flat, impermeable layers occur in the soil; the vegetation is mainly a Prosopis savannah with a grassy layer of Elionurus muticus and Spartina argentinensis. The main tree species of the Chaco forests are strongly tannic Quebracho species Aspidosperma quebracho-blanco (Schinopsis quebracho-colorado and *S*. balansae and others). Of the palms, Trithrinax campestris is common, while Copernicia alba is typical for moist depressions.

◘ Fig. E-28 Chaco in Paraguay covers about 60% of the land area in Paraguay and parts of the Bolivian lowlands. In the wet parts, Chaco has the character of a parkland as shown here in the picture. The dry parts, however, are a thorn savannah (photo: Ilosuna, [https://t1p.de/av1l](https://t1p.de/av1l%22%20%5Ct%20%22_blank)).

The mammal fauna is not species-rich. Termite eaters are Myrmecophaga tridactyla and Tamandua tetradactyla. Of predators, the jaguar (Leo onca), puma (Felis concolor) and many smaller species are or were represented. Rodents are numerous; on trees are found the sloth Bradypus boliviensis, three species of monkeys (Cebidea), the tree porcupine (Coenda spinosus) and the mustelid Eira barbara, in addition to many insectivores or bats feeding on fruits and flowers, and the blood-sucking vampire Desmodus rotundus.

Of the birds, the large ratite Rhea americana should be mentioned, the reptiles are represented by two rare species of caiman, three species of turtles, some poisonous snakes (a total of 25 species of snakes) and various lizards; of anurans, 30 species are known so far. In addition, there are countless invertebrates.

Ecosystem research has probably not yet been initiated. The main human interventions occur through deforestation and grazing, which can lead to scrub encroachment.

In the last few decades the country has been increasingly conquered by large farms and in some cases intensively used for agriculture. The agricultural front is spreading rapidly into the drier areas of the Chaco. The focus is on planting huge monocultures, for example soy, for export, and recently *Jatropha* for biodiesel. The livelihoods of many still nomadic indigenous groups are threatened by the often illegal clearings. In many places the indigenous people therefore see their basic right to food being violated.

5.4 **Savannahs and park landcapes of East Africa**

This area, lying at the foot of the great volcanoes, with the giant crater Ngoro-Ngoro (◘ Fig. E-29), the East African Rift Valley, and the vast Serengeti range, is widely known, especially for its abundance of game (►Fig. E-14; Fig. E-15), which may also be related to the nutrient-rich volcanic soils and thus better plant food. But in this equatorial area with a diurnal and monsoon climate, two rainy seasons occur, one small and one large. Usually, these are separated only by a short drought period, which is hydrologically more favorable. Their effect is similar to that of a summer rainy season, so that with annual precipitation of around 800 mm one encounters similar savannahs and park landscapes as in ZB II.

Fig. E-29 View of Kilimanjaro volcano (5,890 m asl, Tanzania) in East Africa. The volcano's snow cap has completely melted except for a small remnant (Climate change!) (photo: Breckle).

Clearing, annual fires and overgrazing have strongly influenced the plant cover; as a result, different stages of degradation are common. It is often referred to as an 'orchard steppe', but it is a typical tree savannah. When the climate becomes drier, or on dry rocky sites, large candelabra euphorbias (► Fig. E-18) and Aloe species occur (◘ Fig. E-30).

◘ Fig. E-30 Aloe in area of Serengeti National Park in Tanzania with low summer precipitation (ZE II/III) (photo: Breckle).

There are today several National Parks and Game reserves. With colonization, big game hunters began to shoot down animals in large numbers and thus to decimate the populations. This arbitrary killing of wild animals ultimately made it necessary to set up nature reserves in order to protect the savannah habitat and the wildlife there. In the 19th century the area was still grazing land for the nomadic Maasai people. The Maasai, who were not to blame for the destruction of nature, were severely restricted in their freedom in their own homeland by the nature reserves (Poole 2006).

The Serengeti was partially declared a game reserve (Serengeti Game Reserve) as early as 1929 to protect the lions that were previously considered pests. In 1940 it was declared a Protected Area. In 1951, the Serengeti National Park was established, which at that time also included the Ngorongoro Crater. In 1959, the wildebeest rainy season pastures in the southeast of the Serengeti at the Ngorongoro Crater were separated from the national park and declared only a conservation area, in which Maasai herders are allowed to graze their cattle.

The Serengeti is one of Africa's most complex and least disturbed ecosystems, ranging from dusty summer drought to green winter and lush spring. The focus is on the savannah with scattered acacias. To the south there are wide open short grass plains, to the north there are long grasslands covered by thorn trees, along the rivers gallery forest and in the hilly western corridor extensive forests and black clay pans.

5.5 **Monsoon forests in India**

India is located in the south of the largest continental landmass - Asia - and is rightly called a subcontinent due to its large expanses, approximately 3,220 km in north-south and approximately 2,980 km in east-west direction. Connected to Africa, Antarctica and Australia by land bridges until about 180 million years ago, it has been moving northwards ever since, folding up the Himalayas, which also form the natural boundary to the north. This high mountain range is still evolving; the earthquake in May 2015 with its devastating consequences in Nepal is evidence of the steady and current geo-morphodynamics in this region.

The determining factor of the Indian climate is the rain-bringing summer monsoon. It is caused by the summer warming of the inner Asian land mass with the formation of the inner Asian low pressure area. This sucks in air from the summer high pressure area over the Indian Ocean, which is cooler relative to the land mass. The resulting southwesterly air flow (SW monsoon) brings in a lot of moisture from the Indian Ocean and rains down on the mountain flanks of the Western Ghats facing it with an average of 2,500 mm to 3,000 mm of rain per year (also with maximum values of up to 10,000 mm, e.g. in Cherrapunji: ►Fig. A-8) and on the Himalayas.

The climate of India corresponds to the zonobiome II and in the dry NW to the zono-ecotone II-III. It extends marginally to the Afghan border.

Although the Indian flora undoubtedly belongs to the Palaeotropics, it has many peculiarities peculiar to itself. The reason for this is the certain isolation of the subcontinent due to the shielding effect of the mountain ranges in the north, the long coastline in the south and the arid regions in the northwest. Nevertheless, distinct Holarctic influences are found, completely dominating the higher elevations of the north. Isolated elements of Gondwanaland (e.g. the Podocarpaceae) indicate the former land connection to Africa, Antarctica and Australia. The relative isolation, which allowed immigration of new species only slowly and predominantly from the north-eastern flanks, resulted in numerous endemic genera and species via radiation from existing clades. Again, some species just reach across the Afghan border in the subtropical thorn savannahs of the Khost basin and in Nangarhar.

Champion & Seth (1968) classify the vegetation of the Indian subcontinent on the basis of the dominant woody vegetation types. The respective vegetation type depends primarily on the total amount of local precipitation, its seasonal distribution and the relationship between precipitation and evapotranspiration.

The tripartite division of the forests of the Indian subcontinent is summarized in ◘ Fig. E-31 as follows: Numbers 2 to 7 are the monsoon forests proper, Numbers 8 to 11 indicate forests of the hilly and low mountainous regions, and Numbers 12 to 14 those of the mountainous regions of the Himalayas.

