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J. Schultz

The Ecozones of the World

The Ecological Divisions of the Geosphere

With 189 Figures and 48 Tables

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Preface

The preliminary work on this book goes back to lectures and seminars which I held on the subject of an *ecological division of the world* at the Geographical Department of the Aachen University of Technology (RWTH Aachen). The idea of presenting this material in book form arose as I became aware that no modern compendium exists, in either German or English (or in any other language, as far as I know), which could have aided me in preparing these courses or would have helped the participating students to review the material presented in the classroom.

Existing studies on major land ecosystems, some of which are highly detailed, have been published over the past 15 years by firms such as the Springer-Verlag (*Ecological Studies*), the Cambridge University Press (*International Biological Programme*) and the Elsevier Scientific Publishing Company (*Ecosystems of the World*); all suffer from the fact that individual aspects (mainly botanical-ecological ones) are given the utmost consideration, while other aspects (often pedological and geomorphological ones) are almost entirely neglected.

Furthermore, it is most aggravating that the various studies have failed to establish consistent terminology, units of measurement, and organization of the data for all of the global ecosystems, thus making it difficult even for the knowledgeable reader to make comparisons. The individual nature of each ecozone therefore remains unclear, since it is precisely these differences that allow those characteristics peculiar to a specific ecozone to be unmistakably recognized.

Moreover, the book series mentioned (as well as those not mentioned here) deal with only a selection of the major geographical regions. None of them really attempts to give a more or less comprehensive introduction to the great ecozonal divisions of the geosphere.

It is a premise of this book that the large geographical regions of the world should be treated as *geozonal ecosystems*, using quantitative characteristics as far as possible. A rich source of background material for this approach is represented by the large number of regional ecological studies, which have since become available – particularly those published as part of the International Biological Programme. The present book also strives to give those readers who have less knowledge of modern ecological research a brief introduction to a few of the terms and methods applied in quantitative ecosystem analysis (in particular, cf. Chap. 2.5).

Nine terrestrial ecozones are distinguished and described in separate chapters. Each of these regional chapters is subdivided by the same headings, i.e. distribution, climate, relief and hydrology, soil, vegetation and animal life, and land use. The contents of the corresponding subdivisions have similar organizations and use consistent terminology and units of measurement. This should help the reader greatly in finding and comparing information which especially interests him; e.g. he can easily find which soil units are characteristic for each of the ecozones or how ecozones differ with respect to soil units. Other features and processes handled in this way include weathering of rocks, erosion and sedimentation processes, soil formation, solar radiation, growing seasons, moisture regime, vegetation structure and dynamics, nutrient cycling, energy fluxes, ecosystem models, agricultural use and potential.

Soil types are classified and named in accordance with the FAO-UNESCO classification system, which has been utilized in preparing a unique detailed soil map of the entire earth (and an even more detailed one covering the European Economic Community). With this map, internationally applicable soil terminology has been made available for the first time. The terminology may sound somewhat foreign to unaccustomed ears, but this will not be the case for long. The reader should not let himself be put off by foreign-sounding soil names – he will have to learn them sooner or later anyway!

This book was conceived mainly to serve students of geography. I would be pleased if others also find interest in it – students of biology, agricultural sciences or forestry, and geography or biology teachers striving to further their knowledge, and all those interested in ecology and geography who would like more information on the specific characteristics of the major regions of the earth, if only for the purpose of preparing themselves for a journey to another part of our planet. During my stays in foreign regions, I have at times wished for a book which–as is the intended purpose of the present volume – could have provided in concentrated form a summary and explanation of the most significant characteristics of the major regions of the earth and their interactions with one another.

I wish to thank my colleague at the Geographical Department, Prof. F. Ahnert, for critical commentaries on the sections on relief, and Dr. R. Schmidt-Lorenz from the Institut für Weltforstwirtschaft (World Forestry Institute) in Hamburg for his comments on the sections on soil. Prof. H. Beringer from the Landwirtschaftliche Forschungsanstalt Büntehof (Büntehof Agricultural Institute) in Hanover provided many valuable suggestions. Recognition should also go to my students Peter Breuer, Olaf Franken, Susanne Rebig and Anne Salber for the active support they provided. Each of them in his/her own way made important contributions to the completion of this book. The final drawings for the figures were made by our cartographer, Mr. A. Ehrig. I thank all those who helped me in preparing this book, including the many who cannot be mentioned here by name.

Aachen, July 1994 Jürgen Schultz

Contents

1 Introduction: on the Methodology of Dividing the World into Ecozones

Ecozones are global divisions which have their own characteristic interplay of climatic factors, morphodynamics, soil-forming processes, living conditions for plants and animals, and production potentials for agriculture and forestry. Correspondingly, they are distinguished by different climates, landforms, soil units, plant formations and biomes, and land use systems.

As regards their delimitation and the purpose behind it, namely to create a system for classifying natural (and, to a certain extent, cultural) regions of the earth, the ecozones of the world are comparable to those regions referred to by other authors (e.g. Passarge 1929; Maull 1954; Müller-Hohenstein 1981; Bramer 1982; Haggett 1990) as "landscape belts" (Landschaftsgürtel), "geographic zones", "geozones", etc. The former differ from the latter in content, however, in that the ecozones are more distinctly described as *geozonal ecosystems.*

This means that the (more qualitative) description of single-feature complexes such as soils, vegetation and relief is supplemented by the (more quantitative and integrative) analysis of matter and energy reserves and turnovers within and between different ecosystem compartments. The matter *reserves* dealt with include, for instance, the biomass of plants and animals, dead soil organic matter, and mineral nutrients in vegetation and soil; the matter *turnovers* dealt with are those of primary production, animal consumption, secondary production, litter fall, decomposition of organic wastes, and mineral and water cycling; with regard to organic substances and transfers, the *energetic* aspects are also considered. This way of representing ecozonal characteristics has become possible since modern ecological research has provided rich and profound data on a large variety of regional ecosystems.

The term *ecozone is being used here for the first time.* In the (hierarchical) system of natural regions, whose basic unit is the ecotope, this new term represents the highest-class heading. Its advantages over the other terms already mentioned lie in the fact that it is brief, it can be used adjectivally, it is related to the basic term ecotope, and its meaning is self-evident. The prefix *eco* is understood from its usage in terms such as ecology and ecosystem, while *zone,* which appears in the terms climatic zone, vegetation zone etc., is understood as the highest (global) level of regional (planetary) classification (particularly when, as in the present case, the words "of the world" are appended). Most readers will be surprised less at the fact that the term ecozone is being introduced here than at the fact that it did not already exist.

The attempt to subdivide the world into a few ecological regions, i.e. ecozones, which are highly uniform as regards their abiotic and biotic factors, the processes controlling their ecosystems, and their limits and prospects for human exploitation, is difficult for several reasons and has therefore been subject to criticism from some sides (e.g. Hard 1982). The problems, which are difficult to solve and whose existence should not be denied, include the following:

a) *The wide range of small-scale variations in environmental conditions*, which exist everywhere on earth, can only be fitted into an ecozonal classification by applying many constraints and by accepting considerable blurring of the data as a result.

b) *A number of phenomena cannot be classified at all due to the lack of distinguishable environmental influences*; this group includes, for example, the land/sea interface, the overall relief of the earth, the distribution of rock types and mineral resources and many historically related phenomena (classification according to national boundaries, languages and so-called cultural groups). These characteristics and the effects they have, e.g. on the climate or the use of the land, disrupt the process of ecozonal classification, or they fail to fit into such a system at all.

c) *The remaining geographical elements, which are more or less dependent on the surrounding environment (and thus form part of the ecozonal web), seldom have distinct boundaries.* Typically, the changeover from one region to another is gradual and takes place over broad regions, in some cases along very different parameters (exceptions to this are the land/sea interfaces and boundaries formed by mountain ranges). The drawing of boundaries as distinct lines must, therefore, remain a questionable practice; all the more so when, as in the present case, they claim to be the boundaries delineating entire *groups of characteristics.*

d) *Many phenomena found on earth have developed over long periods of time.* For this reason their present form is the result of various environmental conditions to which the areas were subjected. Such regions can either not be classified at all or only with severe constraints.[1]

As a result of the problems just discussed:

1. ecozonal boundaries must to a certain extent be drawn arbitrarily (for example, along climatic thresholds) and are applicable only for a certain number of geographic characteristics; and

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[1] Particularly in the case of landforms, the number of phenomena originating from the geological past is large. A morphogenetic explanation based on the processes predominating today is only possible on a very limited scale. Many soils also exhibit characteristics which have resulted over long periods (paleosoils); and most agricultural practices have strong historical roots.

Much less prevalent are long-term characteristics in vegetation, since changes in environmental conditions cause rapid, sweeping changes in plant life (the postglacial changes of the forests in central Europe are a good example of this); and the climate is completely independent of elements from the past: the present climatic conditions are dictated solely by the global differentiation in energy supply from the sun, the earth's rotation and the existing tellurian and orographic conditions.

2. regardless of how the zonal boundaries are drawn, the variation in conditions in each of the zones must naturally remain large.

Nevertheless, an ecozonal classification of the world is possible and useful– that is the thesis of this book; however, it is subject to the following premises and concessions:

a) *Variations within the ecozones cannot be viewed as being inconsistent with their boundaries.* The decisive point is that at least some highly significant common elements do exist within each of the ecozones. Significance is measured in the case of characteristic factors according to their scale and functional dominance, and in the case of characteristic forms according to their distribution and conspicuousness. Significant factors and form characteristics in this sense are, for example, *inhibited decomposition of organic matter* and *thick raw humus layers on the ground* in the Boreal Zone or *winter rain* and *sclerophyllous (hard-leaved) vegetation* in the Mediterranean-Type Subtropics. To recognize common elements within zones, an adequate (global) yardstick is the most important prerequisite. When this tool is applied, many discrepancies disappear on their own accord. A figurative comparison may be able to clarify this point: when a small section of a small-scale world map is compared to a detailed, large-scale map of the same area, the former is found to be inexact and incomplete, and generalized to the point of being erroneous; but no one would argue that this map is of no value.

b) *Ecozones can only be characterized by the average conditions that predominate in them.* "Average" conditions are found in areas, which

- have no excessive runoff (erosion and denudation),
- exhibit neither considerable input (sedimentation) nor waterlogging,
- are at sea level or slightly above,
- have neither a distinctly continental nor a distinctly maritime climate.

Special cases in an orographic or edaphic sense can be included in the characterization if they are typical for a zone; this applies, for example, to vertisols, saline soils or histosols, which are typical final links in relief-related soil sequences (catenas) of the Seasonal Tropics, the arid lands and the Boreal Zone, respectively.

c) *The drawing of boundaries between the ecozones is of secondary importance.* The main emphasis must be placed on determining the (average conditions of the) core areas.

d) *All quantitative data can only be viewed as guidelines* (even when ranges are indicated, these do not reflect the actual extremes but rather the ends of the spectrum within which most data lie). The data are intended to make the global differences between the ecozones clearer and can serve as a measure for determining local deviations within each zone.

The major aim of this book, by listing and characterizing the ecozones in the manner described, is to aid in establishing a kind of *global classification system* (orientation guide) which

- allows immediate listing of several important characteristics of any area on earth; and
- is suitable as a basis for further detailed investigation (starting with the question: in what way does a certain area in an ecozone differ from the overall characteristics of the ecozone in which it is found?).

The ecozonal approach, in principle, follows a line of research which is of quintessential geographical importance, i.e. it describes and assesses the characteristic features and processes, and their interaction, in a particular area, in this case an ecozone.

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2 General: the Treatment of the Ecozones and Global Overviews of Selected Characteristics

Only the terrestrial regions of the world are considered; marine ecozones are ignored. The land portion is divided into nine ecozones, although an even larger number of ecozones might be justified. For instance, the subdivisions within some of the ecozones could be elevated to the status of ecozones themselves.

Ecozonal classification is performed according to *natural* criteria. Cultural elements are included only insofar as they evidently depend on natural conditions. Such dependencies, are of course present in the case of *land use*, for instance, otherwise they are the exception or of only negligible importance.

Each of the nine (terrestrial) ecozones is described in a separate chapter (Chaps. 3.1–3.9). The order of their appearance is roughly comparable to their order on the earth from the poles to the equator.

For the sake of consistency, each ecozone description is subdivided by the same headings, and the contents of the corresponding subchapters are based in each case on the same selection of features, to the extent that the latter reflect the individuality of each zone.

Chapters 2.1–2.7 describe these selected features in general, providing global overviews for some of them, and explaining abbreviations and special terminology, particularly those taken from biology and soil science. Terminological explanations are meant to serve not only as an aid in understanding the regional chapters which follow, but also as a stepping stone to the extensive biological/ecological and soil science/ecological literature available.

This "rigid" structuring of the way in which the individual ecozones are handled was chosen in order to make it easier for the reader to find and compare information on the various types of features. The reader will thus be better able to verify differences between the ecozones and, I hope, recognize their most salient characteristics.

2.1 Distribution

Location on Earth. Figure 1 gives an overview of the ecozonal division of the world. In addition, each ecozone is shown on its own distribution map at the start of the corresponding regional chapters (3.1–3.9). Where applicable, geographic designations such as taiga, Great Plains, Namib or Sahel are noted. The climatic

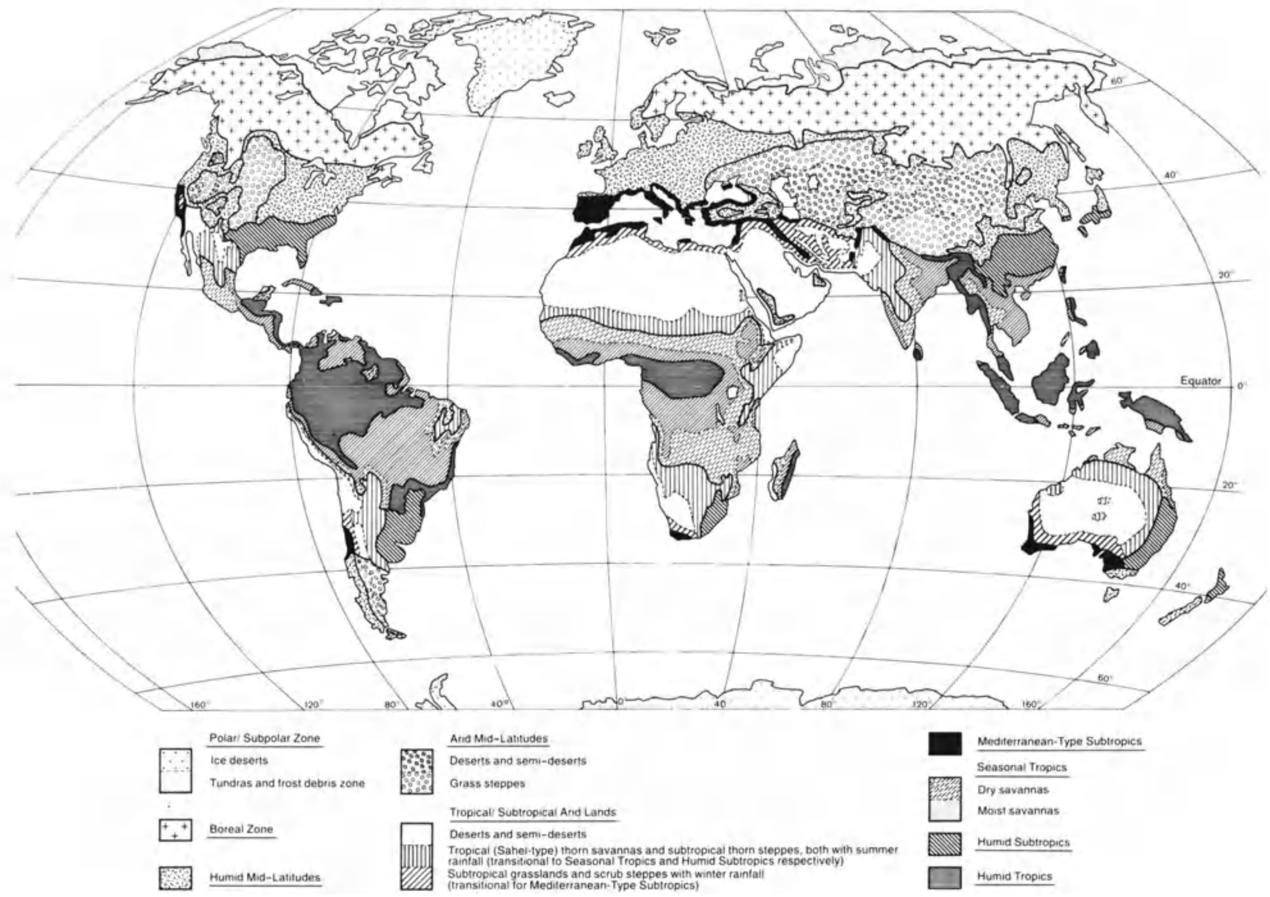

Fig. 1. The ecozonal divisions of the world

diagrams included (from Walter and Lieth 1960–1967) are intended both to show the conditions typical of the zone and to make clear any differences exhibited by the subdivisions; they do not show extreme variations occurring only in small areas. It should be noted that the diagrams of the Southern Hemisphere are transposed by 6 months, i.e. they begin with July rather than with January (see Fig. 3 for further explanations to these diagrams).

Boundaries. The ecozonal boundaries drawn on the distribution maps follow the subdivision of the earth into climatic zones established by Troll and Paffen (1964) in their map on *Seasonal Climates of the Earth.* This is a stopgap measure, but in view of the already-mentioned fact that this book is interested first and foremost in describing the average or most common features and processes in the core areas of the ecozones, the outer borders can be considered of secondary importance.

Some geographical regions are difficult to integrate into one ecozone. These are indicated as transitional regions.

Given the uncertainities prevailing with respect to the boundaries, the *data on surface area* (from Paffen 1980) should be viewed merely as rough estimates (Table 1).

A few of the ecozones are subdivided into comparatively independent *subregions,* such as the Polar/Subpolar Zone, which is divided into the glacier-

Table 1. Ecozones of the world

Ecozones of the world	Approximations to the climatic zones according to		Surface area[a] (Paffen 1980)	Proportion of landmass[a] (Paffen 1980)
	Troll/Paffen[a] (1964)	Walter/Lieth (1960–1967)	Mio km^2	%
1 Polar/Subpolar Zone	I_{1-4}	IX	22.1	14.8
1.1 Tundras and frost debris zone	I_{2-4}		5.8	3.9
1.2 Ice deserts	I_1		16.3	10.9
2 Boreal Zone	II_{1-3}	VIII	19.5	13.0
3 Humid Mid-Latitudes	III_{1-8}	VI	14.5	9.7
4 Arid Mid-Latitudes	III_{9-12}	VII	16.4	11.0
4.1 Grass steppes	III_{9-11}		11.9	8.0
4.2 Deserts and semi-deserts	III_{12}		4.5	3.0
5 Tropical/Subtropical Arid Lands	$V_{4-5}+IV_{2-3,5}$	III	31.2	20.9
5.1 Thornbush and thornscrub savannas and subtropical thorn steppes	V_4+IV_{2-3}		13.6	9.2
5.2 Deserts and semi-deserts	V_5+IV_5		17.6	11.7
6 Mediterranean-Type Subtropics	$IV_1(IV_{1-2})$	IV	2.7 (6.2)	1.8 (4.2)
7 Seasonal Tropics	$V_{2-3}(V_{2-4}+IV_{3-4})$	II	24.4 (36.1)	16.3 (24.2)
8 Humid Subtropics	$IV_{4,6-7}$	V	6.1	4.1
9 Humid Tropics	$V_1(V_{1-2})$	I	12.5 (26.6)	8.3 (17.7)

[a] Values in parentheses refer to extended ecozonal delimitations (i.e. including transitional areas whose classification is not definite).

covered regions (ice deserts), the frost debris regions and the tundras, or the Tropical/Subtropical Arid Lands, which are further subdivided into the deserts/ semi-deserts, and semi-arid shrublands (including the tropical Sahel-type scrubs and the subtropical thorn steppes). The distribution maps show the more important of these regional subdivisions.

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Chapter 2.1: Distribution

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2.2 Climate

The climates are described on the basis of those elements having a recognizable influence on other environmental factors, for instance, on the processes of morphogenesis, soil formation, biological fixation of solar energy, or of agricultural and forestry production; that is to say, mainly those elements belonging to the morphoclimate, soil climate, bioclimate, agroclimate, etc. Such climatic properties can be defined only to a limited extent by quoting the average values of the individual climatic elements; information on the frequency and magnitude of individual meteorological events (e.g. frequency of freeze-thaw cycles, temperature amplitudes, variability of precipitation) is at least equally necessary. The descriptions of climates attempt to do justice to these needs (cf. also Chap. 2.3).

Solar Radiation

In general, this refers only to the short-wavelength (290–3000 nm) solar radiation which reaches the earth's surface as direct radiation or as diffuse skylight and cloudlight *after* penetrating the atmosphere, i.e. the total *incoming (short-wave) radiation* or global radiation.

This must be distinguished from two other types of radiation which are sometimes confused with the term incoming radiation. These are calculated from the geographical coordinates of a location; one type completely ignores atmospheric factors (solar climate radiation), and the other excludes the major disruptive factor, namely cloud cover (incoming radiation under cloudless conditions). Neither of these can be used for geoecological investigations because, in contrast to the actual incoming radiation (which can be measured at the earth's surface), they are not clearly correlated with an ecozone's energy and heat budgets. It is the actual incoming radiation that is the direct source of energy input and that dictates thermal processes (heating, evaporation) and photoenergetic processes (photosynthesis) which are possible in an ecosystem.

Sometimes the radiation data mentioned in climatological/ecological studies refer only to particular portions of the incoming radiation, i.e. the absorbed radiation, net radiation (radiation balance) or the *photosynthetically active (exploitable) radiation (PAR)*. The latter covers the narrower band of the solar spectrum which can be used by green plants for photosynthesis. It lies between 380 and 710 nm and thus is more or less equivalent to the spectrum of visible light. About half the energy input through incoming radiation belongs to this spectrum.

The definition of the two other radiation parameters can best be illustrated by a (simplified) radiation (or energy) balance equation (Box 1). Excess energy present in the case of a positive *radiation balance* leads to a sensible heat flux (increase in temperature) and (if water is present in solid or liquid form) to a latent heat flux, i.e. a transfer of heat-energy required for melting ice (heat of fusion) or for evaporation (heat of evaporation). In the case of a negative radiation balance, namely when outgoing (long-wave) radiation outweighs incoming (absorbed) radiation, which is the case at night or in many areas during the winter months, the latent and sensible heat transfer mechanisms are reversed: the condensation of water vapour and the freezing of liquid water can lead to the release of latent heat of condensation and latent heat of fusion and at the same time to the withdrawal of sensible heat and thus, as is always the case in the long run with negative radiation balances, to a drop in temperature.

Radiation data presented in the climatological-ecological literature are difficult to compare, not only because of the variation in the type of radiation mentioned, but also due to the different *units of measure* used (calories or joules; conversion formula: $1\,\mathrm{J} = 0.239\,\mathrm{cal}$, $1\,\mathrm{cal} = 4.1868\,\mathrm{J}$) and the different relationships to space and time (cm^{-2}, m^{-2}, ha^{-1}, and s^{-1}, min^{-1}, d^{-1}, mon^{-1}, a^{-1}), which in some cases are given special names, e.g. langley ($1\,\mathrm{ly} = 1\,\mathrm{cal\,cm}^{-2}$), watt ($1\,\mathrm{W} = 1\,\mathrm{J\,s}^{-1}$) or lux (1 klx equals about 4–10 $\mathrm{W\,m}^{-2}$, depending on the light source). Where possible and appropriate, all radiation data given in this book have been converted to the uniform units of measure **kJ ha^{-1}** and **kJ ha^{-1} a^{-1}**. This unit of measure is recommended because solar energy is then seen as the supplier of energy for photosynthesis, and thus for the primary production of natural vegetation, as well as of agricultural crops and forests. The latter are usually measured in terms of hectares and years.

To determine the *radiation energy input* in each of the ecozones, i.e. the *solar climate*, world maps of annual or monthly totals for incoming radiation published by Budyko (1963a); Landsberg (1963); Löf et al. (1966) and De Jong (1973) were used. The results are shown in Fig. 2a and Table 7.

The peak solar radiation (highest monthly averages) is similar in all the zones. The differences are due to the unequal length of periods with high radiation gains

1

Simplified radiation (or energy) balance equation

$(Q + q)\ (1 - \alpha) - Lu + Ld = LE + H$,
where
Q = direct solar radiation
q = diffuse atmospheric radiation
α = reflected radiation
Lu = outgoing radiation (terrestrial thermal radiation)
Ld = counter-radiation (atmospheric thermal radiation)

G = global radiation, of which less than 50% = PAR
= Albedo
= Thermal (long-wave) radiation

$G\ (1 - \alpha)$ = absorbed or net incoming (short-wave) radiation
$Lu - Ld$ = effective or net outgoing (long-wave) radiation

$G\ (1 - \alpha) - Lu + Ld = R$ (all wave-length) radiation balance [net incoming (all wave-length) radiation]

LE= latent heat flux: transfer of thermal energy connected with the change in the state of water, without changing the temperature of the latter; i.e. the requirement for evaporation (heat of vapourization) or melting (heat of fusion), or the release of heat during condensation and freezing; heat of sublimation in cases where there is a direct change from the solid to gaseous state, or vice-versa
H= sensible heat flux: (temperature-effective) transfer of thermal energy through molecular conduction at boundary layers; a distinction is sometimes made between heat flux into (out of) the soil (or snow cover) and heat flux into (out of) the atmosphere

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This equation does not take into account lateral (advective) energy transport, reflection of long-wave counter-radiation or the energy fixed by plants through photosynthesis

Box 1

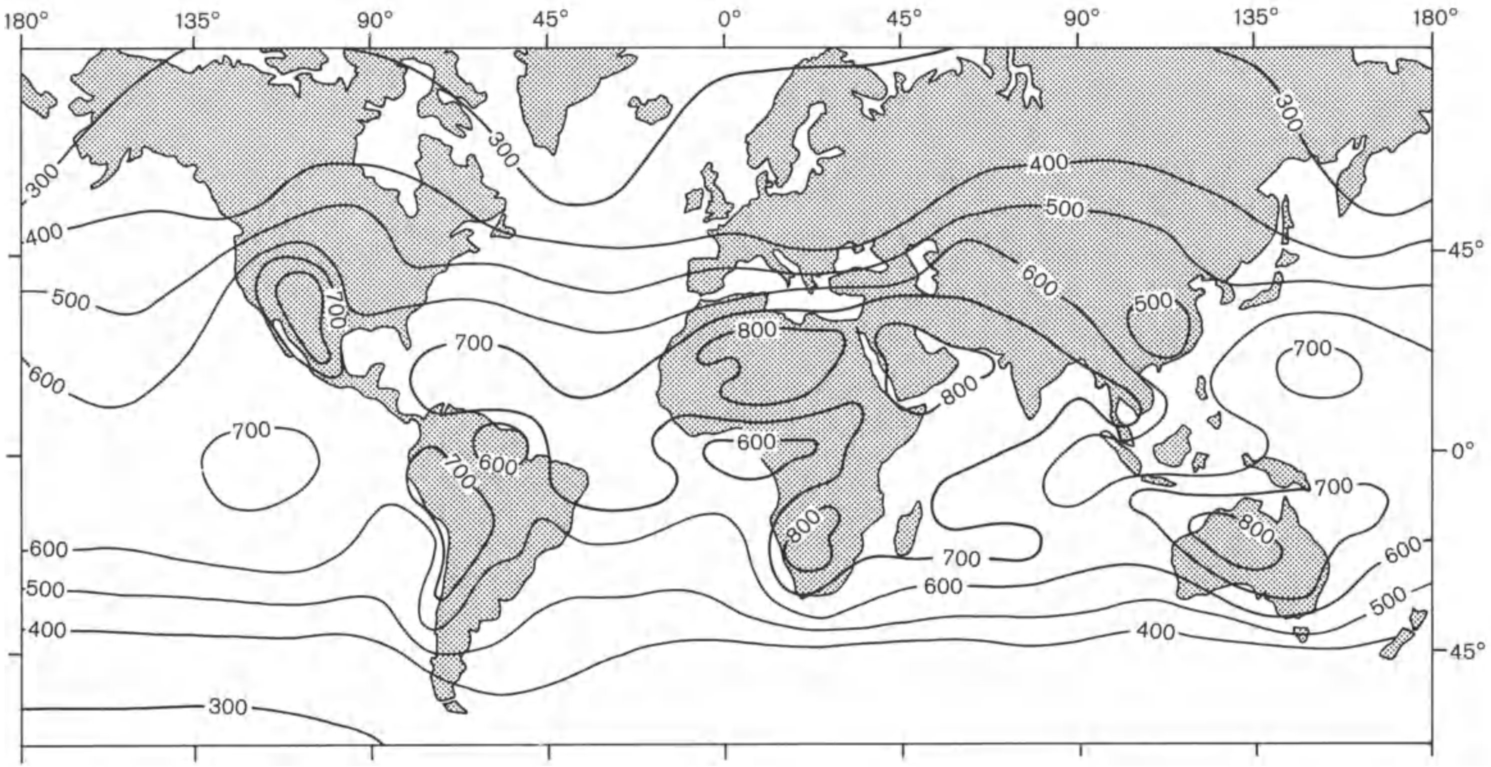

Fig. 2a. Annual global radiation in 10^8 kJ ha^{-1}. (De Jong 1973)

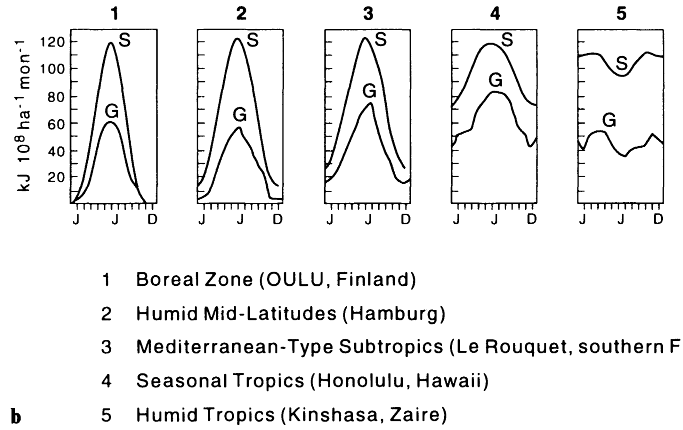

Fig. 2b. Extra-atmospheric solar radiation (*S*) and global radiation at the surface of the earth (*G*) throughout the year at stations representative for five ecozones. (After Galoux et al. 1981)

and of periods with thermal/hygric conditions which allow the plants to exploit the radiation energy input (Fig. 2b).

Growing Season

The period during which climatic conditions allow plant growth is termed the growing season. Its range varies worldwide from year-round to zero. Limitations are dictated by the lack of heat or water, or both.

The assumption is made here that all months with an average temperature (t_m) of at least +5 °C form the growing season as far as *heat requirement* is concerned. The monthly average of +5 °C has been shown through experience in many plant communities to represent the minimum requirement for any notable amount of plant production (growth). In individual cases, the species and growth stages of the plants present can lead to considerable differences in requirements and tolerances.

The temperature +5 °C was selected as the threshold value for practical reasons as well: it makes it possible to determine growing seasons worldwide from the climatic data available much more quickly than would be the case using daily temperature data (of the same or similar level), as is usually done in regional studies.

There are a great number of more or less complex methods of calculating a *hygric threshold* (cf. Giese 1974). This book uses one of the "physically questionable" (Weischet 1983, p. 152) methods of determining humidity which were developed on a purely empirical basis by De Martonne (1926); Lauer (1952); Jätzold (1962) and Walter and Lieth (1960–1967), among others. For practical reasons, the method developed by the last two authors is preferable: their two-volume world atlas of climatic diagrams provides the user with a rapid overview of the significant differences in humidity, in terms of magnitude, between the earth's various regions. This is certainly adequate for the ecozonal dimension.

In principle, the other methods of calculation could also satisfy our purposes. On a global scale they all provide similar guidelines for the length of humid periods; the differences in any given region are for the most part less than half a month and at the most one month, and therefore remain within the range which normally applies to the differences in humidity within the individual ecozones.

The *climatic diagram* from *Walter* (Fig. 3) shows the curves for average monthly precipitation (in mm) versus the average monthly temperatures (in °C), in the ratio of 1 : 2; this means, for instance, that the distance along the ordinates is the same for 40 mm precipitation as it is for 20 °C air temperature. At this ratio, times during which the precipitation curve is above the temperature curve, are considered humid, the remaining periods as arid. Climatic diagrams of this type have come into use worldwide in ecological investigations covering large areas.

The *growing season*, then, is the sum of those months in the year in which the average temperature $t_m \geq 5$ °C and the precipitation level is in the order of P (in mm) > 2t (in °C). The period during which these conditions prevail can be quickly and accurately determined using the climatic diagrams. The data on growing seasons given for the various ecozones in this book are derived from measurements of many such diagrams.

Not only the length of the growing season and the radiation energy available (during this period), but also the air temperature, are of importance to plant production. In the tropics, the average monthly temperature exceeds +18 °C in

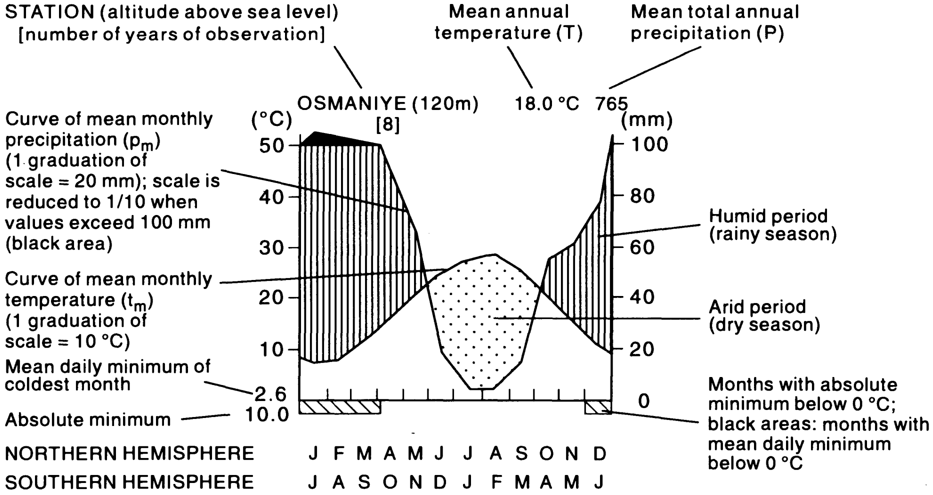

Fig. 3. Explanation of Walter's climatic diagrams (from 1955 onwards)

all months; this is also true for the subtropics during at least 4 months of the year, but at the tree line in the Boreal Zone only 1 month has an average temperature which reaches 10 °C.

Hygrothermic Growth Conditions in the Ecozones

In all ecozones outside the Tropics, i.e. ecozones 1–4 (see Table 1), the air temperatures during the winter months drop to levels (at least 1 month with $t_m < 5\,°C$) which cause an interruption of plant growth. In the tropics and subtropics, i.e. ecozones 5–9 (see Table 1), plant growth can be interrupted due to dryness. The hygrothermic growth conditions in each of the nine ecozones can be characterized as follows:

1. *Polar/Subpolar Zone.* Brief warming in summer allows plant growth during, at most, 3 months; but, even then, the air temperatures remain far below the optimum level for life processes.
2. *Boreal Zone.* The summer growing season lies between 4 and 6 months, with air temperatures which still for the most part (except in areas with distinctly continental climates) remain well below the optimum.
3. *Humid Mid-Latitudes.* The shorter and less severe drop in temperature during winter limits the growing season to only 7–11 months; summer temperatures are somewhat below optimum levels.
4. *Arid Mid-Latitudes.* Low winter temperatures and aridity in the summer both limit the growing season to 5 (5.5) months or less. Air temperatures in summer are very high.
5. *Tropical/Subtropical Arid Lands.* Growth conditions are usually limited all the year round by aridity (at most 5 mildly humid months); summer temperatures are very high and winter temperatures either remain above the freezing point (tropical deserts, semi-deserts, and semi-arid shrublands) or fall slightly below it (subtropical deserts, semi-deserts and thorn steppes).
6. *Mediterranean-Type Subtropics.* Summer dryness limits the growing season period to 5–9 (winter) months or at least significantly restricts plant growth during the summer. Air temperatures during the winter growing season remain well below the optimum levels for life processes.
7. *Seasonal Tropics.* Aridity in winter limits the growing season to 5–9 (9.5) months or at least considerably reduces plant growth during the winter. Air temperatures during the growing season are optimal (at least as high as in ecozone 9).
8. *Humid Subtropics.* The temperature drop in winter is severe enough (frost at regular intervals) for plant growth to be limited for 1–2 months (even though the monthly averages usually remain above +5 °C). Air temperatures in the summer, on the other hand, are as high as in ecozone 9.
9. *Humid Tropics.* Unlimited growth conditions all the year round or slight water stress for at most 1–2 months.

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2.3 Relief and Hydrology

Relief is treated by describing the characteristic (currently active), exogenous morphological processes in each ecozone and the land surface components formed by them. Landforms stemming from tectonic movement and structures or from earlier morphoclimatic conditions (see below) are mentioned only to complement the other data. Such landforms are always azonal. They usually dominate because of the amount of current relief for which they are responsible.

Geomorphic Processes and Landforms

Most of the factors (= conditions acting on the morphogenesis of an area) on which land forming (= morphodynamic processes) is based are (in the final analysis) of climatic origin. A classification of the earth into regions of similar morphodynamic processes (forming mechanisms) thus follows roughly the same scheme as a global classification of climates and can therefore be included in the ecozonal classification method (cf. morphogenetic maps by Stoddart 1969; Wilson 1969; Büdel 1971; Tricart and Cailleux 1972; Hagedorn and Poser 1974; Wilhelmy 1974). This means that many of the ecozones have their own landform characteristics and are, therefore, also morphoclimatic zones.[2]

Morphogenesis varies between the zones according to:

1. Type and rate of *weathering* (= breakdown of rock or mineral components of the soil) whether due to

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[2] There are climatically induced landforms in every ecozone whose presence cannot be explained by the morphodynamics of the prevailing macroclimate (or zonal climate). These have either developed in the geological past under other climatic conditions (paleoclimate), or they are special forms determined by *edaphic* (microclimatic) conditions. Such extraneous landforms are referred to in the first case as *fossil* or *relict* landforms and, in the second, as *azonal* landforms. In describing the various ecozones, the presence of relict and azonal landforms is noted only where they cover large areas (e.g. ice age formations in the Boreal Zone and the Humid Mid-Latitudes).

   a) physical (mechanical) weathering, e.g.
      - frost splitting,
      - temperature weathering,
      - salt cracking; and/or
   b) chemical weathering, e.g.
      - dissolution,
      - oxidation,
      - hydration and/or
      - hydrolysis.
2. Type and rate of *material transport* (erosion/denudation and sedimentation processes) whether due to
   a) gravitational mass movement,
   b) sheet erosion (hill wash, rill erosion),
   c) fluvial erosion,
   d) glacial action and/or
   e) eolian erosion.

Which of these exogenous morphological processes predominates, and thus, which forms/products – if any – of weathering, removal and/or sedimentation result, depends in the final analysis on the moisture conditions (including those in the soil) and on the temperature. Figure 4 shows in a (very schematic) profile from the pole to the equator how the depths and structures of the weathered mantle differ as a function of climates.

Morphodynamic processes are frequently modified to varying degrees by the vegetation cover which, in turn, is also mainly dictated by the climate. In contrast to the climate, which changes continuously throughout the zones, the vegetation boundaries can be much more distinctly drawn along defined climatic thresholds (e.g. polar and mountain tree lines or various boundaries of arid regions); therefore, linear demarcations between climatic-morphological zones are more likely than might have been expected from the climatic/morphological relationship alone.

Not all of the ecozones, which are delimited mainly according to climatic criteria, can claim their own characteristic morphogenesis. All deserts and semi-deserts are morphogenetically similar, for instance, regardless of whether they lie in the tropics/subtropics or the mid-latitudes; the same applies to the humid climates of the tropics and subtropics.

As a rule, *hygric* differences produce stronger morphological effects than thermal ones. *Thermal climatic factors* are important, however, in humid areas where the temperature drops below the freezing point, either often or for extended periods of time, namely in the Polar/Subpolar Zone, the Boreal Zone and the Humid Mid-Latitudes, as well as in mountain ranges outside these zones. The frequency and intensity of freeze-thaw cycles in these zones and at high altitudes differ widely and therefore have quite distinct effects.

Climatic effects on morphogenesis are seldom the result of *average* climatic conditions. The average values, provided by climatologists, are therefore often

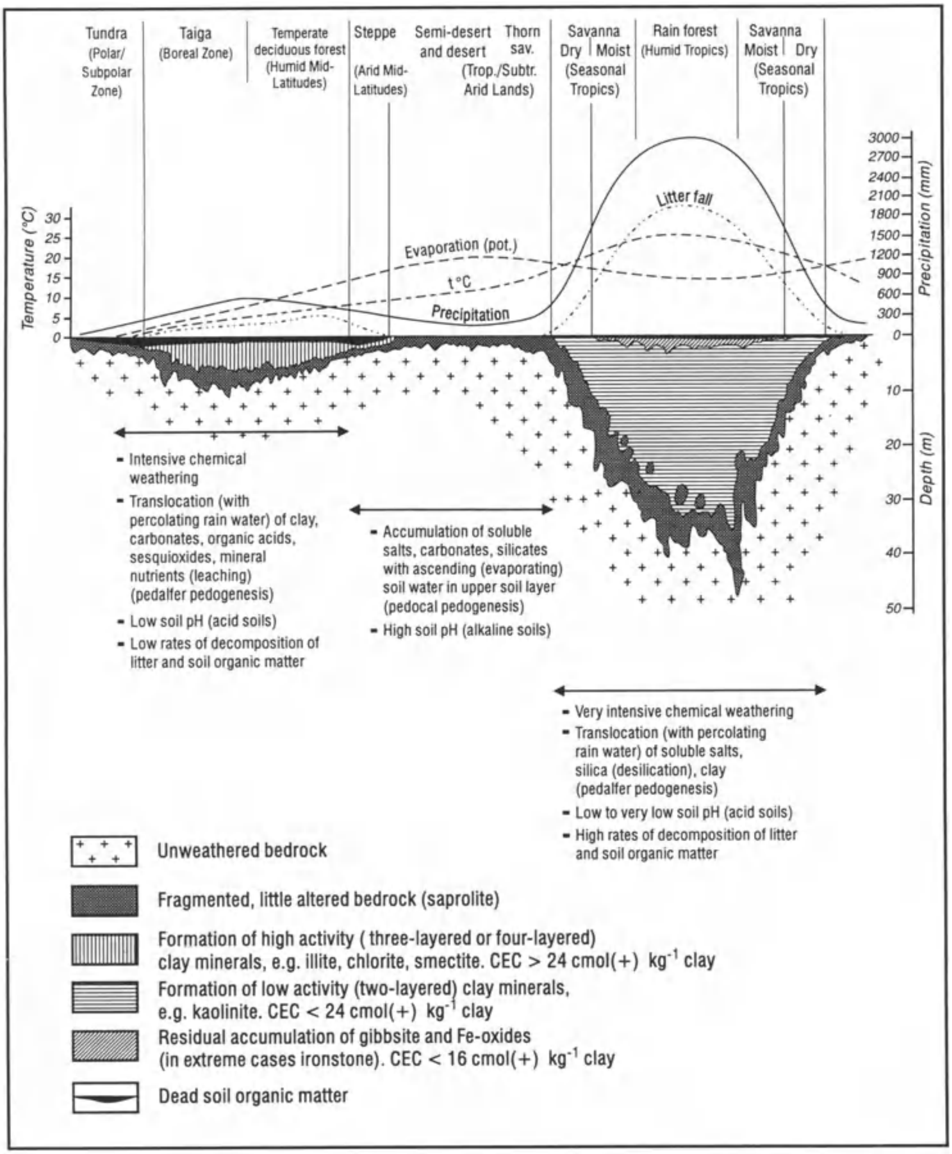
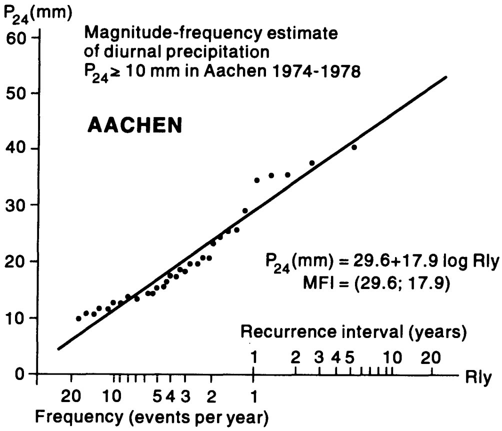


Fig. 4. Schematic depth and structures of the weathered mantle (regolith and saprolite) in different climates. (After Strakhov 1967)

of little assistance to geomorphologists, or even to ecologists and agricultural scientists etc. More meaningful is information on extreme conditions and their frequency, such as the frequency of heavy precipitation, long dry periods, strong winds, deep frosts or freeze-thaw cycles. Such frequency data, which indicate the probability of recurrence, can be calculated by means of *magnitude-frequency analyses* (e.g. Gumbel 1958; Ahnert 1982, 1987).



Ahnert's method takes the data to be investigated, for example daily precipitation values over a specific time period, and "first classifies them according to their magnitude (the highest value receives the ranking 1) and the recurrence interval (RI) for all the other values is calculated. This is the period most likely to pass before an event of equal or greater magnitude than the one observed can be expected to occur" (Ahnert et al. 1982, p. 23). The recurrence interval can be calculated using the equation:

$$RI = \frac{N + 1}{r},$$

where N = the total number of time units (days in this example) and r = the ranking of the event in question (a certain amount of daily precipitation in this example). The values thus calculated are presented in the way shown in the example for Aachen, Germany (which indicates typical conditions in the Humid Mid-Latitudes), using a logarithmic scale for the time data along the x-axis and a linear scale for the precipitation data along the y-axis. The regression line is calculated using the regression formula $P_{24} = Y + A\log_{10}RI_Y$. In this equation P_{24} = the daily precipitation; RI_Y = the recurrence interval in years; Y = a constant for daily precipitation (P_{24}) with recurrence interval RI_Y = 1 year ($\log_{10}RI_Y = 0.0$), A = the coefficient $Y + A = P_{24}$ with RI_Y = 10 years ($\log_{10}RI_Y = 1.0$); $Y + 2A = P_{24}$ with RI_Y = 100 years ($\log_{10}RI_Y = 2.0$).

When combined, the two values Y and A give the magnitude-frequency index (MFI). The MFI (29.6, 17.9) for our example indicates that at least once a year daily precipitation of 29.6 mm, once every 10 years daily precipitation of 47.5 mm (29.6 + 17.9), and once every 100 years a daily precipitation of 65.4 ($29.6 + 2 \times 17.9$), can be expected to occur.

Hydrology

The amount of precipitation which enters the rivers depends on the *water balance* i.e. (in its simplest form) on the difference between precipitation and evaporation.

Table 2. Annual coefficients and amounts of runoff in the ecozones. (Based on UNESCO data 1978)

Ecozones/plant formations	Runoff coefficient Q/P[a]	Amount of runoff
1. Polar/Subpolar Zone: Tundra	0.55	220
2. Boreal Zone: Taiga	0.43	300
3. Humid Mid-Latitudes: Temperate deciduous forest	0.34	350
4. Arid Mid-Latitudes: Moist steppe (prairie)	0.25	200
Dry steppe	0.12	60
Desert/semi-desert	<0.03	10
5. Tropical/Subtropical Arid Lands: Thorn savanna	0.08	50
Desert/semi-desert	<0.03	5
6. Mediterranean-Type Subtropics: Sclerophyllous vegetation	0.15	150
7. Seasonal Tropics: Dry savanna	0.25	250
Moist savanna	0.35	450
8. Humid Subtropics: Rain forest	0.43	650
9. Humid Tropics: Rain forest	0.52	1200

[a] Q = annual runoff (mm); P = annual precipitation (mm).

The left-hand diagram in Fig. 5 shows the global differentiation for both these parameters and their assignment according to ecozones/plant formations (it should be noted, however, that the precipitation data do not take account of the variations in *seasonal* distribution which, particularly in the case of the seasonal tropics and subtropics, are of considerable significance to the water budget; the evaporation data do not reflect actual evaporation, but rather potential values). The right-hand diagram in Fig. 5 shows the relationships between precipitation and *runoff coefficients* for the same zones. These data allow the absolute amounts of runoff to be estimated. Table 2 provides guideline values for the individual ecozones. (See Fig. 82 for an evaluation of water cycles in ecosystems.)

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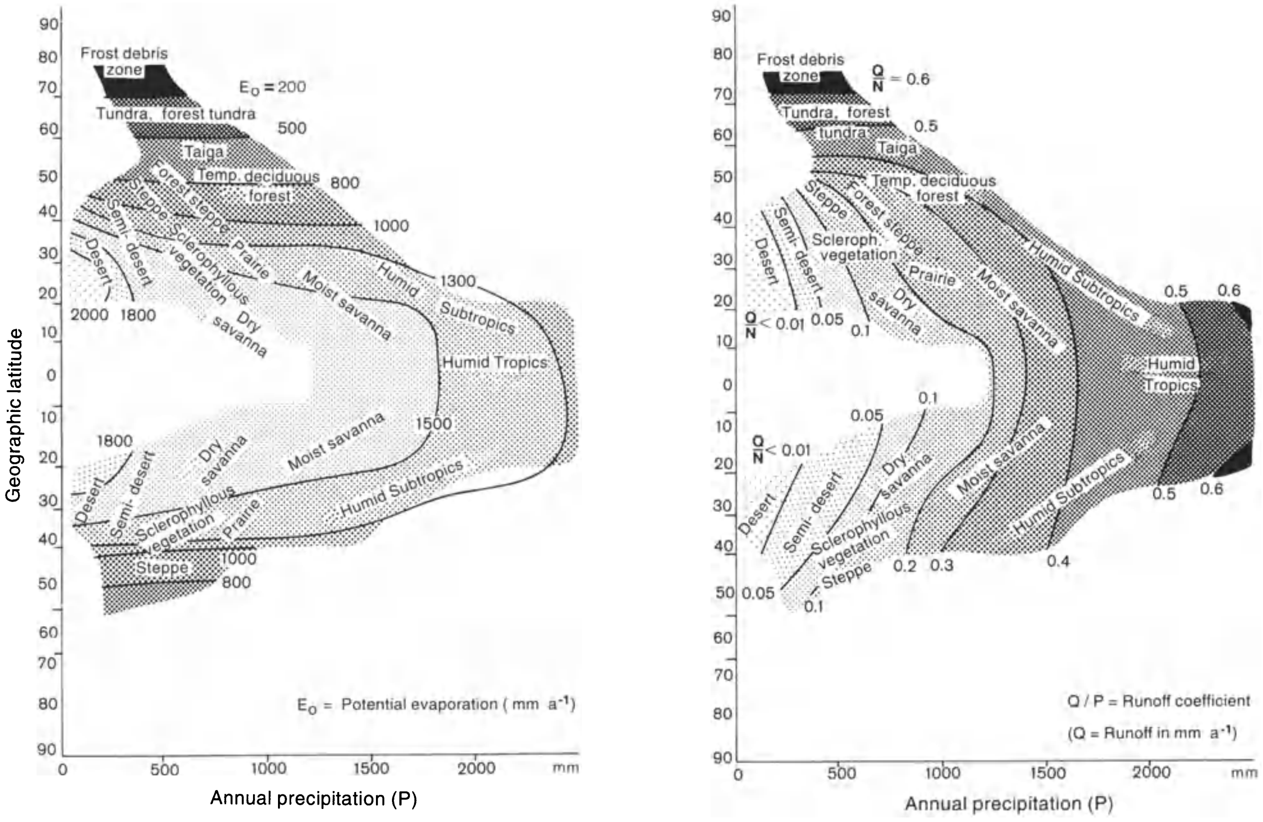

Fig. 5. Water balance of ecozones/plant formations. (Simplified from UNESCO 1978). See text for explanation

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2.4 Soils

The classification and nomenclature of soil units (types) follows the *FAO-UNESCO Soil Classification System*. This system was designed primarily for the legends of the *Soil Map of the World*, drawn on a scale of 1 : 5 million (18 multi-coloured sheets) and published between 1971 and 1981. “One of the most important results of the world soil map project is the creation of an internationally recognized (!) soil nomenclature and thus of a worldwide unified, common soil language. The terminology has already become the international standard for supraregional soil comparison" (Schmidt-Lorenz 1986, p. 53). This is reason enough for us to give the FAO-UNESCO system pre-eminence over other classification systems.

Soil Units and Soil Zones

For the sake of clarity, all *major soil groupings* (first-level soil units) and some of the *soil units* (level 2) of the FAO-UNESCO system are described very briefly in Box 2; in addition, equivalents in some other classifications are shown. The latter can be only approximations since the criteria applied in different classification systems are not fully identical.

For the second-level soil units a binary nomenclature is used: the first element (adjective) indicates this second level, whereas the second element (noun) indicates the major first-level soil grouping to which the soil unit belongs. A separate list in Box 2 explains the meaning of the more common formative elements used for naming (second-level) soil units.

The original legend was revised in 1988 (FAO Rome). With the revision, some major soil groupings and soil units were deleted, whereas others were added. In general, this book follows the new classification and nomenclature, but includes the original version wherever this applies. The original version is needed for understanding the *Soil Map of the World* which has not yet been revised and – most likely – will not be revised in the foreseeable future.

The compilation of the map on *soil zones of the world* (Fig. 6) resulted from a comparison of the FAO-UNESCO maps with the Troll-Paffen map on seasonal climates of the earth. The individual soil units were first grouped according to their ability to fit the given climatic and ecozonal systems, and then the distribution limits of these soil associations, as indicated on the FAO-UNESCO maps, were transferred onto the soil zone map. This means that the soil zones are defined according to climatic coincidence, but their *spatial* delineation follows solely the existing pedological boundaries. Table 3 shows the relationships between the soil zones and the ecozones.

Regional chapters on soil (Chaps. 3.1.4, 3.2.4, 3.3.4 etc.) deal with the characteristic factors and processes of soil formation and describe the major properties of the resulting zonal, and to a lesser extent intrazonal, soils. Additionally, information on soil fertility (suitability for plant growth) is included.

Soil Fertility

In this context, the term soil fertility refers primarily to the *soil nutrient supply* (quantity of mineral nutrients and their availability to plants). Such physical properties as soil temperature, soil air and soil moisture content, whose effects

Main characteristics of FAO-UNESCO soil units and some approximate equivalents of other classifications

2a

FAO-UNESCO Units (1)	Main characteristics	Approximate equivalents from		
		Anglo-American classification systems	German classification systems	French classification systems
Acrisols	Strongly weathered, acid soils with argic B horizon (clay accumulation), low cation exchange capacity (< 24 cmol(+) kg^{-1} clay) and base saturation (< 50%)	Ultisols, red-yellow podzolic soils, leached ferralitic soils	Fersiallitische Böden, Rotlehme, Braunlehme	Sols ferrallitiques lessivés, Sols ferrallitiques lessivés moyenne ou fortement désaturés à horizon B
Alisols (3)	Formerly grouped together with acrisols; separated in 1988 on the basis of high activity clays (CEC > 24 cmol(+) kg^{-1} clay) and high exchangeable Al content			
Andosols	Dark soils developed on young volcanic deposits (e.g. ash), low bulk density, rich in allophane and volcaniclastic material	Andisols, black volcanic soils, humic allophane soils		Sols bruns tropicaux sur materiaux volcaniques
Anthrosols (3)	Soils in which human activities have resulted in profound modification		Anthropogene Böden, Kulturböden, Kultosole, Rigosole	
Arenosols	Soils with sandy texture and low organic carbon (ochric A horizon), exclusive of alluvial (fluvic) materials	Entisols: psamments; (red and yellow) sands		
Calcisols (3)	Soils with accumulation of secondary calcium carbonates (calcic horizon), mainly in arid/semi-arid regions	Aridisols: calciorthids; calcareous soils		
Cambisols	Soils with a weakly to moderately developed structured subsoil, without appreciable illuviation (cambic B horizon)	Inceptisols: ochrepts, umbrepts; brown earths	Braunerden (ohne Parabraunerden)	Sols bruns
Calcaric	Calcareous at least between 20 and 50 cm from the surface		Kalkbraunerde	Sols bruns calcique
Chromic	Strong brown to red subsoil	Rhodic xerochrepts	Terra fusca, Terra rossa	Sols fersiallitiques non lessivés
Dystric	Low base saturation (less than 50 %)	Dystrochrepts, acid brown forest soils	Saure Braunerde	Sols bruns acides
Eutric	High base saturation (50 % and more)	Eutrochrepts, orthic brown forest soils	Typische Braunerde	Sols bruns eutrophes
Chernozems	Soils with a very dark mollic A horizon (to a depth at least 50 cm) and a calcareous subsoil	Mollisols: borolls; black earths of temperate steppes	(Steppen-) Schwarzerden, Tschernoseme	
Haplic	Normal horizon sequence	Haploboroll, typic chernozem	Typischer Tschernosem	
Luvic	Illuvial accumulation	Argiboroll, podzolised chernozem	Ausgelaugter Tschernosem	

Ferralsols	Deep, strongly weathered soils with low activity clays (CEC < 16 cmol(+) kg^{-1} clay), high Fe- and Al-oxide contents and porous and stable structured subsoils (ferralic B horizon)	Oxisols, weathered ferralitic soils, latosols, red earths	Trop. Roterden, Trop. Gelberden, Ferrallitische B., Lateritische B.	Sols ferrallitiques moyenne ou fortement desaturés à horizon B
Fluvisols	Young soils on alluvial deposits (fluvic properties)	Entisols: fluvents; alluvial soils	Auenböden, alluviale Böden, Schwemmlandböden	Sols minéraux brut
Gleysols	Fine-textured hydromorphic soils with reducing moisture regime, related to saturation by groundwater (gleyic properties)	Entisols: aquents; inceptisols: aquepts; meadow soils	Gleye, Gley-Böden	
Gelic	having permafrost within 200 cm of the surface	Pergelic cryaquepts, Tundra gleysols	Tundragley	
Greyzems	Soils with a dark humic topsoil (mollic A horizon) showing uncoated silt and sand grains on structured ped surfaces; having an argic B horizon	Mollisols: argiborolls, aquolls; grey forest soils	Graue Waldböden	
Gypsisols (3)	Soils with accumulation of gypsum (gypsic horizon), mainly in arid/semi-arid regions	Aridisols: calciorthids; soils with gypsum		Sols (bruns) gypseux
Histosols	Organic soils (peats, bogs) with at least 40 cm (or 60 cm if mainly sphagnum) thickness within 80 cm depth	Bog soils, peat soils, organic hydromorphic soils	Moorböden, Torfböden	Sols hydromorphes organiques
Kastanozems	Soils with a dark brown humic topsoil (mollic A horizon) and a calcareous subsoil	Mollisols: ustolls and aridic borolls; chestnut soils (of the dry steppes), brown and dark brown soils	Braune Steppenböden, Kastanienfarbene Böden, Buroseme	Sols châtains
Leptosols (3)	Weakly developed, shallow soils over hardrock or very stony material; include former (in 1988 deleted) lithosols, rankers, rendzinas and 'very stony' regosols	Entisols	Syroseme	
Lithosols (2)	Very shallow soils (< 10 cm) over hardrock	Entisols: orthents	Syroseme, Gesteinsrohböden, Schutt- oder Skelettböden	
Lixisols (3)	Strongly weathered soils with an illuvial clay subsoil (argic B horizon), low clay activity (< 24 cmol(+) kg^{-1} clay) and high base saturation (> 50 %); the low CEC separates them from luvisols and the high base saturation from the acrisols	Alfisols: ustalfs, xeralfs; ferruginous soils		Sols ferrugineux tropicaux lessivés

Box 2

Luvisols	Soils with an illuvial clay subsoil (argic B horizon), a CEC of at least 24 cmol(+) kg^{-1} clay and a base saturation of 50 % or more	Alfisols: udalfs, boralfs; grey brown podzolic soils	Lessivés, Parabraunerden	Sols lessivés
Albic	Albic E horizon		Podzol-Parabraunerde	
Chromic	Strong brown to red argic B horizon	Rhodoxeralfs, haploxeralfs	Terra rossa, Terra fusca	Sols fersiallitiques lessivés
Haplic	Former Orthic; normal horizon sequence	Podzolidized brown forest soils		
Nitisols	Soils with an illuvial clay subsoil (argic B horizon) and an angular blocky structure (in some subhorizon) with shiny ped faces on its elements	Alfisols: udalfs; ultisols: udults, ustults; ferrisols		Sols ferrugineux tropicaux lessivés
Phaeozems	Soils with a dark humic topsoil (mollic A horizon), lacking a calcareous subsoil	Mollisols: udolls; dark grey soils, brunizems	Brunizeme, Prärieböden, Degrad. Tschernoseme	
Planosols	Soils with redox conditions in E horizon (bleaching and mottling) related to saturation by surface water (stagnic properties) for prolonged periods		Pseudogleye, Stagnogleye	
Plinthosols (3)	Separated from ferralsols by content (25% or more) of plinthite (iron-rich, humus-poor mixture of clay etc.)	Oxisols: plinthaquox; latosols		
Podzols	Soils with black to brown-red subhorizons (commonly below a bleached E horizon) due to illuviation of organic matter, Al and Fe (spodic B horizon)	Spodosols	Podzole (Podsole), Bleicherden	
Podzoluvisols	Soils with a bleached lower topsoil (E horizon) tonguing deep into the illuvial clay subsoil (argic B horizon)	Alfisols: glossic great groups	Fahlerden	Sols lessivés glossiques
Rankers (2)	Shallow soils with an acid-humic topsoil (umbric A horizon) over siliceous material	Inceptisols: lithic haplumbrepts	Ranker, Humussilikatböden	
Regosols	Weakly developed, shallow soils on fine-textured unconsolidated material	Entisols: orthents	Lockersyroseme	Sols minéraux bruts
Rendzinas (2)	Shallow soils with dark humic topsoil (mollic A horizon) over highly calcareous material	Mollisols: rendolls	Rendzina, Humuskarbonatböden	

Solonchaks	Soils with high contents of soluable salts (salic properties)	Aridisols: salorthids; saline soils	Salzböden, Weißalkaliböden	Sols salins
Solonetz	Soils with an illuvial clay subsoil and a saturation of exchangeable sodium of more than 15 % (natric B horizon)	Natric soils, alkali soils	Alkaliböden, Schwarzalkaliböden	Sols sodiques à horizon B
Vertisols	Dark coloured cracking and swelling clay soils	Tirs, black cotton soils, regurs, cracking clay soils, grumusols	Pelosole, Smonitzen	
Xerosols (2)	Semi-desert soils with a low organic matter content (weak ochric A horizon)	Aridisols, semi-desert soils	Buroseme, Halbwüstenböden	Sols peu évolués xériques, Sols bruns subarides
Yermosols (2)	Desert soils with a very low organic matter content (very weak ochric A horizon)	Aridisols, desert soils	Sieroseme (Seroseme), Vollwüstenböden	Sols minéraux bruts xériques

(1) All (28) major soil groupings and some of their subdivisions(soil units); (2) deleted 1988; (3) added in revised legend (1988), therefore missing in the soil map of the world (1971-1981).

Formative elements used for naming Soil Units (level 2)	Connotative of	Formative elements used for naming Soil Units (level 2)	Connotative of	2b
Albic	Strong bleaching	Gelic	Permafrost	
Calcaric	Presence of calcareous material	Haplic	Simple, normal horizon sequence	
Chromic	Bright colour	Humic	Rich in organic matter	
Dystric	Infertile, low base saturation	Luvic	Accumulation of clay	
Eutric	Fertile, high base saturation	Orthic	Deleted in 1988; superseded by 'Haplic'	
Ferralic	High content of sesquioxides	Plinthic	Mottled clay materials which harden irreversible upon exposure	
Ferric	Ferruginousmmottling or an accumulation of iron			
		Rhodic	Red coloured	

Box 2. Continued

Common small letter suffixes added to master horizon designations (capital letters, e.g. H,O,A,E,B,C)				**2c**
h	Accumulation of organic matter	t	Accumulation of clay	
k	Accumulation of calcium carbonate	w	Alteration in situ	
s	Accumulation of sesquioxides	z	Accumulation of salts	

Box 2. Continued

on the *productiveness*[3] of the soil can be considerable or may even predominate, are not considered here, since they are more dependent on the climatic environment.

The following properties and processes determine the soil nutrient supply.

The Amount of Weatherable Silicates (Weatherable Residue). Weathering can cause nutrients in primary silicates (those stemming from the parent rock material, e.g. olivine, augite, hornblendes, mica and feldspars) to be released (become mobilized). A high primary silicate content is therefore advantageous (good ability to regenerate soil fertility), especially when these minerals are relatively easy to weather out and a large number of them have particle sizes as low as 0.002–0.02 mm in diameter (= silt). The amount and composition of weatherable residue

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[3] Productiveness, which can be measured as the annual increase in organic substance [organic dry matter (DM) in dt ha^{-1}] or in annual crop or timber yield, is generally accepted as an adequate *measure of soil fertility* (for example, in Germany it is used for performing official soil evaluations). In global comparisons, however, such an *evaluation method* is of little value since the variation in productiveness between the earth's regions is more strongly diversified due to climatic conditions (such as the length of the growing season, the amount of incoming radiation) than to soil factors (as such). If the "yield" criterion were applied, the ferralsols, which are severely lacking in nutrients, but on which high primary production is achieved in the tropical rain forests, would be given a higher fertility rating than the very nutrient-rich chernozems which, due to the prevailing semi-arid climatic conditions, have a much more limited productiveness.

When judging *soil nutrient supplies* it is of major importance whether a soil is covered with natural vegetation or whether this has been removed and replaced by agricultural crops or – to a lesser extent – by timber plantations. Under rain forests, the nutrient supply in ferralsols is not at all bad, due to the rapid return of organically bound nutrients; it is bad only when the forests are cleared and as a result this return is halted. In principle, the same applies to all soils. Differences, however, are found in the rate at which the humus is broken down after return ceases, and in the rate at which the minerals useful to plant life are used up; and, furthermore, there are differences in the feasibility of applying fertilizers to make up for nutrient loss. Most important are the cation exchange capacity and base saturation of the *mineral components* of the soil. If these factors are high, nutrient availability is likely to remain intact after cultivation has begun, or it can be kept at similar levels through the addition of nutrients. If they are low, on the other hand, the soil quickly becomes exhausted and the application of fertilizers will not help very much to stop this.

This means that the nutrient supply of cultivated soil depends for the most part on its clay mineral components, whereas that of natural soil is also influenced by its organic components and their dynamics (litter production and decomposition) as well as their exchange properties.

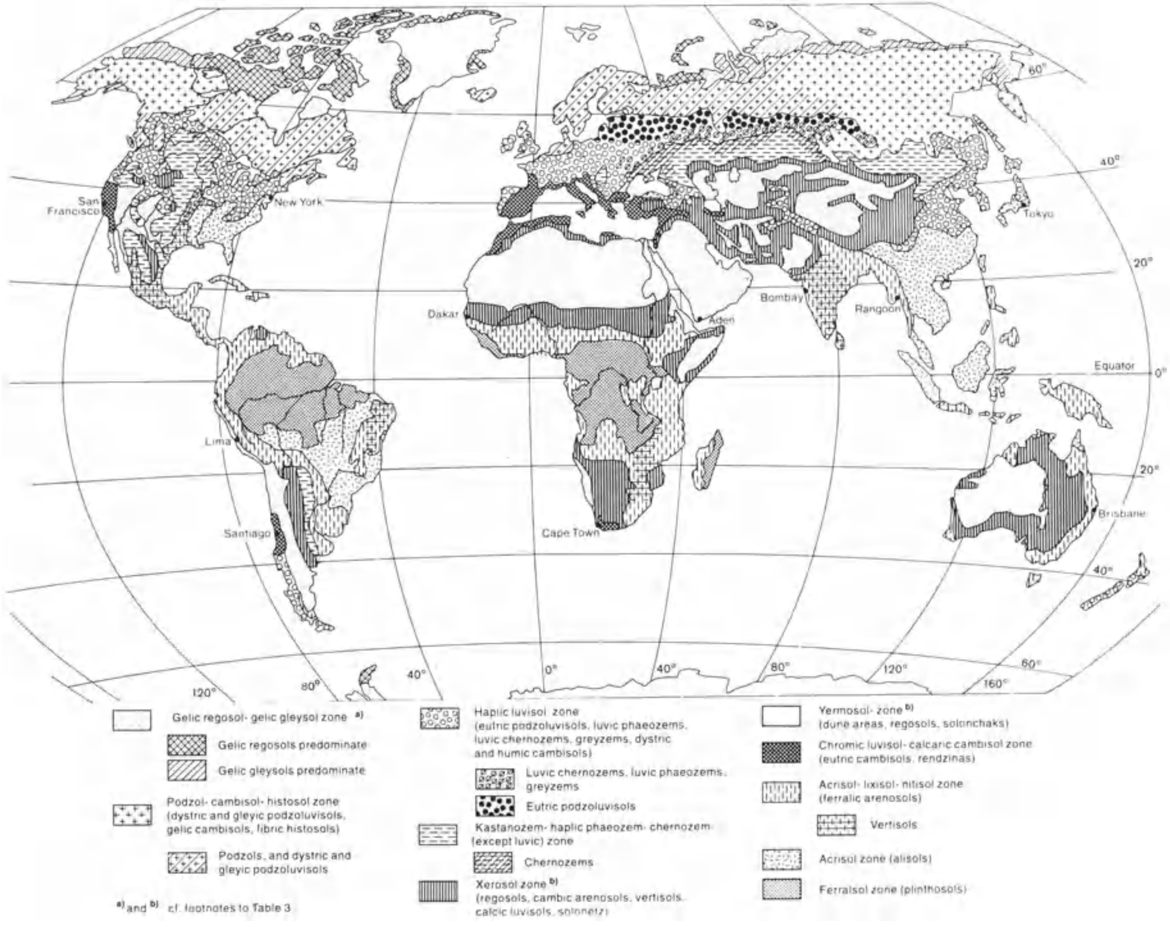

Fig. 6. Soil zones of the world (see text for sources)

Table 3. Approximate correspondence between soil zones and ecozones

Soil zone	Ecozones
Gelic regosol-gelic gleysol zone[a]	(1.1) Tundra and frost debris zone
Podzol-cambisol-histosol zone	(2) Boreal Zone
Haplic luvisol zone	(3) Humid Mid-Latitudes
Kastanozem-haplic phaeozem-chernozem zone	(4.1) Grass steppes (moist)
Xerosol zone[b]	(4.1) Grass steppes (dry) as well as (5.1) Tropical/subtropical thornscrubs and thorn-steppes
Yermosol zone[b]	(4.2) Deserts and semi-deserts in the mid-latitudes and (5.2) Deserts and semi-deserts in the tropics/subtropics
Chromic luvisol-calcaric cambisol zone	(6) Mediterranean-Type Subtropics
Acrisol-lixisol-nitisol zone	(7) Seasonal Tropics
Acrisol zone	(8) Humid Subtropics, Humid Tropics in Southeast Asia and moist savannas in South America
Ferralsol zone	(9) Humid Tropics (except in Southeast Asia and Central America)

[a] Presumably, most gelic regosols consist of very stony material, which means that they have to be grouped under gelic leptosols according to the new FAO-UNESCO soil classification. Accordingly the zonal name has to be changed to gelic leptosol-gelic gleysol zone.

[b] New names are also needed for the xerosol zone and the yermosol zone, since both name-giving soil units have been deleted from the new FAO-UNESCO classification. The problems in both cases, however, are that the new soil units replacing xerosols and yermosols within the respective zones will not be known until the World Soil Map has been renewed (and that seems unlikely to happen in the foreseeable future). Thus, the former zonal names will have to be retained for some time yet. Most likely, they represent the following soil units: – xerosol zone: cambic arenosols, vertisols, calcic luvisols, calcisols and solonetz;

– yermosol zone: regosols, leptosols, calcisols, gypsisols and solonchaks; unconsolidated dunes.

present depend on the parent rock material, the age of the soil and the weathering intensity. In older soils, and especially on acid rock types like granite, sandstone and quartzite, the relative amount of minerals which are difficult to weather out (= resistant residue including minerals such as quartz, magnetite and zircon) build up, particularly with the increasing humidity and temperature of the climate. Accordingly, the weatherable residue of primary silicates is often low in the soils of the Humid Subtropics, and mostly very low in those of the Humid Tropics.

Clay Minerals and Cation Exchange Capacity. The quantity of nutrients which a soil can adsorb in exchangeable form (due to excess negative or positive charges on some of their components), and can therefore easily and quickly make available (most important factor: cation exchange capacity = CEC), depends on the amount and type of secondary clay minerals (and humus, see below) present. For instance, the three-layered (2 : 1-type clays) smectites and vermiculites have a high CEC (usually above 100 cmol(+) kg^{-1})[4], another three-layered clay mineral, illite, has a medium CEC [20–50 cmol(+) kg^{-1}], and the two-layered (1 : 1-type clays) kaolinite and halloysite have a low CEC (5–15 cmol(+) kg^{-1}). The oxides and hydroxides of iron and aluminium (such as goethite, hematite, gibbsite), which go under the name sesquioxides, have extremely low exchange capacities.

Correspondingly, for example, typical vertisols in whose clay contents smectites predominate have a high CEC, whereas tropical/subtropical lixisols, acrisols and nitisols, in which kaolinites predominate, have a low CEC [less than 24 cmol(+) kg^{-1} clay]; soils which not only have a low kaolinite contents but very high free oxide contents, as is the case in some ferralsols, have extremely low CECs [sometimes less than 1.5cmol(+) kg^{-1} clay]. The CEC of most Central European soils is between 40–60 cmol(+) kg^{-1} clay.

The values just noted drop when the CEC is given relative to the entire soil (or fine soil) rather than to the clay fraction. Depending on the clay content, the CECs for our soils range from 5–10 (sandy soils), 10–25 (loam soils), to 20–40 (clay soils); in the humid tropics, on the other hand, where higher clay contents are found, the CEC is often under 10 cmol(+) kg^{-1} soil.

The following *sample calculation* is intended to show what amounts of mineral nutrients useful to plant growth are indicated by the CEC values:

1st assumption. Soil depth (root zone, topsoil) 30 cm, soil density 1.5 g/cm^{-3}, gives 3000 $m^3 \times 1.5 = 4.5 \times 10^6$ kg soil per ha.

2nd assumption. CEC 20 cmol(+) kg^{-1} soil; this yields a total of 90×10^6 cmol(+) for the entire mass of soil.

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[4] The formerly applied unit of measure for exchange capacity was milliequivalent (meq) per 100 fine soil or clay. This expresses how many hydrogen ions (in mg) a soil is capable of adsorbing on its exchangers per 100 g fine soil or clay. Cations of other substances (e.g. potassium, calcium or magnesium) can take the place of protons, in proportion to their charges (valences). For instance, the bivalent calcium ion (Ca^{2+}) takes the place of two univalent hydrogen ions (H^+). The equivalent weights are determined by dividing the atomic weights by the valence; e.g. for Ca^{2+} : 1 meq Ca = 40.08 : 2 = 20.04 mg. The equivalent amount of (univalent) potassium is 39.1 : 1 = 39.1 mg, and that of (bivalent) magnesium is 24.31 : 2 = 12.15 mg.

Recently, the milliequivalent has been superseded by the SI unit (International System of Units) mol(+) or mol_c (c for charge). For comparison: 1 cmol(+) kg^{-1} (1 centimol per kilogram) or 1 mmol(+) 100 g^{-1} (1 millimol per 100 grams) equals 1 meq/100 g. Thus, numerically there are no differences for CEC and AAC values given either in old or new units. Equivalent weights of different exchangeable ions can be calculated as follows:

$$1\ \text{mmol}(+) = \frac{\text{atomic weight}}{\text{valence}} 10^{-3}\ \text{g}\ \ (= \text{milligram})\ \text{or}$$

$$1\ \text{cmol}(+) = \frac{\text{atomic weight}}{\text{valence}} 10^{-2}\ \text{g}\ \ (= \text{centigram}).$$

3rd assumption. Cations adsorbed on the exchangers consist of 90% Ca^{2+}, 9% Mg^{2+} and 1% K^+ [as is the case, for example, in some chernozems in the German Bördeland (loess plain) areas], i.e. the CEC of 20 cmol is distributed as follows: 18 cmol for Ca^{2+}, 1.8 cmol for Mg^{2+} and 0.2 cmol for K^+. The amounts per ha are, therefore:

for calcium: $9/10 \times 20 \times 90 \times 10^6$ centigram $= 16\,200$ kg,
for magnesium: $9/100 \times 12 \times 90 \times 10^6$ centigram $= 972$ kg,
for potassium: $1/100 \times 39 \times 90 \times 10^6$ centigram $= 351$ kg.

4th assumption. Nutrient content of herbaceous plants (dry mass): 1% K, 0.5% Ca and 0.2% Mg (mean values for normally developed crops, taken from Mohr and Schopfer 1978, p. 245). At a net primary production (PP_N) of 10 t ha^{-1} a^{-1}, this gives an annual requirement of 100 kg K, 50 kg Ca and 20 kg Mg per ha. Thus, the supply of K can theoretically be expected to last for 3.5 years, that of Ca for over 300 years and that of Mg for almost 50 years.

The percentage of the exchange capacity accounted for by nutrient ions and sodium, i.e. the magnitude of the *base saturation*, must also be considered. If, for example, this value is 50% (remainder: mainly H^+ ions, in some soils also Al^{3+} ions) the above amounts are halved or, if sodium is also present, they are further reduced in proportion to the sodium content (sodium is not an essential element for most plants).

The *soil reaction* (measured as the pH value) allows the base saturation (BS) to be estimated; a pH of 3.5 is more or less equivalent to 0% BS, pH 8 is about equal to 100% BS. Many soils in humid climates have low pH values and thus low base saturations, those in more arid climates have higher pH readings and higher saturation levels. Hot, humid climates are, therefore, at a disadvantage on two fronts: the soils not only have a low CEC, but also a low BS.

If the *root zone*, i.e. the upper soil portion from which the plants absorb their nutrients, is deeper than the 30 cm given in the sample calculation, the amount of nutrients available to the plants increases (as long as the CEC remains stable over the depth of the soil layer, in proportion to the increase in volume of the root zone). If the plants (or crops) are shallow-rooted, on the other hand, the available nutrients decrease proportionally.

When performing calculations using CEC values, the reference units should also be noted, i.e. to indicate whether the values relate to 100 g clay, 100 g fine soil or 100 g total soil. If the reference is to clay or fine soil, their percentage content in the total soil should be calculated; if these components make up 40%, for example, the nutrient supply calculated from the CEC values also decreases to 40%.

Finally, in the case of acid soils, it should be determined whether the CEC increases with rising pH (i.e. if there is a difference between CEC_{eff} and CEC_{pot} – cf. Chap. 3.7.4).

Calculations of nutrient availability in an ecosystem, using the CEC values as described, can be done as an initial approximation only. More accurate determinations must also take into account *buffer systems* (buffer capacities) in the soil, that is to say, the effects of buffer substances such as $CaCO_3$, H_2CO_3, $Ca_3(PO_4)_2$, $CaHPO_4$, etc., as well as the effects of the mineral and organic exchangers which also act as buffers on exchange processes.

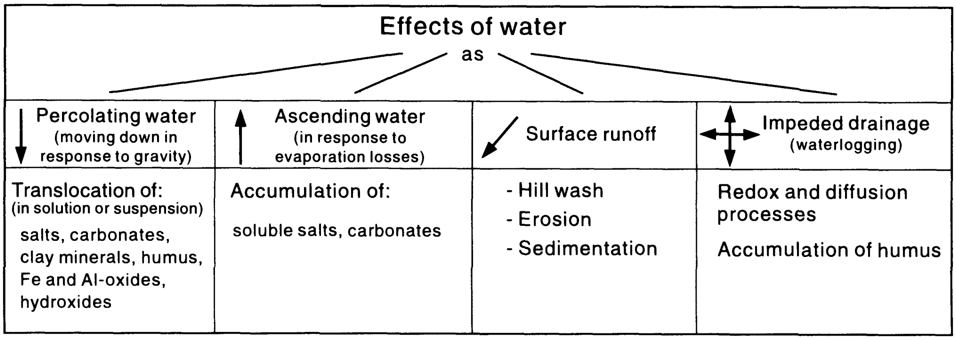
Soil Organic Matter (Humus). In soil science, the term *humus* refers to the totality of dead organic substances in and on the mineral soil (ecologists, on the other hand, do not consider litter layers, or at least the upper layers thereof, to be part of this; cf. Chap. 2.5.2.3). Decomposition (decay) leads to the release of plant nutrients from the dead organic matter (mineralization) or to the formation of rather stable humic material (humification). Soils differ a great deal according to the content of organic matter, its composition from varyingly decomposed litter and humified substances, and its distribution in the soil profile. With regard to soil fertility, it is most advantageous when (1) the bulk of the plant and animal debris mineralizes within a few years, and the nutrients contained therein, again become available to the plants (cf. Chap. 2.5.2.3), and (2) the form of humus which is produced is a *mull* in which large amounts of fine humus are intimately mixed with mineral components; the mull has an unusually high CEC of 200–500 cmol(+) kg^{-1} and has positive effects on the soil structure.

To what degree these or less advantageous circumstances prevail depends on the amount of dead organic substance added to the soil (which is dependent on the PP_N), whether the litter is easy or difficult to decompose (which depends on C/N ratio), and what conditions exist for decomposition to take place (essentially, therefore, what are the living conditions for the soil organisms). The latter may be limited for shorter or longer periods of time and to varying degrees by such factors as dryness, cold, soil acidity or a lack of oxygen in the soil air.

These interactions make it clear why humus content, humus types and nutrient cycling differ so widely between ecozones. The humus content is particularly low in zones with very low PP_N (deserts and semi-deserts in the mid-latitudes and tropics/subtropics) or where – even if the PP_N is very high – the litter decomposes very quickly (humid tropics). Average humus contents are found in areas with a medium to high PP_N but where decomposition is interrupted for long periods during the year (steppes, humid mid-latitudes). The highest humus contents are formed (even when the PP_N is low to very low) in areas where long phases of severely limited decomposition coincide with the input of relatively undecomposable litter (Boreal Zone, tundra). The most common form of humus produced under these conditions is an unfavourable surface layer of raw humus and, when waterlogging occurs, peat.

Translocation and Mixing Processes

Translocation processes occur due to water (in solution or suspension) percolating, ascending, running off at the soil surface and stagnating (Fig. 7). In *arid* regions, for example, (where water ascends during dry periods) the water flow results in the formation of salty, calcareous or siliceous crusts; in *humid* regions



Effects of water as

Percolating water (moving down in response to gravity)	Ascending water (in response to evaporation losses)	Surface runoff	Impeded drainage (waterlogging)
Translocation of: (in solution or suspension) salts, carbonates, clay minerals, humus, Fe and Al-oxides, hydroxides	Accumulation of: soluble salts, carbonates	- Hill wash - Erosion - Sedimentation	Redox and diffusion processes Accumulation of humus

Fig. 7. The effects of water as a soil development factor. (Schroeder 1992). Water affects pedogenesis mainly due to its predominant direction of movement in the soil

(where the predominant soil water flow consists of percolation), water movement may lead (1) to a *translocation of clay* (lessivation), with clay depletion in the upper soil (E horizon) and clay enrichment (illuvation) in the subsoil (argic B horizon) due to illuvial accumulation; (2) to a *translocation of humid acids and free iron and aluminium oxides* (podzolization), with an albic E horizon (below an A or O horizon); and (cemented) enrichment of a combination of organic matter with sesquioxides (spodic B horizon; diagnostic for podzols); or (3) to a *translocation of silica* (desilication), causing a residual enrichment of iron and aluminium oxides and kaolinite (ferralitization), i.e. a ferralic B horizon (diagnostic for ferralsols) is formed. Podzolization is found in moist, cool climates and desilication (ferralitization) in moist, hot climates. Lessivation occurs in the Humid Mid-Latitudes as well as in the Seasonal Tropics/Subtropics (argic B horizons are diagnostic for luvisols, lixisols, acrisols and nitisols). Translocation processes are the main agents for the differentiation of soil profiles into (various) horizons.

Mixing processes can be the result of burrowing by soil-dwelling animals (bioturbation), changes in volume due to freeze-thaw cycles (cryoturbation), or swelling and shrinking processes linked to water uptake or release (hydroturbation). Such processes lead to the thickening of A horizons (e.g. in chernozems), the formation of periglacial involutions (e.g. in gelic regosols, gelic gleysols, gelic histosols) and/or the formation of a gilgai relief (e.g. in vertisols).

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Chapter 2.4: Soils

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2.5 Vegetation and Animal Life

The regional chapters on vegetation and animal life are given particular emphasis. More so than in the other chapters, an attempt is made to provide a synopsis of the individual components (compartments) of the zonal ecosystems, with the ultimate objective of describing the overall conditions for life – not only of plants and animals, but of man as well – that is to say, it is also an attempt to describe the physical background of man's major habitats.

Most of the regional chapters on vegetation and animal life consist of two parts, the first describing the structural characteristics of the biotic communities, and the second dealing with the reserves and transfer processes of organic matter, minerals and energy; the final section of the second part generally presents a model of the zonal ecosystems. In the following, an introduction will be given to the contents of these two subchapters.

2.5.1 Structural Characteristics

The climate classification system devised by Troll and Paffen (1964), on which the ecozonal delineation is based (cf. Chap. 2.1), is one of the so-called *effective* climate classification systems. Such systems classify climates according to their effects on nature and/or land use. Troll and Paffen's system places most emphasis on the effects on vegetation, and their climates are assigned (more or less strictly) to particular vegetation types. It is therefore self-evident that the ecozonal classification coincides in most respects with the earth's vegetation belts, i.e. zonal plant formations.

Plant Formations

Plant or vegetation formations are units (types) of a (mainly) physiognomic classification system for vegetation: In contrast to phytosociological plant communities (e.g. associations), which are derived strictly from floristic analysis and are thus characterized by distinct species compositions, plant *formations* are delimited on the basis of the general appearance of the plants, i.e. the *life or growth forms*, and are thus characterized by particular *life (growth) form spectra* (cf., for example, Chap. 3.6.5.1). The formations covering the largest areas are the *zonal plant formations*, such as the grass steppes, temperate deciduous forests, dwarf shrub tundras and evergreen sclerophyllous forests. Each of the ecozones are (or were) represented by one or just a few of these zonal plant formations.

If one also considers the animal kingdom, the term *bioformation*, or *biome*, for short, takes the place of the term plant formation. A zonobiome is, therefore, a zonal plant formation, including the animals (animal life forms) found in it, that is to say, a large uniform life region within the biosphere (Walter

1990). Transitional zones between different biomes or different plant formations are termed *ecotones*, and those at the uppermost level of the spatial classification system are called *zonal ecotones*.

There are various classification systems for *physiognomic plant types*. This book follows what is probably the best-known life form classification system, namely that from Raunkiaer (1910; Fig. 8). Figure 9 gives an overview of the life forms characterizing each of the plant formations. It also contains information on the distribution of the various plant formations as a function of the following parameters: average annual air temperature and precipitation.

To a certain degree, life forms came into being as *adaptations* to particular site conditions and are, therefore, found in a similar (convergent) manner in completely different species. This allows us to conclude from the physiognomic and structural features (although with varying degrees of accuracy) which abiotic environmental influences have been at work. This means that the physiognomic classification of vegetation is, within limits, at the same time an ecological classification, since it reflects major features of the climatic and edaphic environment; thus it can also be termed a *physiognomic-ecological vegetation classification*.

Changes in Vegetation Over Time

Besides a spatial structure, plant formations also have a temporal structure, which is revealed in seasonal changes occurring over the year and in long-term cyclical or directional changes (successions).

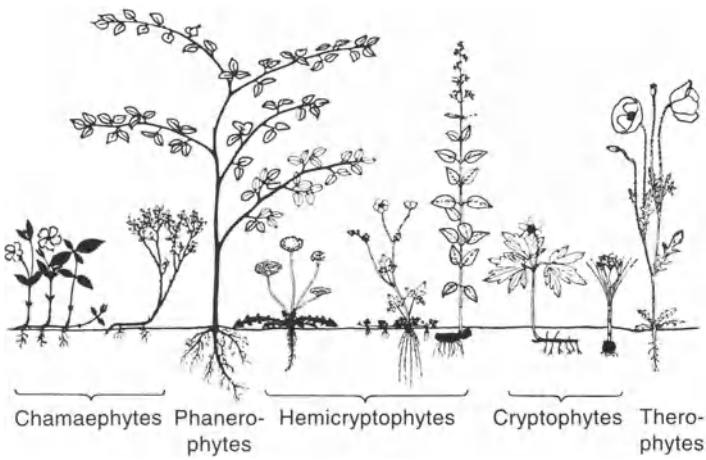

Fig. 8. Schematic of life forms according to Raunkiaer. (Walter 1960). The plant parts shown in *black* survive the least-favourable time of the year (dry season or winter) and the remaining parts die at the start of such periods

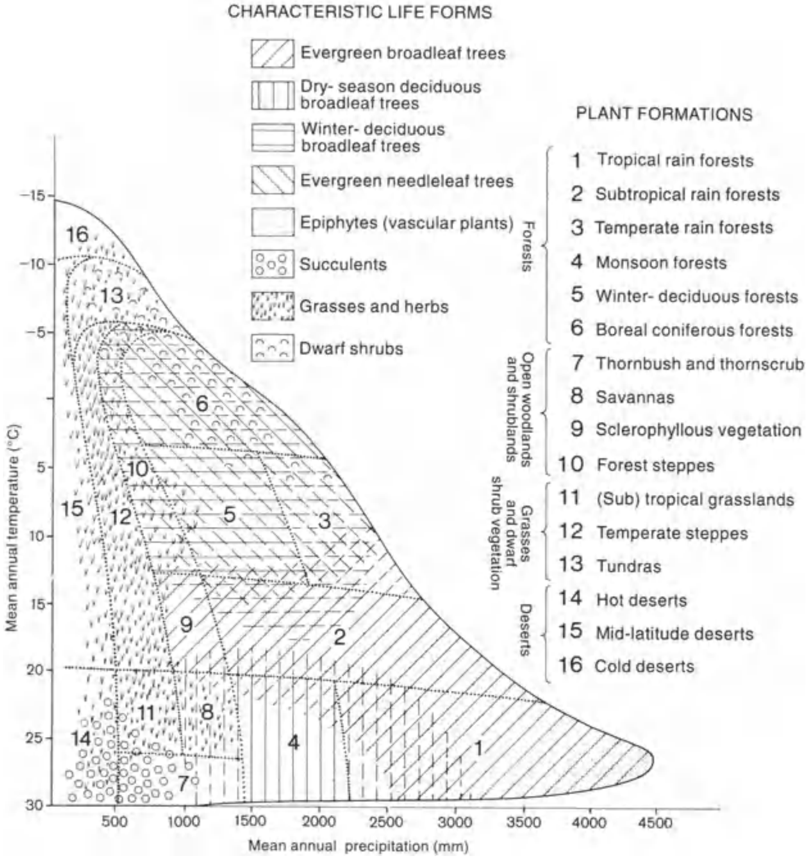

Fig. 9. The distribution of zonal plant formations and life forms as a function of temperature and precipitation. (Strasburger 1983)

Seasonal differences follow the rhythm of developmental changes in plants such as foliation, flowering, seed ripening and shedding. The times at which these occur are determined by conducting *phenological observations* (on a selected number of species). This allows the year to be divided into *natural* (phenological) seasons. Phenological observations also provide information on the length of the growing season (cf. Chap. 2.2). Particularly obvious aspectual changes take place in the Humid Mid-Latitudes (cf. Chap. 3.3.5.1) and the Seasonal Tropics (cf. Chap. 3.7.5.1), as well as in the semi-arid transitional regions between these ecozones and the arid lands.

Long-term cyclical changes are characteristic of all forest formations. In such areas a *mature or optimal phase* in which primary production reaches its peak (Fig. 10) is followed, as overageing occurs in the dominant species, by a *decline phase* in which falling trees tear holes in the fabric of the forest. Re-

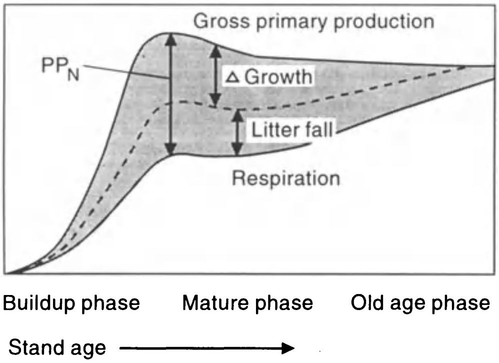

Fig. 10. The changes in primary production, growth increment, litter fall and respiration in a forest formation with increasing stand age. (Kira and Shidei 1967, from Larcher 1984). The highest net primary production (PP_N) is attained during the transition from the buildup to the mature phase; the growth increment (*Δ Growth*) is also highest here. There is a relative increase in respiration after this point, due to the increasingly unfavourable ratio of productive leaves to unproductive trunks, branches and roots, and the PP_N drops again accordingly. Since, at the same time, the amount of litter fall increases in proportion to PP_N, the drop in growth increment is sharper than that of the PP_N. During the old age phase, the rate of litter fall exceeds the net primary production rate, i.e. the amount of phytomass decreases. All changes described here can be mitigated or cancelled out if continuous rejuvenation occurs simultaneously to the ageing process

generation in the spots which then become free, first takes place via pioneer plants, which are characteristic specifically of this *rejuvenation phase*; young specimens of the "mature" vegetation re-establish themselves only gradually. Determinations of phytomass, primary production and nutrient flow in such regions vary widely, depending on the phase during which they are carried out (cf. Chap. 3.2.5.2).

In addition to the cyclical changes, *directional changes in stands or successions* also take place, i.e. new and different plant communities replace each other sequentially at the same site. The first stage in such a development takes place in areas basically free of vegetation (e.g. young moraines, freshly deposited valley sands or abandoned agricultural land) and is initiated by *pioneer communities*. These are followed by *intermediate seral stages*, until a "final" stage is reached which is then termed the *climax community*. The composition of plant species and life forms in such successional communities is dictated by the environmental conditions. If two areas have the same conditions, similar successions will come into being (i.e. the vegetation dynamics of both areas will be similar) (cf. Chap. 3.6.5.1).

If a succession follows an intrusion by man (e.g. clearing of forests), it is termed a *secondary succession*.

The final stage of a succession is considered to be that community which develops within centuries or millennia rather than over geological periods of time, i.e. without a significant change in abiotic environmental conditions having taken place. This stage is also termed *natural vegetation* or, if such is not yet (or no longer) present, *potential natural vegetation.* Natural vegetation which covers a large area and develops in conformity with the overall climate (i.e. ignoring edaphic-orographic influences) is also termed *climax vegetation.* According to this definition, the zonal plant formations representing the various ecozones are therefore climax formations (or, bearing in mind the changes brought about by man, potential climax formations).

2.5.2 Stand Reserves, Matter and Energy Transfer, Ecosystems

Box 3 shows which reserves and transfer processes are of the greatest importance to the biological components and processes in an ecosystem. The following sections will provide an insight into the general correlations existing between matter and energy interactions in ecosystems and will detail the differences between the various ecozones with respect to some of these reserves and transfer processes.

2.5.2.1 Photosynthesis, Primary Production and Phytomasses, Turnover

Every (natural or near-natural) ecosystem begins with the fixation of solar energy (primary energy input) by green plants (autotrophic organisms or autotrophs for short) using photosynthesis (the formation of carbohydrates from water and carbon dioxide as building blocks for use in further synthesis). This produces, in the form of phytomass, what could be called the starting capital of the ecosystem; it is used to feed the remaining components of the system through the transfer of energy-rich organic substances.

Extremely obvious differences exist between the various ecozones with regards to the amounts of phytomass present and to their productiveness. Both these factors indicate great differences in the *potential for (natural and agriculturally promoted) plant growth.* The difference in this potential from one ecozone to another is great enough for it to be used as the sole criterion for differentiation, that is, most zones represent a major region of the earth having its own particular potential for primary production. Figure 11 shows the distribution of phytomasses on earth (terrestrial part only), Fig. 12 the net primary production, and Fig. 13 the correlation between the two.

In general, there is a rise in production with increasing phytomass. However, this correlation does not apply to grasslands (such as steppes and savannas) or to aquatic ecosystems rich in algae; in other words, to those ecosystems whose phytomasses, in contrast to those of woodlands or other woody vegetation types, exhibit a much larger proportion of green (i.e. producing) parts and whose turnover rates are several to many times higher. These two factors provide grasslands and algal populations with high productiveness (growth, reproduction) despite the small amount of material (biomass) present at all stages (cf. Chap. 3.4.5.2).

3

(Selective) overview of the various reserves and transfer processes in an ecosystem

(with special reference to the biological components and processes)

ORGANIC SUBSTANCES **MINERAL NUTRIENTS**

RESERVES

Biomass
- Phytomass[1]
  - Above-ground
    - Fraction of the photosynthetically active organs
    - Fraction of organs merely respiring
  - Below-ground — Fraction of organs merely respiring
- Animal biomass[1]

Litter (L and O horizons)

Dead organic matter in the soil (A_h and H horizons)

Nutrients in phytomass (biomass)

Nutrients in litter

Nutrients in humus

Nutrients in soil solution and at exchangers (CEC, AEC)

Nutrients in primary rock minerals

TRANSFER PROCESSES

Gross primary production

Net primary production

Animal consumption

Litter fall (above-ground litter)

Return of below-ground phytomass (biomass)

Litter (wastes) decomposition

Humification

Nutrient uptake by plants

Nutrient incorporation into phytomass

Resorption of nutrients from the leaves (internal translocation of nutrients)

Recretion (crown wash and stem flow)

Nutrient return from plants through wastes and animal consumption

Nutrient release by decomposition of organic wastes (mineralization)

TURNOVER PERIODS / RATES OF ORGANIC SUBSTANCES[2]

Turnover period/rate of vegetation

$$\frac{\text{Phytomass}}{PP_N} \text{ (years) or } \frac{PP_N \cdot 100}{\text{Phytomass}} \text{ (\%)}$$

Decomposition period/rate of dead organic substances

$$\frac{\text{Litter + dead soil organic matter}}{\text{Return of organic matter (litter fall + wastes from below-ground phytomass)}} \text{ (years) or}$$

$$\frac{\text{Return of organic matter (litter fall + wastes from below-ground phytomass)} \cdot 100}{\text{Litter + dead soil organic matter}} \text{ (\%)}$$

Decomposition period/rate of litter

$$\frac{\text{Litter reserves}}{\text{Litter fall}} \text{ (years) or } \frac{\text{Litter fall} \cdot 100}{\text{Litter reserves}} \text{ (\%)}$$

Turnover period of total plant matter (living and dead)

$$\frac{\text{Phytomass}}{PP_N} + \frac{\text{Litter + dead soil organic matter}}{\text{Return of organic matter (litter fall + wastes from below-ground phytomass)}} \text{ (years)}$$

Turnover period/rate of an animal population

$$\frac{\text{Animal biomass}}{\text{Annual production}} \text{ (years) or } \frac{\text{Annual production} \cdot 100}{\text{Animal biomass}} \text{ (\%)}$$

---

[1] Where the standing dead is included, it is better to speak of standing crop.

[2] Assuming steady-state conditions; 'PP_N' can be substituted for 'return of organic matter', when decomposition processes in the standing dead (cf. Chap. 3.4.5.2) and animal consumption can be ignored.

