I **General part**

**Part A - Ecological basics (auto-ecology)**

**Part B - Ecological basics (synecology)**

**Part C - Ecological systems and ecosystem biology**

[IMAGE]

Research on systematics of plants begins with collecting in the field. This picture shows the Norwegian botanist Per Wendelbo (bare-chested) and the Danish botanist Lars Eckberg (opposite Wendelbo) with their Afghan helper during collection work in northern Afghanistan in spring 1969 (Photo: I. Hedge).

[IMAGE]

Rock sculptures formed by wind and frost at an altitude of 4,700 m on the Bolivian Altiplano, the arid Orobiom II (Photo: Breckle)

**I General part**

**Part A - Ecological basics (auto-ecology)**

1 Ecological factors

1.1 Radiation

1.2 Temperature, frost, heat

1.3 The water factor

1.4 Chemical factors

1.5 Mechanical factors

2 The climate

2.1 General questions

2.2 The radiation balance and astronomical basics

2.3 The heat balance

2.4 The water balance

2.5 The Earth's eco-climates (climate classification)

2.6 Climate representation (thermo-isopleth diagrams, ecological climate diagrams)

2.7 Literature

[IMAGE]

Part of the Great Wall of China north of Beijing in a dust storm with loess (Photo: Breckle)

**1 Ecological factors**

The concept of dividing the landscape into zonobiomes requires clear ecological criteria that take into account the interrelationships of ecological factors. The ecological factors determine for organisms their environment, in which they realise one of their basic functions of existence, namely reproduction. The persistence of organisms in an ecosystem is determined by competition and adaptation. In a floristically uniform area, the structure of the vegetation in the system "climate-soil-plant" is determined by environmental factors and this mainly indirectly by influencing the competitive power of the species occurring in the area. In this interplay, the individual ecological factors often complement each other very differently in their selection effect. ◘ Fig. A-1 illustrates the mutual relationships of the ecological factors.

◘ Fig. A-1 Scheme of interactions between various environmental domains (areas) and plants

The soil type and the vegetation type are shaped by the climate, but for the vegetation the flora (and secondarily the fauna) and for the soil the bedrock and the vegetation (as well as the edaphon) are of great importance. There are such close interrelationships between soil and vegetation that one may almost call it a unit. Both the soil and the vegetation exert a certain influence on the climate, but directly only in the area of the air layer near the ground; that is, they influence the microclimate. All factors acting on plants, or on an organism in general, constitutes its environment, the physico-chemical factors (without competition) being called its site, while the place where it grows is called the growing site, biotope or ecotope. The factors determining the growth and development of the plant can be divided into five groups of primary factors:

1. Radiation: Light intensity and day length - the light factor
2. Warmth: Temperature relations - the temperature factor
3. Water: Hydrological conditions - the water factor
4. Chemical factors: Nutrients or toxins, poisons
5. Mechanical factors: Wind, fire, animal browsing and trampling.

It makes no difference to the plants whether, for example, the favourable warmth conditions are due to the large-scale climate or to the growing location (habitat) on a sheltered south-facing slope (in the Northern hemisphere). Similarly, it makes no difference to the plant whether the necessary soil moisture is due to a favourable distribution of precipitation or the low evaporation on a north-facing slope or, finally, to the soil structure and proximity to groundwater; the main thing is that the plant does not suffer from a lack of water.

The five groups of factors condition in their mutual effect the expression of complex site factors (secondary factors, complex factors), namely climatic, orographic, edaphic (soil) and biotic, as this is shown in the scheme (◘ Fig. A-2) with some essential site parameters.

◘ Fig. A-2 Scheme of the various ecological factors and their effects on the plant.

1.1 **Radiation, light**

All life on earth is kept going by the flow (flux) of energy radiated by the sun and supplied to the biosphere (apart from the special case of deep-sea black smokers with chemosynthesis). Photosynthesis of the plant binds radiation energy in the form of latent chemical energy. It benefits all links in the food chain for the operation of life processes. Radiation is generally the primary source of energy for building organic matter. By regulating the heat and water balance of the earth, it creates the energetic prerequisite for the fulfilment of the life requirements of organisms. However, radiation is not only a source of energy for the plant, but can also be a stress factor. Radiation effects are triggered by the absorption of light quanta and each radiation-dependent process is mediated by very specific photoreceptors. They exhibit a typical absorption spectrum. Important factors are the time, duration, exposure to solar radiation and the spectral composition of the illumination.

1.1.1 **Radiation and plant**

Radiation hits the above-ground parts of the plant from all sides: Direct and scattered sunlight (sky radiation), diffuse radiation when the sky is overcast, and finally radiation reflected from the ground. Many plants arrange their assimilation surfaces in such a way that as few leaves as possible are constantly exposed to direct radiation. Most leaves are in partial shade, where they receive scattered light (Larcher 2001). Upright leaves (e.g. of many monocots and globose pads), leaves in profile position (e.g. of Iris and Lactuca species), drooping leaves (e.g. of Eucalyptus) as well as assimilation organs with curved surfaces (round leaves, scale leaves, needle leaves, assimilation shoot axes) are tangent to the sun's rays at acute angles. This protects the leaves from strong light damage and overheating, but they receive more light in the morning and evening. In the crowns of individual trees and shrubs, a brightness gradient develops from the crown edge to the interior of the crown. Depending on the species-specific ability to develop pronounced shade leaves, a distinction is made between light crowns (pine, larch, birch, umbrella acacia) and shade crowns (many conifers, beech, broad-leaved evergreens). In light crowns, the innermost leaves receive on average 10-20% of the outdoor brightness, while in shade crowns leaves are still active with a light consumption of 1-3% (Larcher 2001).

1.1.2 **Absorption of radiation through the leaves**

Of the radiation falling on a leaf, part is remitted (i.e. diffusely reflected **→** remission), part is absorbed (absorption), and the rest is transmitted (transmission). The light retained by the leaf (remission) consists of the light reflected from the surface and the scattered radiation from inside the leaf (◘ Fig. A-3).

The reflectivity depends on the surface condition of the leaves. Felt hairs increase the reflection considerably. In the visible range, leaves remit on average only 6-10% of the radiation. Highly glossy leaves can reflect visible light up to 12-15%. Due to this scattered light, the interior of such "glossy light forests" is somewhat brightened. Green light is remitted more (10-20%), orange and red the least (3-10%). Ultraviolet radiation is reflected little by leaves (no more than 3%); in the infrared range, however, leaves reflect 70% of the incident radiation (Larcher 2001).

◘ Fig. A-3 Relative reflection, transmission and absorption of a poplar leaf (Populus deltoides) as a function of the wavelength of the incident radiation. After Gates 1965. Optical parameters of leaves of different plant species are given in Gausmann & Allen (1973) (modified after Larcher 2001).

The radiation penetrating the leaf is largely absorbed (absorption). When passing through the leaf, the radiation is attenuated in such a way that the radiation gain of cell layers lying behind each other drops exponentially. Depending on the leaf structure and the equipment of the mesophyll cells with chloroplasts, leaves usually absorb 60-80% of the photosynthetically active radiation (PhAR). The leaves of some herbaceous species that occur in the deep shade of tropical rainforests contain lenticular cells (ocelli → from Latin ocellus = little eyes) in their upper epidermis that focus the weak light onto the chloroplasts arranged in a contracted manner in the mesophyll. The absorption in the visible range is mainly due to the chloroplast pigments. Most of the ultraviolet radiation is retained by cuticular and corked outer layers of the epidermis and by phenolic compounds in the cell sap of the outermost cell layers, so that at most 2-5%, but usually less than 1%, of the UV radiation can enter the deeper leaf layers. The epidermis and hairs are effective UV filters for the assimilating parenchyma: e.g., shield hairs on Elaeagnus leaves absorb 40% of UV-B radiation (Larcher 2001). Lichens deposit colored compounds ("lichen substances") in the upper bark layers that are both UV and light filters. Infrared is absorbed little by leaves in the range up to 2000 nm, but almost completely (97%) in the range of long-wave temperature radiation above 7000 nm. Accordingly, the plant behaves like a black body in relation to thermal radiation (Larcher 2001).

The radiation transmittance (transmission) of leaves depends on the structure and thickness of the leaf. Soft-leaved leaves allow 10-20% of the sun's rays to pass through, very thin leaves up to 40%, thick and coarse leaves are almost impermeable to radiation (<3%). The best transmission is in the green, but especially in the near infrared. Light filtered through foliage is therefore particularly rich in wavelengths around 500 nm and >800 nm. Under a leaf canopy there is a red-green shadow, in the forest darkness only dark red and infrared shadows. Through canopy sheaths and through the bark of thin twigs, up to 0.5-2% of the incident light, mainly long-wavelength light, penetrates both into the interior of the forest and into the interior of the plants, i.e. in the leaves and meristems, where the phytochrome system is active. Apical meristems in buds receive more dark red radiation (700-840 nm) than light red (600-690 nm), and the light red/dark red ratio changes with bud formation and seasonally. These signals are perceived by the phytochrome system, whereupon gene activation triggers the corresponding changes in developmental behaviour and differentiation (Larcher 2001).

Plants adapt to the local radiation climate and to the prevailing quantity and quality of the radiation available at their growing site by modulative (short-term), modificative and evolutionary means. Modulative adaptations occur rapidly and are reversible; after returning to the initial situation, the initial behaviour is soon restored. Examples of photomodulations are: Nastic movements such as the closing stomate cell movements; leaf movements that cause a favorable exposure of the leaf blade to light incidence; the diurnal and weather-related opening and closing of flowers. Modulative radiation adaptations that directly affect photosynthesis proceed via changes in the chloroplasts (Larcher 2001).

Modificatively, plants adapt to average radiation conditions over weeks or months during adolescence. Phenotypic differentiations of organs and tissues are usually not traceable. If light conditions later change, then new shoots sprout and the originally attached, now unadapted leaves age and are shed. Plants that develop in bright light form a vigorous axial system. Their leaves have multiple staggered mesophyll, chloroplast-rich cells, and a dense vein network. As a result of structural adaptation and more active metabolic processes, high-light-adapted plants produce greater dry matter growth, higher dry matter energy content, and better fertility (flowering frequency, flower set, fruit yield). Low-light-adapted plants develop longer internodes and thin leaves with a large surface area. This enables them to cope on sites with low energy supply (Larcher 2001).

Evolutive adaptations to the available radiation are hereditary and determine the site preference of different plant species and photo-ecotypes. The classification of plants into dim-light plants, shade plants (heliophytes) and strong-light plants (which grow in places without shade, e.g. in high mountains, in deserts and on seashores) reflects ecological differentiation by selection and adaptability. The plant's response norm is hereditarily determined. Thus, although sun plants are shade-adaptable, they are not to the same extent as genetically programmed shade plants; the same applies in the opposite direction (Larcher 2001).

Modulative, modificative and evolutionary adaptations overlap and thus give plants the opportunity to use the available radiation as much as possible through finely graduated adaptation. Due to the diversity of growth forms, light-ecological niches in the multi-storey crown horizons of the tree layer of dense forests are exploited by lianas and epiphytes. In addition, secondary effects of radiation (e.g. heat and influences on the water balance) play a role in all adaptations to site brightness. Sun plants are therefore always adapted to higher temperatures, dry air and a temporary stress of the water status (Larcher 2001).

1.2 **Temperature, frost, heat**

The radiation supply is also an important factor for the temperature conditions. Ecologically, thermal conditions are of great importance for vegetation at a site, as life only takes place within certain temperature ranges. Temperature extremes are tolerated differently by different organisms. The heat resistance limit of most plant species is between 50 and 60 °C (◘ Table. A-1). To a certain extent, plants can protect themselves from heat stress by radiation reflection, by transpiration cooling or also physiologically (heat shock proteins).

◘ **Fig. A-4** Temperature dependence of the duration of embryonic development in the bug Eurygaster maura (Pentatomidae) (modified after Tischler 1984).

But much more significant is the cold (**frost**). The cold resistance limit is not as sharp as the heat resistance limit. Besides the plants **sensitive to chilling** or **cold** (mostly of tropical origin), there are the **freeze-sensitive** plants (which avoid ice formation in the tissues, for example by increasing the concentration of cell sap) and the freeze-tolerant plants, which instead of a large central vacuole often form many small vacuoles in which membrane damage by ice crystals is kept small.

With regard to temperature, we distinguish among animal organisms, on the one hand, the cold-blooded or **poikilothermic** species (such as amphibians), whose body temperature depends on the external temperature and changes in the same sense with it; on the other hand, the warm-blooded or **homoiothermic** species (such as humans), which have their own body temperature, largely independent of the external temperature and fairly constant. In these organisms it makes no sensei to measure the external temperature in order to relate it directly to the course of vital functions.

All plants are poikilothermic organisms, even if occasionally, as in the case of the *Arum* family (Araceae), the inflorescence can generate their own heat (Barthlott et al. 2009). The temperature of the surrounding air therefore gives an indication of the governing temperature conditions in the plasma. Certain smaller deviations due to purely physical reasons occur, especially in the case of strong radiation. In ecophysiological studies, they must be taken into account; after all, chloroplasts or mitochondria, for example, can often have over 10 K excess temperature in the leaf during the sunny day compared to the ambient air. In ecological overviews, one will usually have to be content with stating the air temperature.

