CHAPTER 5

Vegetation and animals

Despite interventation by man, the vegetation cover and to a lesser extent the animal world reflect more than any other physical characteristics the ecozonal differentiation. For this reason, the vegetation and fauna are discussed in greater detail than other physical factors in the chapters on the individual ecozones and the components of the vegetation and fauna are described in order to show what the natural environment for plants, animals and man is like and also to indicate the risks and potentials for future development.

5.1
Structural characteristics of the vegetation

The structural characteristics of the vegetation cover include height and density of the cover, expressed by size parameters such as the *leaf area index*, the number of *trunks* and the *basel surface*. Other structural elements include measurements related to the *root penetration* depth and intensity, the species

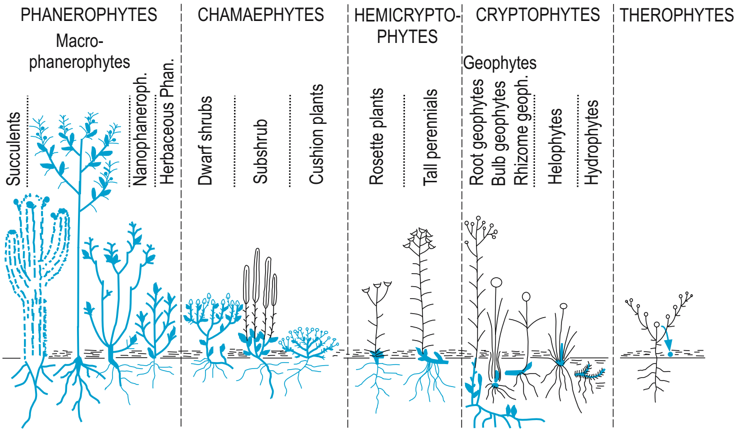


Fig. 5.1. Growth forms. Those parts of the plants drawn in blue survive dry seasons or cold seasons, the remainder die off at the beginning of the dry or cold season. Source: Raunkiaer (from Schubert 1991)

Table 5.1. Plant formations in the ecozones

Plant formations (Climax formations)	Ecozones
Polar desert High arctic tundra Low arctic tundra	Polar subpolar
Forest tundra Lichen forest Closed boreal coniferous forest – Evergreen boreal coniferous forest (dark taiga) – Deciduous boreal coniferous forest (light taiga)	Boreal
Deciduous and mixed forest Temperate rainforest – Evergreen deciduous and mixed forest – Temperate coniferous forest	Temperate midlatitudes
Woodland steppe Tall grass steppe Mixed grass steppe Short grass steppe Desert steppe Temperate desert	Dry midlatitudes
Sclerophyllous forest and shrub formations	Subtropics with winter rain
Subtropical rainforest Laurel forest	Subtropics with year-round rain
Winter wet grass and shrub steppe Summer wet thorn steppe and thorn savanna Tropical and subtropical desert and semi-desert	Dry tropics and subtropics
Short grass savanna (dry savanna) and dry forest High grass savanna (moist savanna) and moist forest	Tropics with summer rain
Tropical rainforest	Tropics with year-round rain

make up in a community, their growth patterns and their spatial distribution. The temporal dimension includes seasonal change, long term cycles in the stand including, aging and *regeneration*, and *plant succession*.

The convergence between the biozonal and ecozonal patterns is based on the convergent development of different plant species which takes place world wide as they adapt to the conditions at a particular location. A small number, compared to the total number of species in the world, of *life-forms* or growth forms have evolved to be similar in appearance and function in the ecosystem, despite differences in their taxonomies. Cactus in the Americas and succulent euphorbias in Eurasia are an example.

Plant cover can be described either in terms of a plant community, which is the species mix within a community, or in terms of a life-form spectrum which measures the relative share of the individual life-forms and their cover

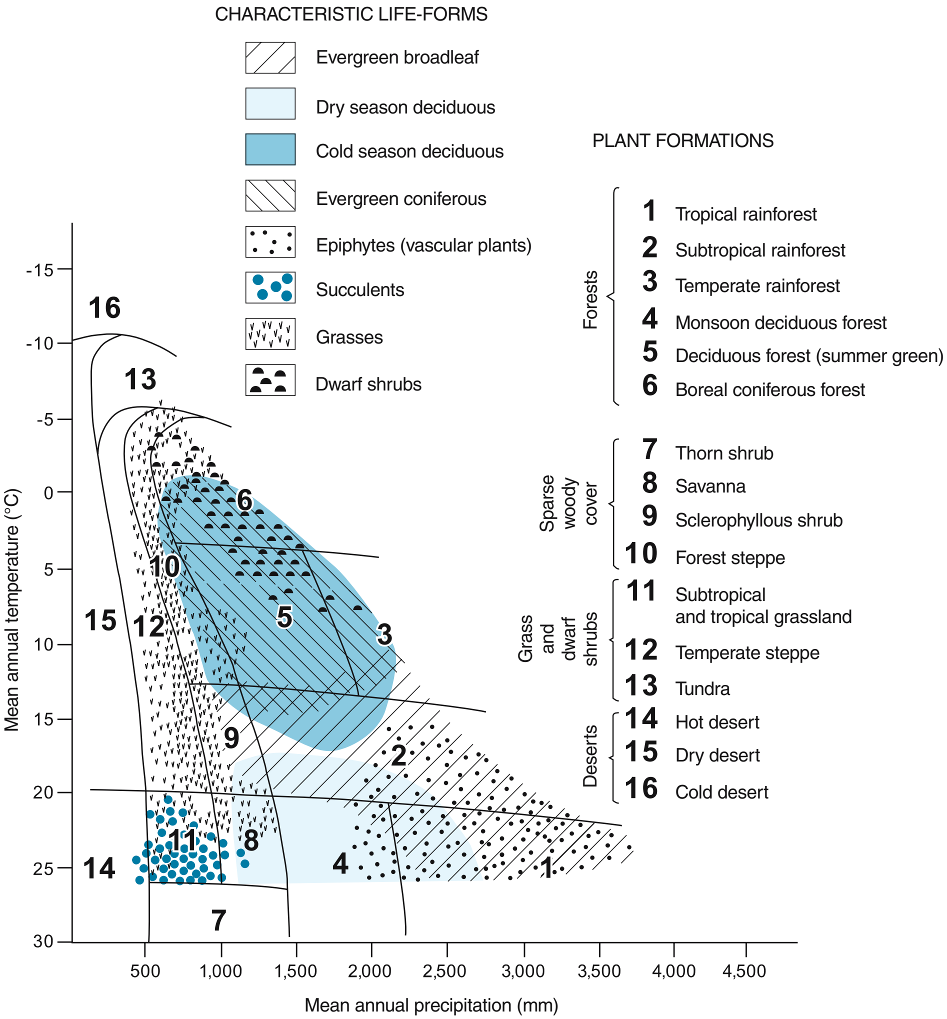


Fig. 5.2. Distribution of life-forms and plant formations in relation to annual temperature and annual precipitation. Source: from Sitte et al. 1998