As an example, the particularly extensive alternating green tropical monsoon forest (4) is described here (◘ Fig. E-32c).

This vegetation type covers the largest area of India and is widespread both in the northern part of the Deccan highlands up to the edge of the Ganges basin and in the southern part. The outer canopy reaches 20 m, is built up of only a few tree species, mostly leafless in the dry season, and is not completely closed. The middle canopy layer is almost completely alternate green, allowing enough light to pass through for a patchy shrub layer with a high proportion of grasses and bamboo. In the dry season, this forest is therefore quite bare (◘ Fig. E-32d).

Representatives are: Tectona grandis (= teak; Verbenaceae), Diospyros tomentosa (Sapotaceae), Aele marmelos (Rutaceae), Butea monosperma, Anogeissus latifolia, Adina cardifolia, Buchanania langan etc. Most probably, human use (grazing) has also significantly altered this forest type and probably favored the occurrence of grasses. Mostly, now this forest type has degraded to open scrub due to intensive grazing (◘ Fig. E-32e).

Fig. E-31 Spatial differentiation of the vegetation units of the Indian subcontinent (modified after Champion & Seth 1968).

The second example is the moist, alternating-green tropical rainforest (**3**), which is often referred to as the actual monsoon forest (◘ Fig. E-32b). A forest type, found in large areas of India with 1,000-2,000 mm of rainfall, it would not have been severely repressed by millennia of continuous use and replaced today by open agricultural landscapes, tea plantations, and planted timber forests. It is found in parts of Assam, in the basin of the Ganges and Godavari rivers, in eastern Sri Lanka and on the western flank of the Western Ghats. In this range alone there are 4,000 species with 1,500 endemics (► Henry et al. 1987, 1989, Nai & Henry 1983, Pascal 1988). With irregular outer alternate green canopy layer, the forest also reaches 40 m or more. The second, lower canopy layer is formed increasingly by evergreen species, and a shrub layer is developed. There are Pterocarpus dalbergoides, Shorea dalbergoides, S. robusta = "Salbaum" (Pterocarpaceae), Terminalia bilata, T. procera (Combretaceae), Albizzia lebbeck (Mimosaceae), Erythrina indica (Fabaceae) with its spectacular red flowers, Bauhinia purpurea (= "orchid tree"; Caesalpiniaceae), the Bengal fig = Ficus benghalensis (Moraceae) which branches out over several hectares, Lagerstroemia parviflora, Adina cardifoia. Bamboo species are widespread as spreading climbers. Massive termite mounds (◘ Fig. E-32f) are common in these partly dry forests.

◘Fig. E-32a: Lianas, epiphytes, and hanging aerial roots characterize tropical ever-humid lowland rainforest in northeastern India (e.g., near Siliguri), but it is also still strongly influenced by the monsoon; b: Tropical moist fallow deciduous forest in Kambalkonda Wildlife Sanctuaryin Visakhapatnam, SE India (photo: Adityamadhav, [https://t1p.de/48vg](https://t1p.de/48vg%22%20%5Ct%20%22_blank)); c: Tropical dry deciduous forest in monsoon area in Mandhya Pradesh (Photo: L.R. Burdak, [https://t1p.de/25lf](https://t1p.de/25lf%22%20%5Ct%20%22_blank)); d: Semi-evergreen in valleys, species-rich dry deciduous forest on slopes at Ajanta and Ellora (with ancient temple caves) and millennia of use; e: Stratified ribs at Nowgong with open tropical deciduous scrub or thorn scrub, valley bottoms cultivated; **f**: Large termite mounds in dry fallow deciduous forest, the typical monsoon forest, here in Orissa (eastern India) during leaf fall in the dry season in February (photos **a,d,e,f:** Breckle).

On the Indian subcontinent, practically all ecosystems known from the tropical-humid, tropical-arid, from humid-temperate and dry-temperate to alpine areas occur - from lowland rainforest (◘ Fig. E-2a), swamp forest and the mangroves to the dry forests, thorn-bush and thorn savannahs (◘ Fig. E-2e) to the semi-deserts (◘ Fig. E-32f) and deserts, from evergreen deciduous and evergreen hardwood and coniferous forests to high mountain tundras. It is certain that this great diversity of ecosystems has led to the high biodiversity (► Wilson 1988, Pullaiah & Ramakrishna 2018) of the subcontinent.

Due to the high relief energy, almost all ecosystems of the orobiomes are represented, both from the tropical-subtropical area and from the temperate latitudes. For the tropical orobiomes, especially in the east of the Himalayan mountain flank, the worldwide peculiarity applies that they are characterized by extremely high monsoon rains. There is no Páramo, since - in contrast to the tropical Andes or the tropical high mountains of Africa - seasons are clearly pronounced in the Himalayas.

Human influences on vegetation have a long tradition, especially in India with its early advanced civilizations. Early migrations led to completely different races with completely different languages and religions settling and using the continent in different waves. For this reason, it is often difficult to even address an original, potential vegetation, although India has a high, independent biodiversity with many endemic species.

5.6 **Vegetation of the Australian ZB II**

With the exception of a few small relicts of deciduous forests in NE Australia with Indomalaian flora elements and some deciduous Eucalyptus species in N Australia, but almost insignificant, this vegetation type does not exist. But parklandscapes also with palms are common in the ZB II area, but with evergreen Eucalyptus species. A little further south, savannahs with a covering grass layer of Heteropogon contortus (also with evergreen eucalypts) occur with lower annual precipitation.

In the detailed vegetation monograph by Beadle (1981) the term 'savannah' does not occur. In contrast, the Australian researchers (Walker & Gillison 1982) count all light forests as savannahs if the grasses of the herb layer have a cover of more than 2%, which would have to include most light eucalypt forests.

One can say now that the largest and still relatively unaffected savannah is in Australia. It extends over an area in the north of the continent that is larger than Western Europe, and since the increasing disappearance and cultivation of the savannah areas in Africa, Asia and South America, it now represents more than a quarter of the world's savannah area.

While on other continents the savannah area - the transition zone between the tropical rainforests and the large desert areas characterized by grass and groups of trees - continues to decline due to urban sprawl and animal husbandry, it has remained largely intact in northern Australia. A network of nature reserves and a relatively thin population - mainly in the form of smaller Aboriginal settlements - are responsible for their preservation.

It is to be hoped that gentle partial development will not also lead to exploitation and desertification.

The Australian savannah cannot keep up with the African savannah in terms of fauna. The previously species-rich Australian megafauna has practically completely disappeared already 50,000 years ago - around the time when Australia was first colonized by humans: the large grazing animals such as the hippopotamus-sized giant wombat *Diprotodon*, the largest known marsupial, as well as the large ones predatory mammals. Only a few "larger" mammal species have survived, including the antelope kangaroo, which is slightly smaller than the gray giant kangaroo that lives in southern Australia.