In most poikilothermic animals, development is very dependent on temperature (◘ Fig. A-4), but usually modified by the water factor, for example humidity. The development time can often be specified very precisely by a corresponding mathematical function (► Fig. A-4), for example by a hyperbolic function. The example in ◘ Fig. A-5 gives not only the duration of embryonic development but also the mortality of the eggs as a function of air temperature and relative humidity. From ► Fig. A-5, it can also be seen that a certain temperature range at relatively high humidity represents the optimum range. Accordingly, one can easily imagine how different, depending on external conditions, the reproduction rates and thus the influence of some insect species in certain biotopes can be from year to year, even without other biotic interactions.

◘ **Fig. A-5** Dependence of the duration of embryonic development and mortality of eggs of the alfalfa weevil (Hypera postica, Curculionidae) on temperature and relative humidity (modified after Tischler 1984).

Freezing is closely coupled with the behaviour of the tissue or cell water in the cell. Freezing of the vacuole with formation of ice crystals usually means a strong rupture of the membranes and thus considerable cell damage. In addition, the supply of water is blocked, so that prolonged exposure to frost often causes the plants to dry out (frost desiccation) rather than real freezing damage.

The different zonobiomes are characterized on the one hand by water availability, on the other hand due to the temperature factor. It is not so much the mean values of temperature that are important, but rather the extremes. And it matters whether frosts in an area occur regularly with the change of seasons or whether they occur episodically. One frost in 20 years in the coffee-growing regions of Brazil damaging the *Coffea*-shrubs causes the world market price of coffee to rise.

◘ **Table A-1**: Temperature resistance of leaves of shoot plants of different climatic regions. Limit temperature at 50% damage (TL50 in °C) after two-hour or longer exposure to cold and half-hour heat treatment (from Larcher 2001)

|  |  |  |
| --- | --- | --- |
| Plant group | Cold damage in the hardened state (°C) | Heat damage during the growing season (°C) |
| Tropics |
| Trees | +5 to -2 | 45-55 |
| Forest undergrowth | +5 to -3 | 45-48 |
| High mountain plants | -5 to -15(-20) | at 45 |
| Subtropics |
| Woody evergreens | -8 to -12 | 50-60 |
| Seasonal green woody plants | (-10 to -15)\* |  |
| Subtropical palms | -5 to -14 | 55-60 |
| Succulents | -5 to -10(-15) | 58-67 |
| C4 grasses | -1 to -5(-8) | 60-64 |
| Winter annual desert herbs | -6 to -10 | 50-55 |
| Temperate zone |
| Evergreen woody plants of winter mild coastal areas | -7 to -15(-20) | 46-50(55) |
| Relict species of tertiary tree flora | -8 to -20(-15 to - 30)\* |  |
| Dwarf shrubs of Atlantic heaths | -20 to -25 | 45-50 |
| Deciduous trees and shrubs with wide distribution | (-25 to -35)\* | at 50 |
| Herbaceous plants of sunny locations | -10 to -20(-30) | 47-52 |
| Herbaceous plants of shady locations | -10 to -20(-30) | 40-45 |
| Tumbleweeds | (-30 to N2\*\*)\* | 60-65 |
| Halophytes | -10 to -20 |  |
| Succulents | -10 to -25 | (42)55-62 |
| Water plants | -5 to -12 | 38-44 |
| Homoihydric ferns | -10 to -40 | 46-48 |
| Winter cold areas |
| evergreen conifers | -40 to -90 | 44-50 |
| Boreal deciduous trees | (until N2)\* | 42-45 |
| Arctic-alpine dwarf shrubs | -30 to -70 | 48-54 |
| Herbaceous plants of the high mountains and the Arctic | (-30 to N2)\* | 44-54 |
| \* Vegetative buds | \*\*Temperature of liquid nitrogen (-196 °C) |

Plants prepare themselves for the annually recurring winter cold. The main frost categories are shown for the whole Earth in ◘ Fig. A-6. Since water freezes by definition at 0 °C and increases in volume in the process, this has very special significance for living organisms. The zero degree limit, i.e. the occurrence of frost, therefore has a decisive influence on the various biomes (◘ Table A-1).

The following applies to the individual zonobiomes: Zonobiome I to III are frost-free (except in the higher altitudes of the mountains). In zonobiome IV and V light (episodic, partly periodic) frosts may occur occasionally. Zonobiome VI already regularly exhibits a typical, albeit short and not very severe, winter with frost. In zonobiome VII, on the other hand, with a continental climate, winters are very pronounced and sometimes severe (cold semi-deserts and deserts). In zonobiome VIII in the taiga, the winter can already be several or many months long and very severe; ZB IX of the tundra is characterized by winter; it is by far the longest season in the annual cycle. The occurrence of frost determines the occurrence of different resistant types of plants. In the equatorial zone with a minimum of not less than +5 °C, cold-sensitive plants predominate. In Zone D (► Fig. A-6), on the other hand, only completely freeze-resistant plants can survive, while in Zones C and B there are also limited freeze-tolerant plants and trees that are at least protected by freeze depression and good super-cooling.

◘ Fig. A-6 The occurrence of frost on Earth. A-C frost-free except high mountains; from D-F increasing frost frequency and intensity at higher latitudes. A = frost-free areas; B = frost-free, but up to +5 °C annual minimum possible; C = episodic frosts down to -10 °C; D = winter-cold areas with mean annual minimum between -10 and -40°C; white line = -30°C annual minimum isotherm; E: long winters, mean annual minimum fall below -40 °C; F = polar ice and permafrost areas (from Larcher 2001).

Only about 30% of the earth's land surface is frost-free, while 42% is regularly subject to severe frost with a mean annual minimum below -20 °C.

1.3 **Water**

For the structure of the biosphere, of all site or environmental factors, the temperature and water conditions are of primary importance. Light is nowhere in the minimum, because the long polar night meets the plants in the winter dormancy. The light factor therefore plays no decisive role in the large-scale structure of the vegetation of the earth.

1.3.1 **Global water supply**

The heat or temperature decreases fairly steadily from the tropics to the poles. Important here, as briefly discussed, is the frost line between the tropical and extratropical regions. The water factor has an even greater differentiating effect. Precipitation is distributed very unevenly over the Earth (◘ Fig. A-7).

The amount of mean annual precipitation varies between over 10,000 mm (◘ Fig. A-8, left: Cherrapunji, India) and practically zero (◘ Fig. A-8, right: Iquique, Chile) in the extreme deserts.

◘ Figure A-9 shows the major vegetation zones for which, in addition to the distributions of precipitation, the temperature conditions are also of particular importance, as expressed in the more or less zonal arrangement parallel to the latitudes (► Fig. A-50).

But not only on a large scale, but also on a small scale, temperature and water have a strongly differentiating effect on the plant cover due to the changing humidity of the biotopes. In general, water plays a very special ecological role in the life of plants, a much greater one than in the case of animals, because plants are location-bound. The water balance can be described quantitatively both at the level of the cell and the plant as a whole, as well as at the level of the ecosystem.

1.3.2 **Water balance types and drought resistance**

Depending on the water supply at the site, a distinction is made between hygrophytes, mesophytes and xerophytes. The hygrophytes as colonizers of evenly moist or wet sites (as well as some shade-loving herbs in the forest) have hardly any water shortage. The mesophytes are already better adapted to certain dry periods. Most species of the temperate latitudes belong to them. The xerophytes have developed many adaptations to the more or less severe and prolonged water shortage at their location. For the mechanisms of drought resistance, Levitt (1972) has characterized different possibilities: Most plants avoid drought by spatial or temporal avoidance; for true drought tolerance, special adaptations are needed, as we will see in some examples of xerophytes (see 1.3.5).

1.3.3 **Soil water**

The availability of water for plants does not depend solely on the water content of the soil. The grain size distribution and thus the pore volume and the size of the capillary spaces in the soil also have a major influence. The maximum amount of water that a soil can absorb is equal to the pore volume, but then there is no soil air and therefore no oxygen left in the soil. Due to gravity, however, part of the water seeps into the depths. The field capacity (FC) is strongly dependent on the grain size distribution, as ◘ Fig. A-10 demonstrates.

◘ Fig. A-7 Global seasonal distribution of precipitation (in cm/month) comparing January (top), July (middle), and year (bottom) (source: NASA 2011; http://is.gd/h916at).

◘ Fig. A-8 Climate diagrams Cherrapunji in India and Iquique in Chile: One of the wettest and one of the driest climate stations (note that monthly precipitation data above 100mm are compressed by a factor of 10).

Beyond the FC, there is a fraction of soil water that is very tightly bound to the soil particles by adsorption forces (by electrostatic, as well as absorption and cohesion forces) in the very small pore spaces. These fractions are not accessible to plant roots. If a soil contains only these tightly bound fractions of water, it is called a "permanent wilting point" (PWP), (► Fig. A-10). In particularly fine-grained clay soils, the total water content may be more than 20%, yet none of it is available to the plant root because of the fine-grained nature of the soil. Accordingly, the water tension (water potential, cm water column, as log pF) of a large water content is particularly high. The PWP is on average slightly above pF = 4 (=104 cm water column), but is variable.

However, the water availability limit is not the same for all plants. Xerophytes and halophytes, which can develop very high suction forces through their roots, are quite capable of still absorbing some water, which means that the permanent wilting point is different for different types of plants.

Thus, with regard to the water factor, the conditions are similarly complicated for plants as they are for animals with regard to temperature.

◘ Fig. A-9 The vegetation zones of the Earth (without edaphic or anthropogenic modifications) (from Schmithüsen Atlas 1976).

Fig. A-10 Relationship between water potential and water content (pF curves) for three different soil types (sandy soil, silt (loess) soil and clay soil), with logarithmic ordinate (after Scheffer & SchachtSchabel 1992). In sandy soils 2%, in silty soils approx. 10% and in clay soils 35-40% of the soil water is not available to plants.

1.3.4 **Water state of the cell**

First of all, one has to distinguish between plants able to change their water content (poikilohydric plants) and those maintaining a rather constant water balance (homoiohydric plants).

Plasma, the cell content, is physiologically active only when it is highly hydrated, i.e. imbibed and hydrated. If cells dry out, then the plasma enters a latent life state (i.e., it exhibits no measurable signs of life) or it dies. The thermodynamics of imbibition (swelling bodies) teaches us that the swelling state depends on the relative activity of the water (a), where a = p/po, i.e. equavalent to the relative vapour pressure.

By definition, pure water has a hydrature of 100% (i.e. it is available to the plant without restriction). The hydrature corresponds to the humidity (also given in %). A certain water vapour pressure is established above salt solutions, which is lower than that above pure water, and the hydrature is correspondingly lower.

Since the vital functions depend to a great extent on the swelling state of the protoplasm, it is important to know its hydrature (or activity of water). In the case of poikilohydric plants, in so far as these plants occur outside water, the hydrature depends entirely on the moisture content of the surrounding air. The lower plants (bacteria, algae, fungi and lichens) belong to them. If they are in contact with water or if the surrounding air is saturated with water vapour, the protoplasm of these species is almost maximally swollen and active. In dry air, on the other hand, severe de-swelling occurs, and the plasma passes into the latent state without dying. The cells of these organisms have no or only very small vacuoles, and the volume changes of the cell contents are therefore small during desiccation and the plasma structure is not damaged. The lower limit of hydration (humidity) at which growth can still be detected is very high in most bacteria, usually from 98 to 94%; in the unicellular algae and molds it varies widely, and in only a few organisms does it fall as low as 70%, a value corresponding to the absolute minimum of hydration for life.

The productivity of poikilohydric organisms is low, their share in the vegetation mass on land is small today. They have therefore received little attention up to now, although they are often much more widespread on the soil surface, namely also in the deserts, than is assumed. Before the conquest of the country by higher plants they might have been already widespread on periodically moistened surfaces, as today on periodically flooded clay surfaces in the deserts (Takyre). These are uninhabitable by higher plants because they offer no root space. However, fossil remains of lower plants are preserved only exceptionally, they are found relatively rarely in the older geological rock formations.

The homoiohydric terrestrial plants play a much greater role. They include all cormophytes, which originally evolved from green algae. Their cells are characterized by a large central vacuole. As a result, the plasma is directly adjacent to the cell sap in the vacuole, and the hydrature of the plasma is largely in equilibrium with that of the cell sap, thus not directly dependent on water conditions outside the cells. The cell sap of the vacuoles constitutes in the higher plants, as has been mentioned, an "inner aqueous medium," the vacuome, and the cell wall of cellulose an "outer aqueous medium," which in the course of phylogenetic development enabled them to pass from life in water to life on land, and to adapt themselves more and more to arid conditions. As long as terrestrial plants succeed in keeping the concentration of cell sap in the vacuole low, the plasma remains imbibed, that is, it has a high hydrature, regardless of the humidity of the surrounding air. This is more likely to be the case the more secure the supply of water from the moist soil through the root and transport system. In the mosses these facilities are only imperfectly developed, and they are therefore generally confined to very moist sites. In the ferns, too, the transport system is still not very efficient. They therefore avoid dry sites, all the more so because the development of the gametophytes is still strongly dependent on moisture. As far as mosses and some ferns (Ceterach, Notholaena, Cheilanthes and others as well as Selaginella species) have penetrated into desert areas, they had to change secondarily to the poikilohydric way of life, i.e. they tolerate desiccation during drought without dying ("resurrection plants"). They regained this desiccation ability, which is otherwise lacking in plants with strongly vacuolated cells, by a cell reduction with reduction of the vacuoles, which solidify even at low water losses, thus preventing deformation and damage of the plasma during desiccation.

