[IMAGE]

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

[IMAGE]

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

**II Special part**

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

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[IMAGE]

Dense dune system with few scattered grasses (Panicum) and shrubs (Tamarix, Calligonum) and feral camels in the Rub al Khali (zonobiome III) in southern Oman (photo: Breckle)

1 **Climatic subzonobiomes**

Deserts together account for more than 35% of the Earth's solid surface. In the subtropical desert zone, in zonobiome III, there is no cold winter season, which is so characteristic of the arid areas of the temperate zone.

The term desert is relative. For someone who comes from the humid east of North America, the southwest of the country is already a desert, even though Tucson (Arizona) receives more than 300 mm of precipitation per year; but an Egyptian who lives in dry Cairo will no longer consider the Mediterranean coast a desert, even though the annual rainfall there barely reaches 150 mm.

The Earth's desert systems are the result of atmospheric circulation. They generally develop in the transition zones of the large wind and precipitation systems. To illustrate this phenomenon, we would like to consider the dynamics of the atmosphere in the course of desertification using the example of Africa (◘ Fig. F-1).

In the inner tropics in the Congo Basin (approximately 0°-10° on both sides of the equator), the convergence of the NE and SE trade winds in the area of the Intertropical Convergence Zone (ITCZ) gives rise to high-pressure thunderstorm cells (cumulonimbus clouds) with regular afternoon showers. Due to the large vertical air mass transport into the higher atmosphere, an area of high pressure develops over the equator in the higher troposphere, while an area of low pressure develops at ground level (equatorial low pressure trough). To compensate for this, monsoon-like westerly winds with abundant precipitation at the western sides of the continents (e.g. Chocó >8000 mm, Cameroon Mountain, Southeast Asia) flow in near the ground. Due to the high insolation and the removal of air masses from the areas near the tropics, a mass deficit is created. Accordingly, cold, heavy air masses flow in from the troposphere, but warm up and dry out on their way down. At ground level, these air masses generate high pressure.

In this quasi-stationary high-pressure belt near the tropics between the tropics (with summer rainfall) and the subtropics (with winter rainfall) are the extensive semi-desert and desert areas of the Earth. Central areas of deserts are not reached by either rainfall regime (◘ Fig. F-2). In "rainier" deserts, on the other hand, the two types of precipitation dovetail (overlap areas). This phenomenon favours the growth of a species-rich flora (e.g. Namaqualand in SW Africa; Sonora Desert in the USA).

In general, therefore, a hot area is called a desert if the annual precipitation is less than 200 mm and the potential evaporation is more than 2,000 mm (up to 5,000 mm in the central Sahara).

In the arid regions of the Earth, the sparse precipitation falls at different times of the year (Walter & Breckle 2004). Accordingly, the zonobiome III is divided into the following subzonobiomes (sZB):

1. sZB with two rainy seasons (Sonora Desert, Karoo)
2. sZB with a winter rainy season (northern Sahara, Mojave Desert, Near Eastern deserts)
3. sZB with a summer rainy season (southern Sahara, Inner Namib, Atacama)
4. sZB with sparse rain possible at any time of the year (Central Australia)
5. sZB of the coastal deserts almost without rain, but with a lot of fog (northern Chilean-Peruvian coastal desert, outer Namib)
6. sZB of the rainless vegetationless deserts (Central Sahara, Central Atacama).

In ◘ Fig. F-3, the climate diagrams of the different sZB are shown with the exception of sZB 5, because the fogs are hardly measurable as precipitation and thus not evident from the diagrams (► Fig. F-36). A very important feature of all arid areas is the large variability of rainfall in individual years. Therefore, the mean values do not mean much. Years with rainfall below the mean are most frequent; however, a few years with very high rainfall occur, which replenish the water reserves in the soil for decades.

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| **Box F-1** The deserts in the arid regions |
| Deserts are arid areas. In these, the potential evaporation is much higher than the annual precipitation. Semi-arid, arid and extremely arid areas can be distinguished. In zonobiome III the "hot deserts" are summarized, in zonobiome VII the "winter-cold deserts". |

◘ Fig. F-1 The atmospheric circulation over Africa in July and the formation of wet and dry areas. The red arrows must be thought of as running obliquely backwards. TC = Tropics of Cancer and Capricorn.

◘ Fig. F-2 The arid regions of the Earth with axes of maximum aridity (as in the central part of the Sahara) or the intersecting areas of tropical and subtropical rain regimes (e.g. in Namaqualand, the Sonora Desert, or central Australia).

◘ Fig. F-3 Climate diagrams from desert stations. Top row from North Africa with winter rain, no rain, and summer rain; bottom row with 2 rainy seasons (Sonoran Desert and Karroo) and rain possible at any time of year (Rawlinna, Australia). ► Fig. F-33.

The variability of precipitation for Cairo (winter rainfall area) is shown ◘ Fig. F-4. A similar skewed distribution has that of Mulka, the most arid station in central Australia, except that the mean is 100 mm and the extremes are 18 and 344 mm, in Swakopmund (outer Namib): The corresponding mean is 15, extremes zero and 140 mm.

The ecological conditions in the individual years are so different that only long-term observations provide a correct picture of the ecosystems in deserts. Each desert must be considered on its own merits, but let us first discuss the few commonalities.

In all deserts the air is very dry (exception: foggy deserts), the irradiation and radiation and thus also the daily fluctuations of the air temperature are correspondingly strong. Only during the mostly very short rainy season are the extremes moderated.

◘ **Fig. F-4 A:**Variability of annual precipitation at Cairo from 1906 to 1953 (modified after Walter 1973) - a markedly skewed distribution of decadal steps. B: Annual precipitation from 1941 to 1996 indicating the big variance (driest year 1958 with 3.3 mm, wettest year 1972 with 68.6mm per year; median M is lower than average m.

2 **Soils and their water balance**

In the deserts one can hardly speak of soils in the proper sense, because they are raw soils (syrosems), which consist of the weathered debris of the rocks, partly altered by wind or water or by strong diurnal heating and nocturnal cooling as a result of intensive irradiation and radiation (mechanical weathering). Therefore, the properties of the often loose parent rocks are decisive, which means that we cannot speak of climatic soils. There is also no definable climatic zonal vegetation in strict sense, but only pedobiomes (lithobiomes, psammobiomes, halobiomes and others).

The water supply of the plants also depends on the substrate. For plants in arid regions, the amount of precipitation is only indirectly important. The decisive factor is rather the amount of adhesive water in the soil that is available to them. It forms only part of the water that falls on the soil as rain, because some runs off and some evaporates (◘ Fig. F-5). The proportion of adhesive water depends on the structure of the substrate. In humid areas, sandy soils are considered dry because they retain little adhesive water, whereas clay soils are considered moist. In arid regions we have to relearn; there it is just the other way round.

◘ **Fig. F-5** Scheme of the fate of precipitation in arid regions. Adherent water is important for plants. The runoff water percolates into the dry valleys and feeds the groundwater, which is rarely reached by plant roots except in wadis.

Infiltration to greater depths down to the groundwater does not take place on leveled terrain in the arid region. Only the upper soil layers are moistened. The depth to which the water penetrates depends on the field capacity of the soil. Let us assume that 50 mm of rain falls on a dry desert soil and that it penetrates completely into the soil. In this case, for a sandy soil, the top 50 cm will be moistened to field capacity. In a fine-grained clayey soil with five times the field capacity, the water will penetrate only 10 cm deep, whereas in a rocky soil with only small fissures, the water will penetrate much deeper, perhaps 100 cm to several meters (◘ Fig. F-6).

**Fig. F-6** Schematic representation of water storage in different soil types after a rainfall of 50 mm in arid regions. h-h = lower limit of soil moisture; e---e = lower limit to which the soil dries out again. The clay soil stores 25%, the sandy soil 90% and the stony soil 100%.

After the rain, evaporation begins. If the top 5 cm of clay soil dries out, 50% of the rainwater that has penetrated is lost. The sandy soil dries out less. But even if the upper 5 cm lose their water, only 10% of the water would evaporate. With rocky soil there is practically no evaporation at all, i.e. all water is stored. It follows that, in contrast to the conditions in the humid region, clay soils are the driest locations for plants in the arid region, while sandy soils provide a better water supply. Ragged rocky soils are the wettest sites, provided that the rain penetrates them unhindered and there is enough fine soil in the rock crevices to store the water.

These considerations are confirmed by measurements in the Negev Desert. For the same annual precipitation, the amount of water exploitable by plants was found to be 35 mm in loess soil, 50 mm in rocky sites with a relatively considerable runoff, 90 mm in sandy soil, and 250 to 500 mm in dry valleys with a strong inflow. That sandy soils in arid regions are more favourable to plants is evident from the fact that the same type of vegetation occurs on sand with less rainfall than on clayey soils. In Sudan, Acacia tortilis semi-desert is found on sandy soils in a zone with 50 to 250 mm of rainfall, but on clay soils only at 400 mm, or Acacia *mellifera* savannahon sandy soils at 250 to 400 mm, but on clay soils only at 400 to 600 mm of annual rainfall. In the shortgrass prairie of the Great Plains, long-grass prairie is found on sandy soils in W Nebraska, which otherwise occurs only farther east at higher precipitation. The more favourable water conditions of rocky soils are often conspicuous in arid areas because of their tree cover amid low vegetation on fine-grained soils.

If in sandy soils or in rock crevices the soil is soaked down to the groundwater, then the roots can grow deep enough to reach the groundwater; the water supply of the plants is then assured. The following example may be mentioned here:

North of Basra in Mesopotamia, groundwater is present at a depth of 15 m, constantly fed by gravel layers from the Euphrates and Tigris rivers. However, since the rainfall is only 120 mm per year, only the upper layers of soil are moistened, and the roots of plants cannot reach the groundwater; the soil covers itself with a scanty ephemeral vegetation after the rains fall in winter. However, the local population have dug wells and use the water to grow vegetables, planting crops in furrows and irrigating several times a day when daily maximum reaches 50 °C. As a result of the greater evaporation, the soil quickly shrivels up, so that the vegetables can only be grown for one year.

