I General part

Part C - Ecological systems and ecosystem biology

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[IMAGE]

Rock wall with an intricate mosaic of waterfalls and remnants of tropical rainforest (Zonoecotone I/II) near Helbourg, Réunion (Photo: Breckle)

1 **Geo-biosphere and hydro-biosphere**

The biosphere comprises the thin layer on the earth's surface in which all life phenomena take place, i.e. on land the lowest layer of the atmosphere, as far as the living organisms permanently reside in it and the plants protrude into it, as well as the rooted layer of the lithosphere, which is called the soil (pedosphere). Besides these, we find life in all waters down to the deep sea. But in this aqueous medium the circulation of matter takes place in a different way from that on land, and the organisms are so different (plankton, for example) that the ecosystems must be treated separately. We therefore divide the biosphere into:

**1.** Geo-biosphere, comprising the terrestrial ecosystems, and

**2.** Hydro-biosphere with the aquatic ecosystems that hydrobiology (and also oceanography) deals with.

Today, numerous results from other sciences are required to capture the essential processes in the biosphere. The observation of large-scale ecological relationships is only possible through interdisciplinary evaluation of results; accordingly, ecology has become a very interdisciplinary science today, reaching beyond the original field in biology, as shown schematically in ◘ Fig. C-1.

2 **The hydro-biosphere**

The hydrosphere comprises all the solid, liquid and gaseous water occurring on Earth from glaciers and ice caps, oceans, lakes, rivers, soil and groundwater, as well as the water vapour in the atmosphere. It is thus a component of the geo-, litho-, bio-, pedo- and atmosphere.

The earth is covered to 71% by water, nevertheless the hydrosphere is to be treated here in this framework only very briefly.

A quantitative overview of the distribution of water on the globe (◘ Table C-1) among the various compartments shows that only 3.5% of all water occurs on the entire mainland (► Table C-1). Most of the water is ocean saltwater. The amounts of water that make up the lakes and marshes are also vanishingly small in total. The amount of water in the atmosphere, despite its short residence time of a few days, exceeds that of all the water bound up in living things in the biosphere by a factor of thirteen.

If only the fresh water is taken into account,  of it is bound as ice. Frozen water, i.e. ice, occurs in large quantities in the polar ice caps, in the permafrost soils of the subpolar regions and in the glaciers of the high mountains on Earth. A distinction is made between compact ice, which occurs in various forms in the various compartments (cryosphere), and the less permanent snow, which may be considered separately as chionosphere. The distribution over specific parts of the Earth is given in ◘ Table C-2. Here, the very large imbalance between land and sea is expressed in the distribution on the two hemispheres, which is ultimately also reflected again in the distribution of the zonobiomes.

**◘ Fig. C-1** The individual spatial sections on Earth and the field of ecology in the context of other sciences.

3 **Division of the geo-biosphere into zonobiomes**

Our object of study is only the geo-biosphere, which is the main habitat of man and therefore of particular interest to us. For its subdivision, the large-scale climate lends itself as a primarily independent environmental factor. This is because both soil formation and vegetation depend on it, it is still hardly (or only slightly, but increasingly) changed by humans and can be recorded perfectly everywhere by the increasingly dense network of meteorological stations (on the principles of subdivision, cf. Walter 1976 and Lauer & Rafiqpoor 2002), see also p. …… .

Table C-1 Quantitative data on the hydrosphere in a global perspective (data from Schönwiese 1994)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Area | Area (106 km2) | Volume (106 km3) | Percentage of the earth's total water volume | Percentage in relation to fresh water |
|
| World Wide Sea | 361.30 | 338.00 | 96.50 | - |
| Mainland | 148.40 | 47.97 | 3.50 |  |
| Groundwater | 134.80 | 23.40 | 1.70 |  |
| thereof fresh water | (134.8) | 10.53 | 0.76 | 30.10 |
| Soil moisture | 82.00 | 0.015 | 0.001 | 0.05 |
| Polar ice, snow | 16.23 | 24.064 | 1.74 | 68.70 |
| Antarctica | 13.98 | 21.60 | 1.56 | 61.70 |
| Grassland | 1.80 | 2.34 | 0.17 | 6.68 |
| Mountain | 0.224 | 0.041 | 0.003 | 0.12 |
| Permafrost | 21.00 | 0.300 | 0.022 | 0.86 |
| Freshwater lakes | 1.236 | 0.091 | 0.007 | 0.26 |
| Saltwater Lakes | 0.822 | 0.085 | 0.006 | - |
| Swamps, bogs | 2.683 | 0.0115 | 0.008 | 0.03 |
| Watercourses |  | 0.0021 | 0.0002 | 0.006 |
| Water of the atmosphere | (510) | 0.0129 | 0.001 | 0.04 |
| Biologically bound water | (510) | 0.0011 | 0.0001 | 0.003 |

Table C-2 Quantitative data on the cryosphere and chionosphere (after **Schönwiese** 1994)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Area | Area (106 km2) | | Volume (106 km3) | Sea level equivalent (in m)\* |
| Landis Land ice | 14.44 | | 32.44 | 81.2 |
| Antarctica | 12.2 | | 29.32 | 73.3 |
| Greenland | 1.7 | | 3.0 | 7.6 |
| Glacier | 0.54 | | 0.12 | 0.3 |
| Permafrost (without Antarctica) | | | | |
| Constantly | 7.6 | | 0.03 | 0.08 |
| Maximum | 17.3 | | 0.07 | 0.18 |
| Sea ice | | | | |
| Arctic | Winter | 14.0 | 0.05 | - |
| Summer | 7.0 | 0.02 | - |
| Antarctic | Winter | 18.4 | 0.06 |  |
| Summer | 3.6 | 0.02 |  |
| Snow | | | | |
| Northern Hemisphere | Winter | 46.3 | 0.002 | Negligible |
| Summer | 3.7 | <0.0001 | Negligible |
| Southern Hemisphere | Winter | 0.85 | Negligible | Negligible |
| Summer | 0.07 | Negligible | Negligible |

\*Potential rise in sea level with complete melting. Data from Schönwiese (1994)

From a climatic point of view, a division of the Earth into zonobiomes should be based on an effective climate classification, i.e. one based on the ecophysiological characteristics of vegetation, because such a climate classification relates to natural vegetation, can best circumscribe the orobiomes, and the ecologist is primarily interested in the climate within the geo-biosphere (Breckle 2011). The climate classification also used here (► Fig. A-50) divides the Earth into five main zones according to the length of the thermal and hygric growing season: A) Tropics, B) Subtropics, C) Cool mid-latitudes, D) Cold mid-latitudes, E) Polar regions.

The climate within the geo-biosphere can be clearly indicated by the ecological climate diagram. It proves to be expedient to further subdivide the very large zone of the mid-latitudes and to combine the subpolar as well as the high-polar to an arctic one. This then results in nine ecological climate zones, which we refer to as Zonobiomes (ZB) in an ecological sense (Walter 1976, Walter & Breckle 1999, Schultz 2008, Olsen & Dinerstein 2002, Wittig & Nikisch 2014), because biome is understood to be a large, climatically uniform habitat within the geo-biosphere. **Humid** refers to a humid (rain-fed) climate, while arid refers to a dry (rain-poor) climate. In the case of double designations, the first refers to summer, the second to winter.