1.3.5 **Xerophytes**

The most perfect adaptation of the water balance to terrestrial life has been achieved by the angiosperms. They have penetrated to extreme deserts. The measurement of their cell sap concentration shows that they are nevertheless able to maintain a low cell sap concentration and thus a high hydrature of the plasma without slowing down too much the gas exchange necessary for photosynthesis. An increase in cell sap concentration and thus dehydration of the plasma and increased osmotic adjustment by appropriate substances (compatible solutes) is generally not a useful adjustment for desert plants, but the sign of a disturbed water balance and a threat to their existence. For the knowledge of the water activity in the plasma, i.e. its hydrature and swelling state, the measurement of the external factors (precipitation, humidity, soil water etc.) is just as insufficient as the measurement of the external temperature in warm-blooded animals.

The determination of the cell sap concentration (and thus of the potential osmotic potential), which is directly related to the relative vapour pressure (= hydrature), provides information as to whether or not the plant is affected by the change in external conditions, in particular by a period of drought, with regard to the imbibition state of the plasma. The measurement of the the water potential, on the other hand, is necessary when dealing with the flow through the plant from the roots to the transpiring organs. This is illustrated by characterizing the individual resistances in the plant in the hydraulic flow model diagram (◘ Fig. A-11).

Some of these flow resistances are constant, others are more or less variable. Especially the stomatal resistance is to be emphasized, because it allows a regulation of the water losses within wide limits. Corresponbding to Ohm's law, the water flow (current) also depends on the resistances and the potential (voltage). The total "voltage" corresponds to the difference in suction force between the ground and the atmosphere. This difference in water potential is almost always very large, even in temperate climates. The suction force (water potential) says nothing about the hydrature state of the plasma, on which the course of all life phenomena depends. Both are closely related, as described by the osmotic characteristics.

While one must provide the usual information on external factors for site characterization, one must additionally refer to cell sap concentration and its change for characterizing the hydrature of the protoplasm, especially when discussing arid areas where the water factor plays a dominant role. Therefore, one must look more closely at the adaptations to drought and point to the osmotic conditions.

◘ Fig. A-11 The flow of water through a plant from the soil to the atmosphere can be compared with a scheme borrowed from electrical resistance analogue. The current (I) is driven by the voltage (U), in this case the water potential difference between the soil and the atmosphere, and limited by the sum of the resistances (R) in the plant, some of which are constant and some are variable (stomatal resistance as a control option for the water flux). Ohm's law (U = R-I) is applicable (according to Hillel 1980).

Studied species are regarded as stable units in the experiment, but they are very changeable during longer observation. Each plant constantly adapts morphologically to the respective environmental conditions. This is necessary for survival. These phenomena are associated with growth and only become noticeable after weeks or months. Ecologically they are particularly significant and in arid regions very noticeable if one examines a plant after a rainy season, i.e. during the drought period until the beginning of the next rainy season.

Adaptations to water deficiency must take into account the different osmotic state variables of the plant parts:

The suction stress (S) = - water potential ( Φ), the potential osmotic pressure ( π\*) = - osmotic potential ( Φs) and the turgor pressure (P). The equations apply:



The state variables are measured in the pressure dimension (today in MPa). **S** and **Φ** as well as **π**\* and **Φs** are numerically always the same and differ only by the sign ( **Φ** and **Φs** are always negative).

It is important to be clear about the importance of the different quantities for the water balance of plants: If one is dealing only with the more physical process of water flow through the plant from the soil to the atmosphere, then one has to measure S or **Φ** respectively. If, on the other hand, one is dealing with the biological processes of the adaptations associated with growth, as is the case here, then **π**\* or **Φs** is the decisive quantity, because it is directly related to the hydrature of the plasma, i.e. its imbibition state, as already mentioned above, and the growth processes of the plants are controlled by the latter.

The adaptations of the plants, which can only be detected after a longer period of time, can be regarded as feedback control loops, which are necessary for the maintenance of a certain equilibrium under changed conditions, in our case a balanced water balance. This is the controlled variable. The disturbance variable is increasing dryness during drought, the set point is a balanced water balance (i.e. water intake = water output). The living plasma acts as a sensor, because when the water balance is disturbed, an increase in **π**\* (decrease in **Φs**) occurs as a result of an increase in cell sap concentration, and this entails a decrease in the hydrature of the plasma, including the hydrature of the plasma of the meristematic cells at the shoot and root apex, which must be regarded as a manipulated variable. Their change, as part of a signaling chain, results in the newly formed organs being morphologically better adapted: The internodes become shorter, the leaves smaller and more xeromorphic, which causes reduced transpiration and allows the water balance to be balanced (already shown by Walter & Kreeb in 1970).

A first example from the Sonoran Desert will explain what has been said: The composite half-shrub Encelia farinosa, about 50 cm high, has large soft hygromorphic leaves during the rainy season, which are greenish and weakly hairy; their **π**\* is 2.2 to 2.3 MPa. In the drought season, water supply becomes more difficult, with **π**\* increasing to 2.8 MPa; this also causes a slight decrease in hydrature of the protoplasm of the meristem cells. The new leaves then formed by the meristem are smaller, more mesomorphic as well as more hairy, replacing the hygromorphic ones. If the drought continues, **π**\* increases to 3.2 MPa and the next leaves are even smaller, thicker and densely white haired, allowing further transpiration reduction. In extremely long droughts, all leaves are shed as soon as 4.0 MPa is reached. Only the terminal buds remain with small leaf systems that do not develop further. The plant's water output is then so low that even with minimal water uptake from the soil, the plants are in a state of water balance.

As soon as the next rainy season starts, the potential osmotic pressure ( **π**\*) drops again to the initial value of little more than 2.0 MPa, the hydrature of the meristem cells increases and the newly formed leaves become large and hygromorphic; as a result of intensive photosynthesis, strong growth sets in with heavy transpiration but still maintained water balance. This cycle repeats itself again and again. Similarly, this is true for many small shrubs and deep-rooted desert plants. In ◘ Fig. A-12, the succulent leaves of Zygophyllum dumosum in the Negev Desert still have both leaflets and are green and turgescent (left). These spring leaves shrivel and turn brown in summer, and the succulent leaf midrib remains green longer (right). Eventually it also wilts and falls off. Then only the woody branches of the small shrub remain, but they consume very little water and thus survive the long summer drought.

It is interesting that roots react differently to a decrease in hydrature of the meristem cells than shoots. Roots become thinner, but longer and do form less side roots. Inhibition of growth only sets in after more severely decreased hydrature while growth of shoots is immediately inhibited.

In general, it must be stated that higher **π**\*, i.e. lower osmotic potential, promotes the transition from vegetative growth to generative. This is also the case with ephemerals; for dwarf plants with higher cell sap concentration always flower first. This confirms the experience of gardeners that when the water supply is more difficult, the plants blossom more, whereas when the water supply is plentyful, they grow mainly vegetatively.

1.4 **Chemical factors and the soil**

1.4.1 **Nutrients and trace elements, mineral supply**

The nutrients and trace elements (micronutrients) and thus the mineral supply are another ecological factor that can control the occurrence of plants. In addition to the main elements C, H and O, several other chemical elements play a role as bio-elements through their participation in the structure of organisms. The bio-elements of plants are listed in ◘ Table A-2.

**Table A-2** Bio-elements in plants (macro- and micro-nutrients, trace elements and essentiality. In addition to C, O and H, the following elements are significant in plants.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Item | Recording as... | Enrichment in ... | Relocatability | Symptoms of deficiency |
| N | NO3-NH4+ | Young shoots, leaves, seeds | Good, in organic form (amino acids) | Stunted growth, premature yellowing (light green) |
| P | HPO42-H2PO-4 | Reproduct. organs | Good, in organic form (amino acids) | Delayed flowering, peak drought, bronze discolouration |
| S | SO42- | Leaves, seeds | Good, in organic form (amino acids), hardly as sulphate | Similar N, intercostal chlorotic leaves |
| K | K+ | meristematic tissues | Very good | Leaf edge wilt, root rot |
| Mg | Mg2+ | Leaves | Pretty good | Scanty growth, intercostal chlorotic, older leaves |
| Ca | Ca2+ | Leaves, bark | Very bad | Disturbed division growth, peak drought, leaf deformations |
| Fe | Fe2+FeIII-Chelate | Leaves | Bad | Chlorosis of young leaves, hardly any bud formation |
| Mn | Mn2+Mn-Chelate | Leaves | More or less bad | Growth retardation, chlorosis, necrosis of young leaves |
| Zn | Zn2+Zn-Chelate | Roots, shoots | Pretty Bad | Dwarfism, white-green old leaves, fructification disturbances |
| Cu | Cu2+Cu-Chelate | Lignified axles | Bad | Peak drought, wilt, spotted chlorosis of young leaves |
| Mon | MoO42- | Roots, leaves | Badly | Growth disturbances, shoot deformations, leaf edge browning |
| B | HBO32- | Leaves, shoot tips, vegetation tips | Bad | Meristem, phloem necrosis, cork disease |
| Ni | Ni2+Ni-Chelate | Leaves of grass | Bad | Fructification disorders in grasses |
| Cl | Cl- | Leaves | Good | Partly wilting, thickening of roots |
| Na | Na+ | Leaves, xylem parenchyma | Good | Growth disturbances (for C4 plants) |
| Se | SeO42- | ? | Bad | ? |
| Al |  | Wood, bark (leaves) | Very low | ? (Ferns) |
| Si |  | Wood, bark, needle leaves | Very low, almost zero | Leaf curvatures in grasses, palms, conifers, Equisetum |
| Co | Co2+Co-Chelate | Leaves? | Bad | ?? (legume nodules) |
| V | VO3- | ? | ? | ?? |
| F | F- | Leaves | Pretty good | ?? |

In animals, iodine must be added as an essential element. Essential elements are generally characterized by the fact that they: 1. Are necessary for very specific functions in the metabolism of plants, and 2. Cannot be replaced by any other element. 3. A deficiency of the respective element produces a very specific deficiency symptom, which can only be eliminated by adding this element and no other.

However, the range of variation between oversupply and malnutrition is very different for each element and also different for each plant species (Adriano 1986). Accordingly, the demands of plants on the nutrients in the soil are species-specific; some plants indicate the availability of the nutrient elements in the soil by their presence: e.g. nitrogen indicator plants, such as Urtica, Rubus, *etc.,* l.

The availability of nutrients and trace elements varies greatly depending on the soil type (Marschner 1986). Certain quantities are absorbed by the plants, which in the case of agricultural crops are withdrawn by the harvest and thus usually far exceed the natural replenishment through weathering of the soil minerals and parent rock. This is the reason that fertilizers have to be applied in agriculture. In general, the soil factor (i.e. the edaphic basis of mineral supply to plants) is an important prerequisite for the flourishing of plants and thus for the normal development and formation of ecosystems and thus shapes the character of the same. The provision of essential nutrients to plants exerts a major influence on thriving, mainly due to the fact that, via water availability to plants at the site, nutrient supply can vary widely.

The necessary, i.e. essential minerals for plants (and animals) ultimately come from the parent rock, from which the individual minerals are released through weathering. The nutrients become available through an increase in surface area of soil minerals and through chemical restructuring. In the course of the processes of soil formation (in interaction with the plants) the material cycles in the ecosystem are fed. Ongoing losses through discharge into the groundwater (◘ Fig. A-13) or dust drift etc. must be supplemented by replenishment, essentially through weathering. Only then can the ecosystem remain sustainable, i.e. sustain itself over a long period of time. The balance of substances in the soil-plant system is balanced in the long term by inputs and weathering and by outputs (► Fig. A-13).

Dust input is also known. Thus, a not insignificant part of the nutrients of the Amazon rainforest is also likely to originate from long-distance transport of fine dust (for example mainly from the Sahara).

Seen as a whole, a very considerable transport of fine material is constantly taking place on the globe. In special weather conditions, Sahara dust can also reach Central Europe (◘ Fig. A-14). The rock particles, minerals, etc. that are released and crushed during weathering sediment for a time or are transported further until they finally end up in the world ocean or, for example, build up large river deltas. The sediment load (◘ Fig. A-15) from the different areas of the earth depends on the one hand on the relief energy and the differences in altitude, and on the other hand on the structure of the material; for example, the easily eroded loess from China is transported in large quantities (via the Yellow River into the Yellow Sea). The dust storms from these loess particles often cause considerable damage to the health of the population in Beijing in connection with increasing fine dust pollution due to increasing traffic. However, the fine dust discharge can sometimes be detected thousands of kilometres away (e.g. in Hawaii).

The material crushed by weathering is transported either by wind or by flowing water. The flow or wind velocity and the grain size of the particles to be transported are of great importance. With increasing particle size, the sedimentation process becomes more and more predominant and can only be overcome by very high flow velocities (◘ Fig. A-16).

◘ **Fig.** A-13 The plant-soil system with the close interconnection of the compartments.

◘ **Fig.** A-14 Dust particles on water lily leaves transported and deposited by atmospheric circulation from the Sahara to Germany and contracted by raindrops (Photo: Breckle).

◘ Fig. A-15 Global overview of sediment loads from medium-sized drainage basins (modified from White et al. 1992).

◘ Fig. A-16 Particle transport by flowing water and its dependence on grain size (in mm) and water flow velocity (in cm.sec-1) (modified after Kuntze et al. 1994).

The wind causes mainly grain sizes around 0.1 mm to move along the ground surface and sediment. These have a particularly low critical shear stress velocity (◘ Fig. A-17), so that saltation (jumping, hopping of grains) is facilitated, leading to the formation of the large sand dunes. In general, the processes of erosion and accumulation play a significant role in changing the site characteristics of ecosystems over the long term. Also, the greatly increased removal of soil material from cultivated areas leads to rapid changes and, in some circumstances, to degradation that does not allow further cultivations.