But between the vegetable plants are inserted salt-tolerant Tamarix cuttings, which easily take root. If in the second year the furrow does not receive water, but the soil is soaked to groundwater due to heavy irrigation in the previous year. As a result, the roots of Tamarix grow deeper and deeper over the next few years until they reach the groundwater. Trees then develop that are cut for firewood every 25 years, but sprout again from the stump as cane sprouts. All former vegetable land turns into a *T*amarix forest in this way. It is thus possible to reforest deserts with groundwater at greater depths, if the first few years after planting the trees are so heavily irrigated that the whole soil is soaked down to the groundwater. However, the question of how long the groundwater supply will last remains open.

This example gives us the explanation that phreatophytes, which are bound to groundwater, reach it with their roots, although there are many feet of dry soil above them. They can only do this after very favourable rainy years, when the soil is soaked from the surface to the groundwater, but then they persist until the woody plants reach their age limit. This need not always be groundwater. Often it is only ground moisture, i.e. adhesive water, which is stored in the soil. As soon as it is deeper than 1 m, it is preserved for a very long time, provided that no or very few plants reach and consume it with their roots. Saline soils occur very frequently in the deserts, and especially in the depressions.

3 **Substrate dependent desert types**

The desert biomes can be subdivided into biogeocene complexes according to soil characteristics, which were first studied in the Sahara. Therefore, mostly the local designations there were generally adopted.

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| **Box F-2** Desert soils as hidden water reserves |
| The hidden water reserves in desert soils are greater than the superficial observer believes. |

3.1 **The stone desert (Hamada)**

When the parent rock formed in the course of geological history is at the surface, it is called a rock desert. Such a one is quite seldom to be found, because arid mountains are often almost completely submerged in their own coarse debris by physical weathering. Coarse rock is also found especially on the elevations of mesas, from which all fine weathering products have been blown out, with strong wind erosion on all projecting rocks due to sand blowing (◘ Fig. F-7a). At the surface, the rock fragments accumulate. They form a stone pavement. The stones are often covered by dark desert varnish (◘ Fig. F-7b). This gives the landscape a somber appearance. Under the stone pavement there may be a water-repellent accumulation soil, rich in gypsum and salt if marine sediments are present, which prevents plant growth. Hamada surfaces are rugged by deep erosional valleys with steep slopes covered by debris (◘ Fig. F-8). Some plants can persist in the crevices and rocky clefts; they are not infrequently xerohalophytes.

3.2 **The gravel desert (Serir or Reg)**

This occurs when the parent rock is heterogeneous, for example a conglomerate. The more easily weathered putty substance decays and is removed by wind. The hard pebbles in turn accumulate at the surface (◘ Fig. F-9).

These autochthonous gravel deserts are contrasted with the allochthonous ones, which are alluvial deposits of earlier rainy seasons from which the fine material was blown out. Beneath the gravel layer, darkened by desert varnish, there may be a hard crust caked by gypsum and lime. The particularly monotonous gravel desert is only slightly undulating. The shallow, broad valleys are filled with sand and are more conducive to plants gaining a foothold. Among them you can find plants of the sandy soil, but also xerohalophytes.

◘ F-7 Hamada types in Egypt (a, photo: Breckle) and in Fuerteventura, Canary Islands (b, photo: Rafiqpoor). The stones of the Hamada are covered with desert varnish and are mostly gloomy and dark.

◘ Fig. F-8 Fish River canyon in the desert in southern Namibia (Photo: Rudi Bosbouer, https://bit.ly/2zmkONe).

◘ **Fig. F-9** Serir in Morocco. The fine material has been blown out of the interstices of the boulders and pebbles and carried away. The stones have a desert varnish coating. This desert also looks gloomy and dark like the Hamada (photos: Rafiqpoor).

3.3 **Sand desert (Erg or Areg)**

They form in the large basin landscapes where the sand blown off the elevations is deposited and contributes to the formation of dunes. If one wind direction prevails, then crescent dunes or barchans form, which slope flat on the windward side and steeply on the leeward side. They move along with the wind direction. If the wind direction changes periodically, only the crest of the dune is rebuilt each time, while the base remains fixed. The sand grains are coated with an iron oxide film on the surface, giving the dunes a bright orange or red colour in dry hot areas (◘ Fig. F-10), as in the Inner Namib. Near the coast, however, with higher humidity, the colouring is yellow-brownish, e.g. in the Outer Namib.

**Fig. F-10** Erg or Areg (sandy desert) usually occupy larger areas compared to the first two types of desert mentioned. In the Wahiba Desert in Oman, large areas are covered by sandy deserts with characteristic crescent dunes, ripple marks, etc. (photo: Breckle).

Movable and therefore vegetation-free dunes are water reservoirs, as rain penetrates easily and evaporates only to the smallest extent. Even with only 100 mm of annual rainfall, a groundwater horizon is formed, so that water extraction from wells is possible or the water escapes in the interdune area.

If the sand cover is not very thick, colonization by plants (non-halophytes, such as dune grasses, Ziziphus and others) can occur. Perennial species or shrubs then serve as sand traps. The plants grow back out of the sand deposited around them, so that new sand is always being accumulated. In this way, each plant forms a cluster dune (several meters high) called a nebkha (◘ Fig. F-11) The whole landscape is given a very typical character by these miniature dunes.

◘ **Fig. F-11** The nebkhas are formed in the sandy deserts by the accumulation of sand on the perennial plants. As a result, mounds of sand form around each plant and are widely spaced. Here a *Salsola* nebkha at Cape Cross in the Namib with fog bank in the background of the picture (photo: Breckle).

3.4 **The dry valleys (wadis or oueds)**

In S Africa these are called riviers (◘ Fig. F-12), in America also washes or arroyos. They are an important landscape element of all deserts. Their formation is usually to be sought in the past, when rainfall was higher (pluvial periods). But even today, every few years or decades so much rain may fall in the catchment area that a broad flood further furrows the wadi valley. The dry valleys begin as barely noticeable erosional gullies that merge into deeper ditches or valleys until they often merge into deep canyons.

The water running off after a rain deposits gravel and sand. The salts are partially washed out and the soil is deeply soaked; favourable growing conditions arise, especially for halophytic woody plants (Tamarix, Nitraria). In the large dry valleys, the bed is devoid of vegetation because the soil is redeposited by the infrequent water floods. Vegetation is confined to the margins protected from the floods and is more abundant the more water is stored in the alluvial deposits. Often a constant groundwater flow is present, then dense non-halophytic phreatophytic woody plants are found as extrazonal vegetation, often in a row (contracted vegetation).

◘ **Fig. F-12** Wadis are the dry valleys in deserts that only carry water during a sudden rain event (river oases). More details in the text (a: Kuiseb-Rivier Southwest Africa, photo: Breckle; b: Morocco, photo: Rafiqpoor).

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| **Box F-3** Hamada - Serir - Erg - Takyr - Sabkha |
| This is often a geomorphological sequence and succession of desert types corresponding in their arrangement to a large catena (here landscape links connected by processes of erosion and deposition) with a substrate sorted by grain size. |

3.5 **Pans (Sabkhas, Dayas or Schotts) and Takyr**

These are the small hollows and depressions or large depressions in which the silt or clay particles carried by the water of the wadis are deposited. If these pans have an underground drainage (in karstified areas), then no bracking occurs.

The same is true of the takyr, the delta-like formations at the mouth of the valleys, from which part of the water slowly drains away in a broad front after particularly heavy rainfall. Their heavy clay soils, however, are unfavourable sites; usually the water hardly penetrates the soil, which soon dries up again after a flood. Therefore, only algae, cyanobacteria, lichens or few ephemeral species grow predominantly on the takyr soils (◘ Fig. F-13).

If there is no drainage and all water evaporates from the basin, salt accumulation is the result. In such salt pans, i.e. halobiomes, solid salt layers form on the deepest parts. At the edge, where the salt concentration is lower, hygrohalophytes appear. Often the groundwater is less saline and salt crusts form only on the surface. If a thin layer of sand is deposited locally on the surface of such a salt pan, capillary rise and thus salt accumulation ceases. Plants settle on these sand deposits, which then serve as sand traps, which in turn creates a pile dune or nebkha landscape around the pan.

◘ **Fig. F-13** Dry takyr surface with mirage and heat flicker in the Verneukpan clay surface in the Great Karoo, South Africa. (photo: Breckle).

**3.6 Oases**

The places in the desert endowed with dense plant growth where low-salt water comes to the surface in the form of common or artesian springs are called oases (◘ Fig. F-14), often also along dry valleys (► Fig. F-12b). Here hygrophilous species can grow. Today, such oases are all densely populated. The natural vegetation has been replaced by cultivated plants or weeds. Oases with strong springs are often adjoined by salt pans (bulkheads, sabkhas) in which the excess water accumulates and evaporates (southern Tunisia, Algeria).

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| **Box F-4** What is the commonality of all deserts? |
| As diverse as the individual deserts of the earth are, they all have one thing in common: The low density of plant cover. |

◘ **Fig. F-14** The Rub Al Khali sand desert in Saudi Arabia and Oman is the largest sand desert in the world. Wide dune valleys, which may be loosely vegetated, are fringed by high dunes (photo: Breckle).

4 **Water supply for desert plants**

The great aridity of arid regions tempts researchers who do not know the desert from their own experience to assume that desert plants possess special physiological properties - a physiological drought resistance - which enables them to grow under arid conditions. In particular, the supposedly high cell sap concentrations that enable the plants to absorb water even from nearly dry soil are repeatedly emphasized. However, in-depth ecophysiological studies have shown that these views are incorrect. The water supply of desert plants is not as poor as one is inclined to assume on the basis of low rainfall. This is because rainfall in millimetres means litres of water per square metre of soil surface; one must therefore also calculate the transpiring surface per square metre of soil surface in order to assess the plant's water supply.