The nine zonobiomes (► Fig. A-9):

ZB I Equatorial ZB with diurnal climate, humid tropical ZB

ZB II Tropical ZB with summer rain, humido-arid tropical ZB

ZB III Subtropical ZB with desert climate, hot arid ZB; sparse rainfall

ZB IV ZB with summer drought and winter rain, arido-humid (Mediterranean) ZB

ZB V Warm temperate (oceanic), humid ZB; mild-maritime ZB

ZB VI Typical temperate ZB with short frost period, nemoral ZB

ZB VII Arid temperate ZB with cold winters, continental ZB

ZB VIII Cold temperate ZB with cool summers and long winters, boreal ZB

ZB IX Arctic including Antarctic, with very short summers, polar ZB.

The zonobiomes are the main large units of the biosphere. In the literature, there are many different models with different names. For the large-scale division into ecological units, the zonobiome division has proven itself. The respective boundaries and size of the transitional areas (zonoecotones) is often a matter of subjective opinion. The two polar ice caps - the Arctic and the Antarctic - are joined by zonobiomes more or less in the shape of a belt around the globe. The difference between the northern and southern hemispheres is considerable due to the unequal distribution of the land mass. It is therefore nonsensical to speak of "anti-boreal", a zone that does not exist in the westerly wind belt of the southern hemisphere - where there is no land, only tiny islands - in contrast to the northern hemisphere, where at this latitude there is almost only land mass with the strongest expression of continentality.

Anti-nemoral should be understood only as the zoogeographic region of the shelf areas of the southern half of the southern continents. After all, no one speaks of the North Desert as an "anti-subtropical" desert or the *Nothofagus* forests of Chile as "anti-nemoral" forests.

The differences between the west and east coasts on the continents are responsible for the wedging out of certain belts or for the small-scale occurrence of the zonobiomes due to the warm or cold ocean currents.

The zonobiomes are clearly defined by climate diagram types; moreover, they correspond largely, if not always, to certain zonal soil and vegetation types, as shown in the overview in ◘ Table C-3.

4 **Zonoecotone**

The climatic zones and thus also the zonobiomes are not sharply delimited from one another, but are often connected by very broad transition zones - the zonoecotones (ZÖ).

Ecotones are, for example, small-scale: a forest with a forest edge is replaced by meadows with a mantle and fringe, or large-scale, for example in Eastern Europe: The deciduous forest gradually merges into the steppe.

In the zonoecotone, both types occur side by side under the same large-scale climatic conditions and are in sharp competition with each other. The decisive factor for the occurrence of one or the other vegetation type is the relief-related microclimate or the soils.

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| Box C-1 Ecotones as transition zones |
| Ecotones are ecological areas of tension; transitional areas in which one vegetation type is more or less gradually replaced by another. |

◘ Table C-3 The soil and vegetation types of the individual zonobiomes

|  |  |  |
| --- | --- | --- |
| Zonobiome (ZB) | Zonal soil types | Zonal vegetation types |
| I | Equatorial brown loams (ferrallitic soils, latosols) | Evergreen tropical rainforest without seasonal change |
| II | Red loams, red earths (fersiallitic soils) | Tropical deciduous forest or savannahs |
| III | Serosemes, syrosemes (grey or red soils, raw soils, saline soils) | Subtropical desert vegetation (rocky landscapes) |
| IV | Mediterranean brown earth (fossil Terra rossa) | Hardwood vegetation (sclerophylls), (sensitive to soil frost) |
| V | Yellow or red forest soils, slightly podsolic | Temperate evergreen forest (lauriphylls), (frost sensitive) |
| VI | Forest brown soils and grey forest soils | Nemoral winter bare deciduous forest (frost resistant) |
| VII | Chernosemes to serosemes (raw soils) | Steppes to deserts with cold winters (frost resistant), short, hot summers |
| VIII | Podsole (raw humus bleaching earths) | Boreal coniferous forests (taiga), (very frost resistant) |
| IX | Humus-rich tundra soils with solifluction (permafrost soils) | Tundra vegetation (treeless) |

◘ Fig. C-2 Horizontal-spatial scales in biology, geography and meteorology. Note the logarithmic scale (modified after Schönwiese 1994).

Fig. C-3 Atmospheric and climatological phenomena in the space-time diagram. Note the logarithmic axes (modified after Schönwiese 1994).

Thereby either a diffuse interpenetration of the two types or a mosaic-like arrangement comes out. First, one type is more strongly represented, then the two balance each other out, until the second becomes more and more predominant and the first disappears completely, with which the new zonobiome begins.

The zonoecotones are named according to the zonobiomes that connect them, i.e. we distinguish the zonoecotones: ZE I/II, ZE II/III, ZE III/IV, ZE IV/V, etc.

Triangular zonoecotones can also occur when three zonobiomes meet (e.g. Pannonian Plain: ZE VI/VII/IV). We treat the most important zonoecotones in short sections of their own at the end of the corresponding zonobiomes.

The geographic distribution of the individual zonobiomes and zonoecotones can be seen from the schematic map of the world (► Fig. A-9) or from the maps for the individual continents ► Fig. C-22 to ► Fig. C-26.

5 **Ecological systems**

On the basis of what we have said so far, we can draw up a scheme for the ranks of both the major and minor ecological units. In addition to the main climatic series, the biomes modified by mountains on the one hand (OB) and by specific soil conditions on the other hand (PB) are thereby marked as corresponding orographic or pedological subsidiary series. This hierarchical scheme of spatial units of ecosystems is used as a basis for the division of the geo-biosphere.

In this context, it should be recalled here once again the very different scales that one has to take care of when characterizing ecosystems (◘ Fig. C-2). This applies not only to the spatial scales of the structures, but also to the temporal scales. In particular, it is atmospheric or meteorological phenomena that determine the scale size in this context. In ► Fig. C-2, the ranks of ecological systems used here are contrasted with those of meteorological processes. Because of the huge differences in scale, such a comparison can only be made on a logarithmic scale. Secondly, this also applies to the time scale on which certain phenomena occur (◘ Fig. C-3).

For the treatment of the individual biomes, the near-ground air layers with their dynamics and the atmospheric-biospheric interactions play the decisive role, as Geiger already pointed out in 1927.

6 **Orobiomes and pedobiomes**

The geo-biosphere is not only structured horizontally, but also vertically by the mountains. It must therefore be viewed three-dimensionally. The mountains stand out climatically from the climate zones and are therefore treated separately from the zonobiomes. We refer to them as orobiomes (OB).

It is characteristic for all orobiomes that the mean annual temperature decreases with altitude. This decrease is about as large per 100 m difference in elevation as that in the Euro-North Asian plain at a distance of 100 km in the direction from south to north. Therefore, the elevational zones in the mountains are about 1000 times narrower than the vegetation zones in the plain from south to north.