Spectacular herds like those in the African savannah are brought about by an involuntary immigrant from Afghanistan: the descendants of dromedaries that were imported to Australia from the 19th century and kept as load carriers by Afghan camel drivers. In the absence of food competition and large predators, they could run wild and fill the free ecological niche. Hundreds of thousands of them live today from the northern grasslands to the arid areas in the middle of the continent and have become a plague that is now being reduced by shooting and control programs.

6 **Ecosystem research - examples**

One of them, the Lamto Savannah, is located in West Africa and is a relict savannah in the rainforest area, the other, the Nylsvley Savannah in South Africa. It borders the Kalahari to the west. Grasses and trees are the components in the savannah. The number of species of grasses is relatively low, more significant is their biomass; the reverse is true for legumes (◘ Fig. E-33). In addition, however, there are numerous other rarer species (about 25%), but their biomass is only about 1.5%.

**6.1 The Lamto savannah**

This savannah is located in the Guinea forest zone (Ivory Coast area) at 5° W and 6° N, still in ZB I. It is burned every year, so that the rainforest adjacent to it cannot advance, even if the soil conditions would allow it. The mean annual precipitation is 1,300 mm. There is a drought period of only one month - in August - on the climate diagram, but the weather pattern varies greatly from year to year; rainfall ranges from 900 to 1,700 mm per year. On the higher part of the relief, a tree or shrub savannah grows on red savannah soils with laterite concretions. On the other hand, in lower parts of the relief, palm savannah grows on waterlogged soils.

The different plant communities were studied by Menault & Cesar (1982) (◘ Table E-4).

Lamotte (1975) dealt with the consumers and destroyers of this savannah: Big game occurs only sporadically. The zoomass (per in kg ha-1) of birds is 0.2 to 0.5; that of twelve rodent species 1.2; that of earthworms 0.4 to 0.6. The mass of termites (grass-, humus- or wood-eating) as well as that of other invertebrates could not be determined.

Soil respiration, which serves as a measure of microbial activity, was determined as per year. The attempt to determine the energy flow during decomposition (Lamotte 1982) resulted in the following:

* 1. Annual fire mineralizes about 1/3 of the primary production. Less than 1% of the primary production is probably eaten by consumers; the decomposition of detritus eaters with the main group of earthworms is also not very effective.
	2. 80% of the primary production is degraded by microorganisms, so that the representation of the energy flux as a pyramid seems very questionable. This confirms that the long cycle via consumers is quantitatively almost meaningless.
	3. Many faunal data for the various animal groups represented in the savannahs can be found in the volume edited by Bourlière (1983).

◘ Fig. E-33 The relative biomass (left column) and the percentage species numbers (right column) of the most important plant families in the African savannah (modified after Müller 1991).

**6.2 The animal world**

The fauna of the Burkea tree savannah and that of the *Acacia* thornbush savannah show striking differences for both vertebrates and invertebrates.

In the entire protected area, 18 amphibian species are found (in the Nyl floodplain), while in the experimental area there are 11 species; far from the water, both the toad Bufo garmani and the frogs Breviceps mosambicus and Kassina senegalensis are found. In terms of reptiles, 3 species of turtles, 19 species of lizards and 26 species of snakes were found in the experimental area.

The number of bird species in the entire protected area is 325, of which 197 are permanent. In the experimental area there are 120 species (14 birds of prey, 71 insectivores, 4 berry eaters, 10 grain eaters and 26 omnivores). Of the 62 mammal species in the reserve, 46 were recorded in the experimental area. Rodent species are the most numerous, along with one species each of porcupines, warthogs, and jackals, and two species of monkeys.

Of the particularly important cloven-hoofed animals, mention may be made of: Kudu (Tragelaphus strepsiceros), Impala (Aepyceros melampus), Deuker (Sylvicapra grimmia) and Ibex (Raphicerus campestris).

The determination of the number of individuals or the living zoomass is difficult and succeeded only in a few cases approximately. Three animals per hectare are reported for snakes, the most common reptile, the gecko (Lygodactylus capensis) is represented with 195 to 262 animals per hectare, the common lizard (Ichnotropis capensis) with 7 to 11 animals per hectare.

The living zoomass of birds is 40 kg per 100 ha in the Burkea savannah, but the number of birds decreases by 25 to 30% in winter, when migratory birds leave the area.

For mammals, catch results were so low and variable that the data mean little. For example, monthly catches of Dendromus melantois yielded about 5 (0 to 15) animals per ha, and only 2 animals per ha for other rodents.

For even-toed ungulates, the following mean values (number of animals per 100 ha) are given: Impala 13, Kudu 2, Warthog 1, Deuker 2 and Ibex 1 to 2 (Reedbuck rare).

The former owner of Nylsvley stated that for the last 40 years he only allowed the area to be grazed between January and April because of losses caused by the poisonous species Dichopetalum cymosum, a geophyte close to the Euphorbiaceae. The cattle biomass in the four months was about 150 kg ha-1 but overgrazing became noticeable in 1975, so that the cattle population was reduced to half in the next few years.

The number of invertebrates is so large that only certain groups of arthropods important for the ecosystem are given: Wood-eating coleopterans, lepidopterans, social insects, root-eaters and spiders.

The zoomass of invertebrates as dry mass was on the woody plants in the average of 135g (minimum in August 60 g, maximum in March 300 g……………… -1 make high index !!!

). The dry mass of insects in the grass layer is greater.

Sporadically, caterpillar masses (Spodoptera exempla) or beetle larvae (Astylus atromaculatus) occurred on the grass species *Cenchrus ciliaris*. Dung is removed by dung beetles (Coprinae, Aphodiinae) 77% of the time in one day during the warm season by burying it directly under the deposition site, while pill bugs (Pachilomera spp.) spread it over a larger area. These coprophages are already leading on to the next group.

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| Table E-4 Ecosystem parameters (extreme values) of a low shrub savannah and a dense tree savannah |
|  | Shrub savannah | Tree savannah |
| Number of woody plants per ha | 120 | 800 |
| Woody plant cover | 7% | 45% |
| Leaf area index (LAI) | 0.1 | 1.0 |
| Phytomass above ground (t ha-1)  | 7.4 | 54.2 |
| Phytomass underground (t  | 3.6 | 26.6 |
| Net timber production  (t |
| ditto, above ground | 0.12 | 0.76 |
| ditto, underground | 0.05 | 0.37 |
| Net production of leaves and green shoots | 0.43 | 5.53 |
| Net production of the grass layer  |
| ditto, above ground | 14.9 | 14.5 |
| ditto, underground | 19.0 | 12.2 |

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| **Box E-4** Burkea savannah biomass |
| The following figures represent dry matter in for *Burkea* savannah and in parentheses for *Acacia* thornsavannah: Acridoidea 0.76 (2.32), other Orthoptera 0.06 (0.02), Lepidoptera 0.05 (0.03), Hemiptera 0.08 (0.08), other 0.05 (0.05), for a total of 1.0 (2.5) . |

Destructive organisms include the saprophagous small animals in the soil and in the litter layer, which eat dead plant parts and animal remains and at the same time break them down, as well as the protozoa, fungi and bacteria, through which complete mineralisation finally takes place.