The landscape in the deserts is therefore not dominated by the plants, but by the bare rock. If one wants to determine the exact relationship between the amount of rainfall and the density of vegetation, one must compare plants of the same life form (for example, grasses or trees with similar foliage) and select an area in which the rainfall changes over a relatively short distance but the temperature conditions remain approximately the same; these should be flat, large areas with similar soil and the vegetation must not be disturbed by human intervention.

Suitable areas are SW Africa with grass cover at rainfall levels of 100 to 500 mm per year and SW Australia with eucalypt forests at rainfall levels of 500 to 1,500 mm. The result of the corresponding studies was a linear function between rainfall depth and plant mass production, or the size of the transpiring area (◘ Fig. F-15). It also applies to creosote bush (Larrea divaricata) stands in SE California as well as to ephemeral vegetation of arid regions with annual precipitation up to 100 mm.

Only at first the grass seedlings consume 16 to 17 mm for the germination process and use the water less well than the perennial grasses, so that the straight line rises more shallowly.

◘ **Fig. F-15** Substance production (aboveground dry matter in t.ha-1) of grasslands in southwestern Africa as a function of annual rainfall (in mm).

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| **Box F-5** Relationship of water supply and transpiring surface |
| It follows that the water supply in terms of the unit of transpiring area remains more or less the same in arid and humid areas (rainfall 100 to 1500 mm per year). |

The drier an area is, the further apart the plants move, the more soil space each plant needs to absorb water.

This rule is confirmed in North Africa for olive tree crops: Intuitively, farmers reduce the number of trees per hectare in proportion to the decrease in rainfall, until eventually there are only 25 trees per hectare (► Fig. A-47). Yet the yield per tree remains essentially the same, a sign that its water supply is not changing significantly. It is also true for cereal crops that seed density must be lower as rainfall decreases. To be able to draw water from a larger soil space, the plant must have a larger root system.

The second essential characteristic is that with increasing aridity the plants reduce their transpiring surface more and more, but develop the root system more strongly. Indeed, it is found that when the cell sap concentration is increased, shoot growth is immediately strongly inhibited, while root length growth is even initially promoted. While in humid regions the greater part of the phytomass is above ground, in arid regions this applies to the underground part. In arid regions the roots often do not penetrate deeper into the soil, as is usually represented, but the root system becomes shallower and more widely branched. This is because the more sparse the rain is, the less deeply it soaks the soil. There is no water at all beneath the top layer of waterlogged soil for the plants to absorb. Only plants that are tied to groundwater (phreatophytes) or whose roots penetrate rock crevices have been observed to have very deep taproots. But this should not be generalized.

If we come to extremely arid areas with precipitation below 100 mm, the plant cover changes: The **diffuse vegetation** with an even distribution of perennial plants over an almost flat surface changes in extremely arid areas into a **contracted vegetation**, i.e. the perennial plants only grow in often hardly noticeable erosion gullies or depressions, while the higher surfaces remain vegetationless. This is related to the distribution of water in the soil.

In the extreme deserts, with the exception of mobile sand, the soils usually have a biological crust on the surface that is difficult to wet (◘ Fig. F-16) and is swollen by dew. As a result, rain, although infrequent but usually falling in downpours, hardly penetrates the soil but for the most part runs off superficially even on sand. The sandy erosion gullies and the depressions therefore receive much more water than corresponds to the rainfall, and this penetrates deeply into the soil. The plants here root as deeply as the soil is soaked, often several feet deep. Groundwater can even accumulate in places in the valleys. Even in the desert near Cairo-Heluan with 25 mm/year of rain, vegetation is present in all valleys. Assuming that 40% of the rainwater drains into the low parts of the relief and that the latter account for only 2% of the total area, the same amount of water is available to plants at 25 mm rainfall by inflow at these growth sites as is available on a plain at 500 mm rainfall. In fact, it has been measured that the annual water output of the plant cover at such a site is 400 mm at Heluan by transpiration. The cell sap concentration of the plants increases only slightly even in the rainless summer, which is an indication of good water supply. The sandy depressions in the gravel desert at the Cairo-Suez Strait constantly contain 2.4% water already at a depth of 75 cm (wilting point 0.8%), so they never dry out and support sparse perennial vegetation. In individual erosion gullies, plant roots can reach depths of over 5 m. This depends on the moisture penetration. Regardless of the high aridity, the flora around Cairo still has 200 species.

◘ **Fig. F-16** In all deserts, especially in the misty coastal deserts (e.g. Namib or in the Atacama), a film of fine dust can develop on the soil surface which is impermeable to rainwater, mainly because a biological crust always develops which is hydrophobic (of cyanobacteria and unicellular algae), later also with mosses and lichens. Then the rare rainwater can run off superficially as here from sand dunes of the Negev (Photo: Breckle).

◘ **Fig. F-17** Shallow channel with several cross dams to accumulate rainwater and retain fine material as soil. The embankments here are planted with Opuntia, and the plots are newly sown with melons and field beans. Tunisia near Sidi Mansour (photo: Breckle).

Thus, the water supply of plants in the extreme deserts is also not as bad as is usually assumed. Where plants grow in the desert, there is at least at certain times always some water available, even if the soil looks superficially still so dry. The plants only have to have the ability to endure long periods of drought. This is made possible mainly by special morphological adaptations. There is no essential plasmatic drought resistance. Cell sap concentration is generally low (the halophytes excepted).

The principle of contracted vegetation has been used by the Berber population in S Tunisia since time immemorial for crops when there is 200 mm or less rainfall per year: Each small gully is provided with a dam impounding the runoff water (◘ Fig. F-17), and date palms or cereals or field beans are cultivated in the moist soil washed up in front of the dam.

Similar run-off agriculture in pre-Arab times by the Nabataeans has also been found in the Negev Desert. The old dams were rebuilt and the experimental cultivation of various crops was successful (Evenari at al. 1982).

5 **Ecological types of desert plants**

People have called all plants that grow in dry areas xerophytes. This is not appropriate. This is because in every arid region there are sites which guarantee the plants a permanently very good water supply, for example in the oases. In such locations species even of the humid tropics can grow. In the rainless desert near Aswan (► Fig. F-3), for example, coconut palms, mango, mate, papaya, batata, cassava, camphor tree, mahogany tree, coffee, pomegranate, and many species of the Indian monsoon forests are cultivated on an island in the Nile with artificial irrigation. In the dense stand, the microclimate is less extreme than in the open desert. Also, under natural conditions, plants can grow in groundwater-bearing dry valleys that are not exposed to water shortages and therefore have no adaptations to drought. Moreover, in most deserts there is at least temporarily a short wet season. It is lacking only in the Central Sahara, the Namib, and the Peruvian-Chilean deserts. Species that develop in these humid periods (therophytes, ephemerals) and survive the rest of the time as seeds (therophytes) or in the soil (geophytes = ephemeroids) also show no special adaptations to water shortage, apart from the strongly developed root system mentioned above.

A distinction between drought-evading and drought-bearing species is ecologically illogical. All endure drought, some as seeds (ephemerals) or tubers, or bulbs (ephemeroids), others in a latent life state such as the poikilohydric low plants (algae, lichens), but also a number of ferns (Cheilanthes, Notholaena) or Selaginella species and even flowering plants, of which Myrothamnus flabellifolia (Rosales) is the best known (◘ Fig. F-18). The succulents and xerophytes persist in a reduced-active state.

**Xerophytes** arethe ecological groups that require some, albeit minimal, water uptake during drought, as they do not have large water reservoirs. They are three subgroups connected by transitions:

1. **Malacophyllous xerophytes** more characteristic of semi-arid areas. They have soft leaves that wilt in drought, with the concentration of cell sap increasing greatly; in prolonged drought they shed the leaves, leaving only the youngest leaf systems in the densely hairy buds. Typical examples are many labiates, Compositae and cistroses of arid regions.
2. **Sclerophyllous xerophytes** with small, hard leaves stiffened by mechanical tissues. They are found especially in areas with a long summer drought. They can reduce their transpiration to a minimum when water is scarce; cell sap concentration increases only under extreme conditions. Examples are the evergreen oaks, the olive tree and others.
3. **Stenohydric xerophytes**, which immediately close their stomata when water is scarce, thus preventing an increase in cell sap concentration; but this brings gas exchange and thus photosynthesis to a halt, i.e. the plants enter a state of starvation. During prolonged drought, the leaves of these species do not wither but turn yellow and fall off. Some non-succulent spurges can serve as an example, but most extreme desert plants belong precisely to this group.

Survival is achieved with incredible tenacity often only miserable cripples. Plants can become very old in the process, often a hundred years and more. Many branches die, but it is enough if some survive, which grow again after rain.

A group by itself are the **succulents**, which store water and during the drought consume this water very sparingly; their small sucking roots often die, so that during the drought there is no absorption of water from the soil at all. According to the organs in which the water taken up during the rainy season is stored, a distinction is made:

1. **Leaf succulents** (Agave and Aloë or Cotyledon, Crassula, Sansevieria and others), which may also become arboreal (◘ Fig. F-18b).
2. **Stem succulents** (cacti, many Euphorbia species, *Stapelia*, Kleinia, Aloë dichotoma and others)
3. **Root succulents** with non-visible underground stores, such as Asparagus species, Pachypodium and others, but there are also some legumes with huge tubers in the sandy areas of the Kalahari.

A more precise classification of succulents has been given by v. Willert et al. (1990). They distinguish the types given in ◘ Table F-1 on the basis of seasonal development.