Box 3

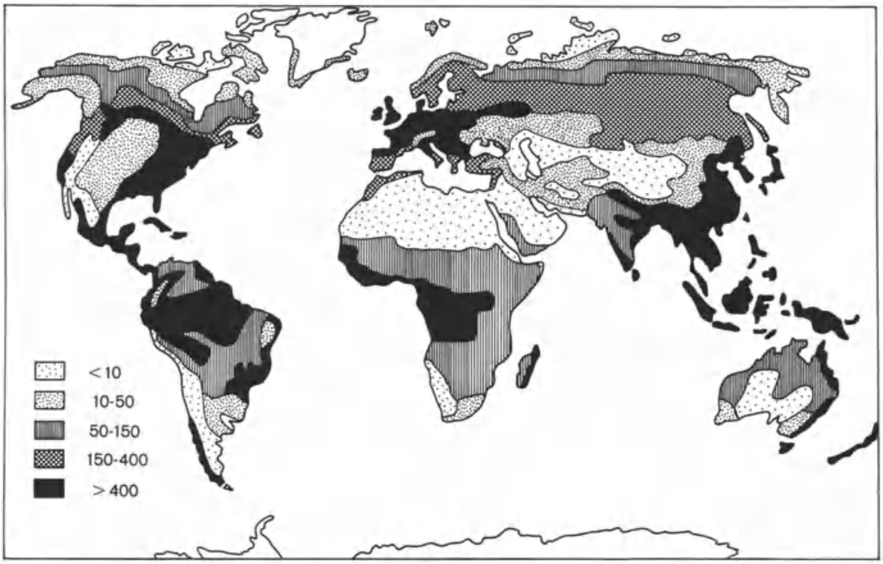

Fig. 11. Distribution of phytomass (above- and below-ground plant material in tonnes of dry matter per ha) around the globe. (Bazilevich and Rodin 1971, from Larcher 1984)

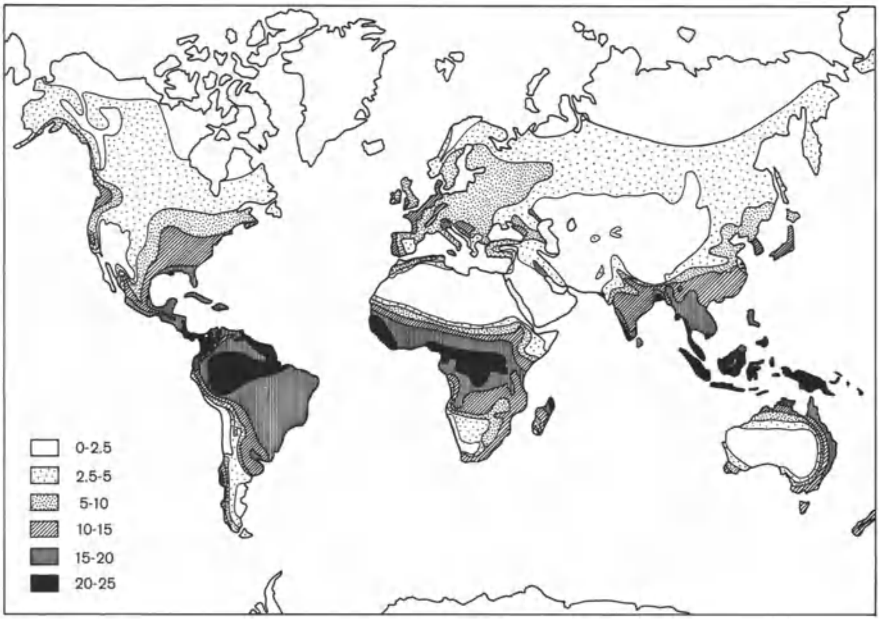

Fig. 12. Annual net primary production (in tonnes of dry matter per ha) around the globe. (Lieth 1964)

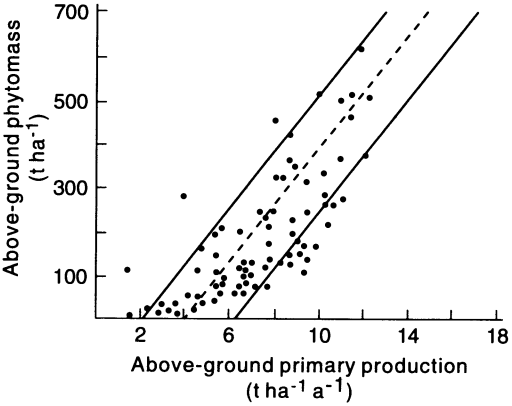

Fig. 13. Relationship between above-ground phytomass and above-ground primary production in forest formations. (O'Neill and De Angelis 1981)

Terms and Units of Measure

Gross and Net Photosynthesis. Some of the photosynthetic products are broken down directly (without the plant receiving any energy) due to the *photorespiration* (light respiration) process which occurs simultaneously with photosynthesis; and a smaller amount (1/2 to 1/5 of the photorespiration) is lost due to the nightly losses of *mitochondrial respiration* (dark respiration) which – as in heterotrophs – serves to release energy for metabolism (cost of biosynthesis, tissue maintenance). The remainder, namely the actual gain in tissue and energy which is at a later stage transferred to the herbivores, saprovores or decomposers, is termed *net primary production* (PP_N), and the physiological production process at its basis is called net photosynthesis, net assimilation or apparent photosynthesis. The sum of net primary production and respiration (R) yields the *gross primary production* (PP_G) and the production process upon which it is based is termed gross photosynthesis or real photosynthesis (Box 4). When the term primary production is used in this book, it is always intended to indicate the *net* primary production.

Losses due to photorespiration increase with rising temperature and are therefore higher in warm zones than in cooler ones. Mitochondrial respiration losses also depend on what proportion of the plant stand is made up of non-productive tissue (Table 4); thus, they are much more severe in forests with high proportions of trunk and branch material than in purely herbaceous formations. When taken together, the two types of loss amount to about 80% of the PP_G in the case of tropical rain forests, about 50% in temperate forests, and about 10–20% in herbaceous formations in the mid-latitudes and in the subpolar dwarf shrub tundras.

The amount of energy diverted to (total) respiration as a part of the gross primary production can be expressed either as the economic coefficient of primary production, PP_G/R (Larcher 1984) or as the production efficiency, R/PP_G (Reichle 1975).

Photosynthesis, primary production and respiration **4**

Gross photosynthesis:
(real photosynthesis)
↓
Gross primary production (PP_G); purely arithmetic measure of effectiveness of the photosynthetic apparatus, does not appear as phytomass; is estimated from net primary production + respiration

Minus respiration losses (R)
(photorespiration = light respiration and mitochondrial respiration = dark respiration)

= Net photosynthesis
(apparent photosynthesis, net assimilation)
↓
Net primary production (PP_N)
↓
Phytomass

When the terms productivity, or rate or intensity of photosynthesis (assimilation) or production are used, for example net productivity, gross photosynthetic intensity, net rate of assimilation, this expresses the relationship to time as long as the time period in question is less than 1 year, e.g. 1 hour, 1 day, 1 month etc. If the relation is one year, only the term production is commonly used; e.g. tundras have an annual *production* of $2–4\,t\,ha^{-1}$ – not an annual productivity or an annual rate of production of $2–4\,t\,ha^{-1}$

Box 4

Phytomass and Standing Crop. The *Phytomass* encompasses the entire mass of living plants (as a rule it does not include the decomposers). Taken together with the *animal biomass*, i.e. the entire mass of living animals (also ignoring the detrivores), these two groups form the total *biomass*, that is, the entire mass of all living organisms. Since, in many cases, the phytomass makes up 99% of the biomass, phytomass and biomass are often considered identical.

Living plants contain a great deal of dead material (which is collectively termed *necromass*), such as tree bark, dead supporting tissue (sclerenchyma) or attached dead parts such as dead branches or roots. Such material is not always considered part of the phytomass; when it is, the more encompassing term *standing crop* should be used (*standing dead* then refers to the dead portions of the standing crop; the standing dead also includes dead trees as long as they are still upright).

In the case of many values given for phytomass, standing crop or primary production in the literature, it is unclear whether the portions below ground were included or whether only the above-ground phytomass, above-ground standing crop or above-ground primary production were taken into account. All references to phytomass found in this book, unless otherwise stated, refer to both above- and below-ground phytomass, including all dead parts still attached to living plants. Analogously, primary production indicates the total production, including that of shoots and roots.

Table 4. Proportion of assimilation organs, axial structures and roots in the total mass (dry matter) of plants. (Larcher 1984). The ratio of below-ground to above-ground phytomass is lowest in forests (often 0.1–0.3), high in grassy areas (often 2–3) and highest under extreme growth conditions in arid regions and subpolar climates (often 4–5). The proportion of above-ground woody trunks and branches is naturally highest in forests, average in shrubby areas and lowest in formations like savannas and steppes containing a great number of herbaceous plants (and zero in areas containing only such plants). When both sets of purely respiratory organs, the axial structures and the roots, are deducted, the photosynthetically active organs (green plant biomass) that are left account for only 1–2% in tropical and temperate trees, for 4–5% in boreal coniferous trees, for 10–20% in tundra plants and for up to 30–50% in savanna and steppe grasses

Plant	Green plant biomass (photosynthetically active organs)	Only respiratory organs	
		Axial structures (trunks and branches)	Roots and below-ground shoots
Evergreen trees in tropical and subtropical forests	about 2%	80–90%[a]	10–20%[a]
Winter deciduous broadleaf trees in the Humid Mid-Latitudes	1–2%	about 80%[a]	about 20%[a]
Evergreen coniferous trees in the Boreal Zone	4–5%	about 75%[a]	about 20%[a]
Steppe plants			
– In wet years	about 30%		about 70%
– In dry years	about 10%		about 90%
Desert plants	10–20%		80–90%
Tundra zone			
– Vascular plants	15–20%		
– Cryptogams	>95%		

[a] A large part of the mass is made up of dead supporting structures.

Units of Measure. Stand reserves and transfers of matter and energy are given in various units of measure in the ecological literature (Box 5). Where possible, the present book limits itself to metric tonnes and kilojoules and uses the hectare as the reference unit of area. The unit tonne refers only to the *dry matter* of the biomass or of the dead organic material found after drying in an oven at 105°C. This total dry matter (tot. DM) should be differentiated from the organic dry matter (org. DM) which is determined by subtracting from the fresh weights not only the water present but also all mineral components. The *energy equivalent* to plant matter is always considered to be 18 kJ per 1 g total DM. The year is taken as the reference unit of time for transfer processes.

Primary Production

Productiveness of Individual Plants and Plant Stands. The primary production of *single plants* can be determined on the basis of the increase in dry matter, the CO_2 uptake or the O_2 release. When described by the increase in dry matter per

Conversions

5

The organic reserves and transfer processes (energy fluxes) in ecosystems are described in different units of measure. The approximate equivalents provided here may help in performing conversions. They apply to the phytomass and to dead organic material of plant origin.

1 g org. TS $\approx$ 0.45 g C $\approx$ 1.6 g $CO_2 \approx$ 19.5 kJ ($\approx$4.7 kcal)
1 g C $\approx$ 2.2 g org. TS $\approx$ 3.6 g $CO_2 \approx$ 42 kJ ($\approx$10 kcal)
1 g $CO_2 \approx$ 0.65 g org. TS $\approx$ 0.3 g C $\approx$ 12.4 kJ ($\approx$3 kcal)

1 kJ = 0.239 kcal $\approx 5 \times 10^{-2}$ g org. TS 1 cal=4.1868 J
1 g org. DM $\approx$ 1 g total DM minus 3--10% (for Wood: minus 0.5%)

1 g total TS $\approx$ 0.42 g C $\approx$ 1.5 g $CO_2 \approx$ 18 kJ ($\approx$4.3 kcal)
1 g total TS $m^{-2} = 10^{-2}$ t total TS $ha^{-1} \approx 18 \times 10^4$ kJ ha^{-1}
1 t total TS ha^{-1} = 100 g total TS $m^{-2} \approx 0.18 \times 10^8$ kJ ha^{-1}

Energy equivalents (caloric values) for plant substances can vary considerably, depending on the type of organic material and the ash content. The caloric values (kJ g^{-1}) shown here are approximations for the following materials:

Carbohydrates (e.g. cellulose)	17.6	Lignin	26
Proteins	23	Fats	39

The mean values for plant material given in the literature are between 16 and 20 kJ (= 3.8-4.8 kcal) per 1 g total dry matter (DM). In the present text, 18 kJ (= 4.3 kcal) is generally used for conversion purposes

Box 5

unit time (day, week etc.), it is given in reference to the initial weight of dry matter (= relative growth rate = RGR) or to the leaf surface (= assimilation) area (= net assimilation rate = NAR). Its magnitude depends to a certain degree on conditions within the plant,[5] but for the most part on external conditions (see below).

The productiveness of *plant stands* (crop growth rate) is calculated from the increase in dry matter per unit time (mostly 1 year or 1 month) in relation to the ground area (m^2 or ha). "Dry matter" includes, in addition to the growth increment (increase in live plant material or phytomass; ΔB), the losses through death (L), herbivory (C) or fire (F), all above and below ground:

$$PP_N = \Delta B + L + C + F.$$

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

---

[5] For example, under optimum conditions, C_4 plants (cf. Chap. 3.4.5.2) attain higher levels of productivity than C_3 plants and these, in turn, are more productive than CAM plants; the leaves of a plant which have developed under sunny conditions are more efficient producers than those of the same plant which have developed under shady conditions.

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:

$$PP_N \approx \Delta B.$$

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:

$$PP_N \approx \Delta B + \Delta W + D.$$

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.

The magnitude of net primary production by vegetation is dictated by:

- The growth rates of the single plants making up the stand.
- The amount of phytomass above ground or (if a great deal of photosynthetically inactive trunk and branch material is present; Table 4) the assimilation area (= sum of all leaf areas).
- Various environmental conditions such as length of the growing season, solar radiation, air temperature, soil fertility etc.

Leaf Area Index and Absorption of Solar Radiation. The assimilation area is expressed as the *leaf area index* (LAI) in m^2 of leaf area (one side only) per $1\,m^2$ of ground area. In deciduous forests of the Humid Mid-Latitudes, this index is often between 5 and 6, in the rain forests of the Humid Subtropics, 7–8, and in the rain forests of the Humid Tropics, 9–10 (Kira 1975, p. 14).

Productivity increases with increasing phytomass and LAI, as long as this causes an increase in the radiation absorption (interception) by the green plants (or green parts). Under the most favourable conditions, this can amount to about 85–95% of the incoming short-wave radiation (global radiation) (cf. Table 30). When this limit is reached (in plant stands at our latitude, this happens at an LAI of 4–8, Larcher 1984, p. 184), a further increase in LAI does indeed cause an increase in the number of production sites, but stand productivity does not increase further, since the assimilation rate per leaf surface area drops in proportion to the decreasing radiation within the stand (due to the increase in plant overlap).

Aside from the LAI, the *angle of incident radiation* is of particular importance to the *efficiency of radiation absorption* or *interception efficiency* [ratio of the absorbed (intercepted) to the total incoming radiation]. This angle is dependent on the solar altitude. The higher the latitude and the lower the altitude of the noon sun, the longer the path length of the sun's rays through the canopy; the longer the path length, the greater the LAI in the direction of the sun's rays. Thus, the same LAI yields increasingly intercepting LAIs with decreasing solar altitudes (Tieszen et al. 1981).

This means that the radiation absorption increases with proximity to the poles, all other conditions being equal (Table 5). On 21 June, for example, an LAI (as usually determined by a vertical projection) of 1.0 provides an intercepting LAI of 3.0, 2.0 and 1.5 at 70°, 55° and 40° latitudes (Tieszen et al. 1981, p. 288). With more vertically inclined leaves, this effect is even greater.

This explains why the radiation absorption at high latitudes, where vegetation development tends to be less lush and the LAI remains lower, always approaches maximum levels. This in turn shows that there can be no important causal relationship between the increase in LAI that exists from the poles to the equator in the year-round humid zones,[6] and the increase in primary production in the same direction.

Primary Production as a Function of Site Conditions. Instead, the decisive causes for the major regional differences in production are to be found in a few external conditions, most importantly, the *length of the growing season* and the *radiation energy available during this season.* The latter forms the solar growth potential.

Photosynthetic Efficiency. 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

Table 5. Radiation absorption as a function of the leaf area index (LAI) and solar declination (geographic latitude). (Tieszen et al. 1981)

Geographical latitude	Solar altitude between 21.5 and 21.8		Same radiation absorption at LAI
	Mean	Range	
70° N	20°	5–45°	1
55° N	32°		1.5
40° N	40°	0–63°	2
0° N	40–45°	0–90°	3

---

[6] With the exception of the boreal coniferous forest, whose LAI of 8 (Reichle 1981, p. 31) is unusually high, even when one considers that the entire surface area of needles (upper and lower sides) is used in the calculation.

as the *relation between the annual primary production (or, more exactly, its energy content) and the incoming radiation during the growing season.*[7]

Values typical for a zone are obtained when the *average annual production of zonal plant formations on average sites* is used in the calculation. Most of the measurements cited in the literature for this type of radiation yield, or those calculated from the results of investigations, lie between 0.1 and 1% (or between 0.2 and 2% PAR). Some authors view 0.5% (or 1% PAR) as a generally applicable value (e.g. Coupland 1979). The magnitude of the primary production for each ecozone was calculated (Table 7, second to last column) using this general value and assuming that the mean energy content of plant matter is $18\,\mathrm{kJ\,g^{-1}}$ (see above).

As far as the *year-round humid ecozones* in cold and temperate latitudes are concerned, the *calculated values* are in good agreement with the *measured values* (or those determined by other means); in comparison to those in the warmer zones, however, they are too low (cf., for example, the summaries of PP_N values from various regions of the earth, given by Rodin et al. 1975, Whittaker and Likens 1975, Lieth 1978, Coupland 1979, Reichle 1981). The PP_N values obviously increase more rapidly with increasing proximity to the equator than do the sums of the incoming radiation during the growing season. This is illustrated by the values shown in Table 6 for various latitudes: the incoming radiation during the growing season (and the length of the growing season) increases from the subpolar tundras to the equatorial rain forests by a factor of 6, while the increase in primary production over the same area increases by a factor of 12–15, or double the rate for radiation.

This suggests that net photosynthetic efficiency increases with air temperature. Investigations conducted on individual plants corroborate this theory (Fig. 14). Many species attain their highest photosynthetic rates at temperatures around +30°C.

The magnitude of the *increase in photosynthetic efficiency towards the equator* can be estimated from productivity data gathered worldwide, when these are related to the radiation received during the growth periods. This indicates that the *mean* photosynthetic efficiencies increase from the poles to the equator from about 0.4 to 0.8% of incoming radiation (or 0.8–1.6 of the PAR).[8] These rates

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[7] Other methods of calculation use, for example, the PP_G instead of the PP_N, the *absorbed* incoming radiation or PAR in place of the total incoming radiation, or they relate these to different time periods; for instance, they calculate the energy yield during phases of particularly intense growth or relate the production to overall annual radiation (not considering that part of the year might be too cold or too dry for plant growth). Depending on which factors are selected, quite different results can be produced in numerical terms.

[8] This is meant to indicate the mean photosynthetic efficiency of zonal plant formations over the long term, i.e. also taking into account those age phases of plant stands in which production is lower. In individual cases, there can be severe deviations from this average, depending on edaphic conditions and plant communities. The most productive stands and the productivity rates during particularly active juvenile/mature phases all exhibit much higher degrees of efficiency. Since many of the investigations so far conducted deal with such special cases, it is of little value at this point to compute an arithmetic mean for the degrees of efficiency in each zone.

Table 6. The polar/equatorial gradients for phytomass, primary production and some environmental characteristics in the humid (moist all the year round) ecozones

Ecozone	Mean geographic latitude (ϕ°)	Phytomass (t ha^{-1})	PP$_N$		Growing season (months)	Incoming radiation during the growing season	Air temperature during the growing season	Net photosynthetic efficiency (%)
			(t ha^{-1}a^{-1})	(10^{8}kJ ha^{-1}a^{-1})		(10^{8}kJ ha^{-1})	(°C)	
Polar/Subpolar Zone: Tundra	70	30	2	0.36	2	100	7	0.36
Boreal Zone	60	200	6	1.1	5	225	12	0.48
Humid Mid-Latitudes	45	300	10 (12)	1.8	7 (−11)	350	14	0.51
Humid Subtropics	30	450	20	3.6	12	575	18	0.62
Humid Tropics	0	500	30	5.4	12	575	26	0.94

Towards the equator, primary production increases faster than the duration of the growing season and the sum of incoming radiation. Since the phytomass, or leaf area (area of assimilation), cannot play a decisive role (see text), this indicates the significance of the temperature factor: as the air temperature increases, the net photosynthesis obviously rises as well. The right-hand column shows the net photosynthetic efficiency calculated for each zone from the PP$_N$ and incoming radiation.

Table 7. Incoming radiation and primary production in the ecozones

Ecozone	Incoming radiation (10^8 kJ ha^{-1})[a]		Net primary production		
	During one year	During one growing season	Energy fixation[b] (10^8 kJ ha^{-1} a^{-1})	Dry weight[b] (t ha^{-1} a^{-1})	Dry weight[c] (t ha^{-1} a^{-1})
Polar/Subpolar Zone	300–350	50–150[d]	0.25–0.75	1 – 4	1 – 4
Boreal Zone	350–450	150–300	0.75–1.50	4 – 8	4 – 8
Humid Mid-Latitudes	450–550	300–400	1.50–2.00	8 – 11	8 – 13
Arid Mid-Latitudes	500–650	150–300[e]	0.75–1.50	4 – 8	4 (3) – 10 (8)
Tropical/Subtropical Arid Lands	650–800	200–350[f]	1.00–1.75	5 – 10	7 (6) – 14 (11)
		100–200[g]	0.50–1.00	3 – 5	4 (3) – 6 (5)
Mediterranean-Type Subtropics	550–700	200–300	1.00–1.50	5 – 8	6 – 10
Seasonal Tropics	650–750	350–550	1.75–2.75	10 – 15	14 (11) – 21
Humid Subtropics	500–650	500–650	2.50–3.25	14 – 18	20 – 25
Humid Tropics	500–650	500–650	2.50–3.25	14 – 18	21 – 29

[a] Compiled from radiation maps by Budyko (1963), Landsberg (1963) and Löf et al. (1966). The ranges given here indicate the boundaries between which most values lie.

[b] Assumptions: (a) mean net photosynthetic efficiency: 0.5% of incoming radiation during the production (growing) period; (b) energy equivalent of the plant mass produced: 18 kJ g^{-1} total DM (dry matter).

[c] Net primary production, assuming that net photosynthetic efficiency varies between ecozones: zone 1: 0.4–0.5%, 2: 0.5%; 3 and 4: 0.5–0.6%; 5: 0.7% (mediterranean-type thorn steppe: 0.6%); 6: 0.6%; 7 and 8: 0.7%; 9: 0.75–0.8%; in parentheses: corrected values for decreased radiation absorption in arid regions; (see text for explanation).

[d] Tundras.

[e] Grass steppes.

[f] Tropical thornbush and thornscrub savannas.

[g] Subtropical thorn steppes.

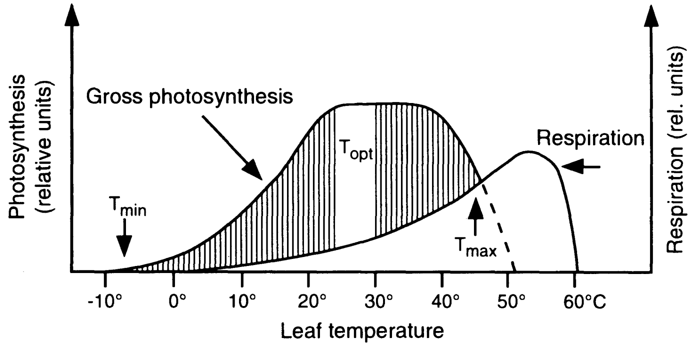


Fig. 14. Schematic of the temperature dependence of photosynthesis and respiration. (Larcher 1984). Net photosynthesis (*hatched area*) is the difference between gross photosynthesis and respiration. In the example shown, it achieves its highest value between +25 and +30 °C

were used in calculating the adjusted productivity values in the right-hand column of Table 7 (cf. Box 6).

In the case of the *arid regions*, additional corrections must be made. It can be assumed, and this is corroborated by high albedo values, that the actual cover of natural vegetation in these regions – at least at the start of the rainy season – remains more or less far below the degree of cover necessary for maximum absorption of incident radiation. The temperature-corrected net photo-

6

Primary production. Calculation of mean annual production of zonal or other spacious plant formations on the basis of climatic parameters.

$$PP_N = \frac{c}{100} \sum_{i=\text{First month of GS}}^{\text{Last month of GS}} (Q+q)_i \frac{10^{-6}\,t}{18\,kJ}$$

where

PP_N = annual primary production of plant stands (t ha^{-1})

c = photosynthetic efficiency [energy fixed by photosynthesis in percent of total (short wave) incoming radiation]. Mean value for plant stands is approximately 0.5 (average of low- and high-productive age phases). Many observations make it very likely that the efficiencies (since correlated with air temperature) drop polewards to approx. 0.4 and increase equatorwards to 0.8.

GS = growing season: sum of months within a year whose mean temperatures are at least +5 °C and whose precipitation (in mm) surpasses twice the air temperature (in °C) (cf. climatic diagrams of Walter and Lieth)

Q+q = short-wave (direct and diffuse) radiation (global radiation) (kJ ha^{-1})

18 kJ = mean energy content of 1 g plant tissue (dry weight)

Box 6

synthetic efficiency in this case cannot be related to the total incoming radiation, but rather to this radiation less the elevated reflection losses present. The productivity values given in parenthesis for the ecozones with a dry season (last column in Table 7) are based on a flat rate subtraction of 20% radiation.

The annual production values thus calculated should be viewed above all as *relative magnitudes of ecozonal vegetation production potentials.* They can also serve as a relative measure of (climate-determined) *agricultural and forest yield potentials* in the individual ecozones. As a rule, crop growth is promoted by a longer growing season, higher solar radiation and higher air temperatures, as is the case with natural vegetation. This means that the growth performance of suitable crops should be at least as high as the primary production found in the ecozone as a whole (in the case of annuals, however, this is the case only if the growing season is fully exploited). The yields can be raised above this level if the growing season is artificially extended (in arid regions through irrigation, in regions with cold winters through the use of greenhouses) or when new varieties of crop exhibiting higher photosynthetic efficiency are developed. Both of these methods have been applied extensively. Table 8 shows the increased primary production values achieved in the ecozones with a dry season, when the growth restrictions during the natural dry periods are eliminated by irrigation.

Rate of Material and Energy Transfer in the Ecosystem

Aside from the magnitude of transfer in an ecosystem, the most important factors are the turnover period (transit time, residence time) and the turnover rate. Under steady-state conditions, in which (at least over the long run) the gains (input, inflow) and losses (output, outflow) of the individual stand reserves balance each other out, that is to say, their magnitudes do not change considerably, the *turnover period* is that time (in years) over which the cumulative inputs and outputs add

Table 8. Primary production under irrigation in ecozones with a dry season (all months with $t_m \geq +5\ °C$)

Ecozone	Incoming radiation during the warm season $t_m \geq 5\ °C$ (10^8 kJ ha^{-1})	Primary production under artificial irrigation		
		Energy fixation (10^8 kJ ha^{-1} a^{-1}) (1)	Dry weight (t ha^{-1} a^{-1}) (1)	(2)
Arid Mid-Latitudes	350–500	1.75–2.5	10–14	10–17
Tropical/Subtropical Arid Lands	650–800	3.25–4.00	18–22	25–31
Mediterranean-Type Subtropics	550–700	2.75–3.50	15–19	18–23
Seasonal Tropics	650–750	3.25–3.75	18–21	25–29

(1) Net photosynthetic efficiency 0.5% of incoming radiation (global radiation) during the production period (warm season).

(2) Net photosynthetic efficiency corrected for temperature, see Table 7.

up to the respective parameters of the stands, i.e., on average, the reserves have been replaced once. The *turnover rate* (in percent) then indicates what proportion of phytomass, animal biomass, litter or humus has been added during the year by means of primary production, secondary production, litter fall and humification, and what proportion is lost due to plant wastes and animal consumption, the death of animals and decomposition.

The turnover period is given as the ratio of reserves to annual input, and the turnover rate as the ratio of annual input to reserves (cf. Box 3). The larger the reserves of living and dead organic substance, the longer the turnover *period* (the turnover *rate* decreases in this direction). Both the turnover period and the rate can be calculated, either for the transfers between individual reserves, or for the entire flow of matter between primary production and mineralization (see Box 3).

2.5.2.2 Animal Consumption and Secondary Production

Animals are *heterotrophic* organisms (or heterotrophs, for short) which directly or indirectly subsist on the organic products of primary producers (and are thus also called consumers). For this reason, their products are considered secondary products and they themselves are termed *secondary producers*. On the basis of their feeding behaviour they are called either *herbivores* (plant eaters, phytophages, primary consumers), *carnivores* (scavengers, predators, zoophages, secondary consumers), *omnivores* (those which feed on both) or detrivores (detritus eaters, saprovores). The first three of these four types can be grouped together to form the *biophages* (animals that feed on living tissue) in contrast to the fourth type, which are also termed *saprophages* (those that eat dead tissue). This latter group is not normally included under the consumers but rather is considered to belong to the *decomposers* (destruents, reducers, mineralizers), at least as far as they belong to the micro- or mesofauna in the soil (body length up to about 2 mm).

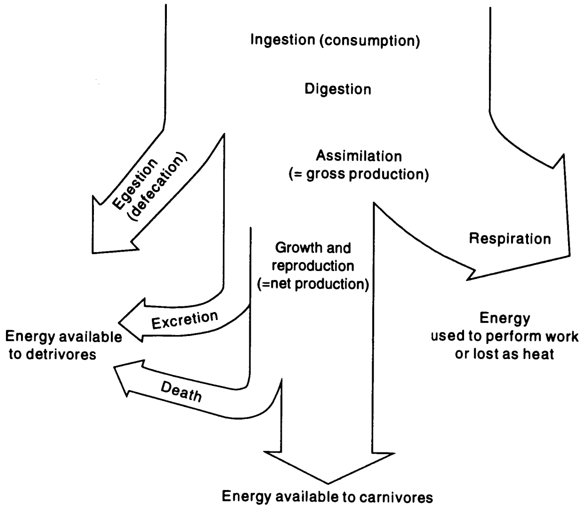
The *quantitative influence of consumers* (biophages) is low in most ecosystems. Usually far less than 10% of the above-ground phytomass is eaten by the herbivores; that is to say, the vast majority of the primary production generally passes by the primary consumers and goes straight to the saprovores. Herbivores play a relatively large role in the overall energy transfer in steppes and savannas rich in game animals and play their smallest role in oligotrophic moors (cf. Chap. 3.2.5).

The *path of food and energy through an animal organism* (or a population) can be divided into a number of single metabolic steps (Box 7). It begins with *consumption* (ingestion), which captures a more or less large proportion of the total food available (remaining portion: ignored food). During *digestion* a portion of the food ingested is directly rejected and egested in the form of *feces* (= unused food, unassimilated food). The remaining absorbed or assimilated portion forms the *gross production*, i.e. the total energy available to the animal for maintenance and production.

7

The path of food (partitioning) and energy through an animal organism (or a population; Ricklefs 1990) and calculation of the efficiency of consumers in the ecosystem

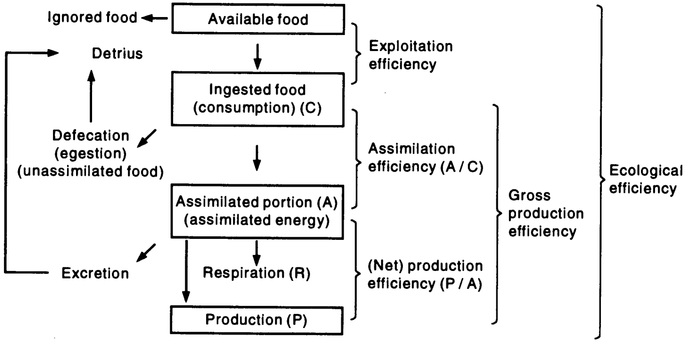
The partitioning of food (energy) within the animal organism



Gross production = ingested food less defecation
= Assimilated portion of food

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

Calculation of energetic efficiencies associated with each metabolic step through the animal organism



Exploitation efficiency[1]: $\frac{\text{ingested food}}{\text{available food}}$

Assimilation (digestion) efficiency: $\frac{\text{assimilation (A)}}{\text{ingestion (C)}}$

(Net) production efficiency: $\frac{\text{production (growth + reproduction) (P)}}{\text{assimilation (A)}}$

Gross production efficiency (also called ecological efficiency): $\frac{\text{production (P)}}{\text{ingestion (C)}}$

Ecological efficiency: $\frac{\text{production (P)}}{\text{available food}}$

Other methods of calculation include the ratio of respiration (R) to ingestion (C), assimilation (A) or production (P) or yield reciprocal results

[1] Proportions are usually given in percent

Box 7

A small fraction of assimilated energy is excreted (urinated) as unusable metabolilc by-products. In the case of most land animals such excretions take the form of ammonia, urea or uric acid. In contrast to the food ingested, excretions and feces are chemically processed or at least mechanically comminuted substances, and thus are easier for the detrivores to decompose.

The largest proportion of the energy won during assimilation is lost during *respiration* (in conjunction with energy-consuming metabolic processes) or it is lost as (partially undesired) heat. Only the energy which remains contributes to the production of new animal biomass. This *net production* is expressed in growth and/or reproduction. It is available to the carnivores of the next higher trophic level in the food chain of the ecosystem, unless the animals die, in which case, their carcasses provide food directly to the detrivores.

The transfer processes just mentioned differ from one type or group of animals to the next with respect to the rate and efficiency of transfer. For calculating the *effects of consumption*, the energy contents involved in the various metabolic steps are compared. For example, *production efficiency* can be calculated as the energy ratio of growth and reproduction to the ingested or assimilated food (gross and net production efficiency respectively). Box 7 provides an overview of the most common efficiency calculations.

Most *warm-blooded (homeothermic) animals* assimilate 80–90% of the energy ingested, whereas many plant-feeding cold-blooded (*poikilothermic*) animals achieve only 20–40% assimilation. Both groups of animals thus differ greatly as to their digestion (assimilation) efficiency. Deviations from this rule are found when the food available is either extremely difficult or easy to digest. On the other hand, warm-blooded animals require a great deal of energy to maintain their high body temperatures, and for this reason the amount of assimilated material which flows to net production (production efficiency) is much smaller than is the case for poikilotherms. This explains why often only 1–5% of the food ingested by homeotherms goes toward growth or reproduction, despite their relatively high digestion efficiency, whereas the value for poikilotherms lies between 10 and 20%. The latter thus have a significantly higher gross production efficiency (sometimes also called ecological efficiency). As a rule of thumb, on average about 10% of the food ingested by consumers contributes to the (secondary) production.

2.5.2.3 Stand Wastes and Decomposition

Below-Ground Wastes

These include primarily dead plant roots (or, in rare cases, below-ground shoots) and, secondarily, dead soil organisms (of the edaphon). The amount of dying roots equals, in the long run, the below-ground net primary production. In contrast to above-ground wastes, which at first form the litter layer, the below-ground wastes directly become part of the humus (meaning all types of dead organic matter **in** the soil; cf. Chap. 2.4).

In soil science, the terms soil organic matter or humus are generally used in a wider sense, including both the below-ground waste portion and the litter layer.

The terms such as low in humus, slightly humous, highly humous, etc. found in soil descriptions refer to particular ranges of *humus content* (in weight percent) in topsoils. These can be used in calculating the *amount of humus* present (in t ha^{-1}, Table 9).

The data provided on soil organic matter in the literature sometimes include living roots and the edaphon. Such values are approx. 10% (max. 20%) above those that take only dead matter into account.

Organic matter is generally determined by analysing the *organic carbon content* of the upper soil layer; for this reason, the humus content is often referred to as the C content. As a rule, 0.5–0.58 g C are considered equal to 1 g of organic matter (or, correspondingly, 1 g C equals 1.72–2.00 g organic matter), although this disagrees somewhat with the ratio found in the substances of living organisms (Box 5). The difference is due to the fact that the C content increases as decomposition takes place.

Above-Ground Wastes (Litter)

As a result of above-ground wastes (leaves, trunks and branches), a layer of litter forms on the soil. The thickness of this layer in an ecosystem varies around a mean value which is determined by both the input and decomposition of litter. Both these processes differ widely between ecozones, and with them also the litter reserves.

Litter input is mainly a function of above-ground primary production. Averaged over a period of years, the annual input will never exceed this value, but it can be lower if herbivores play a role in the transfer process for phytomass or, as has been observed in grassland studies, decomposition already begins with

Table 9. Contents and amounts of dead organic matter in soils. (Schachtschabel et al. 1992)

Description of soil	Organic matter content (dry weight in weight percent) in the topsoil (A_h horizon)	Equivalent to organic matter (dry weight in t ha^{-1}) for[a]	
		A_h = 20 cm	A_h = 30 cm
Humus-poor	<1	<30	<45
Slightly humus	1– 2	30–60	45–90
Moderately humus	2– 4	60–120	90–180
Highly humus	4– 8	120–300	180–450
Very highly humus	8–15	300–450	450–675
Humus-rich	15–30	450–900	675–1350
Peaty	>30	>900	>1350

[a] Assuming a specific soil density (bulk density) of 1.5 g cm^{-3}.

the standing dead (cf. Chap. 3.4.5.2). Herbivores, and possibly carnivores, which live above ground and become part of the litter layer when they die, have body masses between 90–99% lower than the plant and animal tissue they consume. Litter input is also reduced in areas subject to fires, which consume part of the phytomass and possibly of the litter layer as well.

The limitations on litter input mentioned here are most obvious in herbaceous plant formations of the Seasonal Tropics and Arid Mid-Latitudes. In all other ecozones it can be assumed, as a first approximation, that the mean annual litter input is only slightly below the above-ground PP_N for the same time period. As a result, this input is highest in the tropical rain forests and, with the exception of extremely dry and cold regions, lowest in the tundras.

Litter decomposition comprises the processes of the mechanical and chemical breakdown, and also the working of the litter into the mineral soil. Organisms play a major role in all three processes. Either as a whole, or due to their particular function, they are called decomposers, detrivores, saprovores, saprophages (plant saprophages = saprophytes), reducers or mineralizers.

As the transformation and translocation process proceeds, it causes an increasing loss of the original plant structure and finally leads to either inorganic breakdown products (end products of mineralization) or higher molecular secondary compounds (materials of humification), with CO_2 simultaneously being given off; and clay/humus complexes (mull) may be formed (cf. p. 33). The soil profile shows the progress of decomposition over time in a sequence of (continuously merging) layers (horizons) which are identified and defined as follows (starting from the surface):

L = litter consisting primarily of undecomposed organic materials.
O_f = organic horizon with moderately/partially decomposed (fermented) organic matter.
O_h = organic horizon with strongly decomposed (humified) organic matter.
A_h = mineral horizon (at or near soil surface) with well decomposed organic matter.

L, O_f and O_h are taken together to be the surface humus (organic) layer (except in the case of peaty soils, where O_h is replaced by H for histic; cf. Chap. 3.1.4), such as, for example, the raw humus mat which covers certain acid soils; in the FAO-UNESCO soil classification, they are all grouped under the collective term O horizon (cf. also Chap. 2.4).

The *boundary between the litter layer and the (soil) humus* is dealt with in a variety of ways; for example, the humus content of the O_h horizon is often considered part of the organic matter in the soil. Uncertainties also arise due to the fact that the transition between the horizons is fluid, thus making it often impossible to distinguish between them. Unless otherwise indicated, the present book will consider the entire surface organic matter, including the O_h horizon, as part of the litter (and not as part of the soil). However, peat belongs to the soil organic matter (humus), which is otherwise identical to the dead organic matter in the A_h horizon.

The *rate of litter decomposition* depends on the composition of the litter (decomposability) and on the prevailing climatic and edaphic conditions. It is lower, for instance, when woody material predominates, when tannins and waxes are present in large quantities in the organic matter and when dryness, cold, waterlogging or soil acidity impede the breakdown processes, which are mainly biological in nature. Such obstacles to decomposition occur particularly in the arid and cold regions of the earth. Consequently, such regions have the lowest

Table 10. Rate of decomposition of leaf and needle litter in various ecozones. (Swift et al. 1979)

Ecozone	k = rate of decomposition (annual litter input/litter accumulation)	3/k = period (in years) up to 95% decomposition[a]
Polar/Subpolar Zone: tundra	0.03	100
Boreal Zone	0.21	14
Humid Mid-Latitudes	0.77	4
Arid Mid-Latitudes: grass steppe	1.5	2
Seasonal Tropics	3.2	1
Humid Tropics	6.0	0.5

[a] cf. Olson 1963.

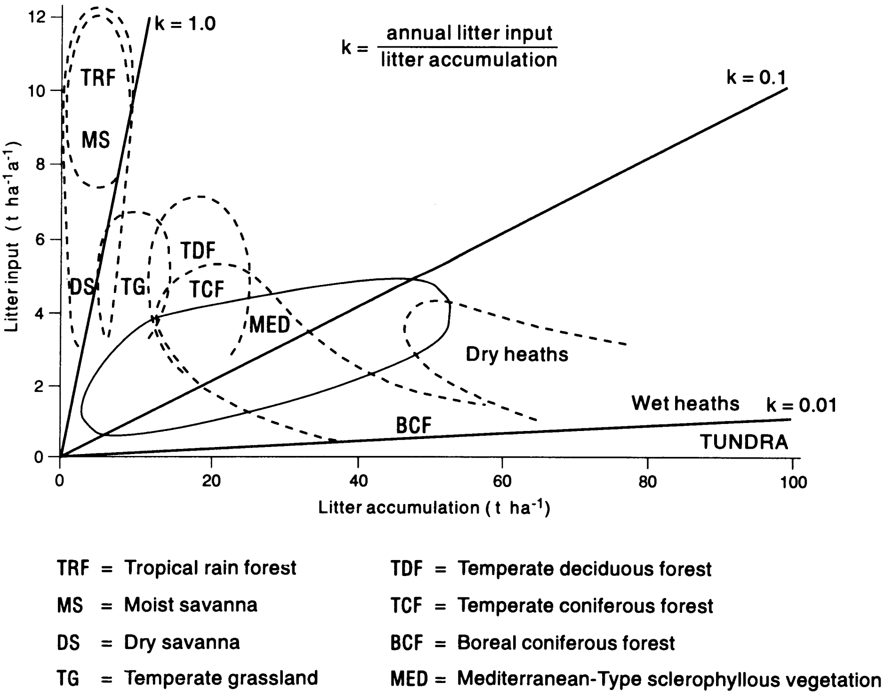


Fig. 15. The relationship between litter input, accumulation and rate of decomposition (k) in selected biomes. (Read and Mitchell 1983)

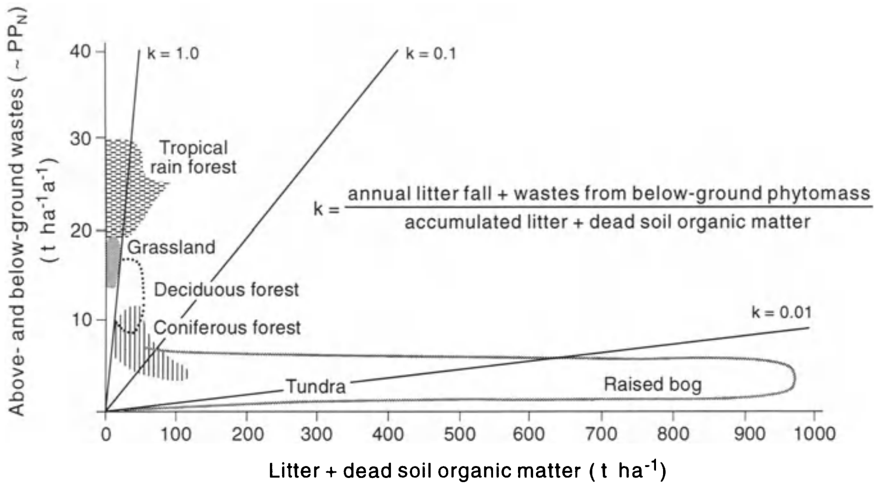


Fig. 16. The relationship between input and accumulation of above- and below-ground wastes and rate of decomposition (k) in selected biomes. (After Heal et al. 1981)

rates of decomposition; the rates are highest in the tropical rain forests. This is illustrated by the *decomposition rates for leaf and needle litter* in selected ecozones shown in Table 10. The breakdown of dead plant and animal tissues in and on the soil is in itself advantageous, since this allows the mineral nutrients bound in this material to be released and returned as a source of food to the plants.

Figures 15 and 16 show the ranges within which the *rates of decomposition (k) of litter* (Fig. 15) *and of the above-ground and below-ground wastes* (Fig. 16) vary for a number of biomes (steady-state conditions are assumed, i.e. the total input of litter and below-ground wastes is equal to the amount of material being decomposed at the same time). Regional differences range from 100–1% (and, in the boreal and subpolar raised bogs, even to below 0.1%); thus, these differences are much greater than those found for turnover rates of phytomasses ($PP_N \cdot 100$/phytomass), which vary between 3 and 30% (cf. Chap. 3.1.5).

2.5.2.4 Nutrient Turnover and Nutrient Stores

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.

The plants' *nutrient uptake can exceed* the amount of nutrients necessary for the synthesis of organic substances (i.e. the amount incorporated into the plants) when a portion of the nutrients absorbed through the roots (1) is excreted again (in mineral form) at the shoot surface (= *recretion*), either immediately or within the same year, and then returns to the soil through *crown wash* or, in the case of trees, also through stemflow; or (2) builds up in the leaves during the growing season, but is not involved in any growth processes.

In the case of perennial plants, the *uptake can be less than the requirement* when a large portion of the nutrients (particularly N, but also K) in the leaves or needles is returned prior to shedding to the remaining shoot portions of the plant and thus becomes available again for (next year's) PP_N. The nutrient uptake from the soil may be decreased by the amount of this *internal resorption (translocation)* (Box 8).

Besides recretion (and a few other pathways of minor importance), *nutrient return* into/onto the soil occurs by means of *litter fall, dying roots and animal consumption*, and the nutrients are released through decomposition processes (mineralization). Each element has its own residence (turnover) time which varies greatly from that of other elements, depending on how it is bound to the organic substances present and on how readily these substances decompose (cf. Chaps. 3.2.5.2 and 3.3.5.3). Potassium, for example, is always released more quickly (since this does not necessarily require the mineralization of organic substances) than, for example, nitrogen or phosphorus. Deficiencies of these latter elements are thus more likely to occur when the mineralization rate is low (Fig. 62).

The *leaves and needles* of trees have much higher *nutrient contents* than do the trunks, branches and roots (accordingly the nutrient requirement for the production of leaves and needles far exceeds that for wood production) and, despite partial nutrient translocation (see above), they still retain a relatively high nutrient content up to the time when the leaf/needle fall occurs. Litter layers of leaves and needles thus also contain relatively high levels of nutrients (Figs. 63, 85, 143 and Table 29). In the case of trees, therefore, the uptake and requirement of nutrients per unit PP_N is not a measure of the average nutrient content of the phytomass produced over the long term through this PP_N; similarly, there is no way to estimate the nutrient release from the litter on the basis of the average nutrient content of the phytomass, which is the source of this litter.

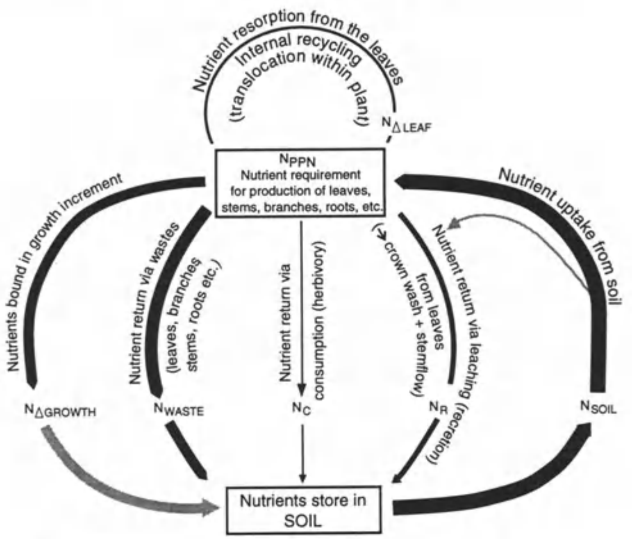
Both the PP_N and the litter fall vary with the *stand age* (Fig. 10), and consequently the nutrient requirement and return rate are also affected. In the build-up phase (rejuvenation phase), the high PP_N causes the nutrient requirement to reach its highest level and the rate of return is at its lowest level, due to the fact that a large portion of the PP_N is invested in biomass (stand increment). This means that soil fertility requirements during this period are extremely high. As the plant stand ages, these relations are reversed.

2.5.2.5 Ecozones as Geozonal Ecosystems

A *natural or near-natural ecosystem* (a bio-ecosystem) consists of a living (biological) community (biocenosis) and its abiotic surroundings (biotope). There

Simplified model of nutrient cycling in a forest ecosystem (for perennial life forms only)

8



Nutrient requirement (N_{PPN}) $= N_{SOIL} + N_{\Delta LEAF}{}^{a}$

Nutrient uptake (N_{SOIL}) $= N_{PPN} - N_{\Delta LEAF}$

$= N_{GROWTH} + N_{WASTE} + N_C + N_R$

Nutrient return, release $= N_R + N_{WASTE} + N_C$

Internal nutrient recycling ($N_{\Delta LEAF}$) (translocation) $= N_{PPN} - N_{SOIL}{}^{a}$

$= N_{PPN\,(leaves)} - N_{WASTE\,(leaves)} - N_R$

External nutrient recycling $= N_R + N_{WASTE} + N_C$

$= N_{SOIL} - N_{\Delta GROWTH}$

The nutrient requirement for primary production (N_{PPN}) is fed from two sources: input (uptake) from the soil (N_{SOIL}) and return (resorption, translocation, internal recycling)from the leaves before they fall ($N_{\Delta LEAF}$). Release of nutrients from their bound form in litter, animal carcasses and dead roots on or in the soil occurs by means of biological-chemical decomposition processes which lead finally to mineralization. The time period during which this occurs can last less than a year or several centuries.
Nutrients returned to the soil by crown wash or stemflow (N_R), on the other hand, are readily available again for use by the forest. This also applies to nutrients involved in internal recycling. Thus, a differentiation can be made between medium- to long-term recycling ($N_{WASTE} + N_C$) and short-term recycling ($N_R + N_{\Delta\ LEAF}$).

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[a] Some authors (e.g. Larcher 1984) include in the N_{PPN} only those elements which become incorporated into the phytomass. Following this definition, recretion losses occur 'below' the primary production level (see dotted line arrow between arrows for nutrient uptake and recretion). The following equations change accordingly:

Nutrient requirement $N_{PPN} = N_{SOIL} - N_R + N_{\Delta LEAF}$

Nutrient uptake $N_{SOIL} = N_{PPN} - N_{\Delta LEAF} + N_R$

Internal recycling $N_{\Delta LEAF} = N_{PPN} - N_{SOIL} + N_R$

Box 8

are many structural and functional interactions between the two. When undisturbed by outside influences, relatively stable, self-regulating (Ellenberg 1973) transformation processes arise, i.e. stores and turnovers of materials and energy gradually settle down to a dynamic equilibrium.

Each ecosystem begins with the chemical binding of radiation energy through autotrophs. In the subordinate organic compartments, i.e. animal biomass, litter and humus, which are controlled by heterotrophs, this energy is step by step converted into heat of respiration, with the concurrent production of CO_2, and thus is ultimately lost again by the ecosystem.

Ecosystems also have spatial dimensions. These range from the small basic unit ecotope through to the planetary ecozone. Although their homogeneity decreases as the spatial dimension increases, this does not alter the fact that the structural and functional similarities which still remain can be viewed and described as an ecosystem. An attempt to do this for the individual ecozones will be undertaken in the regional chapters.

In the interest of comparability, the *descriptions of the ecozonal ecosystems* are presented, wherever possible, in the form of a unified model (Figs. 42, 64 etc.) which follows the basic plan shown in Box 9, assuming *steady-state* conditions. This means (1) the plant wastes (above and below ground) and animal consumption are equal to the PP_N, and (2) the rate of decomposition of dead organic matter is equal to the litter fall and below-ground waste input; all material and energy stores are constant.

Such steady-state conditions are seldom, if ever, found in nature (they are most likely to occur – averaged over the year – in grasslands; cf. Chap. 3.4.5.2) and are instead an imaginary average condition around which the actual stores and rates of transfer fluctuate (sometimes closely, sometimes not; cf. Fig. 10).

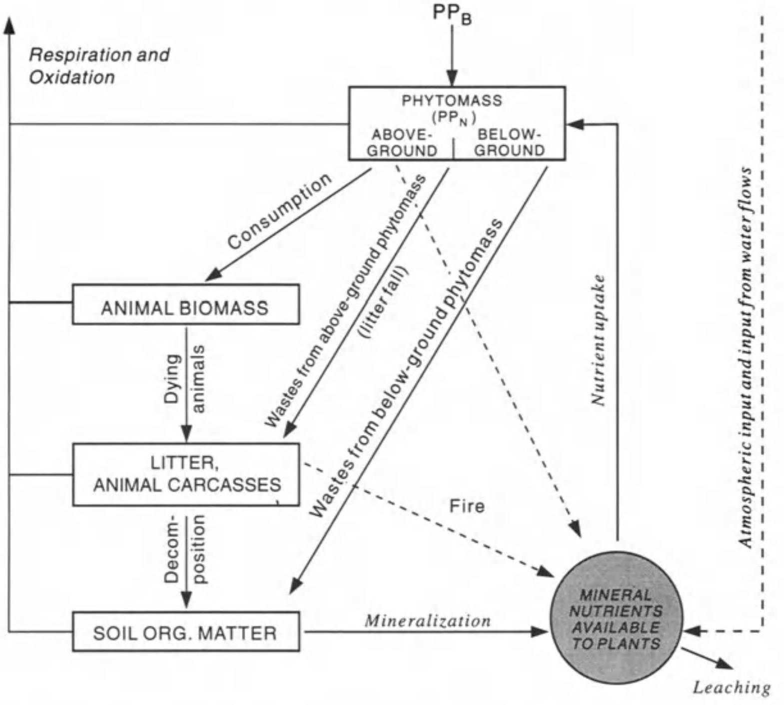
Also, this average condition can be only roughly estimated because, among other reasons, it never occurs at the same time in the different compartments (when, for example, the PP_N and loss of plant tissue are in balance, and the amount of phytomass thus remains constant, the rate of decomposition can lag behind the litter input and thus the litter reserve would grow).

To use this as the basis for rejecting the *steady-state concept* would surely not be advisable, at least as long as there is no other method of describing representative temporal and spatial conditions more accurately. As regards the existing, and in some cases, highly detailed descriptions of ecosystems, it should, however, be noted that their accuracy applies only to the state of a particular plant community for a brief moment under very specific environmental conditions which will – most likely – never occur again in exactly the same constellation. Were the investigations to be repeated at the same location, other results would inevitably be found.

In the *ecosystem models* used here, biomes which are characteristic of the individual ecozones, and their abiotic environments will be described (and not necessarily the average conditions in the ecozones). The numerical values given should be considered rough estimates.

9

Simplified model of a natural or near-natural ecosystem: stores and transfers of organic matter and nutrients; basic scheme for the ecozonal ecosystem models (e. g. Figs. 42, 64, 88). cf. text for further explanation.



Box 9

The areas of the boxes and the widths of the arrows correspond to the quantities of material stores and turnovers; but the circular areas representing the soil nutrients available to the plants (mainly the nutrients adsorbed on the exchangers) reflect only the approximate magnitudes in comparison to those in the other ecozonal systems. The unit of measure for organic pools and turnovers is t ha^{-1} or t ha^{-1} a^{-1} respectively and for nutrient turnovers kg ha^{-1} a^{-1}. The width of the arrows for the inorganic nutrient turnovers are given on a ten times larger scale (e.g. 0.1 t nutrients represent 1 t of organic material). The animal biomass includes for the most part only the above-ground animals which mainly live as herbivores. The litter fauna and soil fauna, which as a rule belong to the decomposer compartment, are not included; the organic substance from these creatures is contained in the litter and humus compartments. Unless more detailed data are provided, the transfer of energy/matter from the animal biomass (through the death of the animals) was calculated as a flat 1/10 of the ingested food (= animal consumption) and the rest was attributed to losses caused by respiration.

Feature[1] \ Ecozone		1. Polar/ Subpolar Zone 1.1 Ice desert 1.2 Tundra and frost debris zone	2. Boreal Zone	3. Humid Mid-Latitudes	4. Arid Mid-Latitudes 4.1 Grass Steppes 4.2 Deserts and semi-deserts	5. Tropical/ Subtrop. Arid Lands 5.1 Thornscrub savannas and subtrop. steppes 5.2 Deserts and semi-deserts	6. Mediterranean-Type Subtropics	7. Seasonal Tropics	8. Humid Subtropics	9. Humid Tropics
Annual precipitation (P)		○	◔	◑	◔ ○	◔ ○	◑	◔	◕	●
Mean annual temperature		○	◔	◑	◑	◕	◕	●	◕	●
Potential annual evapotranspiration		○	◔	◑	◕	●	◕	◕	◑	◕
Runoff	-Amount (Q)	◔	◑	◑	○	○	◔	◑	◕	●
	-Coefficient (Q/P)	●	◕	◑	○	○	◔	◔	◕	●
Annual global radiation		○	◔	◑	◕	●	◕	●	◕	◕
Length of growing season		○ ◔	◑	◕	◔ ○	◔ ○	◕	◕	●	●
Incoming short-wave radiation during growing season		○	◔	◑	◔	◔	◔	◕	●	●
Mean temperature during growing season		○	◔	◔	◑	◕[2]	◔	●	◕	●
Phyto-mass	-Total	◔	◑	◕	◔ ○	◔ ○	◔	◑	●	●
	-Root/ shoot ratio	◕	◔	◔	◕ ●	◑ ●	◑	◑	○	○
Leaf area index		◔	◕	◑	◑ ○	◔ ○	◔	◑	◕	●
Primary production		○	◔	◑	◑ ○	◔ ○	◔	◕	◕	●
Litter accumulation		◕	●	◑	◔ ○	◔ ○	◑	◔	◑	◔
Dead soil organic matter		●	◔	◕	● ○	○	◑	◔	◑	◔
Decay period of organic wastes		●	◕	◑	◔	◔	◕	◔	◔	○

[1] ● Very high (value) ◑ Medium (value) ○ Very small or no (value)
◕ High (value) ◔ Small (value) Without symbol = inapplicable

[2] For thornscrub savannas only

For absolute quantities: cf. respective divisions in General Chapter and Regional Section

Fig. 17. Comparison of ecozones according to selected (quantifiable) features

The difference in residence time between the elements contained in the organic matter (see Table 28) was ignored. Instead, the model is based on the assumption that all the nutrients taken up are released only when mineralization takes place.

Ecosystem imports (from the surroundings) and exports (to the surroundings) depend to a large extent on local conditions and are thus almost impossible to describe on a representative basis for large regions such as ecozones. For this reason, no attempt was made to describe them quantitatively (their presence is simply indicated by arrows). It should be noted, however, that both can have an important influence, for instance in tropical rain forest ecosystems, after the trees have been felled (net exports), and with regard to forest regeneration (net imports) (cf. Chap. 3.9.6).

2.5.2.6 A Comparison of the Ecozones

For certain selected (quantifiable) characteristics, Fig. 17 shows how the ecozones differ from each other. At present, despite the fact that data are available from numerous individual measurements/surveys, it is not yet possible with certainty to give typical zonal quantities or performances. Therefore, only relative, comparative values (very high, high, medium etc.) are mentioned and for the sake of hopefully greater clarity, they are depicted by circles.

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2.6 Land Use

The brief regional chapters on land use deal mainly and succinctly with the natural potential of the ecozones for agriculture and forestry and examine the resultant adaptational systems of agriculture, such as shifting cultivation in the humid tropics, large-scale grain cropping in the temperate grass steppes, or nomadism in the arid regions. They also include some information on settlement and population distribution and the degree of economic development.

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2.7 Synoptic Diagram and Bibliography

Each of the regional ecozone chapters closes with a diagram in the form of a highly simplified ecosystem model which shows the most important characteristics

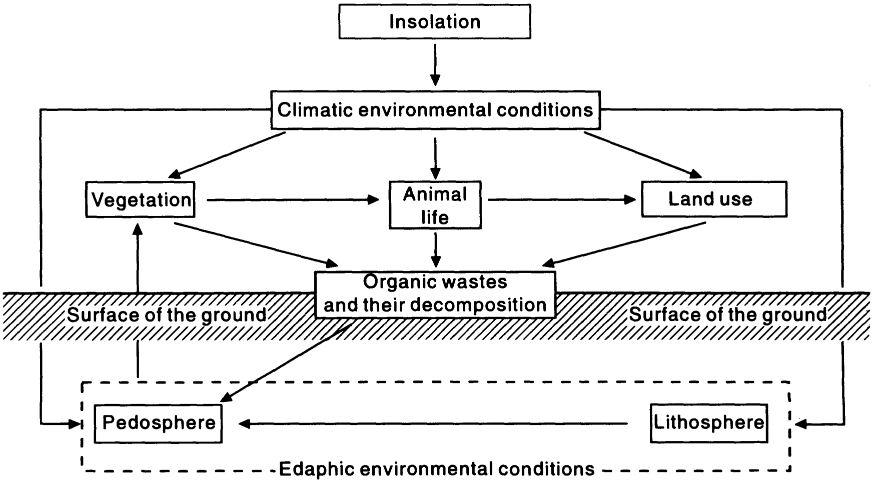

Fig. 18. Model for synoptic diagrams of the individual ecozones

and some of the salient interactions between them. This diagram is arranged as shown in Fig. 18.

Each chapter ends with a Bibliography. The brief selection provided for further reading is limited for the most part to more recent publications and is mainly intended to aid those readers wishing to obtain more information on the various aspects of the ecozone in question. Those titles which are included in more than one Bibliography are quoted in full only in the chapter where first mentioned; in other chapters, the reader is referred to this chapter.

3 Regional Section: the Individual Ecozones

3.1 Polar/Subpolar Zone

3.1.1 Distribution

The Polar/Subpolar Zone is present near the poles in both the Northern and Southern Hemispheres. Towards the equator it is limited by the polar tree lines (see Boreal Zone) or by sea coasts. The entire zone covers 22 million km^2, 15% of the land area of the earth, of which 14 million km^2 are in the Antarctic.

Three-quarters of the Polar/Subpolar Zone is permanently covered by ice and belongs, therefore, to the *polar ice deserts* (Fig. 19). The latter cover almost all of that part of the zone which is situated in the Southern Hemisphere, i.e. the Antarctic.

By contrast, the part that lies in the Northern Hemisphere is, with the exception of Greenland and some islands near the Pole, largely free of glacier ice. Apart from the Siberian tundra, the area became ice-free only about 8000–10 000 years ago, after the end of the last ice age.

The boundaries between the ice-covered and ice-free regions in general follow the *climatic snow line*. Polewards of this line more snow falls on average in the long term than is melted during the summer, while equatorwards of the line the snow normally melts completely in the summer months. The limits of permanent snow and ice do not coincide where ice lobes extend equatorwards beyond their zone of alimentation.

Based on the temperature conditions and the related vegetation, the ice-free regions can be further subdivided into a *frost debris zone* and a *tundra zone*. In the former, the average temperature in the warmest month is less than 6 °C, and plant growth covers less than 10% of the surface. From a vegetation-geographical point of view, the area can be described as a *cold desert*. Summer temperatures in the subpolar tundra are, by contrast, high enough for a low but nevertheless continuous plant cover to develop. In the Northern Hemisphere, the tundra covers almost 5 million km^2 and the frost debris area more than 1 million km^2 (according to Paffen 1980: 4.63 and 1.11 million km^2 respectively). In the Southern Hemisphere, both zones are almost entirely absent (only 0.01 and 0.03 million km^2 respectively).

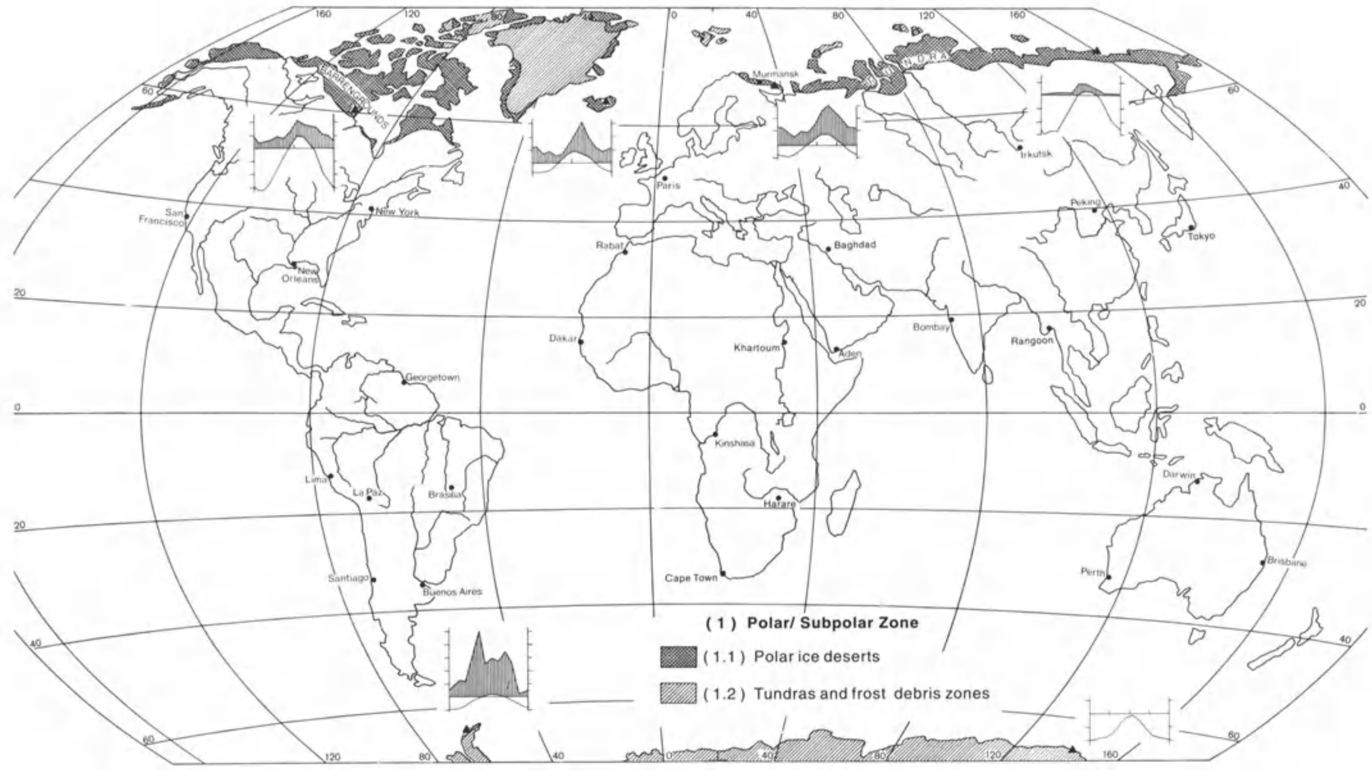

Fig. 19. Polar/Subpolar Zone. The distribution is bipolar. Two-thirds of the zone, for the most part ice climates, lie in the Antarctic. Tundras and frost debris zones predominate in the Arctic

Morphodynamically, the frost debris zone and the tundra belong to the *polar periglacial region*. However, there is no congruence with *permafrost*, the occurrence of which is often used as a criterion to define the boundary of the periglacial area (Karte 1979). The equatorward limits of permafrost extend far into the area of boreal coniferous forest (Fig. 20), where the temperature conditions are continential. On the other hand, there are also some areas within the tundra, for example in Iceland, Lappland, southern Greenland and Kamchatka, where permafrost is absent. As a rule, permafrost occurs only when the mean annual air temperature lies at least 1–2 °C below freezing, and it becomes continuous only if the mean annual temperature is below −6 to −8 °C (Fig. 21).

In contrast to the areas of polar ice climate, where water is almost always present only in the form of ice, the annual change from ground ice to soil water in the soil layers at and near the surface, and also the change from snowfall to rain, are characteristic of the ice-free periglacial zone. Consequently, the permafrost soil develops a thawed layer (the active layer) in summer that extends more or

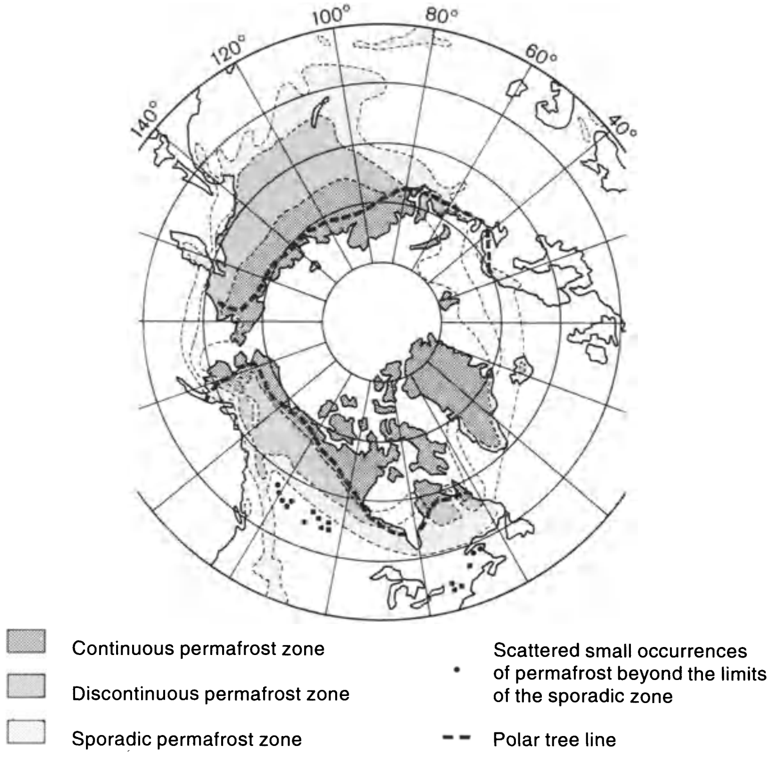

Fig. 20. Distribution of permafrost and polar tree line in the Northern Hemisphere. (Hare and Richie 1972; Karte 1979). There is no correlation between the distribution of permafrost and the polar tree line that limits the Polar/Subpolar Zone towards the equator

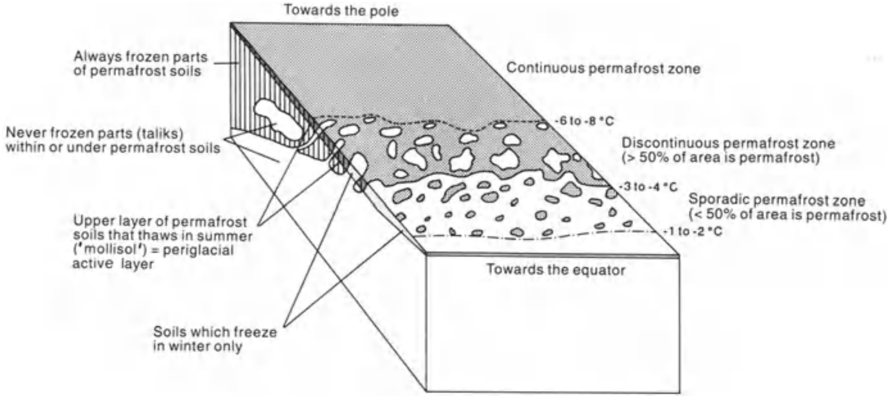

Fig. 21. Schematic block diagram of permafrost distribution. (Karte 1979). The temperatures shown are annual means

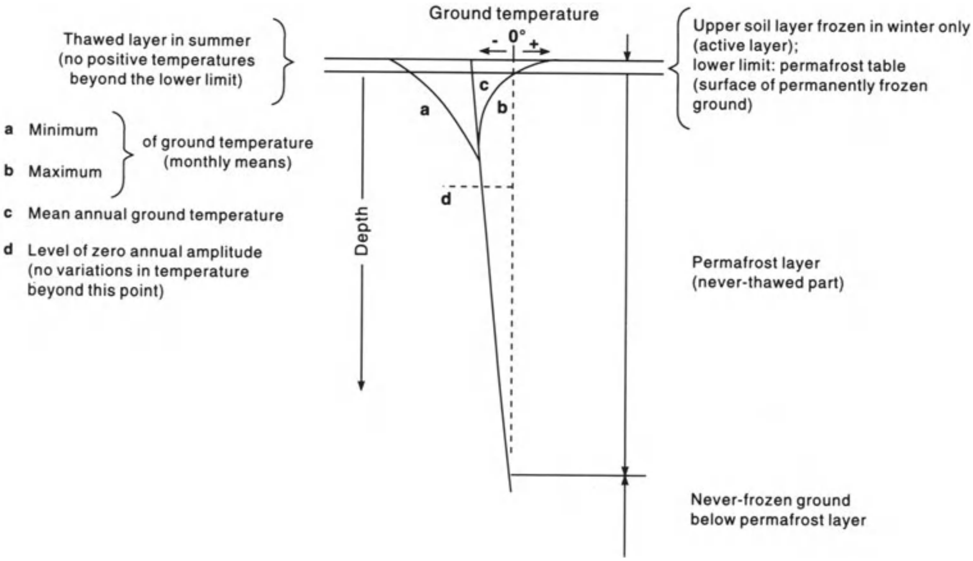

Fig. 22. Temperature profile showing the vertical zonation of permafrost soil and of seasonal variation of freezing in the soil. (Brown 1970; Karte 1979; Sugden 1982)

less deep (Fig. 22). The annual *freeze-thaw cycles* result in very efficient geomorphological processes (frost-dynamic processes) that lead to the development of characteristic surface forms and deposits.[9]

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[9] Freeze-thaw processes are characteristic for the entire permafrost region that lies outside the ice climate area, as well as for many high mountain areas, including those in the tropics. Many of the resulting forms are everywhere the same or, at least, similar. The polar timber line is, therefore, not always a significant boundary for the equatorward limit of the Polar/Subpolar Zone as far as geomorphological aspects are concerned.

The following description of the Polar/Subpolar Zone concentrates on the ice-free regions.

3.1.2 Climate

Cyclones ("polar cyclones") occur over both polar areas in the upper layers of the troposphere. They constitute the extreme limits of the planetary decrease in radiation, temperature and pressure that occur from the equator to the poles (Figs. 68 and 69). In the lower layers of the troposphere, however, high pressure predominates (cold air anticyclones, polar highs) with low temperature throughout. In accordance with the geostrophic laws, the decline in atmospheric pressure from here to the low-pressure zones in the subpolar regions (subpolar lows) results in a belt of easterly winds known as the *polar east wind zone* (Fig. 122).

The subpolar low-pressure belt is composed of dynamically produced cyclones (cf. Chap. 3.3.2) that develop in the planetary frontal zone (polar front) and that tend to veer out poleward from the west wind drift in mid-latitudes, forming a belt on the polar side of the frontal zone.

During the winter in the Northern Hemisphere, the subpolar low-pressure belt is interrupted over the large landmasses of Eurasia and North America by the development of extensive thermal (cold) highs. The remaining low-pressure regions over the oceans are termed Icelandic or Aleutian Lows, depending on where their central areas lie. During midsummer, the subpolar low pressure belt is only weakly developed everywhere, because of the small meridional differences in radiation at this time.

Air Temperatures, Length of Day, Precipitation

Because of the negative annual radiation balance, the *air temperature* is low, with annual averages generally below 0 °C (with the exception of some extremely maritime areas, such as the Kerguelen Islands, where the annual average temperature is a little above 0 °C). Of much greater significance ecologically than these annual values are the actual magnitudes and duration of the *summer temperatures* above freezing and also above 5 (6) °C, the threshold for plant growth. As a general rule, the mean temperature of the warmest month in the tundra is between +6 and +10 °C, with maximally 3, exceptionally 4, months having a mean above +5 °C. Polewards, the highest monthly averages decrease and at the borders of the frost debris zone fall below +5 (6) °C.

The *winter cooling* is minimal in the subpolar maritime areas but increases considerably towards the poles and the interiors of continents. The annual range in temperature (the difference between the highest and lowest monthly means) increases from <10 to >50 °C (Fig. 23). The daily temperature range is, by contrast, small in all areas (Fig. 24).

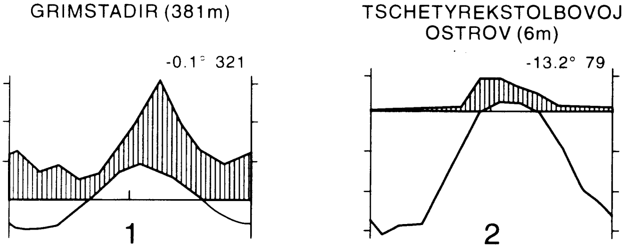

Fig. 23. Climatic diagrams for two stations in polar and subpolar regions. (Walter and Lieth 1960–67). The Icelandic station (*1*) shows subpolar maritime conditions: small annual temperature range, relatively high precipitation. In contrast, the Siberian station (*2*) shows high polar continental conditions: large range in temperatures because of severe cooling in winter, and precipitation is one-quarter of that found at Grimstadir

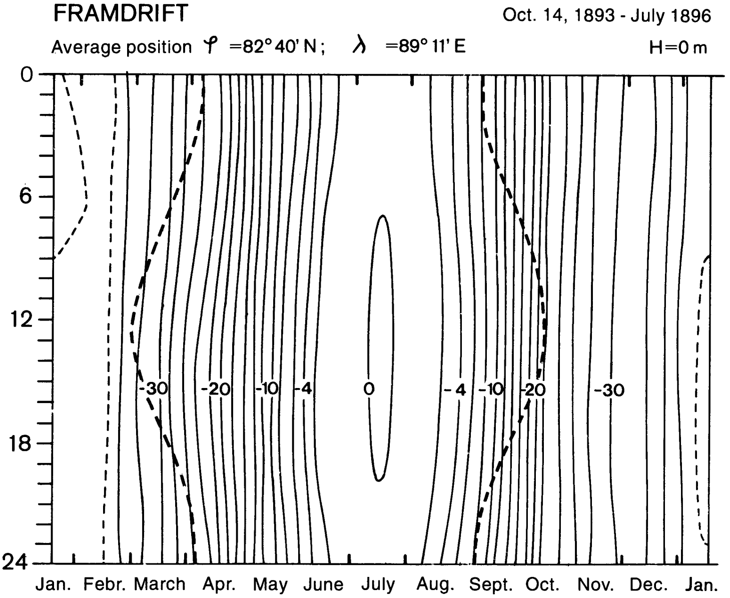

Fig. 24. Thermoisopleth diagram of the Framdrift in the Arctic Ocean. (Troll and Paffen 1964). The *thick broken line* shows sunrise and sunset. Daily variations in temperature are minimal and are non-existent during the sunless winter. In contrast, the annual temperature range is considerable. This is a pronounced seasonal climate which is characteristic of the Arctic

Towards the poles, the *diurnal variations in incidence of sunlight* decrease progressively. The daily change from day to night is replaced by the semi-annual change from polar night to polar day[10]. In line with this, the diurnal variations

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[10] At 70° N, for example, the sun remains above the midday horizon from May 20–July 24. At the summer solstice, the midday sun is at 43° above the horizon, similar to the position of the sun at midday in April in central Europe. From the end of November until the end of January there is no insolation.

of the air temperature diminish so that a thermal and solar *seasonal climate* predominates.

During the winter, when there is little or no insolation (polar night), cold air flows down the slopes and into the valleys and hollows, thereby resulting in a long-lasting temperature inversion. In summer, the air temperatures in the valleys are higher than on upper slopes and hilltop sites (Skartveit et al. 1975).

Exposure to insolation has a limited effect (much less than in mid-latitudes where southern-exposed slopes receive a significantly higher insolation than northern-exposed ones). This is the result not only of the very long path of the sun above the horizon (for some time, it runs all the way round) but also of the high proportion, about 50%, of *diffuse atmospheric radiation* (although not in the Antarctic, where there is a very high proportion of *direct radiation*, because of the general absence of clouds and water vapour). Exposure to wind, not to insolation, is the main factor for the variations in thickness and duration of snow cover that occur frequently over short distances.

Precipitation normally remains under 200 or, at least, under 300 $\mathrm{mm\,a^{-1}}$, not because of the infrequency of precipitation events, but because of their temperature-related low intensities. Precipitation is usually related to warm upper air advection currents. Moreover, in spite of the low annual rainfall, humid conditions prevail throughout the year, at least in the tundra, because evaporation, which is likewise temperature-related, is also low. The winter snow cover is little more than 20–30 cm thick.

Based on the hygrothermal conditions, the climate of the periglacial regions can be termed *cool humid* or *subnival* (less commonly cold arid), and in areas covered by glacier ice it is *nival* (= ice climate).

Annual Variations of Temperature in the Soil and in the Layers of Air Near the Ground

The temperatures of the air layers near the ground and of the soil itself are more significant for soil development, freeze-thaw processes and plant growth than the temperatures measured at weather stations 150–200 cm above the ground. The entire vegetation is limited to a thin layer that extends usually less than half a metre, sometimes only a few centimetres, above and below the surface of the soil. It is here also that the animal population has its most important living space. The annual pattern of temperature change in this layer is represented by the vertical temperature gradients for 5 different days in a year shown in Fig. 25. Based on these gradients, the following features are characteristic.

In winter, the *snow* protects the plants and soil from the very low temperatures that occur in the atmosphere (cf. temperature gradient of Feb. 10). This protection is, however, much less than in the boreal coniferous forests, where snowfall is much heavier (cf. Chap. 3.2.5), although locally it can be greater where the snow has formed drifts.

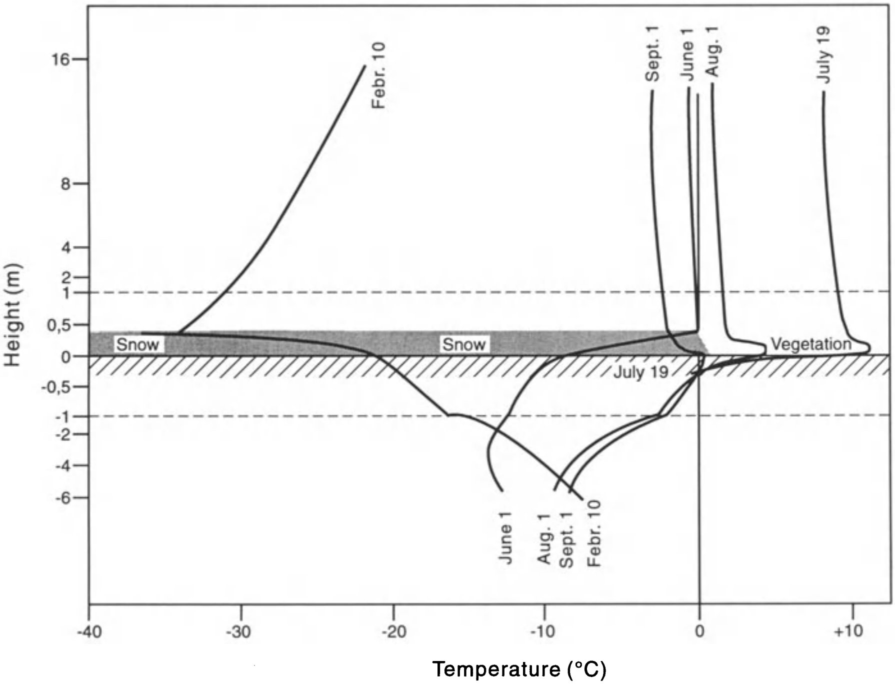


Fig. 25. Typical vertical temperature gradients in the tundra at five characteristic times of the year. (Weller and Holmgren 1974). The thin snow cover protects the soil surface only slightly against the cold winter air temperatures and at the same time clearly delays the warming of the soil in early summer. In the second half of summer, the temperatures of the air layer near the ground are considerably higher than those in the layers above. NB: the scale for heights and depths is relatively expanded between +1 m and −1 m

On the other hand, in spring, the snow prevents an increase in the soil temperature corresponding to the general warming of the air (cf. temperature gradient for June 1). Only after the *snow has melted* do positive conditions return and the sun's rays, which at this time of the year fall directly on to the surface of the ground, result in temperatures near the ground being considerably higher than those in the air above (cf. temperature gradient for July 19). The living world, which until this time has remained largely in a state of winter inactivity, experiences a marked surge in temperature and the growing season begins. The start of the growing season can vary by several weeks within a small area if, due to drifting during winter, the thickness of the local snow cover varies between several metres in some areas and nearly no snow in others; correspondingly, the melting processes may end earlier or later.

Temperatures near the ground remain favourable for growth throughout the summer (cf. temperature gradient for Aug. 1). Even at the beginning of autumn, these temperatures are still above freezing, at a time when temperatures measured at a weather station, or even only 1 m above ground, are already several degrees below 0 °C (cf. temperature gradient for Sept. 1). Therefore, the actual growing season usually lasts somewhat longer than might be expected from measurements made by the weather services.

The cushion-like growth of many tundra plants that is often found, particularly in the high arctic regions, represents the most advantageous adaptation to the favourable temperature conditions of the air layers close to the ground. This type of growth not only uses the warmest temperature zone, it protects the plant from being cooled by winds and contributes to the formation and preservation of the zone of favourable thermal conditions.

With the melting of the snow in early summer, the surface *thawing of the soil* begins. The transfer of heat by meltwater seeping down or collecting in hollows plays an important role. The thawing of the frozen soil continues at a faster rate after the first areas become *free of snow* and, during the short summer, thawing can reach a depth of 30–100 cm. The actual depth depends on the ice and water contents in the soil, the increase in the summer air temperatures (how much and for how long), the amount of "warm" meltwater available and the proportion of organic material in the soil. Soils with a large amount of ground ice or a high water content have a higher heat capacity than dry soils and are, therefore, warmed more slowly. Similarly, soils with thicker raw humus or peat layers that retard the transfer of heat into the soil also remain cooler. For both these reasons, peat bogs are comparatively cold habitats where plant growth begins later and the layer that thaws out in the summer is thinner.

The insulation effect of the (always) low-growing vegetation is estimated to be small (Haag and Bliss 1974). Thus, varying vegetation types do not have noticeable differentiating effects on the thawing processes in the soil.

Because of the locally differentiated thaw processes, the surface of the permafrost (permafrost table) below the active layer has a different configuration than the ground surface (it is not simply the surface pattern projected downward). Accordingly, the runoff conditions (by direction and catchment area) change before and after the thawing of the soil, when a groundwater flow within the active layer takes the place of the initial surface runoff.

Radiation and Heat Budget

The sequence of temperatures and thaw processes that has been described is explained by the radiation budget (Figs. 26 and 27) as follows:

Compared to the rest of the world, the Polar/Subpolar Zone receives the smallest amount of solar energy annually (Table 7, Figs. 2a and 68). The radiation balance is positve only during the short period from April to September in the Northern Hemisphere and from November to February in the Southern Hemisphere. During these periods, however, the daily radiation is relatively high. At the peak period, May to July in the Northern Hemisphere, total daily radiation is comparable to that received in the tropics, although the intensity is only half as great since it is spread over a 24-h period.

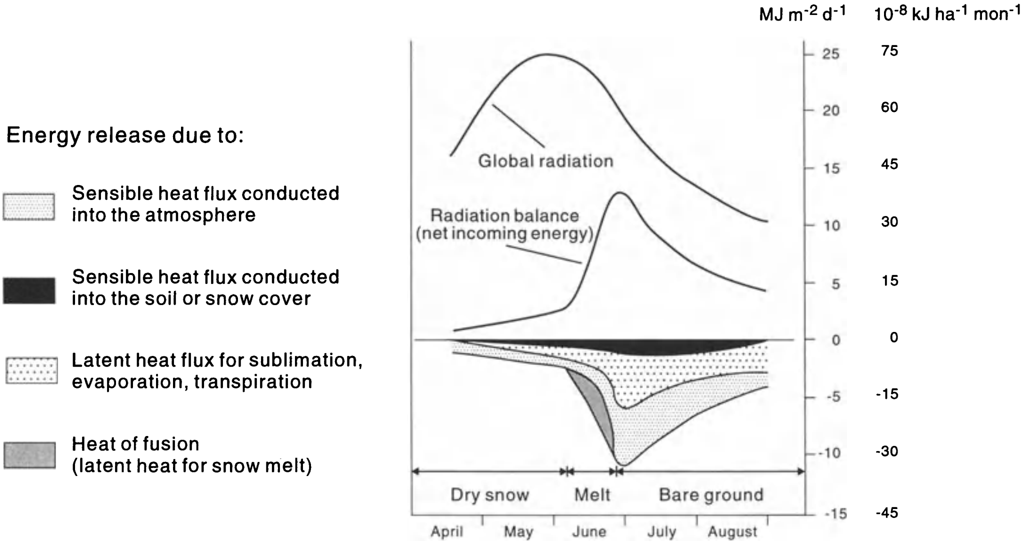
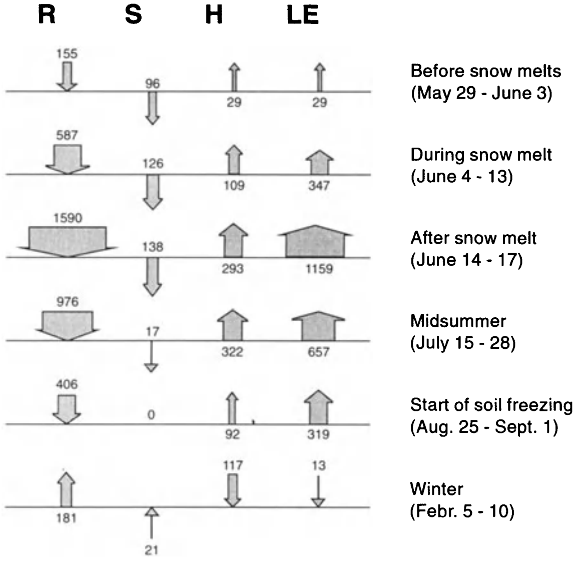


Fig. 26. Summer radiation and heat energy fluxes in the tundra, from measurements taken on Axel Heiberg Island, Canada 79° N 90° W. (Ohmura 1984). The global radiation is virtually unused during the first half of the summer radiation period because, until the snow is melted, very little radiation is absorbed. Even after that, only limited heating of the air and ground occurs, in spite of the large amount of radiation received, because the heat capacity and conductivity of the water (ice)-rich soils is high and much energy is lost as latent heat (evaporation)

Reflection and Latent Heat Flow. The summer heating of both the land surface and the atmosphere progresses very slowly and its optimum also remains far behind that of other ecozones. There are essentially two reasons for this: first, the long-lasting snow cover and second, the very high soil water content after snow melt. The snow cover reflects most of the sun's rays. Only 10–20% of the radiation energy is absorbed, and part of this is also lost by the transfer of heat of sublimation (the amount increases with the increasing temperature of the snow). Only a very small part of the solar radiation contributes, therefore, to the warming of the snow, and the freezing point is exceeded relatively late, usually only shortly before the summer solstice.

Once the snow begins to melt, the amount of radiation that is absorbed rises sharply (the albedo drops from 80–90% down to 10–20%), the excess in the radiation balance triples to about 13 $\mathrm{MJ\,m^{-2}\,d^{-1}}$ (Fig. 26), and the balance can still be positive even at midnight. As a result, all the snow melts away very rapidly (usually in 1 to 2 weeks). The heat of fusion required for this to happen accounts for the largest single amount of energy released.

After the snow has melted, the radiation balance continues to be positive (at the end of July it is still about 7 $\mathrm{MJ\,m^{-2}\,d^{-1}}$). Despite this, the soil and air still warm up only slightly, due to the second reason given above: the active (thaw) layer in the soil is at least saturated with water and quite often it is waterlogged.



The *direction* and *width of arrows* and the *number at the base of each arrow* show the direction and rate (in J cm^{-2} d^{-1}) of the following types of energy transfer:

R Absorbed portion of global radiation minus effective (net outgoing) long- wave radiation [=(all wave-length) radiation balance];

S Sensible heat flux into/ out of the soil or snow;

H Sensible heat flux into/ out of the atmosphere;

LE Latent heat flux for sublimation, melting of snow and evaporation, and for condensation of water vapour and freezing of water.

Fig. 27. Energy balances in the tundra for six characteristic periods. (Weller and Holmgren 1974)

A large portion (probably at least 50%) of the radiation absorbed is used to evaporate this water, and is thus lost as heat of evaporation (latent heat), while a correspondingly small amount is left over as sensible heat.

Heat Budget. The warm-up of the atmosphere over the tundra during the summer months thus remains – in both duration and magnitude – below those expected on the basis of the incoming radiation data and, with the exception of the uppermost centimetres, the soil thaws out only slowly. As a rule, the root zone of the plant cover does not thaw out throughout its depth until a few weeks after the snow has melted. Plant growth cannot begin in earnest until this has occurred. This means that easily the first half of the summer radiation period, and thus most of the solar energy entering the ecozone, remains unused for plant production[11].

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[11] Net photosynthesis begins in spring, even under snow cover and at temperatures well below 0 °C. The amount of this PP_N is, however, relatively insignificant.

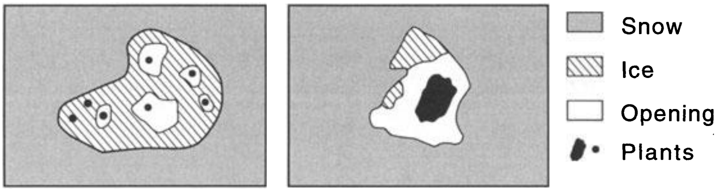

Fig. 28. Ice windows in the Arctic. (Walter 1968). See text for description

Significantly higher net photosynthetic efficiencies could be achieved in *greenhouses* kept relatively dry and free of snow, thus ensuring lower energy losses due to radiation reflection, snow melt and evaporation as well as terrestrial thermal radiation. The long process from the beginning of solar radiation in spring, via the snow melt in June, to soil thawing (a few weeks later), and thus (finally!) to the start of notable plant growth sometime after the summer solstice, could be partially circumvented in this way: solar energy would lead directly to heating of the soil and air and thus plant growth would begin much earlier.

A natural, though tiny, counterpart to the greenhouse is represented by the so-called ice window (Fig. 28; Walter 1968, pp. 529f): if the snow surrounding a plant melts earlier than the remaining snow, because the radiation penetrating the snow warms up the plant somewhat more than it does the snow, a cavity covered with a thin, transparent ice layer is formed in the snow, to create a small "greenhouse" in which the temperature can be up to 14 °C higher than at the surface of the ice. When the ice melts and an opening forms in the ice window, the temperature in the cavity drops sharply.

3.1.3 Relief and Hydrology

3.1.3.1 The Ice-Covered (Glacial) Regions

Glacial cover is characteristic of the land regions in the ice climates. Only in isolated areas do mountain chains (e.g. from bordering mountain ranges in Greenland and the Antarctic) and single mountain peaks (nunataks) project through the glaciers, or dry valleys remain ice-free. For the latter phenomenon to occur, some of the snow cover must be regularly removed by gravity or winds.

The ice cover can reach depths of 3000 to 4000 m (the average depth in the Antarctic is about 2000 m). In contrast to valley glaciers found outside the polar regions, the arctic and antarctic inland ice is more or less free of crevasses and its temperature lies well below the freezing point (cold glaciers). For this reason, subglacial erosion by meltwater streams (as is the case under "warm glaciers" in mountainous areas of lower latitudes) does not take place. Runoff occurs in the form of ice movement only. The direction of this flow and its morphological action through glacial erosion (abrasion) are dictated by the subglacial relief, which has been formed by preglacial tectonic events and subaerial processes.

Frost splitting occurs only in the few ice-free mountainous areas. Within or under the ice, melting and refreezing take place, if at all, only as a result of local pressure differences. This means that the vast inland ice masses carry little or no rock debris with them and create only comparatively small moraines.

3.1.3.2 The Ice-Free (Periglacial) Regions

Quite different conditions and events prevail in glacier-free, i.e. periglacial, regions. The *frost-dynamic or frost-action processes* (frost splitting, cryoturbation, solifluction), which are a result of the change in volume (about 10%) when the water in the soil and rocks goes through freeze-thaw cycles, are particularly characteristic of these regions, as are also the structures which are formed by them. Erosional processes and hill wash by meltwater are also of general importance.

According to Hagedorn and Poser's classification (1974), the periglacial regions belong to the "zone of freeze-thaw processes, intensive sheet erosion and fluvial processes, including thermoerosion". Eolian processes can also take effect in regions with little or no vegatation, where they are promoted by the low level of precipitation and a lack of cohesive (clay-rich) soils.

Frost Splitting

This is the major type of rock weathering (frost wedging, frost shattering, congelifraction); due to the low temperatures, chemical and biological weathering processes play only a minor role, while salt cracking is slightly more important in the driest portions of the frost debris zone. The water entering hairline cracks or fissures in the rock freezes and thereby exerts great pressure capable of shattering even large blocks (block disintegration) or rock outcrops into small to large angular fragments. This *frost debris* can collect at the foot of mountains into huge scree slopes (talus accumulations) in which the mountains, as in arid regions, may finally "drown" (arctic boulder deserts with block slopes, block fields, block streams).

Frost splitting plays an important role in the denudation of steep-sloped reliefs. By breaking the debris into ever smaller pieces, this is also the force which is responsible for the creation of smaller grain sizes, all the way down to coarse clay (for example by splitting the mica flakes parallel and perpendicular to their lamination). The effectiveness of frost splitting depends on the moisture content of rocks (which in turn is a function of the crevices and pore spaces present), the frequency of freeze-thaw cycles and the intensity of freezing in winter. In the subpolar oceanic regions, where high atmospheric humidity and frequent freeze-thaw cycles occur during the long transition periods between winter and summer, frost splitting has more effect than in high polar continental regions where, despite the more severe cooling and longer frost period in winter, freeze-thaw cycles occur only a few times in early summer and fall.

Periglacial Forms on Horizontal Surfaces or Gentle Slopes

In unconsolidated material and under moist conditions, freeze-thaw processes lead to the creation of a large variety of landforms which are highly characteristic of the periglacial region. Those (especially smaller) landforms, developed in level (or gently undulating) terrain, often exhibit a symmetric pattern, such as circles, polygonal nets, or parallel stripes, and are then grouped together under the summarizing term *patterned ground.* With respect to disturbances caused by frost heaving and thrusting within the soil, the term *periglacial involution* (cryoturbation, geliturbation) is used (e.g. Brodelboden, pocket soil).

The following description starts with some of these symmetric structures and then deals with palsas, pingos and thermokarst, before continuing with some of the quite different landforms found on sloping surfaces [solifluction (gelifluction) phenomena]. The sizes quoted in the literature for the various forms of patterned ground and solifluction exhibit a surprising range of variation; therefore the sizes given here should only be considered rough estimates.

Patterned Ground

Frequently, symmetric ground patterns are formed as a result of *material sorting*, which occurs due to the differentiated displacement of coarse and fine material during frost heaving and frost thrusting processes in originally inhomogeneous material. The patterns take the form of *stone circles*, *stone polygons*, *stone nets*, *stone steps*, *or stone stripes* (Fig. 29); stripe-shaped patterns occur in combination with denudative processes (see solifluction). All such patterns are especially characteristic of the frost debris zone and are less evident in the tundra.

The material sorting can, for example, occur due to frost-induced raising of fine substrate or to filling of frost cracks with stones (Fig. 30). Besides sorted forms there are also *unsorted* ones, such as hummocks, mud boils (fine earth islands), and ice wedge polygons (see below), created by frost action.

Patterned ground is found wherever freeze-thaw cycles are frequent, with daily or seasonal intervals, namely in both the tropical/subtropical high mountain ranges and the polar/subpolar regions. The size of patterned ground varies, however: in the Arctic, the polygons attain diameters of 2 to 20 m, whereas they are much smaller in the tropical/subtropical mountains where freeze-thaw cycles are much shorter (often diurnal). Aside from the frequency of freeze-thaw cycles and the intensity and duration of frost periods, other factors such as moisture content, grain size spectrum, thickness of the layer of mobile, unconsolidated material and the slope angle play an important role in the type of patterned ground which forms.