The most important saprophages are the termites. Oligochaetes, myriapods and isopods are of minor importance. Acarines and collembolae feed on bacteria and fungi.

Termites are represented by 15 species, the most common species being Aganotermes oryctes, Microtermes albopartitus, Cubitermes pretorianus and Microcerotermes parvum. Of the 15 species, 4 are humus feeders, the rest feed on dead wood or leaf litter. A mean of 2,540 termites was found in the soil under 1 m2 of area (maximum in November was 8,204, minimum in July was 596).

The fauna of the remaining savannah areas in Africa is particularly rich in large mammals compared to the savannahs and grasslands on the other continents. However, it is known that in the other continents mammal fauna was also considerably richer 11-15 thousand years ago.

Among herbivores, the following functional groups can usually be distinguished:

* Grazers (grazing animals; 'grazers').
* Leaf-eaters (shrub and tree foliage; 'browsers').
* Grain eaters (seed eaters; 'granivores').
* Nectivores ('nectivores').
* Fructivores ('frugivores').

7 **Tropical hydrobiomes in ZB I and ZB II**

With the relatively low potential evaporation, the high precipitation in the humid tropics leads to large water surpluses. As an example, San Carlos de Rio Negro in S Venezuela has a precipitation of 3,521 mm and a potential evaporation of only 520 mm. Thus, insofar as runoff is impeded in flat terrain, extensive swamps are created.

In Uganda, such swamps occupy 12,800 km2 , about 6% of the total area. The catchment areas of the river systems there are not separated from each other by watersheds, but are connected in a network-like manner by swamps. On the flight from Livingstone to Nairobi one sees the large Lukango swamps and furthermore those around Lake Kampolombo and Lake Bangweulu. But the largest swamp is formed by the White Nile in S Sudan. With its left tributary, the Bar-el-Ghasal, it fills with water the large basin situated at 400 m asl. It is the marshland known as the Sudd, the greatest extent of which reaches 600 km from north to south and from west to east; the total area is estimated at 150,000 km2; it varies depending on whether it is high or low tide. Due to evaporation in the Sudd area, the Nile loses half of its water. It is not a free expanse of water with small islands barely protruding above the water, but a green carpet of oscillating grass and floating islands formed by shoots of the grass Vossia lying on the water surface as well as Papyrus.

Also lawns of floating plants, the Eichhornia introduced from South America as well as Pistia play a role. In between one recognizes from the airplane individual free watercourses and smaller water surfaces. A part of the land emerges at low water and forms a grassland with the tall Hyparrhenia rufa and Setaria incrassata. The wettest parts are covered with Echinochloa species, Vetiveria and reeds (Phragmites).

The "Great Pantanal" in Mato Grosso, Brazil, on the border of Bolivia and Paraguay, was formerly thought to be a similarly large marsh from which the southern tributaries of the Amazon and the right tributaries of the upper Paraná rise, but this area is flooded only during the rainy season, but during the dry season it is used for grazing, leaving many annular lakes with riparian forests. It is severely threatened by industrial beef-farms.

Swamps and pools of water are also common in the rest of the humid tropics. The aquatic vegetation consists of some cosmopolitan and pantropical species with floristic features peculiar to each area.

8 **Mangroves as halo-helobiomes in ZB I and ZB II**

Anyone approaching a tropical coast protected by coral reefs from the sea will notice the mangroves, whose treetops barely rise out of the seawater at high tide. Only at low tide do the lower parts of the trunks with their breathing roots become visible (◘ Fig. E-34). These forests grow in the intertidal zone in salt water whose concentration is about 35 gl-1, corresponding to a potential osmotic pressure of 2.5 MPa.

Over 30 species of woody mangroves are known. A distinction is made between the more species-rich eastern mangrove on the coasts of the Indian Ocean and the west coasts of the Pacific Ocean and the less species-rich western mangrove on the coasts of America and the east coast of the Atlantic Ocean. The mangrove reaches its optimum development around the equator in Indonesia, New Guinea and the Philippines. With increasing latitudes, it becomes more and more impoverished, until finally only one species of *Avicennia* remains. The outermost outposts are found at 30°N and 33°S (Sinai, E Africa), at 37 to 38°S (Australia and New Zealand), and at 29°S in Brazil and 32°N in the Bermuda Islands. It can thus be seen that although the mangrove is best developed in the equatorial zone, it extends through the tropical and subtropical zones almost to the winter rainfall area or to the warm temperate zone (Chapman 1976).

◘ Fig. E-34 The mangrove zone with Avicennia (Acanthaceae) with breathing roots on the coast of New Caledonia (photo: Breckle).

The most important genera of mangroves are Rhizophora with stilt roots (◘ Fig. E-35) and viviparous seedlings and Avicennia with thin breathing roots growing out of the soil (not viviparous) (► Fig. E-35). Laguncularia still belongs to the western mangrove, whereas Conocarpus grows only at low salinity. The eastern mangrove also includes species of the genera Bruguiera and Ceriops (both viviparous and with knee roots), Sonneratia (non-viviparous with thick breathing roots), plus Xylocarpus, Aegiceras, Lumnitzera species and others. The individual mangrove species usually grow in distinct zones, rarely in mixed stands. The zonation is related to the tides. The closer to the outer edge of the mangrove a species grows, the longer and the deeper it is in salt water (◘ Fig. E-36).

The tides have a different tidal range (difference in height between low and high water) on the individual coasts; this changes periodically with the position of the moon and the sun. It is greatest at the time of the new and full moon (spring tides) and smallest in between (neap tides). The spring tides are at their highest twice a year at the equinox (equinoxial spring tides).

A distinction is made between coastal mangroves, which grow on flat coasts without water supply from the land and are often many kilometres wide, **estuarine** mangroves, which can be very extensive, especially in the delta region of rivers, and reef mangroves on dead coral reefs emerging from the water, which play a lesser role. The salinity of coastal mangroves in E Africa has been well studied long ago (◘ Fig. E-37).

The coast of E Africa at Tanga has a relatively dry monsoon climate. Potential evaporation is likely to be equal to or greater than the annual rainfall. In addition to a small dry season, a pronounced drought season is present. As a result, the shorter the time the soil is inundated, the greater the inland increase in soil salt concentration in the intertidal area.

The conditions are extreme at the inner edge of the mangrove zone, up to which only the equinoctial spring tides reach (◘ Fig. E-38). Here, the saline water penetrating the soil is strongly concentrated by evaporation during the drought season, whereas during the rainy season the soil can be completely depleted from salt.

No plant species (except cyanobacteria) can cope with these strong fluctuations in concentration, so that these areas are devoid of vegetation. Such areas are found everywhere on the inner edge of the coastal mangroves when the climate is characterized by a period of drought. In N Venezuela, small stands of columnar cacti and opuntia or bromeliads occur in places in the open areas, although these are very salt-sensitive plants. Obviously, the bromeliads take up the water through the leaves and sit here on the ground quite loosely. The cacti, on the other hand, take up the water through shallow roots. They grow here always on small sand mounds, thus root in these, from which the salt is washed out during the rainy season. The salt soil underneath does not disturb them.