Table A-3 shows the erosion rates for a humid area in the USA. According to this, it can be seen that a closed vegetation cover selfevidently is the best soil protection. If one calculates the amount of valuable soil washed away, this example results in 1500 t lost in 10 years for an area of only 1 ha. The soil losses in Germany are somewhat lower, since precipitation is usually less intense and these high values were determined for sloping areas.

**Table A-3** Removal of a sandy loam soil layer by erosion. The time in years required to remove a 10 cm layer in the southeastern USA at a slope inclination of 10 degrees is given.

|  |  |
| --- | --- |
| Vegetation cover, land use | Time (in years) |
| Natural, intact deciduous forest vegetation | 320 000 |
| Dense lawn | 46 000 |
| Arable farming with crop rotation | 60 |
| Cotton cultivation | 25 |
| Corn cultivation | 20 |
| Unvegetated bare ground | 10 |

**Fig.** A-17 Particle transport by wind and its dependence on grain size (in mm) and soil particle velocity (in cm × sec-1). Grain sizes less than 0.01 mm (loess) remain suspended longer and can be transported far by long-distance transport. Fine sand with grain sizes between 0.1 and 0.5 mm is transported along the ground surface mainly by saltation (dunes, ripple marks) (Modified after White et al. 1992).

◘ **Fig.** A-18 The percentages of different cations in the potential exchange capacity (related to pH 7 = 100%) as a function of pH, in a soil with 20-30% clay, predominantly three-layer minerals, and 2-3% humus content (Modified after Scheffer & Schachtschabel 1992).

The minerals pattern and the nutrients available in the system through long-term soil formation determine the productivity of ecosystems quite significantly. The parent rocks, however, hardly play a role in ecosystems of higher age with mature, deep soils, but on younger sites one can very well distinguish the different vegetation units (and thus ecosystems) on limestone, on crystalline, on gypsum, etc.

The availability of nutrients depends, on the one hand, on the inner surface of the soil minerals (and humus) and, on the other hand, of course, on the existing occupancy of the ion exchange sites located on the large inner surfaces. This ion exchange is partly in equilibrium with the pH value; in acidic soils, an increasing proportion of the ion-exchange sites is occupied by protons (◘ Fig. A-18). As a result, the proportion of exchangeable mineral nutrients (Ca, Mg, K) decreases.

In more acidic soils, there is the additional disadvantage that the trivalent Al3+ blocks further sites and thus, for example at pH 3, there are hardly any nutrient cations left in such a soil. In cool, humid climates, soil formation tends towards such acidic, nutrient-depleted soils (Taiga, ZB VIII).

In hot, humid climates, weathering of the parent rock and the formation and conversion of clay minerals proceeds much more rapidly (◘ Fig. A-19). Whereas in temperate climates clay usually occurs as three-layered minerals in the soil (and thus provide a relatively large cation exchange capacity), tropical soils are often characterized by the two-layered clay mineral kaolinite, which has only 5 to 10% in ion exchange capacity compared to three-layered clay minerals. This extreme cation poverty and depletion is one of the most important reasons for the "ecological disadvantage of the tropics" (Weischet 1980).

In dry areas, the accumulations on the soil surface or in the soil at certain soil depths lead to deposits which can be very solid and which can appear as lime or gypsum crusts or also as laterites (iron, aluminium oxides) etc. In humid areas, leaching processes gradually lead to a depletion and acidification (podsolation). Both processes decisively shape the formation of the individual ecosystems in the corresponding zonobiomes. The main types of soils are schematically assigned to certain climatic factors in the ecogram (◘ Fig. A-20).

However, soil genesis is a very long-lasting process. Some important processes are explained schematically in ◘ Fig. A-21. The distinction between climatypical ecosystems and those that are more strongly characterized by pedological processes is only possible in a blurred way because certain pedological processes are themselves zonobiome-specific. Some pedobiomes are therefore actually zonobiome-specific biomes (for example in zonobiome II, where crust formation, laterites, etc. occur).

Soil formation takes place from the parent rock in interaction with the developing vegetation. The soil formation processes, influenced by the climate, lead to certain soil types or groups of soils. It can be seen that the historical aspect is also significant for soils.

◘ **Fig.** A-19 The formation and decay of clay minerals. Illite and montmorillonite are three-layer clay minerals, kaolinite is a two-layer clay mineral (modified after Lerch 1991).

◘ **Fig.** A-20 The main groups of soils in the ecogram of moisture and temperature.

◘ **Fig.** A-21 Schematic of the genesis of soils on silicate rocks depending on various influencing factors.

Natural ecosystems very gradually create their specific soil type, which is then in harmony with the long-term climatic conditions and zonal vegetation at the site.

**1.4.2 Salt: Halophytes and salt soils, halobiomes**

A very important group in many deserts are the salt plants or halophytes. They are bound to the occurrence of saline soils. Many halophytes are succulent, but they should not be grouped with the true succulents. Their succulence is the result of strong saline, or chloride, storage; for this reason their cell sap concentration is often very high and may exceed 5 MPa. In addition to the effect of salt (NaCl), the effects of other ions must always be considered on saline sites, for example, hydrogen carbonate (alkali soils, sodic soils), sulfate, borate. So it is not only the more specific case of exposure to salt (NaCl) in dryland soils that leads to vegetation differentiation.

The halophytes or salt plants colonize the saline soils on the sea coasts and in the deserts. The saline soils may have been conquered by plants evolutionarily relatively late. On these soils, land plants had to solve not only the water problem, but also the physiological effect of the salts.

It is appropriate to start from the plants themselves when defining halophytes: True halophytes are plants that accumulate larger amounts of salts in their organs and are not harmed by them, but are even promoted by them if the concentrations are not extremely high; the corresponding salts are mostly NaCl, sometimes also Na2SO4 or organic Na salts.

The concentration of cell sap in the vacuoles cannot be lower than that of the soil solution, which is usually very high in saline soils. If osmotically active substances were additionally formed in the cell sap, such as sugar, for example, the hydrature of the plasma would have to drop very sharply, which would be unfavourable. The solution of the problem is therefore effected in another way: So many salts are taken up from the soil into the cells that the concentration of the soil solution is equilibrated. Through these absorbed electrolytes (Na+, Cl-) no dehydration of the plasma takes place, but rather an additional hydration, which causes a succulence of the organs. Conversely, additional substances are synthesized in the cytoplasm, which establish the osmotic balance there, but are plasma compatible ('compatible solutes'). These substances can originate from quite different substance classes. They are often typical for certain plant families or genera, i.e. taxon-specific (Popp 1995).

In larger concentrations, salts are toxic. The halophytes must therefore be salt-resistant, but this is only possible to a certain extent, so that very heavily salinated soils remain vegetation-free (◘ Fig. A-22, for example on the shores of salt lakes).

Due to the different behaviour of plants towards high salt loads from the soil, different types of adaptation can be distinguished.

The Non-halophytes (**Halophobes)** (► Fig. A-22 **N**) - the majority of plants - die due to lack of osmotic adaptation when exposed to salts from water deficiency. Salts are toxic to salt-sensitive species. Therefore, these cannot grow on saline soils.

The Facultative halophytes (Pseudo-halophytes) (► Fig. A-22 P) are to a certain extent capable of osmotically adapting their uptake system in the root by salt uptake, but of fixing the salt in the root area and thus keeping the shoot relatively low in salt. Such salt-tolerant plants can withstand a salt concentration that is not too high, but develop better on non-saline soils.

For all halophytes applies, what is also pointed out for the mangroves, that the roots act like an ultrafilter, i.e. they take up practically only almost pure water from the salty soil solution and supply it to the leaves through the conductive pathways. In the vessels of the halophytes, high cohesive tensions were detected.

In Euhalophytes, too, the root system acts like an ultrafilter that allows only a few salts to pass through into the transporting system. However, these salts gradually accumulate in the shoot system and cause their halosucculence by formative differentiation processes: leaf succulence (► Fig. A-22 L) (for example Suaeda) or/and shoot succulence (► Fig. A-22 **S**) (for example Salicornia). Euhalophytes are stimulated in growth by some salt enrichment. On ordinary soils containing only traces of NaCl, they snatch it, so that even then their salinity is relatively high. This stimulation comes from the chloride ion, which has a swelling effect on protein bodies. The consequence of this is a hypertrophy of the cells by a strong absorption of water, that is, a succulence of the organs. The higher the chloride content of the cell sap, the more pronounced is the succulence. Only the chloride ion has this effect, but not the sulphate ion, which has a deswelling effect on proteins. There are halophytes which, in addition to chlorides, also store larger quantities of sulphates in the cell sap; these halophytes are not or only weakly succulent. We must therefore distinguish between Chloride halophytes and Sulfate halophytes. They can grow side by side on one and the same soil. Salt uptake is usually species-specific (Breckle 1976). In studies of the halophyte problem, it is therefore not sufficient to examine the soils for their salt content; for the plant, only the salts with which the plasma comes into contact are of importance. One must always know the concentration and composition of the salts in the cell sap. How different the composition of the cell sap of halophytes and non-halophytes is, is shown in ◘ Fig. A-23.

For the Euhalophytes, too, there is an upper limit to the salt concentration in the cell sap, which varies from species to species. If this becomes too high, the plants will deteriorate, which in the case of the Chenopodiaceae is usually indicated by a red colouration (N-containing dyes: Betalains ◘ Fig. A-24), until they finally die. There is another group of halophytes in whose cell sap Na+ is present in a significantly higher equivalent concentration than Cl- and SO42- combined. Thus, Na ions must be equilibrated by anions of organic acids. After these plants die, decomposition breaks down the organic acids to carbonates. The sodium enters the soil as Na2CO3 (soda ash), making it alkaline. We refer to these halophytes as Alkali halophytes.

◘ **Fig.** A-22 Vegetation profile at the Great Salt Lake (Utah, USA) with indication of chloride contents in the soil (TG) in the individual vegetation belts (modified Kearney et al. 1914, Breckle 1976).

◘ **Fig.** A-23 Content of inorganic ions in the cell sap of green organs of various Halophytes and Non-halophytes from Northern and Central Afghanistan (after Breckle , 1986). Species 1-18 are Chenopodiaceae. Species 1-6 are chloride halophytes, leaf or stem succulent; anion contents(Cl- + SO42-) exceed cation contents (Na+ + K+). Species 7-12 are Alkali halophytes with significantly lower inorganic anion contents, here larger amounts of organic anions are detectable in the cell sap, also clearly leaf or stem succulent. Species 13-18 are Pseudo-halophytes occurring on lower salt sites and are less succulent. Potassium predominates over sodium. Species 19-24 are non-Chenopodiaceae; 19 and 20 are Sulfate halophytes, withstand some salt. The others are Non-halophytes with low salt tolerance. 23 + 24 show in comparison the analysis values of maize leaves of a salt-loaded and an unloaded field; at 23 already with clearly yellowed leaves and salt damage.

◘ **Fig.** A-24 Color change due to betalain incorporation in Salicornia europaea at the beginning (a, photo: Breckle) with increasing drought and with complete salt accumulation beyond the concentration limit on the recently dried lake bottom of the Aral Sea (b, photo: Wucherer).

Among the halophytes there are also species provided with salt glands, mostly not succulent. These Recretohalophytes (◘ Fig. A-25 X) are species that continuously excrete the salt they ingest, such as Limonium, Reaumuria, Frankenia, Glaux, Spartina, and other halophilous grasses. Salt glands are also present in an important tree, the Tamarisk (Tamarix), which is represented by many species in arid regions. When branches of this tree are shaken, salt dust falls from them. Since Tamarix excretes mainly NaCl, sulfates predominate in the cell sap and the leaf organs are not succulent.

Salt excretion is also possible by storage in isolated bladder hairs (Atriplex etc.), which form a coating or can also be shed. Salt excretion is also possible by shedding, for example, old leaves rich in salt. The latter is also known in Facultative halophytes, such as Juncus, where the leaves turn yellow early, or in rosette plants (Limonium etc.), where new leaves are continuously formed. In addition to this more auto-ecological characterization of halophytes (► Fig. A-25), a distributional ecological characterization of the different halophyte types is also used: Obligate halophytes - Facultative halophytes - site-indifferent halophytes - Non-halophytes, which of course largely coincides with the auto-ecological typing.

Along a salt gradient in the terrain, for example around a salt lake, the halophytes usually occur in a certain zonation. On the very inside, Stem-succulent euhalophytes predominate, followed by Leaf-succulent ones on the outside, then there is often a zone with a particularly large number of Recretohalophytes, followed further out by the Pseudohalophytes (► Fig. A-25 P) and then on the outside (without salt pollution) the Non-halophytes. Such a halo-catena is best developed in areas where floristically there are many different halophyte species, as in Central Asia (Breckle 1986, 2002a).

For many halophytes of the arid regions, as already mentioned, the problem is not water, because they grow on wet salt soils of salt pans (Hygrohalophytes), but the salt balance. But there are also those that occur on dry saline soils and often suffer from water deficiency, notwithstanding strong salt storage (Xerohalophytes); these include Atriplex, Haloxylon, Zygophyllum species, and others in which one can often observe a precise reduction in transpiring surface area during drought, tailored to water availability; for example, Zygophyllum dumosum sheds the leaflets first, then the petioles (► Fig. A-12), others the young terminal shoots or even the green bark of leafless previous year's shoots.