within a community. The latter are *plant formations* based on physiognomic-ecological units of vegetation which, to a considerable extent, express the abiotic environmental conditions. Figure 4.2 shows the relationship to climate of the ecozones.

The zonal formations are the largest units of formation types and include boreal coniferous forests, deciduous and mixed forests and evergreen sclerophyllous forests. Their natural development is an expression of the global differentation of climates. They form the climax vegetation. Ecozones are, or in some cases were, represented by one or more *climax formations* (Table 5.1).

A biome includes both the plant formations and the animals within an ecosystem, a zonobiome is the combination of plant formations and animals within an ecozone. Transition zones between two communities are termed ecotones, in its largest extent a zonoecotone.

The growth forms of vegetation have been classified in various ways. Raunkiaer's classification is shown in Fig. 5.1. Figure 5.2 shows which growth forms are characteristic for individual plant formations and the distribution of different plant formations in relation to mean annual temperature and mean annual precipitation.

5.2
Ecosystem model of ecozone

A natural of near natural *ecosystem* is composed of a *biotic* community of plants and animals, or biocoenosis, and its *abiotic* environment, the biotope. A wide variety of functional and structural relationships exist between biotic communities and their biotopes. Conditions, apparently undisturbed from outside, develop a fairly stable structure in which self-regulation and self-regeneration take place and turnovers of materials and energy reach a form of equilibrium in which reserves of organic matter and minerals are constant.

Because ecosystems are dynamic systems in which the individual complexes such as vegetation, fauna or microclimate change continually, there are no real dynamic equilibria and constancy of components. Instead they are derived as mean states, either temporal, such as *aging* or *regenerating cycles* which are present everywhere in an ecosystem, or spatial states which occur all over an ecosystem in mosaic-like pattern of complexes of different ages.

Aging and regeneration cycles are particularly noticable in forests especially in the Boreal zone, the Temperate midlatitudes, the Subtropics with winter rain, and the Subtropical and Tropical zones with year-round rain. In these zones, a mature or optimal phase during which the highest values for primary production are reached, is followed by an aging or decomposition phase during which gaps are left by the dying trees. The vegetation that regenerates in these gaps are the *pioneer plants* that are characteristic for this rejuvenation phase.

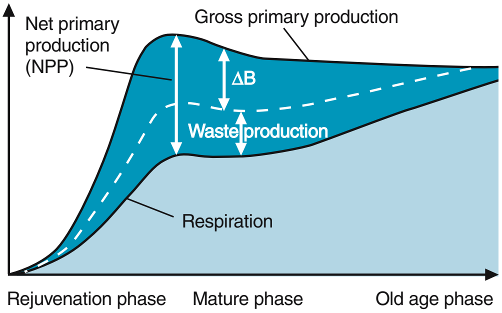


Fig. 5.3. Age-dependent changes in primary production, increment (ΔB), waste production and respiration in a forest formation. Source Kira and Shidei 1967

In Fig. 5.3, the highest net primary production is reached in the transition phase before maturity, when the total increment is also largest. Respiration then also increases relatively rapidly as the relationship between productive leaves and unproductive stems, branches and roots is less favorable and the net primary production declines again. In deciduous forests the increment of wood stops when the share of leaves of the total mass is below 1%. At the same time, because the proportion of detritus production increases, increment of biomass becomes even slower than that of the net primary production. When the old age phase is reached, the rate of *detritus production* is higher than the rate of *net primary production* and the *biomass* decreases. Any of these changes can be modified or stopped when a stand has trees of various ages and aging and rejuvenation are simultaneous. A description of the age dependence of the available supply and turnover for a particular ecosystem can only be interpreted when the age of the stands is known.

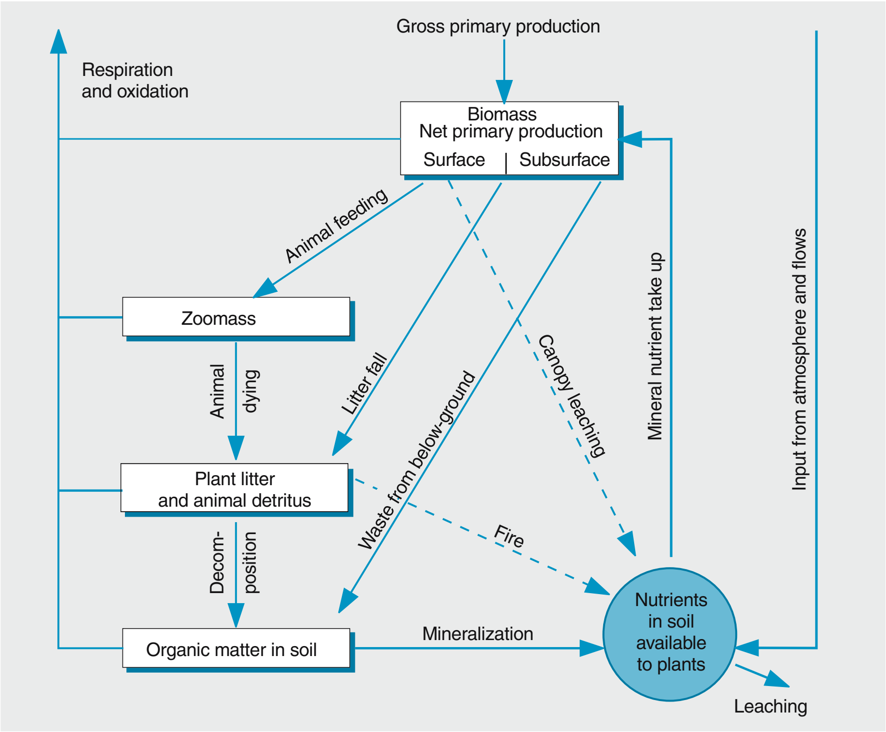


Fig. 5.4. Base model of a natural or near natural ecosystem as applied to typical ecosystems of some ecozones (e.g. Fig. 7.18, 8.12). The areas of the boxes and widths of the arrows correspond to the volume of supply and turnover. The circles represent the availability of nutrients to the plants in the soil, largely the exchangeable nutrients. The area of the circle represents the approximate relationship of nutrient availability in different ecosystems