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| **Box E-5** Mangroves as azonal vegetation  |
| The mangrove is an azonal vegetation tied to the salt water in the tidal area. It always grows on very fine-grained soils, protected from the surf and frost.  |

◘ Fig. E-35 The mangrove forests of Rhizophora mangle (Rhizophoraceae) on the coast of Tulear (SW Madagascar). Rhizophora is viviparous and grows in the mud of the intertidal zone (photos: E. Fischer).

◘ Fig. E-36 Zonation of the East African coastal mangrove. H.W.L. = high water limit, L.W.L. = low water limit (from Walter & Steiner 1936).

◘ Fig. E-37 Concentration of cell sap in bar (or MPa) (lowest and highest) of leaves of mangrove species and soil solutions at different depths (in cm). Coastal mangrove of E Africa (arid type) (from Walter & Steiner 1936).

◘ Fig. E-38 Inner margin of the mangrove zone on the intertidal coast near Maracaibo (Venezuela) with strong fluctuations of the salt concentration in the soil during the dry (high) and rainy (low concentration due to leaching) seasons. Behind the mangroves there are hardly any tides, but constant evaporation in the soil. Partially devoid of vegetation due to high salt concentration. At the right there are stolons of Sesuvium (photo: Breckle).

Neither the cacti nor the bromeliads contain salts in their tissues; they are therefore not halophytes - another example of the fact that one must examine the ecological characteristics of the plants and the soil conditions in each case very exactly.

The conditions are different in the strongly humid region.

◘ Fig. E-39 Scheme of soil salt concentration (red curve) and mangrove structure on humid and arid coasts.

Here, the exposed areas are constantly leached by rainwater, which means that the concentration of soil water must decrease inlandwards, which also applies to the estuarine mangroves upstream. The mangroves thus transition into the freshwater communities via a brackish water zone with the fern Acrostichum, Nipa (a palm), Acanthus ilicifolius, and many other species, without a distinct vegetation-free zone intervening (► Figures. E-35 to E-38). Although mangroves are azonal vegetation, their zonation is also determined by climate. It is different in humid ZB I than in a climate with a pronounced drought (◘ Fig. E-39). In this respect, the zonation of mangroves differs fundamentally between ZB I and ZB II or even ZB III.

All plants rooted in saline soils take up a certain amount of salts, which are stored in the cell sap. This is also true for the mangroves with their strongly succulent leaves, in whose cell sap the salt concentration is about the same as in the soil; to this must be added the nonelectrolytes in a concentration common to tropical species. The typical zonation and potential osmotic pressure in the soil as well as in the leaves of the mangroves is shown in ► Fig. E-36, while the diagram in ► Fig. E-39 highlights the differences between mangroves in the arid and humid regions.

The zoning is the result of competition between the individual mangrove species, for which the salt factor is decisive in E Africa. Avicennia, as the least competitive species, also has the highest resistance to salinity; vestigial specimens of this species therefore form the inner boundary. Sonneratia is probably the most competitive species, but is least able to tolerate an increase in salt concentration above that of seawater. As a result, it can only persist on the outer margin. In mangrove permanently humid areas, zonation is more complicated. Avicennia seems to be bound to sandy soil, while Sonneratia prefers silty soil. Here, soil type and aeration, inundation duration, water movement, and variations in salt concentration are likely to be more important.

An interesting problem is the salt balance of the mangroves. They cannot simply absorb the seawater as such, because a saturated salt solution would form in the leaves in a very short time, since the plants only release water during transpiration and the salts remain behind. Direct evidence has now been obtained that suction forces of 3.5 to 5.5 MPa are generated in the leaves of mangroves, which are higher than the potential osmotic pressure of the soil solution. These suction forces are transferred to the roots by the cohesive tension in the vessels, which at the same time constitute an ultrafilter, i.e. they allow practically pure water to pass through and feed it to the leaves. Only a very small amount of salt penetrates the plant and is stored in dissolved form in the vacuoles of the leaf cells. It is necessary to generate the suction forces.

How the regulation of the salt concentration takes place is not yet entirely clear. An excess of salts could be eliminated from the plant when the old leaves fall off. This is a general principle in almost all species on saline soils. In Avicennia, regulation is also possible by the salt glands located on the underside of the leaves. The concentration of recreted saline reaches 4.1% in Avicennia, which is higher than that of sea water. The excreted salts are 90% NaCl and 4% KCl, which corresponds to the ratio in seawater. Recretion occurs in the dark and is most intense at midday. It reaches 0.2 to 0.35 mg per 10 cm2 of leaf area in 24 hours. In dry periods, the salt accumulates on the underside of the leaf in the form of common salt crystals, which melt and drip off during the night when humidity is high.

It is interesting to note that the viviparous seedlings of Rhizophora are almost salt-free and have a potential osmotic pressure of only 1.3 to 1.8 MPa. Thus, water must be supplied to them through a glandular tissue in the cotyledonary body. As soon as the seedlings drop and root in the saline soil, the salinity increases and the potential osmotic pressure rises to the normal level. The radicle initially appears to be permeable to salt.

The function of the respiratory roots (pneumatophores) has also been elucidated. They have lenticels with fine openings that are unwettable and therefore permeable to air but not to water. When the respiratory roots are completely immersed in water, the oxygen in their intercellulars is consumed by respiration and a negative pressure is created because the easily soluble CO2 escapes into the water. As soon as the breathing roots emerge from the water, pressure equalization occurs and air containing oxygen is drawn in. The O2 content in the intercellulars of the breathing roots therefore fluctuates periodically between 10 and 20%.

The mangroves, together with their fauna, the many fiddler crabs and with the mangrove fish (Periophthalmus) crawling on the trees, are a particularly interesting ecosystem that belongs neither to the sea nor to the mainland. Due to timber exploitation (charcoal burning) and the expansion of crab farming, the mangroves are severely endangered in many places and the coastal regions of the ever-humid tropics have been deserted (◘ Fig. E-40a). Thus, protection against disastrous tsunamis is lacking. In addition, there is contamination from offshore oil and gas extraction (◘ Fig. E-40b).

9 **Shore formations - Psammobiome**

Sandy shore formations of the tropical coasts offer lesser peculiarities. Behind the vegetationless zone exposed to wave action, plants with long runners follow on the sand, of which Ipomoea pescaprae and Canavalia rosea (◘ Fig. E-41) are common, as are the halophytes Sesuvium portulacastrum, Batis maritima, and Sporobolus virginicus. Inland, outside the saltwater influence, the sand in the tropics is very rapidly becomes covered by shrubs and trees. These are species whose floating fruits are found in the tidemark of all tropical coasts. Terminalia catappa (◘ Fig. E-42a; its fruits in Fig. E-42b) is a typical representative; the coconut palm might also be added (◘ Fig. E-42c), though today palms are almost all planted.

**◘ Fig. E-40 a**: Shrimp breeding pools at Playa near the town of Machala, Pacific coast of Ecuador, after total deforestation of the mangrove (photo: Rafiqpoor); **b**: Dead mangrove trees due to oil pollution in Venezuela (photo: Breckle).