◘ **Fig. F-18 a:** Myrothamnus flabellifolius (left) in latent life state (branches and leaves folded) and a Notholaena species (right), two poikilohydre species on the escarpment to the Namib Desert (photo: Breckle), **b:** the arboreal Aloe dichotoma in the Namib with low summer rainfall (photo: Rafiqpoor).

|  |
| --- |
| **Box F-6** Desert plants and dry season |
| In the deserts, it is less important for the plants to produce a lot of material, but rather to survive the droughts at all. There is no competition between the above-ground parts. |

The cell sap concentration of all succulents is very low and does not increase, or increases only slowly, even with large water losses during long dry periods. This is because succulents simultaneously lose organic compounds (sugars, acids and others) as a result of respiration, so that the water content calculated on dry matter can remain unchanged. Many succulents are able to remain alive for more than a year without absorbing water. In many of them the diurnal acid metabolism (CAM - Crassulacean Acid Metabolism) has been proven, i.e. they open their stomata only at night, when transpiration losses are low, take up CO2, whereby this leads to the formation of organic acids, so that the acidity of the cell sap increases strongly. During the day the stomata are closed and in light the CO2 bound at night is assimilated, causing the acidity to decrease again. The necessary gas exchange takes place in this way with minimal water loss (Dinger & Patten 1974).

**Table F-1** Life forms of succulents in the deserts of southern Africa (modified after von Willert et al. 1990)

|  |  |
| --- | --- |
| **Group** | **Lifestyle** |
| 1 | Ephemeral (germination possible after every rain event) |
| 2 | Annuals   * Summer annuals (germination only during summer rains) |
|
|  | * Winter annuals (germination only during winter rains) |
| 3 | Pauciennials (living a few years) |
|  | Perennials (perennial, many years) |
|  | * Geophytes |
|  | * Flowers and leaves at the same time * Flowers and leaves at different seasons |
| 4 | * Root system persistent * Above ground only flowers |
|  | * Above ground persistent plants * No green leaves other than cotyledons * With annual leaf change (rain green) * Periwinkle |

Among the annual succulents, summer annuals are predominantly C4 plants (for example Zygophyllum simplex), while the winter annuals are CAM plants (for example Opophytum aquosum).

A very important group in many deserts are the **salt plants** or **halophytes**. However, they are more bound to the occurrence of saline soils than to the climate. Their distribution often goes far beyond zonobiome boundaries.

6 **Productivity of desert vegetation**

If the individual plants limit their transpiring and at the same time photosynthetically effective surface in times of drought, production decreases. In the case of prolonged drought, it comes to a standstill. On the other hand, in good rainy years the plants develop more luxuriantly, but they cannot use all the water available. The surplus then benefits the ephemerals, which develop particularly strongly and represent, as it were, a vegetation buffer through which the large fluctuations in annual precipitation are compensated.

In bad rain years, the ephemerals almost do not develop or they are represented only by dwarf plants. If the reduction of the surface with the perennial species is not sufficient to achieve a balance of their water balance, large parts of the plants die, because the maximum π\* is exceeded. For survival it is sufficient if the shoot meristem of a branch remains alive and sprouts again after rain. With all woody plants of the deserts, one sees many dead branches as signs of earlier drought years. Reproduction by seed also occurs only after a good rainy year or when several follow each other, which is seldom the case more than once a century. It needs favourable conditions for germination forming seedlings and successful establishment of saplings. Young growth is therefore usually absent altogether. Under these circumstances it is hardly possible to give average values of production.

The leaf area index of perennial species is very far below 1 even in favourable years, and only very abundant ephemeral vegetation can achieve some production in good years.

In the desert near Cairo, the production of ephemeral vegetation has been determined, following a winter rainfall of 23.4 mm, which soaked the upper 25 cm of the soil. Of this amount of water, 68% was lost unproductively by evaporation; the transpiration of the ephemerals during the winter months corresponded to 7.3 mm, i.e. 32% of the amount of rain, which is 730 kg of water calculated per 100 m2 of soil area. The ephemerals produced 9.834 kg of fresh matter or 0.518 kg of dry matter on the same area. This gives a transpiration coefficient of 730:0.518 = 1,409, which is very high compared to the values of our crops in Central Europe (400 to 700). This is due to the very low humidity in the desert.

Similar values were obtained by Seely (1978) for annual grasses in the Namib at very low rainfall. The zoomass in the desert and thus the secondary production is vanishingly small; however, the food chains as control loops for the ecosystem are not without importance in the desert.

As an example, we cite the special production studies on agaves and cacti. They were carried out in the westernmost part of the Sonora Desert in California with a summer drought.

1. Quantitative data (all mean values) are given by Nobel (1976) for Agave deserti, which also occurs in the eastern Sonoran Desert. For plants with a mean of 29 leaves it is stated: Length of leaves 30 cm, area 380 cm2, weight of a leaf fresh 348 g, dry 47 g Stomata30 per mm2. Number of roots per plant 88, their length 46 cm, radially quite flat stroking, so that any rainfall can be used to absorb water.

Stomatal opening occurs during the rainy season (November to May) at a soil water potential of -0.1 bar on 154 to 175 days. If this potential drops to -3 bar at the beginning of the drought, then water uptake no longer takes place, but the stomata open at night on a further eight days. Then they remain closed; a diurnal acid metabolism (CAM) only takes place again after a rainfall.

In 1975, transpiration losses amounted to 20.3 kg per plant, which, converted to the rooted soil area, corresponds to a rainfall of 26.9 mm = 35% of the annual rainfall. The transpiration coefficient, i.e. the ratio of the amount of water transpired to the amount of dry matter produced (both in kilograms), was 25, i.e. very low, which means an extraordinarily economical water use.

Per plant 0.8 kg dry matter was produced in the year. Growth is therefore very slow and only older plants flower once and then die because all the plant's substance and water reserves are used up to produce the large inflorescence.

The following determinations confirm this (Nobel 1977a): The flowering old plant had 68 leaves, which were 4.1 cm thick when the inflorescence just became visible. After formation of the inflorescence they had shrunk, faded and were only 1.4 cm thick.

The entire leaves lose 24.9 kg of fresh weight and 1.84 kg of dry weight during flowering. Water uptake from the soil was not sufficient; 17.8 kg was received by the inflorescence from the leaves. The dry weight of the inflorescence was 1.25 kg and 0.59 kg of dry weight was respired. One flowering plant produced 65,000 seeds, 85% of which were destroyed by animals. Not a single seedling was found in an area of 400 m2 where there were 300 agave plants. Propagation by seed takes place only in favourable years, otherwise only vegetatively by runners. These numerical values make it understandable why agaves are hapaxanthic (monocarpic) species, i.e. they flower and fruit only once and then die.

1. An equally detailed production analysis was carried out in the same area with the globular cactus Ferocactus acanthoides (Nobel 1977b). This is also a species with diurnal acid metabolism (CAM), but in which the effort for the flowering organs is so low that it flowers every year (► Fig. F-25).

The 34 cm high plant with a diameter of 26 cm weighed 10.8 kg with a water content of 8.9 kg. Transpiration losses amounted to 14.8 kg in one year; in addition, 0.6 kg was used for transpiration and the build-up of generative organs. CO2 assimilation produced 1.6 kg in one year, of which one third was respired. The measured annual growth was determined as 9%. The transpiration coefficient was 70, higher than in the agave, but still very low. The opening of the stomata was similar to that of the agave.

7 **Desert vegetation in the different floral kingdoms**

The conquest of the deserts by plants took place in prehistoric times, when the various floral kingdoms had already differentiated. The plant families or generally the taxa of the individual floral kingdoms have a different species population; consequently, the adaptations to the way of life under arid conditions have developed in different directions in the plants of the individual floral kingdoms. Not only are the deserts floristically different, but the life forms need not be the same, although many convergences occur (Walter & Breckle 2004).

7.1 **Sahara**

The Holarctic includes only the northern part of the largest subtropical desert - the northern Saharo-Arabian desert, which in the east passes gradually and directly into the Irano-Turanian and Central Asian deserts with cold winters. The boundary between the two can be drawn by the northern limit of distribution of the productive date culture (e.g., in north-central Iran). In this desert, the Chenopodiaceae are particularly abundant, partly due to the high prevalence of saline soils. Succulent Euphorbia species are found only in W Morocco (◘ Fig. F-19a). Most species are xerophytic dwarf shrubs, some of them broom-like shrubs. Grasses are represented only by xeromorphic forms with hard leaves: Stipa tenacissima and Lygeum spartum (transition zone), Panicum turgidum, Aristida pungens and others. After good winter rains, many ephemeral species appear.

In the vast Sahara, at least today, the central part is not an overlap zone between the northern winter rainfall regions on the Mediterranean and the southern tropical summer rainfall regions, but this central part is a largely rainless desert, an extreme desert with very rare rain events (► Fig. F-2). Nevertheless, although restricted to gullies and wadis, there is definitely still a flora, albeit species-poor. Small localized showers can suddenly cause some annuals to germinate in a narrowly defined area; Zygophyllum simplex (◘ Fig. F-19b) in particular then occurs sporadically.

◘ Fig. F-19 The succulent desert with Euphorbia officinarum at Cap Rhir north of Agadir, Morocco (a: photo Rafiqpoor) and Zygophyllum simplex (b, photo: http://bit.ly/2fkTT4S) typical of shallow gullies even in the central Sahara near Aswan.

The landscape forms are largely determined by the geologically given rock layers with their specific properties in relation to physical weathering (◘ Fig. F-20), often modelling out large blocks or even small inselbergs that are very dark due to desert varnish overlays.

◘ Fig. F-20 Extreme desert of the southern Egyptian Sahara south of Aswan (Egypt) with long-term mean annual precipitation of only 1-3 mm, dark boulder fields and rocky deserts (Hamada) with individual sand dunes (Erg) (photo: Breckle).

Shrubs that are bound to moist sites, i.e. occur contracted in small gullies or wadis, would be Tamarix, Nitraria and Ziziphus. These are already more paleotropical elements, as are the Acacia species in the groundwater-bearing dry valleys.