Ice Wedge Polygons. Cracks occur primarily due to contraction of the permafrost soil during periods of very low temperature (at least −15 to −20 °C) in the winter months (congelicontraction). During the summer snow melt, the initially

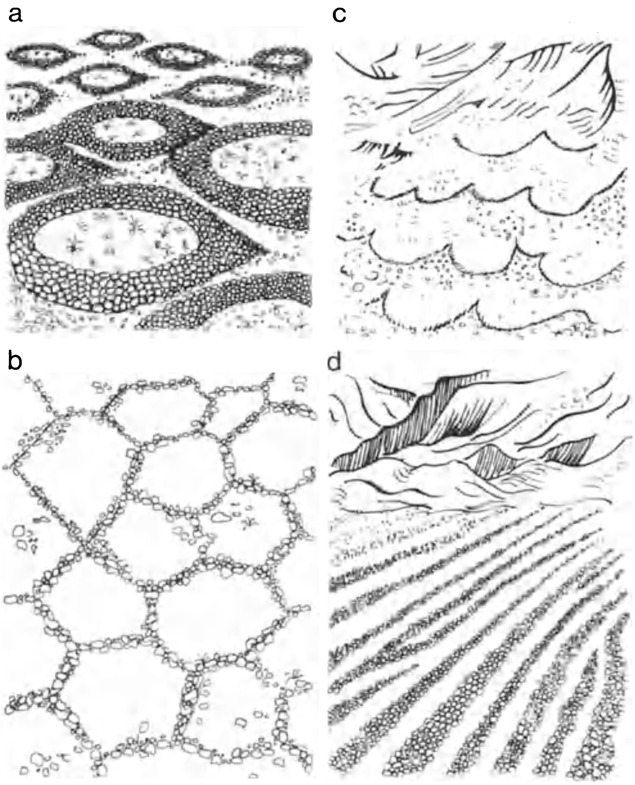

Fig. 29a–d. Types of patterned ground involving material (grain size) sorting. (Schäfer 1959, taken from Ganssen 1965). **a** Stone circles. **b** Stone polygon net. **c** Stone steps. **d** Stone stripes. In the case of stone stripes and stone steps, frost action and gravitational forces have worked together

very fine contraction cracks fill with water, which then freezes in the following winter into (at first very thin) ice veins. Over the centuries, this cycle of winter freezing and cracking, followed by summer thawing and filling, results in the formation of ice wedges (below the summer active layer), whose width at the top can reach more than 1.5 m and whose depth ranges from 3–4 m and more, while at their edges the covering material (the active layer) is forced up into ridges 0.2 to 1 m high. Seen from above, the ice wedges form polygonal patterns often between 10 and 40 m in diameter. The polygonal areas enclosed by the ice wedges usually fill with shallow water (Figs. 31 and 32). Ice wedge polygons are the index formations that identify continuous permafrost regions. Their formation is furthered by a shallow snow cover, a shallow active layer in the permafrost, and by a lack of insultating vegetation.

Sand Wedge Polygons. In their case, the cracks are filled not with ice but with fine material from the surrounding substrate; this may be a primary phenomenon (e.g. in arid regions) or it may take place after the ice in the crack has melted.

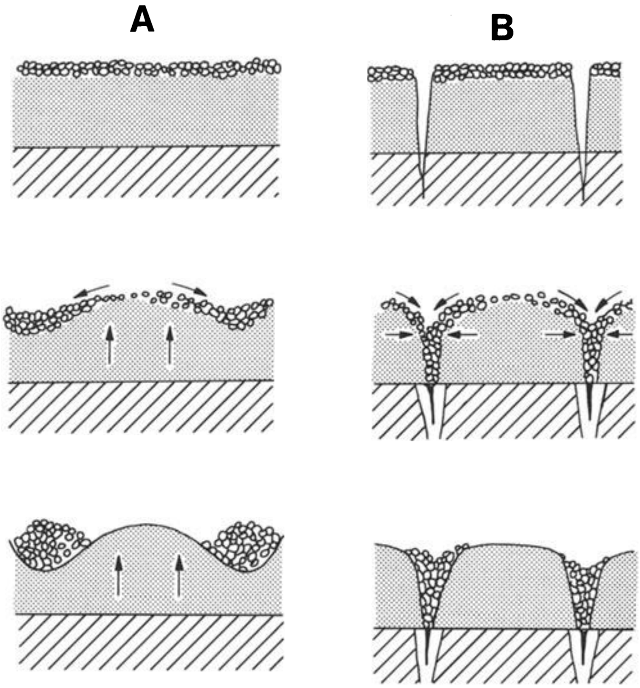

Fig. 30A, B. Origin of a sorted patterned ground. (Jahn 1975, taken from Karte 1979). In inhomogeneous substrate, material sorting can occur due to frost-induced raising of fine material (**A**) or to filling of frost cracks with stones (**B**)

Hummocks (Thufur). These are small mounds with knob-like shapes, up to approx. 50 cm in height and 1 m in diameter, and completely covered with vegetation. Their cores consist mainly (but not always) of inorganic material, and do not contain any perennially frozen soil or ice. Hummocks can develop where permafrost is lacking. Generally, they occur in groups and, in many tundras, particularly the oceanically influenced meadow tundras, they belong to the most prevalent types of patterned ground.

Palsas

Compared with hummocks, these steep-sided frost mounds are much larger (up to 10 m high and 50 m in diameter); they consist of peat and contain a core of (permanently) frozen substrate in which segregated ice is present in the form of ice lenses. The latter form in unsaturated soil which slowly freezes from the top down, while water flows from below to the freezing front at the same rate at which (liquid) water turns to ice (and thus the capillary forces increase, i.e. the matrix potential drops to increasingly negative values). Palsas usually occur in

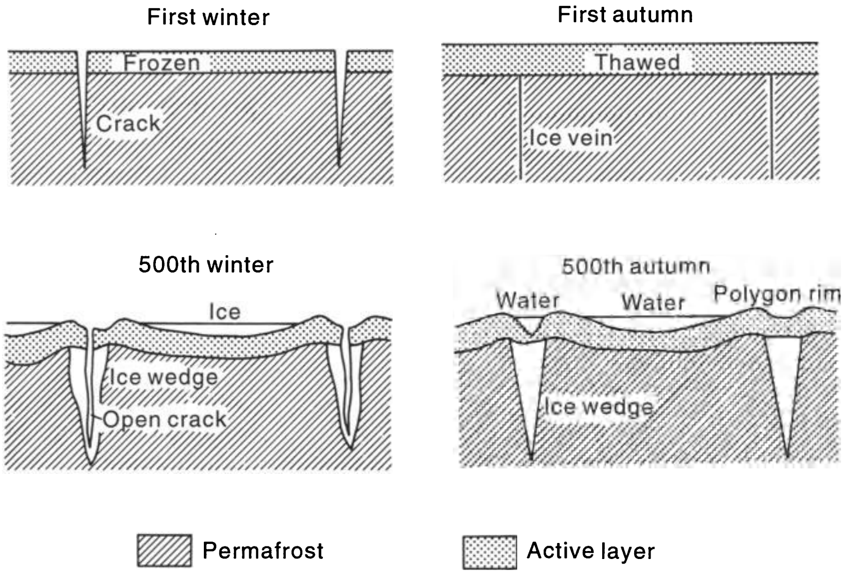

Fig. 31. Origin of ice wedge polygons. (Lachenbruch 1962, taken from Sugden 1982). In summer, the cracks formed due to the low frost temperatures (= thermal contraction) fill with meltwater which freezes during the following winter into ice veins. Over hundreds of years, these veins can grow to the size of huge ice wedges, several of which join to form polygonal structures when viewed from above (see Fig. 32)

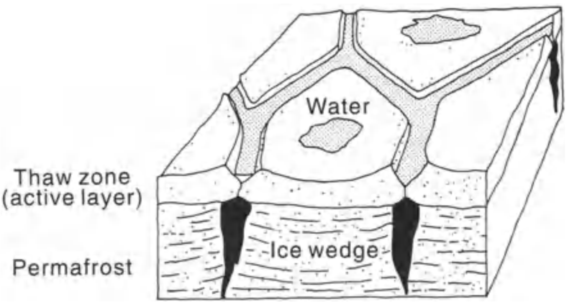

Fig. 32. Block diagram of ice wedge polygons. (Butzer 1976). Surface shows raised rims along the edges of the ice wedges, causing the formation of round depressions within the polygon shapes and furrows overlying the ice wedges. Both may become filled with water during the summer

groups (palsa bogs) and are a widespread zonal phenomenon in the forest tundras of North America and Eurasia. They are index formations for a continentally influenced subpolar frost climate with discontinuous and sporadic permafrost soil (Karte 1979, p. 55).

Pingos

These are also ice-cored mounds (hydrolaccoliths) which are larger than the palsas (maximum height about 50 to 100 m, base about 300 to 1200 m in diameter);

they contain thicker and more often continuous bodies of ice, and have no covering layers of organic origin. They resemble small volcanic cones. Pingos usually occur in areas in which the permafrost soil is still continuous but has begun to thin out or become discontinuous. Closed-system pingos are created by the freezing of taliks (intrapermafrost water) or of local subpermafrost water in areas of discontinuous permafrost (Fig. 33); open-system pingos are formed from the freezing of lateral water inflows. The resulting cryostatic pressure causes the covering layers to buckle upwards.

As the pingos buckle upwards, the ice core exerting the pressure becomes more exposed and is increasingly subject to melting. This may eventually lead to the destruction of the pingo. It is then replaced by a water-filled cavity under which a new talik may form. Lakes and pingos thus form a dynamic equilibrium.

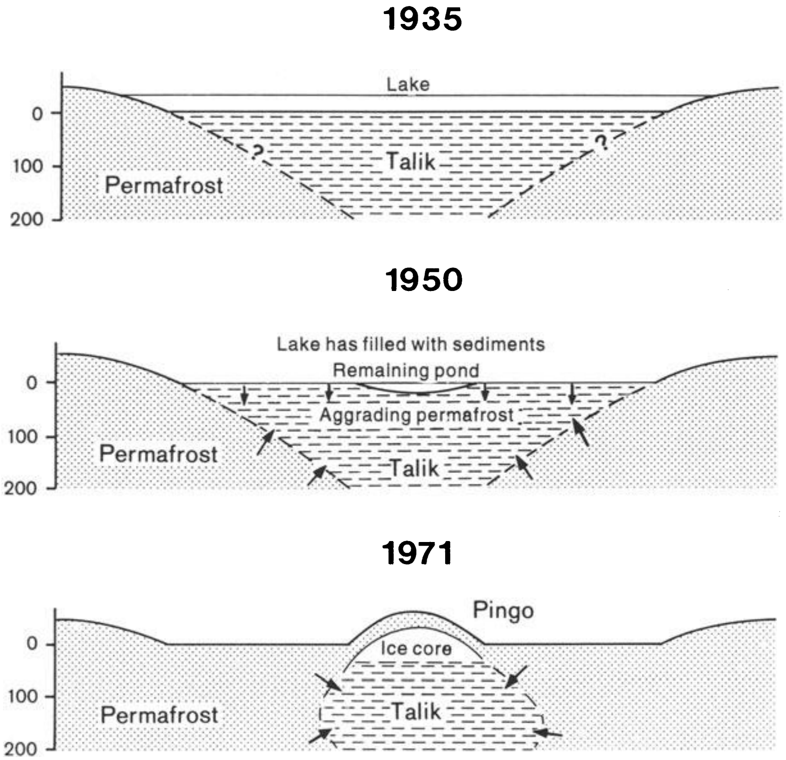

Fig. 33. Origin of a closed-system pingo. (After Mackay 1972). After a lake has filled with sediments, the talik below begins to freeze from all sides. The accompanying increase in volume causes the ground to mound up. Segregated ice (an ice core) is formed within this mound along the downward-moving freeze front

Thermokarst Depressions

Also known as permafrost depressions, depergelation formations, thaw lakes and cryokarst. When ice-rich permafrost soils become degraded or near-surface ice bodies (such as ice wedge polygons, pingos or palsas) melt, subsidence of the terrain may occur which can lead to the formation of closed, spherical (karst-like – therefore thermokarst) cavities (thermoerosion). As a rule, these are no more than a few 100 metres, rarely more than 1000 m, wide and are filled with water to a depth of 1 m, at most 3 to 4 m. After a time, they fill up with silt and a pingo may be formed (see above). In Canada and Alaska, it has been observed that many of these lakes have the same longitudinal axis (N 12° W ± 3 °); this is the result of wind effects ("wind-oriented lakes", Fig. 34).

Locally accelerated melting processes, which cause or reinforce the formation of melt cavities, are a result of disturbances in the thermal equilibrium between a permafrost soil and its surroundings. Such disturbances can be initiated by changes in the natural vegetation cover (which generally acts as an insulator) that occur, for example, due to overgrazing, waterlogging or fire. The degree to which the surface sinks due to melting depends – aside from the thickness of the thaw layer – on the amount of *excess ice* present in the thawing permafrost (that is, as a rule, the amount of ice which exceeds the bulk volume of the soil by 40 to 50%). Depressions which have already formed can become deeper when inflowing meltwater heats up the depression and results in further thawing of the permafrost below (see also Chaps. 3.1.6 and 3.2.3).

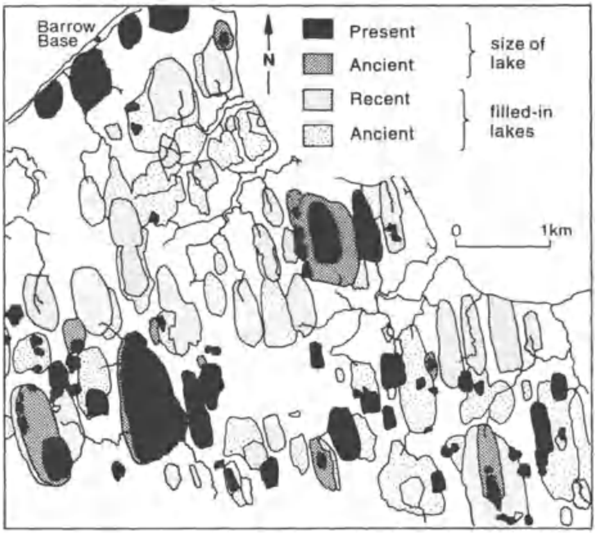

Fig. 34. Wind-oriented thaw lakes. (Carson and Hussey 1962, taken from Sugden 1982). The longitudinal axes of the lakes lie along the predominant wind direction; this means that wind action (wave effects, ice flow drift) plays a large role in forming the contours of the lakes

Solifluction Phenomena

In contrast to the processes and formations just described, solifluction refers to the slow, downslope (clinotropic), mass movement of (waterlogged) unconsolidated material (regolith) as a result not only of *freeze-thaw processes* but also of gravity. Other (at least approximately synonymous) terms for this are gelifluction, congelifluction, gelisolifluction, cryosolifluction etc. The influence of these processes on relief formation is much greater than that of the frost heaving and frost thrusting described above for flat terrains; it extends all the way to the shaping of the macrorelief. The distribution boundary of solifluction processes (solifluction boundary) is thus one of the most important criteria for defining the periglacial region.

Solifluction phenomena can occur on slopes with gradients of as little as 1°. A distinction must be made between two processes (basic mechanisms):

Frost Creep. The downward movement occurs because frost heaving takes place at a right angle to slope inclination, while subsidence during subsequent thawing takes place vertically under the effect of gravitational forces (Fig. 35). The extent of the frost heaving and thus frost creep increases with the water content and the depth of the thaw layer.

Soil Flow (Gelifluction). This downward movement occurs when thawing ice and snow provide moisture, and a frost table in the underlying soil promotes saturation and possibly acts as a slide plane (the latter two factors are the main differences between gelifluction and other soil flow processes).

Solifluction occurs mainly where there is no vegetation cover (e.g. also in high mountain ranges at low latitudes); in regions with deep, frozen soil layers in winter or with deep thaw layers overlying permafrost (e.g. at higher latitudes), it can also occur on slopes covered with vegetation. Because of the great stabilizing effect of roots, however, this requires that the frozen soil layer in winter or the thaw layer (above permafrost) in summer should be deeper than the root space. Deep-rooted trees and shrubs will prevent solifluction from occurring. Depending on whether vegetation is present or not, the process is referred to as *bound* or *free solifluction.*

Frost creep and gelifluction lead to, among others, the following deposits (Washburn 1979):

- *Gelifluction sheets*: characterized by a smooth surface.
- *Gelifluction benches*: characterized by terrace forms with steep fronts varying from a few centimetres to several metres in height, and from a few decimetres to many metres in length.
- *Gelifluction lobes*: tongue-like appearance and also steep fronts.
- *Gelifluction streams*: characterized by a pronounced linear form at right angles to the contour.
- *Block fields*, *block slopes*, and *block streams.*

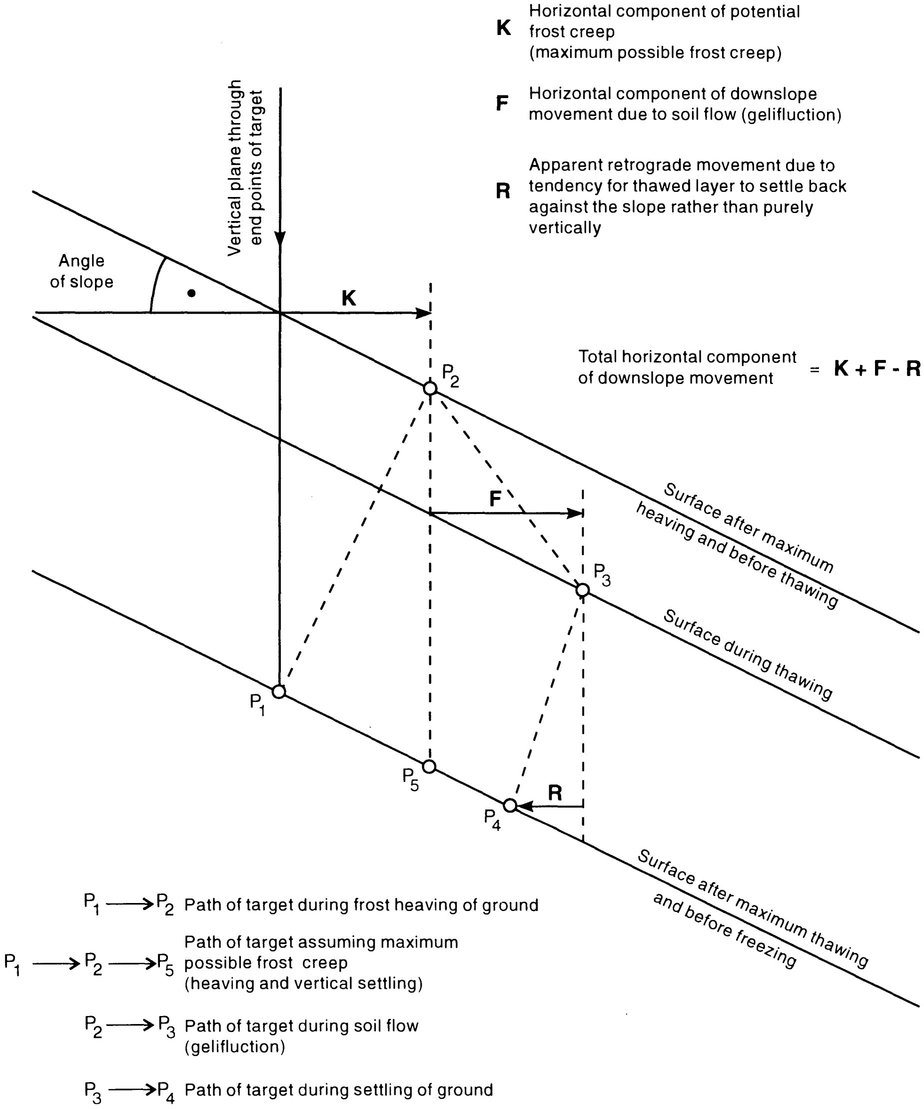

Fig. 35. Measurement of soil creep and soil flow. (Washburn 1979)

In the long term, solifluction produces a level topography, a process which is called *cryoplanation*. The plains are either cut in bedrock, then termed cryoplanation terraces or cryopediments, or built up by deposits, in which case the term solifluction terrace may be applied.

The effectiveness of solifluidal denudation is less than might be expected from the frequency of the resulting landforms. The fact that most slopes are covered with regolith, and that soil has usually developed, shows that the rate of denudation must be lower than the already relatively low weathering rate. In most cases, solifluidal downslope movement can be assumed to be no more than a few centimetres per year.

Morphogenetic Differences Between the Frost Debris and Tundra Zones

These differences are rooted mainly in the varying effectiveness of the *vegetation* as a factor inhibiting frost action. Thus, only smaller frost-related landforms, such as hummocks, palsas and gelifluction lobes and benches are found in the vegetation-covered tundra zone, whereas in the frost debris zone, which has very little vegetation, mainly large formations of patterned ground, block fields, block slopes, ice wedge polygons and pingos predominate. However, such landforms are missing in those areas of the frost debris zone where, due to *lack of precipitation*, little or no ice is held in the soil; under such conditions, the frost debris remains in situ and can accumulate in huge taluses. The block diagrams in Fig. 36 show the distribution of the most important frost-induced landforms in the frost debris and tundra zones.

Runoff Conditions and Fluvial Morphodynamics

Despite the generally low annual precipitation and the correspondingly low amount of runoff (per unit area), fluvial processes and sheet wash can be highly significant morphogenetic factors. This is due to the fact that (1) the percentage of precipitation which contributes to surface runoff is relatively high (50 to 70%; Table 11) because of the low evaporation and the impermeability of the permafrost soil; and (2) the inputs into runoff occur in surges: 80 to 90% of the total runoff occurs within 2 or 3 weeks in June or July, when the snow melts and most of the meltwater runs off in sheets over the still frozen and thus impermeable ground to the rivers, even on slopes with very small gradients.

The later runoff produced by the summer rains (usually between 50 and 150 mm) and by the thawing of the soil ice is much lower (usually less than 10% of the total runoff) than that which occurs during the peak period. Unlike during the snow melt period, the water now drains as subsurface flows within the thaw layer (above the permafrost table). Late-summer runoff is greater in areas in which glacier ablation is an important source.

As soon as the air temperatures drop below the freezing point again in the fall, runoff declines to zero. Seawater enters the coastal sections of some rivers (for example, it penetrates 50 km upstream in the Colville River in Alaska; Sugden 1982, p. 120). The entire runoff process is thus limited to a maximum period of 5 months (May/June to Sept./Oct.); often, it is shorter than this (Fig. 37).[12]

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[12] Other runoff conditions are found in large rivers, such as the Ob, Yenisei, Lena and Mackenzie, which receive considerable inflows of water from temperate climates in the mid-latitudes. In their case, the runoff lasts all year, although in winter it is greatly reduced and for a long time the rivers are covered in ice. Thus, in winter, these rivers are allogenous in character.

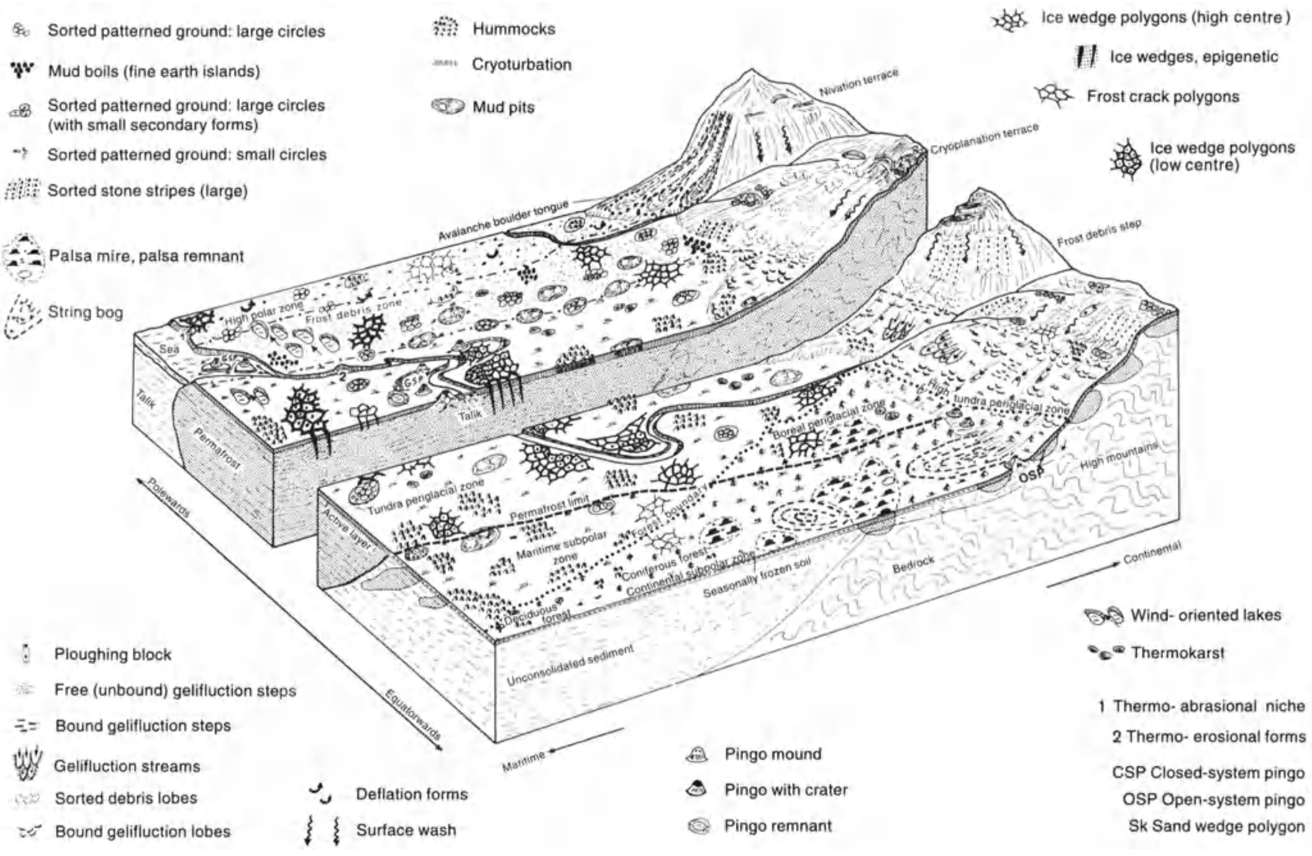


Fig. 36. Schematic block diagrams showing characteristic landforms of the periglacial morphogenetic zone. (Karte 1979)

Table 11. Water balance in the Tundra. (Ryden 1981)

Site	Latitude	Height above sea level	Precipitation			Runoff	Evaporation			Period of measurement (years)
			Snow	Rain	Total		Sublimation of snow	Evapotranspiration	Total	
Devon Island, Canada (Coastal lowlands)	75°33′	10–30 m	137	48	185	84	20	81	101	3
Point Barrow, Alaska (Coastal lowlands)	71°18′	20 m	113	62	175	103	9	63	72	30
Agapa, USSR (Flood plain)	71°25′	20–120 m	186	158	344	230	–	–	115	–
Stordalen, Sweden (Valley floor)	68°22′	351 m	180	150	330	170	24	136	160	5

All values in mm a^{-1}

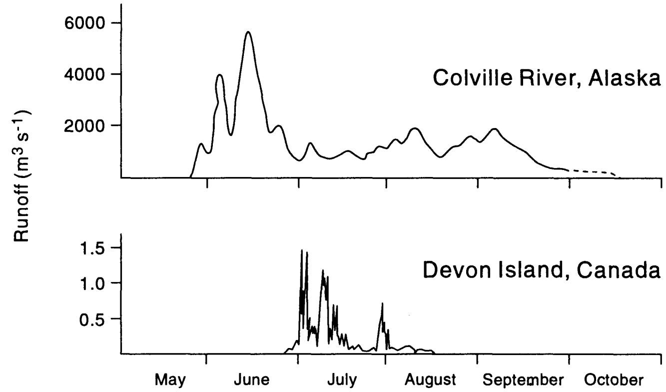


Fig. 37. Runoff regimes of two rivers in the Polar/Subpolar Zone. (Church 1974; taken from Sugden 1982). 80 to 90% of runoff occurs within 2 or 3 weeks during the snow melt. During the rest of the summer, the runoff is fed by rain and groundwater and remains low. Runoff approaches zero when temperatures reach the freezing point

During the (brief) period of high-volume runoff, the rivers, aided by the ice floes they carry, can cause a great deal of erosion. Downcutting may be promoted by frost splitting, which breaks down the rock in the river beds. In spring, bottom ice becomes detached and contributes to the removal of the debris frozen into the ice during the winter months.

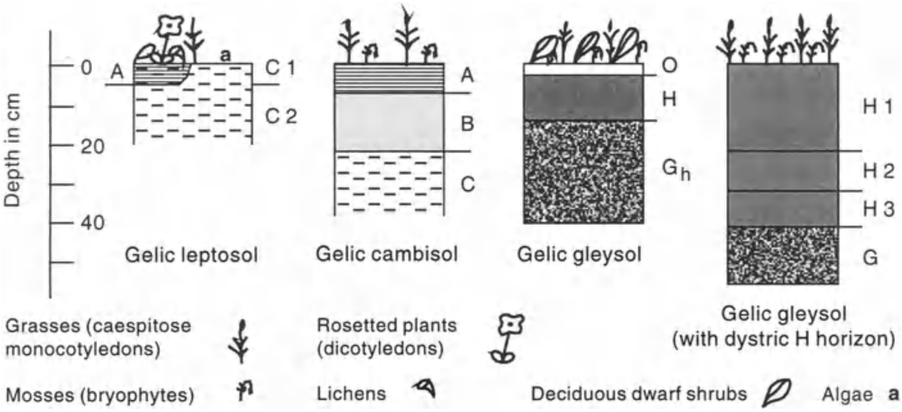
3.1.4 Soils

The following *soil-forming (pedogenic) factors and processes* are active in the tundra and frost debris zone:

1. The permafrost (which is present almost everywhere) hinders the infiltration and percolation of meltwater and rainwater.
2. Soil formation is limited to the thaw layer in summer, which is at most 1 m in depth.
3. Precipitation exceeds evaporation in (almost) all months; this means that humid conditions prevail almost continuously.
4. Since most slopes have low gradients, lateral runoff is hindered.
5. Points 1 to 4 result in waterlogging, or at least in perpetually high soil moisture levels during the thaw phase, and thus in less than optimal oxygen supply to the root space.
6. Soil temperatures are low even during the summer thaw period; they are usually very low in winter.
7. Points 5 and 6 result in severe physical weathering (frost cracking or congelifraction) and freeze-thaw disturbing processes (cryoturbation, solifluction); chemical and biological reactions are impeded.

8. The breakdown of soil organic matter and the concurrent release of the nutrients contained in it, as well as the formation of clay minerals, take place extremely slowly.
9. This means that, despite the low plant production, thick layers of undecomposed detritus can develop in the form of raw humus or peat (decomposition of organic tissue is more severely limited than the PP_N).

The soil type most often found under these conditions is the *gelic gleysol* (tundra gley soil) (Fig. 38). In such soils, a dark and up to 40-cm-thick organic O horizon or a humus-rich A horizon is rather abruptly followed by a blue-grey, loamy cambic horizon with gleyic properties, the upper portion of which may show reddish oxidized mottles. The upper limit of this horizon corresponds to the saturation with groundwater which forms during the summer within the thaw layer above the permafrost table. The adjective gelic indicates by definition, for other types of soil as well, that the active layer of permafrost during the summer months does not exceed 2 m in depth.



Soil type	Location observed	Horizon	Humus content (% org. C)	CEC cmol(+) kg^{-1}	pH	Max. thaw depth (cm)
Gelic leptosol	Queen Elisabeth Islands, Canada 76-78 N	A	2.1	19	7.1	36
		C	0.9	25	7.1	
Gelic cambisol	ditto	A	3.4	17	6.1	43
		B	1.2	9	5.8	
		C	--			
Gelic gleysol	Tareya, Russia 77 N	O	78	--	4.6	38
		H	48	68	5.5	
		Bg	1.5	17	6.8	
Gelic gleysol (with dystric H horizon)	ditto	H1	40	39	4.3	55
		H2	32	51	4.2	
		H3	37	58	4.3	

Fig. 38. Schematic profiles of four common tundra soil types. (Everett et al. 1981)

On very poorly drained sites, where the soil is water-saturated up to the surface for long periods of time, and thus decomposition is restricted even further, peat horizons are formed on top of the mineral base. These are termed *H (histic) horizons* and are diagnostic for histosols (Greek histos = tissue), provided they are at least 40 cm thick or at least 60 cm thick in cases where large amounts of sphagnum (peat moss) and other types of moss are present. In tundra regions, hydromorphic soils of this type always belong to the *gelic histosols.*

Non-gleyic soils are present on sites with better drainage (which are not very prevalent), e.g. on slopes with rapid surface runoff. Some of these soils are *gelic cambisols*, in which an A horizon a few centimetres thick is followed by a dark brown, weakly developed structured subsoil (cambic B horizon). Podzolization processes may occur in such soils where the vegetation supplies large amounts of raw humus (e.g. dwarf shrubs such as *Betula nana*, *Empetrum nigrum*, *Vaccinium* spp.).

If only a thin humus-poor (ochric) A horizon forms and the B horizon is non-existent, that is, if pedogenesis has not advanced beyond the raw soil stage, the soil is termed [according to the (first) FAO-UNESCO classification of 1974] either *lithosol* (now: *leptosol*) or *gelic regosol* (Råmark), depending on whether solid rock or unconsolidated material is present. Gelic regosols are the dominant soils in the frost debris zone and on the (steeper) slopes in the tundra zone, in which otherwise gelic gleysols prevail (cf. Fig. 6: the gelic regosol-gelic gleysol zone is more or less congruent with the tundra and frost debris zone). Gelic histosols and gelic cambisols are found much more frequently in the Boreal Zone and are thus more characteristic of that region (see Chap. 3.2).

According to the revised FAO-UNESCO soil classification (Rome 1988), regosols consisting of very stony material are now grouped together with (former) lithosols, rankers and rendzinas in the new major unit *leptosol.* Very likely this applies to most of the gelic regosols shown on the Soil Map of the World. Thus, the correct name for the soil zone representing the tundra/frost debris zone (Fig. 6) would be gelic leptosol-gelic gleysol zone (Table 3).

3.1.5 Vegetation and Animal Life in the Tundra of the Northern Hemisphere

Common Plant Species and Life Forms

Only relatively few plant species can exist under the extreme climatic conditions in the tundra – a short and cool growing season and a very cold winter. For this reason, vegetation in such areas is limited to communities containing few species, among which dwarf birches, dwarf willows, sedges, cotton grass, mosses or lichens predominate.

Many species (and probably all genera) exhibit a circumpolar distribution. Common genera found among the herbaceous plants and dwarf shrubs are *Vaccinium*, *Arctostaphylos*, *Empetrum*, *Dryas (octopetala)*, *Betula (nana)*, *Rubus* *(chamaemorus)*, *Equisetum (silvaticum)*, *Eriophorum*, *Ledum*, *Salix*, *Carex*, *Saxifraga* and *Cassiope*; among the lichens *Cetraria* and *Cladonia*; among the mosses *Plytrichum* and *Dicranum*. As a result of the ice ages, some species such as *Salix herbacea*, *Ranunculus glacialis* and *Dryas octopetala* have an arctic/alpine distribution.

Regardless of the type of tundra, most of the species present belong to the chamaephytes and (more frequently) to the hemicryptophytes. Therophytes are almost non-existent (they would not have time during the brief, warm summer to form seeds). The superiority of chamaephytes and hemicryptophytes over other life forms is based on the fact that protection against winter frost is optimally combined with advanced vegetative development: snow cover protects the low-growing plants from the extreme cold, and later, in spring, from transpiration losses (which could be deadly as long as soil water is still frozen); when growth resumes in summer, an intact root system – and, in the case of the chamaephytes, a shoot system which, in the (fairly common) case of evergreen dwarf shrubs, even contains intact assimilation organs – is available and ready to function. Thus, without expending much effort, both life forms can produce leaves and blossoms for the purpose of assimilation or reproduction, and the evergreen dwarf shrubs can even begin photosynthetic activity immediately. The overwintering below-ground parts of the hemicryptophytes often function as storage organs; their volume is several times larger than that of the seasonal above-ground parts (up to 20 times larger in the case of wet-site communities rich in sedge, Wielgolaski 1975a). Plants on low-nutrient soils often exhibit xeromorphic growth and those on fertile soils, mesomorphic growth.

Zonal Differentiation of Vegetation

The plant cover in the southern tundra regions is continuous. In the direction of the pole, as climatic conditions become progressively less conducive to growth, plant cover becomes more and more discontinuous until plants are found at only a few advantageous sites (e.g. moraines or river terraces rich in fine material). At the same time, the height of the vegetation decreases, plant communities contain fewer and fewer species and the life form spectra shift towards hemicryptophytes; dwarf shrubs gradually disappear. The soils also change: the amount of humus decreases, the texture of the soil becomes coarser, and the lime, sodium and sodium salt contents increase to levels comparable to those in the parent rock material. In extreme cases, as in hot, arid regions, solonetz and solonchaks can form and salt efflorescences and salt lakes become established.

Aridity can become a limiting factor for vegetation in areas where the general lack of precipitation is compounded by a high permeability of the soil substrate.

In accordance with this south/north change in vegetation and soils, the arctic periglacial can be divided into three circumpolar zones which can be termed the low arctic tundra (> 80% plant cover), the high arctic tundra (10–80% plant cover) and the polar desert (< 10% plant cover) (Fig. 39).

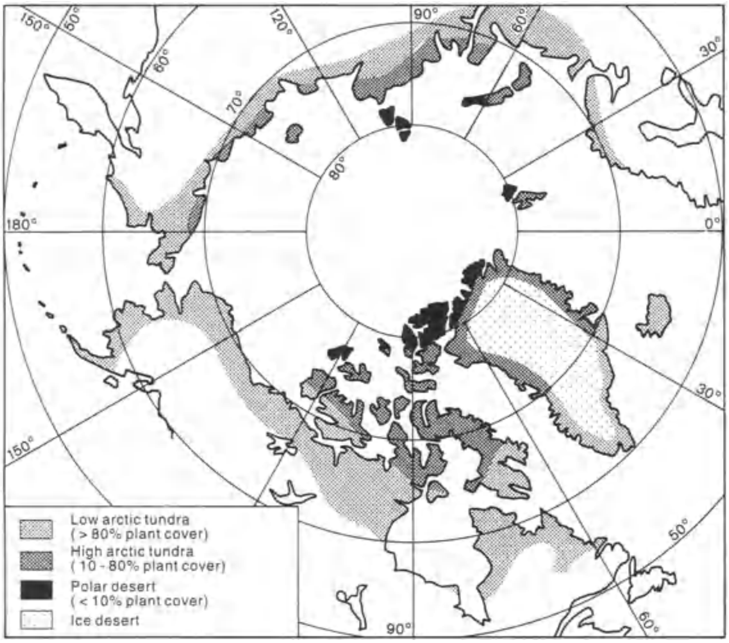


Fig. 39. Subdivision of the Polar/Subpolar Zone according to major types of arctic vegetation. (Ives and Barry 1974)

Small-Scale Subdivision of Vegetation

On the large-scale zonation is superimposed a small-scale vegetational pattern whose units also differ notably from one another according to degree of plant cover, height and species composition. The small-scale differentiation depends on the topography, exposure to wind and the soil substrate. Exposure to wind dictates the thickness and duration of the winter snow cover which, in turn, causes variations in (a) temperature stress during winter and (b) the start of the growing season in the summer; the topography, i.e. the position in relation to relief (e.g. on watersheds, on upper or lower parts of more or less inclined slopes, in valley bottoms), and the soil substrate determine the amount of moisture in the soil, the depth of the active permafrost layer and the effectiveness of cryoturbation (see also Fig. 40). In summer, the thaw layer is deepest in well-drained mineral soils; but, in depressions as well, the energy input from inflowing meltwater can lead to a deeper active layer, even in peaty substrates.

Lichen-rich communities (lichen tundra) are common on many wind-exposed sites (i.e. those with little snow cover), while in areas covered for long periods of time with snow (snow beds), mosses tend to predominate (moss tundra); many of the less winter-hardy dwarf shrubs (e.g. *Vaccinium myrtillus*, *Betula nana*, *Juniperus communis*) find the best growth conditions under the protection of

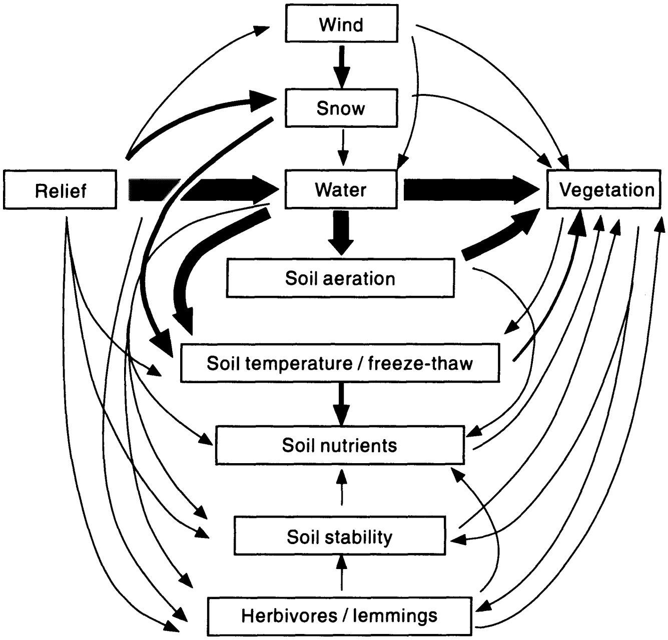


Fig. 40. Interactions between environmental conditions and vegetation in the tundra. (Webber 1978). The major controls are indicated by *heavy arrows*. Local differences in tundra vegetation are primarily relief-related: the relief affects both snow distribution in winter and the flow of meltwater in summer and thus dictates the (re-)distribution of precipitation water in the area; dry, moist or wet sites are then established which also differ as to aeration and temperature, i.e. according to characteristics which are principal components of growth conditions for vegetation

a sufficiently deep but early-melting snow cover (dwarf shrub tundra). In wet locations, dwarf willows predominate or herbaceous plants and grasses form a meadow-like vegetation (meadow tundra; particularly predominant in maritime subpolar regions).

Within these types of tundra (especially in the high arctic zone where the vegetation cover is more or less discontinuous), frost-induced landforms such as sorted and unsorted patterned ground, ice wedge polygons, mud boils, hummocks, gelifluction lobes, streams, steps etc. play an important role in producing a further mosaic-like differentiation of plant cover (which, in turn, makes them more conspicuous).

Primary Production and Phytomass

The growing season begins in June at the earliest and ends in September at the latest. During this period, photosynthesis runs round the clock and, with the exception of very cloudy nights and the time near the end of the growing season, always with a positive result (that is, at any point in time, the gross primary production is higher than the respiration loss). However, this is not able to counteract the disadvantages of the short and cool growing season (extremely different from the Humid Tropics; similar in length to that in the arid regions, but more consistent, and temperatures less favourable) or those of the edaphic problems: the primary production of 1–2 $\mathrm{t\,ha^{-1}\,a^{-1}}$ (max. about 4 $\mathrm{t\,ha^{-1}\,a^{-1}}$) is quite low (the lowest of all humid regions on earth). The photosynthetic efficiency is given as 0.36–0.7% (Wielgolaski et al. 1981, p. 218) and 0.46% (Tieszen 1978a, p. 241), which are relatively low values as well.

Of the vegetational types mentioned above, meadow tundras have the highest PP_N under similar climatic conditions, provided the water level drops significantly during the growing season (which is generally the case at such sites), and litter decomposition is relatively rapid.

As a result of the generally low growth performance, even low-growing shrubs can have a considerable old age (up to about 200 years). The low PP_N is also the explanation for the fact that, despite the very slow decomposition of organic material in the tundra, thick layers of peat are formed only very slowly if at all in raised bogs. For this reason, histosols are more the exception than the rule, in contrast to the climatically more propitious boreal forest areas, and occur more frequently only in the low arctic tundra.

The low productiveness of tundra vegetation also means that it takes a long time to regenerate following destruction (= low resilience). From this point of view, tundras must be classified as sensitive (Remmert 1980).

The phytomass increases with decreasing geographic latitude and altitude (as a result of increasing atmospheric temperature and longer growing seasons) to about 30 $\mathrm{t\,ha^{-1}}$. Parallel to this, the proportion of vascular plants compared with cryptogams (lichens and mosses) increases and the LAI of dwarf shrub tundras increases to about 1.2 $\mathrm{m^2\,m^{-2}}$ (Wielgolaski et al. 1981, p. 213) and more. The below-ground portion of phytomass is generally high; it is highest in areas where shrubs and trees are more common. The portion of photosynthetically active (green) parts is lowest in grassy meadows (where there is a great deal of below-ground phytomass) and in the shrub and forest tundras (which contain large quantities of wood) (Tables 12 and 13).

Animals of the Tundra

In the tundra ecosystem, herbivores play a comparatively important role (their importance is greater only in some savannas and steppes). The majority of animals are represented by the homoiotherms (warm-blooded) species, i.e. mammals and birds. Poikilotherms (whose body temperature varies with the environment) obviously find it difficult during the cool summer to bring their body temperatures up to levels sufficient to allow growth and reproduction. This means that large groups of animals such as amphibians, reptiles, molluscs and insects, which are represented in the warmer ecozones by a variety of species and have achieved

Table 12. Ratio of shoot to root mass and of green to non-green plant parts for various plant formations in the Polar/Subpolar Zone. (Wielgolaski 1981, p. 203)

Plant formation	Ratio of	
	Shoot-to-root mass	Green to non-green parts (vascular plants only)
Polar desert and semi-desert	1: 0.9	1: 2.3
Wet sedge meadow	1:21	1:23
Mesic-dry meadow	1: 5.0	1: 7.7
Dwarf shrub tundra	1: 3.1	1:12
Low shrub tundra	1: 2.0	1:19
Forest tundra	1: 0.8	1:15

Table 13. Phytomass and primary production of some dwarf shrub tundras. (Bliss 1979)

Location	Phytomass ($t\,ha^{-1}$)			Net primary production ($t\,ha^{-1}\,a^{-1}$)		
	Vascular plants		Cryptogams	Vascular plants		Cryptogams
	Above ground	Below ground		Above ground	Below ground	
Peninsula Russia	5.55	12.28	–	1.01	1.34	–
Peninsula Russia	1.70	4.76	–	0.20	0.30	0.24
Devon Island NWT, Canada	1.45	6.71	–	0.17	0.90	0.20
Dempster Highway Yukon T., Canada	1.11	15.24[a]	3.02	0.39	–	1.32
Eagle Creek Alaska	2.49	20.08[a]	0.89	0.72	–	0.34

[a] Including dead and live material

a great deal of importance as consumers (herbivores), are rarely, if ever, found here.

Typical inland mammals include reindeer, caribous, musk-ox, lemmings, arctic hares, wolves and arctic foxes while, at the coast, seals, walrus and polar bears are found. Common sea birds which brood on the coast in large colonies are auks, gannets and fulmars. Birds living inland include rough-legged buzzards, snowy owls, skuas, gyr falcons, ptarmigans and, in particular, numerous water birds such as waders (plovers, curlews, black-tailed godwits, sandpipers), ducks, geese and swans. Mention should also be made of the mosquitoes (mainly of the genus *Aedes*, formerly *Culex*) about which Linné in his *Flora Lapponica* (1737) wrote:

"I am of the opinion that nowhere else on earth is the common mosquito (*Culex vulgaris*) present in such innumerable quantities as in the forests of Lapland, where they compete in numbers with the particles of dust of the ground. They constantly fly around with their sickening buzzing sound and dive onto face, legs and hands . . . . If one sticks out a naked hand, it is soon covered with a black mass of them which settle on it. If one wipes them away with the other hand and kills the whole lot of them, their place is almost immediately taken by new ones. It is virtually impossible to breath freely, because they find their way into nose and throat" (Tischler 1984, p. 275).

There are no land vertebrates in the Antarctic, but seals come to the coasts and islands for the purpose of raising their young; the most common sea bird which is found on the coasts is the penguin.

As is the case for plants, most mammal and bird species (or genera) have a circumpolar distribution. Their total numbers – like those of plants – are very low (only 70 species of bird out of a worldwide total of 8600, and 23 species of mammal out of a worldwide total of 3200 – according to Dunbar 1968, taken from Sugden 1982, p. 117). On the other hand, many species of herbivore are present in large numbers. Wide-ranging cyclic variations in population size are characteristic of the smaller mammals (such as lemmings). The number of species and individuals decreases in the poleward direction.

Most large mammals – such as (usually) reindeer, followed by wolves and wolverines – and most birds migrate southwards in winter. Their number includes hundreds of thousands of geese, ducks, wading birds and gulls which then require sufficiently large wetlands in our latitude in order to be able to overwinter. The draining of such biotopes, which has long been practised in our region, or extensive hunting can thus endanger the animal life of the tundra.

Some mammal and a few bird species spend the winter in the tundra as well. This is made easier for the herbivores among them, e.g. moles, ptarmigans and hares, by the fact that the twigs, leaves and berries of many plants on which they feed are preserved by the rapid temperature drop in late summer (refrigerator effect). Smaller mammals profit from the protective winter snow cover, under which they seek out cavities (Fig. 60), and larger ones grow a thicker coat or plumage. Because some of the herbivores do not leave, a few carnivores can remain behind as well, such as arctic foxes and snowy owls. Hibernation as a strategy for surviving the winter is almost unknown. Winter coats and plumage are often white (e.g. in the case of the arctic foxes, stoats, blue hares, lemmings and ptarmigans); the animals which are white all the year round, e.g. snowy owls, polar bears and arctic hares, are less common.

Herbivorous mammals and birds help to accelerate the turnovers of organic matter and mineral nutrients in the tundra ecosystem. Most important here – as well as in the tropical and temperate grasslands – are the ungulates (hooved animals), rodents and lagomorphs (hares, rabbits), also the ptarmigans and wild geese. Of all these, lemmings and other types of moles seem to play the most important role. In Alaska, a close correlation was found between the availability of plant nutrients (nitrogen, potassium, phosphorus) and the massive increase in the lemming population every 3 to 7 years (Pieper 1964; Schultz 1969). However, it has not been possible to find a generally applicable explanation for this (Liestol et al. 1975). The digging activity of the lemmings also affects soil formation and the genesis of the microrelief.

The role played by *lemmings* (*Lemmus trimucronatus*) at Point Barrow, Alaska, was investigated by Batzli (1981). The scenario found is as follows: every 4 to 6 years the lemming population increases to a density of 200 individuals per hectare or even higher; in between these peaks it drops to less than 1 individual per hectare (Fig. 41). The extreme fluctuations in population are a result of the yearly change in the food supply [which depends on the weather (plant growth conditions) and the density of the herbivore population] and the number of predators (which, with a slight delay, also follows the density of the herbivores). In years with the highest population density the lemmings consume 0.4 t DM (dry matter) ha^{-1} (= 7120 MJ ha^{-1}, Table 14), about one-third of which they assimilate. Almost 96% of this gross production is lost via respiration (mainly for the maintenance of body temperature at 38 °C) and only slightly more than 4% is available for growth or reproduction. This means that the assimilation (digestion) efficiency – no doubt due to the fact that the food is hard to break down – is comparatively low at 33%, whereas the net production efficiency, on the other hand, is relatively high at 4%. Gross production efficiency (also called ecological efficiency), calculated as the ratio of net production to ingested food, is thus almost 1.5%, i.e. growth and reproduction are almost 5 kg ha^{-1} a^{-1} (this is equivalent to an annual production of about 120 lemmings per hectare with a body weight of 40 g each).

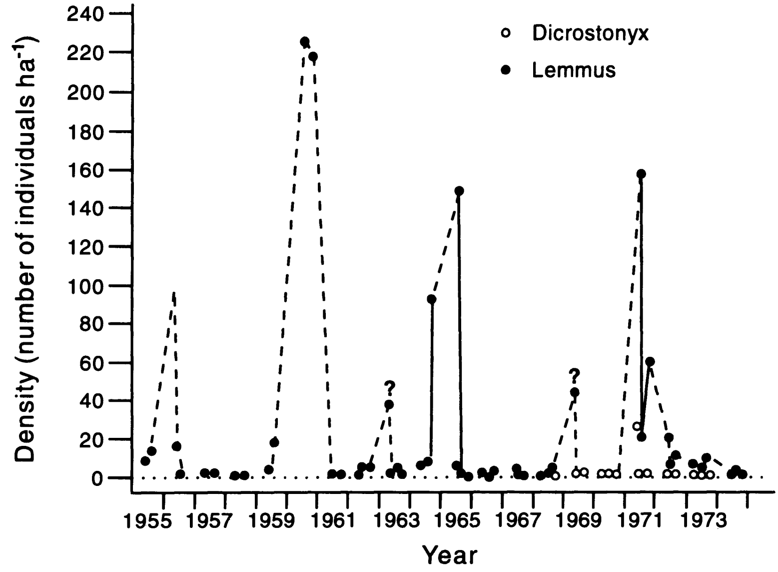


Fig. 41. Variations in density of the brown lemming population during 20 years at Point Barrow, Alaska. (Batzli 1981)

Table 14. Energy transfer (MJ $ha^{-1}a^{-1}$) of three mole (microtine rodents) populations in three tundra areas, in each case for the year with the highest population density. (Batzli 1981)

Species	Location	Ingestion (C)	Gross production (A)	Respiration (R)	Net production (P)	P/R (%)	Gross production efficiency (P/C) (%)
Lemmus trimucronatus[a]	Point Barrow, Alaska	7120	2350	2140	101	4.7	1.4
Microtus oeconomus	Finse, Norway	1630	897	825	28	3.4	1.7
Dicrostonyx groenlandicus	Devon Island, Canada	436	239	222	5	2.3	1.2

[a] Conversions in the text were based on the assumption that 1 g of plant substance = 18 kJ and 1 g of animal substance = 23 kJ

Table 15. Comparative population energetics of reindeer, caribou and musk-ox in tundra ecosystems. (White et al. 1981)

Population parameters	Caribou Alaska	Reindeer Norway	Musk-ox Canada
Density (km^{-2})	0.1–1.0	1.4–2.1	0.03–1.9
Animal biomass (kg DM km^{-2})	4–52	40–177	207
Energy flux (MJ km^{-2}):			
Ingestion (C)	2510–8369	50200	21757
Assimilation (A)	1130–3724	31547	15272
Respiration (R)	1130–3724	9330	15230
Production (P)	25–79	586	837
Efficiencies:			
Assimilation efficiency (A/C)	0.55	0.63	0.70
Ecological efficiency (P/C)	0.010	0.012	0.038
Net production efficiency (P/A)	0.018	0.019	0.055
P/R	0.021	0.063	0.055
Exploitation efficiency (C/available food)	0.1	1.0	1.5
Population turnover time (years) (Animal biomass/annual production)	9.1	2.5	9.6

Similar studies have been conducted on other herbivore populations. Table 15 shows the results for ungulates, the next most important vertebrate group after the rodents.

Total animal biomass (not including decomposers) in many tundras probably attains magnitudes of 0.005 t ha^{-1}. The proportion of the phytomass converted by herbivores is probably between 5 and 10% of the PP_N. This is high in comparison to other ecozones. In view of the generally inhibited decomposition, which in many soils cannot keep pace with the supply of organic wastes, this proportion is very important: the herbivores do a great deal to maintain the nutrient cycle; the plants are therefore just as dependent on these consumers as the consumers are on the plants they eat.

Litter and Humus

Even worse than the ecological disadvantages of the tundra in terms of primary production are the disadvantages associated with the decomposition of dead organic substances; compared with tropical rain forests, the PP_N in this zone is ten times lower, but decomposition takes as much as 100 to 1000 years longer:

	Magnitudes of	
	PP_N (t ha^{-1} a^{-1})	Decomposition time (years)
Tundra	2	100–1000
Tropical rain forest	20	1

Deep layers of litter and a high humus content are thus characteristic of most tundra ecosystems, and they generally exceed the amount of phytomass several times over. None of the other ecozones has a similarly high content of dead organic matter. Decomposition is inhibited by the unfavourable temperature (which strongly limits not only biological breakdown processes, but chemical ones as well), the unfavourable C/N ratio of most litter components and the acidic and often – due to widespread waterlogging – oxygen-poor environment. Of these factors, soil moisture is most important: the highest humus contents (up to several thousand $\mathrm{t\,ha^{-1}}$) are found in areas with constantly high soil moisture (mainly peat) and the lowest in very dry locations (where, however, there is often a deep litter layer). The humus content in moderately moist soils is frequently between 300 and 700 $\mathrm{t\,ha^{-1}}$ (Table 16).

Fungi usually play a larger role in decomposition than do bacteria because they are better able to deal with the acidic environment; but bacteria are more effective in areas deficient in oxygen. Earthworms are rare or non-existent.

The accumulation of humus means that most of the nutrients are present in a form unavailable to plants. This has a negative effect, particularly on the *nitrogen supply* (which is probably the most limiting factor for PP_N in many tundra areas). Legumes with nodule-forming rhizobia in their roots are rarely found, and the fixation of N_2 by bacteria living freely in the soil seems to be severely impeded by the cold, acidic conditions. The most important N_2 fixers are usually free-living blue algae and a few species of lichens (Granhall and Lid-Torvisk 1975, p. 313). The amount of atmospheric nitrogen bound annually is always low, usually between 0.23 and 3.8 $\mathrm{kg\,ha^{-1}}$ (Holding 1981, p. 578). At the sites most affected by nitrogen deficiency – for example in raised bogs – many plants exhibit (xeromorphic-like) peinomorphic growth characteristics with scale- or needle-shaped hard leaves.

The slow decomposition of litter can also limit the availability of *phosphorus* and other nutrients to the point that growth is restricted. Even worse, as a

Table 16. Estimates of organic matter accumulated in the soil at various tundra sites. (Heal et al. 1981)

Site	Plant formation	Soil organic matter ($\mathrm{t\,ha^{-1}}$)	Depth (cm)
Signy Island (Antarctic)	*Chorisodontium*	400	15
	Drepanocladus (wet)	350	23
	Grassland	420	15
Devon Island (Canada)	Beach ridge	90	62
	Mesic meadow	510	31
Point Barrow (Alaska)	Grass-sedge meadow	370	20
Abisko (Sweden)	Stordalen mire	1000	100

consequence of soil acidity (pH usually lower than 4.5), inorganic phosphorus is mainly present in the form of relatively insoluble Fe–P or Al–P complexes.

Model of a Tundra Ecosystem

As always, the ecosystem model (Fig. 42) assumes steady-state conditions. In the case of the tundra, this practice is more questionable than in other zones: it can be assumed that, even under undisturbed conditions, an equilibrium will never be achieved here; it is more likely that, since the PP_N is always larger than the concurrent rate of decomposition, the reserves of dead organic matter will go on increasing. This is particularly true of all wet sedge meadows and

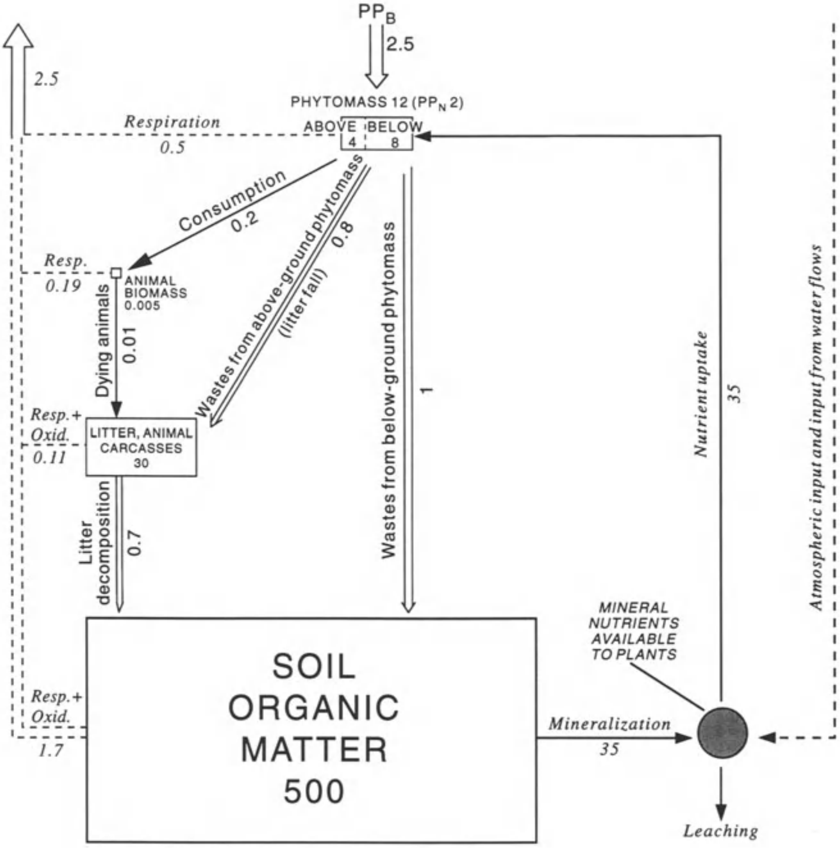


Fig. 42. Simplified ecosystem model of a dwarf shrub tundra on a gelic gleysol (with dystric H horizon), compiled from data taken from Cooper 1975; Whittaker and Likens 1975; Wielgolaski 1975a; Tieszen 1978b; Bliss et al. 1981; Reichle 1981. See Chapter 2.5.2.5 for scheme of the model. A particularly striking feature are the huge reserves of organic matter in the soil (mainly peat) as compared with the small amount of phytomass

cotton grass moors. As a result, the tundras – possibly together with some parts of the Boreal Zone – are a remarkable special case: these are the only regions in which excess organic matter is produced on an ongoing basis; in contrast, all other zonal ecosystems have a long-term balanced input/output cycle of matter.

3.1.6 Land Use

The entire Polar/Subpolar Zone is predominantly free of settlements (of all ecozones, it is the least populated); only in the subarctic tundra has any notable, though still sparse, settlement occurred. Today, about 2 million humans live here (Stäblein 1983). The majority of these are immigrants who mainly arrived during the past few decades. As far as indigenous peoples are concerned, about 90 000 Eskimos still live in Greenland and northern America (a few in northeast Siberia), and about 35 000 Lapps live in northern Europe (Hustich 1979). Many of the current inhabitants are the result of mixed marriages between the original inhabitants and recent immigrants.

Traditionally, Eskimos were highly specialized fishermen and hunters concentrating mainly on fishing, seal hunting and whaling in coastal waters. Today, most of them earn a living by taking ordinary paid jobs. The peoples of northern Eurasia, on the other hand, were originally involved in nomadic to semi-nomadic *reindeer herding*. Many of the current population still are. On an area of about 3 million km^2, there are presently about 3 to 3.5 million (domesticated) reindeer (*Rangifer tarandus*), about 2.5 to 3 million of them in the former Soviet Union (Kryuchkov 1978) and 260 000 in Finland (Epstein and Valmari 1984). Herd management is highly developed in some areas, while in others traditional methods are employed and the animals are used for subsistence. In most places, the herds are kept under surveillance in the winter months with the aid of snowmobiles.

Between 40 and 80 ha of tundra are required as grazing land per reindeer (roughly 1–3 reindeer km^{-2}) (Rieger 1974, p. 761); according to Andreyev (1970), the figure is about 140 ha in the Russian subarctic regions (less than 1 reindeer km^{-2}) and according to Treude (1979, p. 136), even 170 ha in the Mackenzie Delta in Canada. Studies carried out in Spitzbergen yielded considerably higher densities for the smaller reindeer found there (*Rangifer tarandus platyrhyncus*): at an above-ground PP$_N$ of 0.89 ± 0.24 t DM ha^{-1} a^{-1} and with an above-ground standing crop of 11.67 ± 4.06 t DM ha^{-1}, the grazing area required by one animal is only 14–25 ha (4–7 reindeer km^{-2}) (Øritsland and Ødegaard 1984).

Similarly high values of 7 animals per km^2 are given by Thomas (1969, taken from Sugden 1982, p. 117) as the maximum density for (wild) caribou in arctic Canada.

The success achieved with good management points the way to the future: if good management practices are applied everywhere, the experts believe that the tundras could become important meat-producing regions for the world. Hope is also pinned on the possibility of domesticating the musk-ox (*Ovibos moschatus*). Both the meat and the wool of these animals can be used.

In the past, attempts have often been made to introduce reindeer herding into North America, for example in Alaska at the turn of the century, or in the Mackenzie Delta in the 1930s. So far, however, it has not proved possible to develop any lasting interest in this activity among the Eskimos. Future prospects in this direction are also viewed with scepticism, at least as far as the large-scale exploitation of the Canadian tundra is concerned (Treude 1979). It is felt that game ranching of the indigenous, wild caribou (subspecies of *Rangifer tarandus*) offers more hope of success (Riewe 1981).

New interest in exploiting these areas has come to the fore in recent decades. This is partly the result of military considerations (nowadays the Arctic is considered a strategically important region), and partly it is due to the growing requirements for raw materials in the industrialized nations of the Northern Hemisphere: the Arctic has large deposits of many raw materials. For instance, the

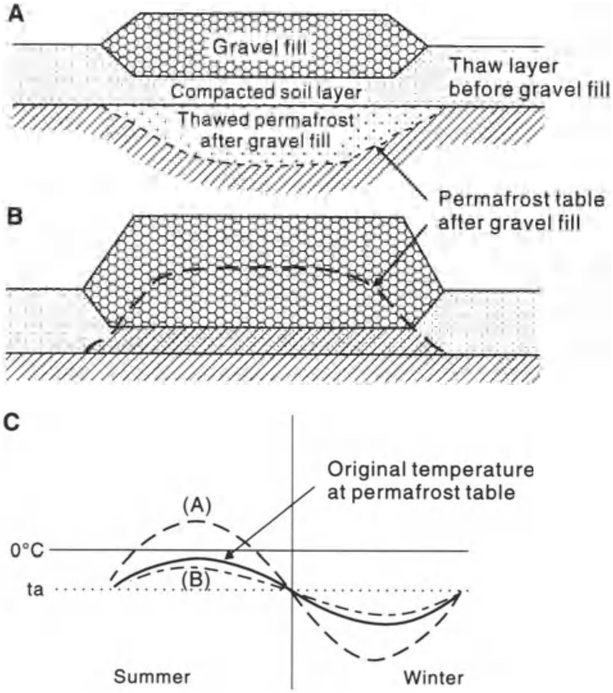


Fig. 43A–C. Effects of a gravel fill (e.g. for road construction) upon the temperature conditions regime and thickness of the active layer in permafrost. (French 1981). **A** Too little fill: increased thermal conductivity leads in summer to deeper thawing. **B** Too much fill: increased insulation causes the permafrost layer to grow upwards. **C** Effects of **A** and **B** upon the thermal regime: too little fill increases the amplitude of seasonal temperature fluctuations at the permafrost table and too much fill decreases it. *ta* Mean annual temperature region contains about 15% (35 billion t) of the world's estimated total 230 billion t of recoverable oil reserves, along with about 50% of the planet's natural gas reserves (Gocht and Pluhar 1978). Considerable reserves of coal and ore are also found here (e.g. 80% of Russian nickel reserves are located in arctic areas – Stäblein 1983). Exploitation of these raw materials has become technically feasible and is being performed today at a growing rate.

Modern settlement and exploitation of these areas encounter a few natural difficulties. For example, there are specific problems related to building and road construction. Due to the flatness of the land in many areas and the impermeability to water of the permafrost layer, the active layer in summer is for the most part saturated with water, marshy in consistency, and covered with patchy vegetation scarcely capable of supporting the weight of a person. This means that the substructures of buildings must be anchored in the permafrost layer and constructed so as to prevent the downward transfer of heat. At the same time, there is danger of upfreezing when, for example, an excessively thick roadbed has too strong an insulating effect, thus allowing the permafrost soil beneath it to extend upwards (Fig. 43).

Supplying the population with *food* is also particularly difficult because the polar boundary of crop production lies far to the south, within the boreal coniferous forest regions. In all areas, however, vegetables can be successfully grown in greenhouses (Rieger 1974, p. 761). Traditionally, the gathering of wild berries (*Vaccinium* spp. and *Rubus chamaemorus*) has played a certain role in nutrition. The *water supply* can be obtained from deep lakes which do not freeze completely down to the bottom during winter. In some locations, groundwater can be

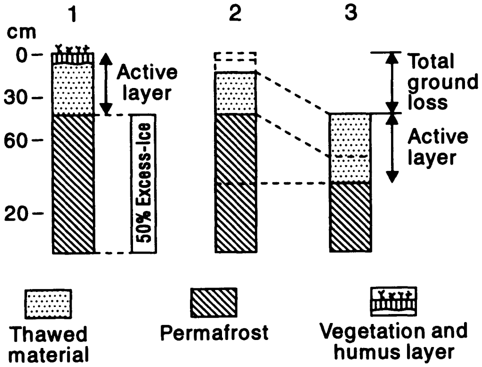
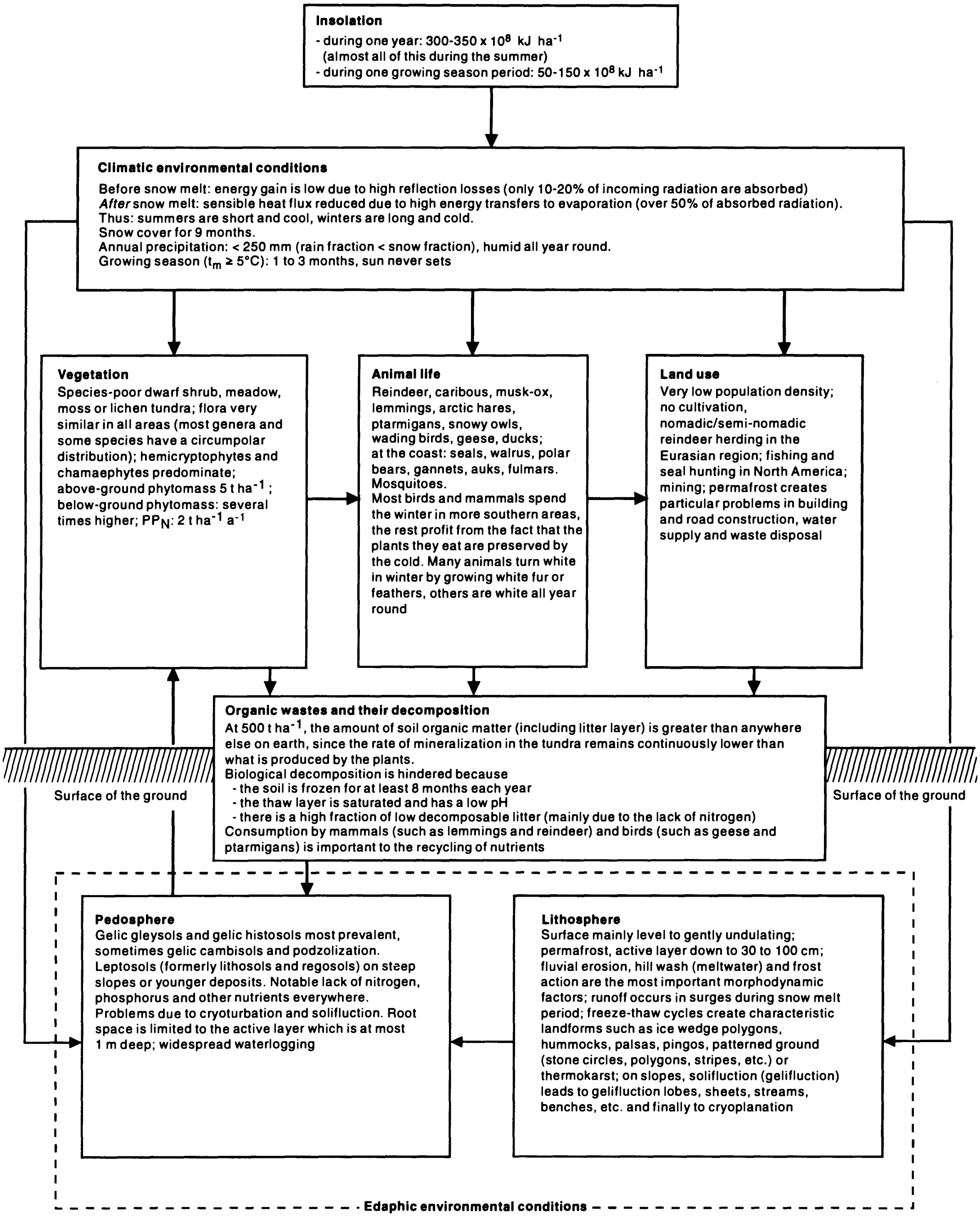


Fig. 44. Diagram illustrating how terrain disturbance of an ice-rich tundra soil can lead to thermokarst subsidence. (Mackay 1970, taken from French 1981). In the undisturbed condition (*1*), namely with vegetation and humus layer intact, the active layer in summer is assumed to be 45 cm deep and the permafrost below it is assumed to have an excess ice content of 50%. If the plant and humus layer (assumed to be 15 cm deep) is then removed (*2*), and thus the insulation layer is lost, the summertime thawing can progress down to 60 cm (*3*). Of this amount, 30 cm lies within the original active layer; the other 30 cm results from 60 cm of permafrost which releases meltwater equivalent to 30 cm of soil depth. The ground then subsides by this amount



Insolation
- during one year: 300-350 x 10^8 kJ ha^{-1} (almost all of this during the summer)
- during one growing season period: 50-150 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Before snow melt: energy gain is low due to high reflection losses (only 10-20% of incoming radiation are absorbed)
After snow melt: sensible heat flux reduced due to high energy transfers to evaporation (over 50% of absorbed radiation).
Thus: summers are short and cool, winters are long and cold.
Snow cover for 9 months.
Annual precipitation: < 250 mm (rain fraction < snow fraction), humid all year round.
Growing season ($t_m \geq 5°C$): 1 to 3 months, sun never sets

Vegetation

Species-poor dwarf shrub, meadow, moss or lichen tundra; flora very similar in all areas (most genera and some species have a circumpolar distribution); hemicryptophytes and chamaephytes predominate; above-ground phytomass 5 t ha^{-1}; below-ground phytomass: several times higher; PP_N: 2 t ha^{-1} a^{-1}

Animal life

Reindeer, caribous, musk-ox, lemmings, arctic hares, ptarmigans, snowy owls, wading birds, geese, ducks; at the coast: seals, walrus, polar bears, gannets, auks, fulmars. Mosquitoes.
Most birds and mammals spend the winter in more southern areas, the rest profit from the fact that the plants they eat are preserved by the cold. Many animals turn white in winter by growing white fur or feathers, others are white all year round

Land use

Very low population density; no cultivation, nomadic/semi-nomadic reindeer herding in the Eurasian region; fishing and seal hunting in North America; mining; permafrost creates particular problems in building and road construction, water supply and waste disposal

Organic wastes and their decomposition

At 500 t ha^{-1}, the amount of soil organic matter (including litter layer) is greater than anywhere else on earth, since the rate of mineralization in the tundra remains continuously lower than what is produced by the plants.
Biological decomposition is hindered because
- the soil is frozen for at least 8 months each year
- the thaw layer is saturated and has a low pH
- there is a high fraction of low decomposable litter (mainly due to the lack of nitrogen)

Consumption by mammals (such as lemmings and reindeer) and birds (such as geese and ptarmigans) is important to the recycling of nutrients

Pedosphere

Gelic gleysols and gelic histosols most prevalent, sometimes gelic cambisols and podzolization. Leptosols (formerly lithosols and regosols) on steep slopes or younger deposits. Notable lack of nitrogen, phosphorus and other nutrients everywhere. Problems due to cryoturbation and solifluction. Root space is limited to the active layer which is at most 1 m deep; widespread waterlogging

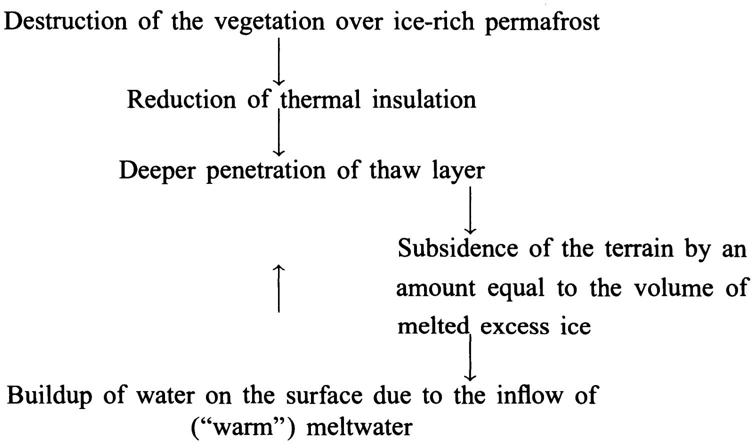
Lithosphere

Surface mainly level to gently undulating; permafrost, active layer down to 30 to 100 cm; fluvial erosion, hill wash (meltwater) and frost action are the most important morphodynamic factors; runoff occurs in surges during snow melt period; freeze-thaw cycles create characteristic landforms such as ice wedge polygons, hummocks, palsas, pingos, patterned ground (stone circles, polygons, stripes, etc.) or thermokarst; on slopes, solifluction (gelifluction) leads to gelifluction lobes, sheets, streams, benches, etc. and finally to cryoplanation

Fig. 45. Synoptic diagram for the tundra

extracted by drilling from below the permafrost layer (Mackay and Loken 1974, p. 111). These deep-lying aquifers are created by the percolation of surface water through gaps in the permafrost, such as are often found under lakes and rivers. Where deep lakes or groundwater are non-existent, the water supply in winter can be secured only by melting ice. The insulating of water pipes is another important task. Finally, it is also difficult to dispose of domestic and industrial waste, since natural decomposition occurs slowly, if at all.

Major problems can arise from the destruction of tundra vegetation, as is common practice in the areas surrounding human settlements. Such destruction eliminates an important source of insulation for the permafrost in the soil, and as a result the thaw layer in summer penetrates increasingly deeper. If the newly thawed layer has a particularly high ice content, the soil subsides by an amount equal to the volume of excess ice (Fig. 44). Such settling of the ground can become exacerbated when "warm" meltwater flows into the depressions formed, i.e. the process may be self-reinforcing, as illustrated in the following diagram:



For these reasons, when carrying out any activity in such areas, efforts should be made to maintain the thermal regime originally prevailing under the intact vegetation cover, even if this means having to use sometimes expensive methods of insulation.

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Chapter 3.1: Polar/Subpolar Zone

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3.2 Boreal Zone

3.2.1 Distribution

Of all the ecozones, the Boreal Zone is the only one that occurs solely in the Northern Hemisphere. It encircles the earth and extends at least 700 km in the north-south direction; at its widest points it has a N-S extent of 1500 km in North America and 2000 km in Eurasia. The southernmost parts of the zone are found on the eastern coasts of the continents, where it extends down to 50° N, while the warm ocean currents (Gulf Stream and Kuroshio) along the western coasts prevent the zone from extending any farther south than 60° (Fig. 46). Leaving aside the tundra areas, the following regions of the earth belong completely or predominantly to the Boreal Zone: Canada, Alaska, Scandinavia, northern Russia and Siberia. When added together, the various regions total almost 20 million km^2 or 13% of the earth's landmass. Thus the Boreal Zone, like the polar and subpolar regions described in the preceding chapter, is one of the larger ecozones. It is certainly the largest when compared with the other *forest zones* of the earth.

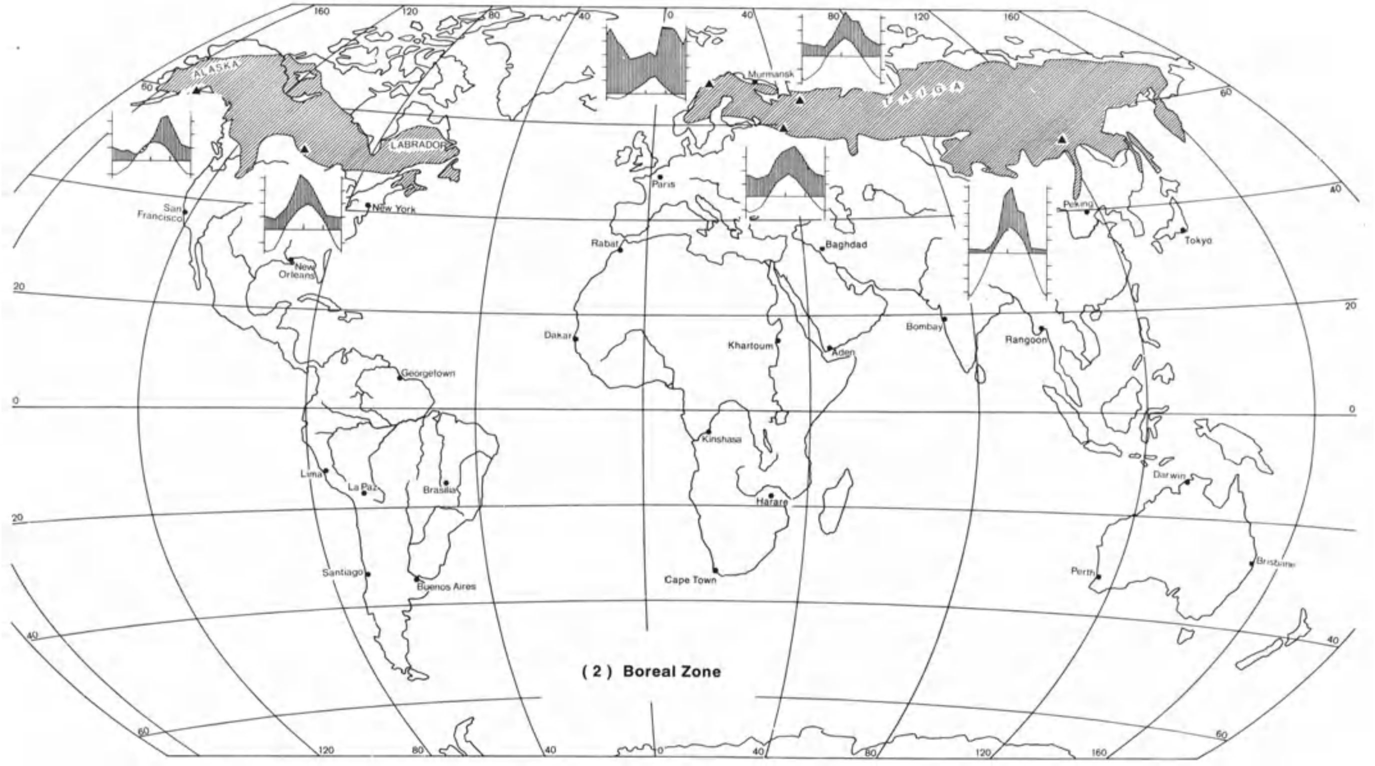

Fig. 46. Boreal Zone. This zone encircles the Northern Hemisphere. The southern boundary extends to about 50° N on the east coasts of the continents and about 60° N on the west coasts. The northern boundary follows the polar timber line

Despite the vast expanse of this zone, the regional deviations found are comparatively insignificant, making subdivision unnecessary. All areas in this zone are or were originally covered by a coniferous forest of very uniform floristic composition or, in a few places, by a mixed forest containing countless lakes and oligotrophic mires.

Along the boundary with the tundra, the forest disappears not suddenly but gradually over a transition zone more than 100 km wide. This ecotone, known as the *forest tundra*, is the one that comes closest to occupying a separate area within the Boreal Zone.

3.2.2 Climate

The growing season is thermally limited to 3 to 6 months: at least 10 months in the year are humid, and of these a minimum of 3 and a maximum of 6 have a mean temperature (t_m) $\geq +5\,^{\circ}C$. The zonal plant formation that establishes itself under these conditions is the *boreal coniferous forest,* which even today is still preserved in most areas. This region is bordered in the south by temperate deciduous forests (Humid Mid-Latitudes), where at least 4 months have a $t_m \geq 10\,^{\circ}C$ and adequate moisture is available, otherwise by steppes and semideserts (Arid Mid-Latitudes). To the north, the *polar tree line* is followed by the subpolar tundra. This transition does not occur at the North Cape until 70° N, but at Hudson Bay it occurs at 53° N. In general, the tree line in Eurasia is nearer the pole because, under the influence of continental climatic conditions, there is a relatively greater temperature increase in summer. The tree line corresponds well to the 10 °C isotherm for July.

Regional climatic differences, particularly those in Eurasia, are due primarily to the west-to-east changeover from maritime to continental conditions. For example, the annual temperature ranges are mainly determined by how far the moderating influence of the oceans reaches into the continents. The ranges are small near the coasts and become increasingly higher towards the interior of the landmasses.

This is perhaps best illustrated by the two climatic diagrams (Fig. 47). The first diagram shows the *cold continental-type climate*: extremely cold winters with minimum temperatures down to $-70\,^{\circ}C$ are contrasted with relatively warm summers with maximum temperatures up to $+30\,^{\circ}C$. The mean annual temperature is correspondingly very low (usually below $-5\,^{\circ}C$) and the annual temperature range is very high – higher than in any other ecozone. There is relatively little snow in winter. Below a certain depth, the ground remains frozen all year round (permafrost).

The second diagram shows the *cold maritime-type climate*: in this case, the summers remain somewhat cooler and the winters notably milder. As a result, the annual temperature range is much smaller and the mean annual temperature is higher (around 0 °C). The snow cover in winter is thicker and permafrost is discontinuous to sporadic, or – more rarely – non-existent in a few places.

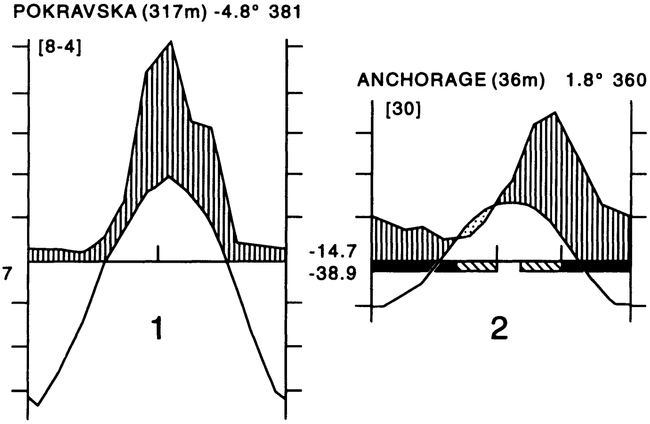

Fig. 47. Climatic diagrams for the cold continental (*1*) and cold maritime (*2*) type climates in the Boreal Zone. (Walter and Lieth 1960–67). As the continental influence increases, so does the annual temperature range and summer precipitation

In addition to the land/sea distribution, latitude also plays a role in the prevailing thermal conditions: in all regions, the degree and duration of summer warming increases significantly from north to south, on average from about 3 months with $t_m \geq +5\,°C$ (1 month of which has $t_m \geq +10\,°C$) up to 6 months with $t_m \geq +5\,°C$ (3 months of which have a $t_m \geq +10\,°C$).

In contrast to the polar and subpolar regions, the *exposure to insolation* is more important here because (during summer) the path of the sun above the horizon is shorter and the percentage of direct radiation is greater. Slopes with a southern exposure thus lose their snow cover earlier in spring, and the summertime temperatures of their soils and of the air layer close to their surfaces are higher. The vegetation responds to the more or less favourable or unfavourable climatic site conditions by displaying a varying species composition: the warm, dry southerly slopes are covered with more productive, e.g. birch and aspen-rich forests, whereas on the cooler, moister northerly slopes, less productive, often spruce-rich forest types are found.

Annual *precipitation*, at 250 to 500 mm (in a few areas up to about 800 mm)[13], is higher than in the tundra, but still quite low in comparison to other humid regions of the earth (it is about twice as high in the Humid Mid-Latitudes).

During the *winter*, precipitation results from low-pressure systems but is less copious due to the low temperatures prevailing. Within Eurasia and North America, cold anticyclones develop over the continents and suppress most precipitation. During the *summer*, however, when continental thermal lows (warm

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[13] Much larger amounts of precipitation (in places well over 1000 mm) are found along the western and eastern coasts and on the islands and peninsulas of Eurasia and North America.

cyclones) are formed above the land masses, convective showers frequently bring much larger amounts of rain (= zone of continental summer rain).

A large amount of the precipitation falls as *snow*, but rain probably accounts for an even larger proportion. The snow cover in winter is deeper (30 to 100 cm) than in the tundra, but the duration, 6 to 7 months, is shorter.

In mid-summer, when the canopy area of the forest heats up considerably and the relative atmospheric humidity drops sharply, *evapotranspiration* can exceed precipitation for 1 or 2 months. However, the moisture deficit usually remains small (since, at the given temperatures, the atmospheric saturation deficit is never very high) and plants are most of the time able to meet their water requirements from the water stored in the soil.

Radiation and Heat Balance. The 150 to 300×10^8 kJ ha^{-1} of solar energy received during the growing season – which is maximally twice as long as in the tundra – is also about twice as high as the amount of radiation reaching the tundra region.

During the growing season, the days are long or daylight is even permanent. As in the tundra, this makes up, if only briefly, for some of the disadvantages stemming from the weaker intensity of solar radiation (as a function of time) compared to areas at lower latitudes. For example, in June, the incoming radiation reaches its highest level of about 60×10^8 kJ ha^{-1}, which is similar to the quantities received in more southerly areas at the same time (Fig. 2b).

Nonetheless, the air temperature remains lower than in regions to the south because, as also (and to a greater extent) happens in the tundra, large amounts of radiation are reflected during the long period of snow cover and are later lost as latent heat when the meltwater evaporates.

The main disadvantage, however, is that the period with high global radiation and a positive radiation balance is relatively short, whereas the heat energy needed to warm up the water-saturated soil (before and after thawing) is exceptionally high due to its high specific heat and high thermal conductivity.

3.2.3 Relief and Hydrology

Landforms

As in the Polar/Subpolar Zone, large areas of the Boreal Zone consist of ancient shields and platforms (Baltic Shield, Siberian Platform, Canadian Shield) which have not undergone any orogenetic changes since the Early Paleozoic. As a result, denudation processes were able to continue unhindered for several hundred million years and to cause extensive planation of surfaces close to sea level. Some of the more significant exceptions are the alpine (Upper-Cretaceous/Tertiary) mountain chains of the North American Rocky Mountains and of eastern Siberia, and the Variscan (Late Paleozoic) folded ranges of the Urals.

As in the case of the polar and subpolar regions, large areas of the Boreal Zone were exposed to the repeated passage of glacial ice during the cold phases of the Pleistocene (Siberia is the only exception). This resulted in large areas being covered with deposits from glaciers (subglacial and terminal moraines) or from meltwater streams (outwash plains, fine lacustrine sediments), and in a great number of erosional (glacial and fluvioglacial) landforms. The current surface, as regards form and material, is thus mainly the result of relatively recent developments (e.g. maximum soil age = about 12 000 years).

Freeze-Thaw Processes and Their Forms. Large portions of the Boreal Zone in Eurasia lie in regions of continuous permafrost and (almost) all other areas – there as in North America – belong to regions of at least sporadic permafrost (Fig. 20). This means that the Boreal Zone also belongs to the *periglacial* region and that freeze-thaw processes still play an important role here (Fig. 48). Widely found periglacial forms include palsas, string bogs, hummocks and thaw lakes (alases). Patterned ground is much less common than in the tundra and frost debris zone.

Palsas and earth hummocks have already been described in the chapter on tundras (cf. Chap. 3.1.3). *String bogs* (string mires, aapa fens, muskegs) are limited to the Boreal Zone. These are oligotrophic mires with gently sloping surfaces on which long, narrow ridges (strings) of peat (moss) and dwarf shrubs form striped and sometimes reticulate patterns, both of which are much more irregular than those found in patterned ground. The lower-lying areas (depressions) in between usually contain shallow ponds. The origin of string bogs is not well known. Solifluction, frost heaving and frost thrusting are likely to be processes of major importance. The ridges, which run in loops perpendicular to the slope, are probably the result of soil flow between the frozen ground and the vegetation cover.

Alases are round to oval thermokarst depressions (see also Chap. 3.1.3.2) with steep banks, often several kilometres in diameter, which are formed due to the (patchy) thawing of ground ice (e.g. ice wedges) and the accompanying downward degradation of a generally flat permafrost surface (Fig. 49). Many of these thaw basins contain shallow pools (thermokarst lakes).

Alases are frequently found in areas of sporadic or discontinuous permafrost where fossil ground ice or ice-rich permafrost melts. In areas of continuous permafrost their development may start with collapsed pingos (in the frost debris zone only), or with forest fires or forest clearings disturbing the thermal equilibrium of the permafrost. Closed stands of trees have an important buffer effect on the air temperature below their canopies and on the near-surface soil temperature (Haag and Bliss 1974), mainly because they prevent the solar radiation from reaching the ground (Fig. 50) and they stabilize the temperature stratification within the stand: while relatively large amounts of solar energy are absorbed by the forest canopies, where correspondingly the temperatures may rise considerably, only a small amount of energy is transferred (by radiation as well as by heat conduction) to the shady ground for warming up the soil and evaporating the meltwater; thus the summer thaw layer of permafrost remains shallow.

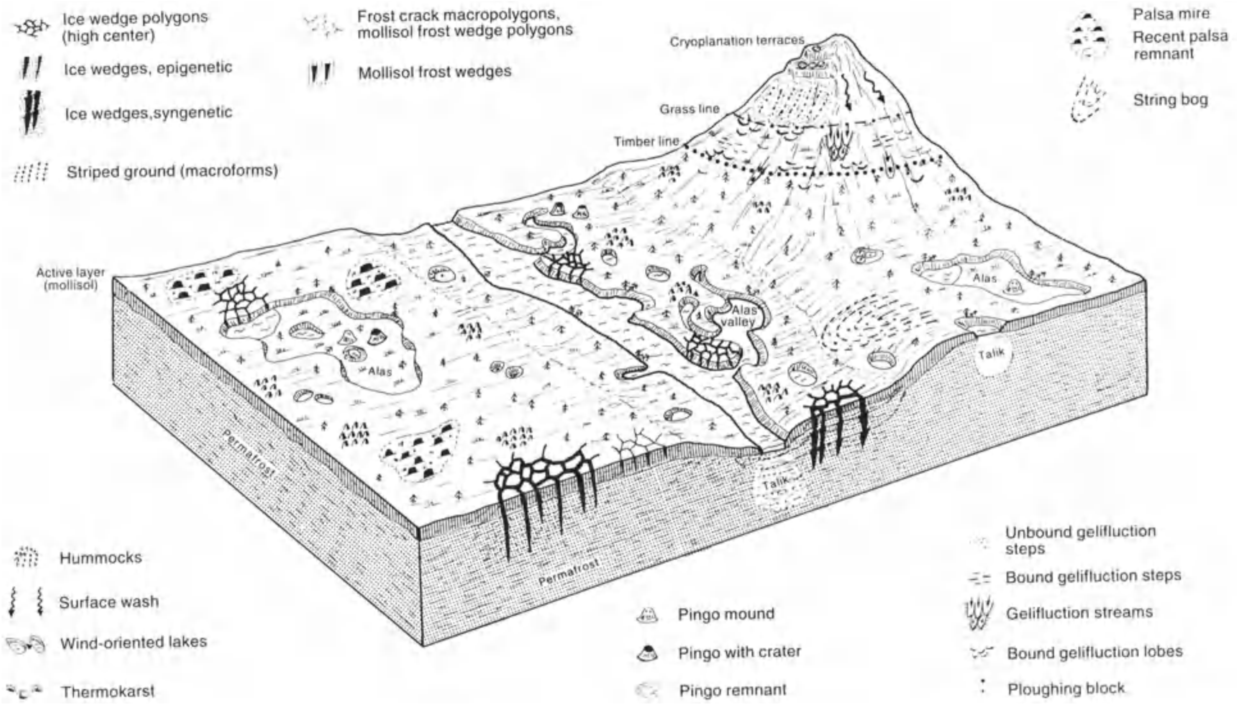

Fig. 48. Schematic block diagram showing characteristic landforms of the boreo-periglacial morphogenetic zone. (Karte 1979)

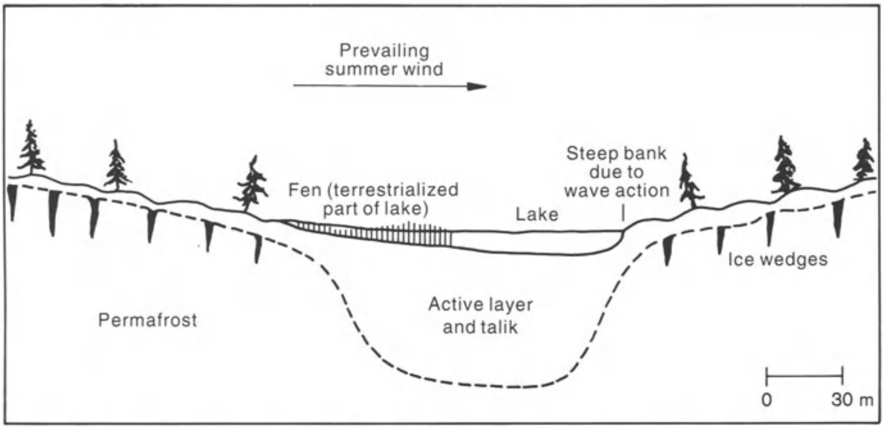

Fig. 49. Thermokarst depression (with thaw lake). (Butzer 1976). Subsidence of the terrain is connected with locally intensified thawing processes

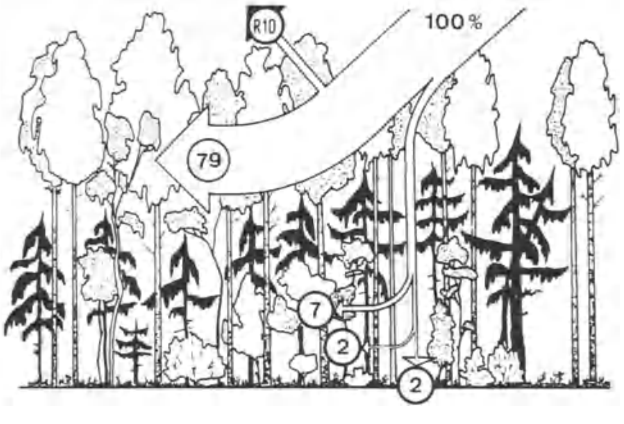

Fig. 50. Radiation distribution in a boreal birch/spruce mixed forest. (Cernusca 1975). By far the largest amount of the short-wave radiation is absorbed by the tree crowns (79%). Only about 10% remains for the low-growing vegetation. Radiation reflected from the stand surface ranges from 10 to 20% (10% in this case)

If, however, the forest is removed, radiation absorption is transferred to levels near the ground or to the soil itself, thus creating drier and warmer conditions there[14]. The direct result is an increase in the depth of the thaw layer. Provided the frozen ground is ice-rich or contains segregated ice, this will lead to the

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[14] This holds true even when it is remembered that there is an increase in reflection losses after forest clearing; investigations by Rouse 1977 near the timber line in northwest Canada showed that the light absorption dropped by 10–15%.

subsidence of the ground surface. The inflow of meltwater will then intensify the thawing process through increased heat transfer (heat stored in the water) which, in turn, will deepen the thermokarst depression, i.e. once formed, the pools steadily enlarge themselves. This process may be further accelerated by the intensified decomposition of soil organic matter resulting from deeper thawing (Heal et al. 1981, p. 629).

The situation is reversed when the thaw lake becomes filled up with sediments or is drained. The vegetation cover which then forms increasingly insulates the ground from insolation. As a result, there is a renewal of permafrost aggradation which, on excessively ice-rich ground, will cause the surface to bulge and eventually (in frost debris zones only) to form pingos (thaw-lake cycle; see Chap. 1.3.2).

Runoff

The density of rivers is usually high. The discharge undergoes tremendous seasonal changes (Table 17). Extreme runoff peaks occur in April and May, when all the snow melts within a few weeks and the meltwater flows off even from gentle slopes, over the frozen ground, and collects in the valleys. There it overflows the at first still frozen river beds, and "epigenetically" seeks new beds. As a result, and also because the non-cohesive material of the river banks crumbles easily when it is undercut, the rivers often change their courses, thus forming braided streams on broad valley floors which the floodwaters temporarily turn

Table 17. Runoff regimes of Eurasian rivers in the Boreal Zone. (Keller 1961)

	Monthly runoff coefficients[a]		
Month	Volga near Tscheboksary 1876–1932	North of Dvina near Ust-Pinega 1877–1930	Ob near Salechard 1877–1935
Jan.	0.415	0.31	0.36
Febr.	0.326	0.249	0.32
March	0.31	0.219	0.26
April	1.99	0.675	0.24
May	4.36	4.09	0.84
June	1.23	2.13	2.74
July	0.61	0.84	2.46
Aug.	0.49	0.658	1.98
Sept.	0.53	0.718	1.02
Oct.	0.57	0.908	0.84
Nov.	0.62	0.766	0.56
Dec.	0.52	0.438	0.36

[a] $= \frac{\text{Mean monthly runoff}}{\text{mean annual runoff}}$

into wide valley lakes. The valley cross sections are often asymmetrical; due to more active solifluction, slopes with southerly exposure are planated to a greater extent than north-facing slopes.