**◘ Fig. E-41** A very salt-tolerant Fabaceae (Canavalia rosea) creeping on calcareous sand, with stolons up to 6 m long (**a**), with inflorescence (**b**) on the beach of a small island off Saba, Borneo (photos: Rafiqpoor).

For the eastern oceans Barringtonia, Calophyllum, Hibiscus tiliaceus as well as Pandanus are typical, for the western Coccoloba uvifera (Polygonaceae), Chrysobalanus icaco and the poisonous Hippomane manicinella (Euphorbiaceae).

Large areas of dunes are absent from the tropics. One of the exceptions is the north coast of Venezuela. Here, in a semi-desert climate near Coro, a lot of sand is blown from the beach by the trade winds blowing constantly from the northeast to the east-northeast, which is collected by Prosopis juliflora. This results in the formation of dunes that continue to grow in the direction of the wind and are repeatedly covered by the Prosopis bush (◘ Fig. E-43). In this way a series of dune ridges is formed, all running side by side parallel to the wind direction and reaching a considerable height. In part of the dune area, probably as a result of logging, shifting sand dunes have developed (barchans), which again merge into dune ridges, but these are oriented perpendicular to the wind direction.

**◘ Fig. E-42** Terminalia catappa (**a, b**) and the fruit of a coconut palm (**c**) washed by ocean currents onto the beach of an island in Saba, Borneo, where it has begun to germinate (photos: Rafiqpoor).

**◘ Fig. E-43** The large sand dunes on the Paraguana Peninsula in northern Venezuela are not covered with Prosopis, but mainly with *Conocarpus* scrub (photo with Prof. E. Medina, Caracas: Breckle).

**10 Orobiome II - tropical mountains with an annual temperature cycle**

While in the case of orobiome I, a short rainless period in the alpine stage does not yet affect the water supply of the plant, the drought period of ZB II has a significant effect depending on the duration even at high altitudes.

It is true that in the montane belt the amount of precipitation increases and the duration of sunshine decreases as a result of cloud cover to such an extent that an evergreen montane forest occurs, but this has a dry season in the cool season, even though a Fog forest may even develop above it in the trade wind or monsoon area (► Fig. D-45).

In the monsoon region of India, even a smaller mountain range already has a very strong effect on the amount of precipitation, less so on its distribution over the year (◘ Fig. E-44).

The whole succession of elevational belts of orobiome II can be traced on the southern slope of the eastern Himalaya, on the very humid Sikkim profile from Darjeeling northward, where it is difficult to distinguish the forest belts. It is further complicated by the fact that in the higher elevational belts the Palaeotropical floral elements are increasingly displaced by Holarctic ones.

At the foot of the mountains a humid deciduous forest with Shorea robusta prevails and on wet soils one with bamboo as well as palms. At about 900 m asl an evergreen tropical montane forest (Schima, Castanopsis) with tree ferns begins, whereby in the upper part already Holarctic tree genera *(*Quercus, Acer, Juglans), also Vaccinium and others are represented.

Above comes a fog forest with Hymenophyllaceae and mosses. The higher you climb, the more predominant Holarctic genera (Betula, Alnus, Prunus, Sorbus and others) are found.

The frost line is reached at 1,800 to 2,000 m above sea level (potential frost).

In the next higher belt one finds many tall Rhododendron and Arundinaria species, which are replaced further up by conifers (Tsuga, Taxus and others).

At 3,000 to 3,900 m asl., an Abies densa fir forest grows with hardwoods. The forest boundary is formed by Abies and Juniperus. The subalpine belt is again characterised by tall Rhododendrons, which become lower and lower in the alpine belt with flower-rich mats until Rhododendron nivale is only a tiny shrub at 5,400 m asl.

Above 5,100m asl., predominantly hemispherical patches occur (Arenaria, Saussurea, Astragalus, Saxifraga and others); the snow line is at 5,700m asl.

◘ Fig. E-44 Increase in precipitation with elevation in the monsoon region of India: Climate diagram of Bombay and two stations above it in the mountains. At the upper station at 1380 m asl., nearly 3,000 mm of rain falls in July. However, the duration of the rainy season is only extended by one month, although the annual rainfall exceeds 6,000 mm.

This orobiome system of the Himalayan mountain ranges is particularly complicated (Troll 1967, Meusel et al. 1971, Miehe in Walter & Breckle 1994, Miehe et al. 2015, Miehe 2021) lying between Zonobiomes.

In the Andes, the altitudinal sequences of the west and east slopes are different, as well as in the inner mountain valleys. A short schematic overview has been given by Ellenberg (1975).

The high plateau of the Altiplano in Bolivia and Peru (◘ Fig. E-45) is populated and grazed by llama herds, and is thus anthropogenically modified. However, the wild vicuña herds also play a role in the devastation of the landscape. According to the climate, on the western slope the succession of steps becomes more and more xerophytic towards the south. The rain green deciduous forest belts reach higher and higher and the evergreen ones become more hard-leaved and small-leaved.

The presence of a warm season results in an elevation of the timberline up to 4,000 m asl.; individual Polylepis stands reach up to 4,500 (5,300) m asl. (◘ Fig. E-46a). Páramos are replaced by Puna, initially moist Puna with cushion plants such as Azorella compacta (◘ Fig. E-47), more southerly dry puna with xerophytic tussock grasses such as Festuca orthophylla (◘ Fig. E-48), Stipa ichu, and others, until a desert puna with many Salars (salt pans) predominates in the orobiome III area (Lauer 1975, Chong-Diaz 1988) (► Fig. E-46**c**,d). Correspondingly, soils of the alpine belt change in a southerly direction from peaty soils to chestnut soils and syrosems to solonez and solonchak.

A very detailed ecological and also microclimatic study of the Puna in NW Argentina between 22 to 24 1/2°S is available from Ruthsatz (1977).

**11 Man in the savannah**

Today, the savannah has been replaced in many places by cattle pastures. Even in earlier times, pastoral nomads were on the move in the vast savannah areas and, with their extensive herds, provided the wild animals with considerable competition for food sources.

Large-scale African grasses have been introduced into neotropical savannahs, drastically reducing the original biodiversity. However, productivity has increased partly to the benefit of extensive cattle grazing (Solbrig et al. 1996).

**Fig. E-45 a**: View from the Bolivian Altiplano (4,100 m) to the Cordillera Real with the glaciated volcano Huaina Potosi near La Paz. **b**: View from the Altiplano to the glaciated volcanoes Parinacota and Pumarape on the Chilean-Bolivian border (West Cordillera, southern Bolivia)**.** The Altiplano in Bolivia is a broad intermontane area fringed on both sides by mountain ranges (Western and Eastern Cordillera). Large parts of this plateau are covered with a semi-arid grassland. Especially in the vicinity of Lake Titicaca near La Paz, the Altiplano (humid Puna) is intensively used for agriculture; towards the south, as a result of the decrease in the humidity of the climate, the extent of field cultivation also decreases, while grazing remains at almost the same intensity (photos: Rafiqpoor).

Due to the frequent grass and bush fires, which are usually deliberately set shortly before the start of the rainy season, the growth of new greenery is to be improved. Over a longer period of time, however, this leads to an ever-increasing nutrient depletion of the soils with greater risk of erosion and thus increasing desertification.