To the Palaeotropis belongs the southern Sahara with the Sahel, as a transition to the Sudanese summer rain area. Here, grasses (Aristida, Eragrostis, Paniceae), with less hard leaves play a much greater role. Shrubs and herbs are also more numerous (Acacia, Commiphora, Maerua, Grewia, Calotropis, Crotalaria, Aerva and others), which are also found in the Thar or Sind deserts.

7.2 **Negev and the Sinai**

They join the Sahara in the east as a bridge to the Arabian deserts. On the Sinai Peninsula, mountain deserts predominate, in which Irano-Turanian plants already occur at high altitudes. The northern Sinai and the Negev are characterized by extensive sand fields, with mobile sand dunes only when grazed heavily (Breckle et al. 2008).

Precipitation shows a very strong gradient from north to south, as shown in the precipitation map (◘ Fig. F-21).

The northeastern part of the Sinai Peninsula and the Negev Desert pass over the Arawa Depression rift valley, the Dead Sea and the Jordan Rift Valley to the Jordanian Desert. Ecological research has been very intensive in this area for several decades. The Negev Desert is therefore one of the best researched deserts (cf. Walter & Breckle 1991, Breckle et al. 2008).

As small as the Negev Desert is in terms of area, as great is its importance in floristic terms as a transitional area between different floral regions. Within a short distance, the Mediterranean vegetation from the north, the Iranian-Turanian vegetation from the northeast, the Saharan vegetation from the west and southwest, and the Arabian desert vegetation from the east meet here. In addition, there are even Sudanic enclaves, especially in the low-lying rift valley, for example with Salvadora persica, Cordia gharaf, Maerua crassifolia. Cyperus papyrus still occurs in the Huleh swamps on the upper Jordan River, where at the same time Nymphaea alba (as a Holarctic plant) reaches here its southernmost point.

7.3 **Arabian Peninsula**

In the same latitude as the Sahara, the Arabian Peninsula continues the desert belt eastward.

Fig. F-21 Annual precipitation in the Negev Desert and in Israel. Note the considerable gradient from south to north.

The precipitation is almost on the whole peninsula between 15 and 100 mm, on some steep slopes they go partly a little beyond 100 mm and in rainier mountainous areas above 2000 m 250 to 650 mm are measured. In the north of Yemen, a distinctive altitudinal sequence is recognizable with a rich vegetation, with evergreen hard-leaved bush forest, in which already numerous tropical genera occur, likewise in the southeastern Oman.

The eastern part of the peninsula is occupied by the Rubal Khali, a vast sandy desert area (► Fig. F-13). The same geomorphologically determined vegetation differentiation occurs here as in the Sahara. The vegetation is almost exclusively contracted. The larger wadis are characterized by rows of *Acacia*, among which a whole range of other woody plants, especially Prosopis, can also be found. In smaller depressions *Tamarix* species, Calotropis procera and Calligonum comosum occur. In the southern areas there are already transitions to *Acacia* thorn savannah (ZE III/II). Occasionally precipitation falls already in summer (for example in Sana or in Salala in Oman). Accordingly, succulent euphorbias and many other tropical-subtropical floral elements occur, such as Adenium (◘ Fig. F-22), Jatropha, etc. On the rocky slopes of the high mountains above 1500 m asl, woody plants include Juniperus spec. (Hall 1984, Fisher 2000) and sporadic Olea europaea (Fuellner 1997); on damp sites exposed to moisture, even mosses (Frey & Kürschner 1988; Kürschner & Böer 1999). Floristically, the flora of Yemen is the richest. Prominent floral elements of the mountains are the genera Euphorbia, Euryops, Dodonaea, Themeda, Lavandula, Solanum, Abutilon and others (◘ Fig. F-23).

◘ Fig. F-22 Boswellia sacra grows in the southern Arabian Peninsula, Oman, Yemen and Socotra. It grows from a tuberous root resembling a lignotuber; sometimes this tree even forms stems that store water (photo: Breckle).

7.4 **Sonora**

In NAmerica only the deserts in SCalifornia and SArizona can be counted as subtropical deserts, but with Holarctic flora elements. The arid areas in NArizona, Utah and Nevada already have very cold winters (ZB VII).

Neotropical are several semi-deserts to desert areas: The Sonora Desert (N Mexico and southern Arizona) is located in N America, but floristically it already belongs to the Neotropics. About this desert (perhaps better semi-desert) extensive investigations are available, which were carried out at the Desert Laboratory in Tucson (Arizona). The stands of tall candelabra cacti (Carnegiea gigantea) are called "cacti forest" (◘ Fig. F-24). These succulents can store so much water that they can last for more than a year without taking up water (◘ Fig. F-25).

◘ **Fig. F-23** West-east profile of vegetation in central Yemen (after H. von Wissmann 1972): **1** Halophilous desert vegetation; **2** Piledunes; **3** Umbrella acacia stands; **4** Semi-desert on alluvions; **5** Semi-desert on rocky slopes; **6** Gallery and canyon forests; **7** Tropical evergreen scrub forest with lianas and succulents; **8** Hardwood shrubs; **9** Semi-desert, partly with Mediterranean species.

◘ **Fig. F-24 a-b** Carnegiea gigantea in the Sonora Desert in Arizona, USA. The gigantic cacti form candelabra-like "trees" that can grow 10-15 m tall. The mechanisms of water uptake are shown in ► Fig. F-25 (photos: Barthlott).

The cacti have very shallow roots. As soon as the upper soil layers are moistened, they form fine sucker roots within 24 hours and fill up their water reservoirs. But apart from succulent cacti, the other ecological types are also represented here: Winter and summer ephemerals, poikilohydric ferns, malacophyllous semishrubs (Encelia), sclerophyllous species, stenohydric and the rain-green Fouquieria, which forms new leaves after each heavy rain.

◘ Fig. F-25 Distribution of osmotic potential or potential osmotic pressure (- π\*) on the transverse section of Ferocactus wislizenii. Isosmoses = lines of equal pressure (cell sap concentration, numbers in atm, highest pressure at \* in the southwest).

If there is a lack of water, many species turn yellow after a short time. Vast arid areas are covered by the creosote bush (Larrea divaricata), which smells of creosote when the leaves are moistened by rain and is particularly drought-resistant. It is also characteristic of the Mohave Desert, which receives only winter rains and is poor in succulents. Larrea is usually joined by Franseria, a soft-leaved composite, but also many Opuntias with flat or cylindrical succulent shoots.

◘ Fig. F-26 Semi-desert with Larrea divaricata (Zygophyllaceae) in Arizona, USA (photos: M. Neumann).

A *Larrea* desertalso extends in the lee at the eastern foot of the high Andes for 2000 km from N Argentina to cold Patagonia. The main species Larrea divaricata is probably identical to that in Arizona (◘ Fig. F-26).

A monograph on the family Cactaceae as a well-studied model group of neotropical drylands, mapping the range of each cactus species (over 1,400 species in total) and including diversity maps of family genera and species, was published in 2014. Quantitative analyses of the centres of diversity of cacti revealed that at the species level they are centred in the Chihuahua-Sonora Desert in North America and in Mexico, while at the genus level they are centred in South America and specifically in the Andes and northeastern Brazil (Barthlott et al. 2015).

◘ Fig. F-27 Tidestroemia oblongifolia is resistant to overheating in Death Valley, USA (photo: Breckle).

The deep tectonic depression of "Death Valley" on California's border with Nevada is characterized by extremely high temperatures in summer. Air temperatures of up to 57°C have been measured there. The basin is heavily salinized, in some places there are freshwater springs. Tamarix species colonize there, but also the very heat-resistant Amaranthaceae Tidestroemia oblongifolia (◘ Fig. F-27) and Cleomella obtusifolia (Capparidaceae), both of which have a photosynthetic optimum above 40°C. The rocky steep slopes at the edge of the basin are a typical hamada, the bizarre rocks are covered with desert varnish (◘ Fig. F-28), very occasionally there are heat- and drought-resistant dwarf shrubs, such as the completely white-looking Atriplex hymen-elytra, in which the typical bladder hairs are glued together to form a radiation shield against overheating.

◘ Fig. F-28 The bizarre rocks on the slopes of Death Valley (USA) are covered in desert varnish (photo: Breckle).

7.5 **Australian deserts**

The arid areas in the Australis show very different conditions. The whole of central Australia is arid. The sand dune areas (Gibson desert, Simpson desert) have desert character, but they are not the climatically driest parts of Australia, and the "Gibber plains", bare areas with stone pavements caused by heavy overgrazing. The vegetation of the driest parts, with infrequent rainfall at any time of year, are the 'Saltbush' (◘ Fig. F-29) (Atriplex vesicaria) and the 'Blue bush' Maireana (Kochia) sedifolia, both Chenopodiaceae. They occur in pure stands, but also mixed (◘ Fig. F-30).

◘ Fig. F-29 Salt Bush formation with single trees of Eucalyptus (with some emus) near Port Augusta in Australia (photo: Breckle).

The soils under Atriplex contain little chloride, about 0.1% by dry weight. However, as the loamy soils dry out considerably, the concentration can be high. This is matched by the high cell sap concentrations of Atriplex (usually 4 to 5 MPa), with the proportion of chlorides reaching 60-70%. Atriplex vesicaria is thus a euhalophyte; growth is promoted by salt. Some salt recretion is possible due to the short-lived and continually regenerating bladder hairs. This semi-shrub lives about twelve years; like most halophytes it has weakly succulent leaves and a root system that extends far laterally over a calcareous crust at a depth of about 10 to 20 cm. The bushes are therefore quite widely spaced.

In contrast, Maireana sedifolia is said to grow very old and to have a deep root system that reaches down 3 to 4 m in the crevices of the calcareous crust, but also about as far laterally. The species grows where rainwater seeps deeper (lighter or stony soils). The cell sap concentration of this species is only half that of Atriplex and the chloride content is also much lower (about 20 to 40%). It is therefore possible that it is a facultative halophyte and comes to predominate as the climate becomes more humid.