In all arid regions there is a constant risk of soil salinization (Waisel, 1972) Although the input of rainwater means only a small supply of salt (on average, rainwater contains 0.001 % NaCl), a considerable amount accumulates in the long term if there is no corresponding discharge, as is more or less the case in all arid areas (by definition: potential evaporation exceeds precipitation). Arid areas are accordingly characterized geomorphologically (► Fig. A-46). They have endorheic basins; runoff generally does not reach the world ocean, but reaches only local basins that represent the erosion base. There, the salt of precipitation water and salt released by leaching of the surrounding rocks is enriched (salt pans or salt lakes, for example Dead Sea, Aral Sea, Great Salt Lake in Utah, Lake Chad, Dashte-Nawor, Hamune-Puzak, etc.).

**Fig.** A-25 Schematic classification of the different halophyte types based on the regulation of internal salinity (after Breckle 1976).

In all arid regions, irrigation (even with irrigation water that contains, for example, only 0.02 % NaCl [= 200 ppm] and is thus of the best quality) leads to slow salinization (Breckle 2009, 2021), unless care is taken to ensure that the enriched salt is washed out of the fields again and again, just as the Nile in Egypt with its annual floods - before the Aswan Dam was built! - has provided for desalination in the Nile valley for thousands of years.

In arid areas, the vegetation mosaic is strongly influenced by soil salinity. The different biomes there are characterized by their salt load. It is not uncommon to find pronounced gradients of increasing salinity (and decreasing soil grain size) towards the basin landscapes. An example from the Great Salt Lake area is given in ► Fig. A-22. Further examples of this are brought in the discussion of arid zonobiomes III and VII.

The long periods of drought in arid areas cause rivers to flow only periodically or even episodically. Since the potential evaporation is higher than the annual precipitation, in arid areas there are sinks without drainage in which all the water evaporates that reaches them through the tributaries. The salts dissolved in the water, as already stated, accumulate more and more in the course of time. A saturated solution may form and the salt crystallize out. Salt lakes or salt basins are characteristics of arid climates. Ultimately, the world ocean is also a terminal lake into which all soluble matter has been transported over billions of years. Most of the soluble salts consist of NaCl, because the hydrocarbonates precipitate early after loss of CO2 as CaCO3, the sulfates somewhat later as gypsum (= CaSO4). The potassium salts crystallize, if at all, at the latest; thus a typical sequence of these evaporites is formed as a sedimentary sequence.

Sodium ions are released by weathering from silicates, whereas chloride ions are present in seawater in quantities of almost 20 g/litre (sulphate only 2.7 g), but chlorine-containing minerals are rare. Thus, little chloride ions can be released by weathering of minerals. Nevertheless, NaCl can always be detected in river water. It is also likely to have been enriched by HCl-containing exhalations from volcanoes over the long history of the Earth.

The NaCl of the saline soils of arid areas can be of various origins:

1. It is sea salt trapped in rocks that were deposited as marine sediments (evaporites). During the weathering of these rocks, the salt is dissolved by rainwater and transported into the drainless depressions. Deserts with marine sedimentary rocks (Jurassic, Cretaceous, Tertiary), for example the northern Sahara and the Egyptian Desert, are therefore highly brackish, whereas arid areas with igneous rocks or terrestrial sandstones have much less saline soils.
2. The arid areas that were lake or sea basins in the recent geological past that slowly dried up, for example the areas around the Great Salt Lake (Utah; Lake Bonneville as a glacial lake), around the Caspian and Aral lakes (Central Asia), around the Tuz Gölü (Central Anatolia), Dead Sea in the Middle East (Lake Lisan as a glacial lake), Lago Enriquillo (Hispaniola), Dasht-e Nawor (Afghanistan) and others, are also depleted.
3. When there is a strong surf on arid sea coasts, seawater is finely atomized, the salt water droplets dry out and the salt dust is blown as aerosol many kilometres inland. It is either deposited as such or added to the soil by rain or fog. This process also takes place in humid areas, but in these the deposited salt is constantly washed out and returned to the sea by rivers (cyclic salt). In arid areas without runoff, on the other hand, the salt accumulates. The brackish conditions of the Outer Namib and the arid parts of W-Australia can be traced back to this cause. If salt flats have developed in the depressions, the wind can blow salt dust from them further. But even far from the coasts, rain (with 10 to 20 ppm NaCl) steadily brings traces of salt with it.
4. Brackage can also occur when spring water loaded with salt comes to the surface, for example in the northern Caspian lowlands. In this case, it is salt from sea basins that dried up in earlier geological times (Permian, Muschelkalk), which forms deposits at greater depths. In arid areas this salt accumulates, in humid areas (salt springs for example in Bad Salzuflen, Salzdetfurth, Salzgitter, Salzburg, all in Middle Europe, with the term “Salz” = salt) it is in turn rapidly discharged to the sea.

In the deserts, after each rainfall, a shift of salt takes place from the higher parts of the relief to the lower ones, so that the depressions dry up. If the sedimentary rocks are very saline and precipitation is very low, as for example around Cairo-Heluan or in central Iran, the soil of the plateau sites may also contain salt. In the rainless central Sahara, no salt displacement takes place, thus salt accumulation in depressions is completely absent.

For the plants, it is not the salt content of the soil - calculated on the dry weight - that is important, but the salt concentration of the soil solution in the rooted soil region. In weakly saline soils, which are dry at the same time, the concentration is often higher than in strongly brackish but wet soils.

Salt displacement is also brought about by evaporation from the soil surface if the groundwater is less than 1 m below the surface, so that it can rise capillary to the soil surface; a salt crust forms at the surface (◘ Fig. A-26), even if the groundwater contains only very small amounts of salt (◘ Fig. A-27). The salt always precipitates where the capillary water flow finds its end; these are the highest points of the micro-relief (◘ Fig. A-28).

◘ **Fig.** A-26 Salinity at different soil depths in an irrigated bed (left) with groundwater rise and an unirrigated bed in the Swakop Valley (Namibia). NaCl = drawn out line, Na2SO4 = dashed line. The salts accumulate only at the surface (modified after Walter 1990).

◘ **Fig.** A-27 Formation of a salt crust by capillary rise (arrows drawn out) of groundwater (dashed horizontally) and evaporation of water (dashed arrows); salt accumulation at the soil surface (modified after Walter 1990).

◘ **Fig.** A-28 Salt accumulation in the Swakop Valley (Namib Desert). The arrows indicate direction and strength of water flow in the soil; the dashed arrows indicate evaporation. Salt concentration increases towards the edge of the valley; salt blooms out at S at the base of the terrace where water flow ceases (modified after Walter 1990).

Where the rule of "no irrigation without drainage" is not followed, crops collapse due to salinization in a few decades, as many "short-lived" development projects show and have shown. A particular example is the Helmand project near Kandahar, SW Afghanistan.

The presence of a salt crust in times of drought does not necessarily impede the growth of plants if they are rooted in the non-brackish groundwater. In the Pampa de Tamarugal in the Atacama Desert, Prosopis trees grow in holes in a half-meter-thick salt crust only because their roots reach groundwater streams with fresh water.

Any field irrigated in arid regions without some drainage constitutes a drainless basin and must in time dry up even if the water used for irrigation contains only very small quantities of salt. In this way vast cultivated areas in Mesopotamia and the Indus region have become salt deserts. This has not yet been the case with the undrained cotton fields of the Gezira in Sudan, because the water of the Blue Nile used for irrigation is particularly low in salt. Small amounts of salt are removed from the field each time the crop is harvested.

Salinization has become one of the most significant constraints on global crop production. More than 20% of the agricultural land in the world can no longer be used productively due ti salinization. There have been tremendous efforts to breed more salt-resistant crops during the last decades (Flowers & Yeo 1995, Munns 2005, Breckle 2002, 2009, 2021, Ibrahimova et al 2021). Still the results are disappointing; The main reason for this is that a plant's salt tolerance is not determined by a few genes, but rather is a comprehensive physiological-biochemical response of the entire plant with far-reaching regulations and formative adaptations. As a rule, this means significantly reduced growth (Cheeseman 2015), but greater competitiveness on salty soils. The potential of alternative splicing mechanisms and targeting gene-editing technologies in understanding salt stress responses and developing salt-tolerant crops (Wani et al., 2020) is apparently overestimated, and often classic eco-physiological knowledge from long-term research on halophytes often seems to be completely forgotten. Nevertheless, halophyte research in the arid zonobiomes and the remediation of their saline soils are of great importance.

1.5 **Mechanical factors**

1.5.1 **Wind, trampling**

Wind and storm, frost formation, driving snow and avalanches, sand drifts and soil movements on slopes, all these are mechanical influences on organisms. But one must also include footfall, trampling and browsing by livestock. A factor that also occurs naturally worldwide is fire, which ultimately destroys ecosystems mechanically and thus affects many organisms.

Many plants in the mountains are adapted to wind and snow breakage; they have very elastic branches and lean on the slope (◘ Fig. A-29).

In the case of sand fill in dune areas, there too are good adaptations of dune plants that grow upwards with the sand fill, but also withstand free blowing of the upper root zone well, as they develop very far-reaching roots. Calligonum is one such genus with numerous species in the Asian deserts (◘ Fig. A-30).

Regular trampling paths in lawns or meadows can be recognized by the fact that tread-resistant plants, often with rosettes lying against the ground, appear preferentially (◘ Fig. A-31).

Herbivory, i.e. the grazing of plants, is an essential process in ecosystems, which will be discussed in the context of material cycles. But every grazing means a mechanical damage of the plants. This can be seen very well in trees standing on pastures or trees at the edge of forests. The lower 1-2 m are kept practically free by grazing (◘ Fig. A-32), higher branches are not reached, apart from some climbing goats.

◘ **Fig.** A-29 The mechanical action of wind on tree crowns in the coastal mountains near Carácas (Venezuela) (a, photo: Breckle) and in Pinus pinaster forests on the SW coast of the island of Sardinia (b, photo: Rafiqpoor).

◘ **Fig.** A-30 In the desert areas of Central Asia, the roots of Calligonum are exposed from the dune sand by the wind. In this state, the water supply of the plant is provided by the main root and the fine root system not yet exposed by the sand (photo: Breckle).

◘ **Fig.** A-31 Plantago major resists mechanical pressure from trampling damage on trampling paths now worldwide (Photo: U. Breckle).

◘ **Fig.** A-32 The lower parts of the trees at the forest edge have been stripped bare by cattle browsing up to a certain height level (a; photo: Breckle). Goats even climb up the trees and eat the leaves at all elevation levels (b: Argania spinosa in Morocco; photo: Breckle). Otherwise, the trees remain intact above a certain height that is not reached by other animals.

1.5.2 **Fire**

One must discuss the fire factor somewhat in more detail. There are a number of plant species in all drier climates that are adapted to fire. This is particularly evident in Australia, but also in all Mediterranean countries. In Australia, we speak of Pyrophytes (fire plants) when these species are virtually dependent on fire to continue to thrive. The fruits, for example, only release their seeds after a fire has passed over them (◘ Fig. A-33) and only then are they capable of germination.

This is due to the fact that a fire burns the hard woody components of the fruit or seed coat and thus mechanically loosens them. The next time it rains, the water can penetrate better and the swelling pressure then opens the fruit wall or seed coat. This can be observed in several species of the genus Eucalyptus, but also in many Proteaceae. In the Mediterranean region, the cork oak (Quercus suber) is particularly fire-resistant. Its thick bark protects the cambium (◘ Fig. A-34). After a fire, new branches sprout from it. But many other plants also sprout new shoots from underground storage organs, well fertilized by the ash.

◘ **Fig.** A-33 Banksia trees represent a good example of Pyrophytes. Their seeds in the cobs in the middle picture are only released (c) and become germinable by the action of fire (photos: a Breckle; b and c: Rafiqpoor).

2 **The climate**

2.1 **General questions**

In everyday life we generally speak of rain, showers, hail, fog and thaw, high and low pressure areas or of the greenhouse effect and global warming. What is weather and what is climate? If you look out of the window in Kabul, or in Tehran, or in Cairo, or in Antofagasta, you may find that the sun shines from a bright blue sky for most of the year. During winter and transitional seasons, one might more or less rarely also observe overcast skies, snow or rain showers, thunderstorms with or without hail, or duststorms. Usually, these short-term observations are then talked about bad weather, but not climate. On the radio and television there are also daily only weather reports, no climate reports. These brief remarks indicate that in determining whether weather or climate, we are talking about a temporal dimension. So weather change (e.g. change from rain showers to sunshine) and climate change are two different dimensions in climatology. The first happens quickly, occasionally even several times a day (so-called "April weather" in Europe), the second slowly and can only be detected over years or better over decades. Weather is therefore something that is happening. It can be interpreted, analysed and put into data. Data collection is always done at climate stations, which in some countries has a dense network, in others (like Afghanistan) a less dense one. The collected climate measurement series usually contain data on radiation, cloud cover, temperature, precipitation, relative humidity, air pressure, wind, etc., i.e. data on the ecological factors that are also important for organisms. From these long series of measurements, it is possible to calculate what the climate was like in recent years. And the further back the first measurements in a country go and the more data are available, the more precisely the climate there can be reconstructed.

So, statistically, climate is a term of something longer lasting. To understand this, one must take into account the spatial and temporal scales and meaningfully move from the small (or short-term) to the large (i.e. long-term).