Close to stationary states of some duration appear when the plant cover reaches a stage of late maturity. By far the largest proportion of the temporal aging cycle and also the spatial distribution within an ecosystem is accounted for by this stage. For this reason conditions during this mature stage are regarded as a steady state and more or less constant and typical for the ecozone or ecosystem. It is also during this stage that the gains and losses in the individual components of the system are in balance for a period of time.

Figure 5.4 shows a zonal ecosystem model based on such an assumption of steady state. It is applicable to several ecozones, not necessarily for the mean states but for the characteristics of the biome or ecosystem in the zone. Clearly it provides only a framework within which the supplies and turnover rates change in the long term as the components in the system develop.

5.3
Available supply of organic matter in the ecosystem

Box 3 shows the various types of organic available supply and the turnovers in an ecosystem.

The *biomass* is the total weight of living components in the ecosystem, i. e. of all producers, consumers and decomposers. In practice, however, *biomass* is used quite frequently as a synonym for *plant mass* or phytomass because in many ecosystems the *zoomass* which is the total mass of all living animals often composes less than 1% of the total biomass.

Living plants can include dead material such as bark, structural tissue or dead roots still attached to the plant. If this *standing dead* is not deducted the term *standing crop* instead of biomass has to be used. The *standing* also includes dead trees that are still upright in a woodland.

Litter and *humus* are composed of dead organic matter lying at or near the soil surface. Soil scientists define litter as part of the humus. Ecologists subdivide the dead organic matter into litter and humus, although not always at the same place. For example, in addition to the organic matter in the Ah mineral horizon, that in the Oh horizon is often considered part of the humus. Boundaries between the O horizons cannot be well defined since most are transitional areas. In this book the entire surface layer, including the Oh horizon is defined as litter. Peat is defined as humus.

5.4
Primary production

5.4.1
Photosynthesis and respiration

Each natural ecosystem begins with a fixing of solar energy in the form of latent chemical energy, the primary energy input, by green, autotrophic plants through the process of photosynthesis. *Photosynthesis* is the production of

3

Selected organic available supplies and turnovers in an ecosystem

Available supplies

Biomass
– Phytomass
- Shoot mass (above surface)
- Root mass (below surface)

Share of photosynthetically active plant components
Share of plant components that only respire

– Zoomass
Litter (L and O horizons)
Humus in soil (Ah and H horizons)

Turnovers

Gross primary production (GPP)
Net primary production (NPP)
Animal consumption and secondary production
Litter production (litter fall)
Below-ground waste production
Litter decomposition
Humification
Mineralization

Duration and rate of turnovers

Duration and rate of turnover of vegetation (productivity)	$\frac{\text{Biomass}}{\text{NPP}}$ (years)	or	$\frac{\text{NPP} \times 100}{\text{Biomass}}$ (%)
Life span of leaves	$\frac{\text{Leaf mass}}{\text{NPP (leaves)}}$ (years)	or	$\frac{\text{Biomass}}{\text{Leaf drop}}$ (years)
Duration and rate of decomposition	$\frac{\text{Litter supply}}{\text{Litter delivery}}$ (years)	or	$\frac{\text{Litter delivery}}{\text{Litter supply}}$ (%)

Duration of turnover = mean period during which a biomass, zoomass, litter or humus is exchanged completely, that is, the input and output cumulate to the total current supply.

Turnover rates = proportion (%) of a supply exchanged within a time unit e.g. mean annual gain by primary or secondary production, litter fall and humification, or loss by animal consumption, animals dying and decomposition.

Turnover duration and rates are measured by flows between individual components of the available supply or total flows between primary production and mineralization.

Note: Units of measure used are tons of dry matter (dry weight of the biomass or dead organic matter, dried at 105 °C) and kilo joules (for energy content and flows; energy equivalent of plant matter estimated at 18 kJ ≈ 4.3 kcal, per 1 gram of dry matter) per hectare and per year. Carbon content of biomass assumed at 45%, of litter about 50% and humus up to 58%. Carbon content increases during decomposition.

carbohydrates from water and carbon dioxide which are used as elements for further synthesis. Photosynthesis can be expressed as follows:

$$6\,CO_2 + 6\,H_2O + 2{,}897\,\text{kJ} \rightarrow C_6H_{12}O_6\,(\text{glucose}) + 6\,O_2 \uparrow$$

A part of the carbohydrate production is lost when respiration takes place and carbon dioxide is released. Respiration is expressed as follows:

$$C_6H_{12}O_6 + 6\,O_2 \rightarrow 6\,H_2O + 6\,CO_2 \uparrow +2{,}826\,\text{kJ}$$

The gross photosynthesis less respiration equals net photosynthesis. The remaining surplus of material and energy which is produced in the plant cover of an ecosystem by means of the net photosynthesis is the *net primary production* (NPP).

The intake of CO_2 and output of O_2 that occurs in photosynthesis and the intake of O_2 and output of CO_2 that occurs in respiration take place in the *stomata* (*pores*) of the leaf surface. Most of the stomata are on the underside of the leaf. In the *transpiration* process the water moves from the roots upwards in the plant and is also discharged through the pores. During a water shortage pores may be closed or narrowed so that photosynthesis is reduced or even ceases.