12 **Zonoecotone II/III**

12.1 **Sahel**

This zonoecotone includes the open, climatic savannahs, such as Namibia. Similar conditions are found south of the Sahara in the Sahel zone, which forms the transition to the summer rainfall area of Sudan (ZB II). But the Sahel has been completely degraded by overcrowding and overgrazing as a result of the recurrent drought years typical of this zone (Müller et al. 2006). It can only tolerate very sparse settlement and correspondingly low numbers of livestock, which used to be enforced by the few natural water points in this area. However, as part of development aid, people wanted to develop the land and drilled many wells. This made it possible to water larger herds, and the population increased accordingly as long as the annual rainfall was above the long-term average. Then, however, followed several years of drought, which led to disaster. Water for people and animals was available, but no pasture, for the grasses withered. Starving livestock perished, and people had to flee the land or be supported by outside relief efforts. But the pasture suffered irreparable damage and became a 'man made desert' as the worst effect of desertification. New programs are planned and have started to protect the Southern regions from further desiccation and desertification. The “Green Belt” is one of the projects, stretching about 8000 km from W to E (Breckle 2021a).

In present-day Namibia, with a similar climate, several drought years in succession also have a devastating effect, but the small number of farmers can survive these years by reducing livestock in time, shifting grazing plans and management, and the economy recovers quickly after a few good rainy years, perhaps because the droughts are also shorter than in the Sahel.

**◘ Fig. E-46** The forest boundary is located at the high volcanoes of the Western Cordillera in Bolivia (e.g. at Sajama) at about 5,300 m asl (**a**, photo Breckle; ► Fig. F-53b) and is formed by Polylepis tarapacana with Lepidophyllum quadrangulare and the tussock grasses from Festuca orthophylla, Stipa ichu etc. (**b**, photo Rafiqpoor). Partially frozen Salar surface of Laguna Hediona (3,900m asl) in the Altiplano of Bolivia with flamingos, salt crusts and volcanoes (**c**, photo: Breckle). In the area of the desert Puna in the southern Altiplano large salt lakes like the Salar de Uyuni occur (**d**, photo: Breckle). In this Salar, at 3,900 m asl near the village of Uyuni, the salt crust is hewn out, crushed and completely dried in the air for further use (lithium extraction).

**◘ Fig. E-47** Azorella compacta (Apiaceae) at a rock site on the Bolivian Altiplano 4,500 m asl (photo: Breckle).

**◘ Fig. E-48** Festuca orthophylla over weathered volcanic fine material on a gently sloping hillside in southern Bolivia (4,750 m asl). Due to the effect of frost heave and the slight slope, the grass tufts are arranged in grass garland structures (photo: Breckle).

12.2 **Thar or Sind desert**

Another zonoecotone II/III is located in the border area between India and Pakistan - the Thar or Sind desert. It is a uniform arid area between the Aravalli Mountains in the east and the heights of Baluchistan in the west, which is also called the "Great Indian Desert" (**◘**Fig. E-49). The aridity increases from east to west.

In the area with over 250 mm of rainfall, savannahs are grazed and degraded as a result of overstocking with livestock, with the annual grass species Aristida adscensionis becoming rampant as a grazing weed.

If the literature often speaks of a Saharo-Sindian desert zone, this is not correct. For the Sahara belongs floristically for the most part as a rainless area or one with little winter rain to the Holarctic and continues eastward into the Egyptian-Arabian Desert to Mesopotamia. The Sind desert, on the other hand, is the last driest spur of the Indian monsoon area and must be included floristically in the Paleotropics. The Indian desert, Thar, is climatically already a zonoecoton II/III, which can be compared with the transition area from the Sudan to the southern Sahara, the "Sahel". Both receive light summer rains, but the Indian area is already north of the Tropic of Cancer, the annual temperatures are therefore 2 to 3°C lower than in the Sahel, and frosts may occur in December to February (► Fig. E-49). Only the area in the Indus lowlands receives an average of less than 100 mm of rain a year and would therefore be climatically a desert; but it is a water-rich irrigated area because of the Indus and its tributaries. The 'Great Indian Desert', on the other hand, is largely a 'man made desert'. The area was inhabited four thousand years ago, became more densely populated from the time of Alexander the Great, and is now completely degraded as a result of overgrazing, logging, and partial cultivation (Mann 1977). By nature, the area was a Prosopis savannah on deep sandy reddish-brown savannah soils, with 400 to 150 mm of rainfall per year, as evidenced by an area that has been protected for several decades not far from Jodhpur (Rodin et al. 1977).

The thorny shrubs there are: Prosopis cineraria, Ziziphus nummularia, Capparis decidua (= C. aphylla) and others. Prosopis grows to 8 m tall at annual rainfall of 500 to 600 mm, forming stands of 150 to 200 specimens per hectare; at 300 to 400 mm it grows only 5 to 6 m tall (stands of 50 to 100 expl. per ha); and at 200 mm it grows only 3 to 4 m tall (stands of 25 to 30 expl. per ha). Similarly, as rainfall decreases, tall grasses (Lasiurus, Desmostachya) are replaced by low ones (Aristida) in the grass layer (Gaussen et al. 1972). Thus, conditions are like those in southwestern Africa (► Fig. E-7).

**◘ Fig. E-49** Climate diagram map of the Sind-Thar desert. Northwest of the line A-B the extremely arid area.

A very open grassland with Lasiurus, Desmostachya, Panicum and Aristida species, with some succulents and the widespread Calotropis procera, is shown in ►**,**while in ► Fig. E-51 a dense Prosopis savannah is shown, with large columnar Euphorbia (Euphorbia caducifolia) in the foreground on rock; the stand structure of the thorn savannah with Prosopis, Acacia, Capparis decidua, Salvadora persica, with the climbing Coccinea grandis is illustrated by ◘ Fig. E-52.

**◘ Fig. E-50** Overgrazed semi-desert near Jodhpur with Calotropis procera (photo: Breckle)*.*

**◘ Fig. E-51** Thorn savannah and open rock slabs near Jodhpur, in the transition area of the zonoecotone II/III to the Thar desert (photo: Breckle).

In the Bikaner district (► Fig. E-47), the soils are very sandy. In the vicinity of settlements, mobile barchans, i.e. vegetationless dunes, form as a result of grazing, giving the impression of a real desert (◘ Fig. E-53). In fact, however, the water content of the sand of such unvegetated dunes is much higher than that of vegetated ones, as shown by data (◘ Table E-5) from an area with 260 mm of rain per year.