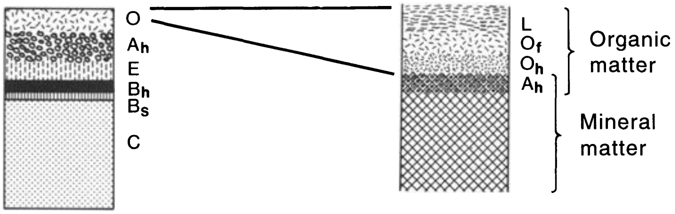
After the snow melt is over, the runoff quickly subsides. Summer rains, which in themselves are not very productive, contribute little to the runoff, since during this period most of the rainwater is evaporated or transpired. It is not until autumn, when lower air temperatures lead to a drop in evapotranspiration, that precipitation gains the upper hand and the water level in the rivers rises again slightly. However, as soon as the winter snows begin, the contribution to runoff quickly approaches zero. Since the rivers are now fed only by groundwater, their runoff declines again until just before the snow melt in the following spring, when it reaches its minimum (Table 17).

Lakes and swamps are conspicuously numerous in the Boreal Zone, due to several factors, e.g. (1) the climate is exceptionally humid despite low precipitation, (2) large areas of the surface are flat or plateau-like, (3) the frozen substrate and bed rock act as water barriers, and (4) great numbers of glacial or periglacial basins (e.g. thaw lakes) are present.

3.2.4 Soils

Raw Humus. The slow decomposition of coniferous needles and of the ericoid leaves of many dwarf shrubs (e.g. of *Calluna*, *Vaccinium*, *Erica*, *Andromeda*), combined with the high acidity of litter and mineral soils, and the fact that conditions for at least a large part of the year are cold and wet, explain why huge litter layers are formed in this zone. Long-term waterlogging (saturation by surface water or groundwater) leads to the formation of *peat*, otherwise *raw humus* is formed. Due to the low rate of mineralization, both types of humus are extremely low in plant nutrients and usually lie on top of the mineral soil without being mixed in with it. In raw humus, usually up to three subhorizons are distinguished according to the grade of decomposition and humification (Fig. 51).

Podzolization. Litter is broken down chemically and, perhaps less often, biotically; in the latter process, it is mainly due to the action of fungi, frequently mycorrhiza. The humic substances (fulvic acids and fulvates) formed during decomposition in acidic environments are of low molecular weight and water-soluble; they are readily carried downwards by percolating water and then precipitate out (are "immobilized") in a deeper layer. Iron and aluminium oxides formed in the process of silicate weathering migrate together with the organic compounds. Leaching of the humic substances and sesquioxides leads to the formation of an ash grey *bleached* or *eluvial horizon* (= albic E horizon) 20 to 60 cm thick, just below the blackish grey, organic surface horizons, and above an approx. 10–30 cm thick *illuvial horizon* in which these substances accumulate (= spodic B horizon of the FAO-UNESCO Classification). The upper section of this layer



O : acidic raw humus (developed on top of mineral soil): usually present in thick layers and differrentiated into L, O_f and O_h horizons (see Chap. 2.5.2)

L : litter

O_f: organic horizon, poorly decomposed

O_h: organic horizon,moderately decomposed

A : mineral topsoil containing strongly decomposed organic matter

E : pale (bleached) eluvial horizon: albic E horizon, from which humic substances, iron and aluminum have been removed

B_h: blackish illuvial horizon (in which humic substances have accumulated)

B_s: brownish illuvial horizon in which Fe and Al oxides (sesquioxides) have accumulated

Spodic B horizon, may be continuously cemented (Ortstein) by a combination of organic matter with iron

C : parent rock (e. g. glacial sands)

Fig. 51. Schematic of a podzol profile. (Schroeder 1992, pp. 47 and 99)

is usually brown-black in colour (B_h horizon), changing to rust brown (B_s horizon) with increasing depth. Parts of the B horizon may be continously cemented by a combination of organic matter with iron or aluminium or with both (Fig. 51). This hardpan (ortstein) seldom acts as a barrier for percolating water, because a large number of coarse pores usually remain, but it may hinder root development.

The leaching and accumulation of humus and sesquioxides, as described here, are referred to collectively as podzolization and the soil type resulting from it as *podzol.*

Podzols are the predominant and thus highly characteristic (zonal) soil type of the Boreal Zone. The main distribution areas include northern Europe and western Siberia, central and eastern Canada and a broad zone along the Pacific from Canada to Alaska. The only notable occurrence of podzols outside the Boreal Zone is found in some areas of the Humid Mid-Latitudes adjoining to the south, namely in coastal regions of northwest Europe and North America, where pronounced maritime (= cool humid) climates are combined with poor sandy soil substrates (probably for the most part Early Pleistocene). True podzols are found only rarely in the tundra.

The *fertility* of podzols is low. Their unfavourable characteristics include a strong acidic soil reaction, low exchange capacity and base saturation, as well as the single-grain structure of the A horizon and the formation of hardpan in the B horizon (Fig. 52). Podzols can, however, be used agriculturally (this is practised already in many areas) provided fertilizer (which also raises the soil

	Podzol	**Eutric cambisol (brown earth)**	**Chernozem (black earth)**
Clay (%)	4.5	16	18
Organic matter (%)	6	3	7
pH (Ca Cl_2)	4.2	6.1	7.0
Saturation (%) with Ca, Mg, K, Na, and (H+Al) ions (area of circle equal to magnitude of CEC)	Mg+K(3) Ca(23) H+Al (74)	Mg(6) K+Na(5) Ca (64) H (25)	Ca (9) Mg+K+ Na(8) H(1)
CEC [cmol(+) kg^{-1}]	12	18	28
Base saturation (%)	26	75	99

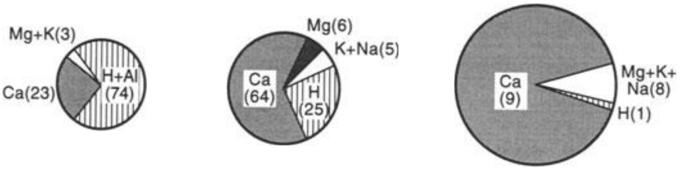


Fig. 52. Cation exchange capacity (CEC), type of cations absorbed and base saturation [= extent to which the exchange complex is saturated with basic (= mainly nutrient) cations] of a podzol in comparison to a eutric cambisol and a chernozem. (Schroeder 1984). The podzol is the least favourable of the soils in all respects: its CEC is one-third smaller than that of the cambisol and less than half that of the chernozem; and only a quarter (26%) of the CEC is saturated with basic ions; i.e. in the podzol only 3 mol(+) kg^{-1} are attributed to nutrient ions. In the case of the cambisol, this value amounts to 13.5 cmol(+) kg^{-1} (three-quarters of 18) and in the case of the chernozem to 28 cmol(+) kg^{-1} (almost the entire CEC). This means that the cambisol has about four times and the chernozem about nine times as many exchangeable nutrient cations as the podzol. The relatively large amount of organic matter present in the podzol, 6% as compared to 7% for the chernozem and only 3% for the cambisol, does not represent an advantage; it is present in the fairly useless form of undecomposed raw humus on top of the mineral soil

pH) is generously applied, and the hardpan layer, if it is not at least 80 cm below ground level, is broken up. Supplementary irrigation might also help to increase yields, because the natural ability of these sandy soils to retain water is very low and there is a danger that they will dry out after only brief periods without rain.

The limits on agricultural activity in the Boreal Zone are thus attributable less to the lack of fertility of the soil than to the short duration (and in maritime regions to the coolness) of the growing season.

Other Soil Types. In the notably continental regions of central and eastern Siberia and the Canadian Rocky Mountains, on the other hand, *cambisols* predominate; in permafrost areas they occur in the form of gelic cambisols, otherwise as dystric or (less frequently) eutric cambisols.

In mountainous areas (gelic) *leptosols* predominate (probably also in most of those regions where gelic regosols are indicated on The World Soil Map), whereas in lowland regions mainly gelic (extensively in western Siberia and some parts of central Canada) or fibric (outside the permafrost region) *histosols* (see Chap. 3.2.5 on bogs) and gelic or dystric *gleysols* occur. A relief sequence (catena) showing some of these soil types is presented in Fig. 53.

In a few southern regions of the Boreal Zone, especially in transitional areas leading to the Humid Mid-Latitudes, podzols and cambisols are replaced by *podzoluvisols* or *albic luvisols*. Both have a whitish grey albic E horizon from

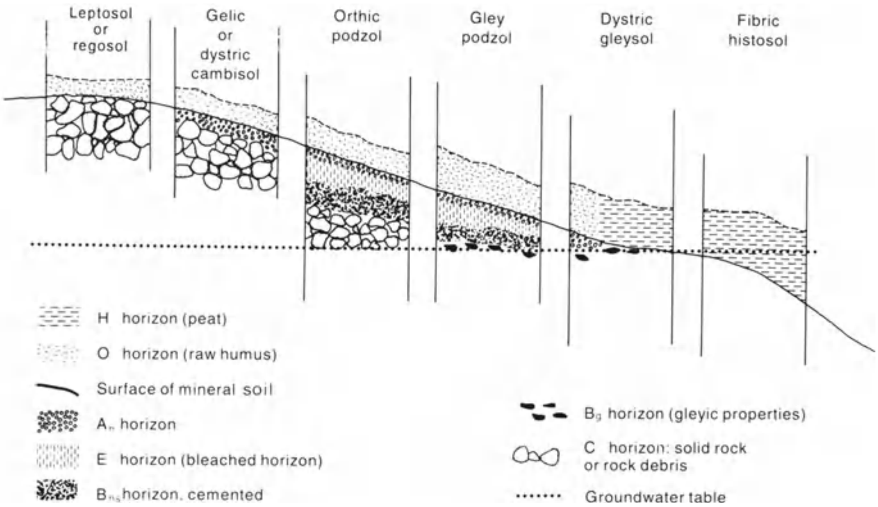


Fig. 53. Relief sequence (catena) of soil units in the Boreal Zone. (Larsen 1980)

which clay and free iron oxides have been removed, overlying an argic B horizon. Podzoluvisols (German name Fahlerde or pale earth) are characterized by the E horizon tonguing deep into the B horizon.

Of the various forms of podzoluvisol, the *eutric* types – like the "true" luvisols – have a base saturation of at least 50%, whereas the dystric types have a base saturation of < 50%. These latter types, as well as the gleyic types, have been included in the soil zone map as part of the *podzol-cambisol-histosol zone*; on the other hand, the eutric types, which represent the most southerly occurrences of podzoluvisols, have been included in the haplic luvisol zone (which is more typical of the Humid Mid-Latitudes.

Similar to the podzols, all other soils in the podzol-cambisol-histosol zone exhibit a considerable lack of fertility.

3.2.5 Vegetation and Animal Life

3.2.5.1 Structural Characteristics

The Boreal Coniferous Forest

Conifers. The boreal coniferous forest (taiga, taiga-type forest) has survived in many areas. The tree layer is dominated by spruces (*Picea* spp.), pines (*Pinus* spp.), larches (*Larix* spp.) and firs (*Abies* spp.), and often thousands of square kilometres are dominated by only a single species of these genera. The deciduous larches are concentrated mainly in extremely continental areas of eastern Siberia, where the annual temperature range is as much as 100 °C. There are huge stands of *Larix dahurica* in this region ("light taiga"), and together with *L. sibirica*, these trees represent the polar tree line throughout Siberia. The main distribution areas of other species of conifer are shown in Table 18. See Fig. 54 for the polar tree line of the four conifer genera referred to above.

In contrast to the firs and spruces in the cool temperate climates, boreal conifers, with crown heights between 15 and 20 m, are smaller and characterized by a more slender form; the latter is not the result of adaptation to heavy winter snow loads but rather the result of difficult growth conditions. The *evergreen* conifers (all except *Larix* spp.), whose cold-resistant xeromorphic needles remain on the tree for at least 2 years, have the advantage over deciduous trees that their photosynthetic apparatus is already fully developed at the start of the brief summer growing season. In addition, their assimilation organs make up 4 or 5% of their total mass (dry mass), a proportion which is more than twice as high as in the case of deciduous broadleaf trees in the Humid Mid-Latitudes (Larcher 1984); at 7–8 $m^2 m^{-2}$, their leaf area index is also relatively high (Reichle 1981, p. 31 gives $7.6 \pm 0.42\ m^2 m^{-2}$ as the mean LAI for nine boreal coniferous forests).

Broadleaf Winter-Deciduous Trees. The predominance of conifers cannot be fully explained on the basis of their "superiority", since broadleaf and mesophyl-

Table 18. Chief tree species of boreal forests. (Hare and Ritchie 1972)

Genus	North America 55° W–160° W	Northern Europe 5° O–40° O	Western Siberia 40° O–120° O	Eastern Siberia 120° O–170° O
Conifers				
Picea (Spruce)	*glauca* *mariana*	*excelsa*	*obovata*	*obovata* *jezoënsis*
Abies (Fir)	*balsamea*	–	*sibirica*	*nephrolepis* *sachalinensis*
Pinus (Pine)	*divaricata*	*silvestris*	*sibirica* *silvestris*	*silvestris* *pumila* *cembra*
Larix (Larch)	*laricina*	–	*sibirica* *sukachzewskii*	*dahurica*
Broadleaf winter-deciduous trees				
Populus (Poplar)	*tremuloides* *balsamifera*	*tremula*	*tremula*	*tremula* *suaveolens*
Betula (Birch)	*papyrifera* *kenaica*	*pubescens* *verrucosa*	*verrucosa* *pubescens*	*ermani*
Alnus (Alder)	*tenuifolia* *crispa* *rugosa*	*incana*	*fruticosa*	*fruticosa* *Alnaster kamschatica*
Salix (Willow)	spp.	spp.	spp.	spp. *Chosenia macrolepis*

Fig. 54. Limits of polar distribution for the conifer genera *Picea* (spruce), *Abies* (fir), *Pinus* (pine) and *Larix* (larch). (Hare and Ritchie 1972)

lic (even though mainly small-leaved) deciduous trees are present in all areas and, in northern Europe, even represent the most northerly occurring specimens of tree. The more common deciduous trees include birches (*Betula* spp.), poplars (*Populus* spp.), willows, (*Salix* spp.), alders (*Alnus* spp.) and ashes (*Fraxinus* spp.) as well as numerous species of dwarf shrub.

Many shrub species produce berries, for instance *Sorbus* (rowans) and *Viburnum* and the dwarf shrubs *Vaccinium* (e.g. cranberries and blueberries), *Empetrum* (crowberries), *Fragaria* (wild strawberries) and *Rubus chamaemorus* (cloudberries). These fruits play an important role in the diet of several animal species; some of them are also edible by humans.

Life Form Spectra and Flora. Aside from the dwarf shrubs named here, and a few others as well, the forest floor is covered mainly by lichens and (in denser tree stands) by mosses. Table 19 shows a typical life form spectrum. An obvious difference in comparison to other ecozones is that, although the proportion of hemicryptophytes is somewhat lower than in the tundra, it is still very high at >50%. Chamaephytes and cryptophytes are also present in large percentages, the number of tree species, on the other hand, is low.

Table 19. Life form spectra (proportion of species in %) of the boreal coniferous forest and other plant formations. (Strasburger et al. 1983)

Zonal plant formation	Phanerophytes	Chamaephytes	Hemicryptophytes	Cryptophytes	Therophytes
Tundra	1	22	60	15	2
Boreal coniferous forest	10	17	54	12	7
Temperate winter-deciduous forest in the Humid Mid-Latitudes	54	9	24	9	4
Tropical rain forest	96	2	–	2	–

All plant communities in the boreal coniferous forest are species-poor (although more species are found here than in most tundra communities). Most plant genera have circumpolar distribution. The similarity in flora between the various regions is significantly greater than would be expected solely from the fact that they all belong to the floral kingdom of Holarctica.

Changes over Time. On a small scale, great changes can occur in the appearance of the boreal coniferous forest, depending on the *stand age.* In most areas, local forest fires, insect damage, windthrow or flooding prepare the way for forest development (successions) to start again and thus for a broad variety of young, mature and old age phases which differ physiognomically and, to a lesser extent, also floristically, to be juxtaposed with one another. While the stands of different ages constantly change their position within the vegetation mosaic, the overall ecosystem remains stable for thousands of years (Tischler 1984, p. 141).

Fire is the most important of the causes of newly initiated successions. It has been estimated that each section of the forests in Alaska burns down once every 100 to 200 years, and in areas with large numbers of black spruce, as often as every 50 years (Viereck et al. 1986, p. 41). Today, most forest fires are started by man. Before the turn of the century, when lightning was practically the only cause of fire, such conflagrations were much less common. Forest fires accelerate the recycling of nutrients, which under normal conditions occurs very slowly, and in this sense they are usually welcome (see below). Sometimes they are set intentionally for the purpose of rejuvenating a forest.

Mires

Aside from coniferous forests, low nutrient status mires, especially peat bogs, are one of the most characteristic components of the vegetation cover in the Boreal Zone. Although such mires are also found in other regions, such as in parts of the Humid Mid-Latitudes with a maritime climate, in the tundras and at moist, high-altitude locations in many mountain ranges, nowhere are they more prevalent (omnipresent) than in the Boreal Zone. In some regions they account for 50% and more of the surface area, such as in western Siberia and in large sections of northern Europe.

The particularly favourable conditions in the Boreal Zone for the *formation of peat* are due, on the one hand, to the relatively high primary production as compared to the tundra and, on the other hand, to the inherent slow rate of litter decomposition as compared with warmer ecozones, due to widespread waterlogging in summer (often above permafrost), the low soil and water temperatures in summer and the long frost period in winter, the general lack of nutrients, and the strong acidity of the soil, rocks, lakes and rivers. All these factors severely suppress the activity of bacterial decomposers. In extreme cases, the pH in raised bogs can drop to between 2.5 and 3.5, i.e. lower than in any other soil substrate.

The formation of peat, in turn, helps to delay the runoff of meltwater and rainwater, thus creating a kind of self-reinforcing effect for the further growth of peat layers. The ability of the major participants in peat formation, namely sphagnum mosses, to store water (sponge effect) can allow growth to continue well above the level of the original water table or waterlogging, and can thus result in the formation of raised bogs (whose nutrients are solely supplied by atmospheric inputs, i.e. mainly by rainfall = ombrotrophic).

Peat bogs are poor in *flora*; only a few species of mosses, grasses and dwarf shrubs, and sometimes also of trees, are found here. As in the case of forest undergrowth, most of the species are hemicryptophytes (here mainly sedges) and chamaephytes; their appearance can be somewhat similar to that of dwarf shrub tundras on acidic soil.

Mires can be classified according to different criteria. Table 20 presents a classification based on the varying amounts of nutrients available to plants (trophism). For the Boreal Zone, oligotrophic and mesotrophic mires are the most frequent. Together (as a group), they can be further subdivided according to their shape into bogs (Hochmoore) and fens (Niedermoore), or, for example, into raised bogs,

Table 20. Mire classification based on chemical properties. (Botch and Masing 1983)

	Ash content	pH	Proportion of the peat deposits in the former Soviet Union
Eutrophic mires (fens)	6–7%	5–7	35.4%
Mesotrophic mires (intermediate types)	4–6%	4–5	18.0%
Oligotrophic mires (bogs)	2–4%	2.5–3.6	46.6%

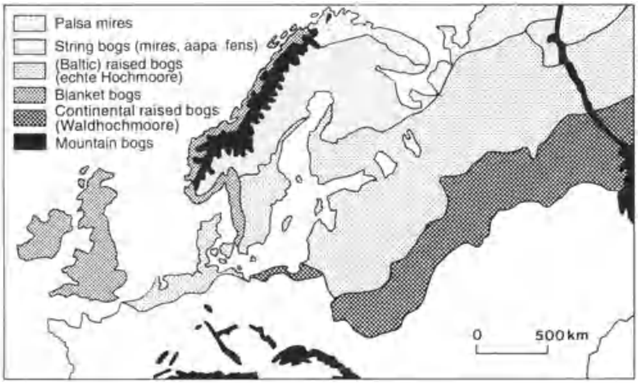


Fig. 55. Distribution of mire types (according to shape) in northern Europe. (Walter 1990)

blanket bogs (upland raised bogs), string mires (aapa fens) and palsa mires. The distribution of these latter types of bogs in Eurasia is as follows:

Blanket bogs are found only in extremely maritime climates, including those of the Humid Mid-Latitudes (British Isles, coastal areas of southern Norway); *true (or Baltic) raised bogs* occur in the somewhat less maritime climates of northwestern Germany and Denmark and in the entire central belt of the Boreal Zone extending right across Eurasia; *continental raised* (wooded) *bogs* are found in the southern belt whereas *string mires* (see Chap. 3.2.3) are distributed north of the raised bog zone, particularly in Fennoscandia and western Siberia. *Palsa mires* are characteristic of the more northerly forest tundra (Fig. 55).

The formation of Holocene bogs in the Boreal Zone began at the earliest about 12 000 years ago after the Pleistocene ice cover had melted away. Mean annual vertical growth since that time has amounted to 0.2 to 0.4 mm in the case of palsa mires and 0.6 to 0.8 mm in the case of true raised bogs. The highest rates of growth, 0.8 to 3.0 mm per year, occurred during the Subatlantic climatic phase (since 500 B.C.), and the lowest, namely 0.2 mm, during the Subboreal climatic phase (about 3000–500 B.C.) (Botch and Masing 1983, p. 101).

Polar Tree Line, Forest Tundra

Boreal coniferous forest and tundra gradually merge into one another. In general, the transition covers a latitudinal zone of more or less 100 km in N-S extension. The somewhat contradictory term used for this zonal ecotone is *forest tundra.* It is either sparsely covered with trees, or tundra and forest combine to form a mosaic pattern, with the tundra fraction increasing in area towards the pole and the forest fraction increasing towards the equator (Fig. 56). The imaginary line connecting the northernmost trees or groups of trees is termed the *polar (or northern) tree line* (timber line), and the northern boundary of continuous forest is known as

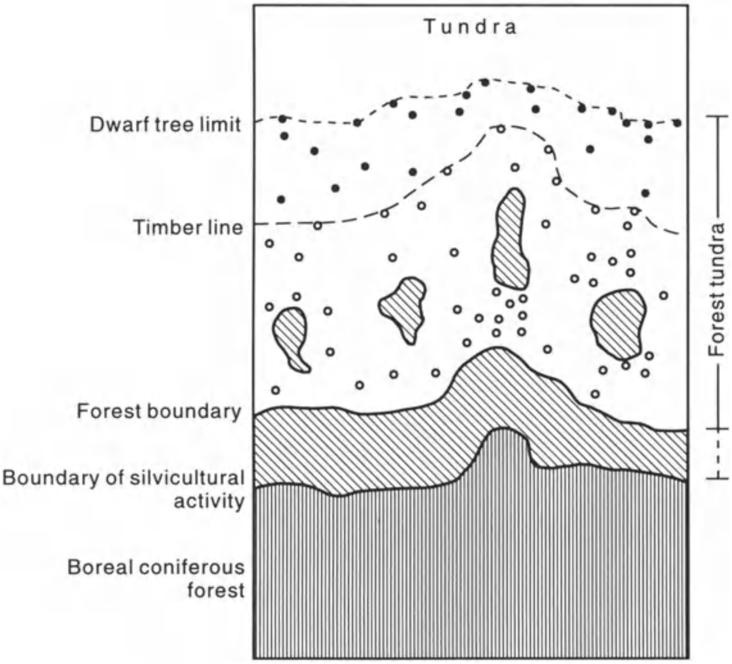


Fig. 56. Forest boundary and timber line in the transition zone between boreal coniferous forest and tundra. (Hustich 1953)

the *polar (or northern) forest boundary*. Conifers are the predominant tree type in the forest boundary belt; only in Scandinavia and Iceland do birches prevail.

The polar boundary for tree growth is not dependent on the degree of winter cold. The centre of lowest temperature (near Verkhoyansk) actually lies well within the borders of the boreal coniferous forest. The presence of permafrost is also of no importance (see Chap. 3.1.1). Instead, the determining factor is the duration and degree of warming during the summer: if the mean growing season drops to less than 3 months with $t_m \geq 5\,°C$ (or fewer than 105 to 110 days with a daily mean $\geq 5\,°C$), or if – in case this period lasts longer – it remains very cool (no month with $t_m \geq 10\,°C$), not even the best-adapted tree species have the chance to develop new shoots and assimilation organs to the point where they will be able to withstand the cold, dry winter to come, i.e. they dry out ("freeze"), and the minimal thermal requirements for generative reproduction, which are higher than for vegetative growth, are hardly satisfied anymore: in the forest tundra, tree seeds capable of sprouting generally can be formed only during summers with well above average temperatures; with increasing proximity to the tree line, the frequency of such exceptional summers approaches zero. As a result, the forest loses its *ability to rejuvenate*. Even south of the forest boundary and approximately down to the northern boundaries of exploitable forest, there are years in which generative reproduction is not possible.

Tree stumps in the tundra bogs are proof of the fact that, during the warmer postglacial period (Boreal: 7500–5500 B.C.), the forest boundary ran considerably farther north. At present, no clear trend for this boundary can be ascertained. In general, the forest in northern Europe is moving northward (Walter and Breckle 1986, p. 487); in northwest Canada, on the other hand, the tree line lies beyond the region where climatic conditions would allow natural reproduction of trees; it is thus a relict boundary marking an area where warmer conditions prevailed in earlier times (Elliot 1979).

The transitional forest tundra is generally considered part of the Boreal Zone, but at the same time it is grouped with the tundra to form the subarctic, which then represents the belt between the closed taiga and the frost debris zone (cf. Blüthgen 1970; Hustich 1979; Tuhkanen 1984 for discussions in defining arctic and subarctic boundaries).

In the more open forest tundra, redistribution by wind can cause considerable regional variation in the depth and thus the duration of *winter snow cover*. This plays a major role in the distribution of trees and other perennial life forms. Disadvantageous sites for plant growth include wind-exposed slopes, where winds remove the snow cover, and sheltered slopes and depressions, where large snow drifts develop. In the former case, the lack of snow cover means a loss of protection against springtime dry-out and mechanical damage by snow storms (the effect of both stress factors is evident from characteristic growth deformations such as *flat-topped growth forms*, cf. Fig. 57); in the latter case, the summer snow melt can be delayed for several weeks. In both cases, only dwarf shrubs, forbs and mosses can grow, whereas trees and patches of forest are found in areas with average snow cover or – regardless of the snow factor – on south-oriented slopes with more favourable temperature conditions.

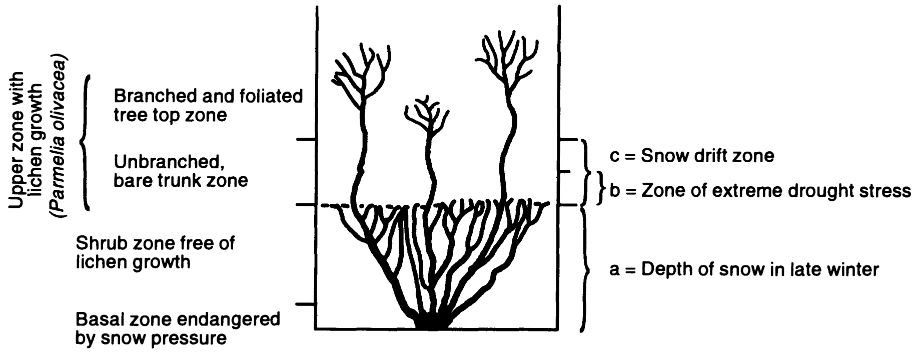


Fig. 57. Schematic of a flat-topped birch tree with a few trunks reaching higher up (candelabra effect). (Blüthgen 1960). The flat top corresponds to the snow surface in late winter. Only a few shoots manage to survive in the overlying zone where there is an extreme danger of snow drifting and of springtime dry-out (due to the relatively strong heating effect of insolation). At a certain point above the snow surface, these stresses ease off and the shoots can again branch as usual

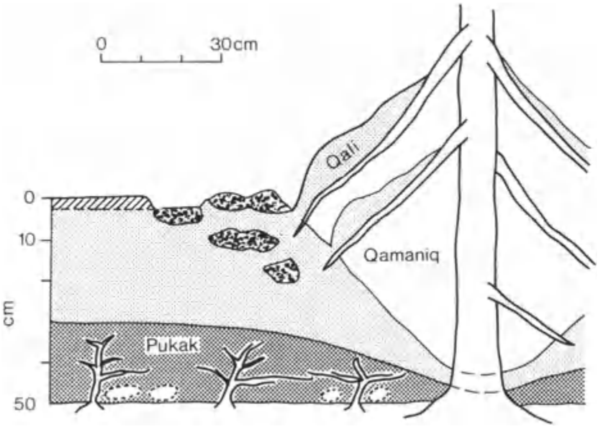


Fig. 58. Schematic representation of the snow profile near a spruce tree. (Venzke 1986). The snow cover is divided into new snow (*lightly hatched*), slightly packed old snow (*medium shaded*), and a "pukak" layer of metamorphosed snow crystals (*heavily shaded*) in which small non-hibernating mammals have dug tunnels. The snow cover underneath the branches is very thin, but that near the canopy drip area, where snow falls from the branches, is deeper

It is characteristic of forests that a great deal of snow remains on the tree branches, and some of it slides off laterally to the ground. This means that the snow cover under the tree crowns is relatively thin, whereas that in the canopy drip area is usually heavier than in open areas (Fig. 58).

3.2.5.2 Ecosystem Matter Reserves and Exchange Processes

Phytomass, Primary Production

In the northern areas of the boreal coniferous forest the *phytomass* is about 150 $\mathrm{t\,ha^{-1}}$ and in the southern areas it is about twice as high (in tree stands of comparable age) (Table 21). The N/S gradient reflects the improvement in climatic growth conditions (longer growing seasons with higher temperatures) with increasing distance from the pole.

In general, climatic conditions also control *primary production*, even though bottlenecks in nutrient supply may hinder growth at times. Averaged over several years, boreal forests produce between 4 and 8 $\mathrm{t\,ha^{-1}\,a^{-1}}$; the higher values are achieved on the warmer soils of slopes with a southern exposure (see Chap. 3.2.2) and in the warmer regions of the southern taiga.

Investigations conducted in the Alaskan "taiga" have shown that the production rates of tree stands vary by a factor of 12, the nitrogen requirement by a factor of 28, and the phosphorus by up to a factor of 50 (Heal and Vitousek 1986, p. 156).

Table 21. Relationship between phytomass and latitude in boreal coniferous forests and adjacent zonal plant formations. (Rodin et al. 1975)

Ecozone	Subdivisions	Phytomass ($t\ ha^{-1}$)
Polar/Subpolar Zone	Frost debris zone	5
	Tundra	28
Boreal Zone	Coniferous forest in the northern taiga on gleysols and podzols	150
	Coniferous forest in the central taiga on podzols	260
	Coniferous forest in the southern taiga on turf-podzolic soils	300
Humid Mid-Latitudes	Broadleaf winter-deciduous forest on greyzems	370–400

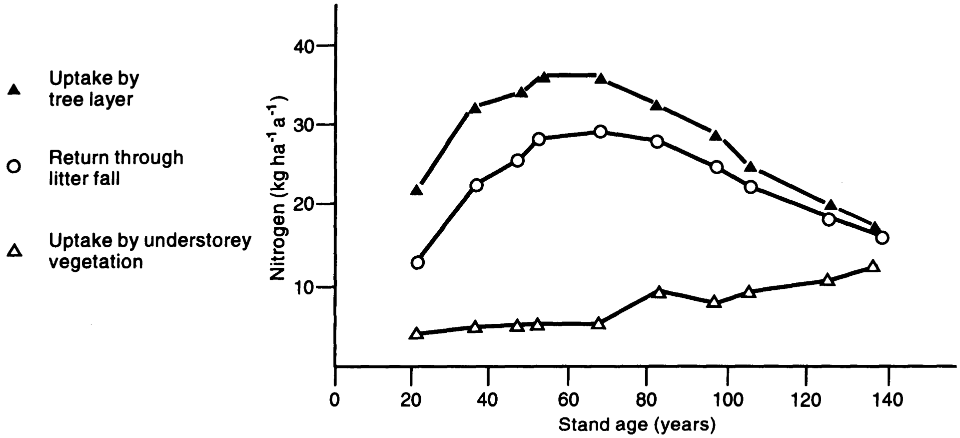


Fig. 59. Changes in nitrogen turnovers with increasing stand age in a boreal coniferous (*Picea abies*) forest. (Kazimov and Morozova 1973, taken from Cole and Rapp 1981). See text for explanation

Kazimirow and Morozova (1973) conducted investigations in Russian spruce forests (*Picea abies*) which showed that variations in production are to a large extent dependent on *stand age*. In a sequence of 22- to 138-year-old tree stands they found that the above-ground PP_N for the 68-year-old stand attained the highest value at $7.4\,t\,ha^{-1}\,a^{-1}$ (the nitrogen uptake was also at its highest level, namely $36.6\,kg\,ha^{-1}\,a^{-1}$), and then decreased again; the 138-year-old stand had a level of only $3.2\,t\,ha^{-1}\,a^{-1}$ (at a nitrogen uptake rate of only $17.3\,kg\,ha^{-1}\,a^{-1}$). On the other hand, the production of the forb/moss layer continued to increase even in the older stands (and its nitrogen uptake finally achieved a level almost equivalent to that of the tree layer; Fig. 59); this phenomenon was obviously favoured by the incipient thinning of the crown canopy in forests with increasing age: the leaf area index (only of the tree layer) for the 138-year-old forest was only 2.4 $m^2\,m^{-2}$ as compared to the maximum, 3.8 $m^2\,m^{-2}$, in the 68-year-old stand.

The (above- and below-ground) phytomass increased continuously with increasing stand age from 31 $t\,ha^{-1}$ in the 22-year-old stand to 162 $t\,ha^{-1}$ in the 68-year-old stand and 255 $t\,ha^{-1}$ in the 126-year-old stand; only in the 138-year-old stand was a slight decrease to 249 $t\,ha^{-1}$ observed.

Consumers

The continuous conifer stands in mature forest regions offer little food for herbivorous mammals and birds. Much more favourable conditions prevail in the early (juvenile) stages of successions, especially those rich in dwarf shrubs, birches and poplars (aspen), which develop in the aftermath of forest fires (see below). Also the plants growing along river banks, lake banks and at the edges of mires, are sources of a somewhat more abundant and varied food supply. In contrast to the steppes and savannas, however, the consumable matter production in all these places is still modest and the number of game animals is correspondingly low.

The most common animal species include moose, deer (e.g. Virginia deer and wapiti), bears, blue hares, beavers, wolverines, wolves and foxes; during the winter, reindeer and caribou are also found in the forest tundra. Poikilothermic land vertebrates (reptiles and amphibians) are rare.

The long and extremely cold winters in this zone require special *adaptations:*

- Most invertebrates and many vertebrates take long rests in winter (diapauses) by adopting a state of torpor (in the case of many arthropods) or by hibernating (in the case of bears).
- Many mammals and insectivorous birds move to warmer regions in the fall and do not return north until the following spring (migration strategy).
- Herbivorous birds and mammals which remain active in the zone during winter profit from the preservation of their food by freezing (e.g. fruit) and from the protection against cold provided by the (long-lasting) snow cover (Fig. 60).

As in the tundra, many animal populations undergo *cyclic changes*: In the case of waxwings, crossbills, jays, squirrels, red-backed voles and lemmings, for example, years in which a good crop of seeds is produced are followed by notable increases in population size. As a consequence, the number of carnivores, such as martens, weasels, buzzards and hawks, which live on these herbivores, increases as well. As the herbivore population decreases, the number of scavengers also drops to its original level.

With the exception of these population peaks, the number of consumers present is insignificant. This applies not only to mammals and birds but also

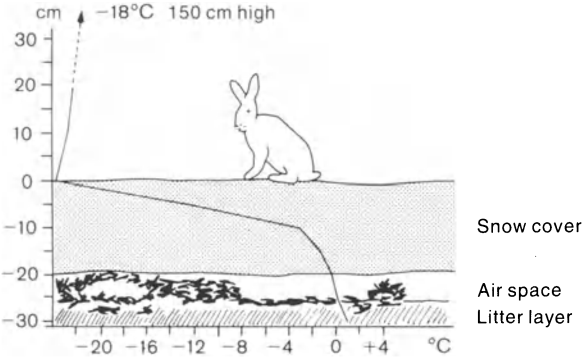


Fig. 60. Ecological importance of snow cover in the taiga. (Coulianos 1962, taken from Tischler 1984). Snow provides protection from the cold, allowing many animals to lead an active life during the winter, both above ground and in the soil

to the invertebrates. The Boreal Zone has the lowest ratio of heterotrophs to total biomass of all the ecozones.

Litter Accumulation and Decomposition

The small number of animals, coupled with the acid soil conditions (similar to the tundra), the relatively non-decomposable plant material (high proportion of resinous needles in the above-ground wastes), and the long winters, all result in a very long mean time between the formation and decomposition of organic substance. Cole and Rapp (1981, p. 357) give 353 years as the time it takes for litter to decompose in boreal coniferous forests (this is the mean value for three forested areas investigated in Alaska). This period is about 20 times as long as in the coniferous forests at our latitude and almost 100 times longer than in our broadleaf deciduous forests (see Chap. 3.3.5). The numerous dead trees in older boreal forests, which stand as bizarre ruins, bare and white, among the living trees or lie scattered over the ground, practically undecayed, are obvious indicators of the extremely slow decomposition of the necromass; almost equally obvious is the *litter layer* on the ground, which is up to half a metre thick and only slightly decomposed (this is the only ecozone in which litter layers of such thickness are found). Litter reserves in older stands can reach levels of up to $1000 \mathrm{t\,ha^{-1}}$ before an equilibrium is established between input and decomposition (at an above-ground phytomass of about $300 \mathrm{t\,ha^{-1}}$) (Fig. 61). Over the long term, namely over several forest generations, however, the mean value for the amount of litter present drops to probably about 50 to $150 \mathrm{t\,ha^{-1}}$ (which is still a considerable quantity).

Some investigations quote significantly higher values for the amount of *humus* than for the amount of litter (e.g. Reichle, 1981). Probably this is because they draw different boundaries between humus and litter; for instance, the O_h horizon (and perhaps also the O_f horizon) might have been considered part of the humus (see Chap. 2.5.2.3). These uncertainties should also be taken into account when

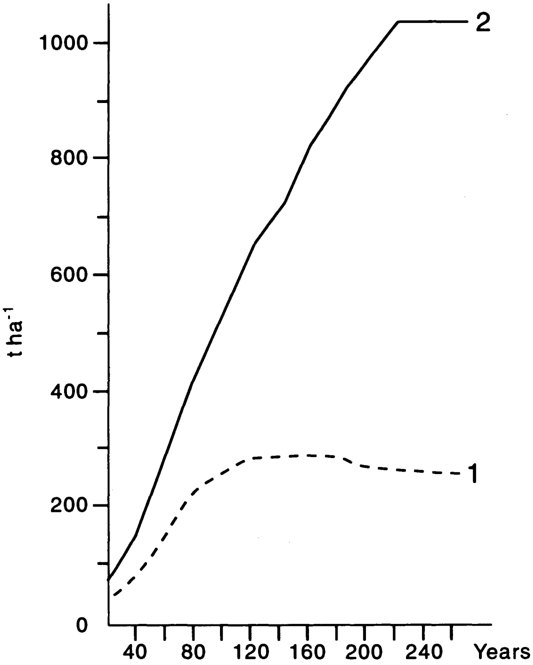


Fig. 61. Changes in phytomass (*1*) and amount of litter (*2*) with increasing stand age in boreal coniferous forests. (Walter and Breckle 1986). The extremely low rate of decomposition leads to the accumulation of litter over several decades until, when a very high level is reached (in this example, at 1000 t ha^{-1} after 200 years), an equilibrium is established between input and decomposition. The increase in phytomass ceases much earlier and at a much lower level (in this example, at 300 t ha^{-1} after 120 years)

comparing this zone with the tundra. As in the boreal coniferous forest, the accumulation of organic material preferably takes place on top of the mineral soil in the form of a rather weakly decomposed and humified organic horizon, which sometimes is classified as a litter layer on top of the soil (proper) and sometimes as raw humus, i.e. as part of the soil.

The uncertainty about what is humus or litter does not exist, however, when the organic layer is peaty, i.e. has been saturated with water for prolonged periods. In this case, it is always considered as properly part of the soil (H horizon). This difference in definition could by itself explain why the tundras are frequently reported to have higher humus contents, whereas the boreal forests are usually found to have higher litter contents: in the first, water saturation and thus peaty properties prevail much more frequently, whereas the organic horizons of the latter are normally well drained.

The slow decomposition of dead organic material gives rise to large amounts of bound nutrients; the formation of peat even removes some of them permanently from the cycling. Particularly affected are the reserves of nitrogen and calcium, and to a lesser extent those of potassium (Fig. 62). Cole and Rapp (1981) found that in boreal coniferous forests the *residence time* for nitrogen in litter and humus was 64 times longer than in mediterranean sclerophyllous forests, 42 times longer than in temperate deciduous forests and 13 times longer than in temperate coniferous forests. The differences were even greater for other elements (except potassium).

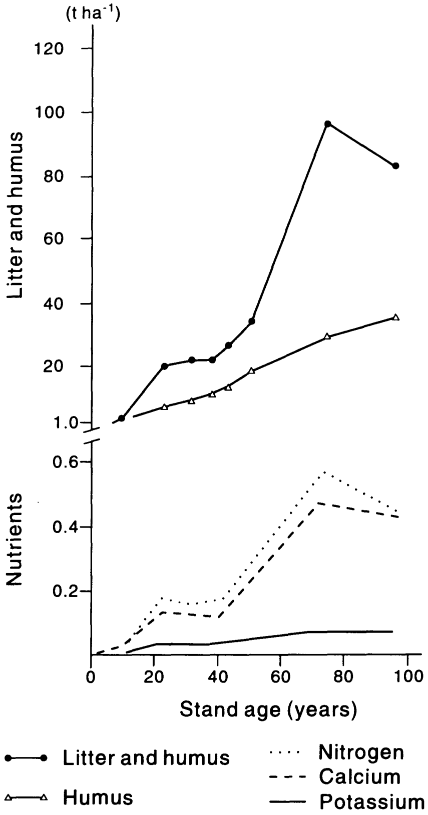


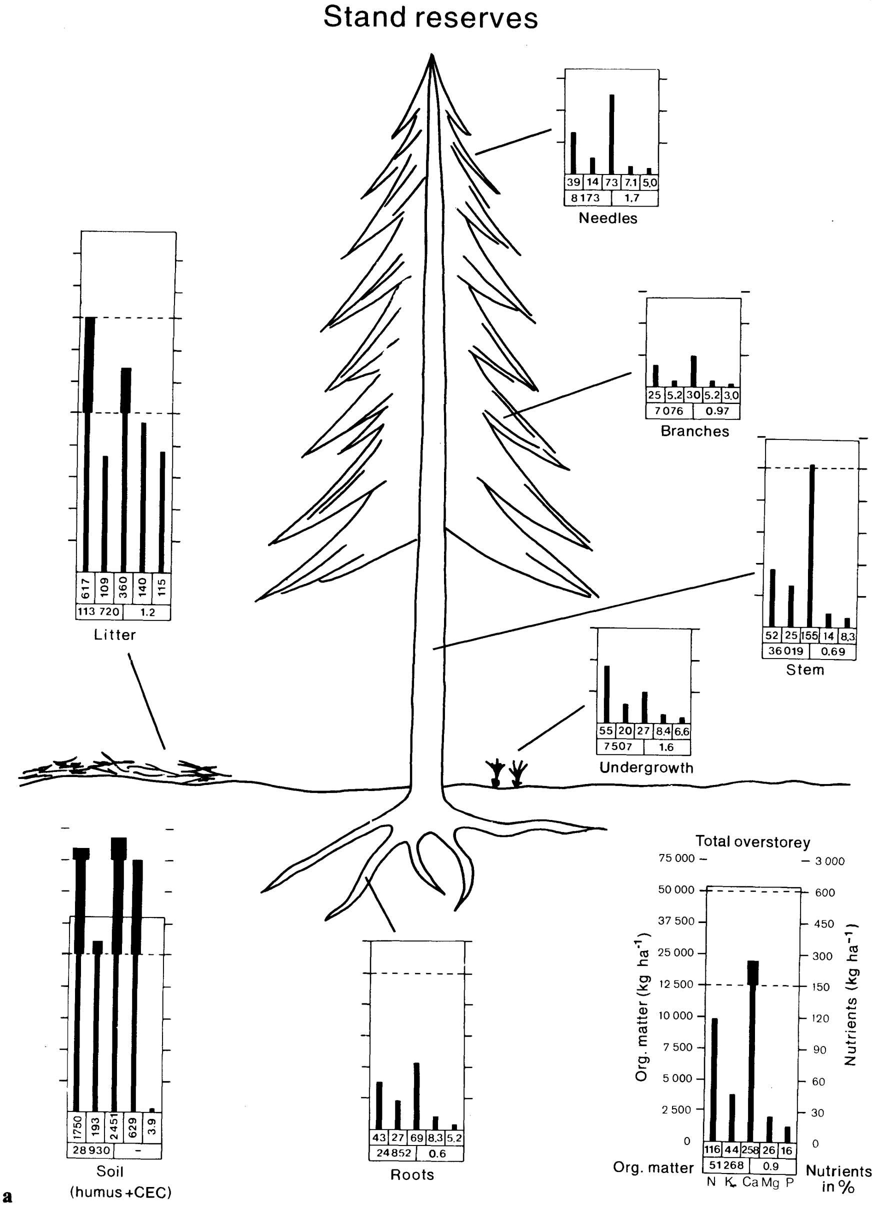
Fig. 62. Accumulation of soil organic matter (litter and humus) and incorporated mineral nutrients, under variously aged stands of boreal coniferous (Douglas fir) forests. (Turner 1978, taken from Cole and Rapp 1981). The amounts of organically bound nitrogen and calcium increase in proportion to the accumulation of litter and humus. Potassium, on the other hand, which is hardly if at all chemically bound in the phytomass (see Chap. 2.5), is released relatively quickly. The supply of potassium to the plants is thus rarely a limiting factor, very much in contrast to the short supply of nitrogen and calcium

The litter layer not only binds nutrients in an unfavourable form, it also has the effect of cooling the ground. Where permafrost is present, this can result in a shallower active layer and thus a decrease in the depth of the rhizosphere. So, in the long term, a forest fire which also destroys the raw humus is positive on two fronts. The release of nutrients also results in an advantageous increase of soil pH (Dyrness et al. 1986).

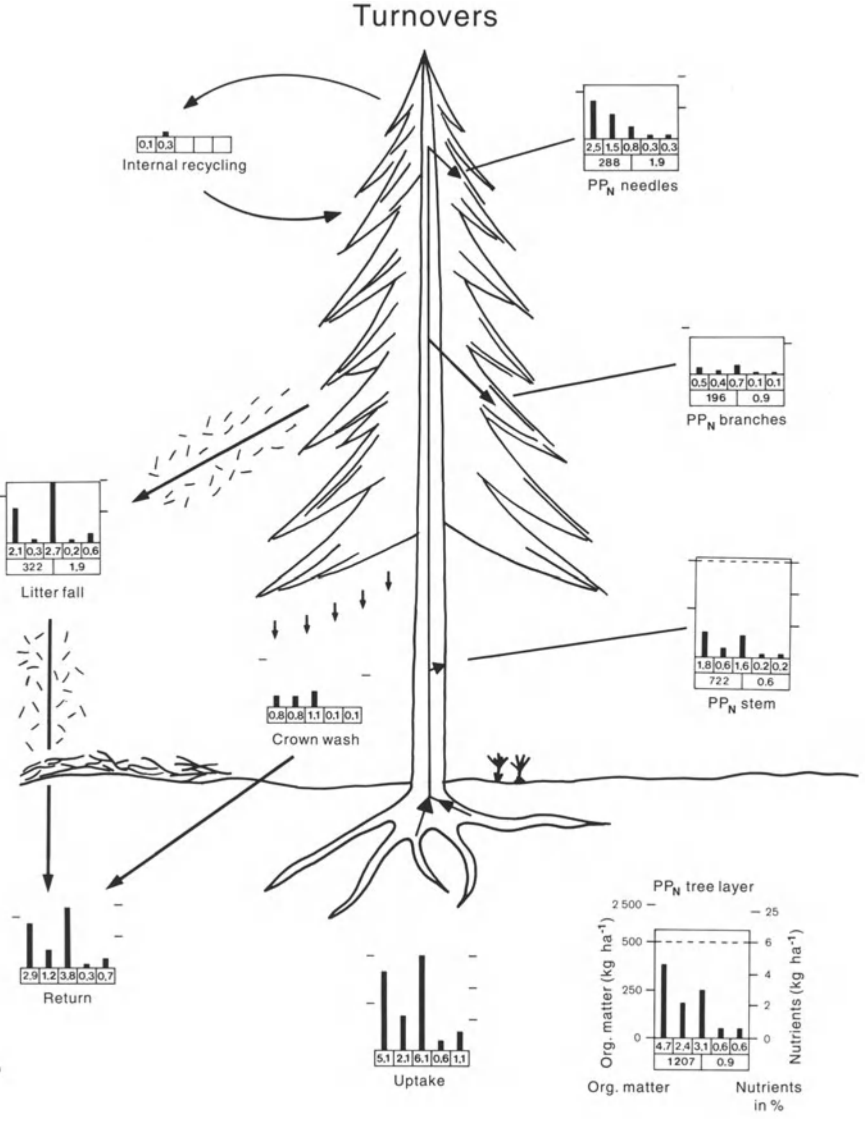
Biological *decomposition* is performed mainly by fungi (for the most part mycorrhiza), and on moderately moist sites by bacteria. There is as good as no soil macrofauna.

Reserves and Turnovers

Figure 63 gives an overview of the most important matter reserves and turnovers in boreal coniferous forests. It is based on investigations which were carried out as part of the International Biological Programme under the leadership of Van Cleve. The values used or reported here are taken mainly from the summary by Cole and Rapp (1981) and a few from Van Cleve et al. (1986). They are



arithmetic means of three Alaskan stands with a large complement of spruce (*Picea mariana*), whose ages were stated as 51, 55 and 130 years. The results are explained in more detail in Chapter 3.3.5.3 in connection with a similar depiction of reserves and turnovers in temperate deciduous forests of the Humid Mid-Latitudes (Fig. 85).



b

Fig. 63a,b. Matter reserves and turnovers in boreal coniferous forests (mean values from three separate stands in Alaska, computed and compiled from data in Cole and Rapp 1981, see also Figs. 85 and 143). Organic matter is represented by *boxes* and the nutrients (N, K, Ca, Mg and P, *from left to right* in that order) *by individual columns.* **a** Stand reserves. The scales are reduced to 1:5 starting at 150 kg (nutrients) and 12 500 kg (organic matter), and to 1:100 starting at 600 kg and 50 000 kg. **b** Turnovers. The scales are reduced to 1:12.5 starting at 6 kg (nutrients) and 500 kg (organic matter)

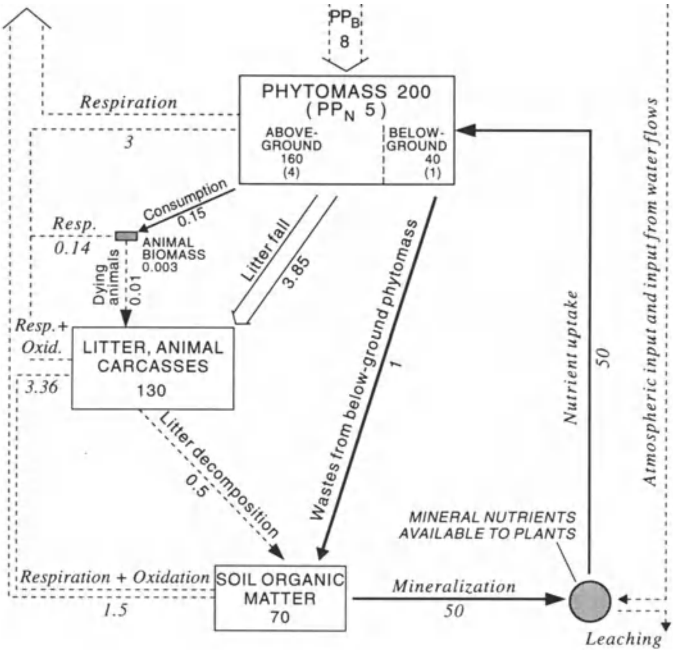


Fig. 64. Simplified ecosystem model of a boreal coniferous forest. (Compiled from data taken from Whittaker and Likens 1975; Wielgolaski 1975; Reichle 1981; Jordan 1983; Walter and Breckle 1986, 1991; and others), (see Chap. 2.5.2.5 for the scheme of the model). A characteristic feature of the boreal coniferous forest is that the reserves of dead organic matter on and in the soil (litter and humus) achieve the same magnitude as the reserves of living matter (phytomass). It is particularly significant that two-thirds of the dead organic matter belongs to the litter layer. This is because of the extraordinarily low rate of decomposition of the litter (barely 3% per annum). The amount of soil nutrients available to plants is very small

The model shown in Fig. 64 is an attempt to depict average conditions in a boreal coniferous forest ecosystem under steady-state conditions.

Vegetation Dynamics in a Boreal Forest

Figure 65 illustrates the changes which take place in plant strategies under conditions of high- and low-resource availability as the forest grows older, or following rejuvenation brought about by external disturbances. Investigations in Alaska (Van Cleve et al. 1986) have shown the following features and interacting processes to be characteristic here:

Early stages of succession, in which broadleaf deciduous trees and shrubs predominate, are characterized by

- A high PP_N (both in absolute terms and in proportion to the phytomass), most of which is above ground.

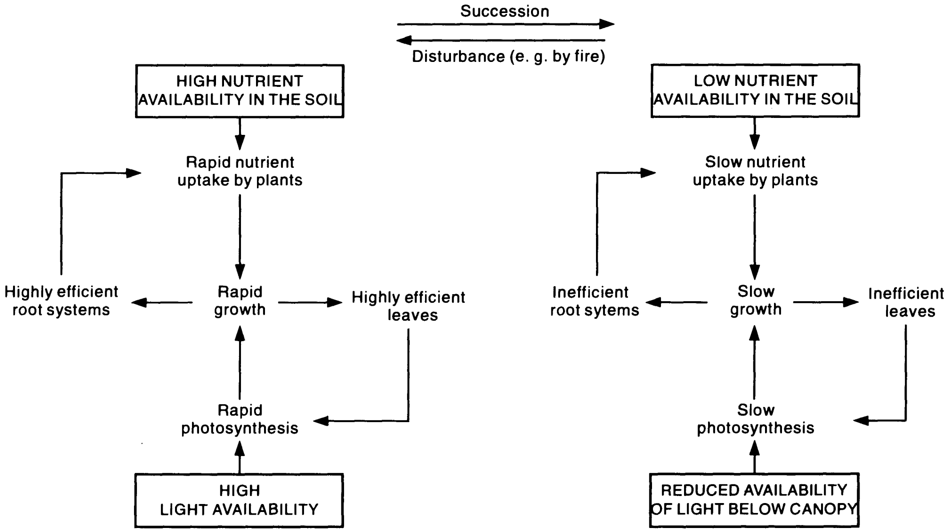


Fig. 65. Changes in plant strategies that occur as consequences of disturbance and succession in boreal forest areas. (Bryant and Chapin 1986)

- A large production of nutrient-rich, easily decomposed litter (favourable C/N ratios).
- Take-off by herbivorous vertebrates plays a relatively important role (more important than in all later stages of succession).
- As a result, the litter layers are thin, and organically bound nutrients are rapidly released.
- Fixation of N_2, particularly by alders (on moist sites), is high (up to $200\,\mathrm{kg\,ha^{-1}\,a^{-1}}$) and sufficient to cover the nitrogen requirement of the vegetation; other non-leguminous plants and free-living microorganisms also participate in the fixation of atmospheric nitrogen.

As the deciduous trees, especially balsam poplars (*Populus balsamifera*), grow up and the canopy gradually closes, the climate within the stand becomes less favourable (cooler and moister). As a consequence, first white spruce (*Picea glauca*) and then black spruce (*P. mariana*) replace the broadleaf trees. The *changeover to evergreen coniferous trees* sooner or later brings about the following changes:

- Decreasing PP_N; the proportion of PP_N in the below-ground plant organs steadily increases.
- Reduction in litter production and in litter quality (compared with leaves, needles have a higher proportion of supportive tissue, a thicker cuticle and high concentrations of tannins and terpenes).
- Steady buildup of a thick litter layer on the ground and the establishment of a moss layer.

- Both, together with the shielding effect of the tree canopy, increasingly prevent the soil from being warmed up in summer. As a consequence, the productivity of the vegetation decreases (see above) and permafrost may form, or perhaps the thickness of the active layer may be reduced in summer, but at least the moisture content of the soil and litter increases. This, in turn, causes further slowing of litter decomposition.
- The continuously accumulating litter layer binds increasing amounts of plant nutrients. This can cause bottlenecks in the plant nutrient supply, particularly with regard to nitrogen, since biological fixation of N_2 is of little or no significance anymore at this stage of succession.

Under such conditions, the increasing density of the root system with increasing stand age, and the association between roots and mycorrhiza, as well as the perennial nature of the assimilation organs, can be considered protective measures against nutrient losses. Denser root systems compensate for the dwindling availability of nutrients, and the retention of needles lowers the nutrient requirement (relatively fewer nutrients are required for the production of trunks, branches and roots than for the production of needles, see Chap. 3.3.5.3). For this reason, evergreen coniferous trees even manage to grow on soil which is very low in nutrients.

While the initial stages of forest development exhibit an open nutrient cycle (there is no direct connection between return and uptake), older stages have a characteristic *closed nutrient* cycle reminiscent of that found in tropical rain forests. Practically the only nutrients available are those released by the decomposition of litter, and forest production depends on the fullest possible exploitation of these relatively scarce nutrients.

3.2.6 Land Use

Boreal forest areas are among the most sparsely populated regions on earth and on the whole have suffered little intrusion by man. The main reason for this is the unfavourable climate, which hampers almost every type of agricultural activity. Wherever permafrost exists, any development project must always be preceded by an investigation into what effect the clearing of trees might have on the depth of the active layer in summer and thus on the possible risk of thermokarst depressions, i.e. lakes or swamps being formed (see Chap. 3.2.3 on alases; also see Chap. 3.1.6).

Hunting and fur trapping were traditionally important forms of animal utilization; they made a major contribution to the relatively early development of the forest areas, but have currently lost some of their significance. In America the possibility of using at least the forest tundra for the controlled grazing of *caribou* is under discussion. Pruitt (1978) believes that once the population has more or less recovered, a number of animals equivalent to 4 million kg of meat could be removed on a sustainable basis every year. It remains to be confirmed whether the practice of game ranching as followed in African savannas is suitable for caribou. There are also hopes of domesticating *moose*.

Game utilization is of such great importance because of the very limited opportunities for agriculture. As a rule, the *polar boundary of cultivation* is about 5 to 10 degrees of latitude below the polar forest boundary. The type of grain grown in the most northerly areas is *summer barley*, which can survive with a growing season of only 91 to 95 days. The polar boundary for this crop in northern Europe is situated at 70 °. The next most common grain types cultivated are *summer oats* and *rye*; both make few demands on the soil and can thus be grown on the nutrient-poor podzols. The *potato* is the most northerly root crop (in Scandinavia it is also grown up to a latitude of 70 °).

Perennial *fodder plants* can be cultivated slightly further north of the grain and root crop areas because these plants can fully exploit the brief growing season from the first day on (no time is lost to tillage, planting and harvesting). During the winter, i.e. for at least 6 months, the livestock (except reindeer) must be kept indoors; feeding in the stall is thus an important characteristic of livestock husbandry in the Boreal Zone.

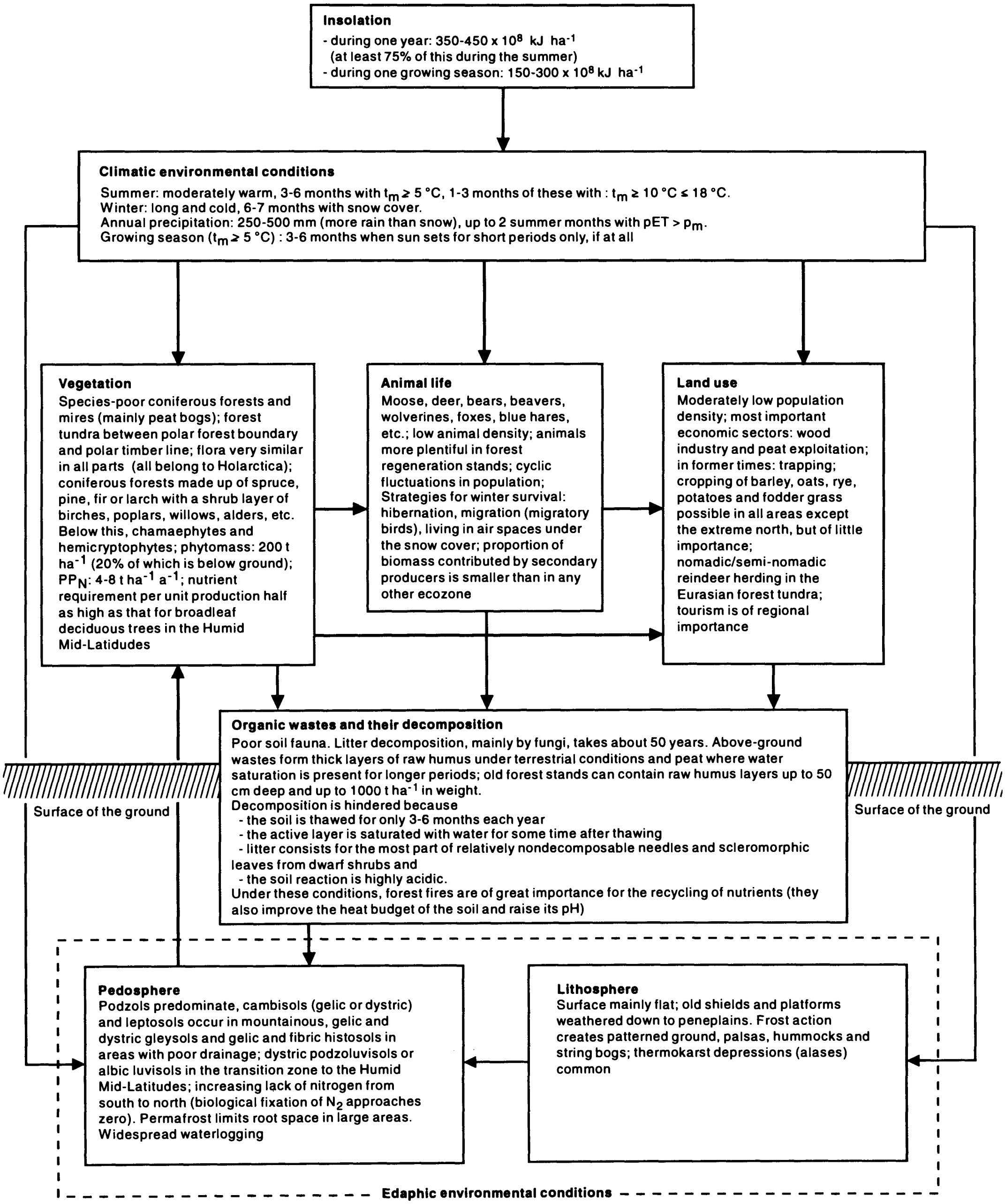
Arable farming and pasturing are often combined in the form of alternate husbandry in which fodder is grown for several years, followed by a few years in which cereal and root crops (summer cereals, potatoes) are cultivated. The soil is tilled either at the end of the final year of fodder cultivation so that no time is lost on soil preparation in the following spring, or a fallow year is interposed for this purpose: crops can thus be planted immediately after the soil has dried up following the spring thaw (Table 22).

More important than the economic activities mentioned is the exploitation of the huge *peat deposits* in the numerous mires, and the *logging* of the natural forests and commercial forests. The peat reserves in the former Soviet Union are estimated at 200 billion tonnes, which represents 66% of the world's reserves, and 22 million tonnes are harvested annually; over two-thirds of this amount is used

Table 22. Crop rotations in Lapland. (Andreae 1983)

Arctic circle ◄——	————	————	——► North Cape
1.–5. Grass crops	1.–8. Grass crops	1.–10. Grass crops	1. Fallow
6. Potatoes, oats	9. Summer barley	11. Potatoes	2. Potatoes
7. Fallow	10. Potatoes	12. Summer barley	3. Fallow
8. Summer barley	11. Summer barley		4. Summer barley

		% land used for		
62.5	72.7	Grass crops	83.4	–
8.0	9.1	Potatoes	8.3	25.0
17.0	18.2	Summer barley Oats	8.3	25.0
12.5	–	Fallow	–	50.0



Insolation

- during one year: 350-450 x 10^8 kJ ha^{-1} (at least 75% of this during the summer)
- during one growing season: 150-300 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Summer: moderately warm, 3-6 months with $t_m \geq 5$ °C, 1-3 months of these with : $t_m \geq 10$ °C ≤ 18 °C.
Winter: long and cold, 6-7 months with snow cover.
Annual precipitation: 250-500 mm (more rain than snow), up to 2 summer months with pET > p_m.
Growing season ($t_m \geq 5$ °C) : 3-6 months when sun sets for short periods only, if at all

Vegetation

Species-poor coniferous forests and mires (mainly peat bogs); forest tundra between polar forest boundary and polar timber line; flora very similar in all parts (all belong to Holarctica); coniferous forests made up of spruce, pine, fir or larch with a shrub layer of birches, poplars, willows, alders, etc. Below this, chamaephytes and hemicryptophytes; phytomass: 200 t ha^{-1} (20% of which is below ground); PP_N: 4-8 t ha^{-1} a^{-1}; nutrient requirement per unit production half as high as that for broadleaf deciduous trees in the Humid Mid-Latidudes

Animal life

Moose, deer, bears, beavers, wolverines, foxes, blue hares, etc.; low animal density; animals more plentiful in forest regeneration stands; cyclic fluctuations in population; Strategies for winter survival: hibernation, migration (migratory birds), living in air spaces under the snow cover; proportion of biomass contributed by secondary producers is smaller than in any other ecozone

Land use

Moderately low population density; most important economic sectors: wood industry and peat exploitation; in former times: trapping; cropping of barley, oats, rye, potatoes and fodder grass possible in all areas except the extreme north, but of little importance; nomadic/semi-nomadic reindeer herding in the Eurasian forest tundra; tourism is of regional importance

Organic wastes and their decomposition

Poor soil fauna. Litter decomposition, mainly by fungi, takes about 50 years. Above-ground wastes form thick layers of raw humus under terrestrial conditions and peat where water saturation is present for longer periods; old forest stands can contain raw humus layers up to 50 cm deep and up to 1000 t ha^{-1} in weight.
Decomposition is hindered because
- the soil is thawed for only 3-6 months each year
- the active layer is saturated with water for some time after thawing
- litter consists for the most part of relatively nondecomposable needles and scleromorphic leaves from dwarf shrubs and
- the soil reaction is highly acidic.

Under these conditions, forest fires are of great importance for the recycling of nutrients (they also improve the heat budget of the soil and raise its pH)

Pedosphere

Podzols predominate, cambisols (gelic or dystric) and leptosols occur in mountainous, gelic and dystric gleysols and gelic and fibric histosols in areas with poor drainage; dystric podzoluvisols or albic luvisols in the transition zone to the Humid Mid-Latitudes; increasing lack of nitrogen from south to north (biological fixation of N_2 approaches zero). Permafrost limits root space in large areas. Widespread waterlogging

Lithosphere

Surface mainly flat; old shields and platforms weathered down to peneplains. Frost action creates patterned ground, palsas, hummocks and string bogs; thermokarst depressions (alases) common

Fig. 66. Synoptic diagram for the Boreal Zone

for improving the soil in agricultural areas and the rest is mostly burned either as fuel in electric generating plants or as a source for heating human dwellings in remote areas (Botch and Masing 1983, p. 133).

The trees felled in the boreal forests cover about 90% of the world's paper and lumber requirements (Müller-Hohenstein 1981). Considerable though this contribution may be, it must be viewed in relation to the enormous forested area from which it comes. From this point of view it is clear – even when no exact data are known – that the productivity of the forest industry per unit area is low. The problems encountered in commercial logging increase in severity from south to north, and include:

- Remote location, i.e. long transportation routes to processing centres and to the consumer (the rivers flow northwards, making them unsuitable for transporting wood, unlike in other areas), local labour is practically non-existent.
- Low temperatures and deep snow cover in winter.
- The useable amount of wood per unit area and the quality of the wood are low: tree stands are relatively sparse and the trees do not attain a great height. The wood is often suitable only for the paper industry or for use as fuel.
- The annual growth increment is low, forest renewal or reafforestation takes much longer than at our latitude before the trees can be harvested again.

In summer, large numbers of *wild berries* ripen in the boreal forests. The gathering of these berries is a major activity in Russia. The most important are cranberries (*Vaccinium vitis-idaea*), whose annual production lies between 0.1 and 1 $t\,ha^{-1}$; the highest yields are found in the transition zone between the southern and the central taiga (Botch and Masing 1983, p. 132).

The boreal forests are the closest primeval forests in which the inhabitants of the densely populated Humid Mid-Latitudes can hike, ski, fish and hunt during their vacations. The number of tourists drawn by these attractions has risen steadily, especially where additional recreational facilities are provided, e.g. in the form of national parks. Aside from the traditional practices of keeping reindeer and trapping, and the more recently established forestry industry, *tourism* is the fourth, and most modern, form of utilization of the northern forest regions (Mikola 1970).

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Chapter 3.2, Boreal Zone

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3.3 Humid Mid-Latitudes

3.3.1 Distribution

The distribution of this zone is fragmented. Most of it is located in the Northern Hemisphere, and only small areas are located in the Southern Hemisphere. The latitudes at which it is found vary slightly due to the influence of cold and warm ocean currents: along the western coasts of the continents it occurs between 40 and 60 ° and, along the eastern coasts, it is located somewhat closer to the equator, between 35 and 50 ° (Fig. 67). Taken as a whole, the various parts of this zone account for a total of about 15 million km^2 or 10% of the planet's landmass. Other more or less synonymous names applied to the Humid Mid-Latitudes are the "deciduous forest belt of the temperate zone" and "temperate nemoral zone".

In the poleward direction, the Humid Mid-Latitudes border on the Boreal Zone; towards the equator, the western parts of this zone border on the Mediterranean-Type Subtropics and the eastern parts on the Humid Subtropics. In the highly continental regions of the Northern Hemisphere the Humid Mid-Latitudes are either missing altogether, i.e. the boreal coniferous forest regions are immediately followed by the cold-winter steppes, or they occupy narrow bands between these two regions.

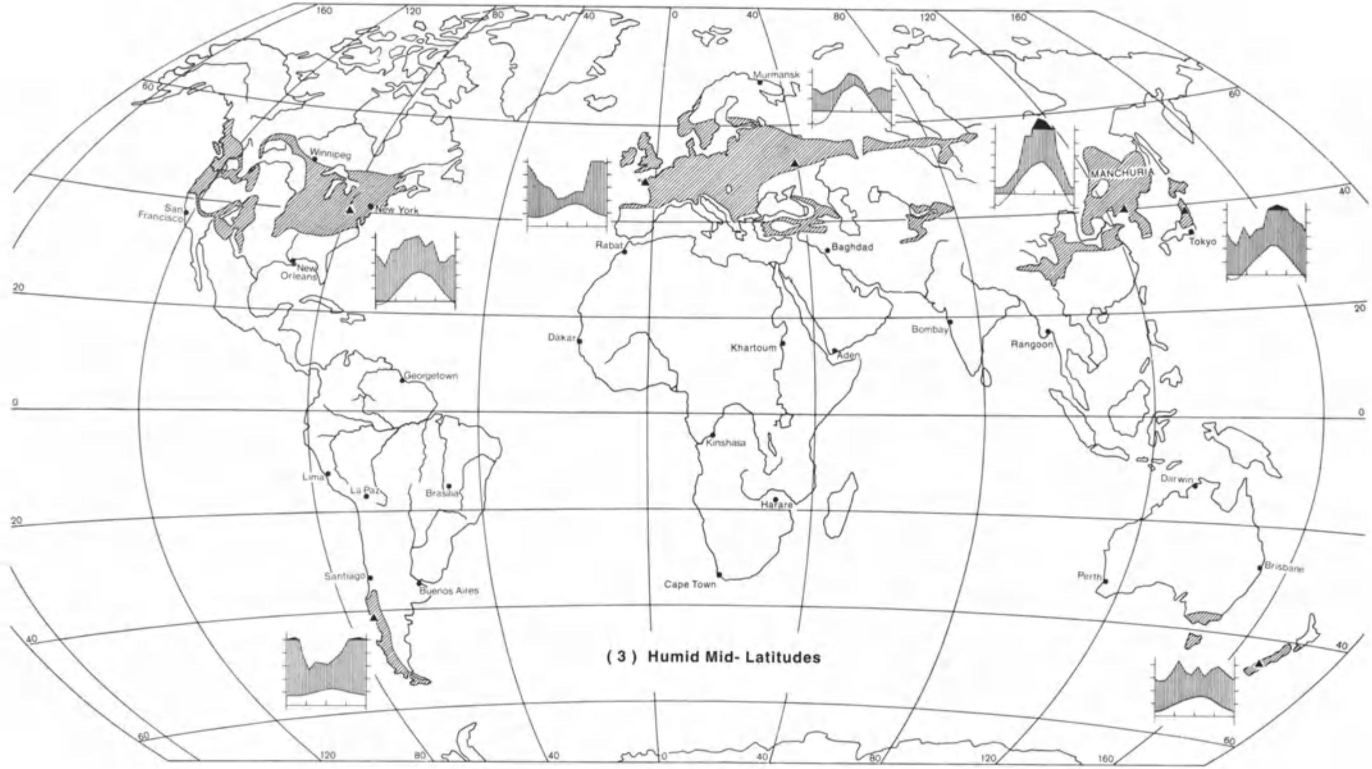


Fig. 67. Humid Mid-Latitudes. The distribution of this zone is fragmented; its major regions are located in the Northern Hemisphere

This zone is distributed over the following areas:

- large parts of western, central and eastern Europe;
- northwest China (Manchuria, Beijing), Korea (with the exception of the southern part), the northern half of Japan;
- the northeast USA (east of 95° W and north of 36° N) and neighbouring parts of Canada;
- western Canada and the northwest USA (British Columbia to Oregon);
- and small areas in the Southern Hemisphere: southern Chile (western Patagonia), southeast Australia (Victoria and Tasmania) and the South Island of New Zealand.

The common locational characteristic of all these regions is their relative proximity to the ocean, or peripheric situation with respect to continental landmasses. Their location is, however, rather central when related to the great divisions of the earth according to natural development potentials: all neighbouring land regions, including the semi-arid steppes, have good natural potentials for various kinds of utilization, whereas those regions that are clearly unconducive to human settlement and economic activity, e.g. those beyond the humid-arid or the polar boundary of cultivation, are relatively far away.

The section of the Humid Mid-Latitudes situated in Europe is most extensively distributed along the Atlantic coast, where it runs from the northwest part of the Iberian Peninsula to Trondheim in Norway. It also covers a wide swath of central Europe, stretching from northern Italy and the northern part of the Balkan Peninsula in the south, to southern Sweden in the north. East of the Weichsel river, the northern and southern borders of this zone converge, leaving only a narrow band which continues eastwards well past the Urals.

3.3.2 Climate

Air Pressure Systems and Winds

Like the two zones already discussed, the Humid Mid-Latitudes also exhibit *pronounced seasonal fluctuations in temperature* due to the still considerable seasonal alternation between a positive and a negative energy balance (radiation balance) as a function of varying solar declination and length of day (see below). On the other hand, the atmospheric *circulation processes* in this zone are completely different. In the middle and lower troposphere of both hemispheres, these processes are dominated by the pressure gradient between the subtropical/tropical belts of high pressure cells and the (much less constant) subpolar lows (subarctic and subantarctic low pressure belt), and by the contrast between warm tropical air and cold polar air (Fig. 122). The air pressure systems, combined with the effects of the Coriolis force, leads to the formation of prevailing *westerly* winds or *cyclonic west wind drift*. However, disruptions in planetary air pressure conditions frequently occur, so that winds blowing from other directions are not uncommon (or, to put it in other words, wind blows from any direction, but the westerly component is clearly predominant).

The formation of the subtropical/tropical high pressure belts and of the subpolar low pressure troughs, as well as the "disruptions" in mid-latitude air pressure conditions, are strongly influenced by dynamic processes along the *planetary frontal zones (polar fronts)* in both hemispheres; but thermal effects also play a role (e.g. in creating cold anticyclones above the landmasses of the Northern Hemisphere in winter).

Planetary frontal zones are the regions between latitudes 30 ° and 50 ° (in the summer they tend to be between 40 ° and 60 °) N and S in which the equator-pole-decline in incoming solar radiation (from the equator region of energy surpluses to the polar regions of energy deficits) is steepest (Fig. 68), and thus where the meridional temperature gradients are highest (Fig. 69). They are also the latitudinal zones in which declining global atmospheric pressure in the *upper* troposphere exhibits the greatest meridional gradients, between the low latitude high pressure belt and the polar low pressure centres. This is accompanied – according to the laws on geostrophic winds – in both hemispheres by a strong westerly upper air flow blowing in a complete circuit around the earth (= belt of upper-air westerlies flowing along the planetary frontal zone, planetary west wind zone; Fig. 70).

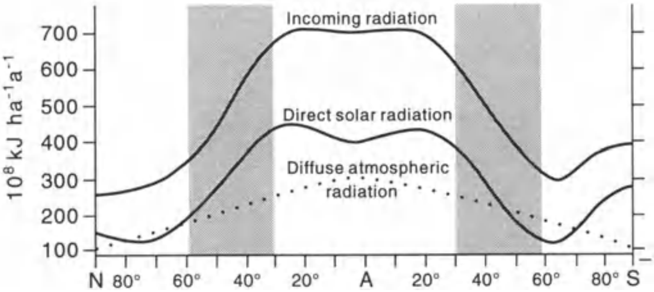


Fig. 68. The equator-pole-decline of incoming radiation (radiation curves from Sellers 1967). The *hatched areas* indicate the latitudinal zones (i.e. mid-latitudes) with steepest decline

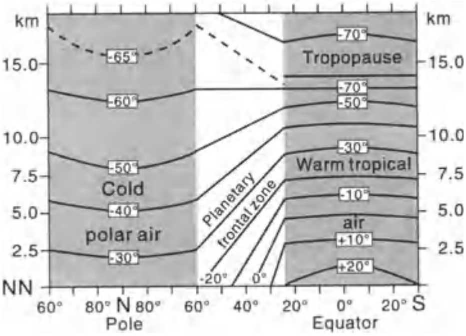


Fig. 69. Schematic meridional section through the atmosphere, showing the vertical temperature stratification. (Weischet 1983). The meridional temperature gradient is highest in the frontal zone

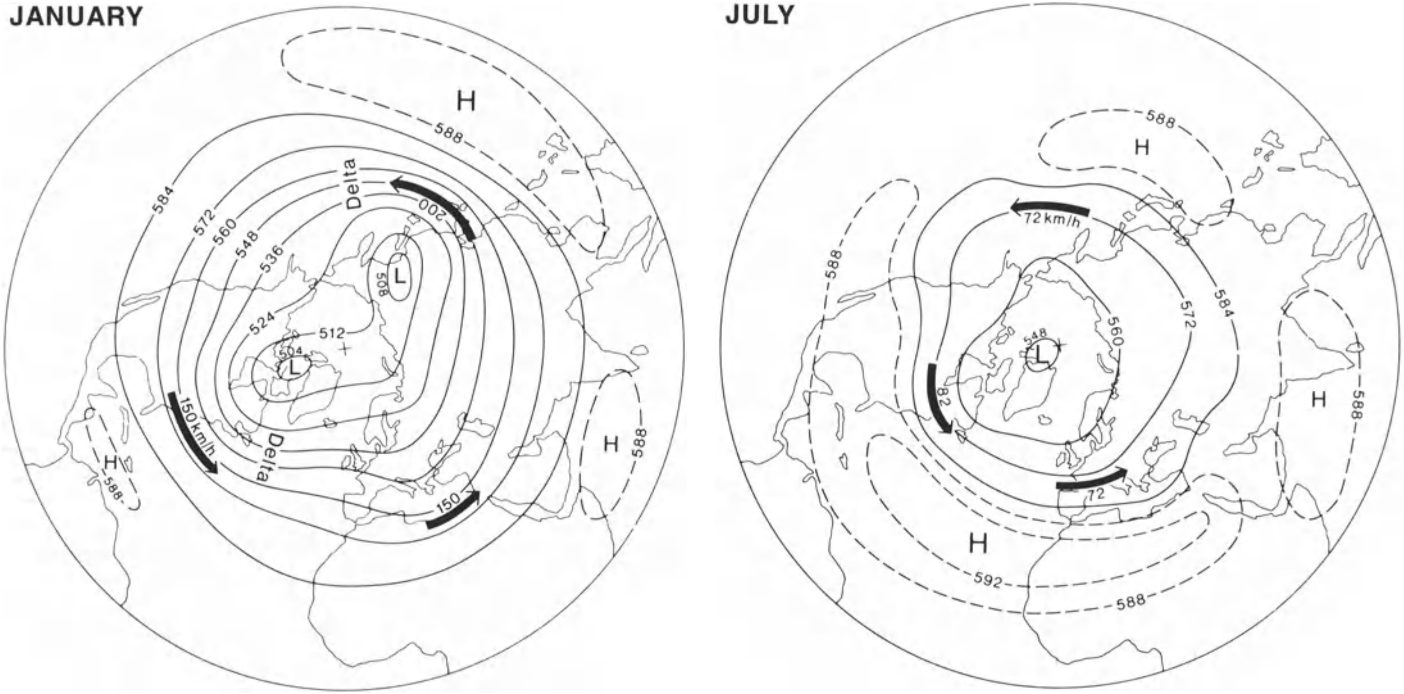
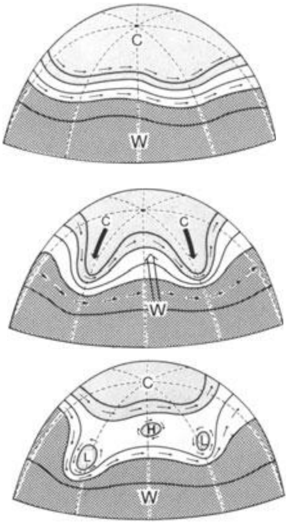


Fig. 70. Mean 500 hPa contours over the northern hemisphere (in geopotential decametres) and the location of jet streams (narrow bands of very high-speed – up to 500 km h^{-1} – upper-air westerlies). (Scherhag 1969 and Estienne and Goddard 1970, taken from Weischet 1983)

(Heat) exchange processes occur along the planetary frontal zone when the uniform flow of upper-air westerlies starts to meander, i.e. large undulations are formed (upper-air waves, Rossby waves; Fig. 71). Then, warm tropical air is deflected polewards and cold polar air equatorwards, and both are transported meridionally for up to several thousand kilometres (thus providing heat exchange on a gigantic scale). Warm air moving polewards causes the formation of high pressure wedges or ridges at high altitudes, whereas low pressure troughs at high altitudes are formed above the cold air masses flowing towards the equator. Cut-off can result in the formation of isolated ridges or troughs, which suppress the westerly drift for a few days (blocking action). Of particular importance to the weather patterns in the lower troposphere is the cold air which flows along the (rear edges of the) troughs towards the equator. It destabilizes the tropospheric stratification and causes a drop in air temperature down to near ground level.

The changes in intensity and direction of the upper westerlies, which result from varying pressure gradients (e.g. jet streams), undulations and the formation of upper-air ridges and troughs, are accompanied by convergences and divergences of flow. In the middle and lower troposphere, the former (on account of the mass influx taking place) lead to increases in pressure, i.e. to *dynamically generated high pressure cells*, whereas the latter lead to decreases in pressure, that is, to *dynamic low pressure cells*. Both these pressure systems travel westwards along with the upper air flow, the highs tending to deflect towards the equator and the lows towards the poles, thus giving rise to the subtropical/tropical high pressure belt and the subpolar low pressure troughs, respectively.

In the Northern Hemisphere, the gradient winds associated with the wandering pressure systems circulate counterclockwise around the low pressure cells



▢ = Cold air (C) } Boundary region: Planetary frontal zone (polar front)
▨ = Warm air (W)
H = Upper-air high pressure cell (warm air)
L = Upper-air low pressure cell (cold air)

Fig. 71. Development of waves (Rossby waves) and cut-off effects in the upper-air westerlies. (Weischet 1983). See text for further explanations

(cyclones), but clockwise around the highs (anticyclones); in the Southern Hemisphere, the directions are reversed. Friction near the earth's surface causes the low pressure systems to deflect convergently and the high pressure systems to deflect divergently. Rising air (which corresponds with the already noted divergence in the upper troposphere) is thus characteristic for cyclones, whereas falling air characterizes the anticyclones (convergence in the upper troposphere). The adiabatic temperature changes which occur in connection with the vertical movement of air create a tendency for cloud formation and precipitation in cyclones and for clearing and fair weather in anticyclones.

Since the cyclones form along the frontal zone (frontal cyclones), they are made up of both warm and cold air (see Fig. 72a). When fully developed, *cyclones possess a wedge of warm air*, typically located along their southern flanks (in the Northern Hemisphere); at the eastern edge (front edge) of this wedge the more rapidly (eastward) moving warm air is forced to ascend when moving into the region of cold air (warm front), while at the western edge (rear edge) heavier polar air forces its way below the warmer air masses (cold front). The lifting of the air masses on both fronts leads to adiabatic cooling and condensation of the moisture in the air (Fig. 72b). Most precipitation in the Humid Mid-Latitudes occurs in connection with such fronts.

Changes in the circulation pattern caused by undulations (etc.) of the planetary frontal zones and by the described pressure systems in the lower troposphere force – often in quick succession – *air masses* of vastly different origin, and thus with different hygrothermic characteristics, to move into the various subregions of the Humid Mid-Latitudes. As a result – both directly and through lifting, upsliding and mixing processes at the borders of the air masses – this zone experiences a highly unstable weather pattern, characterized by frequent precipitation in all seasons, rapid changes in temperature ("cold waves"), and an overall high degree of cloudiness which lowers the actual duration of sunshine to less than half the theoretically possible level. Perhaps as a result of the uncertainty of the weather and the general desire for more sunshine, nowhere else on earth – although this still has to be proved – do the inhabitants spend more time discussing the weather than in the Humid Mid-Latitudes, and millions of them travel to the "sunny south" for their yearly vacation.

Temperature and Precipitation

The *seasonal change in temperature* is pronounced. However, the temperatures do not drop as low as those found in the neighbouring Boreal Zone to the north and do not climb as high as those found in the subtropical ecozones to the south. The diurnal temperature ranges – greater than in the Polar/Subpolar and Boreal Zones but smaller than in the arid regions of the mid-latitudes and tropics/subtropics – also occupy an intermediate position (Fig. 73). Viewed from this standpoint, the thermal conditions in the Humid Mid-Latitudes can be classified as *temperate*, as in the case of the common climatic designation for this zone, namely the

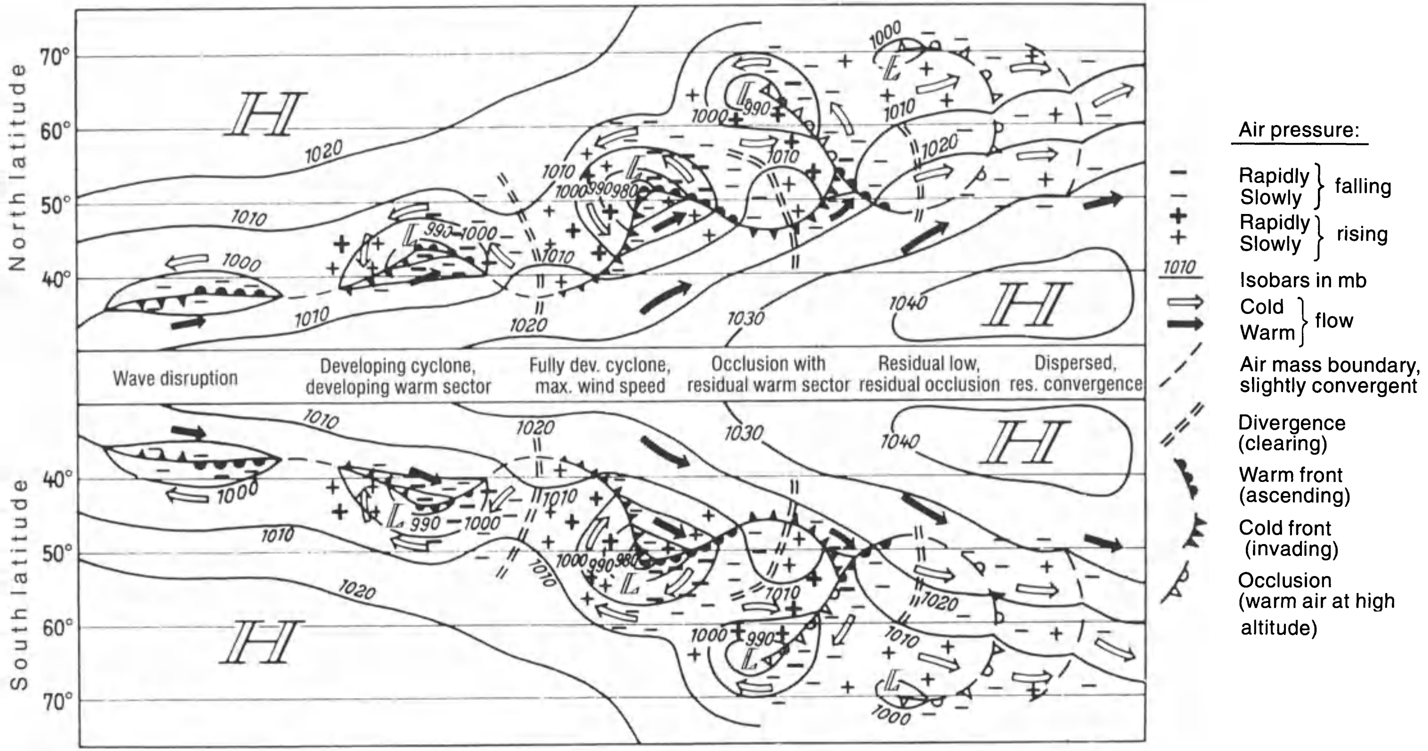


Fig. 72. a The development of frontal cyclones from the initial wave disturbance (*left*) to the fully developed cyclone with a broad sector of warm air (*middle*) up to the occluded residual cyclones (*far right*), taking as an example cyclone families (on a compressed scale) in the Northern and Southern Hemispheres. (Blüthgen and Weischet 1980). The westerly drift of the cyclones generally contains a poleward component

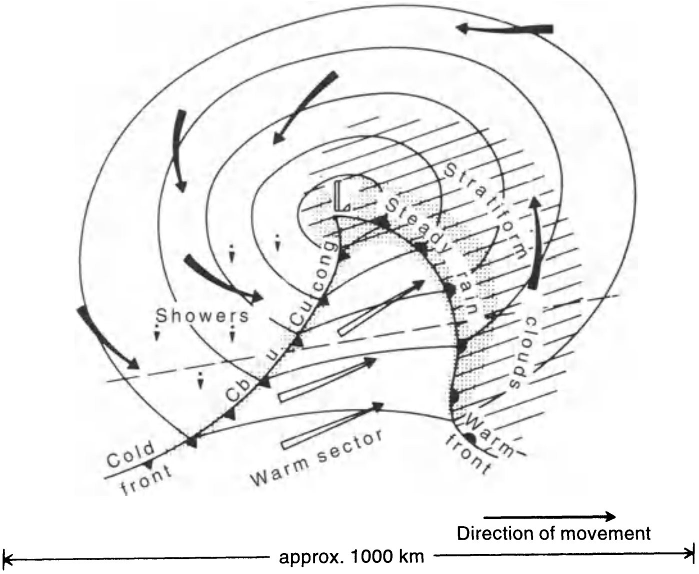


Fig. 72. b Model of a fully developed frontal cyclone. (Weischet 1983)

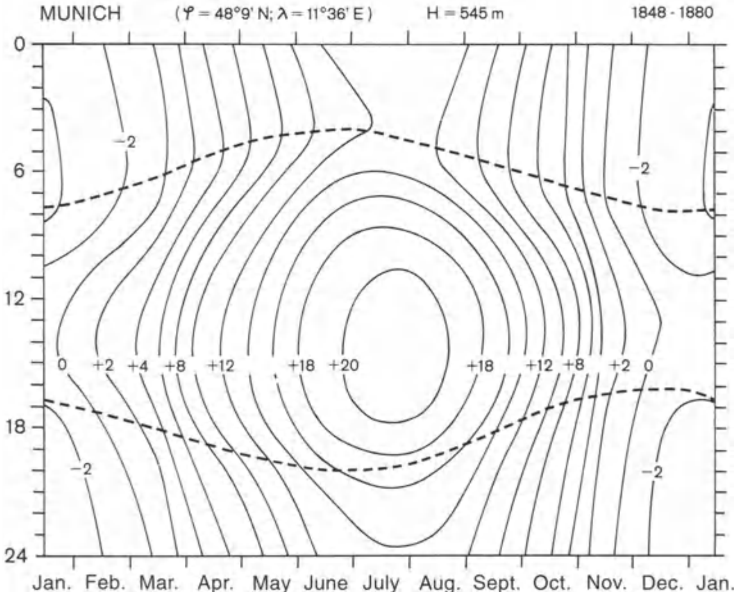


Fig. 73. Thermoisopleth diagram for Munich representing the sub-maritime type of climate in the Humid Mid-Latitudes. (Troll and Paffen 1964). Moderate variations in annual and daily temperatures are characteristic of this climatic type. The *broken lines* indicate sunrise and sunset

cool temperate (forest) climate, or as in the case of vegetation designations, e.g. temperate deciduous forest, which is the prevailing zonal plant formation in the Humid Mid-Latitudes.

Regional differences in climate occur mainly in the east-west direction, i.e. from coastal to inland areas (even more so than in the Boreal Zone) (Fig. 74). The growing season in *highly continental areas* is limited to 6 months and winter temperatures drop below −30 °C. In *climatic regions subject to maritime influence*, the growing season is longer, even year-round in some coastal areas; mean temperatures in the coldest month remain above +2 °C and, in a few areas, even above +5 °C. However, the rise in summer temperatures is also restricted here; the mean temperature of the warmest month normally does not exceed +15 °C. In continental areas it is always above +18 °C. As a result, annual temperature ranges vary widely, from up to 40 °C in continental areas down to only 10 °C in maritime regions (comparison of monthly averages). In some coastal areas the summers remain so cool that cereal crops do not reach maturity (Walter and Breckle 1986, p. 3).

Mean annual temperatures in all areas lie between 6 and 12 °C. Even under highly continental conditions, the maximum monthly temperature of $t_m \geq 18$ °C is achieved in only 3 months of the year (longer in the subtropics).

As regards *daylight conditions*, the Humid Mid-Latitudes again occupy an intermediate position: neither the similarity in the length of daylight, which is found in the tropics, nor the extreme dissimilarity of the summer and winter months, such as is found near the poles, occurs here. At 50 ° latitude the length of day ranges between 8 h at the winter solstice and 16 h at the summer solstice.

The changes in daylight (radiation) and temperature from summer to winter and from winter to summer are such that lengthy (thermic) transition periods oc-

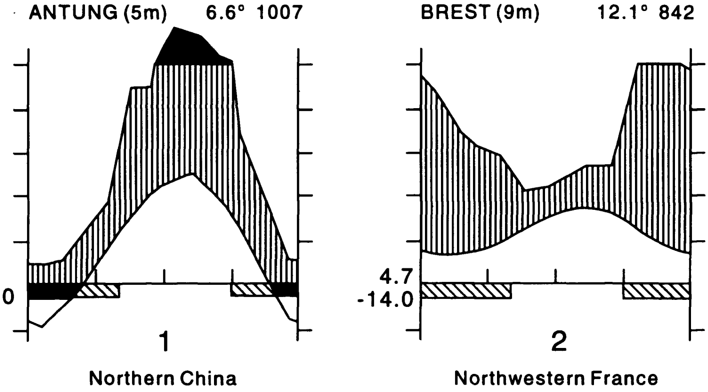


Fig. 74. Climatic diagrams of a continental (*1*) and an (extremely) maritime (*2*) type of climate in the Humid Mid-Latitudes. (Walter and Lieth 1960–67). Under maritime influence, winters are mild (in extreme cases the growing season lasts all year) and summers cool; most precipitation falls in winter. Under continental influence, the summers are warmer and the winters colder (the growing season decreases to 6 months); most precipitation falls in summer

cur in between, dividing the year into *four seasons*, spring, summer, autumn and winter. All four seasons exhibit distinct differences in vegetational characteristics (see Chap. 3.3.5). Only the summer is completely frost-free; late frosts are possible in the spring and early frosts in the fall. Both are particularly dangerous to vegetation and – even more so – to agricultural crops, because the frost resistance developed by the plants through the process of *hardening* each fall is lost again with rising temperature in the following spring. Early and late frosts can thus find the plants unprepared; the damage caused is correspondingly severe.

In summer, about 70% of the incoming radiation is directly received (in winter only about 50%). Since, even in summer, the sun's circuit above the horizon is not very long (at the most 240° at 50°N), southerly slopes receive much more radiation than do slopes with northerly exposure. This relative temperature advantage is, for instance, obvious in the one-sided distribution of vineyards in southwestern Germany.

In contrast to the temperature pattern, there is no marked seasonal variation in *precipitation* and humid conditions prevail year-round (at least 10 months with p (mm) > 2t (°C). Differences in precipitation from year to year also remain slight, at least as far as the annual totals are concerned. Agricultural systems thus profit from the highly *dependable rainfall*. This does not, however, exclude the possibility of dry spells during which, especially on sandy soils, additional watering of the crops is necessary. A small proportion of the precipitation regularly falls as *snow*.

Most areas exhibit annual precipitation totals between 500 and 1000 mm, making this the next wettest ecozone after the Humid Tropics and Humid Subtropics, although, in most areas, the totals in the latter zones are at least twice as high as those in the Humid Mid-Latitudes.

With increasing distance from the oceans, the rain-bringing ability of the cyclones decreases. At the same time, the seasonal distribution changes: winter maxima are replaced – particularly in the high mid-latitudes (see Boreal Zone) – by summer maxima based on rains produced by convection (continental summer rains) and the overall weather pattern becomes more stable.

Frequent cold waves are characteristic of the eastern coasts of the continents. In winter they come from the interior of the continents and in summer from the polar latitudes.

3.3.3 Relief and Hydrology

Compared with the two ecozones already discussed, winter frosts have only moderate morphological effects. None of the frost-generated forms described for the Polar/Subpolar and Boreal Zones are found here, at least not as recent formations and in low-lying areas. Still of some importance, although of much less significance, is the frost splitting on bare rock surfaces (for the frequency of freeze-thaw cycles in the Humid Mid-Latitudes, see Fig. 75).