5.4.2
Primary production from plant stands

The *production capacity* of a plant cover, the crop growth rate, is calculated from the net yield of organic matter in *dry weight* or by its *carbon content*, per time unit (mostly per year, month or growing season) in relation to the ground area (ha or m^2). Included are increases in the living biomass resulting from plant growth or, usually only in older stands, decreases (ΔB) and the losses

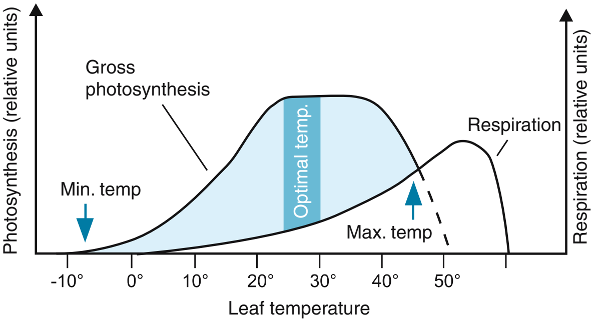


Fig. 5.5. Photosynthesis and respiration in relation to temperature. The net photosynthesis (*blue area*) is the difference between gross photosynthesis and respiration. In this example the highest value is reached between 25 °C and 30 °C. Values are higher if the light intensity increases. Source: Larcher 1994

through death (L) herbivory (C) or fire (F). The net primary production can therefore be expressed as

$$PP_{\mathrm{N}} = \Delta B + L + C + F \ .$$

In some ecosystems, losses due to herbivory and fire are generally (or, with respect to fire, at least for longer periods) of very minor importance; the losses due to death may be negligible during "growing periods" (i.e., assuming that production and death are discrete processes). In such (simplest) cases, net primary production approximates growth increments, and the following simplified equation can be used for determining PP_{N}:

$$PP_{\mathrm{N}} \approx \Delta B \ .$$

Losses due to death equal the increase in the quantity of dead plant material (ΔW), i.e., of dead vegetation (standing dead), litter and dead soil organic matter (above- and below-ground wastes) corrected for the amount decomposed (D):

$$L = \Delta W + D \ .$$

Substituting L in first equation, and still neglecting C and F, the following expression for determining PP_{N} is obtained:

$$PP_{\mathrm{N}} \approx \Delta B + \Delta W + D \ .$$

The definition of B and W may change when live and dead vegetation are difficult to distinguish; then B takes the meaning of standing crop (i.e., phytomass and standing dead) and, correspondingly, W that of wastes only. This shift does not affect the measurements of decomposition; in any case, D has to include the decomposition processes on both the standing phytomass and the ground.

5.4.3
Production capacity of the world's plant cover

The large variations in the *primary production* per spatial unit worldwide are only to a small extent due to differences in the assimilation capacity by photosynthesis of the plant cover (Fig. 5.6). Of greater importance are size and structure of the above ground biomass, or assimilation surface if there is a great deal of photosynthetically inactive stem material present, and the extent to which edaphic and climatic conditions in a location are favorable or unfavorable for plant growth.

The *productivity* of the plant formations in the ecozones is generally higher the larger the biomass (Figs. 5.7 and 5.8). An exception are the grasslands in the steppes and grass savannas and also algae rich aquatic ecosystems which have a higher production capacity from a smaller biomass (Chap. 10).

The *assimilation surfaces* (foliage densities) and their relationship to unproductive organs is a decisive factor in the productivity of a plant cover because

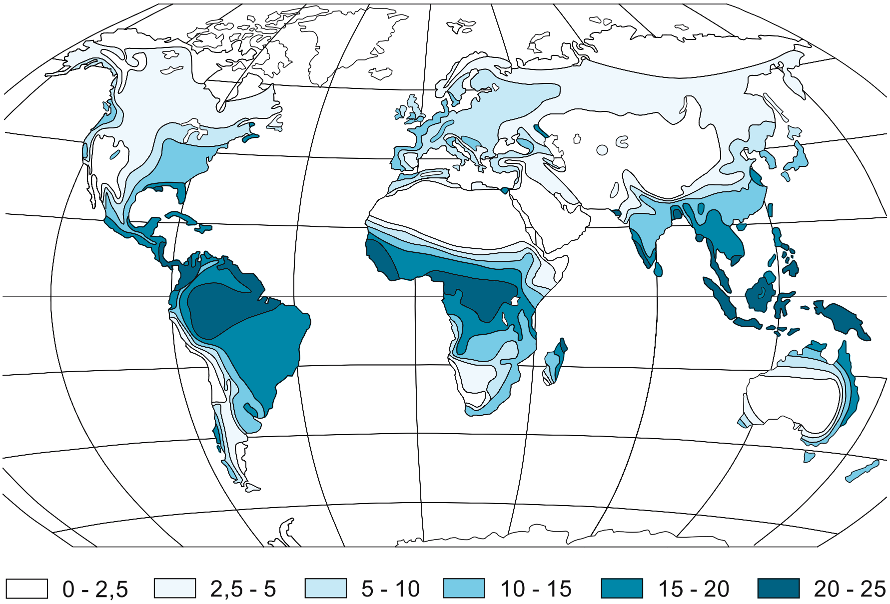


Fig. 5.6. Annual net primary production in the world in tons per hectare. Source: Lieth 1964