Certain similarities of the elevational belts and of the vegetation zones of the higher latitudes are noticeable in Europe and North America on cursory observation, but differences are always present. For, except for the decrease in temperature and the shortening of the growing season with elevation, the mountain climate is different from that on the plains. For example, the length of the day, like the position of the sun, does not change with elevation; on the other hand, the length of the day in summer increases from south to north, while the altitude of the sun decreases at noon. Direct solar radiation increases with altitude, while diffuse radiation decreases. In the plains, the opposite is true in a northerly direction. Precipitation usually increases very rapidly with elevation in the mountains, but is low in the Arctic region.

In addition, the two flanks of a mountain range are almost never symmetrical, but also climatologically different, for example due to foehn effects. As a result, for physical reasons (◘ Fig. C-4a), the temperature gradient is also no longer the same, because moist-adiabatic and dry-adiabatic heating (cooling) differ energetically. As the air cools due to uplift (and volume expansion as atmospheric pressure decreases), the dew point is eventually reached; this is the condensation level at which clouds form ('cloud forest') and moisture 'rains out'. On the other side of the mountains, when there is only dry-adiabatic heating as the air sinks (with pressure rising), the air is ultimately warmer and drier at the same valley level: Foehn effect (◘ Fig. C-4a,b), caused by the released heat of condensation (2.26 MJ●kg-1, ► physical quantities) as the air rises.

Each mountain range within a zonobiome is an ecological unit with a typical sequence of elevational zones (belts), the belts of which are generally referred to as colline, montane, alpine and nival. However, they vary considerably in detail depending on the zone in which the mountain range is located. For example, the elevational belts of mountains in zonobiome I, IV or VI have hardly anything in common.

The further subdivision of the orobiomes is therefore according to the zonobiomes to which they belong. We therefore speak of orobiome I, orobiome II, etc. Furthermore, uni- inter- and multizonal orobiomes (mountains) are distinguished, depending on whether they lie within a zonobiome or between two zonobiomes or extend through many, such as the Urals (from IX to VII) or the Andes (from I to IX). Interzonal mountains are the Alps, the Caucasus, or the Himalayas. They are usually sharp climatic boundaries and the elevational belts on the northern and southern margins must be treated separately. In the case of a multizonal mountain range, it is necessary to divide the same according to the zones into separate sections with particular altitudinal sequences. The Andes are both multizonal and interzonal (west and east slopes are different). The elevational belts are also different for inner mountain valleys with low precipitation and continental conditions (intra-mountain elevational belts).

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| Box C-2 Orobiomes and the elevational belts of the mountains |
| Orobiomes are mountain habitats that are structured according to elevational belts. The individual elevational belts are also referred to as hypsozonal or orozonal vegetation. It is the third dimension that stands out from the associated zonobiome. |

Fig. C-4 Scheme of the Foehn effect. On the windward side, the air masses are lifted (A), then clouds form (B), possibly with precipitation. On the lee side (C) there is warming, dryness and turbulence. The warming is due to the difference between the moist-adiabatic temperature gradient (B) (heat of condensation) during uplift and the dry-adiabatic gradient (C, A) during sinking (with additional radiation in clear air) (modified after Schönwiese 1994). The photo on the right shows the distinct condensation level on the windward side of the mountains in the Eastern Alps (photo: Breckle).

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| Box C-3 Altitudinal and climatic zones |
| Altitudinal zones in the mountains are only superficially a short-circuited repetition of the planetary vegetation zones in the plains toward the poles. |

Not only do the orobiomes stand out from the zonobiomes, but certain areas with extreme soils and azonal vegetation also behave differently. We refer to them as pedobiomes (PB), that is, habitats tied to specific soils. Soils are strongly modified by humans only where soil erosion, i.e. removal of the upper soil layer or the entire soil, has been caused, or where the soil has been processed by agriculture or built over. The large-scale climate affects vegetation unchanged only on the euclimatopes (called "plakor" in Russian), i.e. on flat surfaces with soils that are not too heavy and not too light, so that precipitation does not run off superficially but penetrates into the soil and is retained by it as adhesive water, i.e. does not sink too quickly to the groundwater, it is thus fully available to vegetation. This is not the case with extreme calcareous soils, they are too dry and at the same time too warm biotopes compared to the large-scale climate. On the other hand, the soils may contain harmful substances, such as salts (NaCl, Na2SO4), or the soils are extremely poor in nutrients, so that the vegetation also deviates from the normal of the zonobiome. The vegetation of the pedobiome, which is less influenced by the large-scale climate, but much more by the soil and therefore can occur in almost the same formation on the same soils in several zones, we call azonal vegetation.

The pedobiomes are subdivided according to the soils that are typical for them: Lithobiomes (stony soils), Psammobiomes (sandy soils), Halobiomes (saline soils), Helobiomes (marsh or swamp soils), Hydrobiomes (soils covered with water), Peinobiomes (deficient or nutrient-poor soils, from peine in Greek = hunger, lack), Amphibiomes (= alternating moisture soils) and others.

Pedobiomes can often occupy vast areas, for example, the lithobiome of the basalt covers in Idaho (USA), the psammobiome of the southern Namib, the Rub-al-Khali in Saudi Arabia, or the Karakum Desert in Central Asia with 35,000 km2, the helobiome of the Sudd marsh on the Nile (150,000 km2), the marshlands of western Siberia (over 1 million km2, ► Fig. K-19). Their ecology must also be treated separately from that of the zonobiomes.

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| Box C-4 What are biomes? |
| Biomes are habitats that correspond to a distinct uniform landscape. |

7 **Biome**

By biome (without prefix) we mean the basic unit of large ecological systems.

Biomes are either subunits of zonobiomes (◘ Fig. C-5) or belong to specific orobiomes or pedobiomes, for example, the central European deciduous forest is a biome of zonobiome VI, Kilimanjaro is a biome of orobiome I, the Salt Desert in Utah (USA) is a biome of pedo-halobiome VII, etc.

In this global overview, biomes are mainly treated as the smallest units of a region.

In Anglo-American literature, the term "biome" is used much more broadly and less sharply defined.

8 **Small units of the ecological system: Biogeocenes and synusia**

If one has made a global classification of the entire land surface of the earth within the nine zonobiomes into the next smaller units (biomes), then one can subdivide these in each case according to the state of knowledge into smaller units.

For the delimitation of small ecological units, it is most appropriate to start from vegetation units. In a limited, landscape-geographically uniform area corresponding to a biome, even slight differences in water and soil conditions are important for the formation of vegetation and thus of ecosystems. This is how the typical ecosystem mosaic of a landscape is formed. It is hardly possible to directly measure the decisive environmental factors, which exhibit constant seasonal changes, and to record their interaction. In contrast, we can assume that the natural vegetation, which is in dynamic equilibrium with its environment, reflects the effect of the environmental factors in an integrating manner. Even small differences in an environmental factor cause a qualitative or at least a quantitative change in the composition of the vegetation cover.