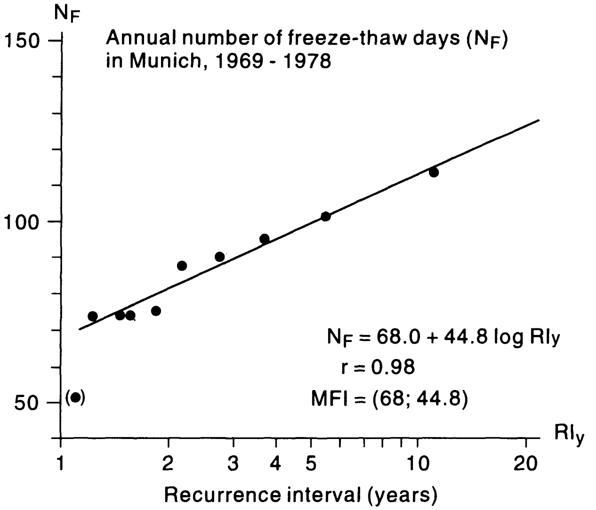


Fig. 75. Magnitude/frequency analysis of annual freeze thaw days in Munich. (Ahnert 1987). See Chapter 2.3 for explanation of method. The average number of freeze-thaw days per year is 68. In 1 out of 10 years, at least 113 freeze-thaw days can be expected to occur

In general, chemical weathering is also not particularly intensive under the cool temperate conditions prevailing; and the (naturally) dense tree cover slows down every type of erosion and denudation process. Changes to the topography thus have occurred only at a retarded rate – more slowly than in the Polar/Subpolar and Boreal Zones and in the arid regions (and probably also in the Mediterranean-Type Subtropics). According to Hagedorn and Poser (1974), the Humid Mid-Latitudes are a zone of *moderate morphological activity*. The debris and gelifluction sheets created under glacial and periglacial conditions during the last ice age have yet to be decomposed (see below).

Weathering

Hydration plays an important role in the weathering of certain primary minerals, e.g. biotite. In this process, the silicates absorb water between their layers, expand and finally split apart, thus causing stress within the rock. More common is the hydration of secondary products such as iron and aluminium oxides. Material changes can occur, such as anhydrite becoming gypsum ($CaSO_4 \cdot 2H_2O$).

Hydration is almost always accompanied by chemical conversion through *hydrolysis*. In this process, the hydrogen ions formed by the dissociation of water molecules replace the basic cations (such as Na, K, Mg, Ca and eventually Fe and Al) occurring in the structure of primary silicates, and this also leads to loosening and finally destruction of the crystal lattice. This is the most important weathering type in the Humid Mid-Latitudes, and probably also elsewhere, involving the disaggregation of consolidated rock and even more the decomposition of soil minerals. The intensity of this reaction increases with increasing H^+ concentration, i.e. decreasing pH, in the soil and with increasing temperature (the conditions most favourable to hydrolysis are thus found in the hot, humid tropics). Hydration and hydrolysis can lead to desquamation and granular disintegration of solid rock. For example, the disintegration of granite is mainly a result of the hydrolysis of orthoclase feldspar and its conversion to clay.

True *solution weathering*, in which mineral substances are dissolved in an aqueous liquid, without chemical reactions as such taking place, seldom occurs in the Humid Mid-Latitudes: easily soluble minerals such as chlorides, nitrates or gypsum are not found under such humid conditions. Solution processes involving less readily soluble minerals can take place, however, if the rainwater is acidulated with carbon dioxide (derived from its passage through the atmosphere) and thus acts as a dilute acid, or – as is often the case in humid climates – the soil water contains acid decomposition products of organic matter. For example, *carbonic acid* is formed by the reaction of CO_2 found in the soil air (CO_2 is more highly concentrated here than in the atmosphere due to the respiration of roots and of the edaphon) and H_2O ($CO_2 + H_2O = H_2CO_3 \longrightarrow H^+ + HCO_3^-$). This carbonic acid attacks calcite and (to a lesser degree) dolomite which are widespread and form the major components of calcareous rocks (limestone and chalk), and some other materials. In the process of *carbonic acid weathering* the calcium carbonate is slowly dissolved and removed in the form of soluble calcium bicarbonate with the percolating water [$CaCO_3 + H_2CO_3 = Ca(HCO_3)_2$]. The intensity with which calcium carbonate is dissolved increases with increasing CO_2 concentration in the water and is promoted by low (!) temperatures. In limestone mountains, the carbonic acid weathering leads to *karst formations* (e.g. karren, dolines, caves with stalactite/stalagmite formation) and in unconsolidated material (e.g. moraines, loess) and soils (e.g. chernozemes) to *decalcification* (which progresses downwards from the surface). In earlier times, lime depletion in the fields was compensated for by applying lime-rich loam taken from the subsoil (marl pits); today, lime fertilizers are used.

In addition to the carbonic acid, *humic acids* can also play an important role in acid-promoted solution weathering. Decomposition processes based on this or on carbonic acid formed from respiration CO_2 (by roots or soil organisms) are grouped together under the term *biological/chemical weathering*. This type of weathering is of importance in all soils with high litter input, dense root networks, and rich soil fauna and flora. It is of comparatively great significance in the Humid Mid-Latitudes due to the fact that other chemical weathering processes, as well as physical types of weathering, play a lesser role. As a result, biological/chemical solution processes are (perhaps besides hydrolysis) the chief means by which plant nutrients are released from rock fragments, formed by mechanical splitting (by frost weathering and by hydration).

Runoff and Landforms

About one-third of the precipitation runs off, compared with almost 50% in the Boreal Zone and over 50% in the tundra (Table 2). But since the amount of precipitation in the Humid Mid-Latitudes is greater than that in these other zones, the absolute amount of water running off per unit area is nonetheless larger.

There is a high density of rivers, all of which are perennial; in winter, ice may form, and frequently does in more continental areas; runoff then occurs under a cover of ice. The *runoff regime* is determined to a much lesser extent than in the Boreal Zone by winter frost and snow melt in spring; of greater importance are the unequal seasonal distribution of precipitation, where present, and the relatively high evaporation losses in summer. The minimum runoff during summer is thus usually much more pronounced than that occurring in winter due to frost and snow; runoff peaks follow the precipitation maxima, i.e. in maritime climates they typically occur in spring and in continental climates in the fall.

Variations in discharge also occur as a result of occasional dry or rainy periods. Both the regular and occasional seasonal variations can be regarded as moderate, insofar as they are less pronounced than those normally found in the adjacent zones to the north and south. On the other hand, the floodwater levels still rise so high in many years that dams are needed to protect settlements and agricultural land wherever rivers flow through plains.

Despite short-term floodwaters, the morphological effectiveness of the rivers remains modest, and linear downcutting by running water correspondingly weak. If, nonetheless, the V-shaped valleys formed during the Pleistocene are still present and steep-sided valleys with broadened floors were frequently able to develop, this is due to the fact that slope degradation is even less vigorous. The reason for this is that, even in winter, when there is little vegetation cover, the land surface is protected by multiple layers of decaying leaves and most soils exhibit good structural characteristics (stable structure with good permeability to percolating rainwater). At the same time, precipitation intensity is low in most cases; even the peak values are far below the intensities frequently occurring in the tropics (see Chap. 2.3 and Fig. 154). Sheet erosion by surface runoff is usually of less consequence than is mass movement through gravity.

Relict Landforms

Parts of the Humid Mid-Latitudes (at least all the higher mountainous areas) were covered with glaciers during the cold phases of the Pleistocene; the remainder were part of the periglacial region and formed areas of frost debris or tundra. Most of the landforms and accumulations created during that period are still in existence and play a major role in defining the topography. In the mountains, for example, U-shaped valleys (trough valleys), cirques (kars) and ice-polished rocks bear witness to the glacial erosion, while further down, terminal basins (today filled with lakes), moraines, drumlins, eskers and kames provide evidence for former ice cover. Outside the formerly glaciated regions, Urstromtäler (broad meltwater valleys along edges of ice sheets) and outwash plains are the most conspicuous forms of fluvioglacial erosion and deposition respectively; and large dune drifts (today afforested with pines) and fertile loess deposits, sometimes accumulated far from the glacial regions, bear witness to the former periglacial climate which did not allow a complete plant cover to develop everywhere. The meltwater streams frequently formed terraces in their own gravel sediments, thus indicating the periodic changes between fluvial sedimentation and downcutting linked with the changes between cold (glacial) and warm (interglacial) phases in the Pleistocene. Terraces above the floodline can today be important areas of economic activity or settlement. Many valley slopes and mountainous areas are still covered with gelifluction sheets, sometimes even when rather steep inclined (such slopes are thus at least as old).

Remains of *Tertiary* peneplains are preserved in some mountainous countries.

3.3.4 Soils

The Humid Mid-Latitudes are characterized by moderately fertile soils, certainly more fertile than those found in any other forest climates. In contrast to the Boreal Zone, in which raw humus predominates, more favourable mull and moder develop and soil acidification is seldom so extreme. When compared with the Seasonal Tropics and Humid Tropics/Subtropics, the more favourable clay mineral formation is of particular consequence. Instead of the low activity (double-layered) clay minerals from the kaolinite group, which predominate in the zonal soils of these latter zones, the cool, moist conditions in the Humid Mid-Latitudes promote the formation of high activity (three- and four-layered) clay minerals from the illite and chlorite groups, which give the soils a much higher cation exchange capacity. This means that the mid-latitudinal soils are capable of storing greater amounts of nutrient ions (in plant-available form).

Many soils thus naturally have relatively high nutrient contents, and nutrients added to the soil by farmers in the form of fertilizer can be adsorbed by the soil over longer periods (than is the case in the Humid Tropics, for example) and taken up by the crops little by little as the need arises. This possibility of adding nutrients through fertilization is a widely accepted and still growing practice in the Humid Mid-Latitudes, where – together with other measures – it has led to a *sustained increase in soil productivity* of in general up to several times the original value.

Most of the soils found in the Humid Mid-Latitudes are *young* (*post-ice age*) soils whose characteristics are strongly influenced by the parent material. The most fertile soils were formed on loess, marsh, moraines of the last Pleistocene glacial phase and carbonate-rich rock; those with a naturally low production potential, on the other hand, formed on outwash plains, eolian deposits (e.g. Pleistocene dune fields), moraines of earlier Pleistocene glacial phases and other carbonate-poor rock types. Moderately to well-developed (mature) soils are generally more fertile than older soils. On slopes subject to degradation, nutrient-poor soils tend to predominate (when the pedogenic processes cannot keep pace with the rate of degradation), regardless of the type of bedrock. The close connection between soil development and rock type (parent material), time (soil age) and relief (soil moisture and, again, soil age) has led widely to the creation of a small-scale (mosaic-like) soil distribution pattern (Fig. 76).

Zonal Soils. Of all soil types found in the Humid Mid-Latitudes, haplic (and, in North America, albic) luvisols, and dystric and eutric cambisols are most widely distributed. Both types could be viewed as the truly zonal soils of the Humid

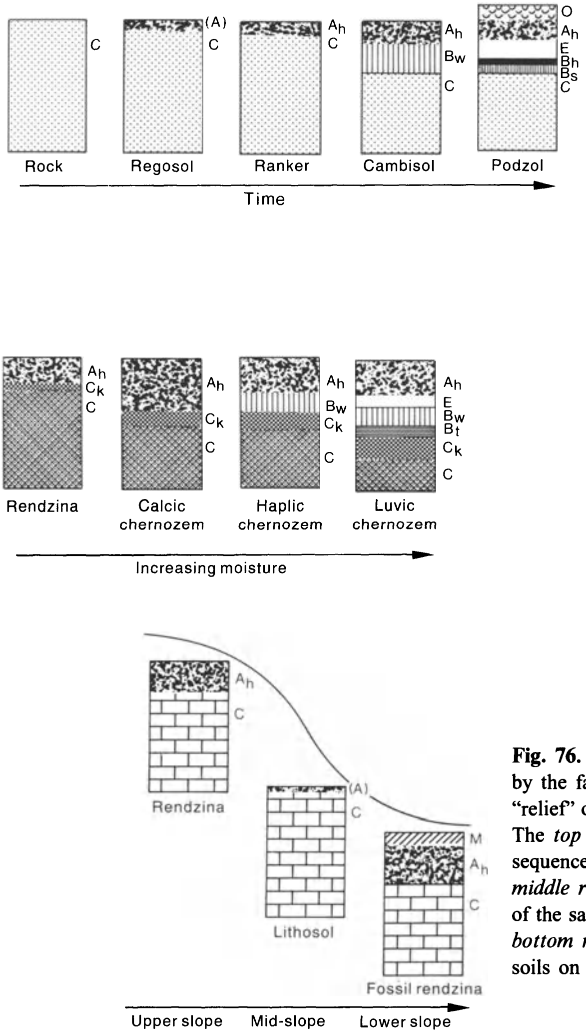


Fig. 76. Examples of the influence exerted by the factors "time", "soil moisture" and "relief" on soil formation. (Schroeder 1984). The *top row* shows a chronological sequence for soils on sandy material, the *middle row* a climatic sequence for soils of the same age on calcareous loess and the *bottom row* a relief sequence (catena) for soils on limestone

Mid-Latitudes.[15] Luvisols are the most common soil types on relatively moist (not water-saturated) substrates rich in $CaCO_3$ but are also found on substrates not containing $CaCO_3$. Cambisols, on the other hand, are more often found on poorer and dryer parent material.

Cambisols (Latin cambiare = change) have a dark humous A horizon which, with increasing depth, gradually changes over to a B_w horizon that is generally brown in colour (weathered in situ, *cambic B horizon*). This is followed, again without a distinct boundary, by the (unchanged) C horizon. Together, the A and B horizons can have a depth of up to one and one-half metres. The change to a brown colour is attributable to free iron oxides and hydroxides (mainly goethite) formed from the iron released during weathering of the primary minerals. The eutric cambisols can be differentiated from the dystric cambisols by their base saturations ($>50\%$ and $<50\%$, respectively). The former develop, for example, on basalt or glacial till, the latter on granite or sands; further development can lead to the formation of luvisols or podzols or of podzoluvisols.

The agricultural value of cambisols varies widely. *Eutric* cambisols (brown earths) are nutrient- and humus-rich (with mull as humus), slightly acidic to neutral, well-structured soils with a correspondingly high production potential. They are frequently used for agricultural purposes. Forestry predominates in those areas – usually mountains – where these eutric cambisols are shallow and stony. The acidic, coarse-textured *dystric* cambisols, whose humus occurs in the form of moder are nutrient-poor, however, they can be greatly improved by the addition of fertilizer (and water) to produce good agricultural yields.

Luvisols (Latin luere = wash out) are characterized by the translocation of clay (lessivation) from the A to the B horizon with the percolating soil water. This yields the corresponding horizon profile A_h E B_t C. In haplic (formerly *orthic*) luvisols, the (eluvial) E horizon, whose clay content is depleted, is somewhat lighter brown in color (in the *albic luvisols* it is even whitish) than the blackish, humous A_h horizon and the dark brown B_t horizon, in which the illuvial accumulation of clay occurs (= argic B horizon). Together, the A_h and E horizons can reach depths of about half a metre and the B_t horizon can be up to several metres deep. The base saturation (measured at pH 7) of the B_t horizon is 50% or more, at least down to a depth of 125 cm, and the cation exchange capacity is at least $24\,\mathrm{cmol(+)\,kg^{-1}}$. The topsoil, which is often sandy, and in which lessivation (leaching) has led to a relative increase in coarse grains, can be more acidic, on the other hand. In general, there is a tendency toward higher saturations in an increasingly dry climate.

Where leaching has been more severe, the eluvial horizon can become strongly bleached, and finally an albic E horizon may result, tonguing deep into the B horizon, which is diagnostic for podzoluvisols. This happens very frequently in the transitional region leading to the Boreal Zone where, in particular, the *eutric*

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[15] Since cambisols (eutric and dystric together with humic types) are found in all mountainous regions of the earth (from the Boreal Zone to the Humid Tropics), they can be viewed as characteristic of the Humid Mid-Latitudes only when they occur in combination with haplic luvisols.

podzoluvisols (with a base saturation still above 50% throughout the argic B horizon, at least within 125 cm of the surface) occupy a large area.

Luvisols develop from (eutric) cambisols or chernozems when carbonate leaching and moderate acidification make clay translocation possible (Schachtschabel 1992, p. 376), i.e. through degradation of these two soil types. Perhaps more often, however, they have evolved directly as mature phases of an age sequence next to rankers or rendzinas. In general, luvisols are considered as favourable sites for various types of agricultural utilization.

Lithomorphic Soils. On slopes, where continuous denudation prevents more mature soils from developing, and in areas in which hard rock hinders soil formation, at best only shallow soils with a poorly differentiated profile are found. Compared with more mature stages of soil formation, these A-C soils (no B horizon !) are more strongly influenced by the characteristics of the parent material; in other words, they have distinctly lithogenic properties. The two most common of these "lithomorphic" soil types are the *rankers*, which are found over silicate or quartz, and the *rendzinas* found over rock rich in calcium carbonate. Even younger stages of soil formation containing only a poorly developed A horizon are termed *lithosols*, if they were formed on solid rock, and *regosols* if they developed on unconsolidated rock.

According to the revised version of the FAO-UNESCO classification (1988), rankers, rendzinas and lithosols are now grouped together under the newly introduced major soil unit *leptosols* (Greek leptos = thin).

Hydromorphic Soils. Many of the soils found at the lower end of relief sequences (catenas) exhibit properties caused by prolonged water saturation from groundwater, flooding or waterlogging. Table 23 provides an overview of these "hydromorphic" soils and the conditions under which they are formed.

Soils in Transitional Areas. The poleward border areas of the Humid Mid-Latitudes (i.e. in the Northern Hemisphere, those next to the podzol-cambisol-histosol zone) include large occurrences of podzols and histosols, wherever both a sandy substrate and a maritime climate predominate.

More equatorwards, acrisols are found (in rather small patches), where the Humid Subtropics follow (see Chap. 3.8.4), or *greyzems*, *luvic chernozems* and *luvic phaeozems*, where a more arid climate (steppes) adjoins (for chernozems and phaeozems see Chap. 3.4.4).

Greyzems are grey A-C soils having a mollic A horizon, and showing uncoated (bleached) silt and sand grains on structural ped surfaces. In Eurasia and North America, these soils occupy a narrow, discontinuous belt in the transitional region between the temperate deciduous forests (in some places: boreal forests) and the steppes. As is the case for the two other soils found in this forest steppe zone, i.e. the luvic chernozems and luvic phaeozems, clay translocation has led to an argic B horizon. In contrast to these two other soil units, greyzems are found predominantly in the moister, forested regions of the transitional zone. They are

Table 23. Hydromorphic soil types in the Humid Mid-Latitudes. (Schroeder 1984)

Determining factor	Waterlogging alternating with well-drained phases	Groundwater (GW) with GW table at different depths and fluctuating at various amplitudes				
		Mineral soils			*Organic soils,*	
		With flooding		Without flooding	GW permanently above the mineral subsoil	
Type of influence	Temporary, periodic	GW table fluctuates with large amplitude (in river valleys), occasional flooding	GW table fluctuates with moderate amplitude (in tidal areas), and frequent flooding	GW table fluctuates with small amplitude	Relatively nutrient-rich groundwater (topogenic)	Nutrient-poor groundwater (ombrogenic)
Processes	Alternating oxidation and reduction processes	Fluvial sedimentation; periodically alternating redox processes, with oxidation processes predominating	Marine sedimentation; periodically alternating redox processes	Permanently reducing moisture regime in lower subsoil, and alternating redox processes in upper subsoil	Accumulation of mainly eutrophic organic substances; reduction processes predominate	Accumulation of mainly oligotrophic organic substances; reduction processes predominate
Characteristics	Mottled brown grey (argic) B horizon, due to segregation of iron; no differentiation into oxidation or reduction horizons	Stratification, usually no reduction horizon, yellow or (red) brown mottles due to oxidation and segregation of iron	Stratification, oxidation horizon above blue-black sulphuric horizon	Grey or blue (reduction) horizon where permanently saturated and, above that, mottled horizon where aeration (oxidation) occurs for some time	Reed and sedge peat horizons above sapropel	Sphagnum peat horizon (histic H horizon)
Site description	Level or depressed topography with poor drainage	Valley floor which receives fresh fluvial deposits at regular intervals	Salt marsh with tidal deposits	(Not alluvial) clay-rich depressions with groundwater at shallow depth	Fen	Raised bog
Soil unit	Planosol	Fluvisol		Gleysol	Eutric histosol	Fibric histosol

considered fertile. In adequately level terrain, they are used for cultivation (mainly of cereals) and in hilly areas for forestry.

Anthrosols. In many areas the soils have been greatly changed through removal or disturbance of original surface horizons etc. For example, the planting of conifers in areas naturally carrying deciduous forests has initiated secondary podzolization processes, or intensive soil improvement measures for agricultural purposes, such as frequent and deep ploughing, fertilization, irrigation or drainage, have produced significantly different soil profiles. Soils of such profound modification are termed 'anthrosols'. They have an especially wide distribution in the Humid Mid-Latitudes.

3.3.5 Vegetation and Animal Life

3.3.5.1 Structural Characteristics

Given their prevailing climatic conditions, the Humid Mid-Latitudes are on the whole a natural location for forest growth. It was the man who destroyed these forests by relentless cutting and burning during many centuries or even millenia of human history. In our time, in most regions, *commercial* forests only are found, restricted to those areas where no agricultural or other interests took precedence.

Natural Forests. No more than a few vestiges of the original forests are found today. These include, for example, floodplain forests which have occasionally been preserved in some valleys, remnants of oak-birch forests on marginal (sandy, dry) sites, and the few "primeval forests" put under official protection, such as are found in Bialowieza in Poland, in order to show us or future generations what our environment was like before we destroyed it.

The original forests, presumably in all their different types, were characterized by a much wider structural diversity, due to a greater species richness, mixed age composition among the woody plants (which then formed several tree layers), uneven distribution (density) of the trees (ranging from thickets to glades), a lush herbaceous layer (forbs in the more open, and mosses, lichens and fungi in the denser parts of the forest), and a large number of animal species, particularly birds, butterflies, snails and amphibians. According to the predominant life form in the tree layer, the prevailing forest types were temperate deciduous forests, mixed forests made up of broadleaf deciduous and needleleaf trees or (as in the Pacific Northwest region of North America) temperate coniferous forests; less often, there were temperate rain forests consisting of evergreen broadleaf trees.

Commercial Forests. The commercial forests of today, frequently dominated by one single tree species only (often a fast-growing conifer), with all trees of the same age and canopy height and usually planted in parallel rows, with at best a discontinuous layer of herbaceous plants, bear little similarity to the original forest types. As is the case for the meadows and fields, these artificial forests are severely depleted of biological diversity. On the other hand, some of the relatively few wild plants and animals still left are present in much larger populations than before, e.g. red deer and roe deer in many Central European forests. These can cause considerable damage to the tree growth.

Heath and Moorland Vegetation. A broad strip of the European Atlantic coast contains extremely little forest, and those parts of the shoreline which are still in their near-natural state are covered with heath or moorland vegetation. Although this vegetation is rather stable, its origins, like those of the garrigue in the Mediterranean region, are nonetheless anthropogenic in many places. Most likely, forests were predominant here in former times as well. The felling of these forests took place very early in human history, and it was followed by a rapid and irreversible degradation of the soils. Due to the cool, moist climatic conditions, the widely prevalent coarse and leached early ice age deposits, and the secondary heath vegetation, it was generally podzols that resulted from this degradation. The podzolization, in turn, stabilized the heathlands and moorlands.

Seasonality

A particular characteristic of the current and former forests is the fact that most of their broadleaf trees and shrubs lose their leaves at the end of the warm season (*autumnal leaf shedding*) and do not grow new leaves until the following spring, when they sprout from protected buds (this is not the case in the rare rain forests; see below). Leaf loss is not facultative but obligate. It is initiated in fall by the shortening of the days and represents an adaptation to the unfavourable conditions of winter; most leaves are not resistant either to cold or to frost-induced dehydration and thus are incapable of surviving long periods at temperatures below 0 °C (Walter 1979, p. 187). Before the leaves fall, some of the organic substances they contain are broken down and some mineral elements such as N, Fe, P and K are *resorbed* by the branches (see below). This is accompanied in many species of tree by a very obvious change in leaf colour (to the reds and yellows of fall foliage). The scars remaining after the leaves are lost are sealed off by a cork layer. This allows winter transpiration losses to be reduced even further than is accomplished through leaf shedding.

As a rule, the above-ground portions of herbaceous plants die in winter; in spring, shoots start at the soil surface (in the case of hemicryptophytes) or from perennating organs (tubers, bulbs, rhizomes) in the soil (geophytes). Therophytes are as good as lacking in the forests (even the original ones); chamaephytes can be found but are not typical.

The obvious physiognomic contrasts between the winter and summer seasons (Table 24) are accompanied by important functional differences. During the *winter months*, photosynthesis ceases, the biological/chemical processes in the soil are slowed and many small mammals go into winter dormancy (badgers, squir-

Table 24. Changing annual aspects of life under central European climatic conditions. (Walter and Breckle 1986)

Season	Months	Vegetation	Birds	Arthropods
Winter	November–March	Winter dormancy	Non-migratory birds and winter visitors	Cold torpor; some species overwinter within the soil
Early spring	March and April	Spring flowers particularly in deciduous forests prior to foliation	Return of migratory birds, delimitation of breeding territories	Re-activation of imagoes that have survived the winter, or hatching of various (larvae) stages
Spring	May and beginning of June	Development of tree leaves	Nest building and brooding	Reproduction
Early summer	Mid-June–Mid-July	Trees fully foliated, ground shady	Raising of young birds	Mass reproduction in some cases
Late summer	Mid-July–Mid-September	Fruits and seeds mature	Migratory birds leave	Still high population densities, some individuals die off after eggs are laid
Fall	September and October	Leaf shedding	Non-migratory birds, first winter visitors	Increased die-off, start of cold torpor, retreat into the soil

rels) or hibernation (hedgehogs, dormice). Almost all the above-ground poikilotherms, such as amphibians, snails, insects and spiders, become torpid or – as is the case with most insects and spiders – the imagoes die, leaving only eggs, larvae or pupae to survive the winter under tree bark or in the soil. Most of the insectivorous bird species migrate in the autumn.

In contrast, most soil fauna remain active during the winter, even though the low temperatures slow their life functions to a considerable extent and force some of them to live deeper in the soil than during the summer. Earthworms, for example, move down to depths of about 1 m, and moles also relocate their burrows to this level (see Fig. 77 for the composition of the soil fauna). Figure 78 shows the seasonal changes that many animal species undergo between their above-ground and below-ground living phases.

In *spring*, life first reawakens on the *forest floor*. Because there is little or no blockage for incoming light at this time (the woody plants have not yet sprouted their leaves, Fig. 79), the litter layer and the top soil warm up much more rapidly than do the overlying shrub and tree layers. The most obvious indication of this initial advantage of the forest floor is given by the numerous herbaceous plants

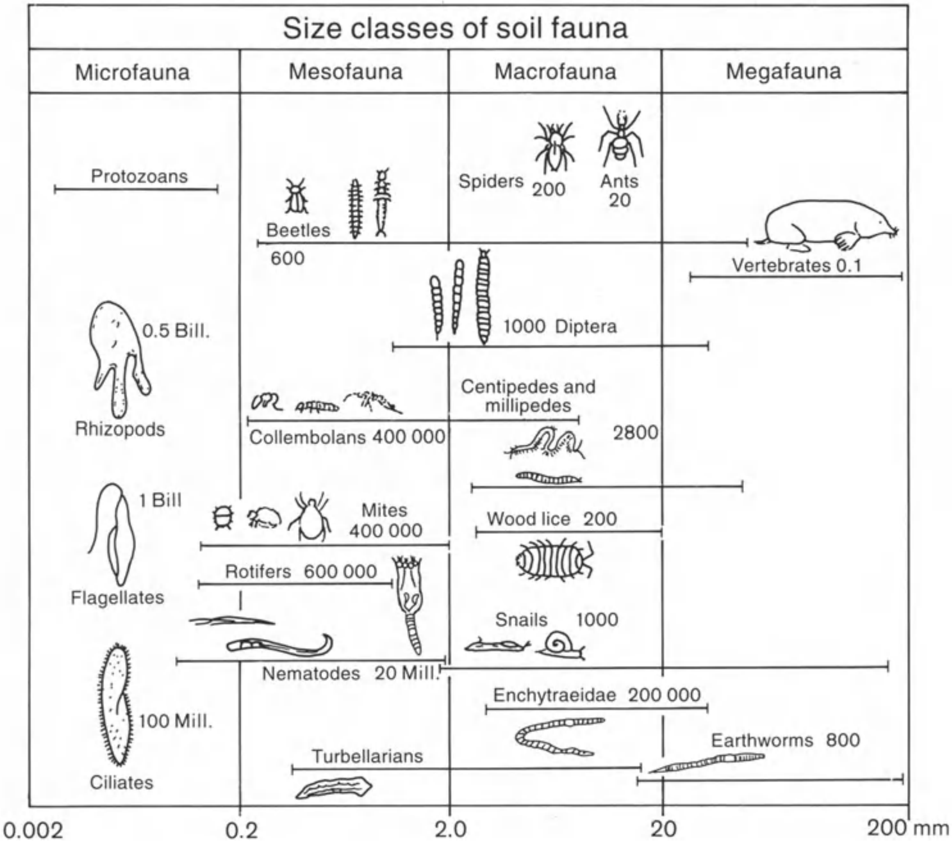


Fig. 77. Size classes of soil fauna showing the most common types in Central Europe. (Walter and Breckle 1986). The scale in mm is given at the *bottom edge* of the drawing; the *lines under individual animal names* indicate the size range of the representatives of the animal group. The *numbers entered alongside* the individual animal groups indicate the average number of individuals in a block of soil measuring 1 m^2 in area by 30 cm in depth. Soils in the Humid Mid-Latitudes are distinguished from others by the particularly high activity of the soil fauna (this is possible because frost rarely has any effects and there are no restrictions due to dryness)

which blossom in spring (mainly geophytes with shallow root systems). As the year advances, so the incoming radiation is absorbed by progressively higher layers in the forest, from the next developing leaves of the lower shrubs and young trees all the way through to the foliage in the uppermost tree canopy which develops last (Tischler 1984, p. 187). After that, forests with dense crown canopies, such as is the normal case, let so little light through to the stem area and to the forest floor that only plants capable of growing in extreme shade and having a low primary production can survive there.

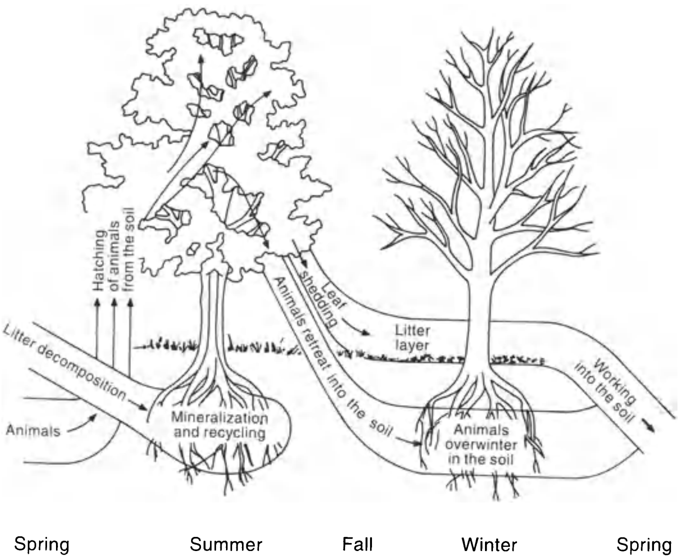


Fig. 78. The annual alternation between the above-ground and below-ground phases of many animal species together with the seasonality of plant growth and return of nutrients through wastes. (Walter and Breckle 1986)

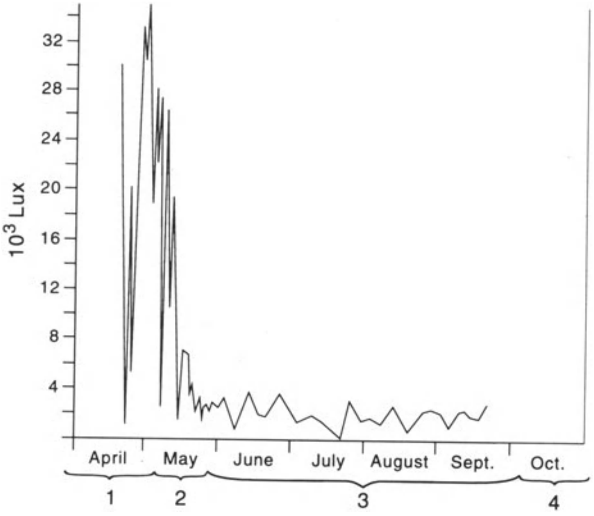


Fig. 79. Change in intensity of daylight in a Russian mixed oak forest during spring and the summer, all values measured at noon. (Walter and Breckle 1983). *1* Spring light phase (prior to leaf development); *2* transition phase (from opening of buds to the start of foliation); *3* summer shade phase; *4* bright fall phase after leaf shedding (see section of curve at *top right*). In evergreen coniferous forests of the Boreal Zone, the forest floor does not exhibit these changes under light conditions

In autumn, woody plants lose their leaves, seeds and fruits, and the above-ground portions of herbaceous plants die, so that most of the above-ground production of the summer is returned to the soil. In many cases, 3 to 5 t (dry weight) of leaf mass per hectare falls to the forest floor within a few weeks, creating a continuous layer of litter several centimetres thick. Decomposition of this layer takes 1.5 to 3 years, depending on the species, namely in increasing order of time: alder, elm, hornbeam, linden, maple, ash, birch, beech and oak. After the trees have shed their leaves, some evergreen plants in the undergrowth, such as asarum (hazelwort) (*Asarum* sp.), evergreen (*Vinca* spp.) and ivy (*Hedera* sp.), can make use of the increased availability of light for several winter months, as long as the temperatures do not fall below freezing.

Since the life cycles of herbaceous plants end at very different points in time, litter input from these plants is distributed over a longer period. Herbaceous wastes are also more rapidly decomposable.

As a rule, each plant species runs through the cycle of budding – flowering – seed (fruit) maturity – wilting/leaf shedding only once during a growing season. The times at which each of these development phases occurs, however, vary depending on the species in question and – even more – on the local climatic conditions.

For example, the members of a species start to grow sooner in areas in which spring warming starts earlier than elsewhere; similarly, the later stages of development in the annual growth cycle, such as seed maturity or leaf shedding, occur later in areas where autumnal cooling starts later (Fig. 80). Data collected through *phenological observations* (of regional differences in the times at which particular stages of development occur for selected plant species) can thus provide insight into regional differences in climate. This kind of bioindication is used by the meteorological services in many countries of this Humid Mid-Latitudes.

In principle, cyclical aspectual changes of plant growth occur in all those regions of the earth where seasons with conspicuously different hygric or thermal conditions alternate with one another; i.e. everywhere except the Humid Tropics, Humid Subtropics and the deserts of the Tropical/Subtropical Arid Lands. However, aspectual changes are relatively inconspicuous in those areas where the floras contain a high proportion of evergreen species, such as in the Mediterranean-Type Subtropics, the Boreal Zone and the tundras of the Polar/Subpolar Zone, or where vegetation is sparse due to dry conditions, such as in the deserts and semi-deserts of the Arid Mid-Latitudes. Despite its broad distribution, the phenomenon of seasonality thus tends to be more a zonal feature, characteristic of the mid-latitudes (and here, especially of the Humid Mid-Latitudes) and of the Seasonal Tropics.

Floral History

The three (four) major areas of temperate deciduous forest – North America (east and west), Europe and eastern Asia – were originally all interlinked. Up to the

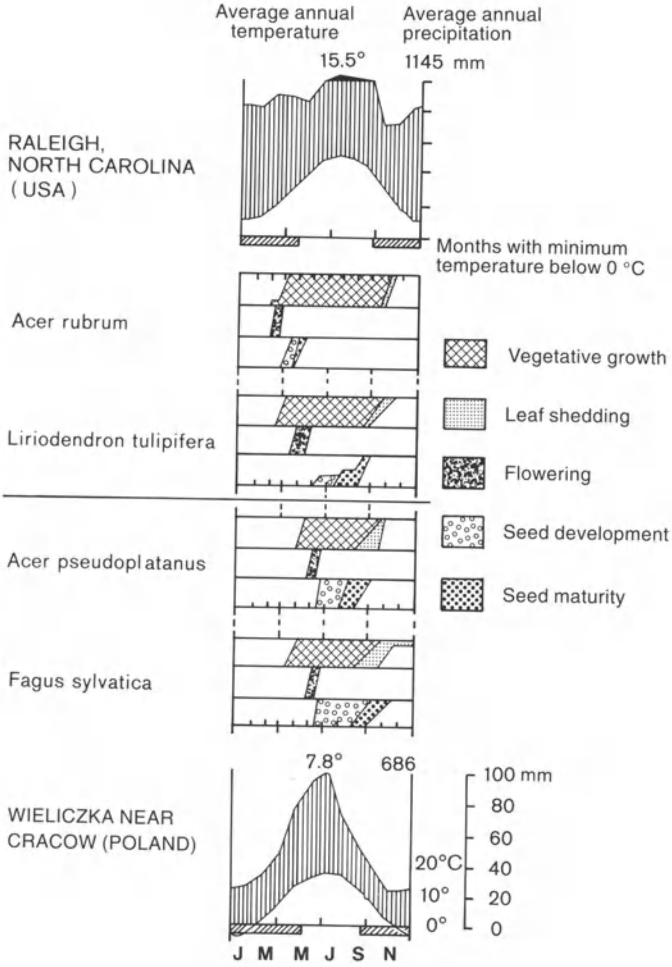


Fig. 80. Phenological data for two (ecologically comparable) tree species in the eastern USA and southern Poland. (Lieth 1971). The more favourable temperature conditions in Raleigh cause growth to begin earlier in spring and continue slightly longer in the autumn

Miocene, they belonged to a common floral belt located somewhat further north of their present position and encircling the globe in the northern hemispheric landmass, which at that time was practically continuous. It was not until the onset of cooling in the Late Tertiary that this *Arcto-Tertiary flora* shifted southwards while, at the same time, the American and Eurasian continents drifted apart, thus isolating the individual areas. This explains that all three (four) northern hemispheric occurrences of Humid Mid-Latitudes, although nowadays far apart from each other and separated by either oceans or arid lands, have many plant taxa in common (or, in other words, many plant taxa have a disjunctal distribution, including temperate locations in North America, Europe and East Asia (Fig. 81).

During the cold phases of the *Pleistocene*, these floras shifted even further southward than at present. In Europe, mountain ranges running east to west (Alps, Carpathians) hindered this southward movement and many species of plants died out. This explains why, in comparison to the floras in the other two distribution areas, where there were no natural barriers of this kind, the European flora contains relatively few species (Table 25).

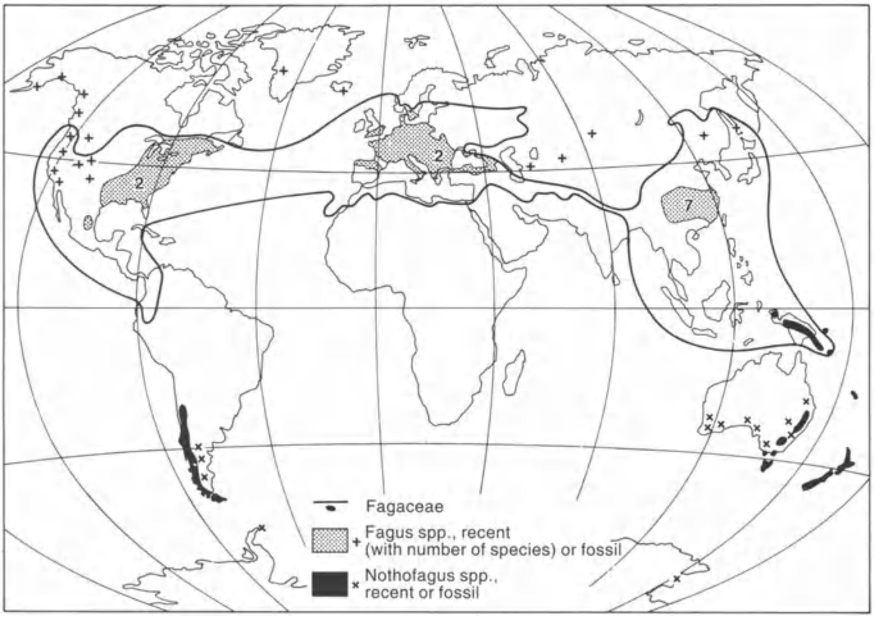


Fig. 81. Present-day distribution of Fagaceae showing the areas containing *Fagus* (beech) and *Nothofagus* (southern beech) and fossil finds of both genera. (Meusel et al., taken from Strasburger 1983)

Table 25. Examples of different species diversity between North American and European deciduous forests. (Tischler 1984)

	Deciduous forests	
	In North America	In Europe
Tree species	800	51
Oak species	70	3

Rain Forests

The (potential) natural vegetation in those areas of the Humid Mid-Latitudes where the winters are mildest (t_m in the coldest month ≥ 5 °C, rarely any frost) are not deciduous forests, as is the case in all other parts, but rather evergreen broadleaf forests (temperate rain forests). These are rich in epiphytes and have a lush undergrowth often containing ferns (including tree ferns). At present they are most widely distributed in New Zealand (South Island), Tasmania and in southern Chile. In all other areas only remnants, if at all, exist.

In Europe, temperate rain forests originally covered a narrow strip along the coast from western France to southwest Ireland. They contained a high percentage of woody Mediterranean evergreens (e.g. *Arbutus unedo*, *Erica arborea*). In North America, temperate rain forests rich in coniferous trees grew along the Pacific coast from Oregon to British Columbia. Some of them still exist.

3.3.5.2 Forest Water Balance

The water balance of the plant stands and of the soil root zone exhibits strongly seasonal fluctuations: great water surpluses in *winter* replenish the soil water reserves (ΔW_S) and supply (by draining = V) an increasing runoff, while the rising losses (water leaving the ecosystem) in *summer*, caused especially by interception and transpiration, can lead to water deficits of varying degrees of severity (Figs. 82 and 83). In spring, the soil water content is usually at its maximum (at the level of the retention capacity) for some time ($\Delta W_S = 0$).

The conditions in spruce-rich forests differ from those shown in Fig. 82 on several counts. For example, stemflow for spruces is practically zero, since the "hanging" branches conduct the water away from the trunk. Interception by the crowns of spruces is higher, both in summer and, since they are evergreen, especially in winter, than in the case of broadleaf deciduous trees; spruces observed as part of the Solling Project (Ellenberg et al. 1986) intercepted an annual average of 27.2% of the precipitation, namely more than 1.5 times the value of 17.1% found for beeches; the latter value is in good agreement with those shown in Fig. 82. As expected, the percentage losses in interception increase in dry years for both tree species.

Another difference between spruce stands and beech forests is the higher total evaporation (in dry years 70% of the precipitation as compared to 58% for beeches) and higher transpiration rates (fluctuating from year to year between 274 and 384 mm as compared to only 245 to 311 mm for beeches); that is to say, in spruce forests (1) a larger amount of energy is consumed for evaporation (leaving a correspondingly lower amount available for warming) and (2) a smaller amount of precipitation is drained to the groundwater and to rivers.

If a relation is established between, on the one hand, the amounts of water transpired by spruces and beeches during a growing season and, on the

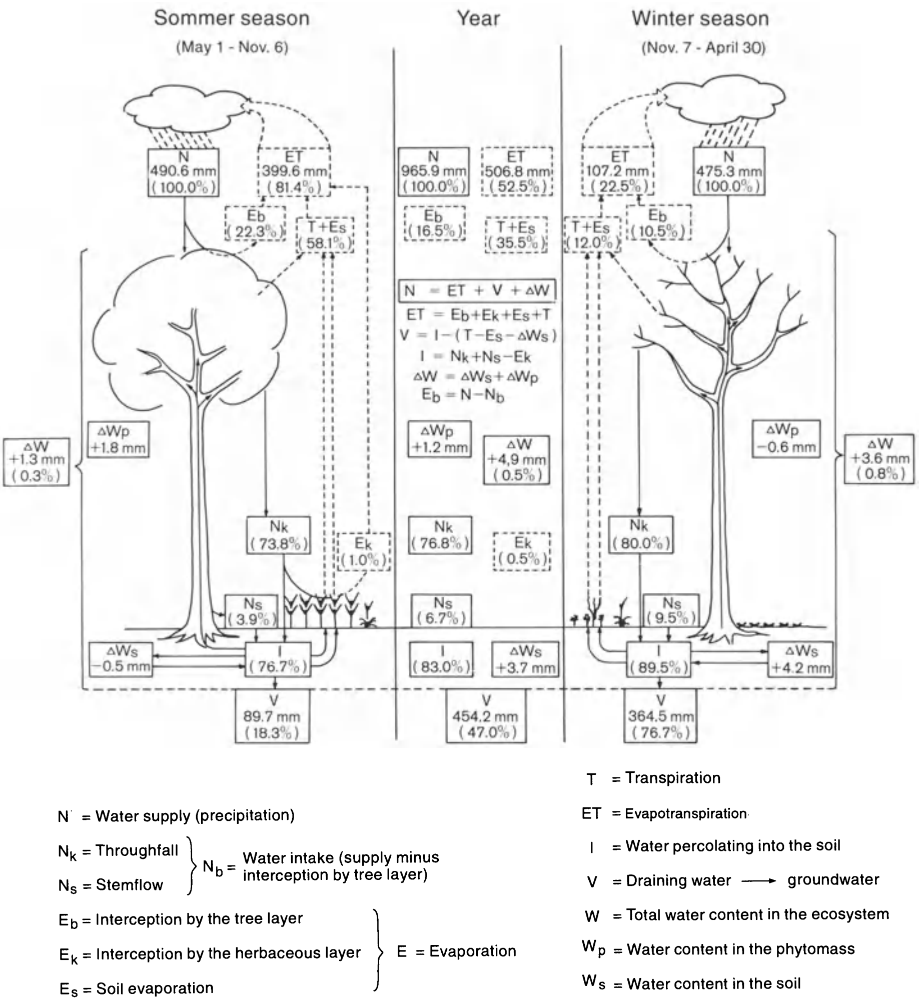


Fig. 82. Water balance in a Belgian oak forest, both with leaves and without (winter). (After Schnock 1971). Annual average precipitation (1964–1968) is 965.9 mm. Of this amount, 506.8 mm (52.5%) evaporate, 454.2 mm (47.0%) run off and 4.9 mm (0.5%) are stored in the biomass. Precipitation is more or less evenly distributed over the summer and winter seasons, but the water balances are nonetheless vastly different: interception losses and transpiration are about four times as high in summer than in winter (399.6 mm as opposed to 107.2 mm). Consequently, much more water percolates into the soil during winter and leaves the ecosystem by drainage (364.5 mm as opposed to 89.7 mm). As a result, the runoff is significantly higher at this time. Soil evaporation is low during both seasons due to the presence of an insulating litter layer

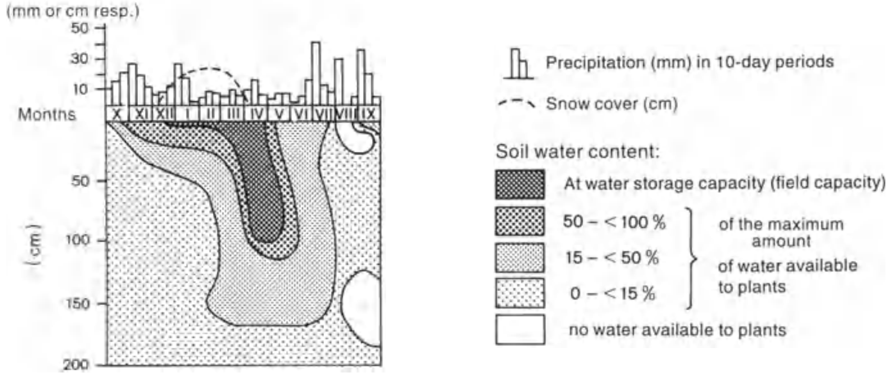
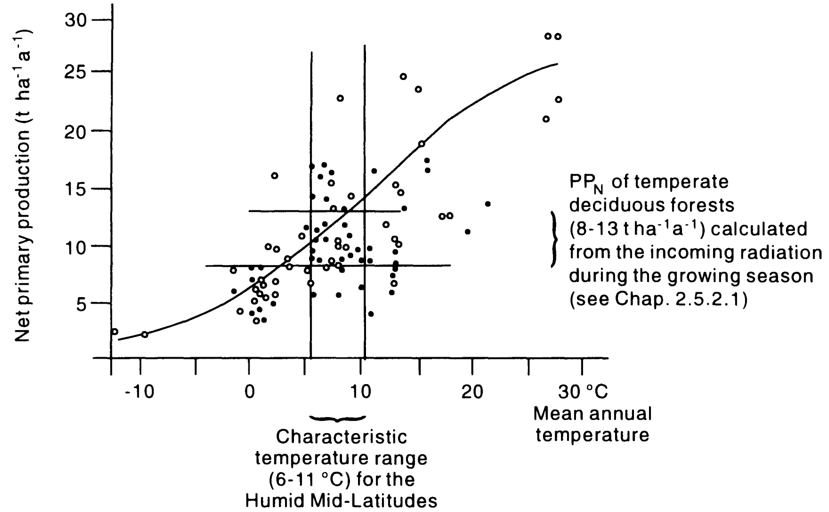


Fig. 83. Chronoisopleths of soil water content under a central Russian deciduous forest during the hydrological year 1958/59, in which almost the normal amount of precipitation fell. (Goryschina 1984, taken from Walter and Breckle 1983). Deciduous forests may suffer temporary water deficits in the summer, when water intake of the forest ecosystem drops below evapotranspiration of the stand, and the soil water reserves, built up during the previous winter, are consumed. Plants react to the decreasing water reserves in the soil by limiting their transpiration so that the soil water content seldom drops below the wilting point. Water consumption is thus highest in early summer when, in the example shown here, it is around 6 mm d^{-1}, compared to only 1–2 mm d^{-1} in late summer

other hand, the amounts of plant substance each produces during the same time, another important difference between the two species is found: Spruce require 220 l kg DM^{-1}. whereas beech need only 180 l kg DM^{-1}, i.e. the latter have a significantly lower *transpiration ratio of production* (or, in other words, higher water-use efficiency); for comparison, C_3 herbaceous plants need about 300–400 l for every kg of dry matter they produce.

3.3.5.3 Stand Reserves, Material and Energy Turnovers, Ecosystems

The *primary production* values calculated from the solar energy supplied during the growing season (Table 7 in Chap. 2.5.2.1) are in very good agreement with the relationship established on a worldwide basis between PP_N and annual average temperatures (Fig. 84): the area on the graph where the temperatures (assumed range for the Humid Mid-Latitudes: 6 to 11 °C) and the calculated PP_N values for temperate deciduous forests (8 to 13 t ha^{-1} a^{-1}) intersect includes a large number of the PP_N values actually measured in this temperature range. The slight preponderance of higher PP_N values in the graph could be due to the fact that many of the stands studied were young to mature and thus of above-average productivity.



○ Data points used by Lieth in his analysis

● Data from the IBP woodlands data sets added by O'Neill and De Angelis 1981

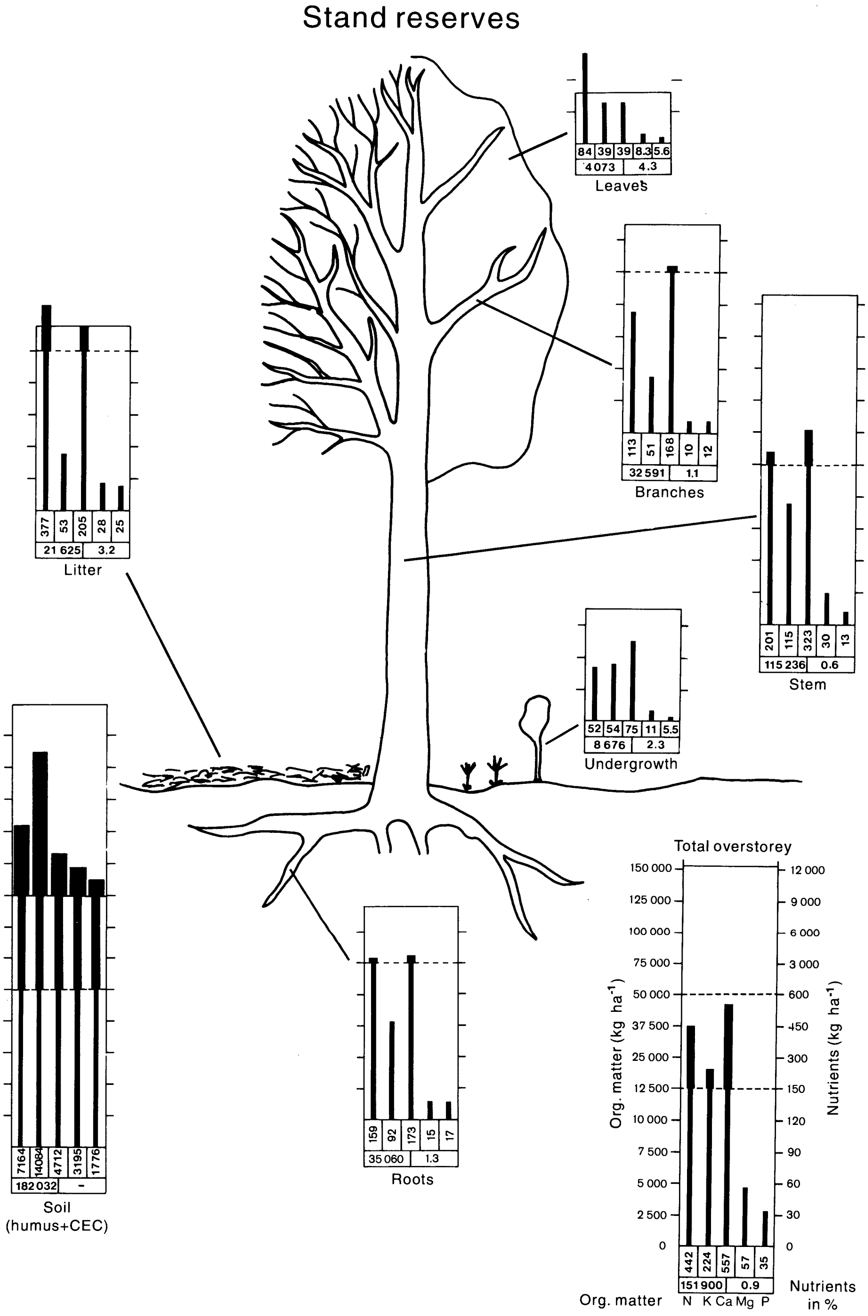
Fig. 84. Relationship between net primary production and annual average temperature. (Lieth 1964, taken from O'Neill and De Angelis 1981); the position of the Humid Mid-Latitudes in this graph is denoted by the *area within the square*

Reserves and Turnover Processes in General

Several detailed studies have been conducted on the reserves and turnover processes in temperate deciduous forest ecosystems in Europe and the USA (e.g. Duvigneaud and Denaeyer-de-Smet 1971; Satchell 1971; Sollins 1972; Duvigneaud and Kestemont 1977; Nihlgard and Lindgren 1977; Bormann and Likens 1979; Jakucz 1985; Ellenberg et al. 1986; Falinksi 1986).

The values for nutrient reserves and turnover processes presented in the following and in Fig. 85 are mean values for 14 temperate deciduous forests in

Fig. 85a,b. Matter reserves and turnovers in broadleaf winter-deciduous forests in the Humid Mid-Latitudes (mean values from up to 14 separate stands in Europe and North America, computed and compiled from data in Cole and Rapp 1981; see also Figs. 63 and 143). Organic matter is represented by boxes and the nutrients (N, K, Ca, Mg and P, *from left to right* in that order) by individual columns. **a** Stand reserves. The scales are reduced to 1:5 starting at 150 kg (nutrients) and 12 500 kg (organic matter) and to 1:100 starting at 600 kg and 50 000 kg respectively. The stand reserves for the tree layer (overstorey) are not equal to the sum of the individual reserves because only 12 values were available for averaging of the branches and stems. Nutrient data on *Soil* (*humus* + *CEC*) refer to values presented by Cole and Rapp under the heading soil-rooting zone. It is unclear whether these values always refer to the nutrients bound in the soil organic matter and the exchangeable fraction.


Stand reserves
84 39 39 8.3 5.6
4073 4.3
Leaves
113 51 168 10 12
32 591 1.1
Branches
201 115 323 30 13
115 236 0.6
Stem
377 53 205 28 25
21 625 3.2
Litter
52 54 75 11 5.5
8 676 2.3
Undergrowth
7164 14084 4712 3195 1776
182 032 -
Soil
(humus+CEC)
159 92 173 15 17
35 060 1.3
Roots
Total overstorey
150 000
125 000
100 000
75 000
50 000
37 500
25 000
12 500
10 000
7 500
5 000
2 500
0
12 000
9 000
6 000
3 000
600
450
300
150
120
90
60
30
0
Org. matter (kg ha^{-1})
Nutrients (kg ha^{-1})
442 224 557 57 35
151 900 0.9
Org. matter
N K Ca Mg P
Nutrients in %

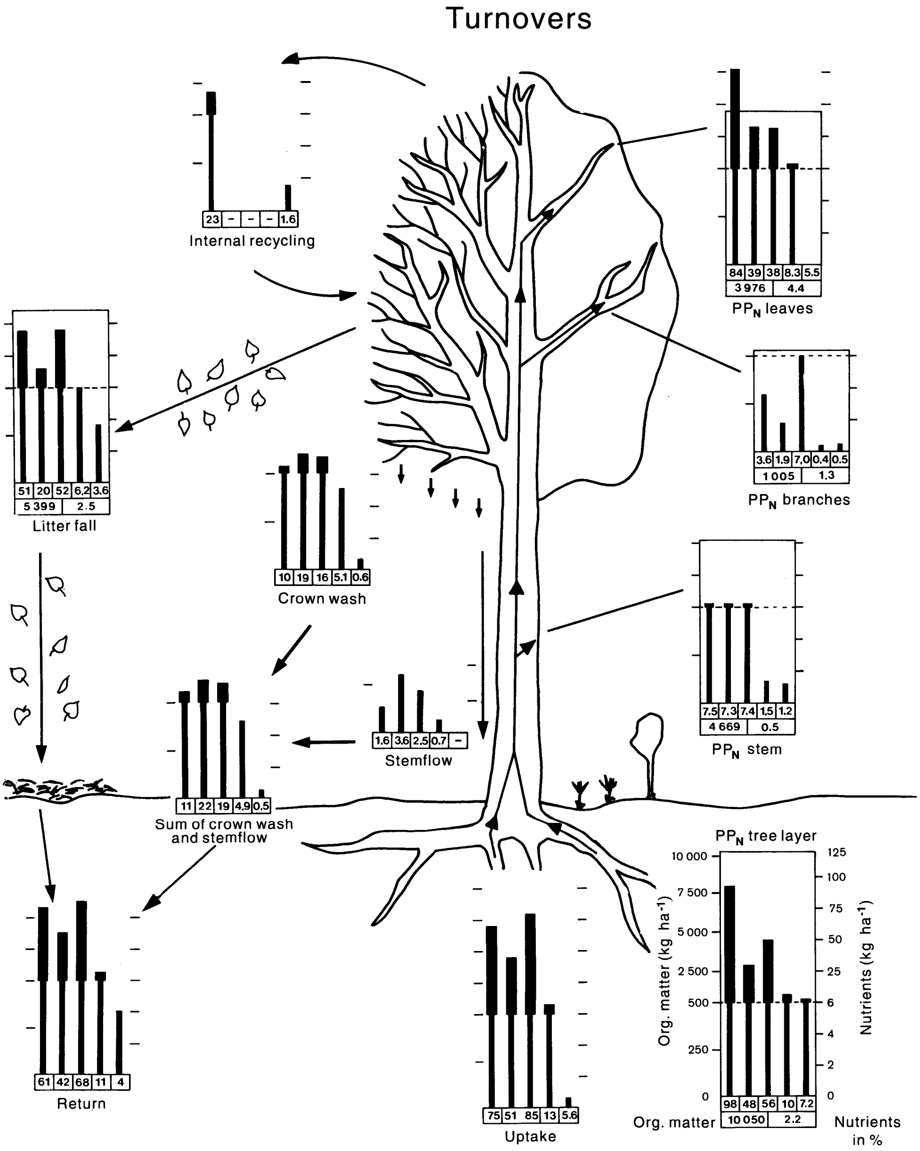


Fig. 85b. Turnovers. The scales are reduced to 1 : 12.5 starting at 6 kg (nutrients) and 500 kg (organic matter). The (minor) differences between the values for PP_N *tree layer* and *Return*, on the one hand, and the sums of the individual values for each, on the other, can be attributed to the fact that the averages taken were based on different sample sizes (depending on the data available for the investigations covered here)

Table 26. The 14 study sites and forest types used in nutrient cycling synthesis for temperate deciduous forests in the Humid Mid-Latitudes (see Fig. 85, Tables 27–29 and the text). (Compiled from Cole and Rapp 1981)

Location	Tree species	Stand age (years)	Studied by[a]
Oak Ridge (USA)	*Liriodendron tulipifera*	50	Reichle et al.
Oak Ridge (USA)	*Liriodendron-Quercus*	30–80	Harris
Oak Ridge (USA)	*Quercus-Carya*	30–80	Harris
Oak Ridge (USA)	*Quercus prinus*	30–80	Harris
Coweeta (USA)	*Quercus-Carya*	60–200	Swank
Hubbard Brook (USA)	*Acer-Betula-Fagus*	110	Whittaker, Likens
Belgium	*Quercus* etc.	Mixed	Duvigneaud
Belgium	*Quercus* etc.	80	Duvigneaud
Solling (Germany)	*Fagus sylvatica*	59	Ulrich
Solling (Germany)	*Fagus sylvatica*	80	Ulrich
Solling (Germany)	*Fagus sylvatica*	122	Ulrich
Merlewood (GB)	*Quercus-Betula*	Mixed	Satchell
Kongalund (Sweden)	*Fagus sylvatica*	45–130	Nihlgård
Cedar River (USA)	*Alnus rubra*	30	Turner

[a] See Reichle (1981) for publications.

Europe and North America which were studied as part of the International Biological Programme. Table 26 shows which forests were involved. The data evaluated here stem mainly from the tabular overviews prepared for the 14 forest sites by Cole and Rapp (1981) and De Angelis et al. (1981).

Figure 85 (like its counterparts, Figs. 63 and 143) is a highly simplified depiction of the nutrient reserves and turnover processes:

- only the macronutrients N, K, Ca, Mg and P are included;
- data on primary production include only the above-ground tree layer without bark growth (the undergrowth and root layers are missing);[16]
- animal consumption is ignored;
- nutrient contents in the soil are not presented separately for humus and mineral exchangers;
- atmospheric inputs and losses due to leaching are ignored;
- biological fixation of N_2 is not included.

Despite these limitations, the most important characteristics of the nutrient cycle in temperate deciduous forests can be clearly seen from Fig. 85. They become even more obvious when comparing this figure to that for boreal coniferous forests in Chap. 3.2.5.2 (Fig. 63). The following description follows this line (Tables 27, 28 and 29).

Organic and Mineral Reserves. In temperate deciduous forest ecosystems, the (standing) phytomass of the tree layer represents almost 40% of the total (living

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[16] In general, the amount of phytomass and production accounted for by the herbaceous plant and shrub layers is low due to the adverse light conditions in the stem area during the growing season.

Table 27. Uptake, requirement and return of nutrients in temperate deciduous forests of the Humid Mid-Latitudes and in evergreen coniferous forests of the Boreal Zone. (Compiled from data published by Cole and Rapp 1981). Uptake and requirement have to be seen in relation to the above-ground PP_N of the tree layer, found at the same time, i.e. 10 050 and 1207 kg ha^{-1} a^{-1} (dry matter) respectively. The values for nutrient return should be compared with those for litter fall, i.e. 5399 and 322 kg ha^{-1} a^{-1} (dry matter) respectively. In this latter case, however, one has to bear in mind that the contributions of crown wash and stemflow, especially for K and Mg, are considerable

	Uptake (kg ha^{-1} a^{-1})		Requirement (kg ha^{-1} a^{-1})		Return (kg ha^{-1} a^{-1})	
	Temperate deciduous forests	Boreal coniferous forests	Temperate deciduous forests	Boreal coniferous forests	Temperate deciduous forests	Boreal coniferous forests
N	75.4	5.1	97.9	4.7	61.4	2.9
K	50.7	2.1	47.8	2.4	41.6	1.1
Ca	85.0	6.1	55.6	3.1	67.7	3.8
Mg	13.2	0.6	10.4	0.6	11.0	0.3
P	5.6	1.1	7.2	0.6	4.0	0.7

Table 28. Mean turnover (residence) time for the litter layer and the nutrients it contains in the Humid Mid-Latitudes and the Boreal Zone. (Cole and Rapp 1981)

Ecozone	Forest type	Turnover time in years						
		Number of sites	Litter	N	K	Ca	Mg	P
Humid Mid-Latitudes	Broadleaf deciduous forests	14	4.0	5.5	1.3	3.0	3.4	5.8
	Coniferous forests	13	17.0	17.9	2.2	5.9	12.9	15.3
Boreal Zone	Coniferous forests	3	353	230	94	149	455	324

and dead) organic matter, compared to slightly over 20% in boreal coniferous forest systems. The difference is attributable to the extremely large amounts of litter present in the Boreal Zone, both in absolute terms and in relation to the phytomass: together with the soil humus (A_h horizon), litter accounts for at least 50% and, in our example, for more than 60% of total organic matter; the amount of dead matter in temperate deciduous forests, on the other hand, is always less than 50%.

Another obvious difference is the fact that the amount of needles in the phytomass of the tree layer in boreal coniferous forests is much higher than the corresponding amount of leaves in temperate deciduous forests (in t ha^{-1}):

	Needle or leaf mass	Phytomass in tree layer
Coniferous forest	8.2	51.3
Deciduous forest	4.1	152.0

Table 29. Average nutrient content of phytomass and litter and the average nutrient requirement for the PP_N of the tree layer in coniferous forests of the Boreal Zone and in broadleaf deciduous forests of the Humid Mid-Latitudes. (Compiled from data published by Cole and Rapp 1981). All values are given in % dry matter

Nutrients	Average of 3 boreal coniferous forests				Average of 14 temperate deciduous forests			
	Above-ground phytomass in the tree layer		Litter layer	Requirement for the PP_N of the tree layer	Above-ground phytomass in the tree layer		Litter layer	Requirement for the PP_N of the tree layer
	Total	Needles only			Total	Leaves only		
N	0.23	0.48	0.54	0.39	0.29	2.06	1.74	0.97
K	0.09	0.17	0.10	0.20	0.15	0.96	0.25	0.48
Ca	0.50	0.90	0.32	0.26	0.37	0.96	0.95	0.55
Mg	0.05	0.09	0.12	0.05	0.04	0.20	0.13	0.10
P	0.03	0.06	0.10	0.05	0.02	0.14	0.12	0.07
Total	0.9	1.7	1.2	1.0	0.9	4.3	3.2	2.2

On the other hand, at 4.3%, the nutrient content of the leaves is more than twice as high as that for needles at 1.7% (Table 29); the difference in the nutrient contents of litter is of a similar magnitude (3.2 and 1.2%, respectively).

Otherwise, the tree layers of boreal coniferous forests and temperate deciduous forests exhibit similar average nutrient contents (0.9% in both cases). However, in absolute terms, temperate deciduous forests do contain slightly higher amounts of nutrients, since they also have more phytomass.

Organic and Mineral Turnovers. More distinct differences are found with regard to all turnovers. The average PP_N of the tree layer in temperate deciduous forests is $10\,t\,ha^{-1}\,a^{-1}$ compared to 1.2 t for the three boreal coniferous forests observed (the *typical* zonal average for temperate deciduous forests is probably somewhat lower and that for boreal forests distinctly higher than these values). In deciduous forests about 40% of the $PP_{N(\text{tree layer})}$ goes into *leaf production*, in other words it is used only to provide seasonal assimilation organs, not long-term stand (growth) increments: each spring, deciduous trees must create new organs with the aid of which they can produce again. Due to the high nutrient content of the leaves (4.3% as compared to only 0.6% for the wood of the stems), the nutrient requirement for leaf production represents a full 80% of the total required for annual production in the tree layer.

In contrast, "evergreen" *coniferous* trees produce mainly nutrient-poor wood; only about one quarter of the $PP_{N(\text{tree layer})}$ and just under 50% of the nutrients required annually are used for *needle production*.

Considerably more nutrients (except for P) per unit of production are therefore required for the PP_N of temperate deciduous trees, i.e. they have a much lower *nutrient use efficiency* (in particular, a lower nitrogen use efficiency). As a result, temperate deciduous forests produce on average only 103 kg organic matter per kg of nutrients, compared with 257 kg for boreal coniferous forests.

Less obvious differences are found in the *nutrient uptake* from the soil, since the deciduous trees meet their higher nutrient requirements, especially for nitrogen, partly from those nutrients which were returned to the branches from the leaves prior to leaf fall in the previous autumn (see below); their uptake is reduced accordingly. On the other side, the nitrogen losses due to crown wash, and the amount of nitrogen no longer available for PP_N because it is stored in older plant tissues, are slightly higher in conifers; both have to be compensated for by higher uptake. Nevertheless, the nutrient uptake still differs considerably. For deciduous trees it is 1 kg for every 134 kg organic matter production, whereas for coniferous trees it is 1 kg for every 237 kg.

Since broadleaf trees also exhibit a higher PP_N, the differences in nutrient requirements and nutrient uptake expressed *per unit area* are even greater: if the PP_N is assumed to be twice that of the boreal forests, both the nutrient requirement and the nutrient uptake will be almost four times as high. According to the data presented in Figs. 63 and 85, the differences are even larger. In temperate deciduous forests a PP_N 8.5 times that of the boreal forests results in a nutrient uptake and nutrient requirement which is 15 to 20 times as high.

Temperate deciduous forests thus place much higher demands on soil fertility (soil nutrient status) than do boreal coniferous forests. Retention of needles over many years (more than 25 in the case of Alaskan black spruce) allows conifers to flourish even on sites of marginal quality. This is confirmed from the IBP woodlands data sets: The mean nutrient contents of humus and exchangers under broadleaf forests are 30 931 kg ha^{-1} compared with only 5027 kg ha^{-1} in the podzols under boreal forests.

Vast differences also exist with regard to *nutrient return*. Total litter fall (leaves, twigs, branches, fallen trees) found on average in the 14 broadleaf deciduous forests studied is 5.4 t ha^{-1} a^{-1}. Due to the large proportion of leaves present (frequently 3 to 5 t ha^{-1} a^{-1} in such forests), the average amount of nutrients contained in the organic matter is a respectable 2.5%. In addition, crown wash and stem flow contribute notable amounts of nutrients in mineral form. This explains why over 80% of the nutrient uptake is returned to the soil annually, although litter fall accounts for only 54% of the PP_N during this period.

All these turnover processes take place on a smaller scale in boreal coniferous forests. Annual litter fall, for example, is only 0.3 t ha^{-1} (= 27% of the PP_N for the tree layer) and it has an average nutrient content of only 1.9%. Taken together with crown wash, this gives an annual return of 60% of the nutrients taken up during the same period.

When the *absolute* amounts of nutrients returned each year by the two types of forest are compared with each other, it is found that the values for temperate deciduous forests are 20 to 40 times higher than those for boreal coniferous forests.

In temperate deciduous forests *N and P uptake is significantly lower than the requirement* (Table 27): the difference is covered by *resorption of nutrients from the leaves*; in the case of N, this represents almost one-third of the requirement. Large amounts of K are also internally recycled, although this is not visible from the data, because the throughfall losses are very high (about 60% of the K uptake). Ca and Mg, on the other hand, are not translocated. For both of them uptake exceeds requirement. Excess Ca and Mg accumulates in the leaves or older needles, and then is returned to the soil when the leaves or needles are shed, or is stored for longer periods in woody parts of the trees.

Despite the considerable amount of wastes they produce, only thin layers of *litter* (in our example 21.6 t ha^{-1}) are encountered in temperate deciduous forests because most wastes are rapidly decomposed. The ecosystem of the boreal coniferous forest behaves in the opposite manner: here, the much smaller amounts of litter produced go together with litter layers about five times as thick (114 t ha^{-1}) because decomposition takes place at a much slower rate. However, the respective absolute nutrient contents of the two litter layers are in a ratio of only 1 to 2 (688 kg ha^{-1} versus 1341 kg ha^{-1}) because the leaf-rich litter of the Humid Mid-Latitudes is much richer in nutrients (3.2% versus 1.2%). If steady-state conditions are assumed (i.e. litter is decomposed at the same rate at which it accumulates), the turnover time for litter in deciduous forests is 4 years as compared to about 350 years for that in coniferous forests (Table 28). The residence time for individual nutrients may exceed or fall short of these values by varying amounts. In both deciduous and coniferous forests, K is released more quickly than other nutrients.

Nutrients bound in the leaves, which are seasonally produced and – after falling – undergo rapid decomposition, thus become available for a renewed utilization much more quickly than those contained in the needles, which have a longer life span and in addition break down less easily.

Despite the higher nutrient uptake of temperate deciduous forests, their nutrient supply is more favourable because the supply of plant nutrients in the soil (nutrient content of humus and exchangeable nutrients) is much better than that in the podzols of the Boreal Zone (in our example: 30 931 kg ha^{-1} versus 5027 kg ha^{-1}).

In *summary* (Fig. 86) it can be said that:

- The temperate deciduous forests in the Humid Mid-Latitudes go through a brief but intense nutrient cycle: nutrient uptake in spring and summer is high, but most of it is returned to the soil along with the leaf fall in the following autumn and then released from the litter (including woody parts) on average within 4 years.

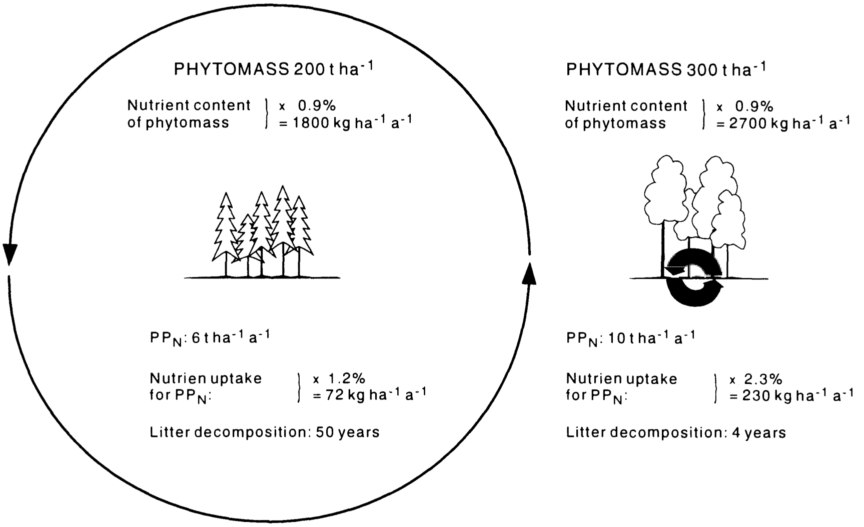


Fig. 86. Diagram of nutrient cycles in broadleaf deciduous forests of the Humid Mid-Latitudes and in evergreen coniferous forests of the Boreal Zone. The percentage nutrient content of the phytomass is similar in both forest types, although the larger amounts of phytomass in deciduous forests lead to higher absolute nutrient quantities. Much more distinctive differences are seen in the fact that nutrient uptake, requirement and return are much higher and turnover processses (only litter decomposition is shown here) are much shorter in temperate deciduous forests than in boreal coniferous forests. This figure assumes steady-state conditions under which the PP_N is equivalent to the litter input, and nutrient uptake equivalent to nutrient return

The coniferous forests in the Boreal Zone, on the other hand, have a lengthy, less intense nutrient cycle: the requirement for the PP_N is low because the relatively nutrient-rich needles are perennial, and thus annual nutrient losses are low; on the other hand, the release of nutrients from the dead organic matter (standing dead, litter, humus) takes considerably longer; bottlenecks in nutrient supply thus occur more frequently in the Boreal Zone than in the more demanding deciduous forests of the Humid Mid-Latitudes.

Energy Turnovers in a Central European Beech Forest

Ellenberg et al. (1986) described the following energy turnovers in a beech forest (*Fagus sylvatica, Luzula* sp.) in Solling, Germany, which they studied as part of the International Biological Programme (IBP). Their data can probably be considered fairly representative of deciduous forest ecosystems in the Humid Mid-Latitudes (Fig. 87).

Almost half the gross primary production is lost through respiration. Of the remaining PP_N, which totals about 14 t ha^{-1} a^{-1} (converted from the calorific values established by Ellenberg et al. for beech stands, see Table 99 in that work), 55% goes into long-term increment and the remainder, about 6.3 t ha^{-1} a^{-1} (at least 3 t of which is leaves) is directly (or within shorter periods) utilized by heterotrophs. Detrivores and decomposers, especially fungi and bacteria, account for 99.5% of this consumption. In comparison, the activity of biophages (consumers of living matter), and particularly that of the herbivores, is of little or

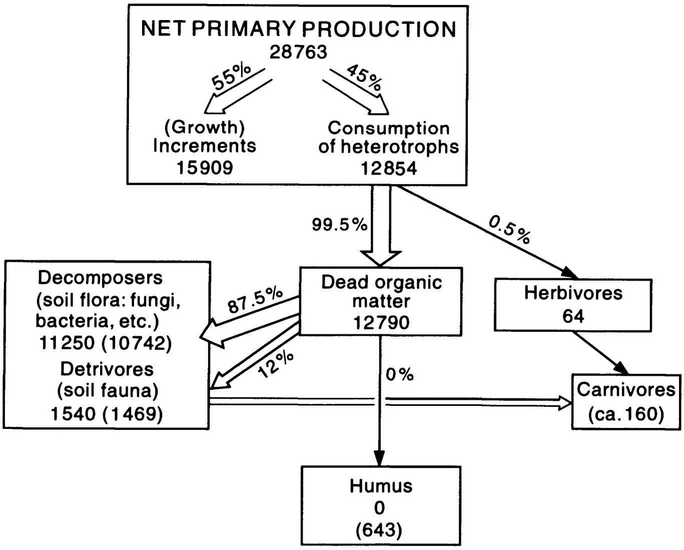


Fig. 87. Energy flow in a beech forest in Solling, in kJ $m^{-2}a^{-1}$. (Ellenberg et al. 1986). See text for explanation

no importance from an energy viewpoint. The slightly more important role of secondary consumers (carnivores) in the energy turnover is attributable to the fact that they also consume detrivores (it is assumed that 10% of all herbivores and detrivores are consumed). A total of 12.5% of the wastes are consumed by animals at the various trophic levels (herbivores, carnivores and saprovores), and 87.5% by saprophytic microorganisms.

The above-ground wastes forming the *litter* layer (here defined as including L and O_f horizons), which has a dry weight of 12.5 $t\,ha^{-1}$, are decomposed within 2 years. In contrast, the dead organic matter in the deeper layers (O_h horizon) and the mineral soil (A_h horizon) is much more stable; complete (final) decomposition of this matter takes decades. During the period covered by their

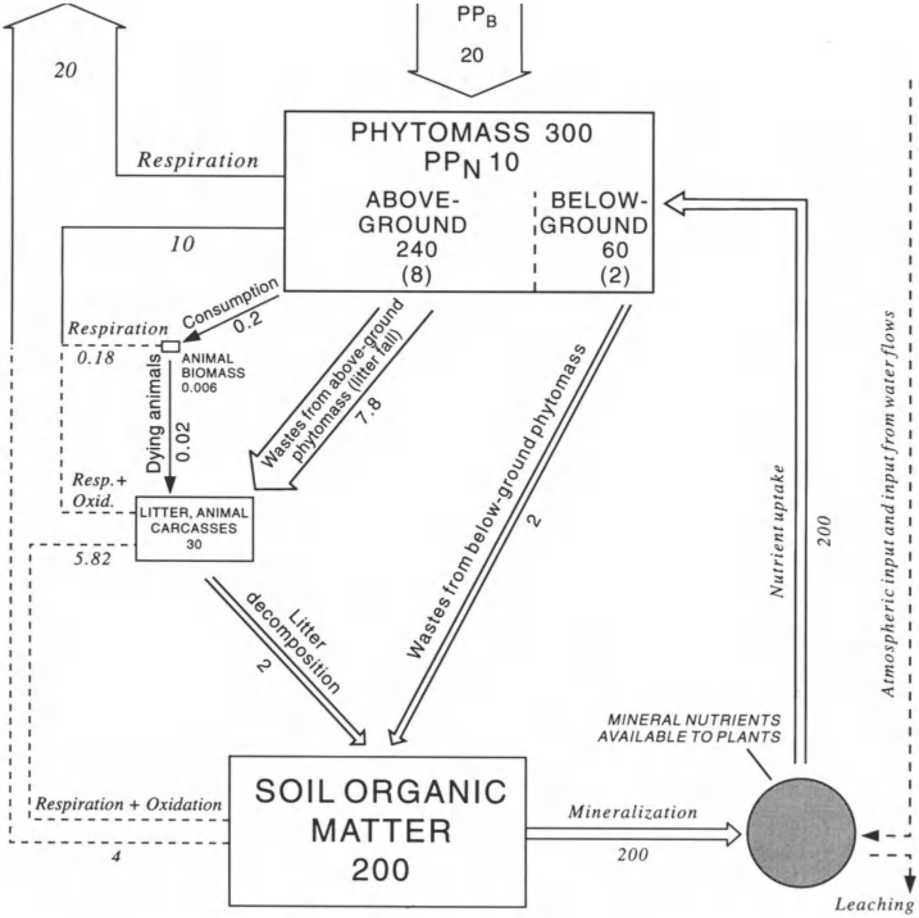


Fig. 88. Simplified ecosystem model of a broadleaf deciduous forest in the Humid Mid-Latitudes. (Compiled from data taken from Reichle 1970, 1981; Duvigneaud 1971; Ellenberg et al. 1986; Satchell 1971; Harris et al. 1975; Ricklefs 1980; Jakucs 1985). See Chapter 2.5.2.5 for the scheme of the model

observations, Ellenberg et al. were unable to state definitively whether a portion of this matter remains undecomposed for ever, i.e. whether it becomes "permanent humus". This is the reason why no percentage is given for this flux in Fig. 87. The value in parenthesis was calculated on the assumption that 5% of the soil organic matter becomes permanent humus, i.e. is continuously stored.

The *ecosystem model* shown in Fig. 88 describes the characteristic (under steady-state conditions) reserves and turnovers for a broadleaf deciduous forest in the Humid Mid-Latitudes in the same manner as was used for the previous two ecozones.

3.3.6 Land Use

The Humid Mid-Latitudes are one of the most densely populated and intensively used regions of the earth. Nature has been altered here more extensively than in most other ecozones.

According to Müller-Wille's calculations (1978), the Humid Mid-Latitudes (which he calls the cool temperate climates) hold 29% of the world's population (1965), i.e. almost three times what one might expect, given the fact that this zone accounts for only about 10% of the dry landmass of the earth. Three of the four major *agglomerations of human population*, namely Europe, the eastern USA and the Far East, lie for the most part within the Humid Mid-Latitudes; only India, the fourth agglomeration, is situated entirely outside this zone (Fig. 89).

Today, the birth rates in most industrialized nations have sunk so low that the *population figures are stagnating* or have even gone into decline. Regional peaks of population growth are now located elsewhere, in particular in many developing countries. If this trend continues, the current population balance will shift towards other, especially tropical, zones so that the Humid Mid-Latitudes will lose their predominance in terms of population.

The Humid Mid-Latitudes are not only the most densely populated but also the *economically strongest regions* on earth: a geography of the Humid Mid-Latitudes is thus "a regional geography of the most important industrialized nations" (Hofmeister 1985, p. 9). These are characterized by:

- high incomes per head and a correspondingly high standard of living of the population;
- high energy consumption by industry;
- low rural/urban population ratio (high degree of urbanization);
- high degree of industrialization (Fig. 90);
- high percentage of area utilized for (labour- and capital-) intensive agriculture (Fig. 91);
- high percentage of people employed in the service sector;
- high share of world trade, thus high degree of international interdependence;
- dense communication networks.

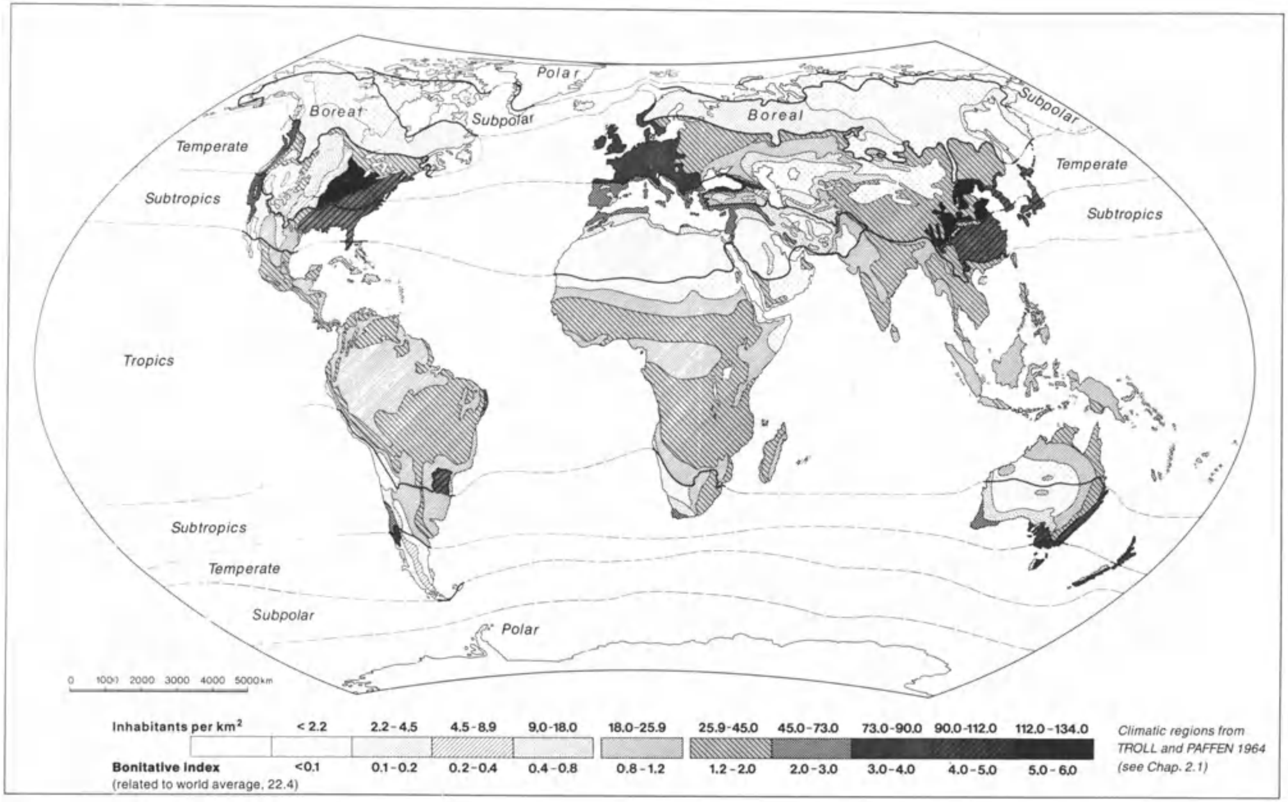


Fig. 89. Mean population densities of the bioclimatic regions and their relation to the world average. (Müller-Wille 1978). *Bonitative indices* Population densities of the bioclimatic regions divided by the worldwide average

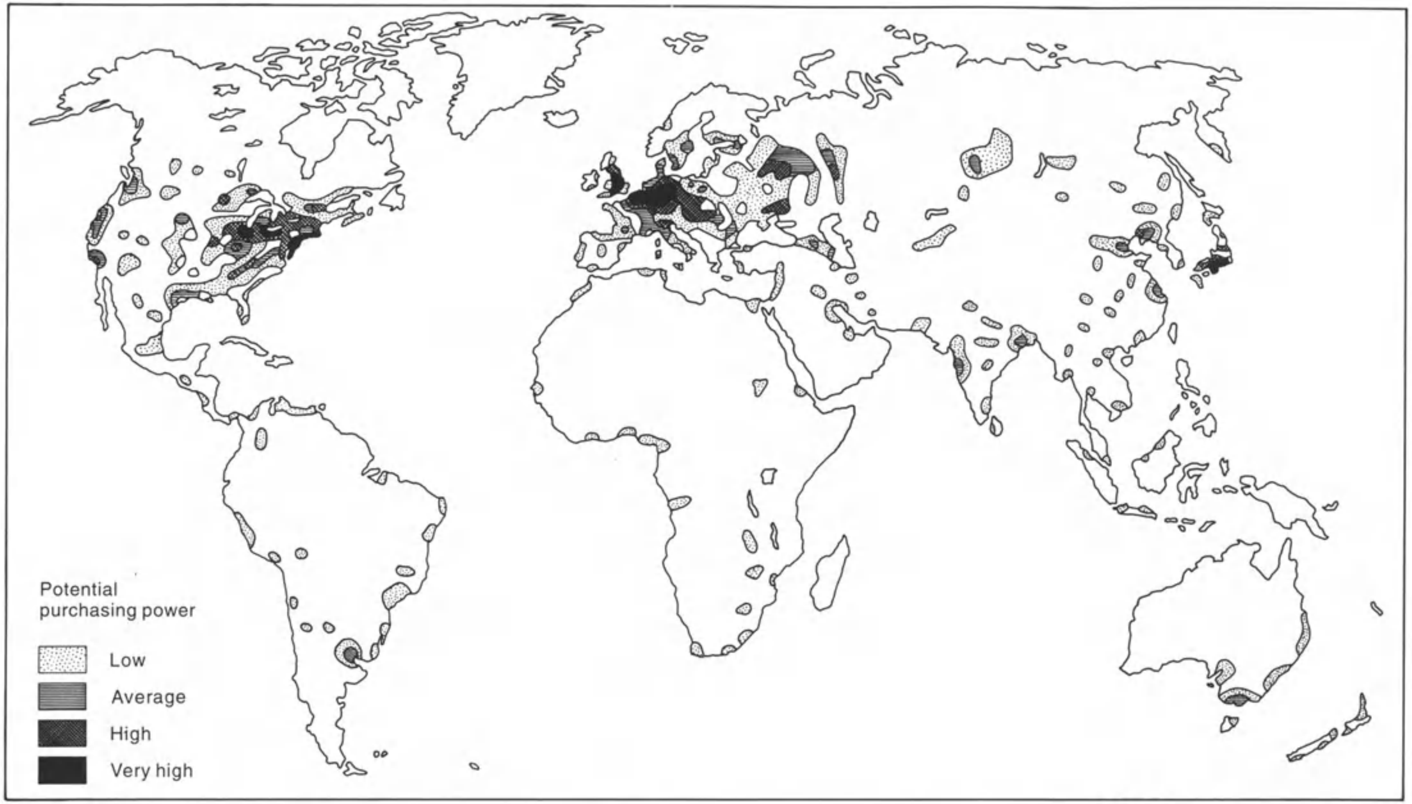


Fig. 90. Relative density of world industrial production in 1964, based on contributions of industrial production to gross domestic products. (Hofmeister 1985)

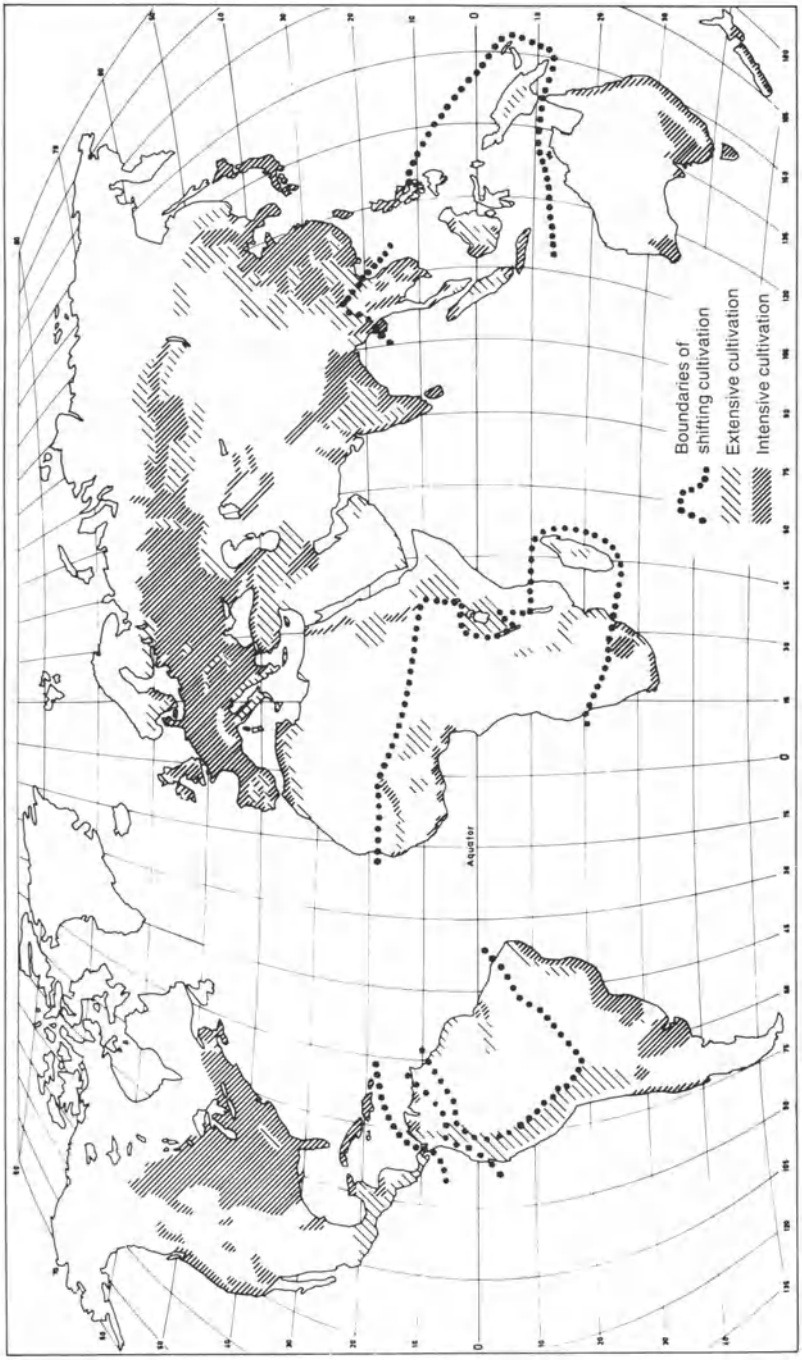
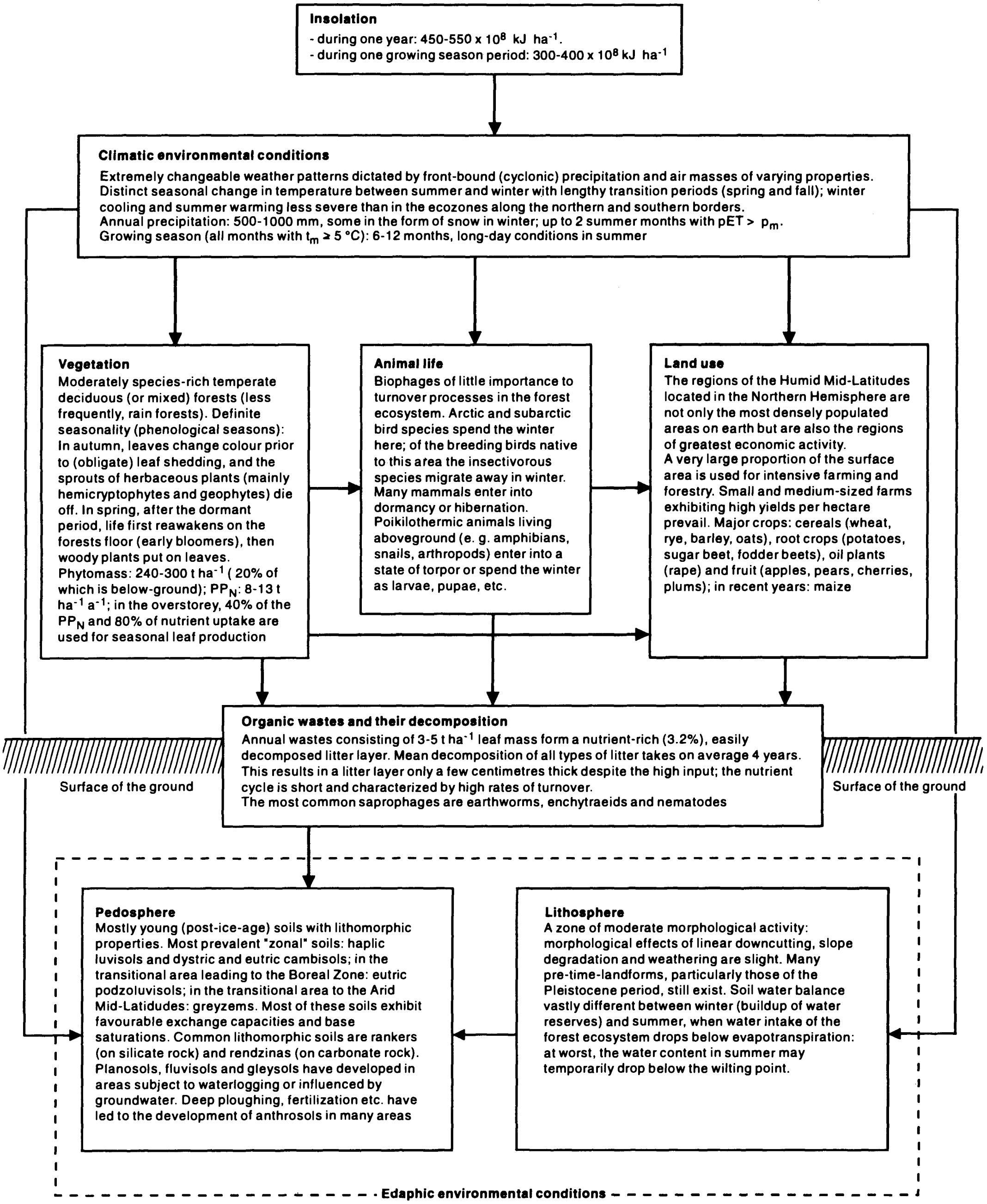


Fig. 91. Intensity of cultivation in the world's agricultural areas and boundaries of shifting cultivation. (Andreae 1983)



Insolation

- during one year: 450-550 x 10^8 kJ ha^{-1}.
- during one growing season period: 300-400 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Extremely changeable weather patterns dictated by front-bound (cyclonic) precipitation and air masses of varying properties. Distinct seasonal change in temperature between summer and winter with lengthy transition periods (spring and fall); winter cooling and summer warming less severe than in the ecozones along the northern and southern borders.
Annual precipitation: 500-1000 mm, some in the form of snow in winter; up to 2 summer months with pET > p_m.
Growing season (all months with $t_m \geq 5$ °C): 6-12 months, long-day conditions in summer

Vegetation

Moderately species-rich temperate deciduous (or mixed) forests (less frequently, rain forests). Definite seasonality (phenological seasons): In autumn, leaves change colour prior to (obligate) leaf shedding, and the sprouts of herbaceous plants (mainly hemicryptophytes and geophytes) die off. In spring, after the dormant period, life first reawakens on the forests floor (early bloomers), then woody plants put on leaves.
Phytomass: 240-300 t ha^{-1} (20% of which is below-ground); PP_N: 8-13 t ha^{-1} a^{-1}; in the overstorey, 40% of the PP_N and 80% of nutrient uptake are used for seasonal leaf production

Animal life

Biophages of little importance to turnover processes in the forest ecosystem. Arctic and subarctic bird species spend the winter here; of the breeding birds native to this area the insectivorous species migrate away in winter. Many mammals enter into dormancy or hibernation. Poikilothermic animals living aboveground (e. g. amphibians, snails, arthropods) enter into a state of torpor or spend the winter as larvae, pupae, etc.