In the salt bush area, sand dunes or sandy areas occur scattered with more favourable water conditions; the soil here is free of chlorides. Shrubs grow here (Acacia, Casuarina, Eremophila).

◘ **Fig. F-30** Blue Bush Formation from Maireana (Kochia) sedifolia in South Australia (photo: Breckle).

The arboreal Heterodendron and Myoporum species, together with Eremophila and Cassia species, are attached to silty soils. The most important species of central Australia is Acacia aneura, known as "Mulga". It dominates on wide areas, which look like a grey sea from the airplane. The shrub reaches 4 to 6 m in height and has phyllodes covered with resin that are thinly cylindrical or somewhat flattened (◘ Fig. F-31). The root system is strongly developed and penetrates through the hard soil layers about 2 m deep. With the irregularity of rainfall, flowering is not tied to any season, but only to rain. After heavy rainfall, the fruits and seeds ripen. At the same time, a flowering carpet of white, yellow and pink immortelles (everlastings, strawflowers), several genera belonging to the Compositae (◘ Fig. F-32), then develops on the ground.

◘ **Fig. F-31** Over 500 Acacia species occur in Australia. We present here some examples. **a**: Acacia cf lasiocalyx; **b**: Acacia cf cuneata, **c**: Acacia sp., **d**: Acacia aneura, **e**: Acacia maidlandii; **f**: Acacia dyctiophylla, **g**: Acacia tetragonophylla; **h**: Acacia pyrifolia (photos: Breckle).

◘ **Fig. F-32** Mulga vegetation in the interior of Australia near Wiluna after rain. Large shrubs - Acacia aneura, small bush - Eremophila spec., ground densely covered with short-lived immortelles, such as Waitzia aurea and white Helipterum species (photo: Breckle).

Acacia aneura is sensitive to salt, but can tolerate long periods of drought. In dry sites, the bushes are widely spaced, while in moist depressions they form thickets. This species as well as Rhagodia baccata and Acacia craspedocarpa were studied ecophysiologically (Hellmuth 1968, 1969).

Another important group is the hedgehog grasses (Triodia, Plectrachne), which are grouped together as "spinifex grasslands". They have coiled, persistent, and very hard leaves with a resinous coating that terminates in a sharp point, and they form large, rounded cushions, hemispheres up to 2 m high in Triodia pungens (◘ Fig. F-33). We can classify these species among the sclerophylls.

◘ **Fig. F-33** Triodia pungens grassland near Ayers Rock Australia is broken up into individual bushes (photo: Breckle).

Triodia basedowii is found on sandy areas in the most arid part of Western Australia. Its dense root system goes 3 m vertically into the depth. Older pads break up into individual festoons. Other characteristic genera, represented by many species, are Eremophila, Dodonaea, Hakea, Grevillea and others. The arrangement of the vegetation is conditioned by the nature of the soil and by stratum floods after heavy rains, creating a complicated mosaic of vegetation.

The quaternary history, derived by Crowley (1994) from pollen diagrams of numerous lake sediments, reveals an increase in rainfall and concomitant decreased salinity for the Australian desert areas at the end of the last glacial period, which increased again 5,000 years ago and became particularly pronounced after the arrival of European settlers.

7.6 **Namib and Karoo**

Of the South African deserts, the Namib and the Karoo are also palaeotropical. Occasionally, Capensian floral elements already occur. The Namib extends along the coast of SW Africa. This coastal Namib, rich in fog, must be distinguished from the southern Namib in the transition area to the Karoo, which as an actual desert lies between the southern winter rainfall area and the northeastern summer rainfall area and intermittandly can have two rainy seasons.

The Karoo extends into the Oranje Free State. The two rainy seasons favour the development of innumerable succulents, on rocky sites with the larger Euphorbia, Portulacaria and Cotyledon species as well as many small Crassulaceae and *Mesembryanthemum* s.l. species on quartzite veins (◘ Fig. F-34). The wide areas are covered with dwarf shrubs (mainly Compositae) (◘ Fig. F-35). In the dry valleys woody plants are found, such as Acacia, Rhus, Euclea, Olea, Diospyros, but also Salix capensis. In the transition area of the Upper Karoo, the grassland of the summer rainfall area is already growing on deep fine-grained soils, while Karoo succulents are still found on the shallow rocky areas (◘ Fig. F-36).

As an example of a biome of the zonobiome III and the subzonobiome of the fog deserts, the Namib on the coast of Southwest Africa will be discussed in more detail, because it differs strongly from the other deserts. Although it is a subtropical and extremely rainless desert, the coastal strip is characterized by high humidity with about 200 foggy days per year and low temperature fluctuations as in oceanic climate areas.

The mean annual temperature (16 °C) on the Namibian coast is about 5K too cool for the latitude because of the cold Benguela Current. The quasi-stationary high-pressure area and the cold Benguela Current here, like the Humboldt Current on the Chilean coasts, cause a pronounced temperature inversion at about 600 to 1,000 m asl with the formation of a blanket of high fog at the inversion lower boundary (◘ Fig. F-37). The thickness of the high fog is about 300 m and depends on the cooling from below. Inland, the temperature increases so that the fog cover dissipates about 50-70 km inland. The vegetation has adapted well to these ecological conditions. In the fog desert area (◘ Fig. F-38), a rich small-leaved succulent flora occurs. Outside the fog zone, where periodic summer precipitation intervenes, a stem succulent flora tends to dominate (► Fig. F-38).

◘ **Fig. F-34** In the Karoo, an exceedingly exotic-looking leaf succulent formation of the Knersvlakte (**a** with Oophytum nanum) has developed on the weathered white quartzite veins from various Mesembryanthemum species and other genera of the Aizoaceae ("Living Stones"), etc. Some examples: **b**: Mesembryanthemum crystallinum; **c**: Malephora purporeo-crocea (Aizoaceae); **d**: Drosanthemum diversifolium; **e**: Argyroderma delaetii; **f**: Mesembryanthemum nodiflorum (Aizoaceae) (photos: Rafiqpoor).

◘ **Fig. F-35** Great Karoo near Laingsburg (South Africa) with succulent euphorbias, Rhigozum obovatum, Rhus burchellii and dwarf shrubs (photo: Breckle).

◘ **Fig. F-36** Vegetation profile through a valley of the Upper Karoo near Fauresmith (South Africa). Plant cover structure conditioned by differences in soil. Scrubland with Olea, Rhus and Euclea.

The temperatures are always cool, hot days are few in the year. These strange conditions are caused by the cold Benguela current (water temperature 12 to 16°C). Above it lies a 600 m high layer of cold air with a fog bank, so that due to the inversion the warm easterly current does not reach the ground. Rather, a sea breeze sets in daily from the southwest, bringing the fog and cool air into the desert (Logan 1960, Besler 1972).

◘ **Fig. F-37** A dense blanket of fog develops on the Peruvian-Chilean coast due to the effect of the cold Humboldt Current. It is so saturated with moisture that water is exuded from it when it comes into contact with objects. This fog humidity leads to the development of fog-adapted flora on the fog coasts of the earth (Southwest Africa, Northwest Africa) (photo: Rafiqpoor).

◘ Fig. F-38 Climate diagram of Swakopmund in the Namib. Almost rainless area, but with 200 foggy days per year (not measurable precipitation).

When the inversion layer is broken, thunderstorms form and rain falls, which is the case in very few years. Exceptions are rare, heavy rains only once or twice in a century, such as in 1934/35 with 140 mm of rain and in 1975/76 with over 100 mm and in 2006 and 2011 there was also abundant rainfall. The long-term annual mean of 16 mm for Swakopmund (other sources: 28mm) therefore means little (► Fig. F-38).

The humidification of the soil by dew or fog is minimal, on average 0.2 mm, maximum 0.7 mm per day; the annual sum of fog precipitation of about 40 mm remains ineffective because the individual fog precipitations evaporate again without being stored by the soil. They benefit only the poikilohydric lichens and soil algae (◘ Fig. F-39b), which cover all the rocks in the fog zone with variegated colours when the humidity is high, as well as the window algae found on the underside of transparent quartz pebbles (► Fig. F-39a), where the fog moisture is retained longer. True mist plants, like the tillandsias in the Peruvian desert, which do not draw water from the soil, do not exist in the Namib.

Only where the drifting mist collides with a rock face does water condense and penetrate deep into the crevices. There plants (mostly succulents, ◘ Fig. F-40) can establish themselves. This is the case with the inselbergs that rise above the almost flat hull platform of the Namib.

This hull plain rises with a gradient of 1:100 from the coast to the east and has a width of 100 km to the foot of the escarpment from the African highlands (Escarpment). The fogs are noticeable up to 50 km inland. They also contain droplets of seawater sprayed by the surf, which come to be deposited so that the soils of the outer Namib are brackish.

Fig. F-39 In the Outer Namib in SW Africa, window algae occur here and there on the underside of quartz pebbles in the area of fog influence (a). Migratory lichens Omphalodium convolutum (b) are concentrated in depressions and gullies (photos: Breckle).

◘ Fig. F-40 Hoodia currorii flowering in front between white marble rocks (Witport Mountains, Namibia) (photo: Rafiqpoor).

Perennial plants are only found in the Namib where the soil contains water at a depth of less than 1m. These water supplies come from good rain years. After the 140 mm of 1934, the desert was green and covered with flowers (◘ Fig. F-41a). These were mainly ephemerals, including especially many succulent *Mesembryanthemum*-species and other Aizoaceae, Portulacaceae etc. (◘ Fig. F-41b). These stored so much water in the shoot that they still flowered and fruited the next year, although the root and the shoot base had already dried out (◘ Fig. F-42). In them, almost the entire supply of assimilates and of water is used to form the fruits and seeds (V. Willert et al. 1990). Many seedlings also grow from the perennial species in such years, their roots penetrating rapidly into the depths and reaching the lower soil layers that remain moist longer. However, they can only survive for the next decades where larger water reserves are stored in the soil.