However, since human interventions are now evident almost everywhere, to a greater or lesser extent, caution is called for. It is necessary to carefully distinguish the effects of natural and anthropogenic factors through a critical analysis and, in the case of the latter, also to take into account human interventions in the past.

In forest communities, human interventions have an effect even after centuries (clear-cutting, type of regeneration, grazing, litter use, etc.). Although it is often believed that the herb layer in the forest is better suited for the assessment of natural conditions, it depends to a particularly high degree on the composition and structure of the tree layer (shading, higher competitive strength of tree roots, leaf litter) and roots less deeply than the trees, so that only the upper soil horizons are decisive for it. Any change in the tree layer by humans also affects the herb layer. Even the removal of old hollow trees and the trunks decaying on the ground is a serious intervention in the ecosystem.

In densely populated areas, however, we will have to accept the fact that only human-influenced ecosystems are present.

The position of the biogeocenosis in the size hierarchy of ecological systems is shown in **► Fig. C-5.**

In an ecosystem, the material cycle, energy flow and phytomass as well as production are mainly determined by the **dominants,** in the forest, for example, by the dominant tree species. Character species that are rare and occur in few specimens may have indicator value for community recognition, but they may not exert the slightest influence on the ecosystem. Therefore, ecosystem research must demand consistency of dominants within an ecosystem type.

Actually, the delimitation of plant communities in the field has to be done after thorough orientation about the prehistory of the individual stands and after exact exploration of the whole area as well as considering the site conditions and the soil profile down to the lower limit of rooting. The ecologist can only examine real (usually heterogeneous) stands and not the abstractly defined associations (plant communities) of plant sociology.

The biogeocene is the basic unit of ecosystems, but not their smallest unit. Within a biogeocene, one can distinguish a number of **synusia.** These are '**working communities**'of species with similar development and ecological behaviour. However, we must not call the synusia ecosystems; for they are only subsystems that do not have their own material cycle. They rather fit into the material cycle of the whole ecosystem, and the production of the synusia is only a small part of the total production of the ecosystem; it is, however, of importance because the turnover in the synusia is usually much faster than in the whole ecosystem.

A typical example of synusia are the different species groups with a similar development rhythm and the same demands on environmental factors, such as the spring geophytes of the deciduous forest (Allium ursinum, Corydalis, Anemone, Ficaria and others), which take advantage of the light phase on the forest floor before foliage emerges (◘ Fig. C-6), or the herbs that persist during the shade phase in summer, or the herbs with evergreen leaves. Synusia of lower plants are the lichens on the tree trunks (◘ Fig. C-7) or the mosses at the base of the trunks (◘ Fig. C-8).

Between the biomes on the one hand and the biogeocenes on the other, there is a large gap that must be filled by units of intermediate rank. These are biogeocene complexes that often coincide with certain landforms and are based on a common genesis, or are linked by dynamic processes. As an example, we mention a biogeocene series on a slope with lateral transport of matter (often with a soil catena, i.e. a sequence of certain interdependent soil types) or lawfully arranged biogeocenes in a river valley or in a basin without drainage, etc. One can also think of biogeocenic complexes with biogeocenes that follow one another in time, as in secondary succession, or biogeocenes that belong side by side to an ecological series that arises in the presence of a constantly changing site factor (decreasing water table or increasing soil depth), etc. The spatial extent of such biogeocenic complexes can be very different. The designations for the individual types diverge greatly. We will content ourselves with using the neutral term, biogeocene complexes.

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| Box C-5 Biogeocene as the basic unit of ecosystems |
| The basic unit of the smaller ecosystems is the biogeocoenosis (short: biogeocene). It corresponds to a concrete plant community in the range of an association, it is so to speak the walkable ecosystem with for example 20 × 20 m size. |

◘ **Fig. C-5** Scheme of the hierarchical organization of the ecological systems of the geo-biosphere.

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| Box C-6 Real and theoretical plant communities |
| The plant community (→ biogeocene as a real spatial unit) is something different from the plant association (→ theoretically defined construct), the Association as a basic syntaxonomic unit of plant communities - it is a type, the overlying type categories are: Alliance, Order, Class. |

◘ Fig. C-6 Spring geophytes in a deciduous forest in the Baybach Valley in the lower Moselle Valley that is not yet green. Before the forest becomes green, the spring geophytes (here Corydalis cava) take advantage of the light phase in the forest floor and can complete their entire generative cycle until the forest is fully green (photo: E. Fischer).

◘ Fig. C-7 Lichens on a tree trunk as special synusia (photo: Rafiqpoor).

◘ Fig. C-8 Mosses grow on tree trunks and stones, especially in forests, as the forest floor between the trees becomes covered with a thick layer of dead leaves; eastern slope of Mt. Kinabalu on Saba, Malaysia (photo: Rafiqpoor).

All ecological units are real. The ecologist is only able to carry out his measurements and studies exclusively on real ecosystems and not on abstract units. Only sufficiently extensive real data collection can serve to formulate theoretical models. These summaries, drafted at a desk on the basis of experience gained, must be based on certain assumptions. They will therefore never fully correspond to real ecosystems, but their clarity and comparative view can facilitate our understanding of ecosystems and the processes taking place within them. Provided that they are based on sufficient experience and constant evaluation, they can even enable predictions to be made about future developments (Wissel, oral comm.).

9 **Ecosystem biology and the nature of ecosystems**

Having pointed out the small ecological units, we need to learn more about the principal structures and processes in ecosystems. Here, one often takes as an example a uniform deciduous forest stand of zonobiome VI, which has a manageable size and is easily 'walkable'.

If the stand comprises a very specific, limited and homogeneous society, for example a forest, a bog, etc., then it is more appropriately called a biocoenosis. A unit of plants and animals, including the rooted soil and the air layer near the soil, into which the plant organs project, is called a biogeocoenosis (in short: biogeocene). The biogeocoenosis 'deciduous forest' describes the static picture, the spatial structure, the organisms. In such a plant community, however, a material cycle and an energy flow constantly take place. Together with the animal organisms and the inorganic environment, the plants form a dynamic structure, an ecosystem, which is not closed in itself, because there is a supply of energy from outside through solar radiation and a supply of matter through precipitation, gas exchange, dust deposition, etc., but at the same time there is also a release of energy in the form of disordered heat energy and matter (water running off or seeping away, through gas exchange, etc.). The dynamic picture of such a spatial section, i.e. the essential structures and processes, is studied by ecosystem biology.

The total plant dry matter in a biogeocene is its phytomass, and that of animals is its zoomass. Together they form the biomass. With regard to the role played by each group of organisms in the ecosystem, a distinction is made:

1. Producers: They are autotrophic plants that store light energy as chemical energy during photosynthesis by forming organic compounds from CO2 and H2O and extracting mineral nutrients and water from the soil.

2. Consumers: These are heterotrophic animal organisms which, as phytophages, use the plants as food and convert a small part of them into animal matter. Predators that eat the phytophages (food chain, food web) also belong to this group.

3. Decomposers (mineralizers): They are mostly found in the soil (saprophages, bacteria, fungi) and ultimately degrade all plant and animal remains to CO2 and H2O. They mineralize the organic material, thus closing the material cycle.