Land use

The regions of the Humid Mid-Latitudes located in the Northern Hemisphere are not only the most densely populated areas on earth but are also the regions of greatest economic activity.
A very large proportion of the surface area is used for intensive farming and forestry. Small and medium-sized farms exhibiting high yields per hectare prevail. Major crops: cereals (wheat, rye, barley, oats), root crops (potatoes, sugar beet, fodder beets), oil plants (rape) and fruit (apples, pears, cherries, plums); in recent years: maize

Organic wastes and their decomposition

Annual wastes consisting of 3-5 t ha^{-1} leaf mass form a nutrient-rich (3.2%), easily decomposed litter layer. Mean decomposition of all types of litter takes on average 4 years. This results in a litter layer only a few centimetres thick despite the high input; the nutrient cycle is short and characterized by high rates of turnover.
The most common saprophages are earthworms, enchytraeids and nematodes

Pedosphere

Mostly young (post-ice-age) soils with lithomorphic properties. Most prevalent "zonal" soils: haplic luvisols and dystric and eutric cambisols; in the transitional area leading to the Boreal Zone: eutric podzoluvisols; in the transitional area to the Arid Mid-Latidudes: greyzems. Most of these soils exhibit favourable exchange capacities and base saturations. Common lithomorphic soils are rankers (on silicate rock) and rendzinas (on carbonate rock). Planosols, fluvisols and gleysols have developed in areas subject to waterlogging or influenced by groundwater. Deep ploughing, fertilization etc. have led to the development of anthrosols in many areas

Lithosphere

A zone of moderate morphological activity: morphological effects of linear downcutting, slope degradation and weathering are slight. Many pre-time-landforms, particularly those of the Pleistocene period, still exist. Soil water balance vastly different between winter (buildup of water reserves) and summer, when water intake of the forest ecosystem drops below evapotranspiration: at worst, the water content in summer may temporarily drop below the wilting point.

Fig. 92. Synoptic diagram for the Humid Mid-Latitudes

All large rivers are utilized as transportation routes; this use may be temporarily impeded by spring floodwater levels and by low water levels in the summer months. During hard winters, ice can also hamper shipping. In many countries, canals complement the natural inland waterways.

Water consumption by private households and industries is generally very high. This has made necessary the construction of ever more and ever larger pumping stations and purification plants. At the same time, the discharge of effluent into rivers has burdened many bodies of water to such an extent that they are becoming increasingly polluted, despite their natural capacity for self-purification.

Most tracts of primaeval forest were cleared for agricultural purposes. The forested areas which still exist have all been drastically altered to serve as commercial forests and are today found only in areas with poor soil conditions or where steep slopes make the terrain unsuitable for agricultural use. Today, the distinct straight-lined demarcation between open agricultural lands and forests, and the division of agricultural land into rectangular fields are conspicuous characteristics of this zone.

Agricultural use is promoted by advantageous temperature conditions and reliable rainfall during a growing season of adequate length, and by comparatively fertile soils, or at least by soils whose fertility can be significantly increased through the use of fertilizers. The zone thus possesses a high natural yield potential. Widely, small and medium-sized farms prevail, with high yields per hectare and high capital investment. The major crops are cereals (chiefly wheat, rye, barley and oats), root crops (mainly potatoes, sugar beet and fodder beets), rape and fodder/forage crops. Maize has become widely distributed in recent years. Fruits and berries (apples, cherries, pears, plums, strawberries and raspberries) are also found in certain areas.

Intensive stock farming (mainly cattle, pigs, poultry) is characteristic of the continental regions of this zone. Areas with a pronounced maritime climate are dominated by dairy farming and – in coastal regions – by sheep farming.

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3.4 Arid Mid-Latitudes

3.4.1 Distribution

Arid Lands in General

The arid regions account for almost one third of all mainland areas on the planet. Approximately two-thirds of them are located in the warm climatic zones (chiefly between 15° and 35° in both hemispheres), thus they belong to the *Tropical/Subtropical Arid Lands*. The *Arid Mid-Latitudes*, which in some areas adjoin polewards immediately on the Tropical/Subtropical Arid Lands, extend to about 55°; they include large parts of central Asia (from the Ukraine via Turan and Kazachstan, Sinkiang and Tibet as far as the Gobi desert in Mongolia) and the Middle West of North America (from Saskatchewan and Alberta in Canada via the Great Plains and the Great Basin in the USA to Arizona and Texas), while in the Southern Hemisphere only eastern Patagonia and a very small area on the South Island of New Zealand belong here (Fig. 93). Taken together, all the separate areas of the Arid Mid-Latitudes cover 16.4 million km^2 or 11% of the continental mass of the earth.

It is difficult to define the outer limits of the arid regions – in the middle latitudes as well as in the tropical latitudes – because the one feature which they have in common, namely climatic aridity, varies regionally according to degree, duration and season, and also the temperature conditions in the individual zones exhibit different characteristics. Quoting the annual precipitation totals (as a rule between 0 and 500 mm) does not permit any direct conclusions to be drawn about the degree of aridity.

A better way of defining the limits of arid regions is to take account of *moisture-dependent site conditions*. Using this criterion, arid lands would be all those zones in which:

- adequately warm-wet conditions exist for plant growth during a maximum of 5 months of the year,
- lack of water remains an important unfavourable factor even during the rainy season (wide variability in precipitation, low reserves of water in the soil),
- rain-fed cultivation is therefore either not possible, or it is a highly risky venture, or it requires the use of special methods (e.g. dry farming, the cultivation of fast-growing or drought-resistant crop species),
- the natural vegetation is characterized by xeromorphic characteristics, the occurrence of halophytes and +/– patchy plant stands, and
- the rivers carry water only episodically and end in sinks from which there is no drainage (endorheic drainage).

The *soil also develops differently* in humid and arid environments. In the wetter regions percolation predominates, and thus soluble weathering products are leached out (e.g. *decalcification*), while on the other hand, Fe and Al oxides and

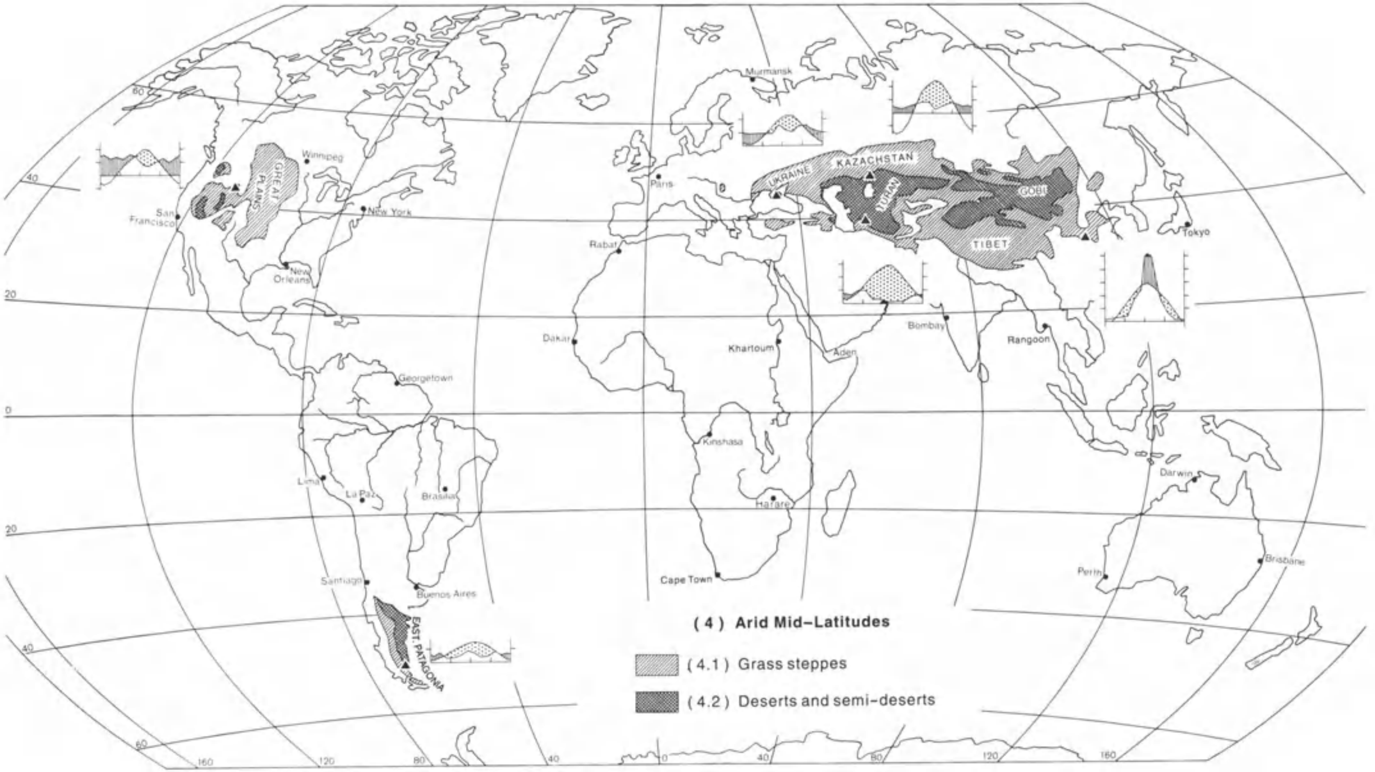

Fig. 93. Arid Mid-Latitudes. These are concentrated chiefly in the continental regions of Eurasia and North America, approximately between 35 and 55° N. In the Southern Hemisphere they are very limited in extent and are found only in eastern Patagonia and New Zealand

hydroxides are relatively enriched (pedalfers); but in the arid regions ascending movements of soil water lead to an enrichment of calcium carbonate, occasionally also of calcium sulphate and soluble salts in the soil profile (pedocals), and as a rule this goes together with a rise in the pH value into the alkaline range and with an increase in the base saturation to 100%.

In the relatively moist steppes (or the thorn savannas of the Tropical/Subtropical Arid Lands), the precipitation may for a certain period of time exceed the evaporation; but even then, at least in the subsoil, the soil water content is not replenished up to the level of field capacity (therefore there is also little or no groundwater runoff) (Fig. 125). Often the subsoil remains dry all the year round.

Arid Mid-Latitudes

Towards the equator, the boundary between the Arid Mid-Latitudes and the Mediterranean-Type Subtropics (with winter rains) runs at approximately 200 mm and the boundary with the Humid Subtropics (with mainly summer rains) runs at about 250 mm annual precipitation, and in each case there are fewer than 5 "humid" months (cf. Chap. 3.8.1). Thermal criteria play a role where Tropical/Subtropical Arid Lands directly adjoin, as is the case between Turan and Iran, the Middle west of the USA and Mexico, as well as between eastern Patagonia and the Pampa: the Tropical/Subtropical Arid Lands begin here as soon as the winter cooling is so slight that there are no thermal restrictions on plant growth, i.e. where the mean temperature of the coldest month no longer drops below +5 °C (in the Arid Mid-Latitudes there is at least 1 month with $t_m < +5$ °C) and the summer warming on average exceeds +18 °C in at least 4 months.

In the regions bordering on the neighbouring non-tropical zones – i.e. the Humid Mid-Latitudes or the Boreal Zone – the summer (growing season) precipitation totals are around 200 mm (the annual sums may go as high as about 500 mm).

The Arid Mid-Latitudes are subdivided into *strikingly different subregions* according to the predominant plant formation (e.g. forest steppes, tall- and short-grass steppes, semi-deserts and deserts; see Chap. 3.4.5.1), as well as according to the prevailing type of agriculture and the potential suitability of land for agricultural use (see Chap. 3.4.6): if at least 100 mm of precipitation fall during the growing season, and if 2–5.5 months are humid, then steppes occur (or originally occurred) where it is usually possible to cultivate wheat; if, on the other hand, less than 100 mm of precipitation falls during the growing season, then only semi-deserts and, below 50 mm, only deserts occur.

3.4.2 Climate

Arid Lands in General

The Arid Mid-Latitudes and the Tropical/Subtropical Arid Lands exhibit a number of features in common which will now be described before proceeding any further.

Most (not all) arid lands have little cloud cover and low atmospheric moisture content. The *incoming solar (short-wave) radiation is therefore higher than elsewhere* in the same latitude and at the same time (in the Tropical/Subtropical Arid Lands it is highest of all). On the other hand, there are high upward fluxes of thermal (long-wave) radiation emitted by the land surface according to its temperature; these energy losses are hardly compensated because (long-wave) counter-radiation emitted from clouds, water vapour in the atmosphere, etc. remains exceptionally low, thus giving a strongly negative net outgoing (long-wave) radiation.

Furthermore, a relatively large amount of the incident radiation is immediately reflected back: arid environments have without exception a higher albedo (reflection coefficient) than humid environments even though, on an individual basis, considerable differences may occur depending on the colour, texture and moisture content of the soil as well as on the plant cover. Most frequently the albedo is between 25 and 30% (Table 30).

High reflection and terrestrial thermal radiation losses are the reason why the (all wave–length) radiation balance (net radiation) is only relatively weakly positive in arid regions, and less positive than in wetter regions in the same latitude.

Despite this, the *surface of the ground* (soil, rocks and plants) is *strongly heated up* in the course of the day because, given the dry substrate, (a) the absorbed radiation energy (net incoming radiation) is apportioned almost totally to the sensible heat flux (there is very little latent heat flow such as otherwise occurs in association with the evaporation of water, Fig. 124), and (b) the thermal conductivity and capacity of the soil (many air-filled and therefore insulation cavities) are low.

The latter explains why the heat stored in the soil during daytime is very much restricted to the uppermost part of the ground and small in amount. Under

Table 30. The albedo of various types of land surface. (Graetz and Cowan 1979)

Arid regions (%)		Humid regions (%)	
Desert	25–30	Pastureland	10–20
Sand dune (dry)	35–45	Deciduous forest	10–20
Sand dune (wet)	20–30	Coniferous forest	5–15
Wadi vegetation	36–39	Arable land	15–25
Dwarf shrub semi-desert	28–33		

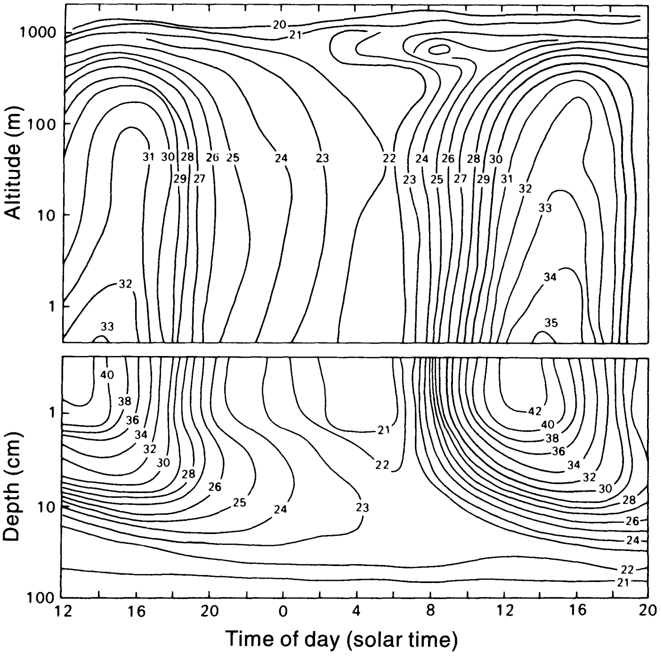

Fig. 94. Diurnal temperature cycle (°C) at various depths in the soil (0–1 m) and at various heights in the atmosphere (0–1000 m), recorded on 24 August 1953 in the Great Plains, USA. (Graetz and Cowan 1979). In the course of the day, the soil warms up to a greater extent (to 40–42 °C) than the overlying layer of air (33–35 °C); however, only the uppermost 10 cm of the soil undergo warming

the conditions of prevailing terrestrial radiation (i.e. at night), the heat is quickly released and thus the temperature rapidly drops. The *diurnal temperature amplitude is therefore high* (Fig. 94).

Correspondingly, rock disintegration processes by thermal expansion and contraction play a relatively important role.

With regard to the net primary production, the nightly cooling is favourable in that it reduces the dark respiration losses (which generally increase with rising temperature; Fig. 14, Chap. 2.5.2.1) (on this topic compare, for example, the unfavourable ratios of gross to net production in the permanently hot tropical rain forests, see Chap. 3.9.5). This may be economically significant for irrigated crops.

The *precipitation varies regionally between almost 0 and 500 (600) mm a^{-1}*; in most or all months, the precipitation is lower than the respective potential evapotranspiration. Even though in many areas it is concentrated in certain seasons, the distribution of rainfall is highly irregular (unreliable): long periods of drought frequently occur within the "rainy seasons", and considerable deviations (in percentage) occur from the annual means. The efficiency of the rare rainfall events is diminished by the fact that, under the (mostly) predominant conditions of high saturation deficit in the air, large amounts of the rainfall are immediately lost to *evaporation.*

Arid Mid-Latitudes

As the Humid Mid-Latitudes, the Arid Mid-Latitudes are also located in the zone of prevailing westerly winds or cyclonic west wind drift. However, in contrast to the former, they occupy a definite *leeward* or *continental position.* For example, in *North and South America* the north-south-oriented chains of the Rocky Mountains or of the Cordilleras form a barrier in the path of the westward-flowing air masses and force them to rise. The resulting adiabatic cooling causes the water vapour to condense, and as a result, orographically induced rainfall is produced in the ascending air masses. This means that the air descending on the lee side of the mountain chains is dry and tends to consume moisture rather than supply rain. In *Eurasia,* where there is no equivalent mountain barrier, the dryness of the internal regions far from the sea is explained by the fact that moist air masses are barely able to penetrate that far inland. In addition, mountain chains at the southern edge of the continent (and at the eastern margin in North America) prevent monsoonal influences from exerting any major effect in late summer and fall. In the arid lands of *Patagonia,* the cold Falkland current prevents moist air masses from penetrating from the east.

Most of the arid regions outside the tropics are *cold in the winter* (coldest month with a temperature of $t_m < 0\,°C$) and have snow cover at least for several days, and frequently for several months. The only places where all the monthly averages remain above 0 °C (= mild in winter) are in southern Turan and in the southern part of the Great Plains as well as in the coastal arid regions of eastern Patagonia and New Zealand. Apart from these exceptions, the Arid Mid-Latitudes can therefore be designated as *arid lands with cold winters* where the vegetation exhibits not only drought-induced, but also cold-induced dormancy.

During the *high summer* the solar radiation attains similarly high levels to those prevailing at the same time in the Tropical/Subtropical Arid Lands, because the greater length of the day compensates for the lower angle of the sun's rays (Table 31). Correspondingly, the summers – with the exception of eastern Patagonia and New Zealand – are hot: the mean monthly temperatures exceed 20 °C and in some areas attain 30 °C, but in each case very much higher daily maxima are recorded.

In the *western sub-areas* of the two arid-land regions of the Northern Hemisphere, where the precipitation falls mainly in the spring and autumn in conjunction with eastward-moving low pressure cells, *four distinctly different seasons* (with the exception of those areas having mild winters) can be identified: a long cold winter is followed here at first by a short wet-warm spring when the soil moisture content is high due to rainfall and snow meltwater; next comes a long dry-hot summer; and finally a short wet-warm autumn with rainfall but without any reserves of water stored in the soil.

Table 31. Height of the sun, length of day and global radiation during the summer in dry regions of the Northern Hemisphere, as a function of the latitude. (Fitzpatrick 1979). The Arid Mid-Latitudes receive the same peak amounts of insolation as the Tropical/Subtropical Arid Lands

Latitude	Height of sun at midday on 22 June	Length of day on 22 June	Global radiation in June, given a cloudless sky[a]
25	88° 7′	13 h 41 min	97.97×10^8 kJ ha^{-1}
40	73° 27′	15 h 01 min	98.39×10^8 kJ ha^{-1}

[a] Converted from Budyko (1963). Since there is usually very little cloud cover in most arid regions, the actual amounts of insolation are not much lower than the stated values.

In the *southern and eastern sub-areas* of the two arid-land regions in the Northern Hemisphere, most precipitation is due to convective processes which occur during the summer, frequently in conjunction with monsoonal events from the south. However, the efficiency of these summer rainfalls is attenuated by the simultaneously high air temperatures and correspondingly high potential evaporation, so that as a result humid conditions rarely if ever form.

The Arid Mid-Latitudes may be *climatically subdivided* according to the regionally differing duration of the wet-warm season (= humid months with $t_m \geq 5$ °C) and the degree of winter cooling (t_m of the coldest months > or < 0 °C). It is then possible to make a distinction between steppe climates with mild and cold winters, each climate having a growing season of 2 to 5.5 months, as well as desert and semi-desert climates with mild and cold winters, each climate having a growing season of less than 2 months.

3.4.3 Relief and Hydrology in the Arid Lands of the Middle and Tropical/Subtropical Latitudes

In all arid lands of the earth, whether in the middle latitudes, subtropics or tropics, morphogenesis proceeds broadly speaking along the same lines. Regional differences are more likely to be linked to fluctuating degrees of aridity than to the temperatures which change with the geographical latitude. It therefore appears appropriate to deal with the Arid Mid-Latitudes and the Tropical/Subtropical Arid Lands together, as far as relief and hydrology are concerned.

Weathering Processes

Chemical weathering processes do take place, as is indicated by the salt content of many weathering products and soils, but they are possibly of secondary importance because moisture is almost always lacking everywhere. This might apply even to those sites which are favourably influenced by inflows of water, because the water always gives a neutral to alkaline reaction and – because of the greatly reduced biological processes – it contains very little carbonic and organic acid; therefore, even when the moisture conditions are similar, the dissolution and hydrolytic processes take place much more slowly than in the seasonal and humid tropics.

On the other hand, very few of the products of chemical weathering are transported away (leached out), therefore, possibly with the help of accumulative processes or ascending soil water movements, they may lead to local (regional) enrichments in near-surface soil strata where they may also harden. For example, *hard crusts* (*duricrusts*) of $CaCO_3$-rich material (calcrete) or SiO_2-rich material (silicrete) are widespread. They occur either at the surface or at low depths and attain thicknesses of up to 1 m, and in exceptional cases up to 3 m. Calcium carbonate enrichments are caused by ascending soil water, silicon enrichments occur as residual or accumulative formations where poor drainage exists.

Duricrusts as well as stone pavements (see below) might affect soil moisture conditions since both of them reduce evaporation and increase surface runoff in the case of rainfall events.

On rock surfaces – even in hyper-arid environments – *biological weathering processes* caused by lichens, algae, fungi and bacteria, which live epilithically or in cavities just below the surface of the rock, have been detected. Many of these microorganisms contribute, in the long term, to the breakdown of the mineral structure and thus cause the rock to crumble. Others are involved in coating formation (see below).

Physical weathering processes, such as salt and temperature weathering, are presumably more important. *Salt weathering* commences when rainwater or dew penetrates via pores and hairline cracks into the rock and dissolves salts (and other substances) which have previously been formed there via chemical (hydrolytic) weathering processes. When the pore water then rises by capillary action during dry phases, these salts are transported to the outer layer of the rock where they crystallize out due to continuing water loss or a drop in temperature. This causes considerable pressure to build up. If water is added once more, then hydrates are formed, thereby causing the volume of the salt crystals to increase still more and thus exert an additional splitting action (wedge effect, salt cracking). Hydration weathering (see Chap. 3.3.3) and stress caused by crystallization in confined space play an important role especially in fog deserts.

Under certain circumstances (which most likely include the presence of certain microorganisms), the capillary ascent of solutions from the interior of the rock may also lead to the formation of hard (lacquer-like) *coatings* ("desert varnish"). These coatings are made up of metallic black to rust-brown-coloured enrichments of iron and manganese oxides at the surface of the rocks which – like the salts – were released by chemical weathering processes. The hard lacquer-like coating is more resistant to weathering than the interior of the rock. When this coating splits open, further decomposition can take place in the form of core weathering inside the protective coating and may thus induce the process of cavernous weathering. Some of the weathering forms produced in this way are called, for example, *tafoni.*

In the case of *temperature weathering,* changes in volume brought about by temperature changes lead to stress buildup in the rock which can be "discharged" in the form of crumbling (granular disintegration), superficial scaling (flaking), spalling (exfoliation) or block disintegration. Since rocks possess low thermal conductivity, and temperature fluctuations occur only in the near-surface layers, weathering-induced spalling and heat cracks probably occur only where pre-existing joints or bedding planes (in the case of spalling the release joint runs parallel to the surface of the rock) facilitate the breakdown of the rock and assists in the processes of hydration and salt wedging. On the other hand, spalling may also come about solely as a result of pressure release, i.e. without any thermal assistance.

Temperature weathering is only able to act on exposed rock. Its effectiveness increases with the size of the rock surface (cumulative effect of the expansion coefficient), with the frequency and amplitude of changes in temperature, and also with the differences in the mineral constituents of a rock according to colour and coefficient of expansion. Consequently, it is most effective in regions with at best patchy vegetation cover, low atmospheric humidity and strong insolation (hence also the name insolation weathering), and in crystalline rocks it is generally stronger than, for example, in sandstone.

In the *Arid Mid-Latitudes* (and to some extent also in the subtropical arid lands) *frost wedging* also plays an important role. Similarly, *frost-induced soil movement* may also be a significant phenomenon. For example, in the cold-winter steppe areas, solifluidal displacements (mudflows) are widespread on the fields, when surfaces thaw out in the spring. These mass movements can be reduced by cultivating winter cereal crops (Semmel 1983). In principle, freeze-thaw processes are more effective in the Arid Mid-Latitudes than in the Humid Mid-Latitudes because the temperatures drop further below the freezing point and the freeze-thaw cycle occurs more frequently; in addition, there is no insulating plant cover and the frosts penetrate more deeply into the soil and the rock.

Because of the physical weathering processes, an *angular debris* ranging in size from sand grains to blocks is formed. Since the available water is inadequate to remove this material (by slope wash and fluvial action) residual block fields of varying thickness are left behind in the mountains and mountainous regions, and debris flows form at the foot of the mountains. In the deserts and semi-deserts the quantities of debris can build up to such an extent that the mountains appear to "drown" in them.

More obviously than in any other ecological zone, those parts of the mountains which are free of debris are characterized by a high percentage of *rock- and structure-determined landforms.* The lack of vegetation and the poor soil development allow the "geology" to stand out.

Eolian Processes

Eolian activity is favoured by drought and a total (or at least partial) lack of vegetation. The landforms which are created by wind action are among the most striking, although they are by no means the most frequent phenomena occurring in deserts and semi-deserts. *Wind transport and deposition* create, for example, dune areas (erg) and loess deposits (both extending in some places over thousands of square kilometres but rarely occupying more than a few percent of the deserts); *wind abrasion* (wind corrasion; operates like a sand-blasting machine) produces windkanters (faceted stones, ventifacts), mushroom rocks, and yardangs (streamlined hills); *deflation* gives rise to desert pavements, deflation hollows and minor blowouts on dunes. Wind erosion also poses a threat to harvested fields. In particularly dry years, dust storms may occur here with catastrophic consequences. Planting shelter belts, as has been done in some steppes (Walter 1968), can provide only limited relief. Wind endangers field crops close to the agronomic humid-arid boundary because it also accelerates the drying out of the soil.

River Action and Slope Wash

Valleys are rare in most regions and the runoff, apart from allogenic rivers, is only *episodic*, i.e. the runoff is fed essentially by rainwater flowing at the surface or close to the surface into the rivers, and is therefore linked to precipitation events; once these come to an end, the runoff also quickly stops (only a subterranean stream might continue under some valley floors). Nevertheless, the redistribution of material caused by flowing water is usually more significant than eolian action, even in the driest regions.

For example, *deep V-shaped valleys, some with a broadened valley floor*, are frequently incised in the inselberg (see Chap. 3.7.3) and mountain regions, and almost level to gently inclined *piedmont plains (pediments)* are formed by sheet erosion in the foreland of mountains; further down, these are followed by broad shallow open valleys or immediately by *alluvial pans as internal (endorheic) drainage basins* (Fig. 95). Where the valleys emerge from the mountainlands thick *alluvial fans (serir, reg)* have usually built up. Because the rivers carry water only intermittently, the material of these fans consists mainly of almost unrounded gravels and coarse sands.

The *pediments* (which may also have been formed under more humid climatic conditions — see Chap. 3.7.3) have angles of inclination ranging from 3 to 8 ° (flattening out towards their lower ends). There is usually a clear change in declivity where the pediments merge with the steeper (usually >20 °) mountain slopes above them. This knickpoint lies in the zone of relatively intense chemical weathering (possibly combined with salt cracking) which is here due to the inflow of water from the mountain slope and thus the greater and longer lasting soaking of the soil. While retaining its angle, the knickpoint moves up the pediment as the mountain slope progressively retreats along a parallel front (Fig. 95). The surface

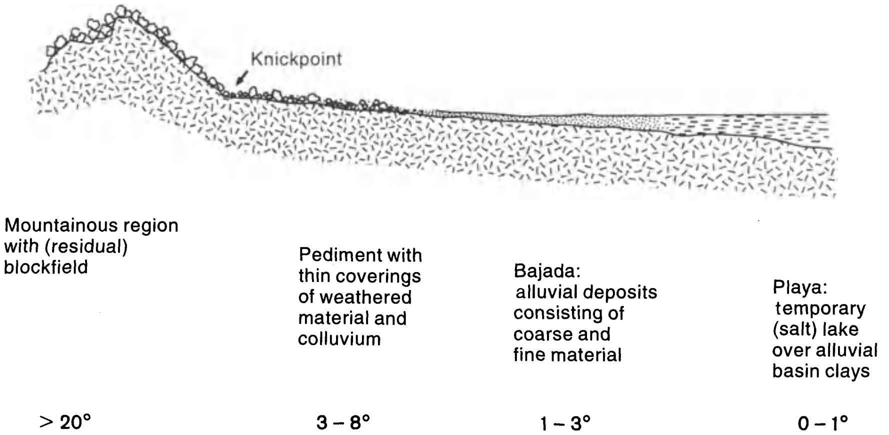

Fig. 95. Typical relief sequence in arid regions. (Amounts shown in degrees = approximate angles of slope)

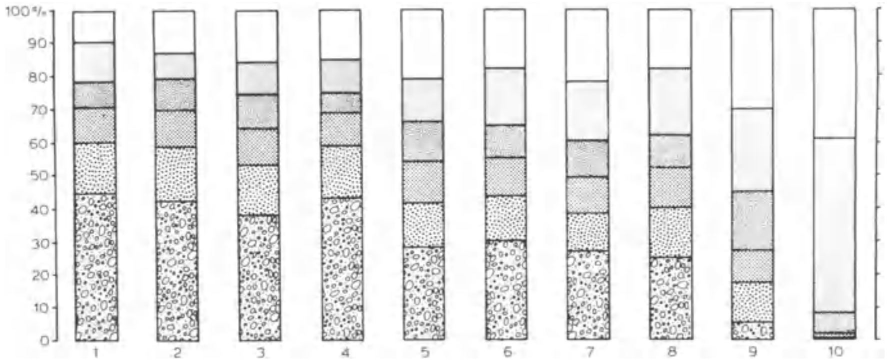

Fig. 96. Mean grain size composition of soil material of a bajada in Arizona. (Phillips and MacMahon 1978). The samples were taken along two traverses running down the slope. *Bar diagram 1* shows the conditions determined at the uppermost and *bar diagram 10* at the lowermost sampling points. The *various shadings* (*from top to bottom*) stand for: clay and silt (*white*), very fine sand, fine sand, medium-sized sand, coarse sand, gravel and very coarse sand (grus, stones)

of the pediments is usually (thinly) covered with a soil substrate, containing large amounts of rock debris along with sand, which for the most part was generated as a sheet wash sediment, but may partially also have been formed as a result of creep processes. Because of the coarse-textured material, but principally because of the erosion and aggradation events, the soil has not developed beyond the stage of a regosol, arenosol, or xerosol.

With increasing distance from the foot of the mountains, the material relocated by fluvial action and slope wash becomes finer in size (Fig. 96) and it is deposited in greater thicknesses on the underlying solid rock. The upper part of the alluvial zone, which is still fairly coarse-grained and gently inclined, is also called a *bajada*, while the lower, clay-rich and extremely level alluvial zone is referred to as a *playa*. During the rainy season, or even after single precipitation events, the playas can turn into shallow (frequently salt) lakes; otherwise, their argillaceous sediments are criss-crossed by desiccation cracks and in many cases are covered with salt blooms or salt crusts up to several centimetres thick (frequently found in semi-arid areas). Other names for such salt pans are, for example, sebkhas or shotts in the Sahara, takyrs in Turan, kavirs in Iran, salars in South America.

The catena-like sequence of landforms (which is associated with a corresponding differentiation of vegetation — see Chap. 3.4.5.3) created as described by fluvial erosion/hill wash, transportation and deposition, is highly characteristic of all arid lands. In the hyper-arid regions, i.e. the deserts and semi-deserts, this sequence goes back essentially to formation processes which took place during the Pleistocene pluvial periods or even earlier, whereas in the semi-arid regions, i.e. the steppes and thorn savannas, it results (at least to a large degree) from shaping processes which are still taking place. In these latter regions the frequency and intensity of periodically occurring heavy rainfall, i.e. during a clearly defined rainy season, are already so large that sheet flows become a major degrading force even today (and their effectiveness is favoured by the discontinuous vegetation cover which lasts throughout the entire rainy season, and by the rapidly declining permeability of the soil which occurs during rainfall events; see Chap. 3.7.3).

In contrast to the Seasonal Tropics, where sheet erosion also predominates (see Chap. 3.7.3), the mantle of weathered material and colluvial deposits of pediments, as well as the alluvial sediments on bajadas, are generally more coarse-grained because the chemical breakdown of the rock takes place more slowly in arid lands. This consequently reduces the morphological effectiveness of sheet flows even further. Another difference compared with the Seasonal Tropics seems to be that the coalescing of adjacent pediments to form (more extensive) *pediplains*, obviously takes place less frequently in arid regions (Rohdenburg 1971, p. 206). The planation surfaces of these regions are therefore only rarely independent relief elements; usually, as described, they are the middle elements in a relief sequence.

Desertification

When the steppe or thorn savanna vegetation is destroyed (e.g. by overgrazing and excessive logging), soil loses its protective cover at the surface and its consolidation in the root zone. Under these circumstances, the heavy rain floods can do their work much more effectively. As a consequence, the surfaces can be gullied (badlands) or individual erosion gorges (in Russian called ovragi, balki), which occasionally run for several kilometres, may be incised; also, increased amounts of fine material are washed out, i.e. a relative enrichment of sand occurs. As a result, the water-retention capacity of the soils decreases and the dryness of the soils increases correspondingly; chemical weathering processes become even less significant. This may result in the topsoil being carried off by the wind and in the build-up of wind-borne sand layers or even dunes (cf. also Chap. 3.5.6.).

3.4.4 Soils of the Steppes

No soil whatever has formed in large areas of the deserts and semi-deserts, for example wherever unconsolidated dune fields, recent rock debris or bare rock form the surface of the ground. Otherwise, *xerosols* and *yermosols* occur in the extreme arid regions both of the middle and of the lower latitudes. These soils are dealt with in the chapter on the soils of the Tropical/Subtropical Arid Lands (Chap. 3.5.4), because this is where they are most widely distributed. In this chapter we will be examining only the soils of the steppes of the Arid Mid-Latitudes, starting with the zonal soil units followed by the intrazonal halomorphic soil units.

Zonal Soils

Under arid/semi-arid climatic conditions the "leaching" (= displacement of easily soluble salts, carbonates, Fe and Al oxides, fulvic acids or clay minerals by percolating water), which is so characteristic of the humid zones, is relatively insignificant or is even exceeded by displacement in the opposite direction (i.e. by ascending water). As a result, *pedocals* take the place of pedalfers (see Chap. 3.4.1). These are characterized by free carbonates and a high degree of base saturation. Quite commonly, their profile displays the following sequence of horizons: $A_h - AC_k - C$, i.e. soils (some phaeozems excluded) having a mollic A horizon (A_h) and an accumulation of calcium carbonates (k) within 125 cm of the surface; there is no strikingly obvious B horizon. The drier the climate, the closer to the surface is located the calcic horizon[17]. The type of humus formed is a *mull* in which high-polymer humic substances and intermediate products of humification form stable, nitrogen-rich organomineral complexes with clay minerals. The soil structure is characterized by good friability. The *exchange capacity and water-retention capacity are both high*; they are the reason for the high potential fertility of these soils. Any restrictions on plant growth are due entirely to the dryness of the climate.

The steppe soils cover a latitude zone ranging from south-eastern Europe to northern China and Mongolia, the Middle West of the USA (Great Plains) and the Gran Chaco region down to the sub-humid pampa in South America (Fig. 6). Depending on the degree of aridity, phaeozems, chernozems or kastanozems predominate (Fig. 97).

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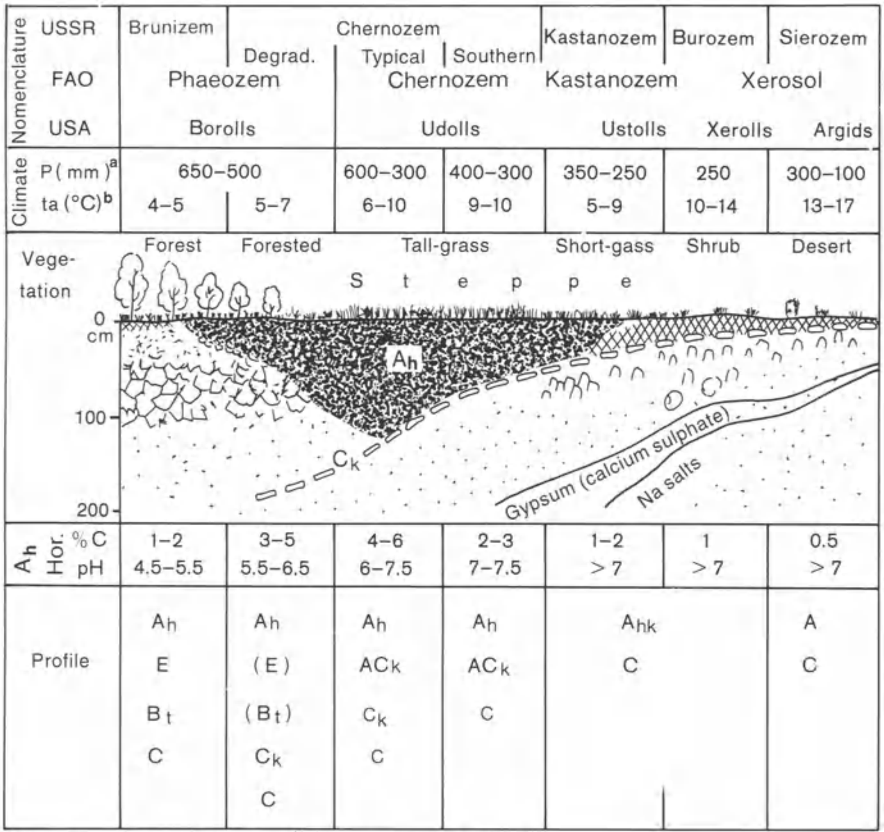
[17] The upper limit of the calcic horizon – in free-draining soils – is probably the depth down to which the leaching takes place as rainwater percolates from the surface; on the other hand, in soils close to the groundwater table, it corresponds to the soil level up to which dissolved calcium carbonate is transported by the capillary ascent of groundwater.



a Mean annual precipitation b Mean annual temperature

Fig. 97. Steppe soils of the former USSR. (Scheffer and Schachtschabel 1992). With increasing aridity, the thickness of the A_h horizon and its humus content (% C) at first increase and then decrease again. In contrast, the other variables change in the same direction as the degree of aridity: the downward translocation of clay (lessivage: E) is reduced, the contents of calcium carbonate (C_k and AC_k), calcium sulphate and sodium salts, and also the pH value, all increase

The wettest sites (roughly between 500 and 700 mm of annual precipitation) are occupied by *phaeozems*. These are dark brown to blackish grey (they derive their name from the Greek word phaios = blackish grey), deep-reaching soils which originated from base-rich sediments (frequently loess). They always contain large reserves of weatherable silicates. The clay minerals belong to the illites and smectites. Base saturation is high to moderate. Carbonate leaching is widespread (no calcic horizon). Clay displacement with the formation of a clay-enriched B horizon (argic B) occurs only in the wettest zones (it is a diagnostic characteristic of the luvic phaeozems, which can be grouped with the haplic luvisol soil zone — cf. Fig. 6).

Phaeozems are the most frequent soils encountered in the North American corn belt from Wisconsin to Missouri (where they were formerly referred to as brunizems or prairie soils); they form the soils of the humid and sub-humid pampa of Argentina, Uruguay and southern Brazil (in the *humid* pampa: *luvic* phaeozems) and they are found at many places in southeastern Europe.

Most phaeozems are considered to be very fertile soils. Their fertility is based, last but not least, on the fact that they have a high water-retention capacity and thus are able to compensate for any moisture deficits during periods of low precipitation (which frequently occur in their distribution regions).

The *chernozems* occupy a middle position, according to the degree of aridity of their occurrences. These are soils with a dark (the name comes from the Russian words chern = black, and zemlya = earth), approximately 50–100 cm thick A_h horizon whose humus content can exceed 10% in well-formed chernozems (in central European black earths the humus content is 2–6%). The generally favourable structural characteristics and high exchange capacities are due substantially to the high humus contents.

The development of the *uniquely thick* A_h *horizon* (apart from certain andosols) is due to a number of favourable factors. These include the quality of the parent material (loose material – frequently loess – containing $CaCO_3$), semi-arid and cold-winter (continental) climatic conditions, the (originally) grass and forb-rich vegetation (tall-grass steppe) as well as the mixing activity of soil-dwelling organisms (*bioturbation*). This constellation of factors results temporarily (during the wet/warm seasons of the year) in a considerable production of biomass (with favourable C/N ratios and thus well utilizable by animal consumers and decomposers); on the other hand, it gives rise to very long-lasting inhibition of microbial decomposition activity (during the warm-dry and cold seasons). The above-ground plant substances, which are thus preserved from decay and merely dry out, are incorporated by steppe-dwelling animals such as susliks, hamsters, prairie dogs (USA) or also earthworms, into the soil where most of them are humified and only a small quantity is directly mineralized. Since the steppe-dwelling animals also retreat into deeper strata of the soil to escape the extreme cold of winter and summer drought, the accumulation of humus extends to a correspondingly deep level. The burrows dug by small mammals are referred to as krotovinas; the material which is brought to the surface in these burrows counteracts the process of decalcification.

Most variants of the chernozem soils exhibit *precipitations of calcium carbonate* and to some extent also *calcium sulphate* (e.g. a calcic or gypsic horizon, carbonate concretions resembling loess dolls, or carbonate blooms) above a depth of 125 cm. Such enrichments are lacking in degraded chernozems occurring under more humid climatic conditions ($> 600\,\mathrm{mm\,a^{-1}}$) (= *luvic* chernozem with an A_h–AE–B_t–C_k profile). When chernozems degrade even further, a luvisol (A_h–E–B_t–C–profile) may be formed.

Chernozems are amongst the soils with the highest potential fertility.

As zones with increasing aridity are approached (i.e. the area of short-grass steppes), the chernozems give way to the *kastanozems*. In contrast to the other two steppe soil units, the mollic A horizon of kastanozems is less thick and is brown in colour (Latin castanea = chestnut; chestnut-coloured soil; in the USA formerly known as: chestnut soil). Secondary calcium carbonate and/or calcium sulphate accumulations occur regularly and less deep than in the chernozems. One indication of the greater dryness is also that water-soluble salts may occur in the subsoil.

Because of the many months of water deficit, the fundamentally high *yield potential* of the kastanozems can only be fully exploited as a rule by the dry farming system or by using artificial irrigation (although the danger of salinization is great in this case). Otherwise, pasturing, in the New World frequently in the form of ranching, is the predominant form of use.

Halomorphic Soils

In the arid regions, also in those of the tropics and subtropics, at sites where there is a tendency for waterlogging to occur, or at sites with a high groundwater table, where in the humid and sub-humid climates mostly gleysols, planosols, fluvisols, or histosols occur, one finds solonchaks and solonetz (halomorphic soils).

Solonchaks (derived from Russian words sol = salt, and chak = salty area) are characterized by high contents of readily water-soluble salts (salic properties; at least 0.2 wt%) in the upper soil (A_Z horizon) and/or in the subsoil (B_Z and C_Z horizons). They are therefore also referred to as saline soils.

The distribution of salt in the soil profile can vary according to the season: in dry periods the salt is transported upwards with the capillary ascent of water, often forming salt blooms or crusts at the surface; during the rainy season, percolating water transports a large amount of the salts into the subsoil. Fluctuations in the groundwater may also influence the salt distribution.

The salts are mostly chlorides, sulphates or (bi-)carbonates of sodium, less frequently chlorides or sulphates of magnesium and calcium. Depending on the type of salt, as well as on the quantity and distribution of the salts, the properties of the solonchak soils can vary greatly. For example, *soda-rich solonchaks* (containing much sodium carbonate) have high degrees of Na saturation ($>15\%$, often $>50\%$) and exhibit a strong alkaline reaction (pH up to >10). When high levels of clay are present they have a tough plastic consistency when moist, but in the dry state they turn hard and dry cracks occur. As a rule, they do not support any vegetation. In contrast, the (more frequent) *chloride-rich solonchaks* have a much lower Na saturation ($<15\%$), exhibit only a weakly alkaline reaction (in general pH <8.5) and have slightly more favourable physical properties. The best soils in ecological terms are the *gypsum-rich solonchaks* (containing mainly calcium sulphates) whose soil reaction is in the neutral range (sometimes also <7). The natural vegetation growing on the last two variants consists of halophytic species which, however, exhibit only modest development. As a result, the humus contents are also low.

In modern pedology the *salinity* is not determined according to type and quantity of salt but indirectly according to the electrical conductivity of the soil saturation extract (ECe). In the case of solonchaks the conductivity within 30 cm from surface is always more than $4\,\mathrm{dS\,m^{-1}}$ (corresponding to 0.2 wt% salt), and usually (in the case of chloride-rich solonchaks and all other soils with pH > 8.5) it is more than $15\,\mathrm{dS\,m^{-1}}$ (corresponding to 0.65 wt% salt)[18].

The soil can be used only after the salts have been washed out. When irrigation is used, however, new salt is also frequently brought in. Flushing with fresh water is only successful in those places where the substrate is permeable and the groundwater table is situated at a great depth (cf. also Chap. 3.5.6, irrigation farming).

Solonetz are characterized by a high degree of *Na saturation in the exchange complex* ($>15\%$ in the upper 40 cm of the argic B horizon (then: natric B horizon = B_{tn}). Hence also the name sodic soil. Because of hydrolysis of the Na clay (formation of $NaHCO_3$, Na_2CO_3 and NaOH in the soil solution), the *alkalinity* is very high, at least in the B_{tn} horizon (pH 8.5–11). The salt concentration is lower than in the solonchak soils (< 0.2 wt% or $< 4\,\mathrm{dS\,m^{-1}}$).

As a rule, solonetz soils form after desalination of Na-salt-rich solonchaks as a result of a drop in the groundwater table or also when there is an increase in climatic humidity. They have extremely little potential for agricultural use. Their unfavourable features include, among others, the highly alkaline reaction, the mechanical processes associated with swelling and shrinkage (sometimes the soils have a pasty consistency with poor aeration and waterlogging, sometimes they form hard clumps with shrinkage cracks) and the low availability of nutrient elements. Occasionally, by supplying calcium sulphate, it is possible to replace the sodium ions with calcium ions (subsequently flushing out the newly formed, easily soluble sodium sulphate).

3.4.5 Vegetation and Animal Life

Both the Arid Mid-Latitudes and the Tropical/Subtropical Arid Lands comprise hyper-arid *deserts and semi-deserts* as well as semi-arid grass/forb-covered areas, or at least grass-rich plant formations, which occur mostly at the edge of the deserts in the form of broad transitional border areas leading to the wetter neighbouring zones. When these grassy or grass-rich formations occur in the mid-latitudes or subtropics they are referred to as *steppes* (in North America as prairies) and in the tropics as *thorn savannas*[19].

The description of the vegetation and the fauna given here and in the following chapter on Tropical/Subtropical Arid Lands follows this three-part structure: the present chapter deals with both the steppes and the deserts/semi-deserts; and the following chapter examines the thorn savannas. The treatment of *all* deserts/semi-deserts, whether in the tropics, subtropics or mid-latitudes, within

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[18] The SI units for the electrical conductivity $1\,\mathrm{dS\,m^{-1}}$ (deci-Siemens per metre) or, correspondingly, $1\,\mathrm{mS\,cm^{-1}}$ supersede the former (non-SI unit) 1 mmho/cm (millimho per centimetre).

[19] The classification of the subtropical grassy formations is not always clear; some authors place them with the savannas.

one chapter is based (amongst others) on the many common characteristics of the plant cover, in particular the numerous ecological convergencies (convergent adaptations) caused by similar stresses (drought, heat, salt) found in each of the various zones. The influences exerted by the stress factor of winter cold, which exists only in the Arid Mid-Latitudes, are less important.

3.4.5.1 Steppes – Structural Characteristics

Types of Steppes and Growth Forms

Different types of steppes have formed as a function of regional fluctuations in the degree of aridity. The following climatic sequence reflects increasing dryness:

Forest Steppe. This is an ecotone in the transitional region from the forested Boreal Zone or the Humid Mid-Latitudes to the semi-arid regions, and it is characterized by a more scattered tree growth and, above all, by grassland occurring as patches within the forested areas. As one gets closer to the steppe proper, the forest breaks down more and more until finally only *patches of trees* are left within a grassland. The predominant soil type is the phaeozem.

Moist Steppe. Patches of trees are found only on stony terrain or in depressions with an inflow of water, due mainly to oro–hydrological conditions and not so much to climatic conditions, as in the case of the forest steppe. In addition to species of grasses and sedges, non-graminoid *herbaceous plants* (i.e. forbs) are also present in great numbers and they may give the steppe a meadow-like appearance (meadow steppe). The grass grows to a height of 40–60cm; therefore, the moist steppe is also referred to as the *tall-grass steppe*. More than 3 months of the year are arid, but the majority of the months are humid (or nival) or at least sub-humid (with precipitations >50% pET); the annual balance (P minus pET) is at most barely negative. In the spring, the melting snows ensure good wetting of the soil. The growing season lasts until the early summer. The predominant type of soil is the chernozem.

Dry Steppe. No trees, apart from the wooded banks of allogenic rivers (riverine forests). The grass grows only 20–40 cm high. Therefore the dry steppe is also referred to as the *short-grass steppe*. If medium-high grass (=mid-grass) occurs, namely a hybrid form between the tall- and the short-grass steppe, then the designation *mixed-grass steppe* is used. In many cases the grasses grow in tussocks. Non-graminoid herbaceous perennials are for the most part lacking. A maximum of 5 months of the year are humid, 7–10 are arid or at least semi-arid. The annual precipitation is between 200 and 500mm; the growing season is only in the spring. The predominant soil type is the kastanozem.

Desert Steppe. Dwarf shrubs or semi-ligneous shrubs, e.g. sagebrush species (*Artemisia* spp.) predominate (shrub steppe) – depending on the climate and also as a consequence of grazing. The numbers of perennial grass and forb species are lower, but annuals occur rather more frequently than in the "genuine" steppes. The stand cover is moderately patchy (degree of cover >50%). The annual precipitation is less than 250mm; usually only one month is humid. The predominant soil type is the xerosol.

Demarcation Between Steppes and Deserts. The desert steppes are frequently (e.g. in North America) counted among the deserts, i.e. grouped together with the deserts/semi-deserts, because they both have a high percentage of *woody* plants. Steppes in sensu stricto are then (apart from the ecotone of the forest steppes) exclusively the formations of the semi-arid mid-latitudinal areas which are *rich in herbaceous graminoids and forbs* (= grass steppe).

The following description is based by and large on this subdivision and starts out therefore by dealing only with the grass steppes.

Growth Forms. The majority of the herbaceous plants belong to the hemicryptophytes; a large number of them may also be assigned to the spring geophytes and therophytes. It is typical of all these life forms that they overwinter either at the surface of the soil or in the soil and this characteristic, in particular in combination with a (merely thin) snow cover of the kind normally present in the winter, obviously provides adequate protection from cold stress.

On the other hand, the *drought stress* of the summer months is harder on the plants. This is obvious from the fact that, among other things, the mass of above-ground sprout organs newly formed each spring and early summer varies considerably from year to year, depending on the weather conditions, which sometimes bring higher and sometimes lower amounts of precipitation. For example, on a dry steppe in southern Russia, fluctuations in the above-ground phytomass of between 4.5–6.3 $\mathrm{t\,ha^{-1}}$ in wet years and 0.7–2.7 $\mathrm{t\,ha^{-1}}$ in dry years have been determined. The below-ground phytomasses, on the other hand, remain the same (Walter and Breckle 1986).

Through their adaptation to the drought stress many of the plants possess *xeromorphic* characteristics. Understandably, as precipitation declines at the growth sites of the plants, so these features become more frequent and more prominent. Thus, when a comparison is made of the above-mentioned types of steppes, it becomes obvious that, in the sequence mentioned, the leaves become smaller and thicker, the epidermis and guard cells decrease in size, the number of stomata per unit of leaf area increases and the density of the venation also increases (Walter and Breckle 1986). The extremely finely branched (intensive) root system found among grasses is also to be understood as an adaptation to the poor water supply conditions; the mass of this root system exceeds that of the shoots in direct proportion to the increase in drought stress.

The steppes of eastern Asia differ from the rest in that they receive their precipitation in the summer (see Chap. 3.4.2), while the winter has little snow (and is cold) and the spring is dry. Consequently, there are no spring-blooming flowers in those areas and the vegetation turns green late in the year.

Animal Life

Originally, the steppes of Eurasia and North America were home to enormous herds of large mammals (ungulates). In the Old World these mammals were for the most part wild horses (tarpans) and saiga-antelopes; in the New World they were represented by bison, and in the 18th century by several million mustangs, the descendants of the horses which escaped during the Spanish expeditions of the 17th century. The tarpans were all killed off by the end of the last century; some saiga-antelopes have survived in small quantities on certain reserves. By 1890, the original population of 60 million bison had all been shot, with the exception of a few hundred specimens.

The animal species which still to this day inhabit the relatively intact steppe regions in large quantities include rabbits and numerous rodents such as susliks, marmots and guinea pigs (South America) as well as several smaller species of rodents [e.g. *Microtus* spp. (voles and lemmings) on the Eurasian steppes – Walter and Breckle 1986]. Periodic population explosions at intervals of several years are characteristic of these small rodents. At peak periods of population increase, they can consume up to 90% of the plant mass. The populations of the large rodents, on the other hand, are more balanced, and their influence on the steppe ecosystem is correspondingly more stable.

Together with the ungulates, the herbivorous rodents contribute to the accelerated turnover of the phytomass. Because of their burrows, which may extend deep into the C horizon of the soils, they also bring about considerable mixing of the soil material (see Chap. 3.4.4).

3.4.5.2 Stand Reserves and Turnovers of Dry Matter and Nutrients in the Steppe Ecosystem

Phytomass and Primary Production

Dependence on Precipitation and Temperature. For *all* the semi-arid to subhumid grasslands (steppes and savannas) of the earth, the rule applies that the differences in magnitude of phytomass and primary production which can occur within the individual zones of latitude, i.e. under similar conditions of sun light and temperature, can be directly correlated with the amounts of precipitation (Figs. 98, 118, 127, 167 and 168). Maximum values are achieved under subhumid conditions, while under markedly humid conditions the values drop again (presumably due to the reduction in insolation).

The decrease in phytomass and primary production which goes together with a drop in the amounts of precipitation affects the shoot mass to a greater extent than the root mass. Therefore, the latter increases proportionately (Table 32).

The figures compiled in Table 33 for phytomasses and production in tropical and temperate grasslands are mean values or mean ranges which Coupland

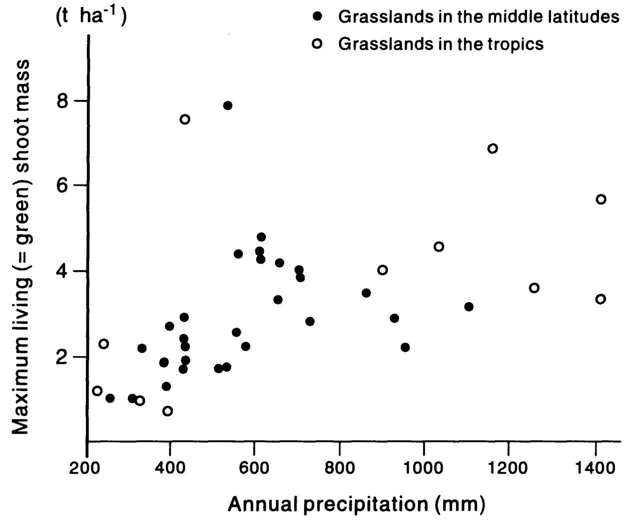


Fig. 98. The relationship between shoot mass and precipitation in semi-arid and sub-humid grasslands in the tropics and middle latitudes. (Coupland 1979)

Table 32. Phytomass and primary production in various types of steppes in Eurasia. (After Bazilevich and Rodin 1965, from Walter and Breckle 1986)

	Wet steppe	Dry steppe	Desert steppe
Phytomass (t ha^{-1})	**23.0**	**21.0**	**9.8**
– Amount above ground (t ha^{-1})	8.0	3.0	1.4
– Below-ground portion (%)	*65*	*86*	*86*
Primary production (t ha^{-1} a^{-1})	**13.0**	**9.0**	**4.2**
– Below-ground portion (%)	*38*	*67*	*67*

Table 33. Phytomass (t ha^{-1}) and primary production (t ha^{-1} a^{-1}) in grasslands under various climates. (Compiled from data taken from Coupland 1979)

	Tropics				Middle latitudes
	Semi-arid		Sub-humid	Humid	
Max. above-ground standing crop (max. canopy biomass)	1.3		13.0	4.0–4.5	3.5–4.0
Average below-ground standing crop		7			16–17
PP$_N$ (above-ground)	0.8	... to ...	34		1–24.3
PP$_N$ total	2.4	... to ...	45.6		7–34.7

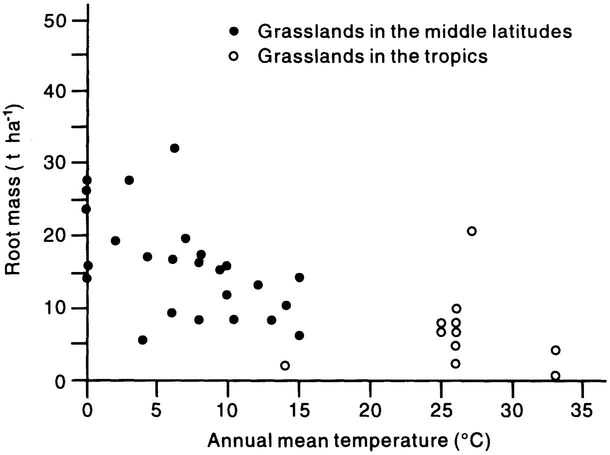


Fig. 99. The correlation between root mass and annual mean temperature in grasslands. (Coupland 1979). In cooler regions the root mass is larger both in absolute terms and (as a proportion of the respective total phytomass) in relative terms than that in warmer regions

(1979) calculated from numerous individual results obtained during studies of grasslands. These results reveal that the proportions of below-ground phytomass are much higher in the temperate grasslands than in the tropical grasslands. This is particularly apparent from the ratios of (mean) below-ground to (maximum) above-ground standing crop: in tropical grasslands these are between 0.2 and 2.6 (on average 0.8), whereas in temperate grasslands they are between 1.4 and 10.3 (average 4.4). Thus, in the tropical grassland areas the root mass is on average somewhat smaller than the shoot mass, while in the temperate grasslands on the other hand it is more than four times as large. Figure 99 shows that the root mass is approximately inversely proportional to the average annual temperature.

The temperate grasslands have higher root masses also in absolute terms: according to the investigations evaluated by Coupland, the root mass values are usually less than 10 t ha^{-1} in the tropics but usually higher than this in the mid-latitudes.

Under comparable humid conditions, the PP_N in the lower latitudes is greater than in the higher latitudes. Since the difference in radiation during the summer growth periods are in many cases insignificant (Table 31), this may be due to the larger proportions of *C_4-plants* in the warmer regions (Fig. 100). C_4-plants have a higher temperature optimum (30–35 °C compared with 10–25 °C for the C_3-plants) and a higher water-use efficiency (transpiration ratio), no photorespiration losses, and they are capable of utilizing higher radiation intensities.

Productiveness. Considering the low amount of phytomass, the production of the steppes is extraordinarily high. In forest and moist steppes where forest stands and grasslands patches occur under the same climatic (merely edaphically de-

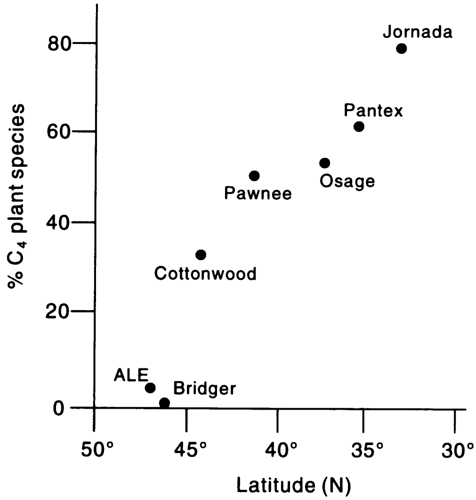


Fig. 100. Percentage amounts of C_4 plant species in the steppe flora in North America, as a function of latitude. (French 1979a). For the position of the individual stations, see Fig. 103

viating) conditions, the photosynthetic capacities can be directly compared. It is found that both formations are approximately equally productive, although the phytomasses of the forests are higher by a factor of 10 to 15. The steppes produce "more economically" because they do not form any above-ground, unproductive (only respiring, i.e. energy-consuming) woody stems but instead *exclusively photosynthetically active organs* are produced (however, compared with trees, the root proportion in the case of grasses is relatively higher). The comparatively balanced distribution of light within the grass layer is also a favourable factor (Fig. 101): because of the mainly steeply oriented leaves, at least half of the photosynthetically utilizable radiation reaches the middle of the stand (*extinction coefficient* less than 0.5). In forests, the drop in available light is much stronger; often only about 10% of the ambient light penetrates the upper canopy (Figs. 50 and 79).

One-Year Growth Cycle. Since most of the aerial phytomass dies off at the latest in the autumn, the amount of litter supplied each year is about as high as the above-ground PP_N of the same year. This (fundamentally easily decomposed) litter breaks down quickly, mainly within 1 year. As a result, large layers of litter do not build up anywhere. However, the seasonal differences in litter decomposition rate are striking. The litter which falls in the autumn months does not start to decompose until the following spring. In the winter season the layers of litter are therefore much thicker than in the summer season; the minimum level is attained at the start of the summer dry period.

The lifetime of the below-ground phytomass is sometimes longer; in the maximum case it is about 4 years for individual roots. This means that the root mass is also relatively quickly turned over. Thus, for the steppe ecosystem the unique

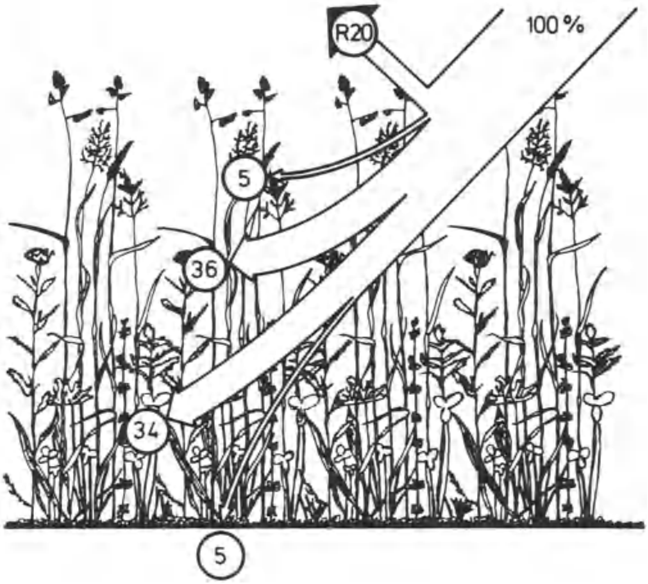


Fig. 101. Attenuation of radiation in a meadow. (Cernusca 1975). In contrast to forests, here a large amount of light penetrates deep into the plant stand (as much as >50% of the ambient light still penetrates to the centre of the grass layer)

case arises where (1) an extraordinarily short, almost 1-year metabolic cycle and energy flow exist and, correspondingly, (2) very approximately steady-state conditions prevail (in all the other ecozones, including the tundra and desert, hoarding takes place over long periods of time, i.e. energy and minerals are fixed in the form of long-lived, ligneous stand increments, until large amounts of stockpiled material are fairly suddenly recycled during a later phase when the stand has aged, or as a result of extreme conditions, e.g. windthrow, fire or extremely dry years).

Nutrient Reserves and Turnovers

Grassland ecosystems are unique in one further point: their phytomasses contain far above average amounts of mineral nutrients; therefore their organic turnovers are accompanied by considerable turnovers of minerals. The mineral cycles in the high-production moist steppes exceed those of all other zonal ecosystems in quantity of materials involved and also in rapidity of throughput. In the drier grass steppes this is true at least in relation to the size of the organic turnovers.

According to the figures compiled by Titlyanova and Bazilevich (1979) for several steppes, the contents of N, K, Ca, Mg and P in the living shoots are on average approximately 4 and 5% and in the roots approximately 2 to 3%.

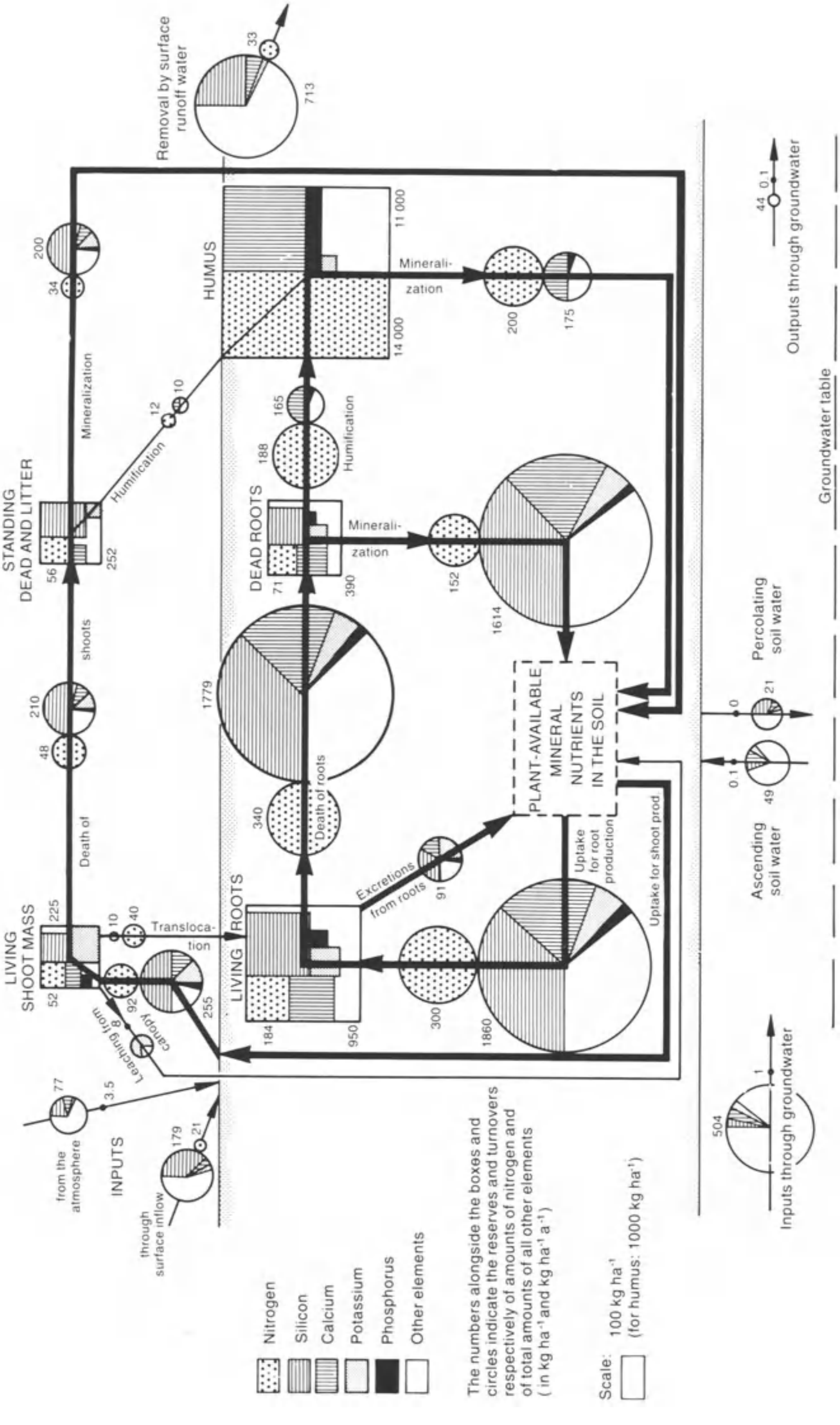
The amounts increase with increasing climatic dryness and concentration of salt in the soil. The above-mentioned elements may also be joined – especially in the case of grasses – by elevated contents of Si, on saline sites by elevated amounts of S, Cl and Na. Compared with the green shoots, the standing dead and litter have lower amounts of K, Cl, Na and S, but higher amounts of Si, Fe and Al; Si can attain several percent (in the green shoot mass it usually reaches only 1 to 2%).

On the other hand, because of the relatively small (compared with all forest ecosystems) amounts of phytomass, the high mineral turnovers go together with low reserves of organically bound minerals (although larger quantities are to be found in the humus).

The mineral cycling of the steppe ecosystem will be described here using as an example a moderately halophytic grassland in the western Siberian steppe region around Novosibirsk, which was studied in detail by Titlyanova and Bazilevich (1979) (Fig. 102 and Table 34). The predominant plant species in this grassland are *Calamagrostis epigeios*, *Poa angustifolia*, *Vicia cracca*, *Artemisia laciniata* and *Galatella biflora*. The system-inherent mineral turnovers were measured, namely (1) uptake by the roots and incorporation into the below-ground and above-ground phytomass, (2) release from dead organic material and (3) formation and decomposition of humus. In addition, the inputs from precipitation, surface inflow and groundwater, as well as the outputs in the form of surface runoff and leaching into the groundwater, were determined. Consumption by animals (presumably this accounts for less than 5% of primary production; excrements and the remains of dead animals are contained in the litter) and also nitrogen exchange between atmosphere and soil (N_2-fixation, denitrification) were ignored.

N and Si, followed by Ca, are the main minerals incorporated into the root mass; on the other hand, in the living *shoot* mass – at least during the main growth phase – K moves clearly ahead of Ca and Si, and sometimes even ahead of N. However, as the growing season progresses, the inflow of Ca and Si also increase relatively more strongly. Towards the end of the growing season, minerals start to be translocated in the opposite direction and finally about 50% of the N and 15–20% of the K and Na are returned to the roots. Further amounts of N, K and Na, as well as of Cl, P and S, are returned to the soil by leaching from the canopy.

Both mineral recycling routes cause the relative proportions of Ca, Si, Fe and Al in the remaining above-ground standing dead and the litter to increase. In the litter, a further increase occurs in the Si, Fe, and Al concentrations because the other elements, this time including Ca, are preferentially released by leaching and decomposition processes. On the other hand, the microbial activity temporarily leads to secondary enrichment of N in the litter whose content as a result may increase to 1.5–2 times that of the above-ground standing dead. Finally, the decomposition of the litter releases approximately 75% of the N and 95% of the other minerals, and thus they are available to be taken up again by the plant roots; the remainder goes into the (permanent) humus.



The numbers alongside the boxes and circles indicate the reserves and turnovers respectively of amounts of nitrogen and of total amounts of all other elements (in kg ha^{-1} and kg ha^{-1} a^{-1})

Only 25% of the N and 10% of the other elements taken up via the roots go into above-ground primary production, while by far the greater proportion ends up in subterranean production. Only a very small part of the minerals contained in the root mass are recycled by being re-excreted; instead, the decomposition of dead roots is the decisive factor; herewith, about 50% of the N and 90% of the other elements are released, and the rest remains in the humus.

Organic Matter and Energy Flow in the North American Prairie

The following remarks relate to the detailed studies which were undertaken within the framework of the International Biological Programme in the North American Prairies near Matador (50° 42′ N, 107° 48′ W, 680 m above sea level) and Pawnee (40° 49′ N, 104° 46′ W, 1650 m above sea level) (Coupland and Van Dyne 1979) (Fig. 103). Matador possesses short to medium-tall grass and is thus a mixed-grass steppe; the predominant species are *Agropyron dasystachyum*, *Carex eleocharis* bailey and *Koeleria cristata*. The mean annual precipitations are 338 mm, and the mean annual temperature is 3 °C. In contrast, Pawnee is a short-grass steppe in which the short tufted grasses *Bouteleoua gracilis* and *Buchloe dactyloides* predominate. The winters are milder, the summers warmer and drier than in Matador; the mean annual precipitation is 311 mm and the mean average temperature amounts to 8.3 °C (Fig. 104). In keeping with its more southerly latitude, Pawnee receives on average 27 000 kJ m^{-2} d^{-1}, namely 400 × 10^8 kJ ha^{-1} of insolation during the growing season, which is much more than Matador (17 000 kJ m^{-2} d^{-1} or 250 × 10^8 kJ ha^{-1} during the growing season; Fig. 105). Probably as a result of greater drought stress, the vegetation in Pawnee is able to use only 0.3% of this energy for net primary production, whereas the vegetation of the more northerly situated Matador is able to use 0.5%

Figure 106 is based on the results of the study carried out at Matador and it depicts the steppe ecosystem based on the model already used for the above-mentioned ecozones. Under steady-state conditions the *turnover period of the above-ground phytomass* (living portion of the above-ground standing crop) can

◄———

Fig. 102. Mineral cycling in a mesohalophytic grassland in the western Siberian steppe region around Novosibirsk. (Titlyanova and Bazilevich 1979). Mineral reserves are indicated by *squares*, mineral turnovers by *circles* arranged along a system of *arrows*. The *sizes* of the squares and circles are proportional to the respective reserves (kg ha^{-1}) or to the turnovers (kg $ha^{-1}a^{-1}$) respectively (a reduced scale is used for the humus). The *subdivisions* of the squares and circles correspond to the proportions of the individual nutrient elements. In the case of the turnovers, *nitrogen* is indicated by its own *separate circles*

Table 34. Amounts of minerals in the organic stand reserves and in the primary production of a mesohalophytic meadow in western Siberia. (Compiled on the basis of data in Titlyanova and Bazilevich 1979)

	Organic matter kg ha^{-1}	Amounts of minerals incorporated therein[a]						Sequence of elements according to their proportions in the organic matter
		Nitrogen		Other elements		Total minerals		
		kg ha^{-1}	in % of organic matter	kg ha^{-1}	in % of organic matter	kg ha^{-1}	in % of organic matter	
Total organic matter (without humus)	29 850					2180	7.3	Si, N, Ca, K
Max. living shoot mass	2400					277	11.5	N, K, Si, Ca
Living and dead root mass	23 300					1595	6.8	Si, N, Ca, K
Above-ground standing dead and litter	4150					308	7.4	Si, N, Ca, K
Humus						25 000		N, Ca
Total primary production	31 000	392	1.3	2115	6.8	2507	8.1	Si, N, Ca, K
PP_N above ground	4200	92	2.2	255	6.1	347	8.3	
PP_N below ground	26 800	300	1.1	1860	6.9	2160	8.1	

[a] Elements measured: N, Si, Ca, K, Mg, P, S, Na, Cl

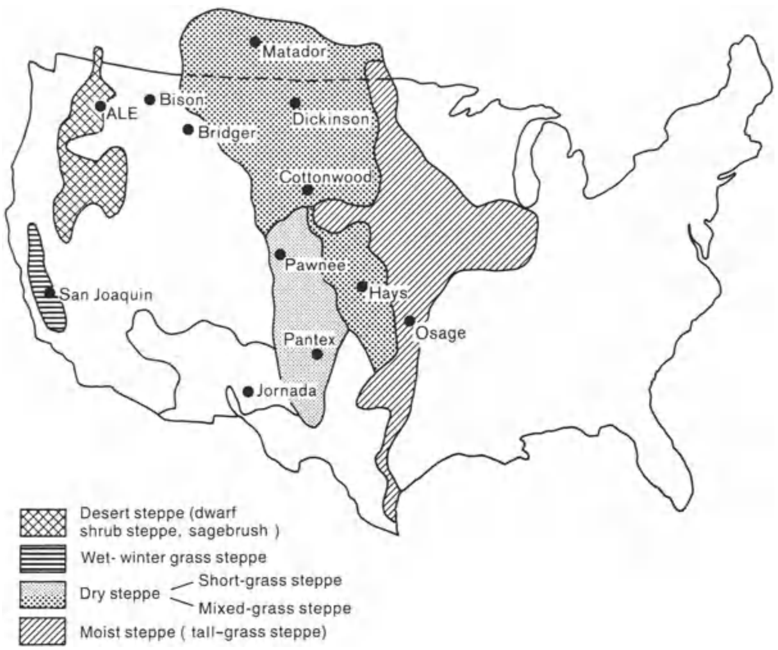


Fig. 103. Original grasslands in North America and location of the IBP study areas. (Sims and Coupland 1979). The values quoted in the text refer to the two stations at Matador and Pawnee

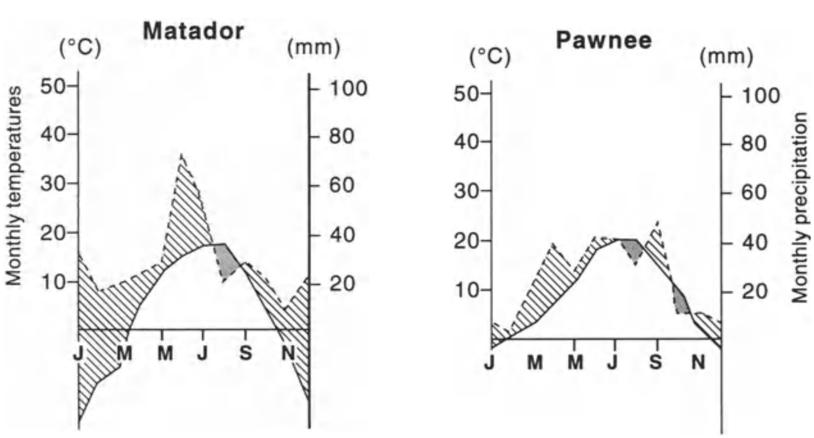


Fig. 104. Climatic diagrams of Matador/Canada and Pawnee/USA. (French 1979b)

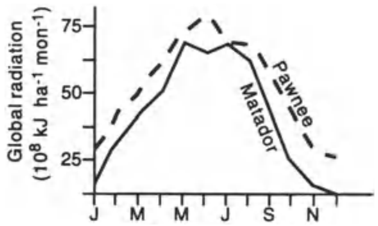


Fig. 105. Annual cycle of global radiation in Matador and Pawnee. (French 1979b)

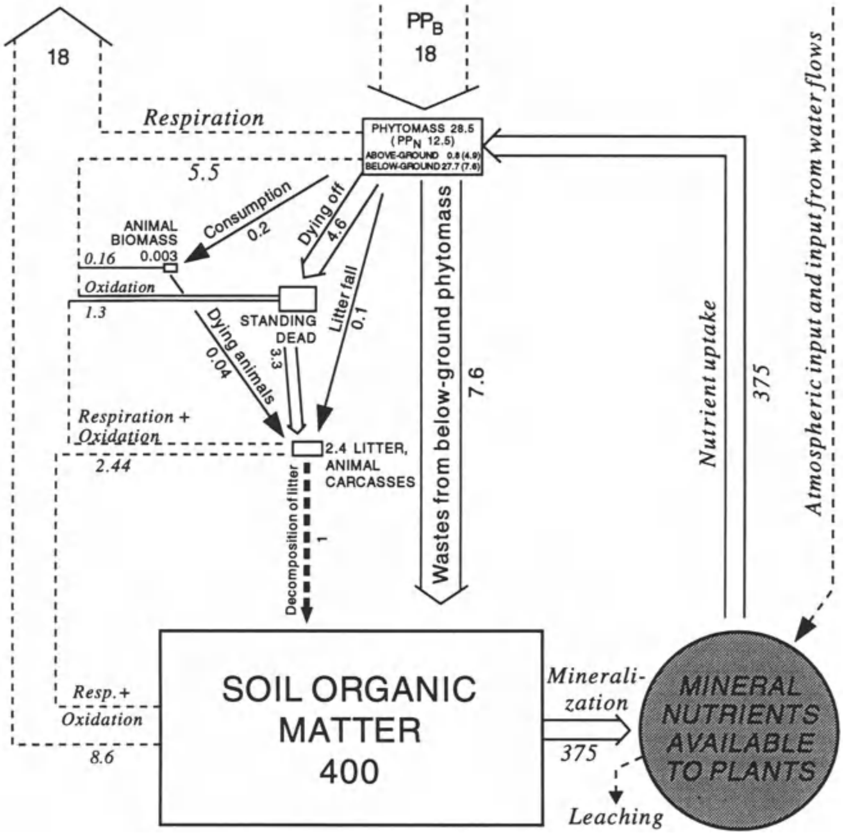


Fig. 106. Simplified ecosystem model of a cold-winter dry steppe (mixed grass steppe). The *numbers* (= mean values) are taken from a study which was performed in 1968–1972 in the prairie at Matador/Canada (Coupland and Van Dyne 1979); *broken lines* indicate estimated additions. For the structure of the model, cf. Chapter 2.5.2.5. The mean shoot mass is 0.8 t ha^{-1}, the above-ground PP$_N$ is 4.9 ha^{-1} a^{-1}. 1.3 t ha^{-1} of the annual shoot production is lost immediately via (presumably non-biological) decomposition processes in the standing dead, i.e. this amount does not end up in the litter where it would be available to the heterotrophs. These above-ground decomposition processes made it necessary to depict the standing dead as a separate compartment, thereby deviating from the scheme otherwise followed in which the standing dead is contained in the box for phytomass. It is characteristic of the steppe ecosystem that (1) the root mass is much greater than the shoot mass, (2) high matter and energy flows occur, both in absolute terms and in particular in relation to the biomass, and (3) the bulk of the organic matter exists in the form of humus

be calculated in relationship to the above-ground PP_N, namely

$$\frac{\text{Maximum living shoot mass}^{20}}{\text{above-ground } PP_N}$$

Correspondingly, the *turnover period of the root mass* (living portion of the below-ground standing crop) can be calculated via the ratio

$$\frac{\text{Maximum living root mass}}{\text{below-ground } PP_N}$$

Thus for Matador, the turnover period for the shoot mass is 0.26 years and for the root mass 4.18 years. This means that (1) the herbaceous parts of the shoots turn yellow and dry on average within three months after their formation, whereas the lifetime of the roots is more than 4 years; and (2) the above-ground PP_N exceeds the maximum living shoot mass by a factor of 4, whereas the below-ground PP_N amounts to only 25% of the root mass. According to Bazilevich and Titlyanova (1980), neither of these values is representative for steppes. From the numerous studies of the steppes which were evaluated by them, it was calculated that the above-ground PP_N generally exceeds the maximum living shoot mass by no more than a factor of 1.2 to 2.7, whereas the below-ground PP_N on average attained a proportion of 0.9 to 1 times the living root mass, i.e. a surprisingly high value, as the two researchers themselves state. This value means that on average the root mass is also turned over within 1 year.

Of the shoot production, totalling 4.9 $\mathrm{t\,ha^{-1}\,a^{-1}}$, 0.2 t are eaten by herbivores and 0.1 t fall to the ground immediately after the death of the plants. The remainder changes to standing dead at first of which 1.3 t are directly (non-

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[20] In contrast to deciduous trees of the Humid Mid-Latitudes, in which the leaf mass formed in the spring and early summer remains largely constant up until the abscission of the leaves in the autumn, the shoots of the herbaceous steppe vegetation continue to grow during the summer, up until the start of the ripening stage which, depending on the circumstances, may occur in early, high or late summer. After that, most of the plants die off. While the plants are still alive, older leaves or large portions of shoots die off but, as a rule, remain attached to the living plant and so, for a certain amount of time, form the standing crop together with the latter. Unless explicitly stated, the values given in the results of the study for the above-ground phytomass refer to the standing crop (this makes sense because this mass represents the total production for the year up to that point).

It follows from what has been said that the living (= green) shoot mass (and naturally also the total, i.e. living and dead, shoot mass) varies considerably over the course of the growing season. This poses the problem of which value to use in drawing up balances. In the present case, the "maximum living shoot mass" was selected; this is the mass which is achieved by the individual plants usually shortly before or at the start of their flowering phase. Since the flowering dates for the individual species are different, that is to say there is not one "peak date" which applies to all species, the "maximum living shoot mass" of a plant stand is of necessity smaller than the sum of the maximum living shoot masses of its individual plants. It further follows from what has been said that the above-ground PP_N is greater than the maximum living shoot mass (in the case of Matador it is about four times as large) and that, in the highest possible case, the maximum standing shoot mass may attain the PP_N of the same year.

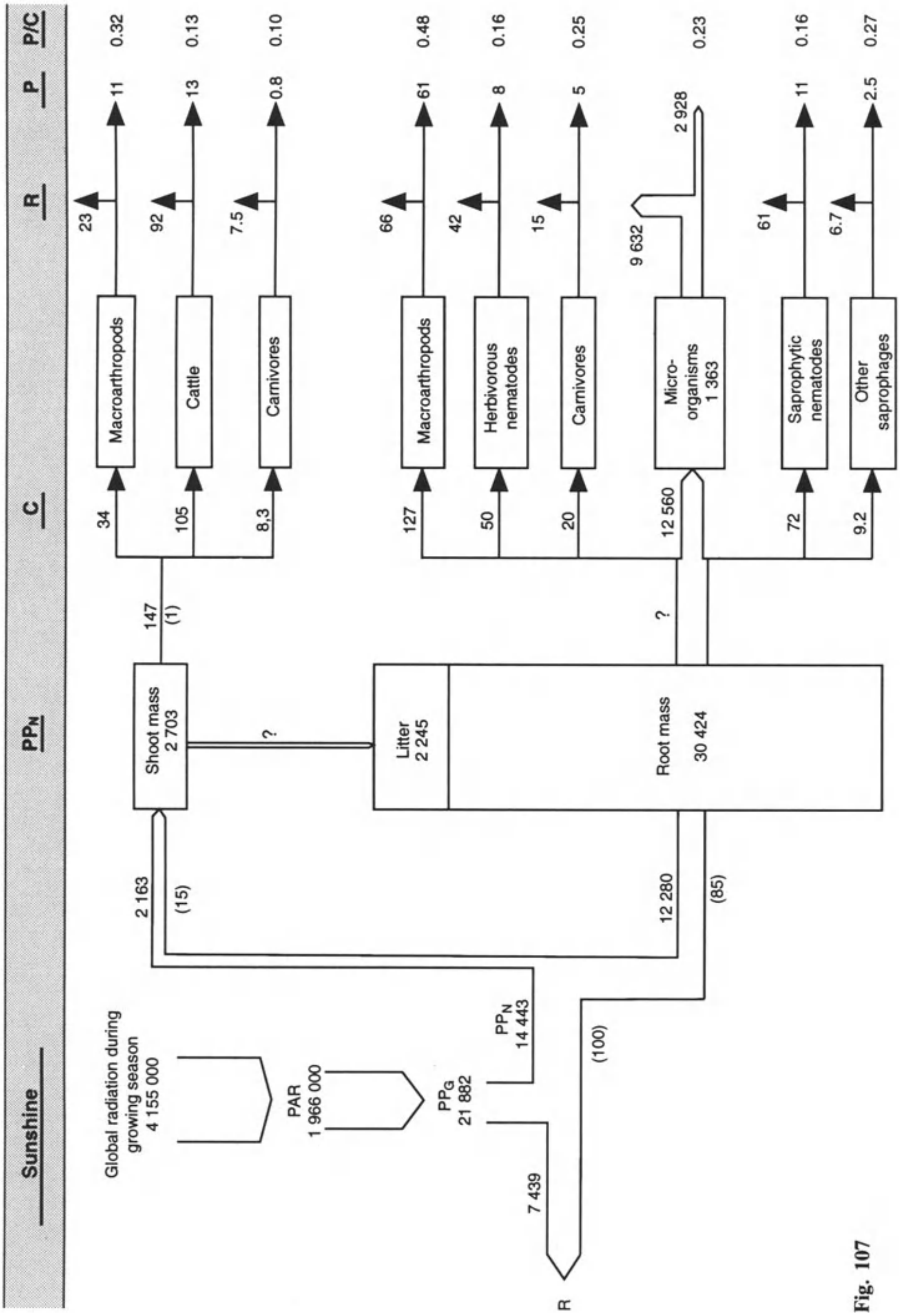
Sunshine
PP$_N$
C
R
P
P/C
Global radiation during growing season
4 155 000
PAR
1 966 000
PP$_G$
21 882
PP$_N$
14 443
7 439
R
(100)
2 163
(15)
12 280
(85)
Shoot mass
2 703
Litter
2 245
Root mass
30 424
?
147
(1)
?
34
105
8,3
127
50
20
12 560
72
9.2
Macroarthropods
Cattle
Carnivores
Macroarthropods
Herbivorous nematodes
Carnivores
Micro-organisms
1 363
Saprophytic nematodes
Other saprophages
23
92
7.5
66
42
15
9 632
61
6.7
11
13
0.8
61
8
5
2 928
11
2.5
0.32
0.13
0.10
0.48
0.16
0.25
0.23
0.16
0.27

Fig. 107

biologically?) broken down. Only 3.4 t (including the small portion of immidiate litter fall) end up in the litter layer, where they are then available to the detrivores and decomposers.

Figure 107 shows the energy flows in the *steppe ecosystem at Pawnee*, taking account in particular of the role played by heterotrophs. Compared with the many studies conducted in other steppe regions, it is surprising that the small herbivorous mammals, which consume sometimes more than 10% of the phytomass growing there, are not listed. The results from Pawnee appear as follows.

Of the shoot mass only a very small amount goes directly to consumers (7% of the above-ground PP_N). Most of the shoot mass ends up on the soil via the litter and is only then taken up by the heterotrophs; a smaller amount is possibly lost via abiotic decomposition (see above). The exact magnitude of this flow, as well as the fate of altogether 1458 kJ (difference between PP_N and the sum of the listed energy flows to the heterotrophs) remains uncertain.

The Pawnee steppe is very little grazed; only a small proportion of the shoot mass with an energy content of altogether 105 $kJ\,m^{-2}\,a^{-1}$ is consumed by cattle (the ability to support cattle is much higher; in Matador, for example, it is estimated to be six times as high as here).

The net production of cattle binds 13% (in Matador 6%) of this energy uptake. Thus, as expected, the gross production efficiency (P/C) is significantly lower than in the case of the invertebrate consumers (16–32%; the value of 48% given for subterranean-dwelling macroarthropods definitely needs to be checked).

It is striking that the microorganisms produce more than twice their own biomass per annum, and the soil invertebrates, whose standing crop was measured at a total of 8.8 $kJ\,m^{-2}$, produce as much as ten times their own biomass (measured in each case according to energy contents). Among the grasshoppers, birds and small mammals in Matador, annual net productions exceeding their respective standing crops by factors of 5, 2 and 5 were measured. In contrast, the weight increase achieved by cattle per grazing season was only about one-third or one-half of the initial body mass.

Large differences also exist in the food uptake with respect to the standing crops of the various groups of heterotrophs. For example, the microorganisms take up 11 times more food energy (12 560 $kJ\,m^{-2}$) than the energy contents of their body substances (1363 $kJ\,m^{-2}$), and the soil invertebrates take up as much as 30 times more. In contrast, during the 6-month grazing season, the cattle

◄———

Fig. 107. Energy flow (in $kJ\ m^{-2}\ a^{-1}$) through the ecosystem of a short-grass steppe at Pawnee/USA. (After Coupland and Van Dyne 1979, slightly modified). The values are derived from surveys conducted in 1972 and relate to a 154-day growing season. The *number in boxes* designate the energy contents of average standing crops, while the *numbers along the arrows* denote energy flows (the proportional amounts of the net primary production = PP_N in percent are shown in brackets). *C* Consumption; *P* secondary production; *R* respiration losses; *P/C* gross production efficiency; *PAR* photosynthetically active radiation; 18 kJ correspond to 1 g green shoot mass; 16.3 kJ correspond to 1 g dead shoot mass; the energy content of litter and roots may be converted into organic dry matter giving 15.1 and 15.4 $kJ\,g^{-1}$ respectively; for animals about 24 $kJ\,g^{-1}$ must be estimated

consume only five to six times their body mass, relative to the energy contents of the foodstuffs and the animals' bodies. This means that the proportion of the animal biomass which is accounted for by the individual heterotrophic groups is not a measure for the proportional role they play in animal off-take (C) or in the decomposition process: in the same standing crop, the food turnovers of the microorganisms and invertebrate soil-dwelling organisms are much higher than in the case of cattle; thus they play a correspondingly more important function in the ecosystem.

3.4.5.3 Temperate and Tropical/Subtropical Deserts and Semi-Deserts

In the deserts and semi-deserts, *woody plants* – predominantly low-growing shrubs and semi-ligneous shrubs (chamaephytes) but also taller shrubs and trees (phanerophytes) – as well as annuals (therophytes) are present in much larger numbers than the herbaceous perennials (hemicryptophytes) which are the typical life forms of grass steppes and thorn savannas. The predominance of non-herbaceous perennials rises with increasing drought and grazing.

The *cover provided by perennial vegetation* remains less than 50%, while in extreme deserts plant growth is lacking altogether. In moderately arid regions the individual plants are fairly uniformly (diffusely) distributed over the terrain. In this case one talks of *semi-deserts* (or of desert steppes where a patchy plant stand exists with a cover of more than 50%). The transition to *deserts* occurs where large coherent areas without any permanent vegetation are found (Jätzold 1984), between more favourable sites with patchy or even closed plant stands. As a rule, the vegetated areas cover less than 10% of the surface.

The degree and type of vegetation cover depend on the water supply. The amount of water available to the individual plant depends on the precipitation, the relief, the soil texture and the amount of available root space. The following comments can be made:

Redistribution of Precipitation by Surface Runoff. Because plant cover is sparse or totally lacking, most raindrops strike the ground directly, where they cause splash erosion. As a result, the surface of the soil becomes puddled and the infiltration rate is considerably reduced. It is therefore characteristic of arid regions that large amounts of precipitation do not infiltrate into the ground at the point of their impingement, but run off at the surface, even in gently sloping terrain, and flow into pans (playas), dry valleys (wadis, oueds, arroyos, secos) or into the zones at the foot of mountain ranges (scree slopes, pediments, bajadas).

In addition to precipitation intensity, the inclination of the terrain, the degree of plant cover and a few other parameters, the precipitation/runoff ratio is especially dependent on the *soil texture* (grain size spectrum), because this determines, to a large extent, the maximum infiltration rate, i.e. the amount of rainwater which is able to infiltrate per unit time into the soil at the start of a precipitation event and as it continues.

The redistribution of the precipitation creates locally more or less "humid" moisture conditions (the inflow can amount to a multiple of the amount which falls directly as rain), and in other places it additionally exacerbates the drought. The redistribution processes may also play a role very locally if the surface of the terrain has only a gentle slope and is divided into separate microareas. Considerable differences in soil moisture content may be found here side by side following precipitation events. The plant distribution may be both the cause and the consequence of this redistribution.

The spatial as well as temporal (see Chap. 3.4.2) concentration of the precipitation water is favourable as far as conditions for plant and animal life are concerned: this is the only way in which sufficient moisture conditions essential for the development of life can be created, at least temporarily, in certain sections of relief sequences and pedosequences.

Water-Retention Capacity of Soils. The *soil texture* also determines what happens to the infiltrating water, since the water-retention capacity of the soil depends on this factor. If the texture is fine and thus the field capacity is high, then the water does not infiltrate to a very great depth (and, correspondingly, the volume of soil which is wetted remains small); also, the percentage of water *not* available to plants is high and there is a large evaporation loss due to the upward capillary movement of soil water. The circumstances are exactly reversed when the soil is coarse in texture and thus has a lower field capacity: the water infiltrates deep or at least deeper into the ground (i.e it is distributed throughout a larger volume of soil); almost all the water is in principle available to the plants, because it is for the most part only weakly bound to soil particles, and it is protected from further evaporation by the uppermost soil layer which dries out (no capillary suction) (Fig. 108). Therefore, under otherwise comparable conditions, soils formed on rocky detritus or sands have more favourable water budgets than soils formed on argillaceous material. In this regard, those soils whose surface is partially covered by "desert pavement", which can be formed, for example, by wind erosion (see Chap. 3.4.3), must also be regarded as advantageous. Removing such pavement would impair plant growth (Evenari 1985).

Space Between Plants. Also, the spacing between individual plants is an important factor for their water supply, because this determines to a large extent the volume of soil which is available for the development of the root system and thus for water uptake. The greater the spacing, the better the opportunity of the individual plant to compensate, to a greater or lesser extent, for deficits in precipitation by developing a more extensive root system. It has, in fact, been discovered that, in arid regions, a sparse plant cover at the surface of the soil corresponds to the development of much denser root systems, which often fill the available space (Fig. 109); in this case, the roots compete (for the water), whereas in humid regions mainly the shoots compete with each other (for the light).