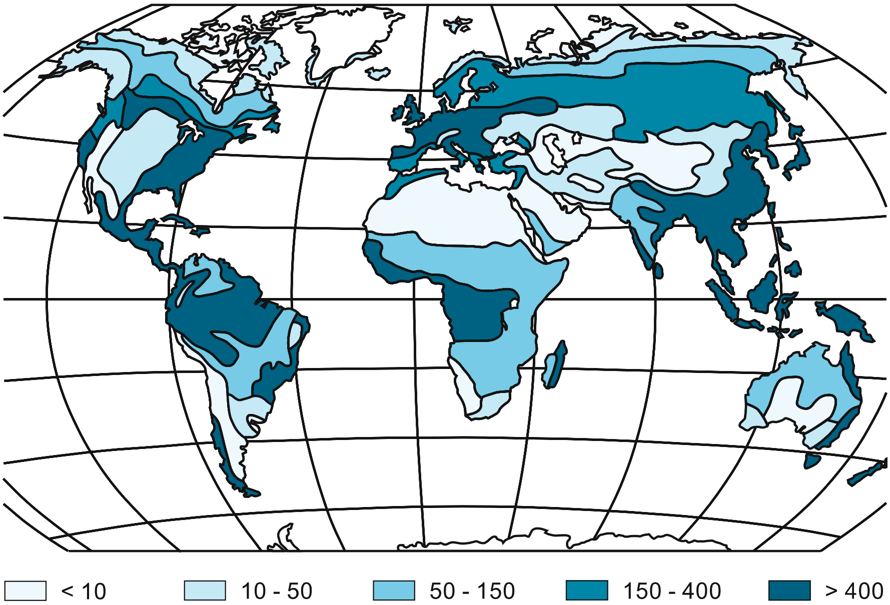
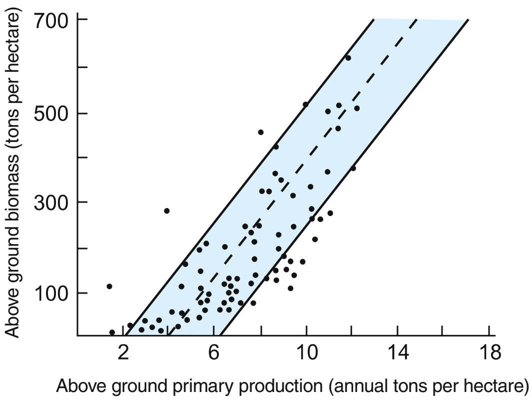


Fig. 5.7. Distribution of surface and subsurface biomass in the world, in tons of dry matter per hectare. Source: Bazilevich and Rodin 1971

Fig. 5.8. The relationship between above ground biomass and primary production in forest formations. Source: O'Neill and De Angeles 1981



only the leaves are involved in the *assimilation of carbon*. If their total area of surfaces above ground is larger and the proportion of only respiratory organs small, other factors being equal, the productivity is also higher. This is shown by the production capacity of neighboring pastures and woodland.

The *leaf area index* (LAI) is the measure of the assimilation surface of a plant cover. This is the total of all leaf surfaces exposed to incoming light energy (projected leaf area) in relation to the ground surface areas beneath the plant. It is expressed as m^2 per 1 m^2 ($m^2\ m^{-2}$) and is basically a measure of light absorption and thereby the energy input of the leaves as well as the decrease of light intensity in the stand. It can also be used to estimate transpiration and interception of rainfall in a plant cover; both usually increase with increasing LAI.

In the deciduous forests of the midlatitudes the index lies between about 5 and 6, in the rainforest of the subtropics from 7 to 8 and in the rainforests of the tropics between 9 and 10. The smallest values are in the dry areas. Production increases with increasing biomass and LAI as long as the radiation interception of green plants increases.

The extent to which primary production world wide is affected by environmental factors depends on the annual length of the growing season, the solar radiation and air temperature and availability of water and mineral nutrients during the growing season.

Growing season, solar radiation, temperature and water availability are determined by climatic factors. The availability of mineral nutrients is also influenced by the climate. As a result of which productivity of the vegetation predominantly changes in relation to latitudinal changes of climate. The highest rates of productivity occur in the tropical rainforests in which the year-round rain, high precipitation totals, high temperatures and intense solar radiation combine to provide optimal conditions for growth.

Solar radiation is the most important source of energy for primary production. It is available in varying quantities world wide. Table 5.2 shows the available range for each ecozone (see also Fig. 2.1 and 2.2). The vegetation

Table 5.2. Global radiation and primary production in the ecozones

Ecozone	Global radiation during a growing season		Net primary production		
	10^8 kJ ha^{-1}	% annual total	Energy fixation 10^8 kJ ha^{-1} a^{-1} [a]	Dry weight t ha^{-1} a^{-1} [a]	Dry weight t ha^{-1} a^{-1} [b]
Polar subpolar	50–150[c]	20–50	0.25–0.75	1–4	1-4
Boreal	150–300	50–75	0.75–1.50	4–8	4–8
Temperate midlatitudes	300–400	75–80	1.50–2.00	8–11	8–13
Dry mid-latitudes	150–300[d]	25–50	0.75–1.50	4–8	4–10 (3–8)
Subtropics with winter rain	200–300	30–55	1.00–1.50	5–8	6–10
Subtropics with year-round rain	500–600	100	2.50–3.00	14–17	19–23
Dry tropics and subtropics	200–350[e] 100–200[f]	25–50 15–30	1.00–1.75 0.50–1.00	5–10 3–5	7–14 (6–11) 4–6 (3–5)
Tropics with summer rain	350–550	50–85	1.75–2.75	10–15	14–21
Tropics with year-round rain	500–650	100	2.50–3.25	14–18	21–29

[a] A mean photosynthetic efficiency of primary production is assumed to = 0.5% of the global radiation during growing season and energy equivalent of the produced plant mass to = 18 kJ g^{-1} dry matter (dry weight including mineral components).

[b] Photosynthetic efficiency increases equatorwards from 0.4 to 0.8%. Values in parenthesis are for dry areas where a reduced amount of radiation is absorbed because of the incomplete vegetation cover.

[c] Tundra [d] Grass steppes [e] Tropical thorn savanna [f] Subtropical steppe

can use only that part of the solar radiation that reaches the surface during the *growing season*, the annual period or periods when thermal and moisture conditions are suitable for growth. That part of the solar radiation received at the surface at this time forms the growth potential for plant cover (Table 5.2, col. 1 and 2).

The utilization of this potential for the production of organic matter depends on the *exploitation of radiation by (apparent) photosynthesis*, i.e. on its efficiency in transforming radiation energy into chemical (biologically useful) energy. This transformation, which is variously called the energy yield or useful effect of photosynthesis, or the *(net) photosynthetic efficiency*, can be calculated in different ways. In this book it will be expressed as the *relation between the annual primary production (or, more exactly, its energy content) and the incoming radiation during the growing season.*

On the basis of the values for productivity of zonal plant formations, a global mean value for the continents of about 0.5% can be estimated, or 1% of PAR (photosynthetically active radiation). These are long term utilizaton rates of zonal plant formation, taking into account lower production related to the aging of stands. Using this value and assuming that the mean energy content of the plant matter is 18 kJ g^{-1}, the order of magnitude of primary production for each ecozone can be estimated (Table 5.2, col. 3 and 4).