Weather is the short-term in this system. Weather is the instantaneous physical state of the atmosphere produced by the meteorological elements and their interaction at a particular time in a particular place (or area). Long period weather (German: Witterung) is a medium term in this system. It describes the general, average or also predominant character of the weather events of a certain period of several days or weeks, rarely also months. A distinction is made between characteristic weather types or weather patterns, each of which is determined by prevailing weather conditions.

Climate is the long term in this system. It is defined as the summary of weather phenomena characterising the mean state of the atmosphere at a given place or in a more or less large area, with all its periodic variations in the course of the year. It is represented by the overall statistical properties (means, extremes, frequencies, durations, etc.) over a sufficiently long period of time. Generally, a period of 30 years is taken as the reference period. In general, however, it must be said that the longer the measurement period, the more reliable the statement about the climatic character of an area! For the compilation of ecological climate diagrams, the entire available measurement series of the meteorological stations are used if possible.

Climate is therefore the result of the interaction of several climatic elements, of which radiation is the most primary and fundamental.

2.2 **The radiation budget and astronomical basics**

The driving force for all climate-determining processes is solar radiation. The interaction of solar (position of the earth as a planet in the solar system), meteorological (physical and chemical processes in the atmosphere) and geographical (land/water distribution, relief, ocean currents, etc.) conditions basically creates the climate.

The radiation incident on the earth from the sun is, as a primary energy source, also the prerequisite for almost all life processes on earth, if one disregards for once the "black smokers" of the deep-sea trenches and their living creatures. The solar radiation arriving at the upper boundary of the atmosphere on a cm2 perpendicularly facing the sun is 8.4 J (joules) per second; this corresponds to an average of 1,367 watts/m2/sec. This amount of radiation, known as the **solar** constant, varies by about ± 3.4% over the course of the year, depending on the position of the Earth relative to the Sun. At the time of solar proximity (perihelion: currently 3 January: 2nd-5th depending on leap year) it increases to 1,420 W/m2/sec and at solar remoteness (aphelion: 5 July: 3rd-6th depending on leap year) it is 1,325 W/m2/sec. The slightly elliptical orbit of the Earth around the Sun with a point a bit farer from the Sun and a point a bit closer to the Sun, but above all the inclination of the Earth's axis to the Earth's orbit around the Sun (◘ Fig. A-35) also explain the sequence of the seasons and their occurrence in the different latitudes and the differences between the northern and southern hemispheres. On average, only about half of the radiation at the upper atmospheric boundary reaches the Earth's surface.

**Fig.** A-35 Scheme for explaining the seasons based on the astronomical conditions of the Earth's orbit and the inclination of the Earth's axis relative to the orbital plane (ecliptic) (solstice line: summer or winter point; equinoctial line: equinoxes, spring or autumn point) (modified from Schönwiese 1994).

In ◘ Fig. A-36, the radiation balance for the vertically directed energy system Earth-atmosphere-space is shown schematically with three balance areas: Earth's surface, the troposphere to the tropopause, and the stratosphere to the mesopause. On average for the entire system, the Earth-space radiation balance is balanced. The radiation balance (S) is the difference between the absorbed global radiation and the effective radiation and can be expressed in:



S = Radiation balance

I = Direct solar radiation

D = Diffuse sky radiation

G = Back radiation of the atmosphere

A = Warm radiation of the earth surface (infrared radiation)

V = Evaporative heat flux (latent heat) in the exchange between earth and the lower atmosphere

L = Convection heat flux (sensible heat) in the exchange between earth and the lower atmosphere

α = Planetary albedo: Unused energy loss as diffuse and direct reflection (26 + 3 + 2 + 2 = 33%: ► Fig. A-36).

The individual energy flows in this system are shown as a percentage of the incoming solar radiation at the top of the atmosphere (100%). The sum of the individual components results in gains (input) and losses (emission) of the Earth-atmosphere-space system. Basically, the solar radiation arriving at the Earth minus the reflected portion is equal to the thermal radiation radiated from the Earth. If more heat is radiated from the Earth as a result of the anthropogenic greenhouse effect, there is excess heat in the atmosphere and consequently global warming.

The diagram (◘ Fig. A-37) shows the spatial distribution of extraterrestrial solar radiation on Earth as a function of latitude. It is noticeable that especially the equatorial regions between 10°N and 10°S receive significantly less solar radiation during the course of the year with 30-35●106 J●m-2●d-1 compared to the marginal tropics, because here, due to the almost constant cloud cover and the resulting high reflection and absorption in the atmosphere, the areas of maximum radiation are shifted towards the marginal tropics around the 30th degree of latitude in the area of the subtropical dry regions. On the other hand, with a radiation amount of >45●106 J●m-2●d-1, the radiation in the polar regions is surprisingly high at the time of the short summers (polar day = 24 hours). This has consequences for the generative cycle (fructification and maturation processes) of tundra and taiga vegetation under long-day radiation climatic conditions.

Despite the radiation-reducing effect of cloud cover, the sum of summer and winter insolation is highest at the equator because of the almost year-round high position of the sun.

**Fig.** A-36 Scheme of the radiation balance of the Earth-atmosphere-space system (modified after Lauer 1999).

**Fig.** A-37 The extraterrestrial solar radiation on Earth during the course of the year as a function of latitude (numerical values in 106 J●m-2●d-1) (modified after Schönwiese 1994).

**Fig.** A-38 Diagram of the theoretical daily sunshine duration (from Junghans 1969, modified after Lauer & Frankenberg 1986).

The solar zenith in summer is located in the area of the respective tropics (approximately 23½°, solstices: summer and winter point: ◘ Fig. A-38 I & **III**). Conversely, the length of day in summer reaches the maximum value of 24 hours (polar day) from the Arctic Circle (ca. 66½°) to the poles, due to the inclination of the Earth's axis against the Earth's orbit. These and the astronomical facts explained below are indispensable for the understanding of the seasons as well as the ecological basics of geobotany and biogeography.

The index numbers (I, II, III) ► Fig. A-38 refer to the reference dates of the equinoxes and the winter and summer solstices. Strictly speaking, only at the vernal and autumnal equinoxes, when the sun is above the equator, is the length of the day twelve hours long (equinoxes: ► Fig. A-38 II). Seen from Earth, the day/night change appears quite different depending on latitude because of astronomical conditions (Earth's orbit around the Sun with 365% days and tilt of Earth's axis with 24-hour rotation). The variations in day length for the two hemispheres result from the difference between the day length at the summer solstice and the day length at the winter solstice. The times of sunrise and sunset can be read very easily from the equator to the poles for selected dates in ► Fig. A-38. The number of astronomically possible hours of sunshine corresponds to the length of the day. The apparent path of the sun in the sky (◘ Fig. A-39) is always almost exactly twelve hours long at the equator; at mid-latitudes, for example Frankfurt/Main, the variation in day length between summer and winter is already considerable at about 11 hours, and at the pole it is night for half a year (polar night) and day for half a year (polar day).

**Fig.** A-39 Apparent path of the sun along the sky at different latitudes (modified after Schönwiese 1994).

**Fig.** A-40 The turnover of solar irradiation energy in the atmosphere and at the Earth's surface and the solar constant as a function of latitude (modified after Schönwiese 1994).

**Fig.** A-41 Scheme of the diurnal variation of solar radiation and terrestrial radiation. The sine curve also corresponds to the temperature curve on clear days (modified after Schönwiese 1994).

The atmospheric processes and the respective latitude-dependent radiation angles ultimately determine what radiation remains at the Earth's surface (◘ Fig. A-40).

In general, the diurnal variation of insolation leads to constant changes in air temperature as a result of the different components of insolation and radiation in the radiation balance (see above). The relative energy turnover reaches its maximum energy gain around midday, the energy losses are particularly large immediately after sunset (◘ Fig. A-41).

The proportion of global radiation is greatest in the Earth's arid regions of marginal tropics, especially in the deserts (Sahara) (◘ Fig. A-42), while the radiation balance is lowest, since the balance values are extremely low due to the high effective radiation and very low water content in the air. Maximum values of the radiation balance occur in the tropics (red), especially over the oceans (dark red).

From ◘ Fig. A-43 it can be seen that equatorial rainforests use >1.6% of global radiation for photosynthetic carbon acquisition, while these values are close to zero in the Sahara, where the maximum global radiation occurs.

The values of radiation use by the plant cover coincide with a high photosynthetic output of vegetation formations in the low latitudes (Lauer & Rafiqpoor 2002). Accordingly, phytomass (► Fig. A-16) and net production (► Fig. A-15) are particularly high in the tropics.

**Fig. A-42** Net radiation at the Earth's surface as the difference between incoming radiation and radiation reflected from the Earth for the month of March (zenith position of the Sun) for the period 1985-1989 prepared by David BICE, Professors of Geosciences, College of Earth and Mineral Science, The Pennsylvania State University as part of the NASA ERBE experiment (source: http://bit.do/bUMme).

◘ **Fig. A-43** Spatial distribution of percent radiation use by plant cover (from Larcher 2001).

2.3 **The heat balance**

The short-wave radiation emitted by the sun is converted into long-wave thermal radiation (sensible heat) at the earth's surface. Temperature is therefore an important climatological parameter as a measure of the thermal state of the air, which is essentially determined by the heat emission of the earth's surface. It only reflects the instantaneous heat state. The air temperature measured with a thermometer at a shaded and well ventilated weather hut is the so-called sensible (sensitive) heat (L) as an expression of the molecular kinetic energy. It provides the heating and is transported further by turbulent air movement (convection). The latent heat (V), or also the evaporation-heat, characterizes the potential-energy, that is consumed during the evaporation-process, i.e. is taken from the sensible heat, is released again through condensation-processes and is transferred into the sensible heat again. These two thermal components, converted by vertical mass transfer, are two important links in the Earth's heat balance. They consume most of the energy from the radiation balance. Since 72% of the Earth's surface is covered by sea, the transport of latent heat of evaporation plays a major role in the global water balance (see below) and participates with 80-85% in the Earth's heat budget (Lauer 1999).

For the thermal differentiation of the zonobiomes of the earth, the ecophysiologically important length of the thermal vegetation period as an expression of the heat balance of an area is of considerable importance. A calendrical month is considered to be thermally favourable if the natural and "cultivated" flora dominating in an area - from the point of view of the heat balance - achieves a clear material gain or fructifies during this month. This happens in the different zonobiomes plant stand typical at different heat levels. Walter (1960) defines the duration of the thermal growing season in the extratropics as the frost-free period of the year on a monthly basis, which is limited by reaching or falling below certain temperature thresholds. The growing season, when woody plants begin to produce matter, begins after they green up, and for many species, when the daily mean reaches the 10 °C mark. When the temperature falls below a specific level in autumn, foliage discolouration sets in and with it the completion of assimilation activity. The optimal temperature range between the beginning and end of the growing season is usually no wider than 10-25 °C for most plants (Larcher 1980). ◘ Table A-4 gives the threshold values for different formations of natural vegetation in the outer tropics and ◘ Table A-5 for cultivated plants.

From such data series, Lauer & Rafiqpoor (2002) determined the length of thermal growing season at global level. The values for the length of the thermal vegetation period vary between 0 and 12 months. One can divide these values into classes according to landscape ecology: 0 = hecistotherm, 1-2 = oligotherm, 3-4 = microtherm, 5-6 = mesotherm, 7-9 = macrotherm, 10-12 = megatherm. The spatial representation of the lines of equal length of the thermal vegetation period (Isothermomena) gives a differentiated picture of the thermal climate on Earth (◘ Fig. A-44).

**Table A-4** Temperature thresholds for the growth and photosynthetic production of different formations of the natural vegetation and cultivated plants of the subtropics and mid-latitudes (after Lauer & Rafiqpoor 2002).

|  |  |
| --- | --- |
| Vegetation formation | Thermal threshold (°C) |
| Boreal coniferous forest | 5 |
| Coniferous moist forest | 5 |
| Temperate deciduous forest | 7 |
| Mixed deciduous forest | 10 |
| Steppes (subtropics) | 10 |
| Patagonian Steppe | 7 |
| Semi-deserts (subtropics) | 10 |
| Deserts (subtropics) | 10 |
| High mountain formations | 11 |
| Subtropical moist forest | 12 |
| Montane coniferous forest | 10 |
| Deciduous broad leaved forest | 10 |
| Sclerophyllous woods | 12 |
| Steppes (mid-latitudes) | 11 |
| Pampa | 11 |
| Semi-deserts (mid-latitudes) | 11 |
| Deserts (mid-latitudes) | 11 |
|  |  |
| Tundra | 5 |
| Subpolar frost-debris zone | 3 |

◘ **Fig. A-44** Length of the thermal growing season on Earth.