This difference is understandable because a Prosopis stand takes about 220 mm of water a year from the soil for transpiration and the often planted grass Pennisetum typhoides also takes about 160 to 180 mm.

|  |
| --- |
| Table E-5 Water content (in mm) of the sand of unvegetated (I) and vegetated (II) dunes near Jaisalmer (after Mann 1976). |
| Depth ranges | Period |
| March | June | Sept. | January |
| Depth (in cm) | I | II | I | II | I | II | I | II |
| 0-105 | 41 | 10 | 33 | 17 | 45 | 10 | 34 | 7 |
| 0-210 | 106 | 39 | 94 | 48 | 120 | 33 | 105 | 28 |

**◘ Fig. E-52** Open species-rich thorn scrub near Jodhpur during the dry season in December (photo: Breckle).

**◘ Fig. E-53** Sand area (Barkhane) in motion in the "Desert National Park" in the vicinity of Huri village about 40 km from Jaisalmer with individual Acacia and Calotropis shrubs (Photo: http://bit.do/bFP6P).

The population exploits the water content in the sand of the unvegetated dunes by planting watermelons at a distance 2x2 m and preventing the sand from blowing away with brushwood. No information can be given about the natural vegetation of the driest part, the Sind Desert in the Indus lowlands. This irrigation area is densely populated; areas of natural vegetation do not exist. Unrationed irrigation has greatly raised the water table, causing secondary salinization of the moist soils. As a result, 40,000 hectares of cultivated land have been lost annually, causing the increase in food production to lag far behind the increase in population. Restoring the brackish soils is very costly in the flat terrain (Breckle 2021b).

Natural saline soils are very common in the south of the Thar Desert on the Gulf of Kutch. Mangroves grow in the intertidal area, followed by salt marshes with Salicornia, Suaeda, Atriplex and the salt grass Urochondra. In the Rann of Kutch area (► Fig. E-49) with high groundwater levels, nearly sterile clayey saline soils spread with few woody plants in favorable places and with halophytes (Haloxylon salicornicum, Aeluropus, Sporobolus) or Cenchrus spp, Cyperus rotundus, and others (Blasco 1977).

12.3 **The Caatinga**

Ecologically difficult to classify is the Caatinga in NE Brazil, the arid area, "Polygono da Seca". It is characterised by extreme fluctuations in precipitation from year to year. For example, in the driest place, Cabaceiras, the good rainy years 1940 to 1946, with rainfall ranging from 664 to 150 mm, were followed by droughts from 1948 to 1958, with rainfall below 80 mm (only 24 mm in 1952, only 22 mm in 1958), with the exception of 1954, with 170 mm, and 1955, with 187 mm. Such an unreliable climate is best survived by large succulent columnar cacti and large spiny Bromeliaceae growing on the ground, as well as much water-storing bottle trees (Ceiba and others) or deciduous shrubs that are leafless for long periods (◘ Fig. E-54). The area is difficult to exploit and is sparsely populated because periods of drought cannot be predicted, forcing the population to leave the land. Similar conditions are found in the trade wind desert on the north coast of South America in the Venezuela-Colombia border area or in the Galapagos Islands. Years with very high precipitation also occur in this arid region.

**◘ Fig. E-54** Caatinga near Rodelas in Sertão NE Brazil (photo: Glauco Umbelino, http://t1p.de/mb49).

12.4 **Tropical East Africa**

Finally, mention should be made of the rather arid areas belonging to the Palaeotropis in the tropical area of E Africa, as well as a small area in the rain shadow between the Pare and W Usambara Mountains with very strange succulents [Adenia globosa, rock-block-like Pyrenacantha, Euphorbia tirucalli (► Fig. E-17), Caralluma, Cissus quadrangularis, Sansevieria (► Fig. E-18), and others]; with an annual temperature of 28°C and only 100 to 200 mm of rain, it may be the driest area along the equator. Much more extensive are the arid areas of N Kenya, W Ethiopia, Somali, and Socotra with Adenium socotranum (Apocynaceae) (◘ Fig. E-55a), which has misshapen succulent stems 2 m in diameter, and Dracaena cinnabari (◘ Fig. E-55b) with a stem diameter of 1.6 m. The various life forms of the thorny succulent savannah are shown schematically in ◘ Fig. E-56. Most of the life forms can be understood as typical adaptations to long dry periods, but they have not been able to penetrate the actual deserts of zonobiome III after all.

12.5 **SW Madagascar**

Madagascar, with its distinctive flora and fauna, has zonobiome I rainforest on the east coast with up to 2,000 mm of rain per year. However, most of the island has a summer rainfall climate and bore deciduous forest. The tree and shrub flora of Madagascar is also very unique overall, with about 94% of the species being endemic. The flora of Madagascar was very rich in species, but today many forests and savannahs have been cleared. Large areas are degraded. Huge areas of grass are burned every year, supposedly to get better pastures for the at least 10 million Zebu cattle, in the dry parts goats are kept.

The driest SW corner of Madagascar is characterised not only by Baobab trees (◘ Fig. E-57) but also by the endemic family of Didiereaceae (four genera with eleven species) (◘ Fig. E-58), which only occurs here and is reminiscent of columnar cacti. With about 350 mm of rain per year, which moreover usually falls very irregularly, a thorn-bush succulent semi-desert develops here. Numerous succulents of the genera Euphorbia, Aloe, Kalanchoe, Crassula occur, plus bottle trees of the genera Adansonia, Moringa, and Pachypodium (► Fig. E-58). Other species are very small-leaved, thorny, or leafless. Poikilohydric vascular plants and ferns also occur.

**◘ Fig. E-55 a**: Adenium socotranum (Apocynaceae) with a trunk diameter of 2 m on western Socotra. **b**: Dracaena cinnabari on the path between Wadi Dirham and the Dicksam Plateau on Socotra. The trunks of the dragon trees have scars left from tapping the resin (dragon's blood). The vegetation along the path shows severe browsing damage (from free-ranging goats). Degraded dragon tree forest is visible in the background. Young trees are largely absent. In the background on the left the Hajhir mountains surrounded by clouds can be seen (photos: Ernst Kluge).

**◘ Fig. E-56** Characteristic life forms of thorny succulent savannah (after Troll 1960). 1 Thorny fine-leaved umbrella trees (*Acacia* type); 2 Stem succulent candle or candelabra trees (*Cacti* type); 3 Succulent and thorny-leaved crested trees (*Aloe* type*)*; 4 Succulent and thorny-leaved crested trees (*Dracaena* type); 5 Water-woody barrel-leaved deciduous trees (Adansonia type); 6 Sclerophyllous trees with thorns (Balanites type); 7 Deciduous trees with xylopodia or lignotuber; 8 Sclerophyllous shrubs and tree-bushes (Capparis type); 9 Stem succulents, low plants (*Stapelia* type); 10 Grasses everywhere in between (after Troll 1960).

**◘ Fig. E-57** *Adansonia digitata* from Madagascar (photo: E. Fischer)

**◘ Fig. E-58** Didierea madagascariensis (Didiereaceae) from Madagascar (a, photo: E. Fischer); b: Pachypodium lamerei from Tsiman-ampetsotsa, Madagascar (photo: [https://t1p.de/cli9](https://t1p.de/cli9%22%20%5Ct%20%22_blank)).

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[IMAGE]

Sand desert (Erg) with pronounced sand dunes in Merzouga (zonobiome III), in S Morocco (Photo: Rafiqpoor)

[IMAGE]

High mountain desert in Eastern Pamir (Orobiome VII [rIII]) with puny hemicryptophyte growth (Photo: C. Opp)