As the net photosynthesis increases with temperature equatorwards, so also does the energy yield of the NPP of the zonal plant formations from about 0.4% in the high latitudes to 0.8% at the equator, The range is probably due to the lower albedo in regions with a high sun angle. Using these zonal variations, an adjusted value for the production can be obtained (Table 5.2, col. 5).

If the water and nutrient supplies decrease, plant production is likely to be reduced. The moisture content and nutrient content at which a reduction occurs, and the extent, depends on the efficiency of the plants involved to utilize the available water and nutrients. This can be expressed as the relationship between production and water consumption and between production and nutrient uptake from the soil.

The relationship between production and water use of a single plant can be expressed by the *water use efficiency* (WUE) in grams of dry matter, or net CO_2 uptake per kilogram (liter) of transpired water. The reciprocal quotient, the *transpiration coefficient* is also sometimes used. This expresses the transpiration in liters per kilo of dry matter production.

The *water use efficiency* of the primary production from a plant cover is determined from the ratio of the production, usually above ground production, of a plant covered area in kg ha^{-1} or g m^{-2}, to the actual evaporationtranspiration (Et) of that area, related to a time period, usually the growing season or a year.

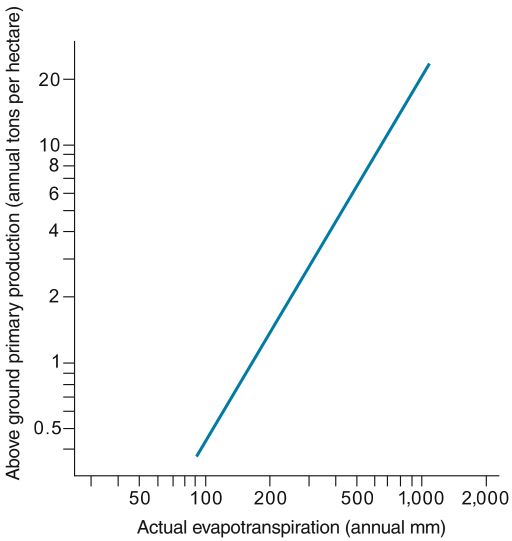
In dry regions it can be assumed that all precipitation is evaporated where it falls and can be equated with the total mean annual precipitation and termed *rain use efficiency* (RUE) of primary production.

Water use efficiency increases with the actual evapotranspiration (Et). For example, with 100 mm Et, there is a production of dry matter of 0.05 g m^{-2} per mm of Et and with 1,000 mm Et, 2.0 g m^{-2} of dry matter per mm of Et (Fig. 5.9).

The increase in production with increasing Et relates to the supply of water to the plant cover. With a larger supply, the vegetation is taller and denser. Also, as the availability of water increases, the proportion of the evaporation that takes place at the soil surface, unused by plants, declines. The correlation between net primary production and precipitation has been measured in several plant cover types (Figs. 10.5, 13.2, 14.10).

The *nutrient use efficiency* (NUE) shows the ratio between production of a plant cover and the uptake of minerals from the soil over a time period. It is expressed as dry matter in kg of NPP of mineral uptake. The NUE is lower for herbaceous plants and leaves that have a short life span and rapid turnover and consequently short mineral cycle than woody plants which have a longer life

Fig. 5.9. Correlation between surface primary production and evapotranspiration, based on data from various formation types. Source: Rosenzweig 1968



span. It is also greater in soil where the mineral supply is better. The nutrient use efficiency for the grass savanna, for example is less than for the savanna woodland which is less than for tropical rainforest; similarly, in dry savanna rich in nutrients (eutropic) the NUE is less than in moist nutrient poor savanna (dystropic) and for deciduous foliage, it is less than for evergreen broadleaf trees and, in turn, less than for needles from conifers.

The nutrient use efficiency can also be used to estimate individual nutrients, nitrogen use efficiency for example. The NUE is of greatest importance in regions that are humid throughout the year. Where the water supply is at least temporarily at a minimum, the water use efficiency plays a greater role in the production capacity of the vegetation.

5.5
Consumption by animals and secondary production

Animals are heterotrophic life forms, *consumers*, that feed directly or indirectly on the organic products of the *primary producers*. They are, therefore, *secondary producers* and their products are secondary products. Depending on their feeding habits, they are classified as herbivores, carnivores, omnivores, or detrivores. The first three are biophages, the consumers that eat plants and animals. *Detrivores* consume dead matter and are often classified as *decomposers*, together with the *saprophytes* which consist mainly of bacteria and fungi, in so far as they belong to the mesofauna and microfauna of the soil up to 2 mm in size (Fig. 5.10).

Quantitatively the importance of the biophages in the ecosystem is small. Only a few percent, at most 10 to 20% of the surface biomass, is consumed by herbivores (Remmert 1992). The highest shares are in the steppes and

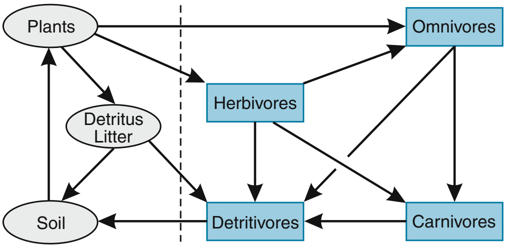


Fig. 5.10. Four main groups of heterotrophic organisms (*blue areas*). The arrows show the paths of organic material transmitted as a result of feeding by heterotrophic organisms

the savannas, where there are large animal populations, the smallest in the oligiotrophic peats of the Boreal zone (Chap. 8). Most of the primary production goes directly to the saprophages.

The material and energy flows through animal organisms is shown in Box 4. The food intake includes a smaller or larger part of the available food, the remainder is disregarded food. During digestion, part of the intake is returned unused as feces, the remainder is assimilated and becomes the gross production. This forms the total of materials and energy available for growth and reproduction by the animal (the net production) and respiration.

The turnover rate varies in speed and efficiency from one animal species to another. The efficiency of animal consumption of different species is shown in Table 14.2. Warm blooded animals assimilate 80 to 90% of the energy intake, many cold blooded animals only from 20 to 30% if they are herbivores. A large share of the energy assimilated by the warm blooded animals is used to maintain body temperature.That part of the assimilated matter which goes into net production is proportionately smaller than in the cold blooded animals. In general about 10% of the food consumed by animals is used for secondary production.