As the simplest ecosystem, one can imagine the interplay of producers and decomposers (without consumers) (◘ Fig. C-9). Indeed, there are terrestrial ecosystems in which consumers play only a very minor role.

The total organic matter produced annually by the photosynthesis of plants is called gross production; the matter remaining after deducting the amount respired by the plants is called net or primary production; the matter formed by animal organisms is called secondary production. The latter is much smaller. Generally, only a few percent of primary production is consumed by consumers (long cycle, ◘ Fig. C-9); most of it ends up in the soil and is almost completely decomposed by the decomposers (short cycle, ► Fig. C-9, ◘ Fig. C-10), producing H2O, CO2, and mineral salts. The dead organic matter (litter) is previously crushed by lower animals - the saprophages or mould eaters - during the feeding process. The CO2 escaping from the soil is called soil respiration. The short cycle plays the main quantitative role in terrestrial ecosystems (► Fig. C-10).

The long cycle runs via the consumers, i.e. via the herbivores or phytophages, and via the zoophages or predatory organisms or via the omnivores, which eat both plants and animals. In addition, there are consumers of the 2nd or even 3rd order, but their metabolic rate is vanishingly small (► Fig. C-10). We must also include the parasites of plants among the consumers.

The excreta and corpses of the animals also re-enter the soil where they are prepared by animal organisms (coprophages, necrophages) for decomposition by microorganisms.

Although the long cycle is quantitatively only of minor importance, it plays an even greater role in regulating the balances in the entire ecosystem. Consumers could therefore also be called regulators. As soon as a certain plant species increases disproportionately in the ecosystem, the number of animals consuming it usually also increases. This reduces the population density of the plant species, which then leads to a decrease in phytophages. However, the settling to an equilibrium is rarely constant. Rather, one usually observes cyclic oscillations of population densities, each with typical phase shifts. Such a phase shift exists again between the phytophages and their zoophagous enemies. These regulatory processes, which can be described cybernetically as control loops with feedback, ensure that the ecosystem is kept in a dynamic equilibrium (steady state). It is true that population densities will always fluctuate to a certain extent, but only within certain limits. Such fluctuations are also caused by changing weather conditions in the individual years, which sometimes favours one plant species over another in the competition.

◘ Fig. C-9 Scheme of the simplest ecosystem (left) with material cycle and energy flow (E: energy flow; energy = ability to do work); R: respiration, respiratory energy; the same with the consumer compartment (right).

Fig. C-10 A: Scheme of the short and long metabolic cycles in a deciduous forest biogeocene. R: Respiration (breathing). Thickness of arrows approximates turnover rates. B: Scheme of the energy flow.

The interlocking control loops are based, on the one hand, on direct control processes by animals such as pollination (zoogamy) or fruit and seed dispersal (zoochory), and, on the other hand, on food chains that begin with herbivory. The long cycle consists of a whole series of such food chains, which would usually have to be described more accurately as food webs and which, despite all fluctuations, give the ecosystem great stability on average. By destroying the predators or by further interventions, man disturbs just these food chains, whereby the whole ecosystem gets into disorder or even collapses (Gigon 1974), or is replaced by another one.

It will continue to be an important task of zoo-ecologists in the future not so much to elucidate the quantitative ratios of secondary production as the various food chains in all their details. For the phytophages and the predators are often strictly specialized in particular species on which they feed. Despite their low density, they have great regulatory importance. A wealth of different adaptations plays a role in this.

Another of many amazing examples from the tropics are the close dependencies between ants and plants. On the one hand, there are the leafcutter ants, which bring pieces of leaves into their nests and grow mushrooms on them (i.e. engage in agriculture), which are their main food source (◘ Fig. C-11). The close dependence of some ants on Cecropia species (of the Neotropics) or Macaranga species (of the Palaeotropics) should also be mentioned (◘ Fig. C-12). The hollow stems of the rapidly growing pioneer trees are colonized by the queen ant through entrance holes preformed by the plant. As the young trees grow, the ant colony increases and continually colonizes new internodes. In addition, protein- or fat-rich food corpuscles are formed on the leaf bases by the plant, which additionally attract the ants. The investment is worthwhile for the plants, because the ants keep the plants free from other herbivores, so to speak as a protective police force.

As can be seen from this, not only the quantitative magnitudes of certain processes, but also the qualitative significance of some processes are quite essential for the stability of natural ecosystems through the interconnectedness of processes.

Parallel to the material cycles, the flow of energy takes place. Solar energy is converted into chemical energy during the photosynthesis of the producers, which is used by themselves, by the consumers and the decomposers for the maintenance of the life processes. In the process, chemical energy is constantly lost as heat in the respiration and fermentations of the microorganisms, until finally, after complete decomposition, it is entirely consumed. This energy flow is shown in ► Fig. C-10.

The composition of an ecosystem and its structures can only ever be represented as a model, and there are numerous ways of doing this. Another example is shown in ◘ Fig. C-13, where above all the functional compartments and their interconnections are highlighted.

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| Box C-7 Regulatory importance of phytophages in ecosystems |
| As an unusual example, Witheringia solanacea from the tropical rainforest of Costa Rica should be mentioned. The berries contain a natural laxative, so that the birds empty the intestine in less than ten minutes and thus distribute the seeds on the forest floor. After this short intestinal passage, 70% of the seeds are still germinable, with longer intestinal passage the rate drops to 20%. |

◘ Fig. C-11 A road of leafcutter ants in the lowlands of Tena, Ecuador (photo: Rafiqpoor) and single specimens of these ants transporting a leaf section (taxi!) on a tree trunk, Costa Rica (photo: Breckle).

Quantitative data of the different ecosystems are helpful for a comparison. ◘ Table C-3 shows essential ecosystem parameters for an oak forest.

The phytomass of forest communities (► Table C-3) is so high because dead wood mass is stored in the stems (heartwood 150 t•ha-1). But even without this, the phytomass is more than 1000 times higher than the zoomass.

For the latter, the following figures are given in European forests: Reptiles 1.7 kg•ha-1, birds 1.3 kg•ha-1, mammals (mainly small species, rodents) 7.4 kg•ha-1. Much larger is the mass of invertebrates, especially subterranean (up to 14 kg•ha-1 TG, 90% dipteran larvae). Figures are available for an American deciduous forest with Liriodendron (Reichle 1970) as TG (each in kg•ha-1): Aboveground: phytophagous arthropods 2.43, predatory A. 0.61. In the litter: Larger invertebrates 8.42, smaller W. 3.42. In the soil: earthworms (Octalasium) 140, smaller invertebrates 2.2.

In the mixed oak forests of Eastern Europe, it was found that after clear-cutting of oaks by caterpillars, the wood increment of ash and lime trees increased due to the better light conditions and overcompensation occurred; in the four years after the caterpillar epidemic, there was a total wood increment of 10%.