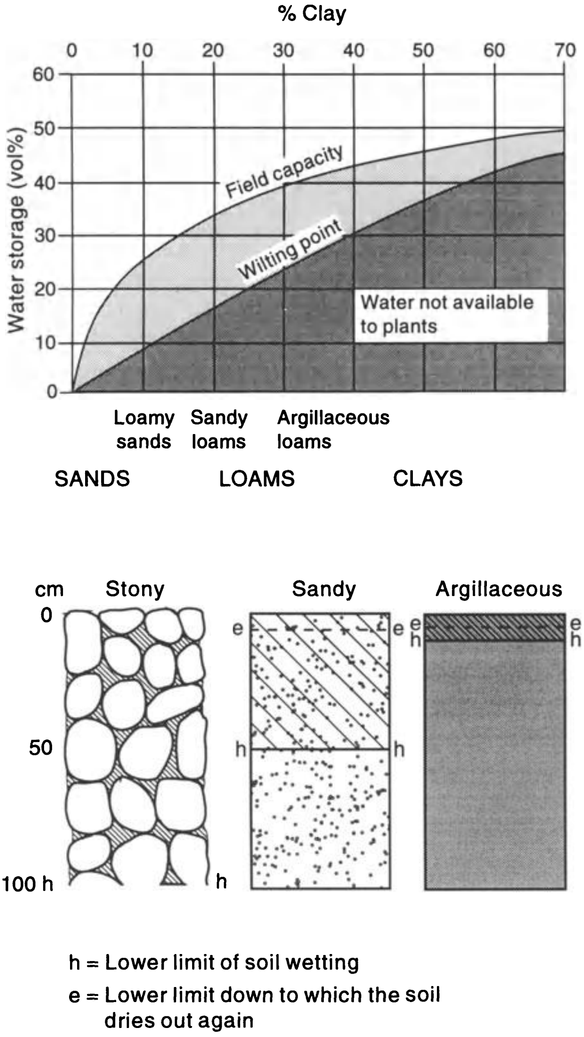

Fig. 108. Water-storage capacity of soils having different grain-size spectra. (Walter and Breckle 1983; Achtnich and Lüken 1986). The maximum possible soil water content (field capacity) increases with declining grain size (The following assumption has been made regarding the soil substrates shown in the bar diagrams: stony = 5%, sandy = 10%, argillaceous = 50%). Therefore, the coarser the grain size of the soil, the deeper the same amount of rain (50 mm of rain has been assumed) infiltrates into the substrate (stony = 100 cm, sandy = 50 cm, argilllaceous = 10 cm). Of the amount of water which infiltrates, the plants have access basically only to that portion which is bound to the soil particles, adsorptively or by capillarity, with a pressure (matrix potential) of less than (approx.) 15–60 bar (depending on the root suction pressure (osmotic potential) of the plants in question). This portion of the water is very much lower in fine-grained than in loamy soils; in sandy soils virtually all the soil water is available to the plants. That portion of the soil water which is subject to evaporation, because (either primarily or as a result of capillary ascent) it is close to the surface, is lost before the plants can take it up. This loss is greatest (about 50% in the assumed example) in clay soils, but much lower (10%) in sandy soils and in stony substrates (0%)

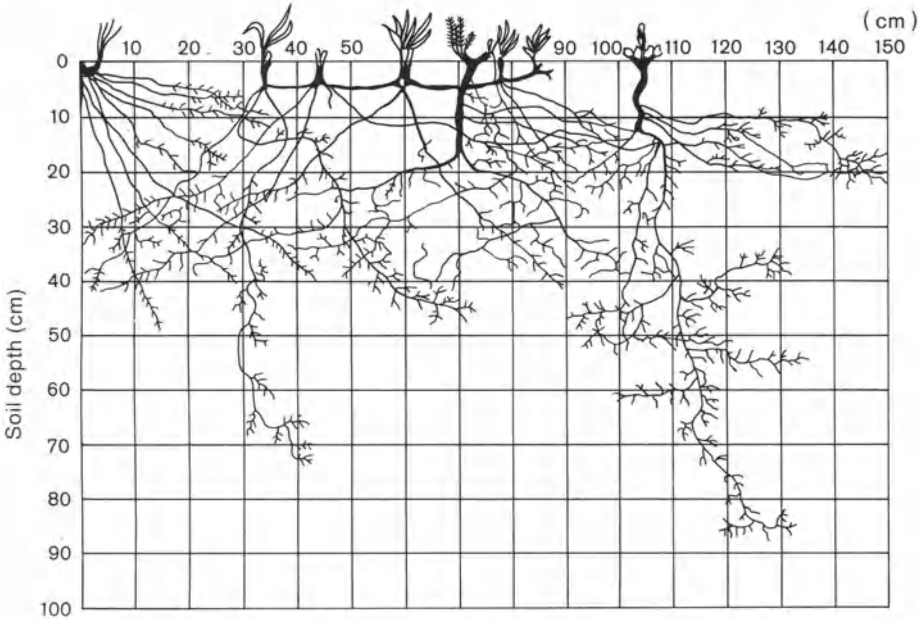

Fig. 109. Root systems of the *Artemisia rhodantha–Stipa orientalis* alpine semi-desert in Pamir (Walter and Box 1983). *From left to right*: *Stipa orientalis*, *Carex stenophylloides*, *Oxytropis chiliophylla*, *Artemisia rhodantha*. The cover provided by the plant shoots amounts to 8–15%. The soil is totally permeated by roots down to a depth of 40 cm. The depth of penetration of the roots is 25–45 times greater than the shoot height of the plants; the root mass is a multiple of the shoot mass

Therefore, the increase in the spacings between plants from desert steppes to semi-deserts is a form of adaptation to the reduction in water supply per unit area along this gradient. The (more or less equally) scattered distribution (diffusion) of plants disappears only when an increase in the volume of root space alone is insufficient to provide an adequate supply of water to the plants (in the Arid Mid-Latitudes this happens approximately at annual precipitation of less then 100 mm); under such conditions plant growth is able to develop only at those places where surface inflow and better water-retention capacity of the soil create sites with better than average moisture content. This means that a vegetation of patchy or linear configuration forms on surfaces where there is otherwise no vegetation (Fig. 110). Depending on the favourability of the site conditions, the vegetated areas may be formed by individual plant stands, as in semi-deserts, or they may even consist of a closed cover, similar to steppe or savanna vegetation; grasses with intensive root systems predominate on argillaceous soils, and trees with extensive root systems are the predominant form on sandy substrates.

Soil Salt Content. The salt content can also influence the distribution of plants (Fig. 111).

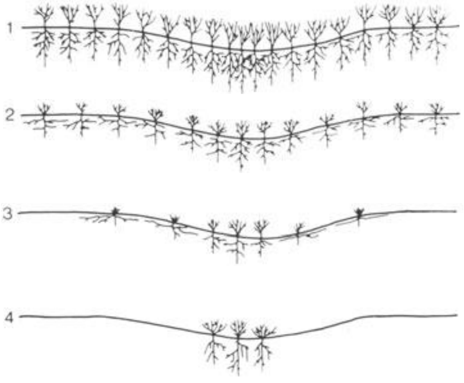

Fig. 110. Schematic presentation of the transition of "diffuse" vegetation (*1, 2*) into a "contracted" form of vegetation (*3, 4*) when precipitation declines in extremely arid regions. (Walter and Breckle 1983). In semi-deserts, as compared with less arid lands, the vegetation moves apart (i.e. becomes "diffuse") so that more root space for water uptake is available to the individual plants. In full deserts, plant growth is limited ("contracted") to those sites where water flows collect together on the surface (or also below ground, e.g. in wadis). The depth of root penetration corresponds to the depth of wetting

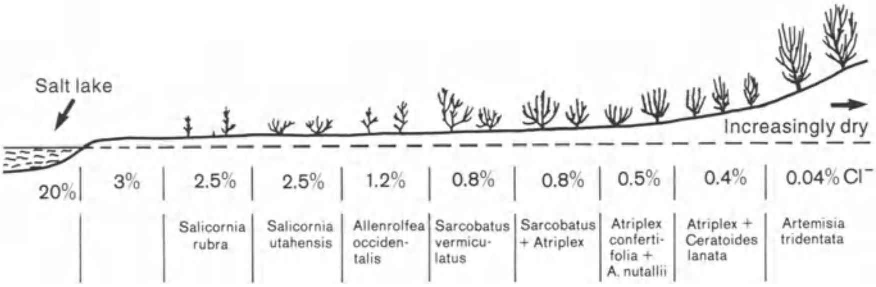

Fig. 111. A normal halosequence on the Great Salt Lake/Utah (USA), showing the Cl^{-1} contents (in % of soil dry weight) in the individual vegetation belts surrounding a salt lake. (Walter and Breckle 1983)

The Spatial Sequences of Plant Cover. Plant sequences in relation to changing climate, relief and soils, which in the final analysis are all linked with the water supply, are surprisingly similar in all arid/semi-arid regions of the world, not only with respect to physiognomy but also – in the the Northern Hemisphere[21] – with respect to the predominant taxa. Thus, they represent an extremely characteristic common feature, especially of all the desert steppes, semi-deserts and deserts.

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[21] Phytogeographically, the Eurasian and North American deserts, semi-deserts and steppes all belong to the Holarctic. In fact, their flora are extremely similar all the way down to the taxomic level of the genera. On the other hand, in Patagonian steppes, most of the taxa are indigenous to that particular region.

The *relief-related and soil-related sequences* commence either with mountains having little or no vegetation, or with unconsolidated sandy regions, and they end in highly saline pans (takyrs etc.) which are equally lacking in or devoid of vegetation. In between the two extremes, depending on the transition from coarsely textured to increasingly fine-grained soil substrates (Fig. 96), we find initially plant communities rich in trees/shrubs and later grasses, which ultimately merge into tracts of herbaceous plants containing many halophytes, until the salt concentrations become too high even for these; thus plant growth disappears completely. However, following flooding of the pans or wetting by precipitation, an *ephemeral algal growth* may form with a phytomass of 0.5–1.4 $\mathrm{t\,ha^{-1}}$ according to Walter and Box (1983).

The *climate-related sequence* of the Arid Mid-Latitudes, which extends from the forested steppe to the desert, has already been described (see also Chap. 3.4.5.1). The climate-related sequence of tropical arid regions, which is different, is described in Chapter 3.5.5.

Mountain ranges and hilly areas often behave differently from the relief sequence described above. In these areas, quite commonly, the redistribution of rainwater through runoff and inflows on the land surface involves relatively larger amounts of precipitation (here frequently somewhat heavier than elsewhere) which, together with petrographic variations, creates a pronounced spatial differentiation that permits the growth of a large number of plant species with widely varying requirements. Such areas are therefore characterized by the relative richness of their flora, while elsewhere usually only a few species (specialists) are present (see below).

Survival Strategies of Plants in Arid Regions

Perennial Vegetation. In order to adapt to the stress induced by drought plants have developed a variety of survival strategies (Fig. 112). All *perennial* species are characterized by *drought resistance*: they can either survive water losses without suffering any damage or, by reducing transpiration or storing water, they are able to protect themselves from suffering excessive water losses during dry periods. The first type of plants, known as *poikilohydric plants*, are rare amongst the cormophytes (regularly, only their seeds exhibit poikilohydric development stages); therefore generally they are not so important. On the other hand, water-storing species, known as *succulents*, are very common in many arid regions. Depending on the storage organ, they are classified as leaf, stem/shoot or root succulents. Many of them are characterized by root systems running just below the surface of the soil and by a CAM (Crassulacean Acid Metabolism) pathway for CO_2 assimilation. In this type of photosynthesis, the CO_2 is taken up at night with stomata wide open (CO_2 dark fixation) and it is then used during the day with closed stomata (to protect against transpiration!), in combination with light energy, to build up organic substances.

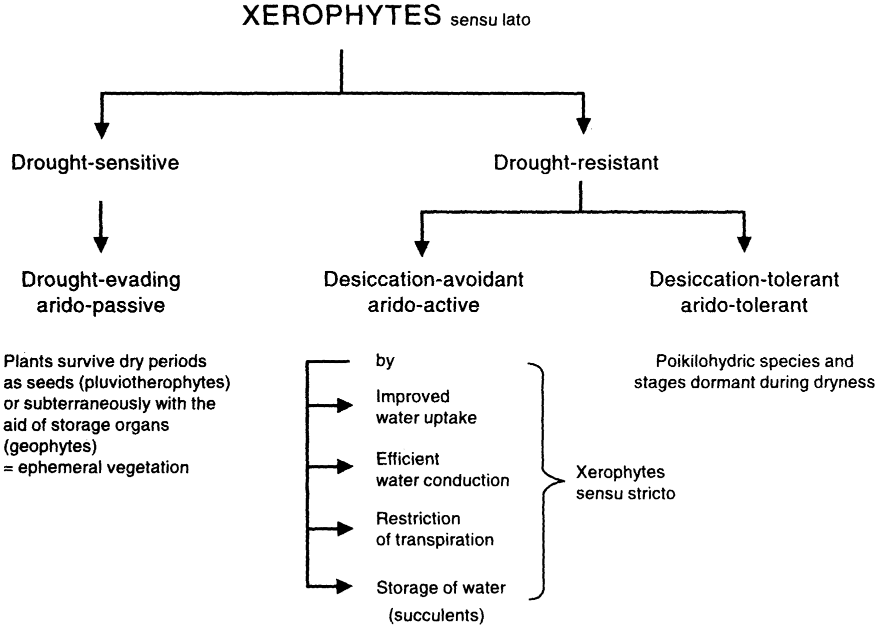

Fig. 112. Survival strategies of plants in dry regions. (Larcher 1984)

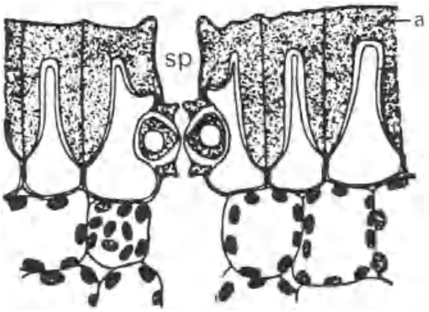

Fig. 113. Anatomical adaptations of the leaves of plants growing at extremely dry and hot sites. (Strasburger 1983, p. 191). The cross section through the epidermis of a leaf from the desert plant *Gasteria nigricans* reveals the highly thickened and cutinized outer wall of the epidermis (*a*) and a sunken stoma (*sp*)

The so-called *arido-active plants*, which do not store water, and which are referred to by many authors (e.g. Walter and Breckle 1983) simply as *xerophytes*, may possess a number of features which reduce transpiration, such as leaves with thickened cuticula, sunken and smaller stomata etc. (Fig. 113), or the leaves are shed during dry periods. Many of them also possess means for improved water uptake and water conduction. Such means generally include the development of large below-ground phytomasses (e.g. in the form of dense and/or deep-reaching root formations), more or less exceeding the above-ground parts; this relatively reduces the transpiration surface of the plant and increases the soil volume from which water can be taken up (Fig. 109). Another means is the capability, when required, to develop higher osmotic suction pressures (by increasing the cell sap concentration). This is important because the suction pressure of the soil, i.e. the force by means of which the soil water is bound adsorptively and by capillarity, increases with decreasing soil moisture content.[22]

Water stress is created for the plant when the *matric potential* falls below the *osmotic potential* and thus the water balance (uptake minus loss) of the plant falls into deficit. The plant can counter the stress by lowering its osmotic potential and by restricting its water losses through a reduction in its growth height (e.g. in grasses the internodes become shorter) and by forming smaller leaves. Both means of stabilizing the water balance are available to plants in humid as well as in dry climates. However, there are significant differences in the extent to which this can be done. Xerophytes can react much more rigorously to the water stress than mesophytes. For example, they are capable of increasing their root suction pressures to more than 60 bar, while mesophytes can usually only achieve 10–20 bar (species in sunny sites can reach approximately 40 bar), and they are able to reduce their transpiration losses much further via growth adjustments. But even they have their limits, namely when they are no longer able to reduce their water potential below that of the soil, i.e. their *permanent wilting point* is reached.

Ephemeral Vegetation. Besides the drought-resistant plants, there are *drought-sensitive (arido-passive) plants* whose shoots exhibit mesomorphic characteristics, i.e. they have no special anatomic/morphological adaptations to water stress. Instead, their adaptation is of physiological nature: they all go through extremely short development phases [of just 1 to 2 months from the start of vegetative development (e.g. germinating) to the stage of seed ripeness] whenever (occasionally) favourable conditions occur, i.e. they grow as if according to the motto "hurry before it is too late", in contrast to the strategy adopted by perennial xerophytes, which develop over many years more according to the motto "slow and

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[22] In recent years, the parameters regarding the state of the soil water content have usually been expressed in terms of *energy potentials*, namely the soil suction pressure which is given as "matric potential", and the root suction pressure which is given as "osmotic potential". What is meant in each case is the energy which must be supplied in order to make the water available (pure water, whose potential is taken as equal to zero, is used as the reference base). The dimensions of water potential are energy per unit mass or per unit volume, e.g. $\mathrm{erg\,cm^{-3}}$ or $\mathrm{J\,kg^{-1}}$. Matric and osmotic potentials are always given as negative values, whereas the pressure potential (in the case of turgor pressure of plant cells) is always positive. Values of energy per unit volume can easily be converted into values of force per unit area, as is frequently the practice; the conversion factor being approximately $100\,\mathrm{J\,kg^{-1}} = 1\,\mathrm{bar}$. The latter units are numerically identical with the values of the suction pressures, except they have a negative sign. This means that, with increasing soil suction pressure, the matric potential drops to increasingly negative values and, correspondingly, the osmotic potential drops with increasing root suction pressure.

steady wins the race" (Ludwig and Whitford 1981, pp. 294 f.). The arido-passive plants survive periods of drought in the form of seeds (pluviotherophytes) or with the aid of below-ground storage organs (geophytes), thus evading drought. Because their short-term appearance is linked to rainfall events, they are as a group referred to as ephemeral vegetation and contrasted with the other plants which are known as permanent vegetation.

Pluviotherophytes also exist in the most extreme deserts. Their production was investigated in the desert near Cairo (Walter 1990), where the pluviotherophytes were caused to germinate by a winter rainfall event of 23.4 mm which resulted in a thorough wetting of the upper 28 cm of soil. Of this quantity of water 68% evaporated, i.e. was unproductively lost. The rest – i.e. 73 000 kg per hectare – was taken up and transpired by the ephemerals which allowed a production of 51.8 kg phytomass on the same area. This means, the *water-use efficiency in production* (dry matter production per water consumption) was very low, correspondingly the *transpiration ratio of production* (litres of transpired water per dry matter produced) was very high. The latter amounted to 1409 (73 000 : 51.8) compared with the more usual ratio of 400–600 in our field crops. This is explained by the fact that the *potential* evapotranspiration in the desert is much higher.

Stunted Growth. The water stress permits the plants to make full use of the rich supply of solar energy for, at most, a short period of time. Normally, they must keep their stomata more or less closed in order to protect their water budget and thus they inevitably reduce their gas exchange to a level which limits photosynthesis (Fig. 114). Therefore, the xerophytes, sensu stricto, all exhibit stunted growth. This is described by the general rule which states that individuals of the same age in a species of plant tend to be smaller the drier their growth site, and the growth height of a plant community is reduced in proportion to the decline in precipitation (Shmida 1985). It is also characteristic that the diversity of species (also in the case of fauna) decreases per unit area with increasing water stress (this does not always apply to pluviotherophytes whose seeds can usually be carried by the wind over great distances and in all directions).

Fluctuations in Phytomass and Primary Production. The water stress inhibits not only primary production, but it also makes it difficult for the arido-active plants to survive; during the dry seasons, many of these plants reduce their shoot components, and others die off completely. Consequently, not only the productivity but also the phytomass are amongst the lowest for all plant formations (even when the phytomass reaches its maximum value, see below); in order of magnitude it is most closely comparable with that of the Polar/Subpolar Zone.

Like the ephemerals and the poikilohydric plants, most arido-active plant species and most animal species are capable of adapting their development phases to the episodic availability of water. Therefore, the seasonal periodicity typical of the Seasonal Tropics and the cold-winter non-tropical zones is lacking (naturally this applies only with reservations to the non-tropical arid regions where at least

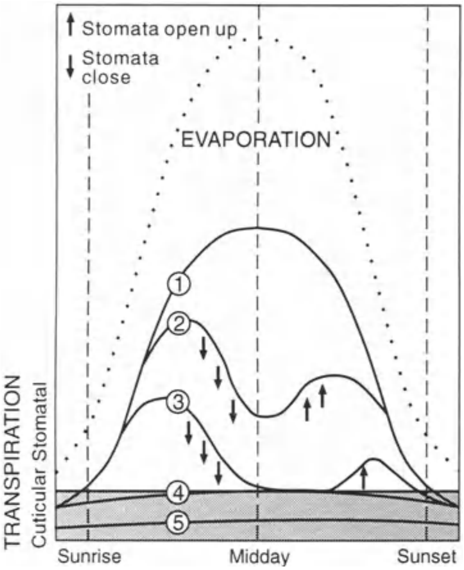


Fig. 114. Diagram of the daily changes in transpiration under conditions of steadily declining availability of water. (Larcher 1984). The *arrows* indicate the opening and closing movements of the stomata which are triggered by the changes in the water supply. The *shaded area* depicts the zone of exclusively cuticular transpiration. *1* Unlimited transpiration; *2* restriction of transpiration at midday as the stomata begin to close; *3* total closure of the stomata during the midday period; *4* complete elimination of stomatal transpiration caused by long-term closure of the stomata (only cuticular transpiration continues); *5* greatly reduced cuticular transpiration due to loss of turgor (membrane shrinkage). When transpiration is restricted by regulation of the stomata, the gas exchange is also reduced along with the efficiency of the photosynthetic reactions. When the stomata are completely closed, photosynthesis drops to zero

the winter cooling results in a certain seasonal regularity in the developmental processes).

On the other hand, the ability of desert plants to react flexibly to moisture impulses is essential for ensuring that the primary production can start up vigorously when particularly large amounts of rainfall occasionally occur, and then attains volumes of above-ground phytomass which are several times greater than those encountered in dry years. Ephemeral plants often make large contributions (50% and more) to these amounts of phytomass.

The considerable fluctuations in the above-ground biomass lead to short-term instability in the arid ecosystems; but, on the other hand, the cause of this instability, namely the highly flexible characteristics of the producing plants, guarantees the opportunity for recovery to take place after phases of decline, and thus creates long-term stability (Evenari 1981, p. 566).

The fluctuations which occur in the below-ground biomass are much less pronounced than those in the above-ground biomass, presumably because the environmental conditions in the soil are on the whole more balanced. The belowground biomass, which is in any case much greater by weight, can therefore be regarded as a kind of security capital (reserve) for the renewal of the aboveground parts of the plants, as soon as adequately favourable conditions for this to happen exist.

Secondary Producers

The bulk of the PP_N is not consumed by herbivores but goes directly to the decomposers. The interrelationships between plants and animals are therefore relatively insignificant; dynamic changes in one of these biotic components have almost no impact on the other.

Most animal species, which at the same time constitute the bulk of the animal biomass, live in the soil (geozonts) where they inhabit "air-conditioned" cavities (with relatively higher relative humidity and more moderate temperatures with a much lower diurnal amplitude). Large mammals (e.g. saiga-antelopes, oryx, gazelles) are rare today, because their populations have been reduced with the aid of modern weapons and they have been replaced by domesticated grazing animals. Birds such as sand grouses and bustards, finches and buntings are widespread; large birds of prey are also frequent, although the sizes of their populations fluctuate as a function of the populations of small mammals. Snakes and lizards are another characteristic faunal element from the group comprising the vertebrates. The most frequent invertebrates are insects and spiders. In terms of the role which they play in secondary production, arthropods are probably the most important group, followed by small mammals and reptiles; birds account for the smallest proportion.

Decomposition of Litter

The mineral contents of the litter, in particular halophyte litter, are extremely high (frequently more than 10% of the dry matter). This applies also to the nitrogen and phosphorus contents, although these two elements in particular are partially taken back into the living shoots before the leaves or branches die off.

The mesofauna appears to be particularly important for the decomposition of litter, because the organisms undertake the task of mechanically breaking down the litter and working it into the soil, without which the microbial decomposition process of the mostly dry litter layer would be relatively ineffective. Controlled use by grazing animals, i.e. grazing which is properly adapted to the given fodder reserves, may also promote the mineral cycle (see below).

The activity of the soil organisms (also of N_2-fixing microbes) commences at very low soil-moisture levels at which higher plants cannot yet start to grow.

The efficiency of the precipitation in the case of the soil organisms is therefore quite different from what is found in the case of the primary producers.

Of all the minerals, *nitrogen is* probably the one for which a deficit most frequently exists and thus exerts a limiting effect on the growth of vegetation. Its cycle in arid ecosystems is depicted here using as an example the semi-desert and desert steppes of North America where cold winters exist (Fig. 115). An astonishingly large amount of nitrogen is supplied by biological N_2-fixation, chiefly by blue algae and lichen crusts. About 90% of this and of the atmospheric input (e.g. via precipitation) is, however, directly lost again from the system via denitrification and in the form of volatile ammonia, without having been used by the plants.

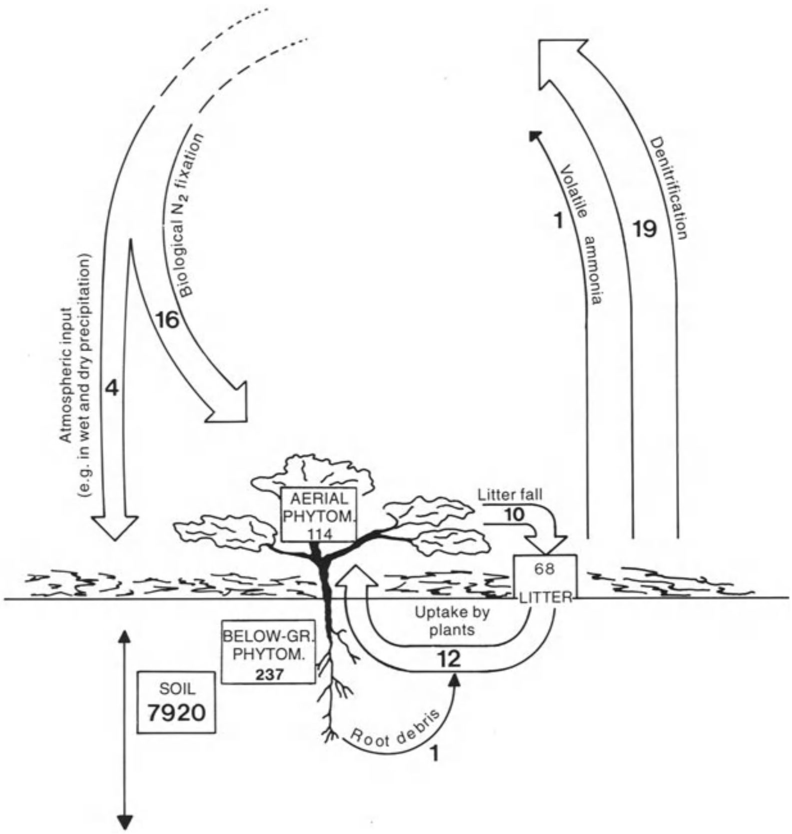


Fig. 115. The most important reserves (kg ha^{-1}) and turnover rates (kg ha^{-1}a^{-1}) of nitrogen in the winter-cold semi-deserts and desert steppes of North America. (West and Skujins 1977). The model depicts average conditions and is based on the assumption that a state of equilibrium exists. The *arrows* indicate turnover rates, the boxes show the reserves

3.4.6 Land Use

All the arid regions of the earth are thinly populated. In striking contrast, the steppes of the Arid Mid-Latitudes and sometimes also of the subtropics are utilized to a large extent for agricultural purposes, either extensive crop cultivation or extensive pastoralism. Crop cultivation takes place in the former moist steppes and in the transition regions to the former dry steppes; pasturing predominates in the dry and desert steppes (Fig. 116). In between lies the so-called *agronomic humid-arid boundary*, i.e. the boundary up to which rain-fed agriculture is possible. In the warmer southern steppe regions this is reached at an annual

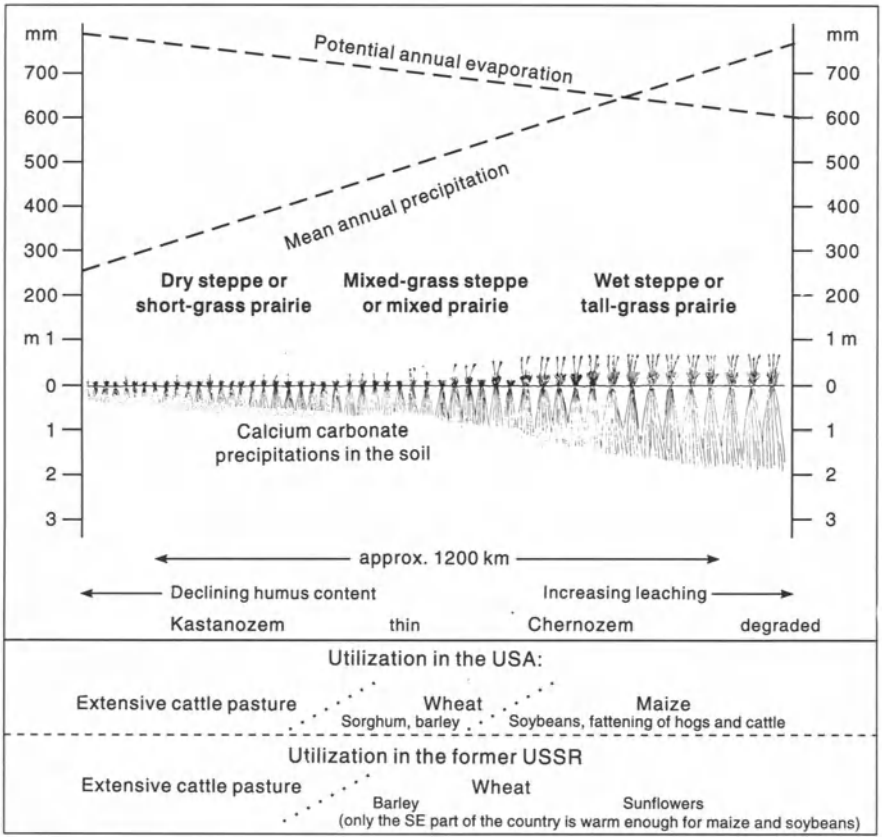


Fig. 116. The agrarian use of dry and wet steppe regions in the former Soviet Union and in North America. (Jätzold 1984). The large-scale cultivation of cereals dominates in the former mixed grass steppes and the still relatively dry adjacent zones of the former moist steppes, while extensive pasture farming predominates in the dry steppes. The American corn (maize) belt is located in the wet steppe regions

amount of 300–500mm and in the cooler northern steppe regions at an amount of 250–300 mm of precipitation; but given favourable rainfall distribution and high moisture storage capacities of the soils, the cultivation of particularly drought-resistant species of crop, and the use of special techniques (see below), rain-fed agriculture can be carried on even at lower annual precipitation levels.

Large-Scale Cultivation of Cereal Crops

The main cereal is *wheat*. In contrast to the Humid Mid-Latitudes and the Mediterranean-Type Subtropics, where wheat is also an important crop cultivated especially by small to medium-sized, often mixed farming operations, in the steppe regions wheat is cultivated by large farms on very large fields (large-scale farming) using giant machinery with minimum input of labour (capital-intensive, labour-extensive farming). By adopting a highly commercialized and mechanized, large-scale form of production the costs of producing the wheat were reduced to such an extent that cereal cultivation was able to compete with ranching, which was formerly much more widespread in the steppes and prairies.

In the central and western parts of the USA the expansion of wheat growing (wheat frontier) peaked around 1930 and in the southern part of the former USSR in the 1950s. During those periods in both regions, marginal lands were tilled which in the long term were too dry to permit reasonably reliable cultivation of wheat. This became evident soon afterwards when periods of drought resulted in considerable eolian erosion (dust bowls) on the fallow fields, and heavy rain also caused irreversible erosive damage (badlands).

Returning these regions to pastureland is not only technically difficult, because it is not easy to establish sod in semi-arid regions; it is also economically problematical, because pasture operations require at least four times the amount of area, i.e. changes have to be made to the land-ownership structure.

The present areas in which large-scale cereal cultivation is focussed are listed below:

- North America: the mid-west from northern Texas via the states of Kansas, (eastern) Colorado, Nebraska, North and South Dakota and Montana and far into Canada (Alberta, Saskatchewan); in addition, the Columbia Basin in the states of Washington, Oregon and Idaho also belongs here.
- Former USSR: the temperate steppe regions east of the Volga and in particular in western Siberia; west of the Volga wheat is also an important marketable crop; however, it is cultivated there mostly on mixed farms.
- Argentina: the subtropical steppe regions from Cordoba and Santa Fé through the pampa humeda to Bahia Blanca in the south.
- Southern Australia: the subtropical steppe regions in southeastern Australia and around Perth in southwestern Australia.

For a long time, wheat has been quantitatively the most important foodstuff sold on world markets. The largest wheat-exporting countries are the USA and

Canada (together accounting for about two-thirds of the total), followed by Argentina and Australia. Despite its own high rate of production, the former USSR must normally import grain.

Because of their *considerable contribution to the feeding of mankind* (even in remote areas of the globe), the principal areas of wheat cultivation referred to above, in which more than 50% of the world's wheat is produced, are known as the bread baskets of the world. Their superiority is founded on certain natural advantages, namely the high degree of soil fertility, the large amount of insolation and the broad extent of flat terrain, which favours the use of large machinery and thus farming on a large scale.

In the cold-winter steppe regions summer cereals are cultivated, whereas in the regions with mild winters winter cereals with a higher yield are grown. Apart from wheat, barley may also be cultivated. In addition, sorghum (especially in the vicinity of the humid-arid boundary) linseed, alfalfa and sunflowers, as well as maize and soybeans (particularly in former forest steppes) may be sown in rotation with one another.

The *yields per hectare* are all significantly below those which are achieved elsewhere by commercialized agriculture. This is due partly to the water stress to which the crops are exposed in semi-arid steppes especially close to the humid-arid boundary, but it is also a consequence of the extensive farming methods which attempt to keep the use of fertilizer and labour to a minimum. The cereal-fallow-system used in the western part of the USA is the most labour-extensive farming system in the world: only about 8 h of human labour per hectare are needed for all the operations from seeding through to harvesting. In this region, the ultimate goal is to achieve the maximum possible production per worker, because human labour is expensive and in short supply, while land is plentiful. The farms are correspondingly highly mechanized.

Unless a changeover is made to drought-resistant crops such as millet, groundnuts, chickpeas or sesame, the *dry farming system* must be used, or artificial irrigation is needed, in the boundary regions of rain-fed agriculture. In the case of dry farming, the farms interpose bare fallows which reduce transpiration losses otherwise caused by field crops. In the following year, the crops can thus utilize 2 years' worth of rainfall. Depending on the precipitation deficits, fallow periods of this kind are required every second, third or fourth year, correspondingly the areas put down to fallow vary in amount from 50 to 25% of the cultivated areas (Table 35). The effect which the fallow exerts on the various annual yields per unit area is shown in Fig. 117. Instead of bare fallow, pastures using shallow-rooted fodder plants, such as clover, may be established. After several years, the water reserves of the soil are increased beneath such cover as well.

Extensive Grazing

In the arid lands of the earth, this is practised either in the form of (semi-)nomadic herding or as ranching. The former is the traditional form of pastoralism in the

Table 35. Changes in wheat-fallow rotations with increasing precipitation. (Andreae 1983)

	Tunisia, north of the line Hammamet-Le Kef			
Precipitation (mm a^{-1})	Less than 350	350 to 400	400 to 500	Over 500
Crop rotations	1. *Fallow* 2. Wheat or barley	1. *Fallow* 2. Wheat 3.–4. Alternating pasture 5. Wheat	1. *Fallow* 2. Wheat 3. Barley, oats, forage crops 4. Legumes (peas, chickpeas, small field beans)	1. Forage crops 2. Wheat 3. Legumes 4. Barley, oats
In % of area under cultivation:				
Fallow	50	20	25	–
Forage crops	–	40	12	25
Legumes	–	–	25	25
Cereals	50	40	38	50
	State of Kansas/USA, from West to East			
Crop rotations	1. *Fallow* 2. Winter wheat	1. *Fallow* 2. Winter wheat 3. Winter wheat, sorghum	1. *Fallow* 2. Lucerne [alfalfa] 3. Maize 4. Winter wheat	1. Maize 2. Sorghum 3. Winter wheat
In % of area under cultivation:				
Fallow	50	33	25	–
Winter wheat	50	50	25	33
Miscellaneous crops	–	17	50	67

arid lands of the Old World, from the deserts to the steppes or savannas. Nowadays, it is found mainly in the tropics/subtropics, and it will therefore be dealt with in the chapter on that ecological zone (see Chap. 3.5.6). *Ranching*, on the other hand, is the modern form of extensive grazing which has been developed by European settlers in America and Australia, and from there it has been transferred to certain areas in the Old World (e.g. southern Africa). Ranching is mainly concentrated in the short-grass steppes of the mid-latitudes, so it is justified to deal with the topic at this point.

Ranching is a stationary and commercially operated form of pastural economy which, like nomadism, has been increasingly displaced into arid lands by the pressure of arable farming interests. However, in the case of ranching the operational humid-arid boundaries are more tightly drawn than in the case of nomadic livestock farming, i.e. wherever the availability of food and water for the animals makes it impossible to carry out stationary livestock farming. On

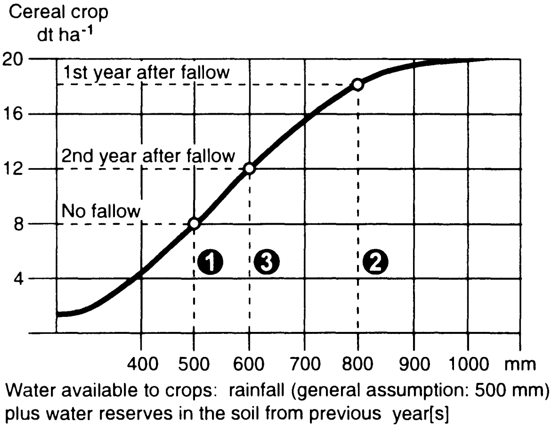


Fig. 117. The effect of fallow in the dry farming system. (Andreae 1983). The highest yields per unit area are achieved with rotation 3

❶ **Continuous cropping (no fallow)**
available water per crop: 500 mm precipitation;
annual harvest: 8 dt ha^{-1}a^{-1}

❷ **Fallow every second year**
available water in the cropping year following
a fallow year: 500 mm precipitation plus 300 mm
soil water reserves from the previous year;
average annual harvest: (0+18) : 2 = 9 dt ha^{-1}a^{-1}

❸ **Fallow every third year**
available water in the first cropping year following
a fallow year: 800 mm, in the second cropping year: 600 mm;
average annual harvest: (0+18+12) : 3 = 10 dt ha^{-1}a^{-1}

the "humid" side, crop farming is generally more competitive wherever the annual precipitation would permit a fodder capacity of 30–40 livestock units (1 LU corresponds to 500 kg live weight) per 100 ha of grazing area.

Typical characteristics of ranching are as follows:

- Extremely large farms covering 500–100 000 ha. The largest farms are located in the driest areas, where mainly sheep farming, otherwise cattle farming is practised.
- The animals feed either exclusively or predominantly on natural pastures. Sometimes the pasture land is improved by sowing suitable fodder grasses. Grazing is carried out under controlled conditions on large fenced-in paddocks.
- The number of animals, the investment of labour and capital, also the operating yield, are all extremely low relative to the area covered. On the other hand, a high initial capital investment is required to establish a ranch.

Ranches may be classified on the basis of intensity characteristics, e.g. the subdivision of the grazing areas and the way in which the alternation of grazing areas is organized, the density of the watering points, the quality of the pasture (possibly after improvements), the performance capabilities of the various breeds

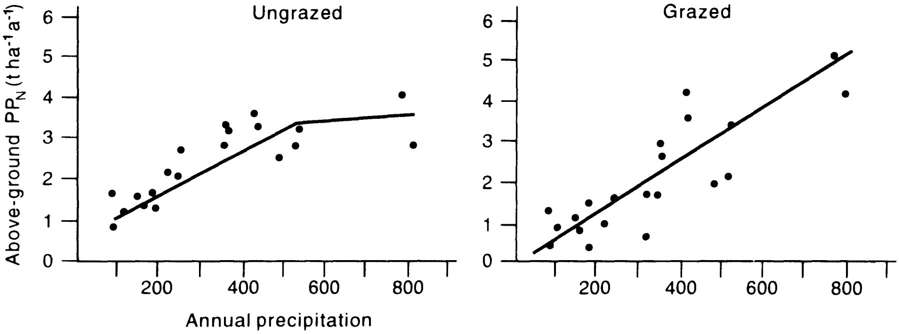


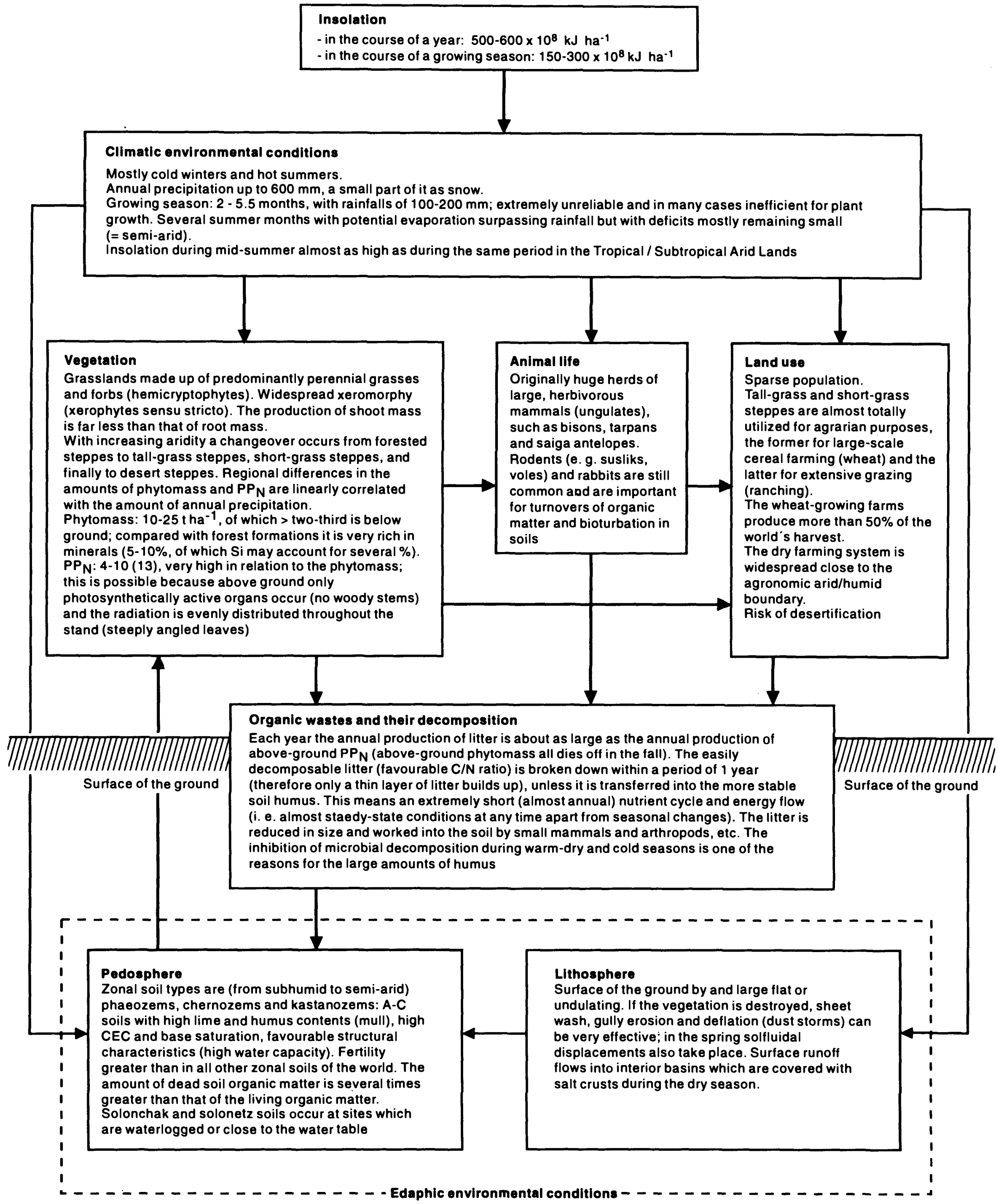
Fig. 118. The relationship between shoot production and precipitation in the steppes of the mid-latitudes. (Sims and Coupland 1979). The above-ground PP_N initially (up to about 500 mm) exhibits a linear dependence on annual precipitation for grazed and ungrazed grasslands. However, the PP_N on grazed areas is situated at a slightly lower level. The reason why the production curve for ungrazed areas flattens out from about 500 mm onwards, while for grazed areas it continues to rise linearly, may be that in the first case the organically bound minerals are returned solely via the litter, and therefore much more slowly than through the digestive tracts of grazing animals; therefore, on ungrazed steppes, there is a tendency for a lack of minerals and thus a growth-limiting effect to occur. It is also reported from the Eurasian steppes that light grazing is necessary to achieve optimal development of the steppe. (Walter and Breckle 1986, p. 174)

of animal, and the attention given to veterinary services. The degree of intensity is expressed in the stocking density which may vary between 2 and 50 LU/100 ha.

As a rough approximation, the potential stocking density may be calculated from the above-ground primary production of suitable fodder plants, whose maximum yield is in turn primarily limited by the amount of precipitation (Figs. 118 and 127). The application of the above-mentioned measures makes sense only up to the point where the fodder potential naturally determined in this way is approached (unless artificial irrigation is carried out). Consequently, the intensity characteristics of a ranch and the natural grazing potential are as a rule matched to one another. The ability of various steppe regions to support cattle and sheep may therefore be assessed solely according to the parameter of annual precipitation, taking into account, however, the amounts of biomass which can be used in each case for fodder.

In the case of the western part of the USA, the following approximate relationships may be derived from a comparison of two maps (Andreae 1983); one of these maps shows the amount of pasture per individual bovine, and the other shows the distribution of annual precipitation:

Given annual precipitations of	The number of cattle per 100 ha is
< 250 mm	3–5
250–500 mm	5–16
500–750 mm	16–50



Insolation
- in the course of a year: 500-600 x 10^8 kJ ha^{-1}
- in the course of a growing season: 150-300 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Mostly cold winters and hot summers.
Annual precipitation up to 600 mm, a small part of it as snow.
Growing season: 2 - 5.5 months, with rainfalls of 100-200 mm; extremely unreliable and in many cases inefficient for plant growth. Several summer months with potential evaporation surpassing rainfall but with deficits mostly remaining small (= semi-arid).
Insolation during mid-summer almost as high as during the same period in the Tropical / Subtropical Arid Lands

Vegetation

Grasslands made up of predominantly perennial grasses and forbs (hemicryptophytes). Widespread xeromorphy (xerophytes sensu stricto). The production of shoot mass is far less than that of root mass.
With increasing aridity a changeover occurs from forested steppes to tall-grass steppes, short-grass steppes, and finally to desert steppes. Regional differences in the amounts of phytomass and PP_N are linearly correlated with the amount of annual precipitation.
Phytomass: 10-25 t ha^{-1}, of which > two-third is below ground; compared with forest formations it is very rich in minerals (5-10%, of which Si may account for several %).
PP_N: 4-10 (13), very high in relation to the phytomass; this is possible because above ground only photosynthetically active organs occur (no woody stems) and the radiation is evenly distributed throughout the stand (steeply angled leaves)

Animal life

Originally huge herds of large, herbivorous mammals (ungulates), such as bisons, tarpans and saiga antelopes.
Rodents (e. g. susliks, voles) and rabbits are still common and are important for turnovers of organic matter and bioturbation in soils

Land use

Sparse population.
Tall-grass and short-grass steppes are almost totally utilized for agrarian purposes, the former for large-scale cereal farming (wheat) and the latter for extensive grazing (ranching).
The wheat-growing farms produce more than 50% of the world's harvest.
The dry farming system is widespread close to the agronomic arid/humid boundary.
Risk of desertification

Organic wastes and their decomposition

Each year the annual production of litter is about as large as the annual production of above-ground PP_N (above-ground phytomass all dies off in the fall). The easily decomposable litter (favourable C/N ratio) is broken down within a period of 1 year (therefore only a thin layer of litter builds up), unless it is transferred into the more stable soil humus. This means an extremely short (almost annual) nutrient cycle and energy flow (i. e. almost staedy-state conditions at any time apart from seasonal changes). The litter is reduced in size and worked into the soil by small mammals and arthropods, etc. The inhibition of microbial decomposition during warm-dry and cold seasons is one of the reasons for the large amounts of humus

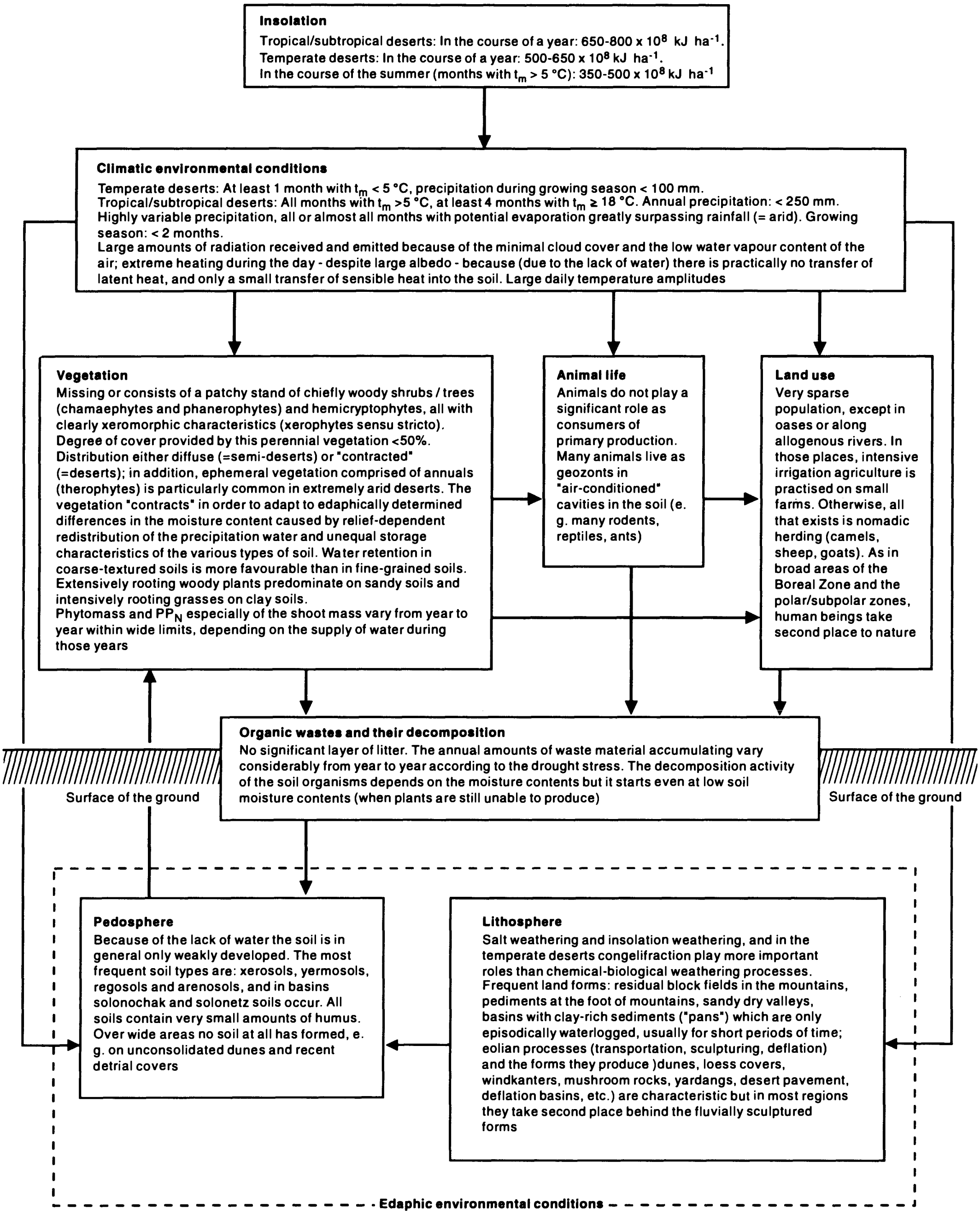
Pedosphere

Zonal soil types are (from subhumid to semi-arid) phaeozems, chernozems and kastanozems: A-C soils with high lime and humus contents (mull), high CEC and base saturation, favourable structural characteristics (high water capacity). Fertility greater than in all other zonal soils of the world. The amount of dead soil organic matter is several times greater than that of the living organic matter.
Solonchak and solonetz soils occur at sites which are waterlogged or close to the water table

Lithosphere

Surface of the ground by and large flat or undulating. If the vegetation is destroyed, sheet wash, gully erosion and deflation (dust storms) can be very effective; in the spring solfluidal displacements also take place. Surface runoff flows into interior basins which are covered with salt crusts during the dry season.

Fig. 119. Synoptic diagram depicting conditions in the steppe regions



Insolation

Tropical/subtropical deserts: In the course of a year: 650-800 x 10^8 kJ ha^{-1}.
Temperate deserts: In the course of a year: 500-650 x 10^8 kJ ha^{-1}.
In the course of the summer (months with t_m > 5 °C): 350-500 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Temperate deserts: At least 1 month with t_m < 5 °C, precipitation during growing season < 100 mm.
Tropical/subtropical deserts: All months with t_m >5 °C, at least 4 months with $t_m \geq$ 18 °C. Annual precipitation: < 250 mm.
Highly variable precipitation, all or almost all months with potential evaporation greatly surpassing rainfall (= arid). Growing season: < 2 months.
Large amounts of radiation received and emitted because of the minimal cloud cover and the low water vapour content of the air; extreme heating during the day - despite large albedo - because (due to the lack of water) there is practically no transfer of latent heat, and only a small transfer of sensible heat into the soil. Large daily temperature amplitudes

Vegetation

Missing or consists of a patchy stand of chiefly woody shrubs / trees (chamaephytes and phanerophytes) and hemicryptophytes, all with clearly xeromorphic characteristics (xerophytes sensu stricto). Degree of cover provided by this perennial vegetation <50%. Distribution either diffuse (=semi-deserts) or "contracted" (=deserts); in addition, ephemeral vegetation comprised of annuals (therophytes) is particularly common in extremely arid deserts. The vegetation "contracts" in order to adapt to edaphically determined differences in the moisture content caused by relief-dependent redistribution of the precipitation water and unequal storage characteristics of the various types of soil. Water retention in coarse-textured soils is more favourable than in fine-grained soils. Extensively rooting woody plants predominate on sandy soils and intensively rooting grasses on clay soils.
Phytomass and PP_N especially of the shoot mass vary from year to year within wide limits, depending on the supply of water during those years

Animal life

Animals do not play a significant role as consumers of primary production. Many animals live as geozonts in "air-conditioned" cavities in the soil (e. g. many rodents, reptiles, ants)

Land use

Very sparse population, except in oases or along allogenous rivers. In those places, intensive irrigation agriculture is practised on small farms. Otherwise, all that exists is nomadic herding (camels, sheep, goats). As in broad areas of the Boreal Zone and the polar/subpolar zones, human beings take second place to nature

Organic wastes and their decomposition

No significant layer of litter. The annual amounts of waste material accumulating vary considerably from year to year according to the drought stress. The decomposition activity of the soil organisms depends on the moisture contents but it starts even at low soil moisture contents (when plants are still unable to produce)

Pedosphere

Because of the lack of water the soil is in general only weakly developed. The most frequent soil types are: xerosols, yermosols, regosols and arenosols, and in basins solonochak and solonetz soils occur. All soils contain very small amounts of humus. Over wide areas no soil at all has formed, e. g. on unconsolidated dunes and recent detrial covers

Lithosphere

Salt weathering and insolation weathering, and in the temperate deserts congelifraction play more important roles than chemical-biological weathering processes.
Frequent land forms: residual block fields in the mountains, pediments at the foot of mountains, sandy dry valleys, basins with clay-rich sediments ("pans") which are only episodically waterlogged, usually for short periods of time; eolian processes (transportation, sculpturing, deflation) and the forms they produce)dunes, loess covers, windkanters, mushroom rocks, yardangs, desert pavement, deflation basins, etc.) are characteristic but in most regions they take second place behind the fluvially sculptured forms

Edaphic environmental conditions

Fig. 120. Synoptic diagram depicting conditions in the deserts and semi-deserts of middle and tropical / subtropical latitudes

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3.5 Tropical/Subtropical Arid Lands

3.5.1 Distribution

Like the Arid Mid-Latitudes, the Tropical/Subtropical Arid Lands comprise not only deserts and semi-deserts but also semi-arid transitional regions leading into the more humid neighbouring zones, in this case the tropical (Sahel-type) thorn savannas (thorn bush and thorn scrub) (represented e.g. in Africa by *Acacia* and *Commiphora*, and in Australia by *Acacia aneura*), the subtropical thorn steppes with summer rainfall and the subtropical grasslands and scrub steppes with winter rainfall (Fig. 121); for the delineation between these transitional regions and the Seasonal Tropics and the Arid Mid-Latitudes respectively, see also Chapters 3.4.1 and 3.7.1[23]. The total area covered by the Tropical/Subtropical Arid Lands is 31.2 million km^2 or 20.9% of the mainland area of the earth.

The outer boundaries and internal subdivisions of these regions follow approximately the *annual precipitation* values quoted in Table 36. The lower threshold values in the poleward boundary areas are due to lower air temperatures and correspondingly reduced transpiration loads on the plants found there. It is only to a limited extent possible to link this regional subdivision with certain values for the *duration of humidity*. Quite commonly, the threshold values between deserts, semi-deserts, thorn savannas and dry savannas are given at 1, 2 and 4.5–5 humid months respectively; but this only makes sense where the precipitation is concentrated in short, clearly defined rainy seasons, i.e. all the months with (significant) rainfall are humid and the arid months remain for the most part rainless. On the other hand, in those regions where the low annual totals of precipitation are distributed over longer periods of time or throughout the entire year (e.g. in parts

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[23] Support for classifying the semi-arid transitional regions in the arid lands can be found in the English-language literature – and to some extent also in German texts – on the subject: it is customary to refer to many of these semi-arid transitional regions as deserts (e.g. the Kalahari Desert, Karroo Desert, Victoria Desert, Chihuahua Desert).

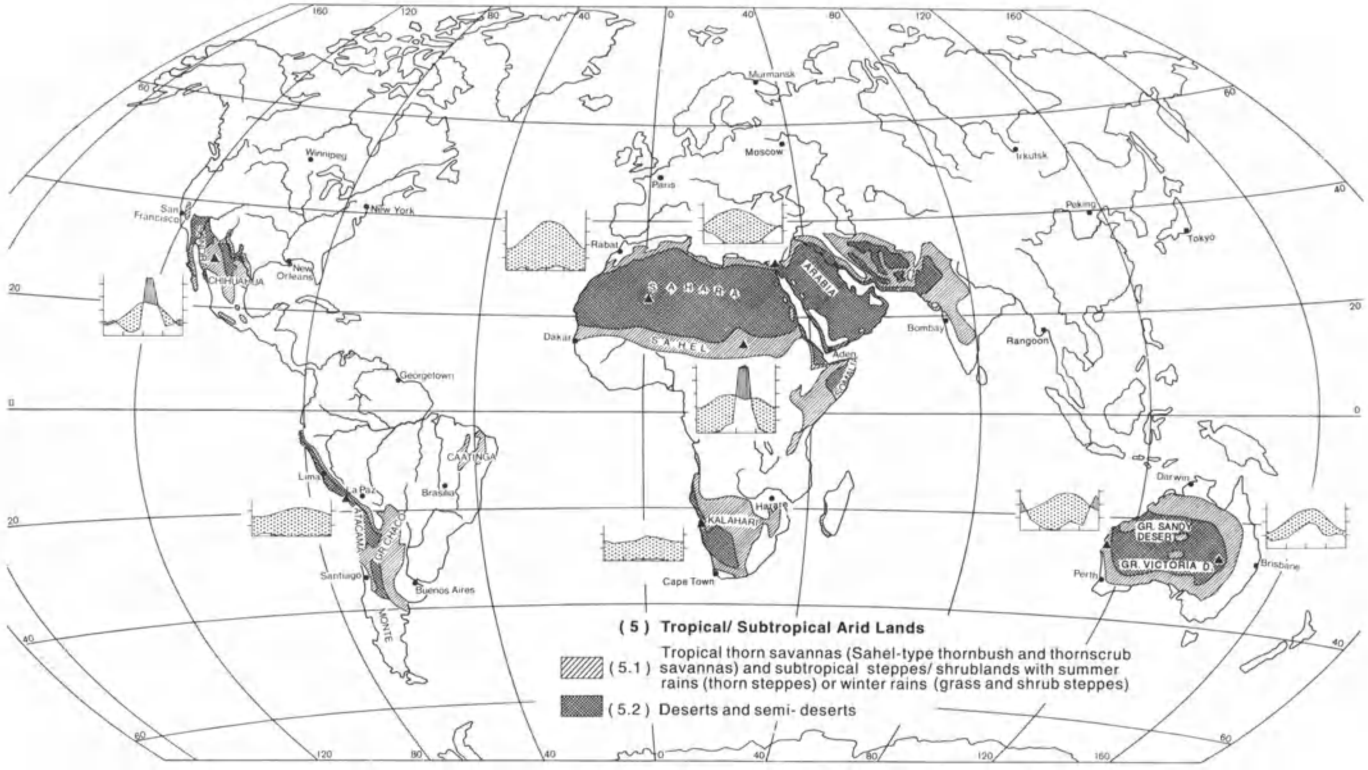


Fig. 121. Tropical/Subtropical Arid Lands

Table 36. The outer limits and subdivisions of the Tropical/Subtropical Arid Lands as a function of the annual precipitation

	Boundaries between	Correlate with an annual rainfall of approx. (mm)
Equatorwards	Desert–semi-desert	125
	Semi-desert–thorn savanna	250
	Thorn savanna–Seasonal Tropics (dry savanna)	500
Polewards	Desert–semi-desert	100
	Semi-desert–wet-winter Steppe of the subtropics	200
	Wet-winter steppe–Mediterranean-Type Subtropics	300(400)

of central Australia and eastern Africa), and therefore possibly no single month is "humid" (but on the other hand no month is totally arid), vegetation can nevertheless develop so that semi-deserts or even thorn savannas or thorn steppes occur. Many drought-adapted plants have the ability to flourish even under conditions of low monthly rainfall far below the "normal" humidity threshold. Full deserts do not occur until at least 11 months are totally arid (Jätzold 1986).

3.5.2 Climate

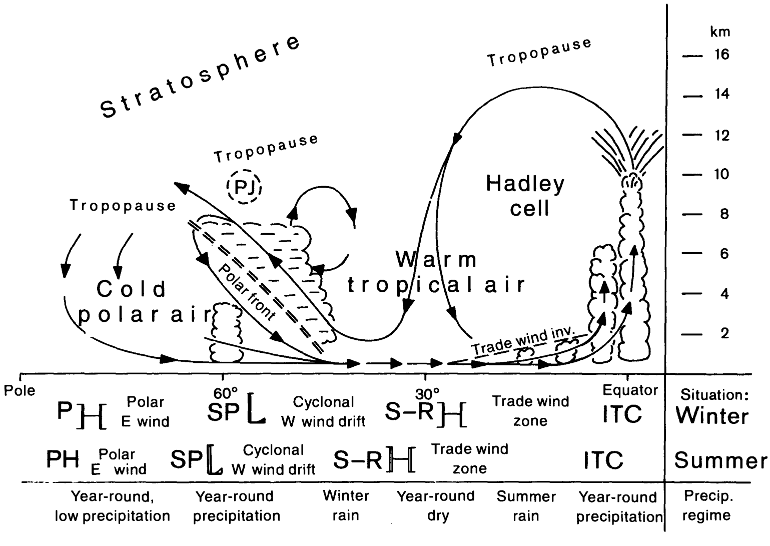
In contrast to the Arid Mid-Latitudes, the occurrence of most tropical and subtropical arid lands is due directly to the planetary atomospheric circulation, i.e. the lack of rain in those regions is primarily a consequence of their latitude (≈ 15°–35°). The coastal deserts in southwest Africa and in the western part of South America, which extend further towards the equator, are among the exceptions to this rule. In those regions, the cold coastal currents help to stabilize the atmosphere. The interruption of the arid belt in the Northern Hemisphere over Southeast Asia is also a striking feature (for the explanation see the chapter on Seasonal Tropics).

Apart from these exceptions, at least the core areas of the hot arid lands are located within a *subtropical/tropical belt of high pressure cells* (Fig. 152) encircling the earth on both sides of the Tropics of Cancer and Capricorn. These high pressure cells are characterized by permanently descending, powerful air flows. Consequently, the air is warm and dry and the stratification of the atmosphere remains stable up to great altitudes. Advective movements of air play only a minor role in the core zones (horse latitudes).

According to the classical model, the descending air masses in the subtropical/tropical high pressure regions are interpreted as elements in a closed tropical meridional circulation (*Hadley cell*, Fig. 122); the complementary flow components include vertical updrafts in the equatorial convection zone (ITC, see Chap. 3.7.2), poleward-oriented high altitude outflows and equatorward-oriented return flows in the lower strata of the troposphere – collectively known as the trade winds. In view of the fact that the subtropical/tropical highs are at the same time the areas from which the trade winds originate, the deserts which are widespread in this region are also known as *trade wind deserts.*

According to more recent knowledge, the thermal model of the Hadley cell requires correction. To start with, the subtropical/tropical belt of high pressure cells is by no means simply the counterpart of the equatorial low pressure trough, but instead derives also from dynamic processes occurring in the planetary frontal zone of the mid-latitudes (see Chap. 3.3.2). It is therefore also an element in the tropical/mid-latitudinal exchange of air masses.

The dynamic origin or reinforcement of the subtropical/tropical high pressure regions also explains why the pressure gradient from here to the equator extends very high and thus can permit a correspondingly high-extending easterly flow to develop. Measured against the vertical extent of this *primary trade wind* and against the westerly flow which occurs above it in the uppermost troposphere, altogether up to about 15 km, the trade winds blowing obliquely to the equator and extending to a height of several 100 but no more than about 2000 m, account



P = polar
SP = subpolar
S-R = subtropical-tropical
ITC = Inner Tropical Convergence
PJ = Jet stream

Fig. 122. Schematic vertical section through the meridional circulation in one hemisphere, showing the seasonal shift in the circulation elements and the consequences for the precipitation regime. (Weischet 1983)

for only a relatively small part of the movements of air masses in the tropics. Therefore, there is no need for a pronounced counter-flow in higher strata (as postulated by the Hadley cell model, although it cannot explain this phenomenon because approximately geostrophic winds would have to prevail at those altitudes); instead, weak meridional components in the easterly or westerly high altitude flow could be sufficient to maintain the equilibrium.

A counter-flow occurs regionally near the ground when thermal lows build up over the mainland masses in the respective summer hemispheres: poleward-oriented SW or NW winds develop between the subtropical/tropical highs remaining over the oceans and these lows and replace the trade winds (particularly on the westward sides of the oceans) (Fig. 152). The summer SW monsoons of Southern Asia (see Chap. 3.7.2) and West Africa or the summer NW monsoon of Australia are examples of the "reversal" in the flow conditions which then occurs.

On the *eastward sides of the continents*, the normally dry trade winds (see Chap. 3.7.2) can bring such large amounts of orographically induced rainfall that rain forests or moist savannas are able to flourish there. As the windward effect decreases further inland (see also Chap. 3.8.2), so the arid lands start to appear, firstly in the form of thorn savannas/thorn steppes, then giving way to semi-deserts and finally full deserts in the interior of the continent (this East-West sequence is particularly apparent in all the southern continents).

Off the *western coasts of the continents* the trade winds, which are blowing offshore in these areas, help to bring cold seawater to the surface, and its cooling effect frequently gives rise to the formation of fogs (hence also the name *fog deserts* for the coastal deserts which are widespread here). As they move inland, these fogs usually break up quickly. They are of little importance as sources of moisture, but they do play an important role in that they partially block out the sun and thus have a cooling effect.

Apart from these fog deserts, *atmospheric humidity* and *cloud formation* are both extremely low in all Tropical/Subtropical Arid Lands, whereas the solar radiation and the warming of the air are very intensive phenomena. This can give rise to considerable thermal convection currents. If, nevertheless, precipitation is rare, this has to do with the stability of the atmospheric stratification, referred to above, and also it is a result of the large saturation deficit of the air masses. On the other hand, whenever rainfall occurs, it is of short duration but high intensity.

The generally low atmospheric humidity and cloud formation also explain why the nighttime terrestrial radiation losses are high. The diurnal temperature cycle is correspondingly characterized by large differences between day and night, which are in the order of magnitude of the annual amplitude (Fig. 123).

Finally, a third consequence of the lack of clouds and water vapour in the atmosphere is that the *direct* insolation attains the extraordinarily high level of approximately 75% of the global radiation (in dry periods it is even higher). Uniquely large differences therefore exist in the exposure to the insolation, and there are correspondingly wide deviations between heat buildup and evaporation on the variously exposed slopes. The regional distribution patterns of vegetation

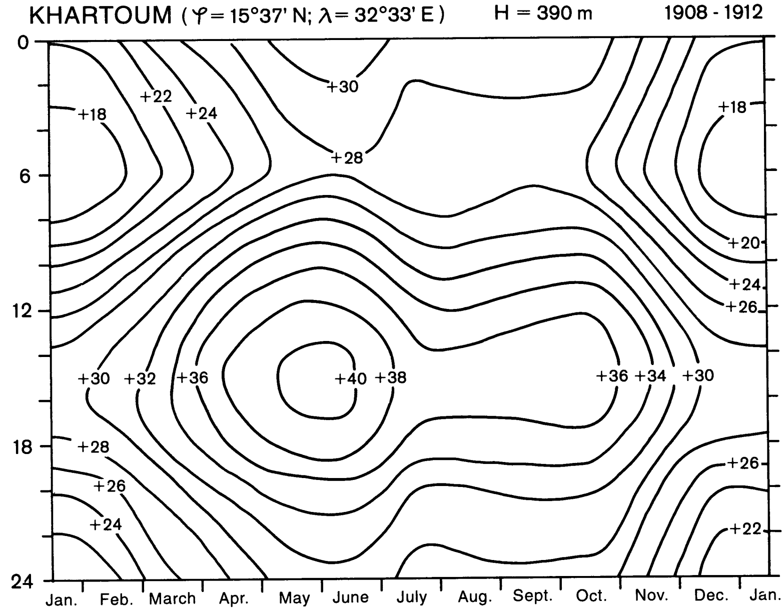


Fig. 123. Thermoisopleth chart of Khartoum, used as an example of an arid tropical climate. (Troll and Paffen 1964)

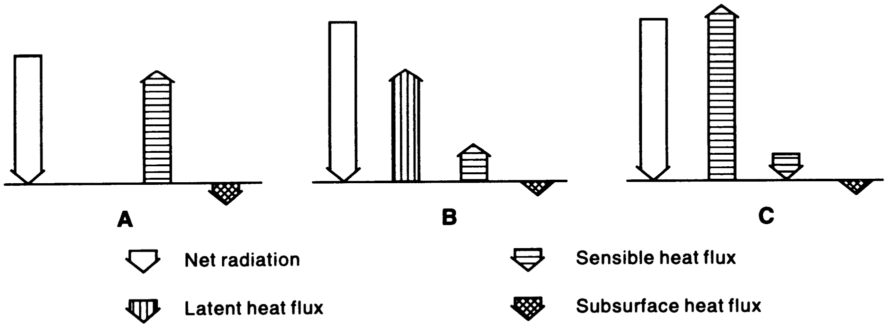


Fig. 124. Types of energy balance: in a desert (*A*), in a humid environment (*B*) and in an oasis (*C*), in each case during the daytime. (Rouse 1981). See text for explanations

cover and weathering debris (in particular rock disintegration by thermal expansion) may reflect this.

The *energy budget* of the desert (Fig. 124) is a special case in so far as the emission of latent heat can decline to zero with declining moisture content (Fig. 124 A), while in humid climates this energy transfer process in particular is usually the most important source of heat loss (Fig. 124 B). The portion of net incoming (all wave-length) radiation (cf. Box 1), which results in the buildup of heat (transfer of *sensible* heat) is thus very high both in relative terms and – given a clearly positive radiation balance – also in absolute terms.

The conditions are different at an oasis or in the narrow moisture zones of an allogenous river (Fig. 124 C). Here the transfer of *latent* heat plays an important role in the energy balance. As a rule, it even exceeds the amount of net radiation energy originally available for evaporation because hot, dry airstreams from the surrounding atmosphere supply additional heat energy (advective energy input, shown in diagram C by the downward-pointing arrow for sensible heat flux). This *oasis effect* also means that the losses of water from water reservoirs and irrigation projects may be much higher than the values calculated from the amounts of radiation energy absorbed at those sites.

In contrast to the generally low and widely varying, i.e. unreliable, water supply, most of the other environmental factors, e.g. air temperature, solar radiation and also in many cases – away from the mountains and dune regions – the supply of mineral nutrients in the soils, are favourable in all areas, all the year round. This means that hot-dry ecosystems are primarily moisture-dependent systems.

3.5.3 Relief and Hydrology

The morphogenesis and morphodynamics of the Tropical/Subtropical Arid Lands have already been dealt with in the chapter dealing with relief in the Arid Mid-Latitudes (see Chap. 3.4.3), because there are many common features between both regions. However, in the Tropical/Subtropical Arid Lands frost weathering (congelifraction) and solifluidal processes do not occur (except high up in the mountains).

Taking as an example a tributary river of the Senegal, Fig. 125 shows how much the river regimes depend on the course of precipitation during the rainy season: the discharge peaks are in each case linked to individual precipitation events (or rapid sequences of such events); once the precipitation is over, the discharge also quickly returns to zero because little if any (long-term) groundwater recharge occurs. This means that the stream discharge is essentially *episodic*.

3.5.4 Soils

Apart from the general dryness, which fundamentally delays the development of soil, the *wind* is the most limiting/disturbing agent for pedogenesis in the *extremely* arid lands. It is responsible for redepositing soil and rock material (by deflation and accumulation), and in the process the materials are sorted according to grain sizes (so that, for example, desert pavement or deposits of loess or sand form). In each case, soils have only been able to develop wherever eolian redistribution has been insignificant for a long period of time. According to the World Soil Map of FAO-UNESCO, the zonal soils found on such consolidated

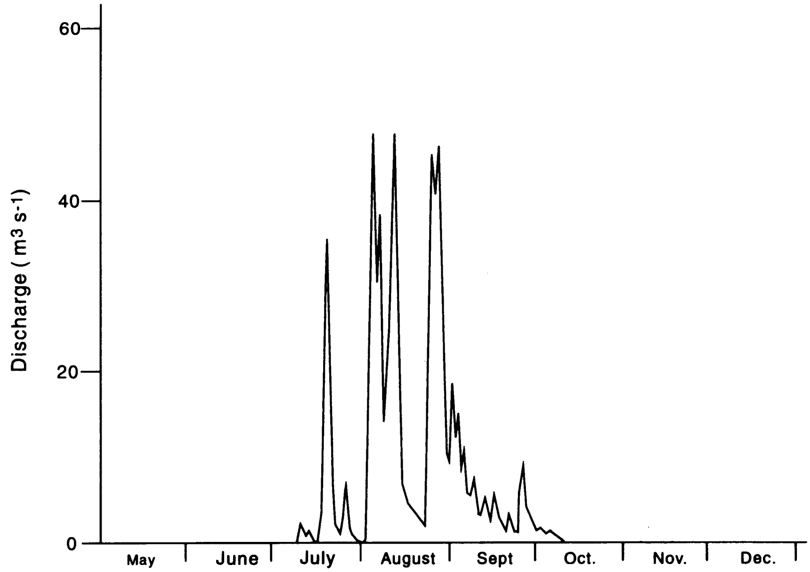


Fig. 125. River regime (= mean daily discharge) of the Térékolé (right-hand tributary of the Senegal) in Yélimané during the 1980 rainly season (Nippes, unpubl.). The size of the drainage basin at Yélimané is 7410 km^2. For further explanations, see the text

substrates are for the most part yermosols or regosols and, in the salt pans, solonchaks.

In the *semi-arid* marginal regions (thorn savannas, thorn steppes), where under natural conditions a more or less continuous plant cover occurs, the wind plays little or no role in pedogenesis. In these areas the *water factor* is much more important: redistribution of precipitation water by surface runoff even from minor slopes and associated erosional and sedimentary processes cause wide fluctuations in the texture and moisture contents of the soils within short distances. The most widely distributed soils – again according to the World Soil Map of FAO-UNESCO – are xerosols, arenosols, regosols and vertisols, and in salt-rich pans solonetz and solonchaks occur; fluvisols (from the Latin fluvius = river) are found in the low-salt and low-sodium alluvial plains of allogenous rivers.

Xerosols (the name comes from the Greek work xeros = dry; other names are burozems, sierozems; see Kubiena 1953) are soils found in semi-deserts. *Yermosols* (the name comes from the Spanish word yermo = desert) are soils found in full deserts. The FAO system defines them as soils which occur under an "aridic" soil moisture regime and which possess a weak or very weak *ochric A horizon* respectively. "Very weak" means that the content of organic matter in the upper 40 cm is no more than 1 wt% in the case of clays and less than 0.5 wt% in the case of sands. Xerosols have slightly higher humus contents, and this goes together with their slightly more luxuriant (although still incomplete) vegetation cover. The fact that the soils are never thoroughly wetted, or if at all then only for short periods of time, means that in recent times there has not been any substantial chemical weathering of the silicates nor has leaching occurred to any significant extent; instead, easily soluble salts may have accumulated. The brown or red soil colours and also the clay-enriched subsoils which occasionally occur extensively in arid lands are therefore to be interpreted as relics of wetter climatic conditions.

Xerosols and yermosols are no longer contained in the new classification used by FAO-UNESCO. Delineating these soil units according to the aridic moisture regime of their occurrences contradicts the normally followed principle of classification which proceeds from the *intrinsic* characters of the soil. Distinguishing between these soil units on the basis of the different humus content of their ochric A horizons has also failed to stand up in practice. Since 1988 the soils are assigned, depending on their characteristics, to the fluvisols, leptosols, cambisols, arenosols etc. Soils which are characterized by enrichments of calcium carbonate and/or calcium sulphate (gypsum) are classified as *calcisols* and *gypsisols* respectively.

Arenosols (the name comes from the Latin word arena = sand) are coarsely textured soils with an extremely low content of fine-grained components, which have developed from (eolian, fluvial, colluvial or marine) relocated (quartz) sands. The weakly humus A horizon (ochric A) may be followed by a weakly developed B horizon. Arenosols are (lithomorphic) soils which are determined by the parent material. Accordingly, they may occur in various climates. Their inherent production potential (capacity to store, retain and release plant nutrients, capacity to store plant-available water, etc.) is low to extremely low. In the Tropical/Subtropical Arid Lands mostly *cambic*, less frequently *luvic, albic* or *ferralic* arenosols occur. No arenosols are shown for the Arid Mid-Latitudes on the soil map prepared by FAO-UNESCO.

The *regosols* (the name comes from the Greek word rhegos = blanket) are weakly developed (A-C-profile), low-humus (at the most ochric A) soils from unconsolidated material (e.g. rock debris, stabilized dunes), whose development has been suspended as a result of the lack of water at a crude soil stage. The variants most frequently encountered are *eutric* and *calcaric* regosols. According to the new FAO-UNESCO classification (1988), former coarse-textured regosols are included in the arenosols and former very stony regosols are grouped under leptosols. By following this classification not many regosol occurrences will remain in arid lands as compared to the previous mapping.

Of the other soil types which occur in arid lands, the *fluvisols* are described in Chapter 3.3.4, the *solonchaks* and *solonetz* in Chapter 3.4.4 and the *vertisols* in Chapter 3.7.4. The humus-rich soil types of the Arid Mid-Latitudes, namely the phaeozems, chernozems and kastanozems of the semi-arid grass steppes which were described in Chapter 3.4.4, do not have any counterparts in the Tropical/Subtropical Arid Lands: not only the soils of the deserts and semi-deserts, but also the soils of the semi-arid thorn steppes and thorn savannas all have humus contents of less than 1%. This is due essentially to the more rapid breakdown of vegetable and animal remains which takes place uninterrupted by a cold winter season in the tropics/subtropics. Another factor may also be that the primary production in the thorn savannas is consistently lower than in the temperate grass steppes.

3.5.5 Vegetation and Animal Life in the Thorn Savanna

On the vegetation of deserts and semi-deserts see Chapter 3.4.5.3.

Like the vegetation of the wetter types of savannas or core savannas (i.e. dry savannas and moist savannas; see Seasonal Tropics, Chap. 3.7.5), that of the (sahel-type) thorn savanna belt may comprise *all transitional forms from pure grasslands to closed tree stands.* However, all the formations are characterized by the fact that the grass cover is sparse and comprises perennial species less than 80 cm high, and woody plants, if and when they occur, are "diffusely" distributed in the grassland and not in groups, as in the forested steppes. Also, the presence of trees in the thorn savannas is by no means an indication of wetter growth sites than usual, but at best points to certain water-retention properties of the respective soils (see Chap. 3.4.5.3). This is apparent from the ecozonal position of the thorn savannas between extremely arid regions and in some respects physiognomically similar savannas on the wetter side; on the other hand, forested steppes are ecotones which represent a transition from wet types of steppes to forest formations.

Many woody plants are protected from drying out by forming small, sometimes delicate leaves (mimosa-type) and/or by reducing their assimilating organs to thorns, while many others are capable of storing water through succulence. Figure 126 provides an overview of these and other frequently encountered *life forms.* Thorns occur so often that they are the source of the name for this type of formation. Practically all the trees/shrubs are used in various ways by the inhab-

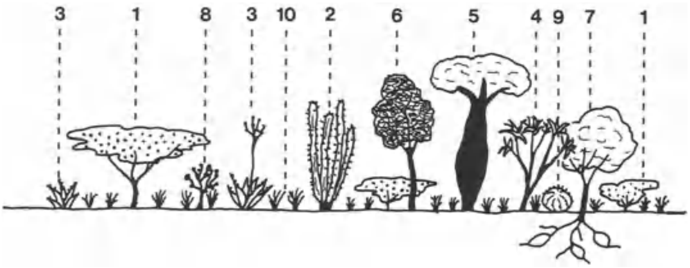


Fig. 126. The characteristic life forms of the thorn-succulent-savanna. (Troll 1960). *1* Thorn-bearing, finely pinnate-leaved umbrella trees and scrubs (*Acacia* type); *2* stem-succulent candle or candelabra trees (cactus type); *3* herbaceous plants bearing tufts of succulent and thorny leaves at the end of their stems or branches (*Aloe* type); *4* trees bearing tufts of succulent and thorny leaves at the end of their stems or branches (*Dracaena* type); *5* water-retaining, barrel-shaped deciduous trees (*Adansonia* type); *6* sclerophyllous trees with spines (*Balanites* type); *7* deciduous trees with xylopodia; *8* sclerophyllous bushes and tree shrubs (*Capparis* type); *9* Stem-succulent, low-growing plants (*Stapelia* type); *10* grasses

itants of the arid lands (for example as sources of food, animal fodder, tannins, fibres, dyes or medicines).

Many of the life forms illustrated occur in all the thorn savanna regions distributed over three continents, although there are very few common taxa between the floras of these regions (they belong to three different floral kingdoms, namely the Paleotropical, Neotropical and Australian kingdoms). Those life forms are thus *convergent adaptations* which developed under the selection pressure exerted by similar environmental conditions. They include, for example, trees with barrel or bottle-shaped trunks (e.g. *Chorisia* and *Bombax* in America, *Adansonia* in Africa, *Sterculia* in Australia), stem succulents (Cactaceae in America, Euphorbiaceae in the Old World) and trees with succulent leaves arranged in tufts at the end of their stems or branches (*Yucca* in the New World, *Dracaena* in the Old World).

Most woody plants lose their leaves during the dry season, and the aboveground parts of grasses dry out. New leaves and shoots do not emerge until towards the end of the dry season or at the start of the rainy season. Around this time, annuals may account for significant proportions of the herbaceous cover (they are present in large numbers where the grass cover has been severely damaged by over-grazing). If fire breaks out during the dry season, and this happens every year in many of the thorn savannas, then as a rule only the leaf litter and the dead grass stalks are consumed by the flames. Immediately after the fires have passed through, possibly long before the next rainy season starts, the grasses begin to put out shoots once more (see Chap. 3.7.5.2). The danger is then rather great that these shoots will suffer drought damage or the grasses will die off completely. Frequent fires can therefore endanger the perennial grass stand.

3.5.6 Land Use

Altogether, the Tropical/Subtropical Arid Lands lie beyond the *agronomic humid-arid boundary*. Where rain-fed agriculture is nevertheless pursued, for example in parts of the African Sahel, crops such as various species of millet and groundnuts, which do not require much water, are cultivated although the harvests are unreliable and there is an increased risk that the soil will be destroyed. The fields are established mainly because the population is desperate and sees no other way of obtaining a supply of food. Economically and ecologically it makes more sense to practise irrigation agriculture and pasturing (and traditionally these are also the main forms of agrarian use). Both will be briefly described in the following.

Nomadic Herding

Pasturing was and is practised in the arid lands of the Old World mainly in the form of *nomadic herding* (see Chap. 3.4.6 for ranching = stationary form of extensive livestock farming). The most frequent form (nowadays) of nomadic herding is known as *transhumance*; full nomadism is rare. In the case of transhumance, subgroups or family members of the owners of the herds (frequently women and children) remain all the year round in permanent settlements near watering points where they practise modest agriculture. The driving of the cattle, which is supervised in particular by the men, follows traditionally prescribed routes and in the course of a year the animals are taken to two or more pasture areas which, depending on the altitude, climate and plant cover, are capable of supporting the livestock at different times.

In the *Tropical/Subtropical Arid Lands the herding of the cattle is linked to the alternation of dry and rainy seasons*: during the dry seasons the herders move into the high-altitude regions, which for the most part are still wetter at that time, and during the rainy seasons they move down into the lowlands again. In the deserts and semi-deserts, the herds consist for the most part of camels, sheep and goats, while in the thorn savannas, cattle predominate. Natural (traditional) selection has favoured those animals which have proved particularly hardy and capable of survival under harsh conditions of life (drought, low quality fodder, long migration routes). Other breeding goals, such as good meat or milk production, were of secondary importance and consequently the productive capacity of the animals is usually correspondingly low.

The low productivity of pastureland necessitates a *very high demand for area per grazing animal.* The lower the amount of precipitation per year, the greater the area required. Ruthenberg (1980) mentions the following relationships:

Annual precipitaion (mm)	Area required (ha) per livestock unit (sustainable density)
50–100	More than 50
200–400	15–10
400–600	12–6

Le Houérou (1980 quoting from Walter and Breckle 1984, p.197) states that in the Sahel 1 kg ha^{-1} of grazeable dry matter (total above-ground dry matter = 2.64 kg ha^{-1}) is produced there for each millimetre of precipitation. In Namibia the correlations between grass production and annual precipitation shown in Fig. 127 were found (for comparison with grass steppes of the mid-latitudes, see Fig. 118).

The generally low ability to support grazing animals means that the population densities are also very limited; but on the other hand, the anthropogenic effects on the natural landscape must inevitably be disproportionately high even if the number of animals is low.

In the recent past, the nomads have in many places not only lost their formerly important function as traders, but also their grazing areas have been increasingly reduced in size by advancing crop cultivation. Nowadays, nomadic herding is found only in those areas where more extreme conditions of drought exist. In the thorn savanna belt, these occur wherever the annual precipitation drops to less

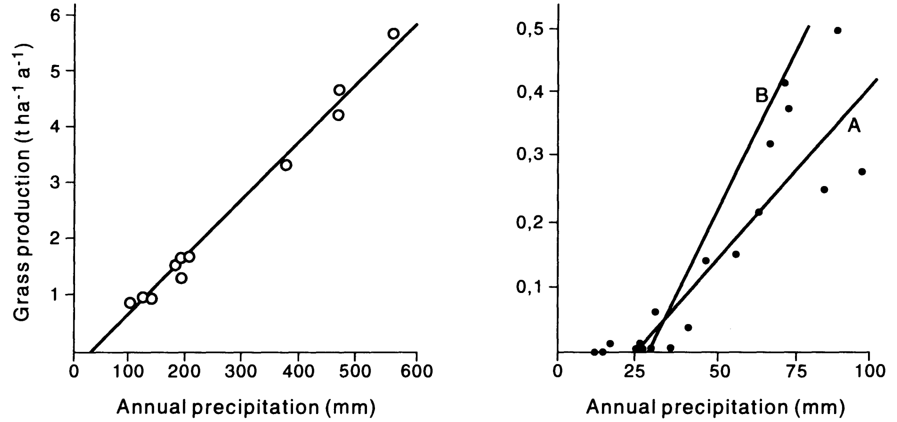


Fig. 127. The dependence on precipitation exhibited by the grass production of the thorn savanna/thorn steppe and desert regions of southwest Africa. [*Left-hand graph* Walter 1973; *right-hand graph* Seely 1978 (*A*) and Walter 1939 (*B*)]

than 400 mm, i.e. far below the minimum rainfall limit down to which rain-fed cultivation was practised in former times under less population pressure.

The fact that the nomadic lifestyle has become progressively more difficult to maintain has encouraged the *trend towards sessility*. This gives rise to new hopes as well as to problems. The hopes spring from the fact that it then becomes possible for the first time to introduce improvements in animal breeding, veterinary care, grazing controls, management of fodder supplies etc. In the past, practically no such measures were ever taken.

The problems which are associated with the adoption of a settled way of life and the implementation of some of these "improvements" (including the provision of veterinary care and the construction of wells) derive from the fact that these trends go hand in hand with an increase in the density of the settlements and intensity of grazing per area. As a result, in many cases rapid and progressive felling occurs of important useful trees/shrubs [e.g. in Sahel *Adansonia digitata* (baobab), *Salvadora persica* and *Tamarindus indica*, as well as species of *Acacia*, *Balanites*, *Bauhinia*, *Prosopis* and *Ziziphus*] and the grass cover is destroyed by overgrazing and trampling. Because of this, wind action and erosion following rainfall can have increasingly serious effects, and can lead to deflation of fine material and sand deposition or hillwash and gully formation over wide areas. As soon as this advanced stage of *desertification* is reached, it no longer seems possible to re-establish the former ecological equilibrium. Examples of this can be found over wide areas in the African Sahel. They show clearly how urgently necessary it is to adopt *controlled* grazing without overstocking of animals.

It also seems conceivable, on a moderate scale (i.e. without placing excessive stress on the slender reserves of soil water), to *cultivate fodder plants*, for example (possibly salt-tolerant) fodder *trees/shrubs* (e.g. some of the above-mentioned species), in particular legumes which bind atmospheric nitrogen. Without woody fodder plants, it is fundamentally impossible to practise year-round grazing in tropical arid lands.

However, controlled grazing and cultivation of fodder crops can only prevent overstocking if at the same time the density per unit area is reduced, because the production of fodder per unit area is strictly limited in each case by the lack of moisture. Furthermore, neither method is at all suitable to permit utilization of the natural grazing potential which exists in remote areas of the arid lands. Only "mobile" utilization systems would be capable of doing this by transporting the herds with trucks to those grazing areas which are far from the settlement areas, thus practising a kind of *advanced nomadism.*

Irrigation Farming

This is the only form of agrarian land use in the arid lands which guarantees reliable (climatically independent) and high yields, even on a global scale, because year-round use (perhaps with several harvests per annum) is possible, fertile soils exist in many areas, and the input of solar energy attains otherwise unknown peak values. All this results in a uniquely high natural *yield potential,* the exploitation of which depends solely (regarding natural conditions of production) on providing an adequate supply of water, i.e. enough to meet the requirements of the plants (cf. Table 8).

The *water requirement* is determined by the consumption of the plants, i.e. the water transpired and stored in the plant tissue, and also by the direct evaporation of intercepted water and soil water. Under the dry-hot conditions which normally exist in arid lands, transpiration and evaporation (referred to together as evapotranspiration) are very high, and the water requirement per unit area is correspondingly higher than for irrigated crops in other ecozones.

The *amount of water required for irrigation is usually calculated* via a potential evapotranspiration derived from various climatic elements (e.g. net radiation, temperature, length of day or duration of sunshine, atmospheric humidity or saturation deficit, wind speed), i.e. by determining the amount of water which is evaporated and transpired from a planted area, given an unlimited supply of water and full utilization of the soil moisture content by the plants. With respect to transpiration losses, the varying water requirements of the different species of crop and of the different age stages must be taken into account.

The *irrigation water required can be supplied* by diverting water from allogenous rivers, withdrawing groundwater or by capturing rainwater. A range of different techniques varying in cost and magnitude are used to exploit and exert better control over these resources. For example, river water can be stored behind giant dams to provide water for major irrigation projects, or surface runoff can be locally concentrated in the fields by sealing the surface of other sections of the terrain, or by building small dams (e.g. "crescent-shaped embankments") or ditches (Thames and Fischer 1981). Groundwater may be supplied to the fields through pipelines or tunnels from higher ground, sometimes over considerable distances, or it can be raised by pumps, water wheels etc. directly from wells.

The foggara and qanats, which are widespread in North Africa and the Middle East, are a very old form of water supply system. Using this method, water which collects in accumulations of debris at the foot of mountain slopes is collected in long tunnels or conduits and supplied to the fields located further downslope on better soils (Fig. 128).

Problems are encountered in the use of many irrigated crops in arid lands *because of the high salt or sodium contents* of the soil. Some of the salts and the sodium are original components which have become enriched in the course of halomorphic pedogenesis (primary salinization or alkalinization), some are secondary formations which were supplied with the saline irrigation water.

In most arid lands halomorphic soils account for only 1–5% of the area (Young 1976, p. 202). Nevertheless, their potential for cultivation of crops is almost always (disproportionately) large because the remaining areas are usually even more unfavourable tracts of land covered with wind-blown sand or with stony materials. The particular advantage of such soils is that they have a deep-reaching, fine-grained texture, and also, because they all occur in shallow depressions, on valley floors or on alluvial planes, they are suitable for artificial irrigation. The problem of high salt concentrations is – in principle – to solve by leaching (e.g. by initially supplying excess amounts of water and possibly by laying drainage pipes in the subsoil), while the problem of high alkali contents (Na^+ at the exchangers) is much more difficult to deal with (e.g. by introducing Ca^{2+} and H^+ ions; see p. 221).

In many cases, the water supplied for irrigation contains salts. In order to avoid (renewed) salinization, more water must then be added than is evaporated from the surface of the soil and transpired by the crops. The amount of excess water required (*leaching requirement*) depends on the salt content of the irrigation water and on the salt tolerance of the respective crop plants. The amount can be determined according to the following formula (taken from Young 1976):

$$LR = \frac{EC_w}{EC_e} 100 ,$$

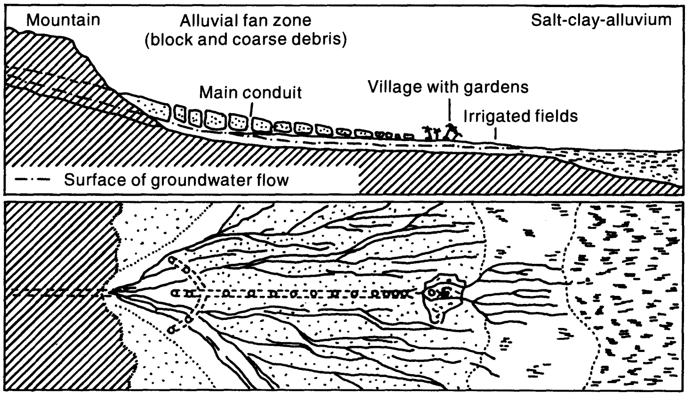


Fig. 128. Diagrammatic plan view and profile view of an Iranian qanat. (Troll 1963)

where LR=leaching requirement, EC_w = electrical conductivity[24] of the irrigation water, EC_e = electrical conductivity of the soil saturation extract which is tolerated by the crops.

If, for example, the tolerance level is $8\,\mathrm{dS\,m^{-1}}$ and the salt concentration of the irrigation water is $2\,\mathrm{dS\,m^{-1}}$, then the leaching requirement is 25%, i.e. the amount of water supplied must be 125% of the anticipated amount lost to evaporation and transpiration. A salinity of $2.25\,\mathrm{dS\,m^{-1}}$ (approx. 0.15 wt% salt) is generally regarded as the permissible upper limit for irrigation water.

Other danger points for the irrigation process may lie in the fact that large amounts of sodium, boron or calcium bicarbonate are supplied with the water.

Although it is basically desirable to expand irrigation agriculture in arid lands, this intention usually flounders on the problems encountered in supplying the water. The possibilities which can be developed with traditional methods are already being used everywhere, and new resources can only be developed by implementing technically complex and capital-intensive projects. Suitable sites probably still exist in several regions.

Non-agrarian Use

A much more modern use is currently being made of many desert areas by establishing military training and testing grounds; another possible use might be to capture solar energy. Desert areas are also nowadays regarded as tourist attractions, in particular in North America, but also in the Old World and in Australia (Sutton 1981).

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Chapter 3.5: Tropical/Subtropical Arid Lands

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3.6 Mediterranean-Type Subtropics

3.6.1 Distribution

The Mediterranean-Type Subtropics cover only 1.8% of the mainland area of the earth, i.e. barely 2.7 million square km^2, and are therefore the smallest of all the ecozones; in addition, they are the most "fragmented" of the ecozones since they are distributed around the world in five relatively small regions which are separate from each other (Fig. 129).

The individual regions are located between approximately latitudes 30° and 40° in both hemispheres, in all cases on the *western sides of the continents*, between the Tropical/Subtropical Arid Lands and the Humid Mid-Latitudes; the

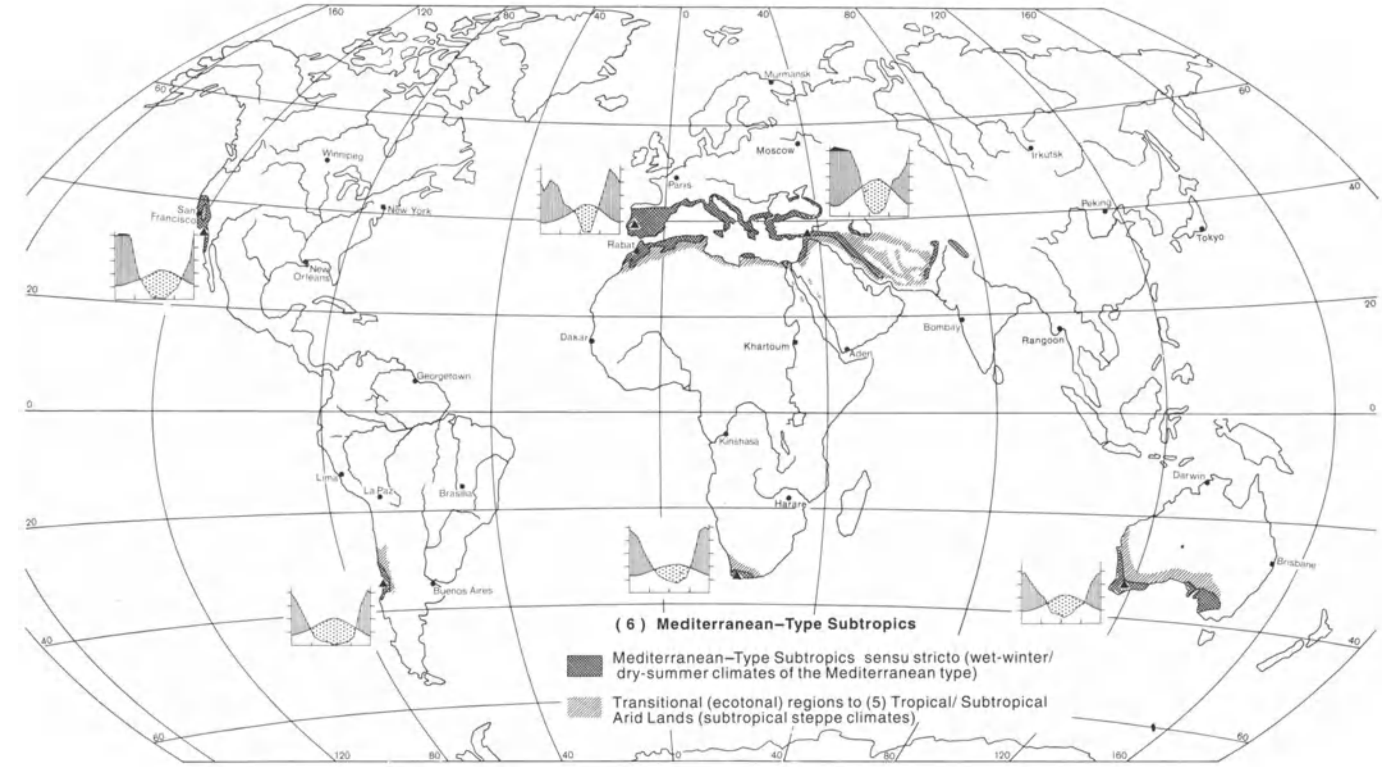


Fig. 129. Mediterranean-Type Subtropics. Of all the ecozones, they cover the smallest areas and are most fragmented. The individual regions are located in both hemispheres, in each case approximately between latitudes 30° and 40°, on the western sides of the continents

Humid Subtropics are found in the same latitude range on the eastern sides of the continents. Mediterranean-Type and Humid Subtropics are usually separated from each other by arid lands. Only in South Africa and in southeastern Australia are they immediately adjacent to one another. In contrast to the Humid Subtropics, the Mediterranean-Type Subtropics are also isolated from the Humid Tropics by arid lands.

The Mediterranean-Type Subtropics usually occupy only narrow coastal strips extending a few 100 km inland (maritime location). Only in the Mediterranean region do they penetrate far to the East into the Old World continent, but even there they basically remain close to the coast, here of the Mediterranean Sea. It is also in this region that they extend to a latitude of approximately 45°, which is the closest they come to either pole.

A number of *designations* are customarily applied to the Mediterranean-Type Subtropics, such as wet-winter climates (areas), dry-summer subtropics, Etesian climates, areas with a mediterranean climate or mediterranean subtropics. The term mediterranean is applied to all *subtropical climates with a winter rainy season* because of the outstanding position of the European Mediterranean region: it covers more than 50% of the total area of all wet-winter regions and – from time immemorial – it has been the focus of more attention and studies on wet-winter regions than any of the other occurrences of this type of climate. In this book (in keeping with the terminology used by Di Castri et al. 1981) the term mediterranean is used as synonymous with wet-winter/dry-summer subtropical; if only the actual Mediterranean region is meant, then this will be indicated by capitalizing the name, i.e. Mediterranean.