5.6
Waste and decomposition

The above ground litterfall of dead leaves, shoots, branches etc. forms a litter layer on the ground. The thickness varies around a mean value which is determined by the rate at which litter is supplied and decomposed, as long as herbivores, fire or decay of standing dead do not play an important role. Rates at which litter is added and decomposed vary greatly in different ecozones, as does the total amount of litter.

The *decomposition* of litter and below ground waste includes processes of mechanical breakdown, chemical decomposition (dissimilation) and their transition into mineral soil. The soil fauna are important in all three processes, the soil flora also in the chemical process. Many of the detrivores (detritus feeders, saprovores) and saprophytes are microscopic and include algae, fungi, actinomycetales, bacteria and numerous animal organisms.

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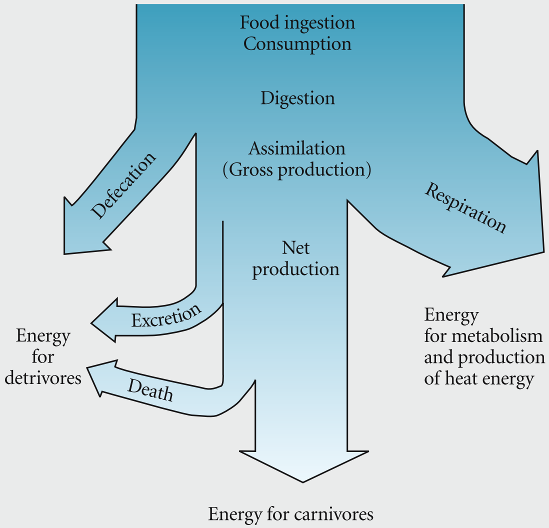
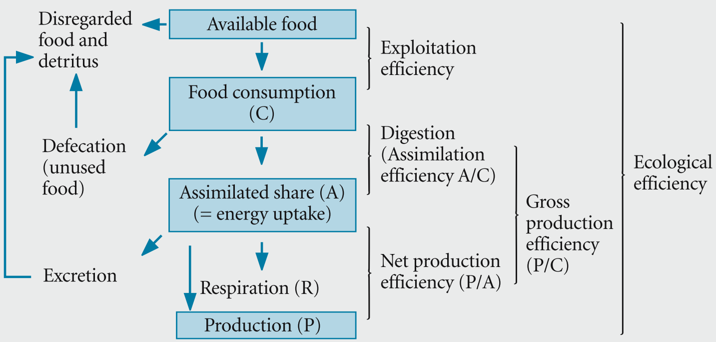
Material and energy flow through an animal organism (or population) and estimated ecological effect



Gross production = Food intake
less defecation
= Assimilated food

Net production = Gross production
less excretion and respiration
= Growth and reproduction

Ecological Efficiency



Exploitation efficiency (Use efficiency, degree of exploitation)	$\frac{\text{Food intake}}{\text{Available food}}$
Digestive (assimilation) efficiency	$\frac{\text{Assimilation (A)}}{\text{Food intake (C)}}$
Net production efficiency	$\frac{\text{Production (Growth + Reproduction) (P)}}{\text{Assimilation (A)}}$
Gross production efficiency	$\frac{\text{Production (P)}}{\text{Food intake (C)}}$
Ecological efficiency	$\frac{\text{Production (P)}}{\text{Available food}}$

Note: efficiencies are usually expressed in %.

Source: Ricklefs 1990

Table 5.3. Decomposition rates of broadleaf and needle litter in selected ecozones

Ecozone	Decomposition rate (k) $\frac{\text{Annual litter input}}{\text{Litter accumulation}}$	Duration of decomposition ($3/k$) Years until 95% decomposed
Polar subpolar Tundra	0.03	100
Boreal	0.21	14
Temperate midlatitudes	0.77	4
Dry midlatitudes grass steppes	1.5	2
Tropics with summer rain	3.2	1
Tropics with year-round rain	6.0	0.5

Source: Swift 1979, see also Olsen 1963

The *rate of decomposition* depends on the composition of the detritus, whether it is coarse or fine, the chemical and biological properties, the climate and edphaic factors. The rate is lower when coarse, woody components dominate in the detritus, especially if they have a high lignin content, and there are high shares of cutin, tannin and wax. Additional factors slowing the rate are low mineral content, especially if there are unfavorable C/N (carbon/nitrogen) or C/P (carbon/phosphorus) ratios, dryness, cold, stagnant water or soil acidity. Favorable C/N-ratios lie between 10:1 and 30:1; wood has a ratio of 100:1 (Larcher 1994). Limiting conditions prevail largely in cold or dry regions. The highest decompositon rates are in the tropical rainforests where humidity and temperature are high (Fig. 4.2). An annual decomposition rate can be estimated from the relationship between the annual supply of waste and the mean stock of available waste (Table 5.3) (Schultz 2000a).