Even in a pure pine stand of different ages, compensation occurred over time after infestation with Dendrolimus pini by promoting the suppressed and less infested trees. Wood increment in the 2nd year decreased to 76% and in the 3rd year to 56%, but it increased to 150% and 194% in the 4th and 5th years, respectively (► Walter & Breckle 1999). Even moderate grazing of grasslands stimulates vegetative growth of grasses to such an extent that total annual production increases when the amount eaten is taken into account (► Walter & Breckle 1999). A similar situation probably applies to the material balance in tropical forests when individual trees are cut almost completely bare by leafcutter ants (Wirth et al. 1997).

Primary production is of particular importance for the ecosystem. As production analyses show, the level of primary production depends less on the intensity of photosynthesis, nor on the leaf area index or the total available leaf area, but rather on the assimilate balance of the producers (Walter 1960), i.e. on the way in which the assimilates are used in the course of the growing season (specific investment of organic matter in growth of producing or stabilizing tissues and organs). If they are used productively, in that new assimilating leaves are constantly being formed, then growth increases exponentially. If they are used non-productively to build up lignifying organs, the benefits of which only become apparent after years, then this corresponds to a long-term strategy. However, this is very different in individual biotopes and depends on the respective life forms.

◘ Fig. C-12 Cecropia trees are conspicuous from a distance in the rainforests of the New World because of their shimmering silver leaves. The hollow stems of Cecropia are inhabited by ants that live in symbiosis with Cecropia (photo: left: Rafiqpoor, right: Barthlott).

◘ Fig. C-13 Simplified schematic representation of the structures and processes in an ecosystem (modified after Ellenberg et al. 1986).

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| Box C-8 Influence of animals on biomass in a forest |
| During caterpillar epidemics of the gypsy moth (Lymantria dispar) in oak forests, the mass can increase sharply: At 106 to 107 caterpillars per hectare, their dry mass is 75-150 kg • ha-1, with 1-2 t • ha-1 of dry leaf mass destroyed and 500-1000 kg • ha-1 of excrement excreted. This throws the whole ecosystem out of balance. But this is true only for forest monocultures of the same age. Deciduous forests usually recover, coniferous forests may even die. |

Table C-3 Important ecosystem parameters of an oak forest of the Belgian Ardennes with a hazel shrub layer (Querceto-Coryletum) and a sparse herb layer (after Duvigneaud 1974)

|  |  |  |  |
| --- | --- | --- | --- |
| Leaf area index | Tree layer | | 3.87 |
| Shrub layer | | 1.83 |
| Total | | 5.70 |
| Phytomass (t • ha-1) | | | |
|  | Aboveground: | | 260.8 |
|  | thereof | Tree Leaves | 3.5 |
|  | Twigs and branches | 58.3 |
|  | Tribes | 180.2 |
|  | Shrub layer | 18.1 |
|  | Herb layer | 0.7 |
|  | Belowground: | | 55.4 |
| Total phytomass: | | 316.2 |
| Primary production per year (t • ha-1 • a-1) | | | |
|  | Aboveground: | | 15.3 |
|  | thereof | Total litter | 6.2 |
|  | Lost by herbivores | 0.5 |
|  | Tree growth | 5.9 |
|  | Shrub growth | 2.1 |
|  | Herbal growth | 0.6 |
|  | Belowground: | | 2.3 |
|  | Entire production: | | 17.6 |
| Dead organic matter in soil (t • ha-1) | | | 122 |

◘ Fig. C-14 Fruits of sunflower (top) and beech (bottom). The seedlings of both plant seeds produce very different amounts of dry matter in the first year due to different growth strategies (photo: Breckle).

The difference in investment strategy can be illustrated: If, for example, one sows single-seeded fruits of the beech (Fagus sylvatica, beechnut) and the sunflower (Helianthus annuus) (◘ Fig. C-14) under the same conditions in good soil in Central Europe, the beech seedling produces only 1.5 g of dry matter in the first year, whereas the sunflower, even in a climate that is not favourable for it, produces about 800 g.. This is because it continually forms new large assimilating leaves, whereas the beech seedling is content with two or three small leaves, and then uses the assimilates to build up a long primary root and a woody stem. It is true that the intensity of photosynthesis in the sunflower is about twice that of the beech, but this does not explain its production, which is 500 times greater. Here, then, the 'compound interest rate' effect of investment in organs of production plays the decisive role. In this the essential types of life differ fundamentally.

For the different forests, the general relationships between net primary production and the main ecological factors, such as temperature and humidity, can be illustrated (► Fig. C-15).Of course, this is only true for a limited range; in both dependencies there are typical upper limits, as shown in ◘ Fig. C-15A and ◘ Fig. C-15B; in addition, the relationships are not particularly pronounced.

On a global scale, in the case of net primary production (NPP), one can see the high productivity of warm-humid zonobiomes, where the growing season can be more or less year-round. The shorter the growing season and the colder and drier an area, the lower the NPP. The average value of 10 to 15 t- • ha-1 • a-1 for the central European beech forest is a relatively high value compared to the rest of the world; most dry areas are far below this value. In the tropics, however, values of up to 25 t • ha-1 • a-1 are reached (◘ Fig. C-16).

In the tropics, the standing, aboveground phytomass (◘ Fig. C-17) sometimes reaches well over 500 t • ha-1, with the belowground phytomass adding a further 20 to 30%. In the humid temperate latitudes, the total phytomass is often just as high, and the belowground phytomass is usually even significantly greater than in the tropics. The forested areas of the world usually yield more than 50 t • ha-1, but in deserts and semi-deserts the stand stock is often less than 10 t- • ha-1 (► Fig. C-17).

10 **Highly productive ecosystems**

Over large areas, NPP in the hot humid tropics reaches average values of up to 25 t•ha-1•a-1, as shown in the previous section. However, the plant communities of the tall shrubs are also characterized by a particularly high primary production. Like annual plants, tall perennials produce mainly assimilating leaves throughout the growing season and flowering organs and fruits only at the end of the growing season. However, since, unlike a seedling, they have much larger reserves at their disposal when they sprout in the spring, having been laid down the year before, they can build up the richly leafy shoot in a very short time, whereas the seedling of the annuals requires a long start-up time for this, until the leaf area has reached its maximum size. This is why summer cereals need ten weeks to produce the first quarter of the total dry yield, two more weeks for the second quarter, but only one week for the last half (according to the usual exponential growth curve).

In contrast, tall perennials can use almost the entire vegetation period very productively, which explains the very large developed above-ground phytomass and the considerable underground reserves built up in autumn for the next year.

A detailed production analysis of a tall herbaceous stand is shown in ◘ Table C-5. Primary production could be determined by monthly determination of above- and belowground phytomass.

The annual net primary production of about 18 t • ha-1 is in the same order of magnitude as that of a West European mixed oak forest, but slightly below that of a 50-year-old evergreen Castanopsis cuspidata forest in the warm-temperate climate of Japan with an aboveground primary production of 18.3 t•ha-1•a-1 on average.

Fig. C-15 Net primary production of forests as a function of annual precipitation (A) and mean annual temperature (B) (modified after Ehlers 1996).