**Tab. A-5** Threshold values of the minimum and optimum temperature requirements of important crops in the subtropics (modified from Lauer & Rafiqpoor 2002).

|  |  |  |
| --- | --- | --- |
| Crops | Minimum temperature range (°C) | Optimum temperature range (°C) |
| Coconut Palm | 24 | 26-27 |
| Yams | 20 | 25-30 |
| Sugar cane | 18-20°C, at 15°C growth stops | 25-28 |
| Cassava | 20 | >27 |
| Cocoa | >20 | >27 |
| Coffee | 18 | >22 |
| Pineapple | >18 | >20 |
| Tea | 18 | 28 |
| Millet | 12-15 | 32-37 |
| Sweet Potato | 10 | 26-30 |
| Tobacco | 15-20 | 25-30 |
| Rice | 12-18 | 30-32 |
| Olives | 12-15 | 18-22 |
| Sesame | 12-15 | 25-27 |
| Pumpkin | 10-15 | 37-40 |
| Cotton | 18 | 30 |
| Peanut | 15 | 30 |
| Corn | 12-15 | 30-35 |
| Potato | 8-10 | 16-24 |
| Winter wheat | 4-6 | 15-30 |
| Spring wheat | 6-8 | 20-30 |
| Rye | 4-6 | 15-25 |
| Barley | 4-6 | 15-25 |
| Oats | 4-6 | 20-30 |
| Sugar and beta beets | 4-5 | 20-30 |
| Meadow grasses | 3-4 | c. 25 |

2.4 **The water balance**

Water is the sine qua non of all life on earth. Only about 0.001% of the total water on earth is in the atmosphere. Nevertheless, water is extremely important for the climatic processes in the atmosphere and can exist in all three aggregate states (solid, liquid, gaseous). It enters the atmosphere by way of evaporation (Evaporation and Transpiration = Evapotranspiration, ET). Evaporation occurs both over the oceans and through evapotranspiration over the land. The motor for this process is latent heat (see above), which initiates the evaporation process by changing the state of aggregation (from liquid to gaseous state).

Due to the ascent of the air into the atmosphere via the turbulent exchange processes, the gaseous water condenses in clouds (water droplets or ice crystals) by way of cooling. With higher condensation and millionfold enlargement of the water droplets or ice crystals around a condensation nucleus, precipitation occurs (rain, snow or hail ...etc.).

The vapour pressure of water depends on the temperature. The vapour pressure saturation is not linear, but increases steeply with increasing temperature, as shown by the curve of the saturation vapour pressure as a function of temperature (◘ Fig. A-45). For dry air, for example, with a vapor pressure like point X at temperature Ta and a vapor pressure of ea, the relative humidity can be expressed as a fraction of Y. If one reduces the temperature, the relative humidity increases - for the same absolute humidity - e.g. up to 100% at point Z at a temperature Td; this Td is called the dew point. At temperatures below 0 °C, the saturation vapor pressure is very low (ordinate enlarged, ► Fig. A-45). It is somewhat lower over ice than over water. If the air cools from Tb to Ti, the air is still somewhat unsaturated with respect to water droplets in supercooled clouds, for example. This means that at the same temperature these will release water to ice crystals, a significant process for precipitation from clouds (White et al. 1992). Overall, this also means that precipitation can be much more abundant at high temperatures, as in the tropics, than in cold regions. At water vapour saturation, 30 °C warm air contains about 45 mbar of water vapour, i.e. 9 times as much water compared to 0 °C warm air with 5 mbar, or even -20 °C air with only 1 mbar.

Precipitation makes life on Earth possible and is regionally very unevenly distributed (humid and arid areas). In an arid region, evaporation predominates in the hydrological water balance. Thus, in contrast to a humid area, no closed, permanent river system will form. Basin landscapes there contain only small terminal lakes (see p. xxx) that become saline (Dead Sea, Great Salt Lake in Utah, Aral Sea, Lop-Nor, Hamune-Puzak, Dashte-Nawor) (◘ Fig. A-46).

Fig. A-45 Changes in the water vapour saturation of the air as a function of temperature (modified after Lambrecht, Göttingen).

◘ **Fig.** A-46 Dashte-Nawor is a dry saline basin in a high plateau in central Afghanistan with clearly formed belts of halophyte vegetation (photo: Breckle).

In humid regions, such basin landscapes (for example Lake Constance, Germany) have an overflow and are filled "to the brim" with water. The internal water cycle of larger regions is thus very different, depending on whether they are humid or arid.

Baumgartner & Reichel (1975) calculated the water balance for the Earth and presented it in maps. A new model of the water balance has been produced by the Max Planck Institute for Meteorology in Hamburg and made available to the public (◘ Fig. A-47).

According to this, annual precipitation over the world's oceans averages 386.103 km3 and evaporation 469.103 km3, which is about 97.103 km3 more than precipitation. Of the total 469.103 km3 of water evaporated over the oceans, about 40.103 km3 is transported to land. This amount is returned to the oceans by surface and subsurface water flows (40.103 km3). The major portion of precipitation over the mainland comes from the small water cycle (81.103 km3) through evapotranspiration (ET). The sum of ET over the mainland (81.103 km3) and water vapour transport from the oceans to the mainlands (40.103 km3) gives the total annual precipitation (121.103 km3) over the mainland. The measured data of precipitation and evaporation are in good congruence with the data resulting from the model calculations (► Fig. A-47).

◘ **Fig. A-47** Scheme of the hydrological cycle on Earth with the measured and modelled proportions of precipitation, runoff and evaporation of various systems on Earth. (source: Max Planck Institute for Meteorology, Hamburg: [https://t1p.de/0dqz](https://t1p.de/0dqz%22%20%5Ct%20%22_blank)).

In general, the water conditions of a biogeocenosis, a specific area, an entire landscape section or an entire country can be quantified with the water balance equation. According to this equation, the input variable into the system is precipitation N.

**Water balance equation of an ecosystem:**



N = Precipitation

I = Interception

A = Surface runoff

E = Evaporation

T = Transpiration

S = Infiltration

ΔW = stored water supply in the system

The discharge can take place in different ways, on the one hand by evaporation **E** (from the soil) and by transpiration **T (**by the plants), in addition there is interception **I** (superficial moistening of the leaves and subsequent evaporation), furthermore discharge is possible by surface runoff **A** and by infiltration **S** into the soil (underground runoff to groundwater). The soil itself, or the entire ecosystem, has a certain water reserve as a storage quantity **ΔW**, which can increase (+) or decrease (-).

Often **E** and **T** together (with **I**) are referred to as evapotranspiration (**ET**). The surplus water that is not released back to the atmosphere by **ET** benefits groundwater and thus the feeding of neighbouring springs, and ultimately the formation of a stream and river system (intact water cycle).

At sites affected by groundwater, allochthonous water can be added to the system, so that in addition to precipitation, upwelling water is also added and the loss variable of leachate is reversed.

In arid areas, most of the water will be lost to **ET**, and there will be no groundwater recharge (arid areas, with interrupted water cycle).

Of particular importance for survival in arid regions is the development of a sufficiently large root system. If the rootable soil volume is large enough, perennial plants may be able to survive several dry years if water is accessible in deeper layers. Some plants with particularly deep roots even seem to be able to lift this water ("hydraulic lift") in such a way that even other plants can benefit from it, as Caldwell et al. (1991) were able to show.

The drier the area, the greater the rooted soil volume of olive trees, for example. In Tunisia, from farmers' experience, the distances between planted trees are much greater in the south than in the north (◘ Fig. A-48).

◘ **Fig. A-48** In Tunisia, farmers increase the distances between the individual trees in olive plantations from north to the south of the country so that a sufficient crop yield is achieved despite the drier climate and lower amount of available water (Photo: Breckle).

For the large-scale landscape differentiation of the Earth into zonobiomes, the determination of the humid and arid months as an expression of the **hygric growing season** over a sufficiently long time series is an effective tool. The hygric growing season is defined by the length of the moisture-determined growing season expressed by the number of humid months (isohygromenes) (Lauer & Rafiqpoor 2002). A month is considered humid if, in it, the precipitation amount at least reaches (N = ET) or exceeds (N ≥ ET) the potential evapotranspiration (ET) of the site flora. The methodological principles of calculating potential evapotranspiration are discussed in detail in Lauer & Rafiqpoor (2002). The water balance in temporally resolved form gives a 12-scale of the number of humid months from perarid (12 arid months) to perhumid (12 humid months). These can be divided into 6 humidity levels of ecological relevance: 0 = perarid, 1-2 = arid, 3-4 = semiarid, 5-6 = semihumid, 7-9 = humid, 10-12 = perhumid. The spatial representation of the lines of equal length of the hygric vegetation period (isohygromenes) gives a differentiated picture of the hygric climate on Earth (◘ Fig. A-49).

◘ **Fig. A-49** Length of the hygric growing season on Earth (isohygromenes).

2.5 **The Earth's eco-climates (climate classification)**

Lauer & Rafiqpoor (2002) developed a system of ecoclimate classification in which they used the length of the thermal and hygric growing season on a monthly basis for climate typing of the Earth. They analyzed data from over 2000 climate stations and designed maps for isothermomenes (length of thermal growing season on a monthly basis) (► Fig. A-44) and isohygromenes (length of hygric growing season on a monthly basis) (► Fig. A-49). From the intersection of these two maps, they developed a map of Earth's eco-climate types whose boundaries can be clearly determined empirically (◘ Fig. A-50). The solar radiation belts were used to divide the major climate zones. This is done using the threshold values of the annual daylength variation, which is determined by latitude. Based on this clear mathematical division of the earth, five main climate zones result [tropics (A), subtropics (B), cool mid-latitudes (C), cold mid-latitudes (boreal zone D), polar regions (E)]. They provide the basic framework for the division of the Earth into zonobiomes, which are the basic concept of this book.

From the comparison of the ecoclimate types (► Fig. A-50) and the zonobiomes on Earth (► Fig. C-22 to Fig. C-27), there is clear congruence in the zonation of the two systems:

ZB I = Megatherm, perhumid climates of the inner tropics

ZB II = Megatherm, humid climate of the outer tropics

ZB III = Megatherm-macrotherm, perarid desert climates of the marginal tropics and subtropics

ZB IV = Macrotherm, humid-semihumid climates of the Mediterranean winter rainareas

ZB V = Macrotherm, perhumid-humid subtropical climates (mostly) of the eastern sides of the continents

ZB VI = Mesotherm, perhumid-semihumid climates of the cool mid-latitudes

ZB VII = Mesotherm, semi-arid and arid climates of the cool mid-latitudes

ZB VIII = Microtherm, perhumid-semihumid climates of the cold mid-latitudes

ZB IX = Oligotherm, perhumid-semihumid climates of the subpolar and polar regions

These zonobiomes can further be differentiated into zonoecotones and biomes according to the degree of continentality and small-scale regional differences, and into different orobiomes according to altitude differences. All these units can be found on the map of the Earth's ecoclimates (► Fig. A-50).

◘ **Fig. A-50** The Earth's eco-climates.

2.6 **Climate representation: Thermo-isopleth diagrams, ecological climate diagrams**

Temperature can be recorded in the form of maxima and minima, mean and duration values, and as diurnal and annual variations, and can be represented in diagrams and maps, from which the typical climatic characteristics of the individual zonobiomes can be identified. However, the thermal climate of an area is most easily read off from thermo-isopleth diagrams based on daily and annual fluctuations in air temperature (Troll 1943).

Thermoisopleth diagrams (◘ Fig. A-51) provide a quasi-three-dimensional picture of the thermal conditions at a climate station. In a thermoisopleth diagram, the months of the year are plotted on the abscissa and the hours of the day are plotted on the ordinate and connected with lines of equal temperature (to form an isopleth diagram). The graph is extremely informative. Not only the individual values of the diurnal and the annual cycle, but also the fluctuation magnitude (range) and the relationship of the fluctuation values to each other can be made visible through the curve. When comparing individual diagrams, the affiliation to corresponding climate zones is visible at a glance. They are thus suitable instruments for characterising the thermal homoclimates (i.e. climates similar in type) on Earth.

In the tropical and bordering tropical, maritime regions, the isolines show a stretching in the direction of the abscissa (► Fig. A-51: Belem). This means that here the seasonal variations remain only slight, since only slightly different temperature values occur at a given hour on each day of the year (diurnal climate). The diagrams of extratropical stations, on the other hand, show a stretching of the isolines in the direction of the ordinate (► Fig. A-51: Helsinki, Irkutsk, Eismitte), which indicates greater seasonal fluctuations (seasonal climate). The dense stratification of the lines, especially in the polar regions (► Fig. A-51: Eismitte), reflects the rapid change in temperature during the day or in a season, revealing the degree of continentality of an area. Images of stations in the subtropical transition regions (► Fig. A-51: Cairo) make it clear that the course of the curve in summer and during the day is more similar to the tropical type, whereas in winter and at night the basic shape of the curve is more indicative of extratropical conditions.

◘ **Fig.** A-51 Thermopleth diagrams of selected stations in the tropics (Belem), subtropics (Cairo), midlatitudes (Helsinki), continental region (Irkutsk), South Pacific (Macquarie Island), and polar region (Eismitte) (modified from Troll 1943).

The hygrothermal behaviour of the regions can be illustrated most simply with the help of ecological climate diagrams. It is a pictorial representation of the overall climate in the area near the ground. However, such a representation must be clearly arranged, i.e. it must contain only the most important data for ecosystems. These are the temperature and precipitation conditions over the course of a year. Almost 9,000 climate diagrams from meteorological stations all over the world had been already included in the Climate Diagram World Atlas by Walter & Lieth (1960-1967).

The explanation of some typical diagrams is given in ◘ Fig. A-52. The climate diagrams given there are examples of the nine zonobiomes, each from stations at lower elevations, and with an updated lay-out.

In addition, climate diagrams of orobiomes (OB) are shown in ◘ Fig. A-53. OB I with diurnal climate (Páramo) and the other orobiomes II-IX. Orobiome IX (Vostok, in Antarctica), with a mean annual temperature of -56 °C, is probably one of the coldest stations on Earth.

From the climate diagrams not only the temperature and precipitation values can be seen, but also the duration and intensity of a relatively humid and relatively arid season, as well as the duration and intensity of a cold winter and the possibility of the occurrence of late or early frosts.