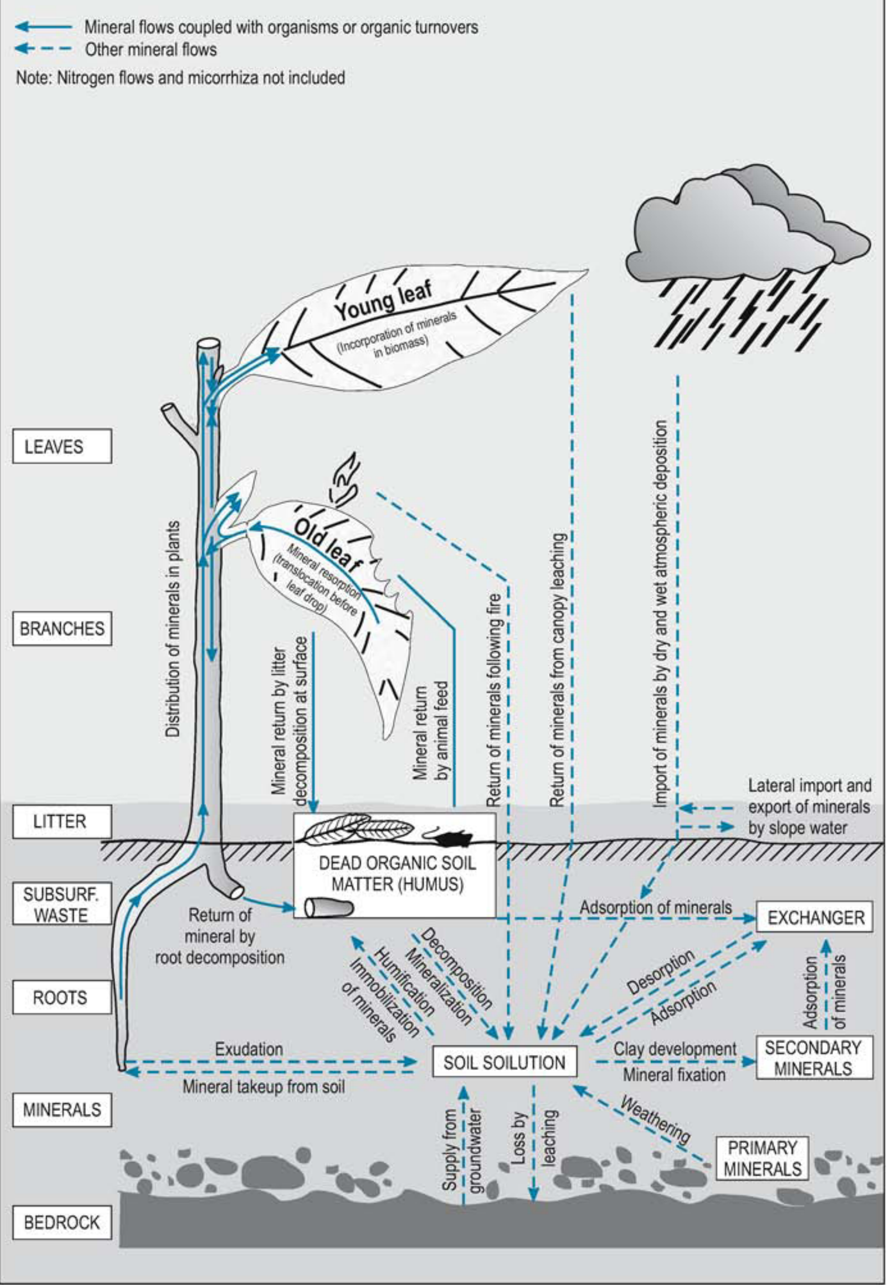
5.7
Turnover of minerals

For the various biochemical synthesis following the photosynthesis, plants require several *mineral nutrients* from the soil. Nitrogen, potassium, calcium, magnesium, phosphorus and sulphur are macro elements with from 0.2–2% of dry matter. Trace elements with a content of at most 0.02% of dry matter include boron, molybdenum, chlorine, iron, manganese, zinc, and copper and, in some plants, silicon and sodium.

The amount and composition of the nutrient requirement for plants is determined by the magnitude of the PP_N and by the mineral contents of the organic substances produced (Box 5). The incorporation of mineral nutrients varies according to the species and also with the various parts of the plant.

The occurrence and flows of mineral nutrients

5



Leaves and needles have a much higher mineral nutrient content than stems and roots. The minerals reach most higher plants with the water from the roots and are, therefore, tied to transpiration on the shoots. If drought or other stresses occur stomata may close and mineral uptake is lower. The uptake of minerals can exceed or fall short of the net primary production requirements. It can exceed them if the nutrients on the shoot or foliage surfaces are washed out in mineral form and during rainfall returned to the soil as *drops* or *trunk flow*. This is termed *canopy* or *foliage leaching*. The uptake can also exceed NPP needs if cell sap is enriched in the leaves during the growing season but not used in the growth process. The uptake can fall short of the requirements for the

Box 5 continued

The mineral reqirements for primary production are usually from two sources: uptake from the soil and internal recycling (the return of minerals by resorption and retranslocation from leaves before they fall). The release of minerals into and on to the soil from litter, dead animals and dying roots in an organically bound form is the result of biological and chemical decomposition processes.

The time span required for mineralization ranges from less than 1 year to several hundred years. Minerals returned by canopy leaching or precipitation are available to the forest for immediate use, as are minerals from plant internal recycling. Indirect recycling which takes place in the middle and long term and direct recycling which takes place in the short term can therefore be separately estimated. Mineral budgets in plant covers and ecosystems are usually estimated in kilograms per hectare and year. If it is assumed that the return of minerals occurs mostly by means of the surface and subsurface waste, the following relationships are valid.

$$\text{Mineral uptake from soil} = \text{minerals incorporated in biomass} + \text{minerals returned from canopy leaching}$$

Mineral incorporation in biomass

$$= \begin{matrix}\text{Minerals}\\ \text{in biomass increment}\end{matrix} + \begin{matrix}\text{Mineral return by litter fall}\\ \text{and below ground waste}\end{matrix}$$

$$\begin{matrix}\text{Turnover}\\ \text{of minerals}\end{matrix} = \frac{\begin{matrix}\text{Mineral return by litter fall and below ground waste}\\ + \text{Mineral return from canopy leaching}\end{matrix}}{\text{Mineral uptake from soil}}$$

$$\text{Mineral use efficiency} = \frac{\begin{matrix}\text{Minerals in biomass increment}\\ + \text{Mineral return by litter fall}\\ \text{and below ground waste}\end{matrix}}{\text{Mineral uptake from soil}}$$

NPP if minerals incorporated in the organic matter of the leaves or needles are translocated to the shoots or roots that do not drop or die off in the autumn or at the beginning of the dry season. These minerals are, therefore, available to the net primary production during the following years.The share of translocated nutrients can be estimated by measuring the difference in minerals between mature and old leaves or recently fallen leaves, taking into account the effects, if any, of leaching. Nitrogen and potassium are often involved in the translocation process.

The return of minerals to the soil takes place in mineral form following canopy leaching or fire and in organic form in the litter, subsurface waste or animal feed. For the release of organically bound nutrients from plant waste and animal remains there are varying time spans depending on their composition and the rate of decomposition of organic matter. Potassium, for example, is released more rapidly than either nitrogen or phosphorus. Where rates of mineralization are low, the release of both nitrogen and phosphorus is at a minimum with a limiting effect for plant growth.