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| Box C-9 Influence of environmental factors on productivity |
| Rule of thumb: The higher the temperature, the higher the productivity. The higher the precipitation, the higher the productivity (◘ Fig. C-15). |

◘ Fig. C-16 Net primary production (dry matter per m-2 • a-1) on Earth (after Larcher 2001).

◘ Fig. C-17 Phytomass (t • ha-1) on Earth (modified after Schulz 1995; original by Bazilevich & Rodin 1971).

**Table C-5** Production values of a pure stand (in t•ha-1•a-1) of the adventitious goldenrod Solidago altissima in a river floodplain in Japan (Iwaki et al. 1966, cf. Walter 1979); vegetation period from April to October.

|  |  |
| --- | --- |
| Growth of the above-ground parts | 12.01 |
| Growth of rhizomes and roots | 2.94 |
| Parts dead during the growing season | 2.83 |
| Total production | 17.78 |

Kamchatka belongs to the subarctic zone with low Betula *ermanii* forests. The growing season is 90 to 110 days (mean frost-free period only 64 days), mean temperatures are 3.5°, June 10.6°, July 14.3°, August 13.3° and September 7.2 °C in May. Tall shrubs reach 3.5 m in height, with Filipendula camtschatica, Senecio cannabifolium, and Heracleum dulce dominating (◘ Fig. C-18). According to Hulten (1932), bears sleep in them during most of the day, catching salmon in the river. The maximum standing phytomass reaches 31 t • ha-1 (of which 10 t • ha-1 are underground). Because some of the shoots die during the growing season, primary production is higher than the maximum herbaceous phytomass and probably exceeds 16 to 20 t•ha-1•a-1 despite the short growing season. The tall herbaceous plants are used as livestock feed in the form of silage. On southern Sakhalin, which is much further south (about 45°N), with a warmer climate and mixed deciduous and coniferous forests, even higher values were obtained. The frost-free period on Sakhalin is 145 to 155 days and the mean temperature of the warmest month is 18°C. The tall shrubs here grow up to 4.5 m high, and their composition is similar to that on Kamchatka, but they are more heterogeneous, as different species dominate locally. A leaf area index of 13 to 14 is given for stands dominated by Filipendula, and as high as 18 to 21 when Polygonum sachalinense is dominant, which is only possible if the tall shrubs receive additional side light, for example from the river side. This might explain the enormous annual above-ground phytomass produced, reaching 30 t • ha-1 • a-1 (total phytomass 70 t • ha-1) when Polygonum dominates. Thus, small-scale primary production could reach the record value of over 38 t•ha-1•a-1.

Whether the primary production of high Papyrus stands in the tropics is even higher is not known. It must be borne in mind that in the tropics the respiration losses due to the high night-time temperatures are very great, so that despite the high values of gross production, net production is greatly reduced.

Very lush tall shrubs are also known from the western Caucasus Mountains (► Fig. C-18, right) from the subalpine belt (Walter 1974) and not quite as tall in the Alps in the area of the likewise subalpine Alnus viridis stands, which indirectly assimilate atmospheric nitrogen, which also benefits the soil. However, exact production values are probably not available in either case.

Tall perennial grasses on moist, nutrient-rich sites also produce a large phytomass annually, for example, about 35 t • ha-1 of phytomass (annual production 18 t • ha-1) is reported for the 2.3 m tall reeds (Phragmites) on the lower Amu-Darya.

11 **Peculiarities of the material cycles of different ecosystems**

With the exception of the narrow shore zone, the littoral, aquatic ecosystems have autotrophic algae floating in the water as producers. They constitute a part of the plankton. By dividing, they can multiply very rapidly. Since they need light for photosynthesis, they only occur in the upper layers of the water bodies. They serve as food for the animal organisms of the micro- and macroplankton, which in turn feed larger animals up to fish and aquatic mammals, as well as birds of prey that take their food from the water. All dead organic waste is mineralized by decomposers in the water or in the mud layer at the bottom of the water bodies.

The phytomass present in the waters is small, yet the primary production may be very high due to the rapid reproduction rate of the algae. Since this primary production serves as food for the animals and is then incorporated to a considerable extent into their body substance (secondary production), the zoo mass is very large compared to the phytomass. The ratios, as we have seen, are quite different in terrestrial ecosystems. The corresponding mean ratios are given for comparison in ◘ Table C-6.

**◘ Table C-6** Ratios of phytomass and primary production of terrestrial and aquatic ecosystems

|  |  |
| --- | --- |
| Ecosystem types | Phytomass :  Primary production |
| Terrestrial ecosystems | 10-20 |
| Aquatic ecosystems | 1  :  300-400 |

In terrestrial ecosystems, much unproductive biomass is accumulated in producers; in aquatic ecosystems, biomass is more accumulated in consumers.

Even the scheme of the deciduous forest ecosystem (► Fig. C-13) is by no means universally valid. Various deviations occur, so that examples must be given below because of their great importance.

Almost all forest trees and most herbaceous plant species (except the Brassicaceae), but especially the Ericaceae and orchids, form a mycorrhiza with fungi, which functionally can be understood as a strong extension and fanning out of the root system. This facilitates the uptake of mineral nutrients from humus-rich soils. The mycorrhizal fungi are also able to supply their host plants with organic substances. This is proven by holosaprophytes among orchids (Neottia, Corallorhiza and others), Pyrolaceae (Monotropa and others) and other families. In addition, there are certainly hormonal effects. Whether the mycorrhizal fungi also supply organic compounds to the forest trees and the Ericaceae has probably not yet been proven, but could be possible in stands on extremely poor sands with a layer of raw humus. In this case, the short cycle would be even more shortened because the litter does not need to be mineralized.

A particularly strange case of an ecosystem without producers was discovered in the dune area of the Namib Mist Desert: The organic mass, which is a prerequisite for the material cycle, is blown into this almost vegetationless dune area by the wind from the neighbouring or distant areas and accumulates on the leeward slope of the dunes or in sandy depressions. It serves as food for the saprophages (beetle species and others), these are eaten by small predators (reptiles and others), which in turn are the food of larger predators. In this way, a rich animal life with very strange adaptations to life in the mobile sand has developed even without plants, that is, an open ecosystem without producers.

12 **The importance of fire for ecosystems**

Well secured is the fact that fire can often replace the decomposers and a very rapid mineralization of the enriched litter is achieved. In this respect, fire also represents a special impact on the material cycle of ecosystems. Natural fires triggered by lightning have always existed, even in the forests of the coal age (Carboniferous). They are typical for areas with a drought, i.e. for all grasslands of the tropics and subtropics, for the steppes of the temperate and cold regions, for the woody vegetation of the winter rainfall areas and for all coniferous forest areas, even without human intervention, and are even necessary for the vegetation if the destruents are not able to decompose all the dead litter. In Grand Teton National Park (USA), all fires were suppressed for a long time, resulting in a bark beetle disaster in the *Pinus* forestsbecause the beetles were able to proliferate in the enriched dead wood. Since the natural fires are no longer extinguished, the balance in the ecosystem is maintained. However, larger and large-scale fires of varying intensity occur again and again, causing a mosaic of fires in the landscape. Even steppes or prairies (as well as grasslands and savannahs) and natural parks that are completely protected from fire degenerate when litter accumulates that is otherwise periodically mineralized by natural fires. In certain Australian heaths, if the dead organic plant parts do not burn at least every 50 years, the material cycle comes to a halt, because otherwise the mineral nutrients are stored more and more in the accumulating litter, in the large woody fruits of Banksia, and also in the hard dead leaves of grass trees. Many Eucalyptus, Banksia, Grevillea and *Hakea* speciesin Australia renew only after fire events. Many annuals also take advantage of open ground, freshly fertilized by ash, after rain and germinate. Many geophytes also sprout suddenly at the same time, and new shoots emerge almost synchronously from many burned stumps (◘ Fig. C-19).