The schematic representation of the climate diagrams provides the basis for the assessment of the climate in ecological terms. The indication of the aridity or humidity of the seasons is obtained on the climate diagram by applying the ordinate scale 10 °C ≅ 20 mm precipitation. The temperature curve thereby approximately replaces the curve of potential evaporation (whose values are mostly unknown) and can thus be related to the representation of the water balance in comparison with the precipitation curve. The vertical extent of the dotted area, that is, the drought period, is a measure of its intensity, and the horizontal extent is a measure of its duration. The same is true of the humidity area. Gaussen has found the ratio 10 °C ≅ 20 mm rain for the Mediterranean region to be particularly approximate with actual weather conditions. For steppe and prairie diagrams, however, it is expedient to use in addition the 10 °C ≅ 30 mm scale (Odessa, ► Fig. A-52), in order to bring to the representation a dry season which is less extreme than the arid drought season.

The climate diagrams shown in ► Fig. A-52 belong to the following zonobiomes:

**ZB I** (Humid, equatorial diurnal climate):

Yangambi on the middle Congo; Bogor on Java

**ZB II** (Tropical summer rain climate): Harare in Zimbabwe

**ZB III** (Subtropical desert climate): Cairo on the Lower Nile

ZB IV (Mediterranean winter rain climate): Tunis in Mediterranean North Africa

ZB V (Warm temperate climate): Cheju in the south of South Korea

ZB VI (Temperate, nemoral climate with short cold season): Essen in Germany

ZB VII (Temperate semi-arid steppe climate with long dry season and low drought): Odessa at the Black Sea

ZB VIIa (Temperate arid semi-desert climate with pronounced drought): Astrakhan on the lower Volga River

ZB VII (rIII) (Extreme arid desert climate with cold winters): Nukuss in Central Asia

ZB VIII (Cold, temperate climate with very long winters): Arkhangelsk in the boreal taiga zone

ZB IX (Arctic tundra climate with July mean below +10 °C): Karskije Vorota (Vaigatsch Island).

**Fig.** A-52 Explanation of the climate diagrams with typical examples, at the same time examples for the different zonobiomes (see below). Abscissa (horizontal axis): In the northern hemisphere months from January to December, in the southern hemisphere from July to June (warm season is therefore always in the middle of the diagram. Ordinate (vertical axes): Temperature in °C, precipitation in mm. 1 graduation line = 10 °C, or 20 mm precipitation (numbers are often omitted).

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| **The designations and numerical values on the diagrams mean:**a = station (region);b = height above sea level;c = mean annual temperature;d = mean annual rainfall;e = number of observation years (possibly first number for temperature and second number for precipitation);f = observation period;g = geographical coordinates;h = mean daily minimum of the coldest month;i = absolute minimum (lowest measured temperature);j = mean daily maximum of the warmest month;k = absolute maximum (highest measured temperature);l = mean daily temperature variation (for tropical stations).m = curve of mean monthly temperatures;n = curve of mean monthly precipitation (1 scale division = 20 mm, i.e. in the ratio 10 °C = 20 mm);o = relative aridity (drought) for the climatic region in question (dotted in red);p = corresponding to relatively humid season (vertically shaded blue);q = mean monthly precipitation exceeding 100 mm (scale reduced to 1/10, blue area = perhumid season;r = precipitation curve, lowered, in the ratio 10 °C = 30 mm, above horizontal yellow dashed area = relative dry season (only for steppe stations);s = months with mean daily minimum below 0 °C (black) = cold season;t = months with absolute minimum below 0 °C (diagonally shaded), i.e. late or early frosts may occur;u = number of days with mean temperatures above +10 °C (duration of the growing season);v = number of days with mean temperatures above -10 °C.Not all data are available or given for all stations. If they are missing, the corresponding places in the diagram remain empty. |

The arid season (drought season) shown in the climate diagram is to be regarded only as relatively arid in comparison with the humid season of the climate type in question. The temperature curve, which we use instead of the curve of potential evaporation, is not identical with it, but only runs more or less parallel to it. It is an approximation. The more arid or windy (e.g. Patagonia) the climate in question, the more it lags behind the latter in quantitative terms. More precisely constructed hydroclimate diagrams have been compiled by Henning (1994), and ecological by Lauer et al. (1996) and Lauer & Rafiqpoor (2002). In absolute terms, the greater the aridity of the overall climate, the more arid the season on the ecological climate diagram; that is, an arid season on the climate diagram of a station in the steppe, for example, is not as extreme as that of a Mediterranean station or even one in the Sahara. This is favourable from an ecological point of view, because the drier the climate in which plants are native, the more their sensitivity to drought diminishes. For the species of the tropical rainforest, even a non-perhumid month (less than 100 mm of rain) is relatively dry; the xerophytes growing on dry sites in Central Europe would be more likely to be classified as hygrophytes in the deserts.

We will include the corresponding diagrams when discussing the vegetation areas, as this will allow us to avoid long tables and thus provide a quick overview.

The climate diagrams are particularly suitable for finding out homoclimates, which is extremely tedious when using extensive climate tables.

One only needs to compare the given climate diagram with those in the Climate Diagram World Atlas from areas where homoclimates are suspected. ◘ Figure A-54 shows the homoclimates of Karachi (Pakistan) from zonobiome III (slight transition to ZB II) and of Bombay (very typical of ZB II) in another part of the world. Knowledge of homoclimates is very important for new crop introductions in areas where they are not yet known.

If one looks at climate diagrams of mountain regions, then these are very similar to the diagrams of the surrounding lowlands over the course of the year; however, the temperature curve is more or less lowered depending on the elevation, the precipitation can often be increased. As a result, the aridity usually decreases significantly with increasing altitude. Corresponding mountain stations of the respective zonobiomes are shown as examples in Fig. A-53 (for more details see p.).If you want to get a quick overview of the climate structure of larger areas, you can use climate diagram maps. These are obtained by inserting the climate diagrams from the Climate Diagram World Atlas in the geographically correct position on large wall maps of individual continents or countries. The clarity is increased if the area of the drought periods in the diagram is marked in red and that of the humid periods in blue. Then the division can be overlooked at a glance. Such climate diagram maps of all continents in large format (black and white) have been published elsewhere (WALTER et al. 1975). Here, as an example, we can only bring the climate diagram map of Africa to ◘ Fig. A-55 in small format with only a few climate diagrams (of Africa, the World Atlas contains over 1,000 diagrams). Climatic diagram maps of selected regions are also available on the web (www.s.breckle.name/KlimaDiagrKarten/).

◘ **Fig. A-53** Examples of mountain stations of the different oribiomes: OB I: Páramo de Mucuchies in Venezuela; OB II: San Antonio de Los Cobres in the Peruvian Puna; OB III: Calama in the northern Chilean Desert Puna; OB IV: Cedres in Lebanon; OB V: Hotham Heights in the Snowy Mountains (Australia); OB VI: Zugspitze in the northern Alps; OB VII: Pikes Peak in the Rocky Mountains above the Great Plains of North America; OB VIII: Aishihik in southern Alaska; OB IX: Vostok on the ice cap of Antarctica.

◘ **Fig. A-54** Homoclimates of the two stations Karachi (Pakistan) and Bombay (India) in other continents.

◘ **Fig. A-55** Example of a climate diagram map with 66 stations. Zonobiomes from north to south: IV-III-II-I-III-IV, but north of the equator the east is relatively too dry (monsoon), whereas south is relatively too humid (SE trade winds).

3 **Literature**

Adriano D.C. 1986: Trace elements in the terrestrial environment. Springer/New York 533pp.

Barthlott, W., Szarzynski, J., Vlek, P., Lobin, W. et al. 2009: A torch in the rainforest: thermogenesis of the Titan arum (Amorphophallus titanum). Plant Biol. 11 (4): 499-505. Doi: 10.1111/j.1438-8677.2008.00147.x

Baumgartner, A. & Reichel, E. 1975: Die Wasserbilanz. Niederschlag, Verdunstung und Abfluss über Land und Meer sowie auf der Erde im Jahresdurchschnitt. Oldenburg-Verlag, München

Breckle, S.-W. 1976: Zur Ökologie und zu den Mineralstoffverhältnissen absalzender und nichtabsalzender Xerohalophyten. Habil.-Schr. Bonn, 170 S., Cramer (Diss. Bot.)

Breckle, S.-W. 1986: Studies on halophytes from Iran and Afghanistan. II. Ecology of halophytes along salt gradients. Proceed. Roy. Soc. Edinburgh 89B: 203-215

Breckle, S.-W. 2002: Walter’s Vegetation of the Earth. The Ecological System of the Geo-Biosphere. Springer Verlag, Heidelberg, 527 p.

Breckle, S.-W. 2002b: Salinity, halophytes and salt affected natural ecosystems. In Läuchli A., Lüttge U. (eds.) Salinity: Environment-Plants-Molecules. Pp. 53-77. Kluwer/Dordrecht

Breckle, S.-W. 2009: Is sustainable agriculture with seawater realistic? In: Aschraf, M., Ozturk, M. & Athar, H.R, (eds.): Tasks for Vegetation Science, Vol. 44: 187-196

Breckle, S.-W. 2021: Bodenversalzung (Aridität und Fehler bei der Bewässerung, Meeresspiegelanstieg). In: Lozan, J., et al.: Warnsignal Klima: Böden und Landnutzung. Hamburg (in press)

Caldwell, M.M., Richards, J.H. & Beyschlag, W. 1991: Hydraulic lift: ecological implications of water efflux from roots. In: Atkinson, D. (ed.): Plant root growth - an ecological perspective. Blackwell, Oxford

Cheeseman, J.M. 2015: The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. New Phytol. **206**: 557-570

Flowers, T.J., Yeo, A.R. 1995: Breeding for salinity resistance in crop plants: where next? Aust. J. Plant Physiol. **22**: 875-884

Henning, I. 1994: Hydroklima und Klimavegetation der Kontinente. Münstersche Geogr. Arb. 37: 144 S.

Hillel, D. 1980: Applications of soil physics. Acad. Press, New York

Ibrahimova, U., Kumari, P., Yadav, S. et al. 2021: Progress in understanding salt stress response in plants using biotechnological tools. J. Biotechn. **329**: 180-191

Junghans, H. 1969: Sonnenscheindauer und Strahlungsempfang geneigter Ebenen. Abhandlungen des Meteorologischen Dienstes der DDR 85, Berlin.

Kearney, T.H., Briggs, L.J. et al. 1914: Indicator significance of Vegetation in Tooele Valley, Utah. J. Agric. Res. 1: 365-417

Kuntze, H., Roeschmann, G. & Schwerdtfeger, G. 1994: Bodenkunde. 5. Aufl., Ulmer, Stuttgart 424 S.

Larcher, W. 1980: Klimastress im Gebirge – Adaptationstraining und Selektionsfilter für Pflanzen. Rheinisch-Westfälische Akad. Wiss., N 291: 49-88

Larcher, W. 2001: Ökologie der Pflanzen. 5. Aufl., Ulmer, Stuttgart

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

Lauer, W. & Frankenberg, P. 1986: Eine Karte der hygrothermischen Klimatypen von Europa. Erdkunde 40: 85-94

Lauer, W. & Rafiqpoor, M.D. 2002: Die Klimate der Erde – eine Klassifikation auf der ökophysiologischen Grundlage der realen Vegetation. Erdwissenschaftliche Forschung, Bd. XL. Franz Steiner Verlag, Stuttgart

Lauer, W., Rafiqpoor, M.D. & Frankenberg, P. 1996: Die Klimate der Erde. Erdkunde 50: 275-300

Lerch, G. 1991: Pflanzenökologie. Akad.-Verlag, Berlin 535 S.

Levitt, J. 1972: Responses of plants to environmental stresses. Vol. 1+2; (1980: 2nd. edit.) Acad. Press, New York 497 + 606 p.

Marschner, H. 1986: Mioneral nutrition of higher plants. Acad. Press Harcourt/London 674 pp.

Munns, R. 2005: Genes and salt tolerance: bringing them together. New Phytologist **167**: 645-663

Popp, M. 1995 Salt resistance in herbaceous halophytes and mangroves. Progress in Botany 56: 416-429

Scheffer, P. & Schachtschabel, P. 1992: Lehrbuch der Bodenkunde. Enke, Stuttgart 491 S.

Schmithüsen, J. 1956: Die räumliche Ordnung der chilenischen Vegetation. Bonner Geogr. Abh. 17, 86 S.

Schönwiese, C.-D. 1994: Klimatologie. UTB1793, Ulmer, Stuttgart 436 S.

Tischler, W. 1984: Einführung in die Ökologie. 3. Aufl. Fischer, Stuttgart, 437 S.

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

Waisel, Y. 1972: Biology of halophytes. Acad. Press New York/London 395pp.

Walter, H. 1960: Standortslehre. 2. Aufl., Ulmer, Stuttgart. 566 S.

Walter, H. 1975: Über ökologische Beziehungen zwischen Steppenpflanzen und alpinen Elementen. Flora 164: 339-346

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

Walter, H. & Kreeb, K. 1970: Die Hydratation und Hydratur des Protoplasmas der Pflanzen. Proto-plasmatologia, Bd. II C 6, Wien. 306 S.

Walter, H. & Lieth, H. 1967: Klimadiagramm-Weltatlas. Fischer, Jena

Wani, S.H., Kumar, V., Khare, T. et al. 2020: Engineering salinity tolerance in plants: progress and prospects. Planta **251**: 76, 29pp.

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

White, I.D., Mottershead, D.N. & Harrison, S.J. 1992: Environmental Systems. Chapman & Hall. London 616 p.