◘ **Fig. F-41** The flowering Namib Desert in Namaqualand in October 2008. The gently sloping slopes and the entire area is transformed into a sea of flowers of annual Asteraceae, Mesembryanthemaceae etc. after the first episodic rains (see also Cowling et al. 1999) (photos: Rafiqpoor).

◘ **Fig. F-42** Mesembryanthemum cryptanthum in the Skeleton Coast near Möve Bay, Namib even after many months of drought with thick-fleshy leaves and fruits (photo: Breckle).

After rare heavy rains, the water flows in wide, sand-filled channels, the Riviers (wadis) to the sea, without reaching it. Rather, it seeps into depressions filled with alluvial soil and penetrates deep into the ground. Only the upper soil layers dry out to a depth of 1 m (less deep in sandy soil). Below that, the water persists for decades and can be exploited by deep-rooted plants. In the gullies, the sand is desalinated by the rainwater run-off; in the depressions, on the other hand, the salt is washed in. This results in two distinct sites - in the small and large erosion gullies with non-halophilic biogeocoenoses (Citrullus, Commiphora, Adenolobus and, where there is more groundwater, the shrubs Euclea, Parkinsonia and Acacia spp.), while on the wide flat depressions halophilic species settle. These are mainly Arthraerua (Amaranthaceae), Zygophyllum stapffii and Salsola species (Chenopodiaceae), with sand blown onto each plant from which it grows above. Low mounded dunes form, creating a typical Nebkha landscape (◘ Fig. F-43; ► Fig. F-11). It can be assumed that all the plants germinated in the same rainy year; they are also fairly equal in size and can last as long as the water supplies in the soil last; if no new rainy year comes for a long time, they slowly die and the dune sand is blown away. If, on the other hand, they receive good rain again in time, they continue to grow.

◘ **Fig. F-43** Arthraerua leubnitzia-Nebkha (Amaranthaceae) in the Namib near Swakopmund (photo: M. Loris).

For the survival of these plants, fog (caused by cold ocean currents) plays a major role; because in water-saturated air, the plants can assimilate CO2 without significant transpiration losses. Their water consumption is thus low. Arthraerua is now thought to be able to absorb fog moisture from the air with specially constructed, low-lying stomata at the end of capillary passages (Loris 2004).

Apart from the three biogeocoene complexes with salt-free sandy soil and the brackish depressions near the coast, the oases of the large Rivier valleys (dry valleys) should be mentioned: Omaruru, Swakop and Kuiseb in the Central Namib (◘ Fig. F-44), in the northern Namib: Ugab, Huab, Uniab, Hoanib, Hoarusib and Khumib up to the Angolan border at the Kunene. In the sand Namib, only the Kuiseb (border river between rock and sand Namib) reaches the Atlantic Ocean, Tsondab and Tsauchab seep into the sand masses beforehand.

◘ Fig. F-44 The dry riverbed of the Kuiseb (Wadi, Rivier) near Gobabeb with tree population of Acacia albida, A. erioloba, Tamarix usneoides and Salvadora persica. In the background the mighty dunes of the Sand Namib (photo: Breckle).

The Riviers all originate on the highlands with summer rains (average 300 mm) and are partly cut deep into the Namib platform. The riverbed is filled with sand, in which the water seeps away after rains on the highlands and only after very good rains it flows down to the sea. But the rest of the time there is a constant flow of groundwater in the sand, so that water can be obtained from wells. Partly it is slightly brackish due to the inflows from the Namib. This groundwater creates the possibility for the development of gallery forests of Acacia albida, A. erioloba, Euclea pseudebenus, Salvadora persica or in somewhat brackish places Tamarix and Lycium species. Where the woody plants are protected from the high tides, the forests can reach a great age. On the often shifted sand grow Ricinus, Nicotiana glauca, Argemone, Datura and others, on sand dunes the thorny and leafless Acanthosicyos (Naras gourd) and Eragrostis spinosa - a woody thorny grass; where the ground water forms pools, Phragmites, Diplachne, Sporobolus and Juncellus stand.

All these plants are abundantly supplied with water and have a high productive power. These oases are also rich in animal life: Birds, rodents, reptiles, arthropods and others. Even today, elephants (◘ Fig. F-45) and giraffes roam the Rivier valleys. Elephant and rhinoceros used to be abundant. They have been almost exterminated by man. Only the baboons have persisted in the rocky gorges.

The fauna of the Nebkha landscape is poor. There are: Some rodents, reptiles and scorpions, as saprophages and beetle species. More species are found in the inselbergs, especially if they are further inland and already receive frequent summer rains, so that there are waterholes between the rocks and shrubs can grow in crevices. In the Sand Namib, too, the fauna is much richer in species.

The given description referred to the outer Namib. As soon as one moves further than 50 km from the sea, the inner Namib begins with sparse summer rains and changing grass growth. The desert conditions are not so extreme and give the mobile game the opportunity to find food and visit individual waterholes. This part is rich in game. The most common animals are: Zebra, oryx antelope, springbok, hyena, jackal, occasional lion as well as ostrich and other birds. This is because this uninhabited area has been declared a nature reserve in the central Namib; it is explored from the Namib Desert Station Gobabeb.

In the central Namib, on the border between the outer and inner Namib, the famous Welwitschia mirabilis occurs in numerous specimens. It grows in wide and very shallow erosion gullies with hardly noticeable slopes (◘ Fig. F-46), where the sparse summer rains converge and penetrate deeper into the soil. Welwitschia absorbs this water with its roots, which reach well over 1.5 m deep. Underneath is a hard crust of lime. If this species is absent in the deeper erosion gullies, it is probably because Welwitschia seedlings are very sensitive to flushing water and to being filled in with sand. At present it only rejuvenates in the northern Namib.

◘ Fig. F-45 Big game at the waterhole in the Etosha Pan in northern Namibia (a); elephant family in the Huanib Rivier, Namibia (**b**) (photos: Breckle).

Welwitschia has only two ribbon-shaped leaves, which constantly grow from a meristem on the turnip-shaped stem and dry up at the tip. In good rainy years the living part is quite long, in bad ones the leaves dry up almost to the meristem, so that the transpiring surface is greatly reduced, whereby the transpiration falls almost to zero. The leaves are very xeromorphic anatomically and have sunken stomata. There is no evidence of dew uptake. An age determination with the C14 method gave an age of about 2,000 years for the oldest measured specimen. The wood shows annual rings and tracheae.

Transpiration and photosynthesis were studied by v. Willert et al. (1982): Welwitschia is a C3 plant; the water consumption of a medium-sized plant is about one litre per day. Calculated on the rooted area, this would correspond to a rainfall of 2 mm per year. Thus, water supply is guaranteed even in this arid area. They are pollinated both by the wind and by a species of bug (Probergrothius sexpunctatis) that feeds on the nectar of the female flowers (◘ Fig. F-47).

Unique are special ecosystems of the Namib:

1. The almost vegetationless dunes south of Kuiseb (► Fig. F-43)
2. The Guano Islands
3. The mating grounds of the seals
4. The lagoons behind the beach.

In the dune valleys, organic detritus is found from blown-in grass remains, protein-rich animal remains and perished insects (butterflies). The detritus is eaten by psammophilous wingless tenebrionids (black or darkling beetles), which in turn are eaten by small predators (spiders, solifuges) or by larger lizards, snakes living in the sand and goldmouths (Chrysochloridae) (Kühnelt 1975).

◘ **Fig. F-46** Welwitschia mirabilis on the Welwitschia vlakte between Khan and Swakop Rivier (photos: Breckle).

◘ **Fig. F-47** Male (**a**) and female inflorescence (**b**) of Welwitschia mirabilis and its pollinator the bug Probergrothius sexpunctatis (**c**) (photos: Breckle).

◘ Fig. F-48 A mist-catching tenebrionid on Namib sand dunes in the early morning (photo: M. Seely).

Since the sand heats up to over 60°C during the day, almost all animals hide in the cool sand and only come out at night. The water source is the mist, which they ingest in a special way (Seely & Hamilton 1976, Hamilton & Seely 1976). Some species have comb-like appendages on the hind legs with which to comb out the mist droplets, while others stand perpendicular to the wind and suck up the mist droplets, which condense on the hind legs and abdomen and then drip towards the head (◘ Fig. F-48). The fauna is rich in endemics.

The guano islands are the nesting sites of, among others, the cormorants, which find their food in the cold seawater rich in fish. In the rainless climate, the birds' excrement accumulates and prevents any plant growth, but it is decomposed as guano (phosphate fertilizer). Similar conditions prevail on the mating grounds of the seals (Cape Cross).

The lagoons are cut off from the sea by sand bars, with only occasional waves breaking over during storms. The evaporated water is replaced by seawater that seeps from the sea through the sand. They are therefore aquatic ecosystems with very high concentrations of salt, which we will not go into details. Like the Namib, each desert has its ecological specificity and must be treated monographically (cf. Walter 1973 and Walter & Breckle 2004).

7.7 **Atacama**

The Peruvian-Chilean coastal desert is very strongly divided into subregions (◘ Fig. F-49). In its extreme part it is as rainless as the Namib, but the fog here has a greater effect only in the coastal region, because the coast rises steeply in places. Here the only known true fog plants among the flowering plants are tillandsias (Bromeliaceae), which cannot absorb water from moist air like lichens, but nevertheless suck in the condensation droplets during fog directly with special scales on their leaves. They sit as epiphytes on columnar cacti or lie loosely as rosettes on the sandy soil (◘ Fig. F-50).

◘ Fig. F-49 General map (top) and transect (bottom) of northern Chile and region of the Atacama Desert proper between the Pacific Ocean and the Andes (modified after Wickens 1993).