◘ Fig. C-19 Macrozamia in the understory of a tall Eucalypt forest north of Melbourne (Australia) with fresh shoots after forest fire (photo: Breckle).

After a fire, the material cycle is stimulated again by the ash components. The conditions are similar in the large *Protea* standsaround Cape Town, in the fynbos, where even shorter fire periods occur naturally, such as on the slopes around Junkershoek, where this was studied. There, on average, a fire occurs every two to three decades, i.e. relatively frequently even under natural conditions. During this time not so much litter and dead matter has accumulated, so that in many places the fires are not too hot and therefore not very devastating. The Cupressaceae Widdringtonia can thus always regenerate; it is only competitive enough against other shrub and tree species when exposed to fire. The fynbos (◘ Fig. C-20) thus remains a species-rich mosaic of the most diverse age stages.

Fire is thus very often an important natural environmental factor in maintaining balance in ecosystems. Accurate statistics of forest or grassland fires caused by lightning in the United States are available for the years 1961 to 1970. There were 34,976 = 37% of all fires in the Pacific states, 51,703 = 57% in the Rocky Mountain states, 13,733 = 2% in the Southeastern states, but only 1167 = 1% in the humid Northwest (Taylor 1973).

However, today man-made fires for slash-and-burn etc. have become so devastatingly rampant, especially in the tropics, that thousands of fires can be located in the satellite image every night.

The working group 'Fire Information for Resource Management System' (FIRMS) at the University of Maryland, USA constantly collects comprehensive data from the satellite MODIS, GIS data, Google Earth data etc. about the fire frequency in forests worldwide. NASA creates weekly images of wildfires and makes it available to the public on a platform (for more information ► NASA's archive: [https://t1p.de/kxqs](https://t1p.de/kxqs" \t "_blank)). We bring to illustrate the scale of forest destruction four world maps of forest fires in ◘ Fig. C-21. From these images we can see the seasonal change of forest fires and that the fires are not limited to the forests of the tropics, but also leave equally devastating traces in the forests of the taiga. The smoke particles are distributed throughout the atmosphere, so they contribute a share to the change in radiation absorption and thus to the global climate that is difficult to estimate.

13 **The individual zonobiomes and their distribution**

The sequence of zonobiomes arranges itself on both sides of the equator, but not quite symmetrically, because the land masses in the southern hemisphere are smaller and the climate is more oceanic as well as cooler. Note here that zonobiomes VI through IX are small-scale in the southern hemisphere. Zonobiome VI and VII are weakly developed in the southern hemisphere, ZB VIII is completely absent, and ZB IX is represented only by the sub-antarctic islands and the southern tip of South America, if one disregards the icy and almost vegetationless Antarctic.

The sequence from the equator to the poles does not always correspond to the numerical order, for example ZB VII in Eurasia is partly inserted between ZB V and ZB VI and represents a very dry variation (Krutzsch 1992 calls these climate facies areas), which even often has a precipitation cycle of ZB IV, but with cold winters and great continentality. The large zonobiomes are usually further subdivided into subzonobiomes (sZB) due to certain variations.

As a basis for a more detailed discussion of the individual zonobiomes, ◘ Figures. C-22 to ◘ Fig. C-27 show their distribution on the continents. Additional signatures indicate minor variations within the zonobiomes.

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| Box C-10 The importance of fire in pyrophytes |
| Plant species that require episodic fire in an ecosystem for maintenance or reproduction are called obligate pyrochorous plants. Their reproduction is tied to fire events. |

◘ Fig. C-20 Proteoid fynbos at the Cape of Good Hope (South Africa) with hardleafed shrubs of various Proteaceae and Widdringtonia (Cupressaceae), which can only rejuvenate after fires (photos: Rafiqpoor).

◘ Fig. C-22: Australia and New Zealand with zonobiomes I-V.

◘ Fig. C-23: North and Central America with zonobiomes I-IX.

◘ Fig. C-24: South America with zonobiomes I-VII and IX.

◘ Fig. C-25: Africa with zonobiomes I-V.

◘ Fig. C-26: Europe with zonobiomes IV-IX, plus the Near East.

◘ Fig. C-27: Asia with zonobiomes I-IX (see Fig. C-26 for the Near East).

In Western Europe, the zonobiomes run more from north to south as a result of the influence of the Gulf Stream, whereas in Eastern Europe the normal west-east extension can be seen. They are from north to south: Zonobiome IX (tundra zone) with zonoecotone VIII/IX (forest tundra), zonoecotone VIII (boreal coniferous forest zone), zonoecotone VI/VIII with zonoecotone VI, both of which, however, are tilted to the east (mixed forest and deciduous forest zone) and finally zonoecotone VII (steppe zone). Zonobiomes IX, VIII, and VII find their immediate eastward continuation in Asia (◘ Fig. C-26). Southern Europe belongs to zonobiome IV (Mediterranean), which is still weakly noticeable in Iran and Afghanistan. Zonobiome III is completely absent from Europe. Only zonoecotone IV/III occupies a small semi-desert area in south-eastern Spain, the driest part of Europe. In Central Europe, the zonation is strongly modified by the Alps and the other mountains. The zonation in mountainous Balkan Peninsula is also very complex.

In ◘ Fig. C-22 to ◘ Fig. C-27 the major ecological subdivision of the continents (modified after Walter et al. 1975) is shown. Signatures I - IX correspond to zonobiomes (ZB); zono-ecotones (overlapping hatchings) and mountains (gridded) are shown between them.

◘ Fig. C-21 The extent of wildfires in different seasons for 2014 (from top to bottom: spring, summer, autumn, winter) compared using NASA nighttime satellite imagery (taken from: [https://t1p.de/kxqs](https://t1p.de/kxqs" \t "_blank)).

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◘ Fig. C-22 Australia and New Zealand with zonobiomes I-V.

◘ Fig. C-23 North and Central America with zonobiomes I-IX.

◘ **Fig. C-24** South America with zonobiomes I-VII and IX.

◘ Fig. C-25 Africa with zonobiomes I-V.

◘ Fig. C-26 Europe with zonobiomes IV-IX, plus the Near East.

◘ Fig. C-27 Asia with zonobiomes I-IX (Near East see Fig. C-26)