At an altitude of 600 m, the blanket of fog known as "Garua" in Peru lingers for months during the cooler season. The soil of the slopes is so heavily wetted that a carpet of herbs - the "Loma vegetation" - develops, which is grazed. Woody plants are absent, but were formerly present. Under planted eucalypts, dripping of condensed fog could collect amounts of water equivalent to 600 mm of precipitation. In the coastal cordillera itself in N Chile, sporadic, mighty columnar cacti (Echinopsis atacamensis) up to 8 m high are found, densely covered with lichens (◘ Fig. F-51), but only on slopes exposed to the fog. Further south at Fray Jorge (now a national park in central Chile), even a true cloud forest occurs.

◘ Fig. F-50 Tillandsia straminea (a), Tillandsia purpurea (b) in the Atacama Desert of southern Peru forms festoon structures (c) but without forming roots in the soil. They comb out the water they need from the fog with special suction scales (photos: Rafiqpoor).

◘ Fig. F-51 Echinopsis atacamensis (a: on an island in the Salar de Uyuni, Bolivia) grows about 8 m high in the Atacama Desert. When exposed to fog, they are used as a base by epiphytic tillandsias and lichens (b: Chile). Salt lakes have formed in the closed basin landscapes (photos: Breckle).

In NChile in the area of the large saltpetre deposits, shielded from the coastal fog by the coastal cordillera, the desert is devoid of vegetation. Plant populations and cultures can only be found along the river courses, which are fed by the snowfields of the high Andes.

The inner basins lie at higher altitudes. However, up to the high altitudes of the Andes and into southern Bolivia, they are characterized by huge salt pans (► Fig. F-51a): Salars in which not only NaCl but a number of other minerals have accumulated (probably due to the extremely active volcanism and the arid climate). The extreme conditions allow only a few species to make a meagre living (◘ Fig. F-52). Only above 3500 m, where even occasional summer rains occur, is there a puny dwarf shrub semi-desert (with Baccharis, Fabiana, Parastrephia, etc.), which from 4100 m changes into the tussock grass mountain desert (Ichu grass: Festuca chrysophylla, F. orthophylla, Stipa venusta), in which lama and guanaco, but also nandu, graze.

For the western slope of the Andes in NChile Ellenberg (1975) gives a perarid full desert up to the montane belt, then a subalpine dwarf shrub semi-desert and above 4,500 m asl in the alpine altitudinal belt a tropical andine grass semi-desert or "desert puna". But even between 5,200 and 5,500 m there are still dwarf shrubs, for example at the volcano Ollagué (approx. 5,900 m) and in the lava debris even occasional shrubs or small trees of Polylepis tarapacana up to 4 m high (Wickens 1993). A snow line is hardly detectable (◘ Fig. F-53).

◘ **Fig.** F-52 Salt-encrusted extremely halophilous cushion-shaped Salicornia pulvinata in the Salar regions of Bolivia (photo: Breckle).

◘ **Fig.** F-53 In the highlands of the Andes on the eastern edge of the Atacama: Ollague volcano (5,900 m) (a). Mountain flank with high altitude desert. Even at 5,800 m there are hardly any remnants of snow: the area is so dry that a climatic snow line cannot be defined. b: At Sajama Volcano (6,542 m), which lies somewhat further north in the Bolivian altiplano, the upper forest line rises to 5,300 m (b), a lower forest line is at about 4,400 m (► Fig. E-46a) (photos: Breckle).

8 **Orobiome III - the desert mountains of the subtropics**

In extreme deserts, the air contains so little water vapor that there is no uphill rain even at high altitudes. We have already met orobiomes in the previous sections as well.

In the Tibesti Mountains (3,415 m asl) in the Central Sahara, only annual precipitation of 9 to 190 mm has been measured at 2450 m altitude (four years) with frequent cloud cover in the winter months. Accordingly, arid conditions persist to high altitudes; but the occurrence of a number of Mediterranean elements suggests somewhat humid conditions. Erica arborea was found in gorges at 2,500 to 3,000 m asl, and Olea cuspidata, a wild form closely related to the olive tree, was found as a relict in the Hoggar Mountains at 2,700 m.

In the sequence of stages in the much less arid Sonoran Desert in S Arizona, one finds a belt with Prosopis grass savannahs and many leaf succulents (Agave, Dasylirion, Nolina) above the Larrea or giant cacti desert, then several elevational belts with evergreen *Quercus* species and Arctostaphylos, Arbutus, and a *Juniperus* shrub layer, followed by coniferous forest belts: Pinus ponderosa ssp. scopulorum (higher with Pinus strobiformis), Pseudotsuga menziesii with Abies concolor, and only on San Francisco Peak in N Arizona on north-facing slopes to nearly 3700 m asl Picea engelmannii. Here, annual precipitation increases very rapidly with elevation. This varies greatly among deserts. However, this does not apply to the altitudinal zones in the Andes on the Atacama side (► p. 259).

9 **Man in the desert**

The inhospitable conditions make it seem astonishing that people have lived in all deserts, in some cases for a very long time. They have adapted their way of life, almost always travelling as nomads in order to maintain a livelihood in a larger area (◘ Fig. F-54). Settlement was in each case confined to the oases; these therefore served as base stations for the long migrations. Livestock served as a food reserve (pastoral nomads with sheep and goats) and the camel as a versatile transport and livestock animal.

There are very different ethnic groups living in the desert. They are groups of people that have to keep moving in caravans in search of places with water and food, defying the greatest risks: sandstorms, silted up wells and loss of bearings due to the lack of points of references. Some of these peoples among others are the Berbers of North Africa, that include the Kabilis and the Tuaregs, the Bedouins of the Arabic deserts, the Bejas in Namibia, the Sans in the Kalahari desert and the Australian Aborigines.

In the peripheral areas of the deserts, as well as in the mountains, simple agriculture was possible as rain-fed agriculture (run-off, Lalmi). Irrigation cultures became the basis of developing early cultures only in the area of the large foreign rivers (Egypt: Nile; Mesopotamia: Euphrates and Tigris).

◘ **Fig.** F-54 Bedouin tents in the southern Egyptian Sahara, at Wadi Allaqui, today near the eastern bank of the Nasser reservoir of the Nile. Supplies are stored on stilts (photo: Breckle).

10 **The zonoecoton III/IV - the semi-deserts**

Where at the edge of the deserts, as a result of the increasing winter rains, the contracted vegetation changes into a diffuse one, the boundary between the desert proper and the semi-desert can be drawn. It is not, however, always sharply marked. The ground cover in the semi-desert is up to about 25% of the total area. The floristic composition of this vegetation is as different in the individual floral kingdoms as that of the deserts. North of the Sahara the most important species are the malacophyllous Artemisia herba-alba and the sclerophyllous grasses Stipa tenacissima (half-grass) and Lygeum spartum (esparto grass). Artemisia grows mostly on heavy loess soils or clayey soils. In Tunisia, calcareous precipitates were found at a depth of 10 cm. Dense rooting was present at 5 to 10 cm depth, with individual roots going as deep as 60 cm. Stipa tends to grow on elevations covered with stone pavement. A soil profile shows the following: 2 to 5 cm of stone pavement, with loamy soil well rooted to 30 cm below, followed by a firmly crusted gravel that appears to be an obstacle to roots, but probably also provides a water reservoir (lots of capillary water that can be absorbed by roots through close contact). The tufted roots originating from the base of the tussock sweep widely horizontally at a depth of 10 to 20 cm, so that the 0.5 to 1 m (2 m) apart tussock touch each other with their root systems. In both cases, scattered Arthrophytum plants are found between them. The soils are not brackish, Lygeum spartum, on the other hand, is characteristic of gypsum soils and also tolerates some salt.

Stands of half-grass are cut and provide material for wickerwork, for making coarse rope or for papermaking. Stipa tenacissima is distributed from SE Spain and E Morocco only as far as Al-Khums in Libya; the natural habitat is sparse Aleppo pine forests. Artemisia herba-alba s.l. also occurs in the Near East; it has spread in many cases at the expense of former grassland as a result of overgrazing.

With further increases in precipitation, solitary trees appear in northern Africa, such as Pistacia atlantica in the west and P. mutica in the east, or Juniperus phoenicea. The sparse tree stands finally lead over to the hardwoods (ZB IV).

In California, Artemisia californica occurs in the transition zone along with semi-shrubby Salvia and Eriogonum species (Polygonaceae).

In NChile, in the transition zone, one finds a dwarf shrub semi-desert with Compositae (Haplopappus) as well as columnar cacti and Puya (large Bromeliaceae), after which a savannah with Acacia caven begins: the grass layer is now formed by annual European grasses.

In S Africa, the Renoster formation (Renosterbos with Elytropappus rhinocerotis, Asteraceae) can be considered typical of the low rainfall winter rainfall area.

In Australia, the Mallee formation forms the transition (◘ Fig. F-55), consisting of shrubby Eucalyptus species whose branches arise from an underground, tuberous stem (◘ Fig. F-56). However, sparse stands of Eucalyptus with Maireana sedoides understory may also occur.

◘ **Fig.** F-55 Mallee formation in Australia with shrubby eucalypts (photo: Breckle).

Fig. F-56 In Australia, Eucalyptus species in many places form a mighty lignotuber from which new shoots emerge after fire (photo: Breckle).

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[IMAGE]

Typical maquis on the Cap Corse of the island of Corsica (Zonobiom IV) with white-flowered Cistus salvifolius, C. monspeliensis and the evergreen oaks Quercus coccifera and Qu. ilex in the background (Photo: Rafiqpoor)

[IMAGE]

Fruiting dragon tree (Dracaena draco var. ajgal) in southern Morocco (Zonoökoton III/IV). It was only recently described as a new taxon from the Anti-Atlas (east of Agadir) (photo: Breckle).