Because the mediterranean ecozone is divided up into individual regions located far apart from each other, it is understandable that there are *great differences between the individual occurrences*, for example, with regard to the flora and animal life as well as to the culture and economic development. We must therefore ask whether the remaining common features are adequate to permit all the individual occurrences to be grouped together in one single ecozone; or, to put it another way, whether the characteristic climatic conditions, i.e. the concentration of rainfall in the cold (cool) season of the year, which is a feature common to all the individual regions, truly has such a strong and far-reaching effect that convergent developments have occurred in significant areas (vegetation, soils, landforms and agriculture) throughout the ecozone.

It is not possible to provide a totally convincing argument for or against such a grouping. Depending on the range of characters on which attention is focussed, sometimes more points in common and sometimes more differences will be detected. The decision taken here to regard the wet-winter subtropical regions as an ecozonal unit is based on the consideration that, in view of the large distance between the individual regions, the *common features* are much more important than the *differences*, which, seen from this point of view, must really be regarded as normal. One of the surprising common features is that the natural (and near-natural) ecosystems are all very similar as regards structural and functional characteristics (despite the different phylogenetic origin of the organisms involved), i.e. they are similar in appearance (landscape impression) and by and large exhibit the same nutrient cycles and energy flows (see below). In addition, the developments which have occurred in the agricultural regions share some common features.

Support that all five disjunct wet-winter regions clearly belong together comes also from the fact that they were classified at a very early date (Grisebach 1872; Drude 1890; Schimper 1898) as belonging to one specific zonal type, defined essentially on the basis of its climatological features and vegetation physiognomy. This classification remains in common use to this day.

The *affinity between the individual regions* is very unequal. The greatest degrees of affinity exist between California and Central Chile, as well as between South Africa and southern Australia; then come the Mediterranean region and California and – one step further down – the Mediterranean region and Chile. A number of specific features are also shared in the three regions of the Southern Hemisphere (Fig. 130). In the following, a few of the affinities in the California – Central Chile complex and the Australia – South Africa complex will be mentioned (from Di Castri et al. 1981).

California–Central Chile complex: the geological-tectonical structure is similar (see Chap. 3.6.3), as is also the associated zonation of climate and vegetation. Both regions have frequent coastal fogs in the summer months; and there are many floristic and faunistic affinities which probably go back to migrational exchanges across the Cordilleras. However, the basic stock of flora and animal life is different in the two regions. Convergent historical developments occurred in the course of colonization, which was carried out at approximately the same time in both cases by the Spanish.

Australia–South Africa complex: compared with the previously described complex, the concentration of rain in the winter months is less pronounced; wet-summer regions adjoin immediately to the east. In contrast to all the other

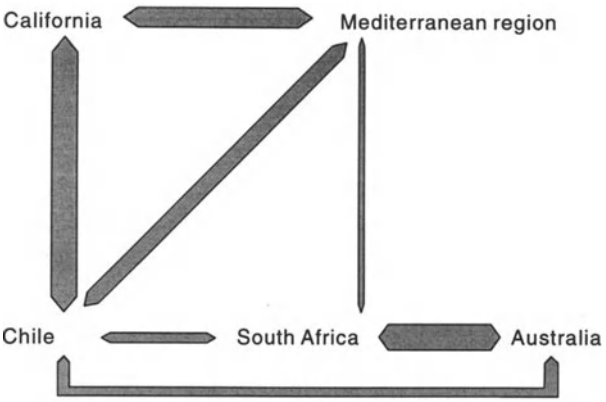


Fig. 130. Degrees of affinity between the five wet-winter regions of the earth. (Di Castri et al. 1981). The *thickness of the arrows* is proportional to the degree of similarity

mediterranean regions, there is (with the exception of the southeastern subregion in Australia) no contact with temperate humid climates (Humid Mid-Latitudes), which otherwise follow in a poleward direction. The macrorelief is determined by a geologically older orogenesis (see Chap. 3.6.3), the landforms are correspondingly more mature and subdued, and the soils, because they are older, are largely depleted of phosphorus and other mineral nutrients (Fig. 134). In general, they are also very deficient in nitrogen. Under extreme conditions, only a heath-like vegetation flourishes and the sclerophyllous shrub formations which are otherwise typical of mediterranean climates are limited to sites with better soils.

The *demarcation of the Mediterranean-Type Subtropics* from the adjacent ecozones causes some problems. The boundaries can be determined only to a limited extent on the basis of the vegetation, for example the distribution of the *evergreen sclerophyllous shrub formations* (for the Mediterranean region see Fig. 136), because so many modifications have been introduced throughout the regions by human beings. Even the attempt to demarcate these regions via the distribution of some typical mediterranean tree or crop species, such as the olive tree (*Olea europea*), or the evergreen (or holly) oak (*Quercus ilex*) or the Aleppo pine (*Pinus halepensis*), is not fully satisfactory. For example, the olive tree (Fig. 131) is regarded as one of the most abundant and conspicuous plants of the Mediterranean basin (Rikli 1943, p. 41). In fact, its distribution coincides extremely well with the region which, for other reasons, in particular climatic ones, is classified as mediterranean; but the olive tree cannot play such an indicator role in the other regions of the Mediterranean-Type Subtropics because, if it occurs there at all, it was only recently introduced and nowhere has it reached the limits of its climatic distribution (e.g. in California where its occurrence is greatly limited by competition with other

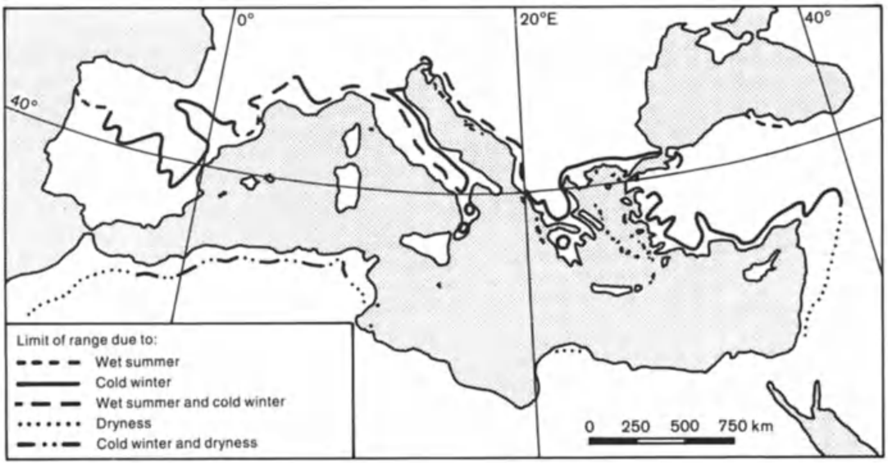


Fig. 131. The olive-tree boundary in the Mediterranean region. (Rother 1984)

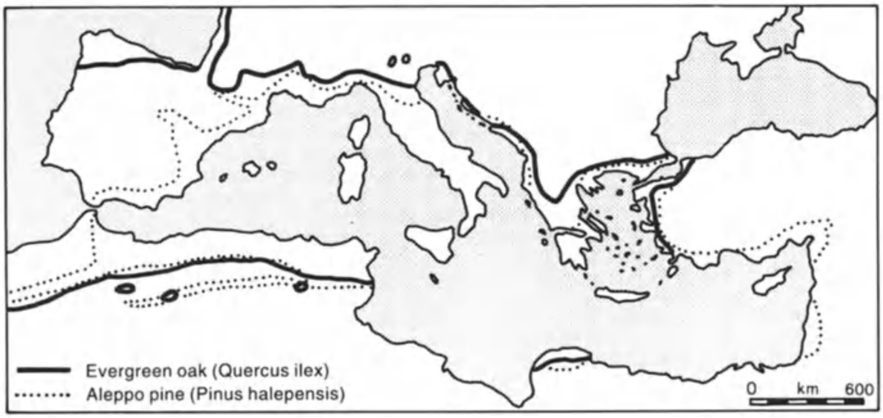


Fig. 132. The natural distribution areas of the evergreen oak and the Aleppo pine in the Mediterranean region. (Rikli 1943–1948)

oil-bearing plants). The same restrictions apply to the indicator value of the evergreen oak and Aleppo pine (Fig. 132).

Clearer and (above all) globally applicable statements can be made on the basis of climatic measurements, although the threshold values (e.g. the percentage of winter rain in the total amount of annual precipitation, or the degree and duration of summer drought) are disputed (e.g. Emberger 1955; Ozenda 1975; Quezel 1976; Di Castri and Hajek 1976).

3.6.2 Climate

During the summer the Mediterranean-Type Subtropics are influenced by the subtropical/tropical belt of high pressure cells. Sunny weather and drought predominate (= *summer dry season*). On the other hand, during the winter as the atmospheric circulation pattern shifts towards the equator, the cyclonal west wind drift of the mid-latitudes prevails. As in Central Europe, rainy weather with front-bound precipitation alternates with sunny periods during high pressure conditions; inflows of cold air masses can cause frosts even in the low-lying areas, and occasionally even long periods of frost occur; at higher altitudes, less frequently also at sea level, snow may fall (= *winter rainy season*).

The eastward extent of the Mediterranean-Type Subtropics depends essentially on how far the mountain massifs can stop the cyclonal west wind drift. This happens least in the European Mediterranean region where the east-west extent is correspondingly very large. In contrast, the wet-winter region in Chile is extremely narrow, because the Cordilleras rise to several thousand metres no more than 200 km inland from the coast.

One disadvantage that all the individual regions of the Mediterranean-Type Subtropics have in common is that in the summer, i.e. when the most favourable temperature and insolation conditions prevail (!), there is a water deficit. However, differences exist with regard to the length and the degree of aridity of the dry period, the amount of winter rainfall, as well as the annual temperature cycle. Subdivisions can be made on that basis (see below).

The outer *demarcation* of this zone to arid lands depends on the importance attached is the climatic differences. According to the ecozonal classification followed in this book, all those wet-winter regions are excluded (see Chap. 3.4.2) where the dry season covers the major part of the year (on average at least 7 months are arid) and the total precipitation remains low (at the poleward boundary $<200-250\,\mathrm{mm\,a^{-1}}$ and at the equatorward boundary $<300-350\,\mathrm{mm\,a^{-1}}$). The sclerophyllous phanerophytes which are characteristic of the Mediterranean-Type Subtropics reach the limits of their range here; beyond this boundary grass and shrub steppes adjoin with chamaephytes as the predominant life form.

The mean annual precipitation reaches values of 800–900 mm in the more humid regions; elsewhere it is frequently in the range 500–600 mm. At least 5 months are humid. In the most favourable case the summer dry period covers just a few (semi-arid) months with low rainfall; but here, too, the soil water content drops so low that plant growth is temporarily restricted.

Within all five individual regions, the amounts of precipitation and the duration of the rainy season increase as a rule towards the poles. The boundary with the Humid Mid-Latitudes is drawn where the summertime restriction on plant growth is no longer clearly evident.

Because of the proximity of the sea and the relatively low temperatures of the coastal waters (cold marine currents everywhere), the *summer warming* is less intense than elsewhere in the same latitude range. In most regions the mean monthly temperatures exceed 18 °C during at least 4 summer months, but they hardly if ever reach 20 °C. Distinctly hot summers occur only in the Mediterranean region (which is explained by its more continental location).

The winter cooling also stays within certain limits. For example, apart from a few poleward (= sub-mediterranean) marginal regions, the average temperatures even of the coldest months usually do not drop below +5 °C (although occasional frosts are the rule). Therefore, low temperatures do not exert an undue limiting effect (no long, thermally induced period of dormancy); but in the spring and – after the first rainfalls – in the autumn, the moisture-temperature combination is more favourable for plant growth and crop cultivation than in the winter. The (only) real stress period is the summer, and the most important selection factor is the restricted or interrupted availability of water, which lasts for various lengths of time.

However, this description must be qualified when we talk of the *high-lying zones*, which cover a large percentage of the area in almost all the mediterranean regions, frequently even larger than that covered by the lowlands. At elevated altitudes, the low temperatures in winter may very well have a limiting effect for varying periods of time. Any climatic-regional subdivision of the Mediterranean-Type Subtropics which wishes to include the varying growth conditions of vegetation and crops (i.e. the phytoclimate) not only in the lowlands but also in the hill and mountain regions, must therefore also take the temperature factor into account as, for example, Emberger (1930, and most recently in 1955) attempted to do with his *pluviothermic quotient (Q)*. Q is a measure of aridity and is calculated according to the formula

$$Q = \frac{2000\ R}{M^2 - m^2}$$

in which R = annual total of precipitation in mm, M = average maximum temperature of the hottest month in °K, m = average minimum temperature of the coldest month in °K. The smaller the value of Q, the drier the climate.

In the *Emberger climagram*, the Q values are plotted against the mean minimum temperatures of the coldest months (m) in a right angled system of co-

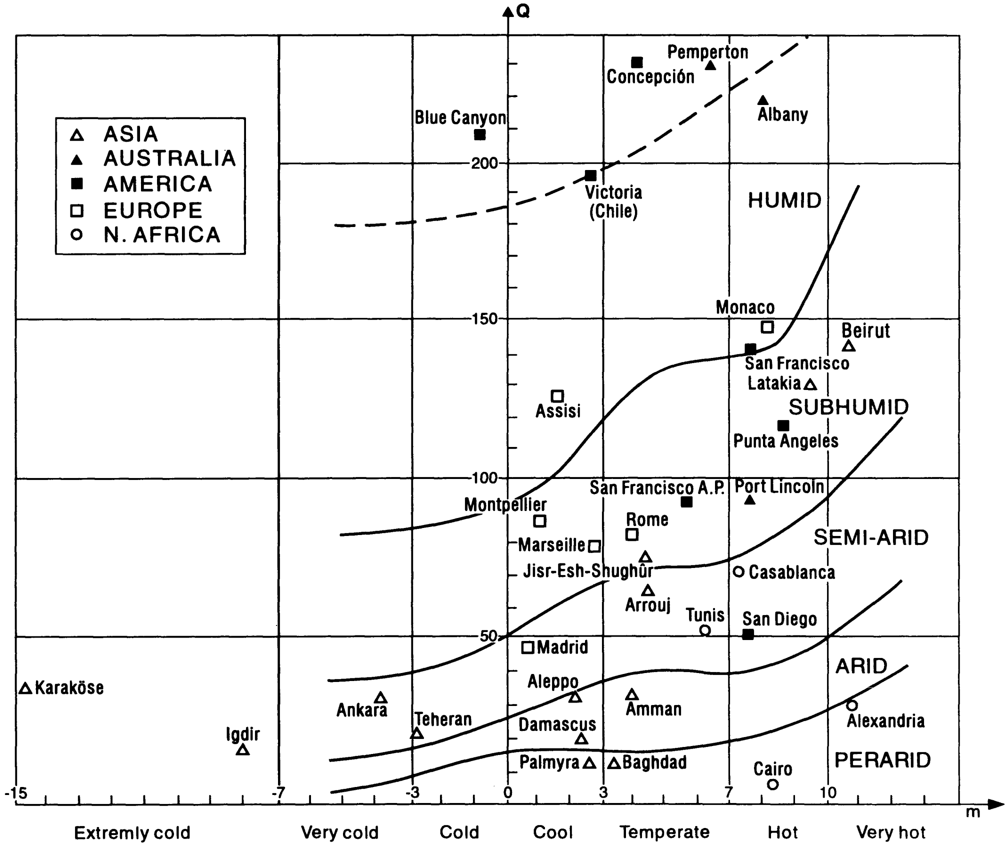


Fig. 133. Emberger climagram (Nahal 1981). It shows the pluviothermal quotient (Q) and the mean minimum temperature of the coldest month (m) for a number of localities in the Mediterranean-Type Subtropics. The vertical lines denote climatic stages according to temperature; the more horizontal curves denote climatic stages according to degree of aridity. For further explanations, see text

ordinates in which the y-axis represents Q and the x-axis represents m (in °C). Figure 133 demonstrates that considerable differences in climate exist behind the basic scheme of wet winter/dry summer which applies equally to all the stations mentioned here.

The intra-mediterranean cold-winter high-lying areas could, for example, be referred to as *alto-mediterranean*, in order to distinguish them more precisely from the also winter-cold *sub-mediterranean* areas, which are meant to be the transitional zones between the Mediterranean-Type Subtropics and the Humid Mid-Latitudes. Both thermal special cases would then be contrasted with the *eu-mediterranean* climatic region, the mediterranean climate sensu stricto, which is usually meant when the climatic conditions in the Mediterranean-Type Subtropics are described as a whole, although this climate often only prevails in narrow coastal strips and in a few valleys.

The macroregional climatic zonation is overlain by a *microregional differentiation* which (with the exception of the mediterranean regions in southern Australia) is linked to changes in exposition and slope inclination of the land surface (see Chap. 3.6.3): mountain belts close to the coast may profit from the water condensing from the frequent fogs (above the cold marine currents), while further inland they profit from the adiabatic rainfall; valleys located in the rain shadow and slopes facing away from the rainfall may, on the other hand, receive extremely low amounts of precipitation; these differences may be reduced when water from high altitude regions, which receive larger amounts of precipitation, flows into valleys with a low rainfall; or, the differences may also be reinforced if, for example, additional runoff losses occur on the lee slopes, which are already at a disadvantage. Finally, the supply of water to the vegetation may vary due to differences in the water-retention capacity of the soil and rock. If there are large differences in altitude, then the hygric conditions just described are also accompanied by significant thermal differences.

3.6.3 Relief and Hydrology

With the exception of southern Australia, where plains predominate, all the individual regions of the Mediterranean-Type Subtropics are characterized by a *dissected relief* in large parts, with maximum altitudes rising to above 2000 and occasionally 3000 m above sea level, while in California and Central Chile mountain peaks attain heights even in excess of 4000 m or almost 7000 m respectively. This wide amplitude of relief was created in the course of the mid-Tertiary–early Quaternary Alpine orogeny, and in the case of South Africa as early as in the Carboniferous-Permian Variscan orogeny. In the Mediterranean region, the relatively young and rugged ranges of folded and faulted mountains frame in many cases older (Mesozoic) masses having only moderate relief and varying in extent, thus creating a large number of small compartments, such as the basin landscapes of Greece. On the other hand, California and Central Chile are characterized by three landform elements, namely, from west to east, coastal range—longitudinal valley (central valley)—high mountains. Both in the Mediterranean region and in North and South America, the mountain–building movements have been accompanied by fossil, subrecent and recent volcanism and frequent earthquakes. Sometimes extensive marine beach terraces (abrasion terraces) have formed in the course of the tectonic uplifts, but also as a result of phases of transgression and regression in the world's oceans.

The *recent geomorphodynamics* are characterized by intensive slope wash and periodically strong fluvial processes (Hagedorn and Poser 1974), although there are significant quantitative differences between the regions. According to Wilhelmy (1975), when viewed from a morphoclimatic standpoint, the Mediterranean-Type Subtropics occupy a transitional position between non-tropical regions with intense fluvial processes and tropical/subtropical regions with intense sheet wash: "The linear erosion which still predominates at the polar margin is gradually replaced towards the equator by sheet erosion" (Wilhelmy 1975, p. 364). The reason for this is the decline in the amount of precipitation towards the equator and the gradually shorter rainy season coupled with the simultaneous increase in potential evaporation.

One common fact which applies to all regions of the Mediterranean-Type Subtropics is that fluvial and denudative processes are limited to a more or less long phase in the *winter season.* However, during that time these processes can assume quite considerable proportions, particularly after a heavy rainfall, and when they are favoured, at least at the beginning of the rainy season (i.e. after the summer drought), by a patchy vegetation cover (in the Mediterranean region 60–70% of the erosion takes place from September to November – Le Houérou 1981, p. 516); in many areas the erosion is, in addition, promoted by high relief energy, shallow soils or impermeable marls (so that in each case large amounts of rainwater run off at the surface). The discharge in the rivers is therefore very strongly dependent on precipitation and the water flows in intermittent surges. "Even small rivers can turn into raging torrents within a short period of time" (Rother 1984, p. 49). Such floods occasionally cause dams to fail and lead to catastrophic flooding, deep gullying and also uncontrolled aggradation. During the summer dry season, many of these rivers turn into tiny streams or dry up completely.

Slope wash and gravitational mass flows (soil slips and landslides) are particularly large where the natural plant cover has been destroyed by human intervention (which is frequently the case) and easily erodible clays and marls are exposed. In this case the runoff is 5 times, and the sheet erosion 50 times greater than on densely forested slopes; per annum between 5 and $30\,\mathrm{t\,ha^{-1}}$ of materials are eroded, corresponding to a soil layer of 0.4 to 2 mm (Le Houérou 1981).

The winter flood waters of the rivers flowing towards the coasts therefore carry very high sediment loads (frequently $> 50\,\mathrm{kg\,m^{-3}}$, with peaks as high as three and four times this amount – Le Houérou 1981) consisting of boulders, pebbles, sand and fine sediments. Coarser sediments fill the broad beds of the rivers in flood, where the rivers emerge from the mountains and the gradients become less steep. In the summer, for the most part only narrow channels remain at these points and in each case they have to find their path again through these wide gravel fields.

The finer grain sizes are carried all the way to the mouths of the rivers far from the mountains. In the weakly tidal Mediterranean Sea they form – occasionally extensive – *deltas* (e.g. the Po, Rhône, Ebro) or they fill up lagoons. These alluvial plains are in sharp contrast to the otherwise precipitous coastlines.

In keeping with the morphoclimatic transitional position of the Mediterranean-Type Subtropics, there are no landforms which are peculiar only to this ecozone; but some landform types occur so frequently on a regional basis that they may be regarded as more or less characteristic. These include the erosional forms known as frane (singular = frana; small-area slides) and calanche (singular = calanci; badland-like ravining of the rock on steep slopes) which occur in geomorphologically soft material; tors and accumulations of boulders which occur on resistant granite; various karst forms such as karren, dolines, uvalas and poljes as well as subterranean rivers and cavities found in limestone substrates. The widely occurring (recent and pre-recent) limestone crusts (calcretes), which are interpreted in the older literature as deposits left by ascending soil solutions (ascension theory), have in more recent times come to be regarded as fossil B_{ck} or C_{ck} horizons (B or C horizons with calcareous accumulations in concretionary form) of decalcified soils (descension theory; Rohdenburg and Sabelberg 1969; cf. also Blümel 1981) (Rother 1984, p. 64).

3.6.4 Soils

In conjunction with the petrographic differences (e.g. carbonate rock, silicate rock), the erosion caused by human activity (soil erosion, karstification, flood damage) and paleoclimatic changes (relict soils), the close-knit hygro-orographic differentiation has led to the occurrence of a large number of (frequently azonal) soil types within a small area. Many of these soil types differ considerably as regards fertility; in the poorer types the lack of phosphorus and nitrogen is particularly widespread. In South Africa and Australia, where low nutrient rocks (basement rocks, quartz sands) predominate, oligotrophic soils cover a wider area than in the other individual regions (Fig. 134). The natural vegetation which is adapted to these soils is a heath-like dwarf shrub formation (e.g. fynbos in the South African Cape region).

Disregarding the numerous special cases (which, however, can add up to very large cumulative areas), and instead looking more closely at gently or moderately inclined slopes where the soil has developed undisturbed over a long period of time, we find that, despite all the variety, one particular type of soil recurs over and over again, and therefore must be regarded as a zonal formation. The soil in question is the *chromic luvisol.* This is a usually bright red to brownish red-coloured sol lessivé, which normally develops on carbonate rock, has a fairly high base content and is low in humus. It tends to be shallow (because it is susceptible

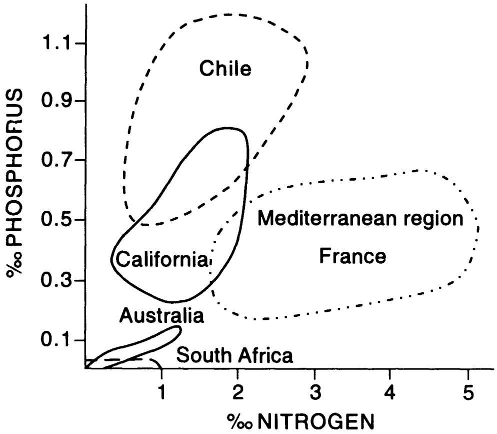


Fig. 134. Phosphorus and nitrogen contents of the soils in the five regions of the Mediterranean-Type Subtropics. (Di Castri et al. 1981). The soils of the Australian and South African wet-winter regions are particularly low in nutrients

to erosion) and to become hardened during dry periods. The red colour is due to hematite distributed in the soil.

Also widespread and similar by its conspicuous red colour are *chromic cambisols.* In the Mediterranean region both these (and perhaps even other red to brown) soils are called *terra rossa* or *terra fusca.* It has been proven that many of them formed as early as in the Tertiary or in the warm periods during the Pleistocene, that is to say they are *relict* formations.

Chromic luvisols cover very large areas in the Californian, Central Chilean and Cape Province regions of the Mediterranean-Type Subtropics, and moderately large areas in the European Mediterranean region; but they occur only occasionally in the Australian wet-winter regions.

In many areas the next most frequent types of soil are the *calcisols* and the *calcaric cambisols,* which are characterized by the accumulation or presence of calcarous material, as well as the *eutric cambisols* which have already been described in Chapter 3.3, Humid Mid-Latitudes. The *dystric* cambisols, which were also dealt with in that chapter, may occur as well, mostly on acid rocks in the wetter mountain regions where pedogenesis is less advanced and therefore the characteristics of the parent rock are still strongly evident.

Chromic luvisols are also characteristic of some drier sub-regions (dry savanna climates) in the Seasonal Tropics. There they occur in combination with *vertisols* (see p. 336). Vertisols have also developed here and there in the Mediterranean-Type Subtropics on clay-rich substrates, but the combination with cambisols is more typical of this region.

In particularly dry areas, ascending, saline groundwater can cause salt accumulations in the top soil and salt blooms at the surface of the soil during the dry season. This occurs quite frequently in depressions and on clay-rich alluvial plains, but is also found on surfaces with weak relief. During the rainy season this process is reversed. The soil types which form under these conditions are the (solodic) *planosols* (pseudogley) and (gleyic) *solonchaks* (see Chap. 3.4.4). Despite the salt content, many of these soils can be used for growing field crops and trees (e.g. for rice and vineyards) – occasionally in conjunction with irrigation to remove the salt.

On sites subject to severe erosion, *rendzinas* or *rankers* predominate, depending on whether carbonate-rich or low-carbonate rock is involved. In extreme cases, only very weakly developed lithosols and – on the recently aggraded material in the valleys and at the foot of the mountain regions – regosols (eutric and calcic regosols) occur. More than their low nutrient content, it is the low water-holding capacity of these soils that makes them into extremely unfavourable sites for vegetation and agricultural use. Deep-rooted olive tree or vine plantations offer the best chances of success in these areas.

According to the recent FAO-UNESCO soil classification (Rome 1988), rankers, rendzinas and lithosols are grouped under the newly introduced major grouping of *leptosols*. The same applies, most likely, to most of those soils formerly classified as regosols.

3.6.5 Vegetation

3.6.5.1 Structural Characteristics

Vegetation Dynamics

Apart from on the driest sites and those with the lowest nutrient contents, all the regions of the Mediterranean-Type Subtropics were originally covered by forests of mostly *evergreen sclerophyllous* species of trees (for the western Mediterranean region see Fig. 135). Although the five wet-winter regions cover no fewer than

Fig. 135. Natural distribution range of *Quercus ilex* forests (*oblique shading*), *Oleo-Ceratonion* communities (*dotted shading*) and *Argania* shrublands (*vertical broken lines*) in the western Mediterranean region. (Walter 1968)

four floral kingdoms (namely the Australian, South African and Neotropical in the Southern Hemisphere, and the Holarctic in the Northern Hemisphere) and thus are floristically extremely different, these forests were (and the vestiges that still exist today are) physiognomically very similar (convergent) to one another.

In the Mediterranean region the original forests were mostly composed of evergreen oak. As can be seen today from vestigial stands, the main features of these forests (*Quercetum ilicis*) were as follows (Walter 1990):

Tree layer: 15–18 m, closed canopy, made up solely of *Quercus ilex*.
Shrub layer: 3–5 (12) m high, *Buxus sempervirens, Viburnum tinus, Phillyrea media, Ph. angustifolia, Pistacia lentiscus, P. terebinthus, Rhamnus alaternus, Rosa sempervirens* etc.; *Smilax, Lonicera* and *Clematis* as lianas.
Herbaceous layer: about 50 cm tall, sparse, *Ruscus aculeatus, Rubia peregrina, Asparagus acutifolius, Asplenium adiantum-nigrum, Carex distachya* etc.
Moss layer: very sparse.

Human activity – which has been going on for thousands of years in the Mediterranean region and at least for hundreds of years in the other regions – has greatly modified or destroyed these sclerophyllous forests. They have been replaced largely by sclerophyllous *shrub* formations which also exhibit a great deal of convergence in appearance all around the world. Nowadays, they predominate in the mediterranean landscapes of all climatic sub-regions (humid to semi-arid, cold to hot; see the Emberger climagram, Fig. 133) to such an extent that their range is occasionally used as a criterion for demarcating the Mediterranean-Type Subtropics (Fig. 136).

It is not always certain how the individual occurrences of the shrub formations should be interpreted: whether partially also as *climax communities*, as quasi-permanent (long-term stable) anthropogenic *substitute communities*, or as relatively short-lived *degradation (regression) stages* (post-forest indicators) or

Fig. 136. The distribution of the maquis and the garrigue scrublands in the Mediterranean region. (Quézel 1981)

(advanced) regradation (progression) stages (post-agriculture indicators). There is agreement that the natural regeneration of the vegetation, when it takes place under conditions which are not too cold and dry, always leads first via forb or sward communities to sclerophyllous shrub communities before sclerophyllous forests can establish themselves again (Fig. 137) at various times following the anthropogenic intervention, and depending on its severity. Only under semi-arid and warm-hot conditions does the *secondary succession* seem to stop at the sclerophyllous shrub communities and therefore, only here they would be climax communities.

Under more humid (and usually also cooler) conditions, of the kind found in the sub-mediterranean region, such sclerophyllous shrub communities are on the other hand often totally lacking. Instead, broad-leaved, (winter-)deciduous species predominate, in the shrub stages as well as in the forests.

Matorral

The mediterranean sclerophyllous shrub formations can be grouped together under the collective term matorral (Tomaselli 1981, p. 95). Differentiations are made in the first instance according to the height of the shrubs, e.g. high (> 2 m), middle (< 2 > 0.6 m) and low (< 0.6 m) matorral, and in the second instance according to the density of the shrub stand, e.g. dense (degree of cover > 75%), discontinuous (50–75%) and scattered matorral (< 50%). A further subdivision can be made according to the proportional significance (numbers of individuals, percentages of cover or weight proportions) of certain life forms (e.g. of thorny xerophytes or of coniferous trees/shrubs).

Here we will use a simpler subdivision into two types, namely a high and a low matorral, which is frequently employed in the literature (Fig. 138). The following are some of the regional designations used for the high matorral: maquis (French) and macchia (Italian) in the Mediterranean region; matorral denso and espinal in central Chile; chaparral in California; and mallee in Australia. Depending on the linguistic region and occurrence, the low matorral is referred to as garrigue (French), tomillares (Spanish), jaral (Chile), phrygana (Greek), or fynbos (South Africa). The names *maquis* and *garrigue* are also used beyond their regional frame of reference in the general meaning of high sclerophyllous shrub formation and low sclerophyllous shrub formation respectively.

The *high matorral* is characterized by the following features: frequently very dense bush, a few metres high, comprising a large number of species of shrub and small trees, many of which produce beautiful flowers in springtime. Most woody plants are more or less xeromorphic, ranging from leafless shrubs with green twigs, and shrubs with very small scale-like (degenerated) leaves, up to those with rather large laurel-like (dark green leathery) leaves. Many leaves are spiny, and fairly often their surfaces are waxy, giving them a shinning bluish or greyish colour (see also below). Several plants give off the fragrance of ethereal oils. In very dense stands the undergrowth is often missing, otherwise dwarf shrubs

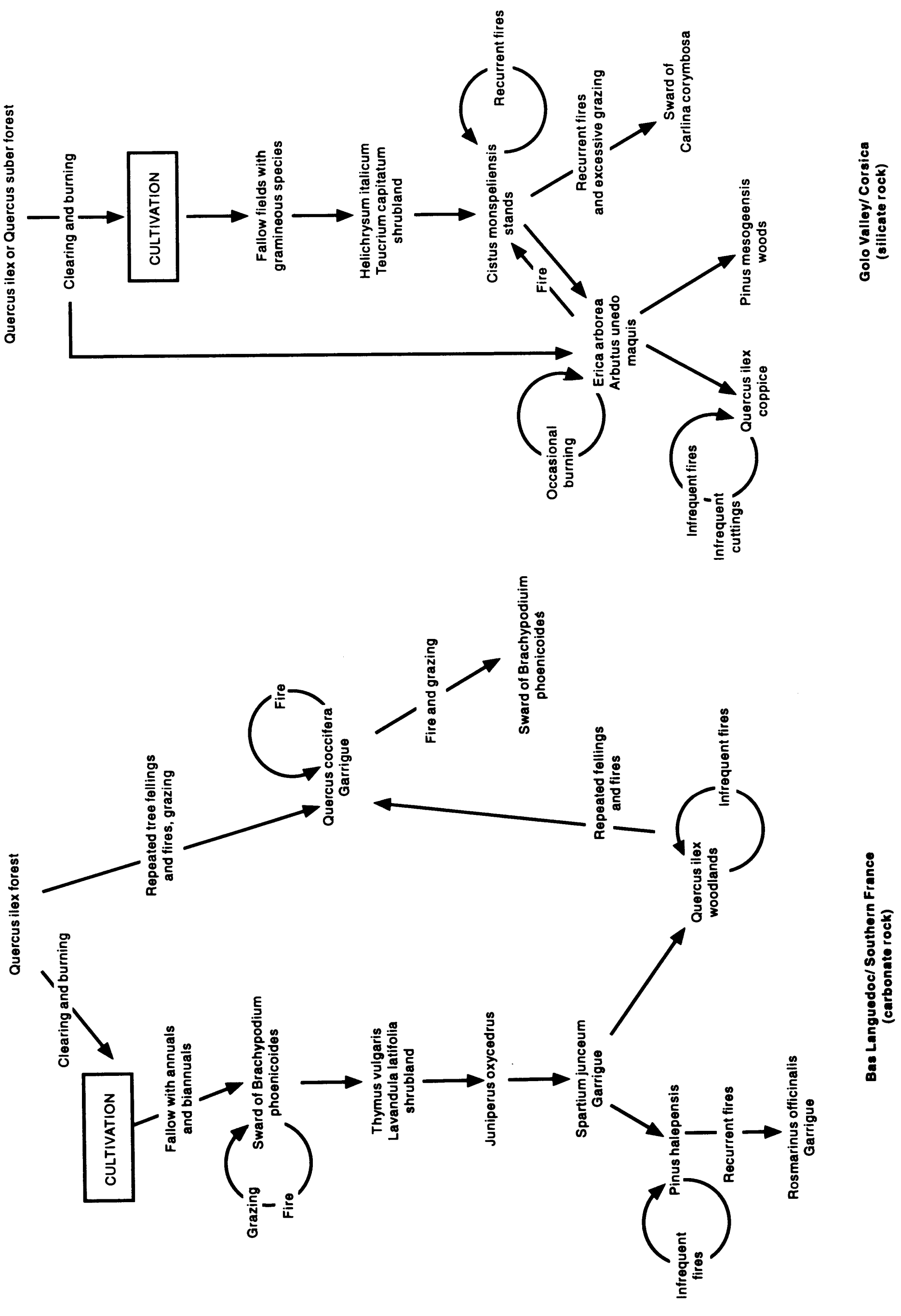


Fig. 137. Successions of plant communities in various wet-winter regions, as a function of the type and intensity of use. (Trabaud 1981)

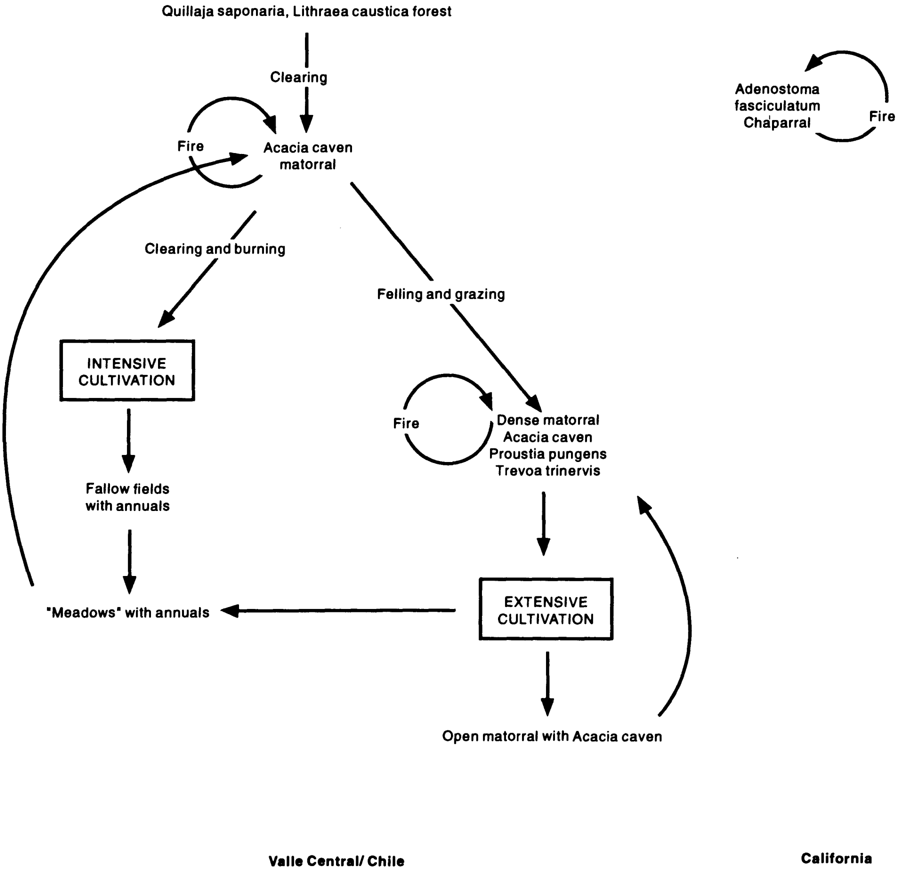


Fig. 137. Continued

and semi-ligneous undershrubs, and in less dense areas bulbous and tuberous geophytes, are present in very large numbers (Schmithüsen 1968).

In the extreme case, the *low matorral* is a dense to patchy stand of often spiny and heath-like shrubs growing to knee height (chamaephytes), between which bulbous and tuberous geophytes are often strongly represented. As soon as anthropogenic influences (grazing, burning) recede, mostly taller shrubs appear, and under their protection hemicryptophytes (perennial grasses and forbs) can spread out. The dwarf shrub formations then appear to exist only on the driest sites (with the lowest supplies of nutrients).

The height (and density) of the shrub/tree layer and thus the distribution of the high and low matorral also depends on the degree of aridity (Fig. 139). With increasing dryness low-growing (and patchy) shrub formations predominate more and more.

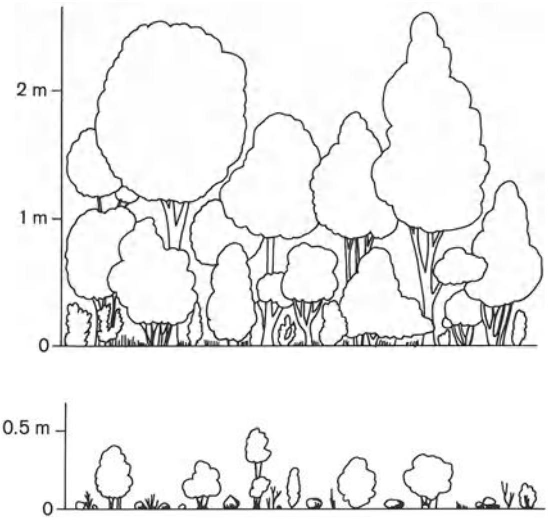


Fig. 138. Structure of a high dense matorral (maquis) and of a low scattered matorral (garrigue). (Tomaselli 1981)

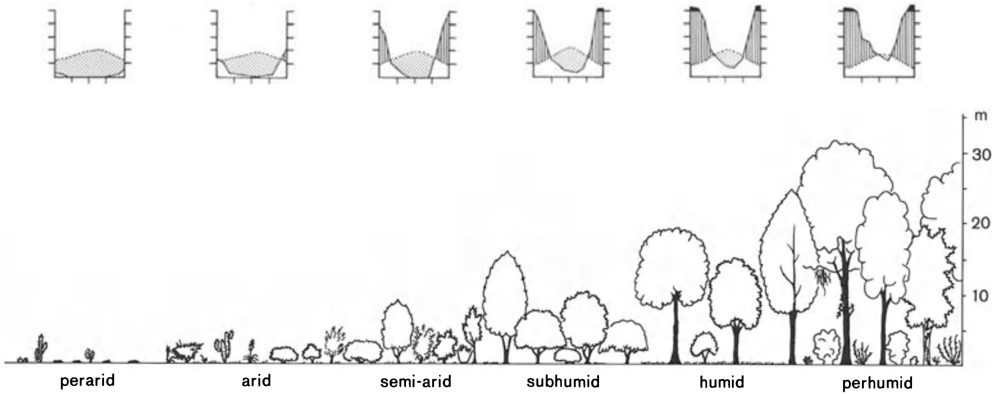


Fig. 139. The types of vegetation in the wet-winter region of Chile as a function of the aridity/humidity. (Di Castri 1981). *Perarid* type (Copiapó, 27°21′S): semi-desert with *Copiapoa*, *Trichocereus* and *chamaephytes*. *Arid* type (La Serena, 29°54′S): open shrub with *Puya*, *Baccharis*, *Trichocereus*, *Lithraea caustica* and *Adesmia*. *Semi-arid* type (Llay Llay, 32°50′S): matorral with *Retanilla ephedra*, *Lithraea caustica*, *Cryptocarya alba*, *Trevoa trinervis*, *Colletia spinosissima*, *Satureja gilliesii* and *Kageneckia oblonga*. *Subhumid* type (Talca, 35°26′S): sclerophyllous woodland with *Cryptocarya alba*, *Lithraea caustica*, *Aristotelia chilensis*, *Quillaja saponaria* and *Azara petiolars*. *Humid* type (Chillán, 36°36′S): mesophilous woodland with *Laurelia*, *Myrceugenella*, *Quillaja saponaria* and *Nothofagus obliqua*. *Perhumid* type (Traiguén, 38°15′S): hygrophilous forest with *Nothofagus dombeyi*, *Persea lingue*, *Drimys winteri*, *Chusquea* and epiphytes

Sclerophyllous Woody Plants and Semi-Ligneous Shrubs

Despite the pronounced seasonality of the climate, many plant species are evergreen, i.e. do not reduce their transpiration surfaces during dry seasons in the manner that is characteristic of plants in the wet-summer tropics and subtropics. They can do so because they possess special adaptive features which protect them against excessive transpiration losses. The most obvious of these is the hardness of their perennial leaves or *sclerophylly* (opposite: malacophylly = having soft leaves): the leaves are stiff (brittle) and leathery due to the fact that they contain large amounts of sclerenchymatic material (supporting tissue). Even when they suffer great water losses, they do not wilt.

Sclerophylly has been developed in similar fashion by representatives of many plant families (e.g. Fagaceae, Oleaceae, Fabaceae (= Papilionaceae), Ericaceae, Liliaceae, Proteaceae and Restionaceae). It is regarded as a perfect example of environmentally induced convergence. Together with sclerophylly, the following characteristics are widely distributed.

The *stems* have a thick bark or cork layer; the often gnarled branches emerge low down and form broad crowns; the trees grow to a height of 15 to 20 m; the coniferous trees for the most part have broad crowns. The branches and branchlets are frequently oriented in such a way as to encourage rainwater to run down the stem, thereby ensuring advantageous soaking of the root zone.

The typical *leaves* have a thick cuticle and strong outer walls of the epidermis; their surfaces are shiny (wax, resin or lacquer coatings); hairy on the undersides; they are rich in extremely pungent ethereal oils (e.g. in the case of thyme, lavender, rosemary); medium-large to small (reduced overall surface area); greyish green in colour; and for the most part they have unbroken edges with an oval to elliptical, sometimes also needle-like, ericoid or scale-like shape; spiny leaves are also relatively common. The cuticular transpiration is extremely low.

The *stomata* of the leaves are very small (their total area is only 0.2–0.5% of the leaf area, compared with about 1–2% in the case of malacophyllous plants); on the other hand, they are very numerous (400–500 mm^{-2}). This permits the sclerophyllous plants to react rapidly to changes in their *water potential* (= osmotic potential of the water bound to macromolecular structures (protoplasm) and to dissolved substances in the cell sap), and thus, to maintain a balanced water budget even in the case of long-lasting drought (this means that they are relatively *hydro-stable*, whereas the malacophyllous plants tend to be hydro-unstable).

Compared with the dry-season deciduous plants of the tropical savannas, the evergreen sclerophyllous plants have the advantage that they can resume photosynthesis immediately and on a large scale when favourable moisture conditons return: their photosynthesis apparatus is always "at the ready"; the tropophytes of the savannas, on the other hand, must first completely redevelop their leaves after periods of unfavourable moisture conditions and they react more slowly to changes in their water potential. This may be one reason why many mediterranean

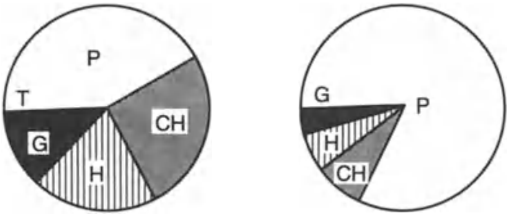


Fig. 140. Life form spectra of *Quercetum rotundifoliae* from Aragonia. (Schmithüsen 1968). *Left* calculated according to the number of species which represent each life form; *right* calculated according to coverage achieved by each life form group; *P* phanerophytes; *CH* chamaephytes; *H* hemicryptophytes; *G* cryptophytes (geophytes); *T* therophytes

plant species have a favourable *transpiration ratio* (i.e. they give off relatively little water per quantity of dry matter produced).

Other Life Forms

Other forms of adaptation to the stress of summer drought occur particularly frequently under modified climatic conditions. For example *seasonal dimorphism*, i.e. the formation of smaller leaves during dry seasons, is found under increasingly arid climatic conditions in more and more chamaephytes (Orshan 1964, 1983). *Succulence* gains abundance in Chile and California as soon as the water supply is particularly critical, and the percentage of winter-deciduous plants increases as the winters tend to become increasingly cold; the evergreen sclerophyllous vegetation ends where regularly hard frosts occur.

Even in those areas where the sclerophyllous woody plants predominate in terms of individual numbers and/or shoot mass, other life forms account for high percentages in relation to the number of species (Fig. 140). Chamaephytes and hemicryptophytes are particularly frequent, but geophytes (cryptophytes) and therophytes are also noticeably numerous.

3.6.5.2 Ecosystem Matter Reserves and Exchange Processes

Phytomass and Primary Production

The productiveness (performance capability) of the mediterranean vegetation suffers from the fact that the *optimum moisture and temperature levels occur at different seasons of the year*. During the warm season a lack of water, and during the rainy season a (moderate) lack of heat, inhibit the production of phytomass. On the other hand, it is advantageous that many woody plants are sclerophyllous and evergreen. This permits them to go on growing (at a reduced level) even during the dry season (year-round photosynthetic activity), or they can at least quickly switch to production as soon as the moisture conditions permit, e.g. after occasional rainfall during the dry season. However, even under optimal moisture conditions, their rates of production never attain those of malacophyllous plants under similar conditions (Mooney 1981, p. 251; Fig. 141).

As is to be expected, the productivity of the vegetation per unit area is determined mainly by structural characteristics of the plant stands (Table 37). Maximum values are achieved where, as in the case of the *evergreen oak forest* studied, the phytomass and the leaf area index attain high values (319 t ha^{-1} and 4.5 m^2 m^{-2}) and the root/shoot ratio is small (0.19). The PP$_N$ is much lower in the case of the Greek *phrygana* where – under severely arid and anthropogenically disrupted conditions – the phytomass and the leaf area index amount to only 27 t ha^{-1} and 1.7 m^2 m^{-2} respectively and the root/shoot ratio increases to 1.48. The fact that the (photosynthetically active!) foliage in the phrygana accounts for a relatively larger amount of the above-ground biomass, namely almost 20% compared to 3% in the case of the oak forest, may have a somewhat compensatory effect.

The annual values for PP$_N$ (only above ground) measured under these conditions in the oak forest and in the phrygana amounted to 6.5 t ha^{-1} and 4.12 t ha^{-1} respectively. For two further stands (Table 37), a French *garrigue* and a Californian chaparral, values of 3.4 and 4.12 t ha^{-1} a^{-1} are mentioned. As shown by many measurements not listed here, these four values define very well the

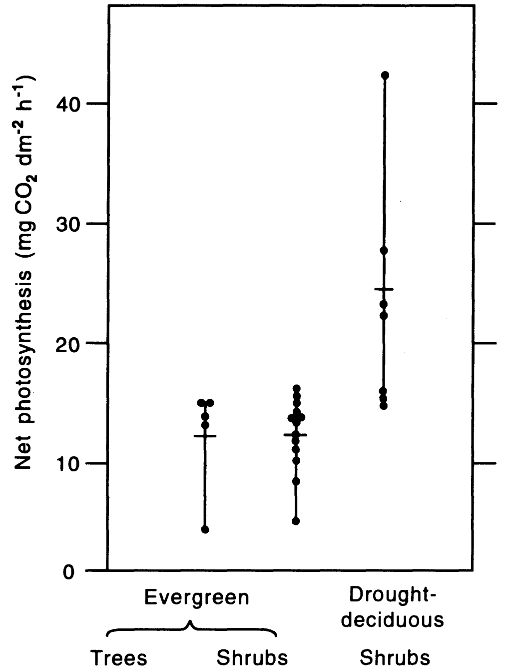


Fig. 141. Photosynthetic capacity of evergreen and deciduous woody plants in the wet-winter regions. (Mooney 1981). The measurements were taken during the rainy season on a large number of plants in Chile, California and in the Mediterranean region. The capacity of photosynthesis was determined via the CO$_2$ uptake per leaf surface area (dm^2)

Table 37. Production characteristics of some mediterranean plant formations (Mooney 1981)

Plant formation	Evergreen oak forests	Evergreen scrub formations		Subligeneous scrub
		Chaparral	Garrigue	Phrygana
Locality	France (Le Ròquet)	California	France (St. Gély)	Greece
Stand age (years)	150	17–18	17	–
Height (m)	11	≈ 1.5	0.8	<1
Leaf area index ($m^2 m^{-2}$)	4.5	2.5	–	1.7
Phytomass (t ha^{-1})				
Shoots	269	20.39	23.5	10.95
Wood	262	16.72	19.5	8.86
Leaves	7	3.67	4.0	2.09
Roots	≈ 50	≈ 12.23	–	16.18
Total	319	32.62	–	27.13
Allocation (%)				
Wood (in % of	97.4	82.0	83.0	80.9
Leaves shoot mass)	2.6	18.0	17.0	19.1
Shoots (in % of	84.3	62.5	–	40.4
Roots phytomass)	15.7	37.5	–	59.6
Root/shoot ratio	0.19	0.60	–	1.48
Primary production (t $ha^{-1} a^{-1}$)				
Above-ground increment	2.6	1.3	1.1	2.02
Litter fall	3.9	2.82	2.3	2.1
Shoot, total	6.5	4.12	3.4	4.12
Litter reserves (t ha^{-1})	11.4	13.59	–	–
Litter decomposition (t $ha^{-1} a^{-1}$)	3	2.64	–	–

range within which the production of most (not excessively disrupted) mediterranean plant formations falls. Thus, as mentioned at the beginning, because of the unfavourable environmental conditions the PP_N in the Mediterranean-Type Subtropics is actually rather low compared with other ecozones (Fig. 142). The energy fixed in the annual primary production (i.e. net photosynthetic efficiency) comprises only 0.17–0.3% of the annual incident solar energy.

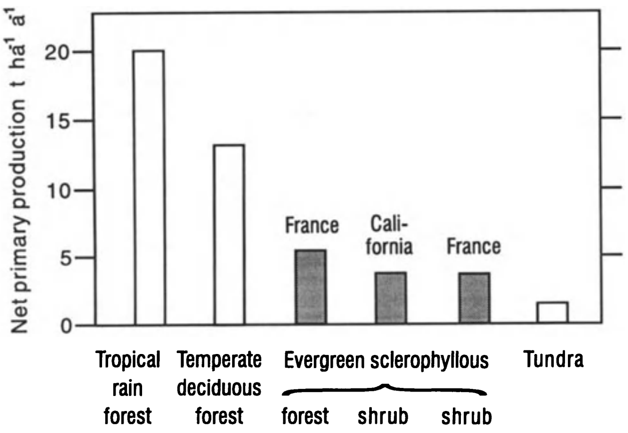


Fig. 142. Net above-ground primary production of mediterranean sclerophyllous formations compared with some other plant formations. (Mooney 1981). The sclerophyllous forests produce less than the deciduous forests of the less sunny Humid Mid-Latitudes; together with the boreal coniferous forests they "bring up the rear" of the zonal forest formations

Stand Reserves and Turnovers

These will be presented here, using as an example a holly (evergreen) oak forest (*Quercus ilex*) at Le Rouquet and two garrigue stands (*Quercus coccifera*) at Saint Gély du Fesc and at Grabels, all located in southern France (Lossaint 1973; Lossaint and Rapp 1971; Cole and Rapp 1981; Rapp and Lossaint 1981). The two garrigues are degradation stages of holly oak forests. The holly oak forest at Le Rouquet and the garrigue at Saint Gély are identical with the oak forest (Column 1) and the garrigue (Column 3) listed in the above-mentioned Table 37.

Holly Oak Forest at Le Rouquet. The material reserves and turnovers are depicted in the same way as in the diagram already used for the Boreal Zone and the Humid Mid-Latitudes (Fig. 143; cf. also Figs. 63 and 85, and the explanations given there). It should be noted that here only the results from the study of a single stand were evaluated, whereas in the other cases, the averages of 3 and 14 stands respectively were analyzed. Therefore, any generalizations are even less reliable. With the appropriate reservations, therefore, the following features were found to be characteristic of Mediterranean sclerophyllous forests.

The primary production is approximately as high as in the boreal coniferous forests, and thus significantly lower than in the temperate deciduous forests. On the other hand, only moderate differences exist with regard to size and allocation (root/shoot) of the phytomasses between these three forest formations.

The proportion of leaf mass to phytomass in the tree layer is 1:38, i.e. as low as in the temperate deciduous forests (1:37), and it is thus also significantly

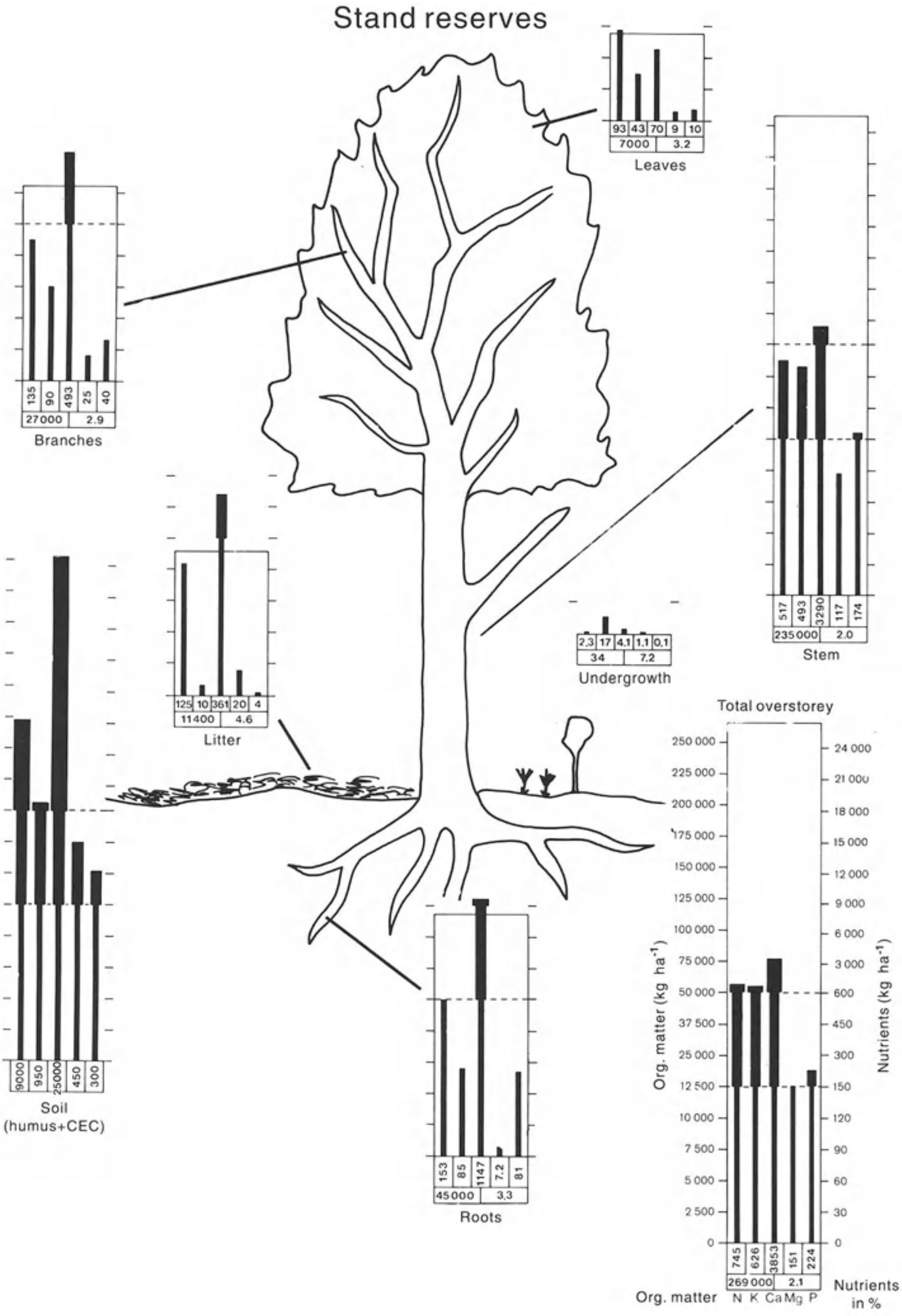

Stand reserves
93 43 70 9 10
7000 3.2
Leaves
135 90 493 25 40
27000 2.9
Branches
517 493 3290 117 174
235000 2.0
Stem
125 10 361 20 4
11400 4.6
Litter
2.3 17 4.1 1.1 0.1
34 7.2
Undergrowth
9000 950 25000 450 300
Soil
(humus+CEC)
153 85 1147 7.2 81
45000 3.3
Roots
Total overstorey
250 000
225 000
200 000
175 000
150 000
125 000
100 000
75 000
50 000
37 500
25 000
12 500
10 000
7 500
5 000
2 500
0
24 000
21 000
18 000
15 000
12 000
9 000
6 000
3 000
600
450
300
150
120
90
60
30
0
Org. matter (kg ha⁻¹)
Nutrients (kg ha⁻¹)
745 626 3853 151 224
269 000 2.1
Org. matter
N K Ca Mg P
Nutrients
in %

Fig. 143a

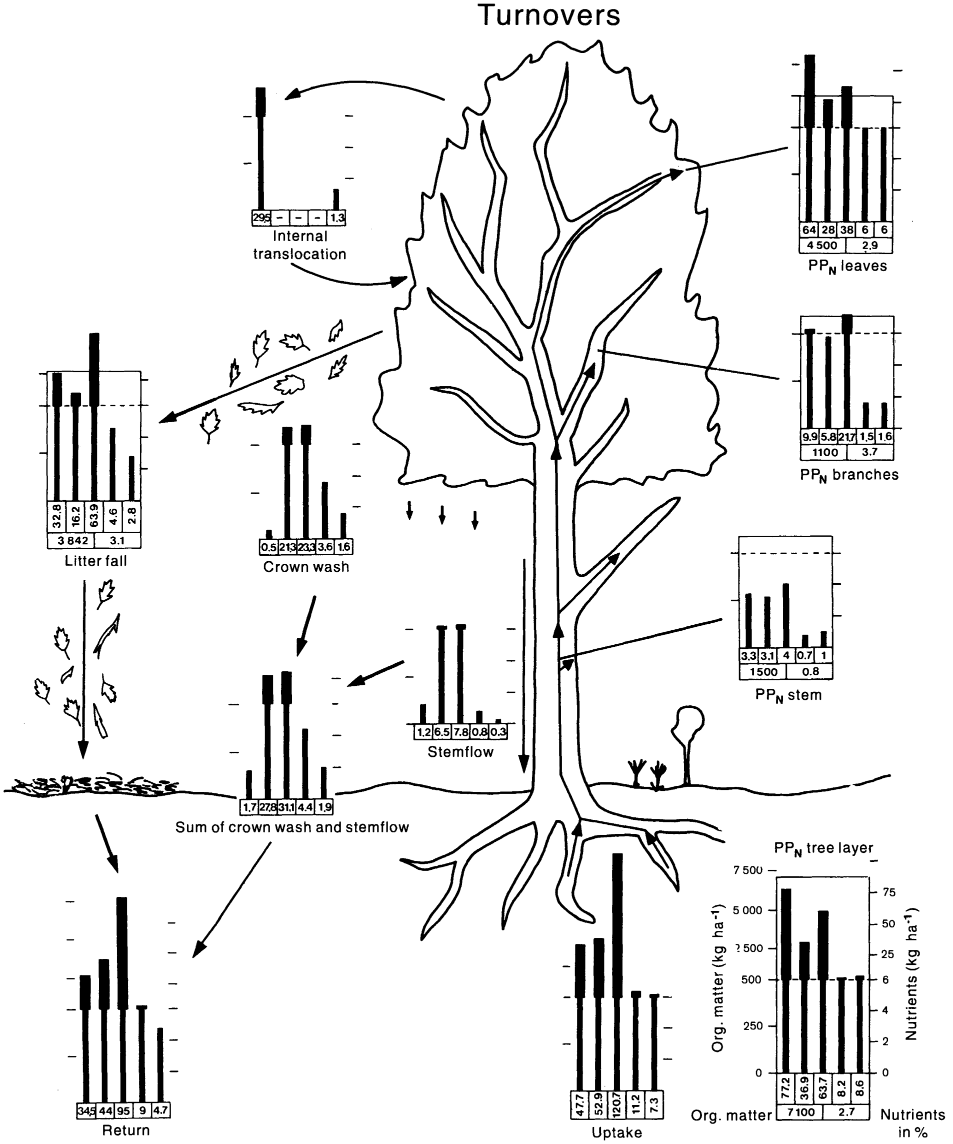


Fig. 143a, b. Matter reserves and turnovers in mediterranean sclerophyllous forests, using the example of a holly oak (*Quercus ilex*) forest in Le Rouquet, southern France (calculated and compiled using data from Lossaint 1973; Cole and Rapp 1981). For explanations, see text; cf. also Figs. 63 and 85. The organic substances are denoted by boxes and the minerals (N, K, Ca, Mg and P, always in that sequence *from left to right*) are denoted by individual columns. **a** Stand reserves. From 150 kg (minerals) and 12 500 kg (organic substances) onwards, the scales are reduced to 1:5, and from 600 kg and 50 000 kg respectively onwards they are reduced to 1:100. **b** Turnovers. From 6 kg (minerals) and 500 kg (organic substances) onwards, the scales are reduced to 1:12.5

lower than in the boreal coniferous forests (1 : 6 = average of the data from 3 forests in Alaska). The mineral contents of the scleromorphic leaves are, at 3.2%, slightly lower than those of the mesomorphic leaves (4.3%), but still significantly higher than those of the needles in boreal forests (1.7%).

Of the 7 t of leaf mass, 4.5 t were formed in the year when the study was conducted and 2.5 t were formed in the previous year. From this we can calculate a mean lifetime of only 1.6 years for the leaves. Therefore, even in the case of the "evergreen" sclerophyllous plants, a large portion of the annual PP_N must go into the production of leaves. According to the figures submitted, this proportion, at more than 60% (of the above-ground production of the trees), is still higher than in the temperate deciduous forests (40%); the amount of mineral nutrients required for this purpose is 73% of the total requirement for the primary production in the tree layer (compared with 80% in deciduous trees).

As a consequence, the nutrient requirement per production unit is similar to that in the temperate deciduous forests and thus significantly higher than in the evergreen coniferous forests. For example, the evergreen oaks produce nearly 92 kg of organic above-ground substance per 1 kg N (the deciduous trees produce 103 kg and the boreal coniferous trees 257 kg).

Only barely two-thirds of the nitrogen required for the above-ground primary production of the trees must be taken from the soil, the rest is supplied by resorption from the older leaves before abscission occurs. As a result, relative to the amount of N taken up from the soil, the production per 1 kg N (nitrogen use efficiency) increases to just under 150 kg organic substance, again similar to deciduous trees. In absolute terms, however, the mineral requirement of the sclerophyllous forests is lower than that of the temperate deciduous forests, to the same extent that the overall PP_N is also lower.

Despite the high annual supply of litter, the layer of litter is thinner than in the boreal coniferous forests and in the temperate deciduous forest. The reason for this is that the litter breaks down more rapidly. In the case of the holly oak forest considered here, this happens within the space of only 3 years. However, this is not representative of mediterranean plant stands (see below). Because of the high percentage of leaves in the litter, the mineral content of the litter is disproportionately high compared with the other organic stand reserves.

Two Garrigue Stands. One of these, near Saint Gély du Fesc, is 17 years old and 0.8 m tall, and the other, at Grabels is 30 years old and 1.1 m tall. The principal mineral reserves and turnovers in the garrigue at Saint Gély are compiled in Fig. 144.

It is striking that in the two garrigues about 50 kg ha^{-1} of minerals are supplied each year by rain. Of these minerals, sodium (20.9 kg) and magnesium (1.6 kg) come from seawater and the remainder come from atmospheric pollutants caused by industrial emissions and by dust naturally swirled up into the atmosphere (14.6 kg N, 2.9 kg K, 10.4 kg Ca and 0.9 kg P).

When a comparison is made with the holly oak forest dealt with above, it is seen in both garrigue stands that, as the forest is destroyed, not only is there

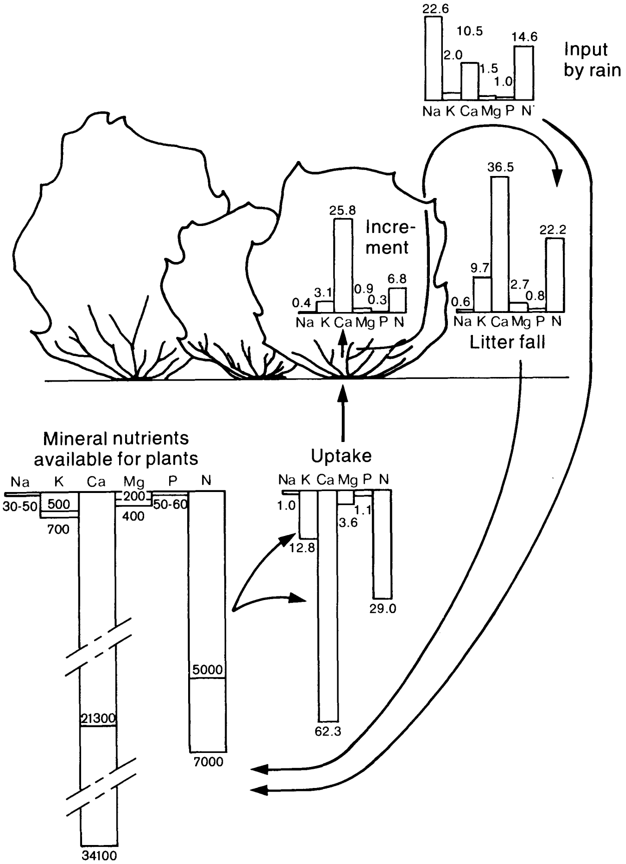


Fig. 144. Nutrient stores and cycling of nutrients in a garrigue near Saint Gély du Fesc (in kg ha^{-1} and kg ha^{-1} a^{-1}). (Rapp and Lossaint 1981). *Available* refers to exhangeable nutrients within the upper 30 cm of the soil; the ranges of the values measured at the various sites are given for each of these nutrients

a considerable loss of phytomass, but also the productivity declines: the above-ground phytomass accounts for only 23.5 and 37.1 t ha^{-1} respectively, and the annual above-ground net primary production is only 3.4 and 3.7 t ha^{-1} respectively. If any further degradation of the garrigue occurs, and possibly a sward of *Brachypodium ramosum* forms, then both values drop even lower. In a highly degraded garrigue, a phytomass of 3–6 t ha^{-1} and a PP$_N$ of 0.6–1.2 t ha^{-1} a^{-1} (in each case above ground only) were measured, and the above-ground phytomass of a sward of Brachypodium was measured as less than 1 t ha^{-1} (Le Houérou 1981, p. 515f).

Garrigue stands which have renewed themselves by coppice growth following (repeated) burning are characterized by a relatively high root mass; in the Saint Gély example, this root mass is twice as high, at 46 t ha^{-1}, as the above-ground

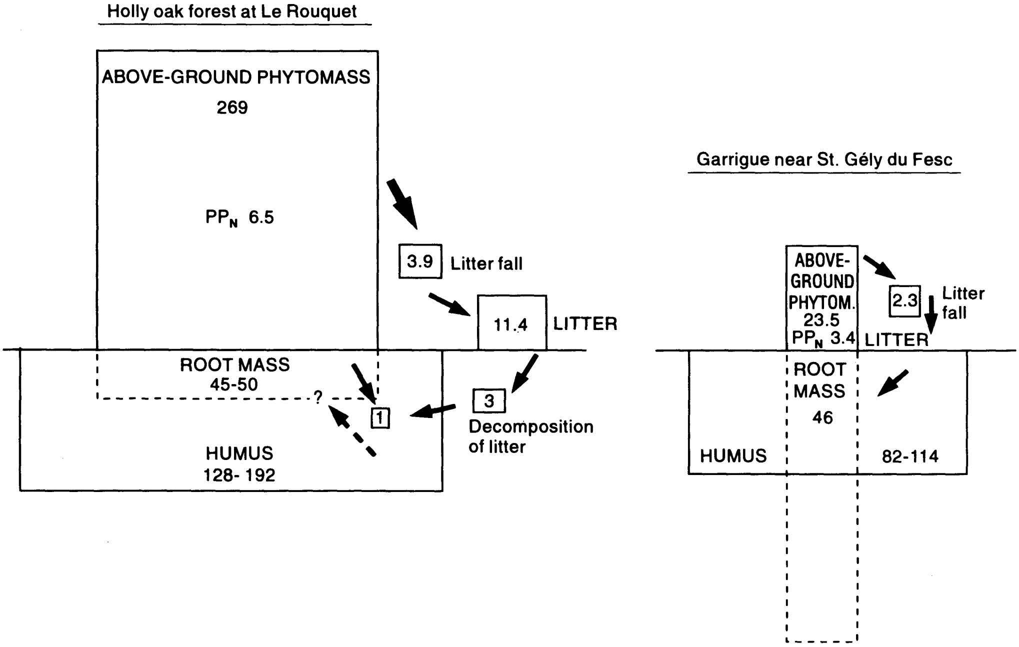


Fig. 145. Organic stand reserves ($\mathrm{t\,ha^{-1}}$) and turnovers ($\mathrm{t\,ha^{-1}a^{-1}}$) in a holly oak forest (*Quercus ilex*) and in a garrigue (*Quercus coccifera*), both in sourthern France. (Lossaint 1973; Rapp and Lossaint 1981)

biomass. Again, the dead organic matter in the soil is more than twice as much, namely 82–114 $\mathrm{t\,ha^{-1}}$. For comparison: beneath the holly oak forest it is between 128 and 192 $\mathrm{t\,ha^{-1}}$ (Fig. 145).

The high humus content, in particular that of the garrigue, is surprising at first sight because the annual input of dead organic substances is low. The explanation is that the decomposition of the waste material is complicated by the conditions of long summer dryness and by the large amount of sclerenchymatic tissue in the litter (unfavourable C/N ratio). The layer of litter can therefore amount to 50 $\mathrm{t\,ha^{-1}}$ (Fig. 15). As far as mineral recycling is concerned, the biological decomposition is frequently less important than fire.

Fire

Reports about extensive bush/forest fires, which sometimes even threaten human lives and settlements in the Mediterranean region or in California, are almost regular events every summer. Le Houérou 1981 estimates that in the Mediterranean region alone, areas totalling 2000 $\mathrm{km^2}$ are burned each year.

In this latter region, it has been a traditional practice for several thousand years, that the farmers and cattle breeders deliberately set fires in order to obtain arable land and grazing land or to keep pastures free of tree and shrub growth. The influence exerted on the vegetation and flora is therefore considerable: almost all the original forests have been destroyed and only relatively fire-resistant species of shrubs (pyrophytes) have been able to survive. Depending on the frequency with which the burning is carried out, or the time which has elapsed since the last fire, different, but in each case characteristic, succession plant communities (seral stages) become established (cf. Fig. 137).

The mediterranean vegetation is particularly endangered by fire because heat and drought coincide seasonally and ethereal oils and resins make the sclerophyllous foliage and wood highly inflammable. The bush and forest fires are therefore much more disastrous than the often only fleeting grass fires in the dry-winter tropical savannas: they often destroy all the above-ground plant mass.

On the other hand, the extreme susceptibility to fire goes together with a high capacity for regeneration (resilience). Many of the species of trees and shrubs are able to form renewal shoots (suckers) from roots or other subterranean organs, and the growth increment rates attain peak values in the first years following the fire (Fig. 146), a fact which is surely connected with the better supply of nutrients and water.

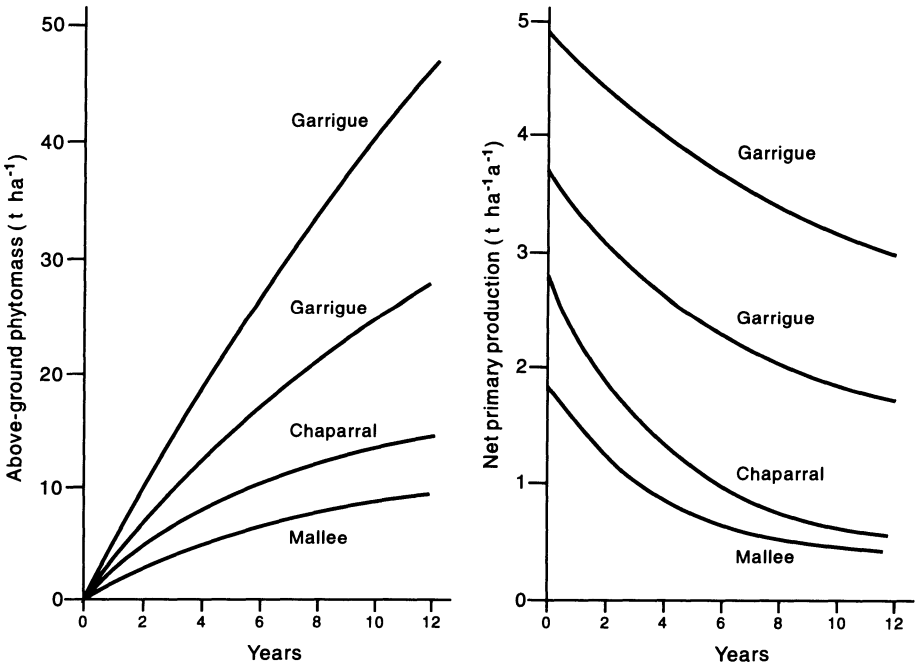


Fig. 146. Above-ground phytomass accumulation and current annual growth increment in some sclerophyllous shrub formations during the first 12 years following a fire. (Specht 1981). The two garrigues are located near Montpellier in southern France, the chaparral near San Dimas in California and the mallee near Keith in southern Australia. As the fire-initiated succession continues, the annual stand increments diminish and thus the further increases in the phytomasses slow down

Because of their large capacity for recovery, the mediterranean shrub formations soon regain their initial status, and even repeated fires, as long as they do not follow too soon one after the other, do not necessarily result in permanent, but usually only transitory changes (Fig. 137); the lack of fire is more likely to bring about a floristic-physiognomical change (e.g. caused by the emergence of certain fire-sensitive tree species and the suppression of all those species which produce seeds only in post-fire years, i.e. which require fire for reproduction purposes). Many of the shrub formations therefore have the rank of *fire climax communities*.

One advantage of the burning is that the mineral nutrients bound in the organic substance are released earlier than would be the case if solely biological-chemical decomposition were to take place (see above). However, when all aspects are considered, the disadvantages outweigh the advantages. For example, as the biomass declines, so also the productivity per unit area declines, and soil erosion and leaching can occur on the burnt areas, and downstream of such areas unwanted sedimentation can build up. Therefore, as in the wet-dry tropics, in many areas people are trying to counter these dangers by *controlled burning*, for example of the undergrowth in forests at the start of the dry season, and thus at the same time to obtain the positive mineralizing effect of the burning. Fire protection is particularly important in the pine forests, which are most exposed to the risk of fire.

3.6.6 Land Use

The proximity of the sea and the long duration (high percentage of possible amount) of sunshine in the summer months are advantageous for economic activity. The location is favourable for shipping and fishing, and the combination of coast and sunshine benefits the tourist trade. In Europe, millions of people in search of rest and recreation travel during the summer months to the Mediterranean region, because it is the closest tourist region to them where they can find (guaranteed) sunny, warm to hot weather conditions. A large number of tourists also visit the Mediterranean region in the spring and autumn because of the mild, warm temperatures compared with those in their home countries, and because of the evergreen (especially in the spring), richly blooming plant life.

In other respects, the *natural potential* – partly as a result of the anthropogenic destruction of landscape – must be classified as rather low. The unfavourable factors include:

- The summer drought; no matter how attractive this may be to the tourists, it is extremely disadvantageous for agriculture because the optimum temperature and sunshine conditions during the summer cannot be utilized by rain-fed cultivation.
- The decline of river discharge during the summer dry season (many rivers dry up completly); this limits the establishment of irrigated crops, and oc-

casionally makes it difficult to supply drinking water and process water to settlements and industries.

- The generally accidented relief; this is disadvantageous not only for crop growing but also for land-based transportation.
- The generally high rate of soil erosion in mountain lands and the uncontrolled aggradations in the lowlands; both processes endanger agricultural areas, and at least reduce their natural yield potential.
- The shrub formations arising after human interventions (clearing, burning, grazing) are of extremely low value as far as silviculture and grazing are concerned.

Despite these problems, all five regions of the Mediterranean-Type Subtropics have acquired considerable agricultural and economic importance, although in different ways and with different results. Therefore, although this ecozone is (rather) physiogeographically homogeneous, it differes widely in economic and cultural geographical terms. Striking similarities across all five regions are found only in the area of agricultural land use, where dependence on the climate has forced people throughout the ecozone to adapt in similar ways. The similarities include:

Cultivation. Rain-fed agriculture is limited to the winter season; agriculture is possible in the summer season or on a year-round basis only when irrigation is used. In keeping with the relatively cool winter temperatures, it is mainly crops of the temperate climatic zones, e.g. wheat, barley and potatoes, which are cultivated in the rain-fed fields. In the Mediterranean region the winter cereal crop is sown in September and frequently harvested as early as in May. The cultivation of onions, lettuce, cauliflower, artichokes, eggplants etc. is also widespread.

Irrigated crops are common (Fig. 147). They permit not only the warm and sunny summer days to be utilized, for example to cultivate the above types of vegetables, but also field crops such as rice and cotton, which need heat and are sensitive to cold, can be grown.

There are a number of *special crop cultivations* which are extremely typical of this ecozone, such as vineyards, olive groves which are traditional in the Mediterranean region, orchards (peaches, apricots, citrus fruits) as well as almond and fig tree plantations. Grape vines and wine production are nowadays characteristic of all the regions of the Mediterranean-Type Subtropics. While citrus plantings, since they come from humid subtropical climates (of Southeast Asia), must be irrigated during the dry season, the other species of fruit tree can survive the summers by drawing on the reserves of water which build up in the soil during the rainy season. Only the occasional supplementary application of water is necessary. While the areas of arable land are concentrated in the coastal lowlands, the orchards are planted up the slopes of the hills and mountains.

Pastoralism. In the Mediterranean region *sheep and goat herding* is an important activity. Fodder crops are for the most part not cultivated. Grazing still takes place to a great extent on natural pastures, i.e. on the rocky heathland and in the

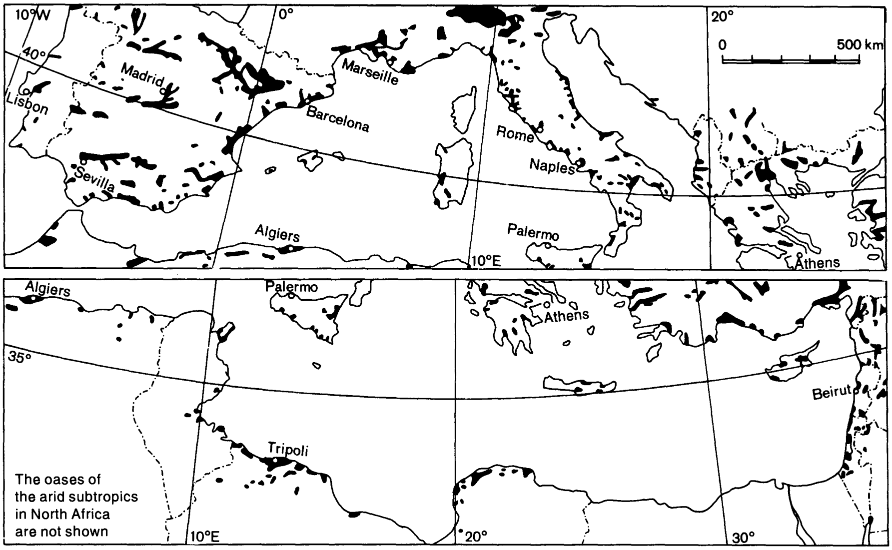


Fig. 147. The irrigated areas in the Mediterranean region. (Rother 1984)

garrigue and maquis stands which – as described above – cover considerable areas; on the other hand, they are a very scanty source of fodder (it is not possible to keep cattle here). Le Houérou (1981, p. 499) writes that in the Mediterranean region almost all the area not used for crop cultivation serves as pasture land (commercially productive forests are very rare). During the dry season the harvested fields are additionally available as grazing areas. As a result, the percentage of temporarily grazed areas increases to about 75% of the total area, namely at least 1.2 million km^2.

Cattle herding is made difficult by the long summer drought. Traditionally, *transhumance* was the answer to this (Fig. 148): in the summer, the herders moved with their cattle into the high mountain lands where better grazing was available. In the process, they covered considerable distances across the regions. Overall, transhumance is on the decline, but it is still common in parts of Greece, Italy, the former Yugoslavia, Spain and North Africa.

The *amount of fodder available to the grazing animals* depends in the first approximation on the primary production, and secondly on the percentage of utilizable plant material. Both are to a certain extent dependent on precipitation (Fig. 149). The annual fodder production can be considerably increased by measures such as applying phosphorus fertilizer and sowing legumes (e.g. *Vicia sativa* or *Lathyrus sativus*); in southern Australia the fodder yields obtained in this way were between 3.5 and 5.5 t ha^{-1} (Biddiscombe 1987). This is already in the lower yield range of temperate pasture land.

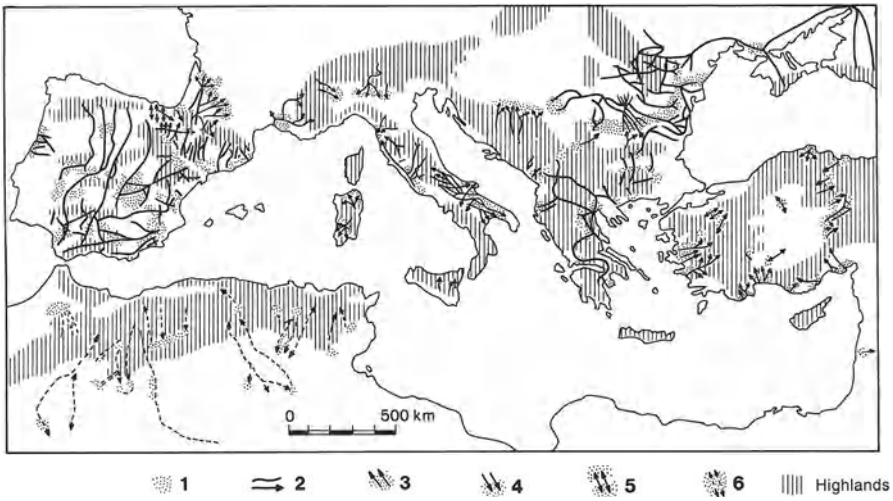


Fig. 148. The distribution of transhumance in the Mediterranean region. (Grigg 1974) *1* Winter pastures; *2* transhumance routes; *3* direction of migrations; *4* herds belong to lowland-dwellers: transhumance routes lead into highlands (normal transhumance); *5* herds belong to the highland-dwellers: transhumance routes lead to lowlands (inverse transhumance); *6* undifferentiated; *7* herds belong to the inhabitants of settlements at medium elevation: transhumance routes lead to the highlands as well as to the lowlands (double transhumance)

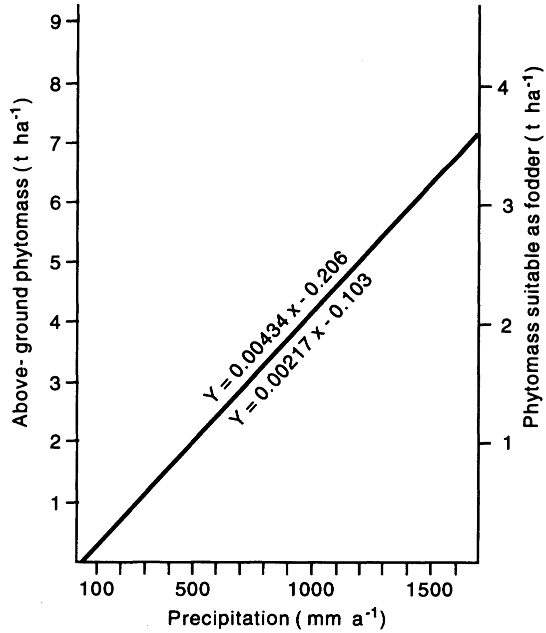
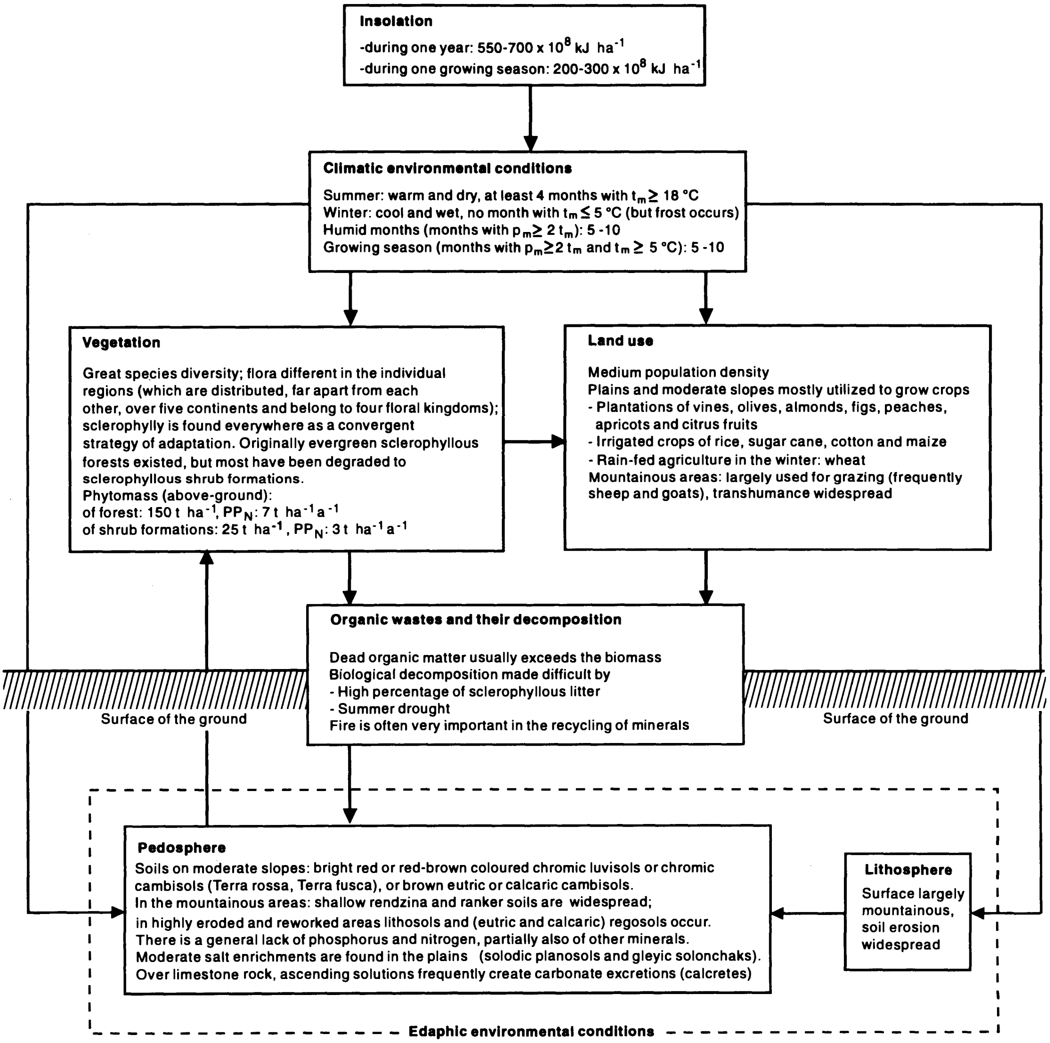


Fig. 149. The above-ground primary production, and the amount of this which is suitable as fodder for grazing animals in mediterranean sclerophyllous shrub formations, as a function of annual precipitation. (Le Houérou 1981)

Resumé. The wet-winter climate is propitious for a large number of temperate and subtropical types of crop, and there are some seasonal advantages – for example several types of vegetable can be harvested and marketed in the winter and spring; taken together, these factors create good opportunities for the mediterranean regions to export to the densely populated Humid Mid-Latitudes which adjoin immediately polewards. In fact, since they are integrated into the system of world trade, the Mediterranean-Type Subtropics can be classified as supplementary farming areas serving the Humid Mid-Latitudes.



Insolation

-during one year: 550-700 x 10^8 kJ ha^{-1}

-during one growing season: 200-300 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Summer: warm and dry, at least 4 months with $t_m \geq$ 18 °C
Winter: cool and wet, no month with $t_m \leq$ 5 °C (but frost occurs)
Humid months (months with $p_m \geq 2\,t_m$): 5 -10
Growing season (months with $p_m \geq 2\,t_m$ and $t_m \geq$ 5 °C): 5 -10

Vegetation

Great species diversity; flora different in the individual regions (which are distributed, far apart from each other, over five continents and belong to four floral kingdoms); sclerophylly is found everywhere as a convergent strategy of adaptation. Originally evergreen sclerophyllous forests existed, but most have been degraded to sclerophyllous shrub formations.
Phytomass (above-ground):
of forest: 150 t ha^{-1}, PP_N: 7 t $ha^{-1}a^{-1}$
of shrub formations: 25 t ha^{-1}, PP_N: 3 t $ha^{-1}a^{-1}$

Land use

Medium population density
Plains and moderate slopes mostly utilized to grow crops
- Plantations of vines, olives, almonds, figs, peaches, apricots and citrus fruits
- Irrigated crops of rice, sugar cane, cotton and maize
- Rain-fed agriculture in the winter: wheat

Mountainous areas: largely used for grazing (frequently sheep and goats), transhumance widespread

Organic wastes and their decomposition

Dead organic matter usually exceeds the biomass
Biological decomposition made difficult by
- High percentage of sclerophyllous litter
- Summer drought

Fire is often very important in the recycling of minerals

Pedosphere

Soils on moderate slopes: bright red or red-brown coloured chromic luvisols or chromic cambisols (Terra rossa, Terra fusca), or brown eutric or calcaric cambisols.
In the mountainous areas: shallow rendzina and ranker soils are widespread;
in highly eroded and reworked areas lithosols and (eutric and calcaric) regosols occur.
There is a general lack of phosphorus and nitrogen, partially also of other minerals.
Moderate salt enrichments are found in the plains (solodic planosols and gleyic solonchaks).
Over limestone rock, ascending solutions frequently create carbonate excretions (calcretes)

Lithosphere

Surface largely mountainous, soil erosion widespread

Fig. 150. Synoptic diagram of the Mediterranean-Type Subtropics

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3.7 Seasonal Tropics

3.7.1 Distribution

The Seasonal Tropics extend on both hemispheres between the equatorial rain forests and the Tropical/Subtropical Arid Lands. Depending on their outer demarcation, they account for 15 to just less than 25% of the total surface of the earth (see below). The vegetation in this gigantic region is very non-uniform in floristic and physiognomical terms, on the microscale as well as on the macroscale. This makes it difficult to determine the outer limits of the region and also, since the differences are frequently anthropogenically caused, it is difficult to make ecologically meaningful subdivisions within the region.

Despite the rich variety of vegetation, the term *savanna* (occasionally preceded by a specific epithet, e.g. tree savanna, shrub savanna or grass savanna) has gained general acceptance as a summary designation for almost all the plant stands in the Seasonal Tropics, and the collocation *savanna zone* (or savanna belt, savanna climate) has come to be used as an approximate synonym for this entire ecozone.

Despite the criticism levelled at this linguistic usage from some quarters, it will nevertheless be retained in this book – not only because this is nowadays the common practice, but also because, from an ecozonal standpoint, many of the noticeable differences in vegetation are insignificant: as a rule these differences are based on edaphic peculiarities, or they are the result of degradations or secondary successions caused by fire or utilization factors and are of no ecological importance. In addition, despite all the variety, there is one vegetation characteristic, namely the grass (under)growth, which is common to all the plant formations of the Seasonal Tropics.

While the equatorward boundary between the savanna zone and the tropical rain forest could be relatively clearly defined, at least in the early stages (namely where the *leaves are not shed* during the dry season, or only a few species of trees are without leaves for a very short time), opinions vary widely on where to draw the boundary in the other direction, namely away from the equator. Sometimes thermal and sometimes hygric criteria are adduced as arguments. The map showing the distribution of the Seasonal Tropics (Fig. 151) attempts to do justice to these controversies by using different types of shading.

If it is assumed that the savanna zone is characterized primarily by:

1. strict seasonality, as a rule a summer rainy season and a winter dry season and
2. a vegetation consisting of a continuous grass (forb) layer as well as (frequently) a discontinuous tree or shrub layer,

then it is found that this also applies to some regions (see broken-line shading on the distribution map) which extend polewards beyond the *tropical boundary* (no matter how it is defined; cf. for example Manshard 1968; Lauer 1975). Thus the savannas in the sense used above must be regarded as *tropical and near-tropical (subtropical) ecosystems* (Tothill and Mott 1985; Walker 1987).

Nevertheless, some vegetation/climatic-based classifications of the earth or larger parts of it (e.g. Troll and Paffen 1964) show the “savannas” ending abruptly at the tropical boundary. The continuation of the savannas on the other side of the boundary are then called (subtropical) steppes. This is usually done while pointing out that freezing temperatures may occur once the tropical boundary is crossed, which allegedly are never recorded on this side of the boundary; the distribution of many “tropical” plant species (also crop species) is said to end at the *frost boundary* and thus a clear difference exists between the flora and agriculture on both sides of the boundary (e.g. von Wissmann 1948).

This probably applies to the *humid* transitional regions (i.e. from the Humid Tropics to the Humid Subtropics) e.g. with respect to some perennial crops such as cacao and oil palms, but it does not hold true for the transitional zone from the Seasonal Tropics to the seasonal subtropics. Here, the possible periods of frost occur during the dry season when the fields have long been harvested and the vegetation has entered a dormancy phase. The woody shoots of the, by then mostly defoliated, trees and shrubs, as well as the below-ground parts and the seeds of the dried-out grasses and herbaceous plants are all resistant to (slight) frosts. Therefore, frost damage does not usually occur. It is also not correct to

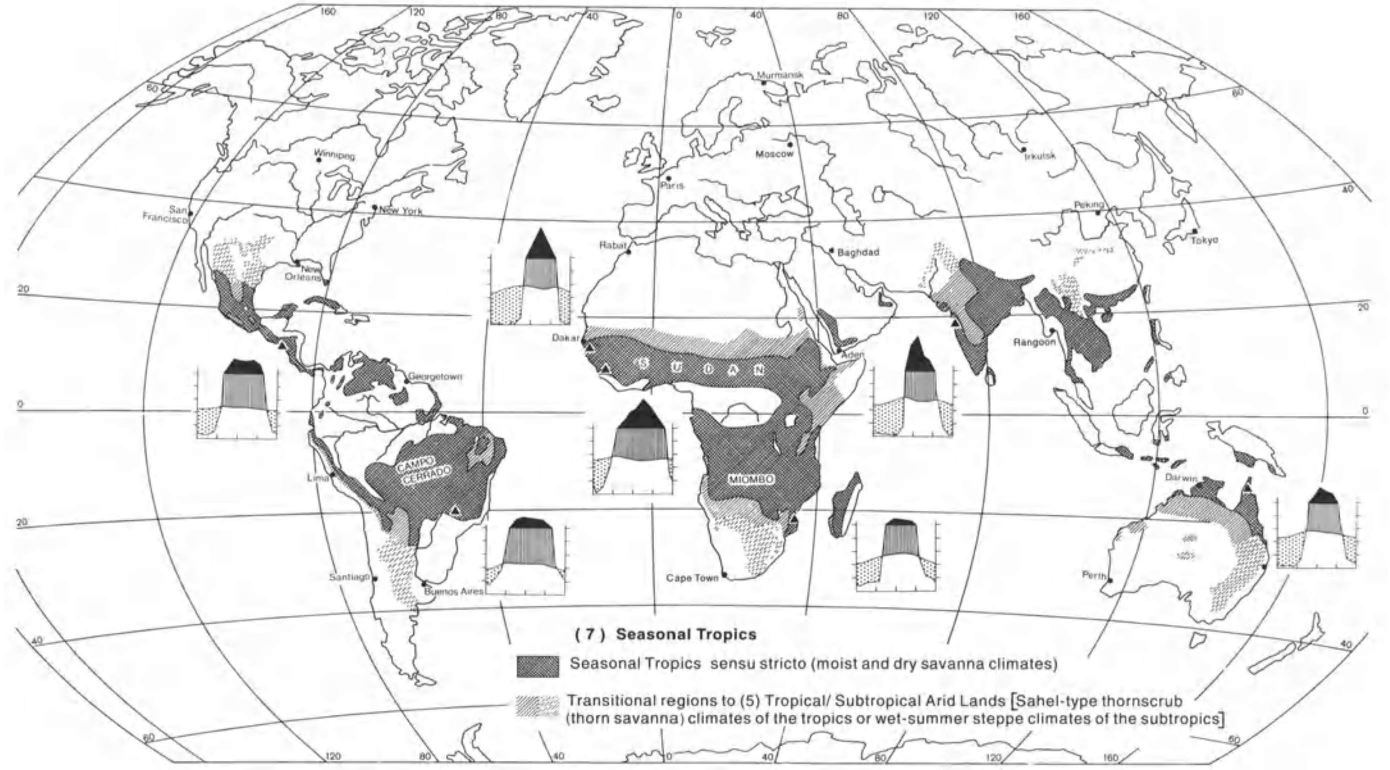


Fig. 151. Seasonal Tropics. In both hemispheres, their range extends as far as the equatorial rain forests. In the direction away from the equator they can be delimited, from the Tropical/Subtropical Arid Lands, on the basis of various hygric and thermal criteria. The map shows the possible boundaries that can be drawn

assume that freezing temperatures are completely missing in the tropics. In fact, they occur in many tropical regions, not only within the narrow altitude ranges of the mountains, but also over large areas, namely wherever plateau regions are situated at an altitude of several hundred to more than 1000 m above sea level (for example in east and south-central Africa).

The winter (dry season) temperature differences on both sides of the tropical boundary are therefore not particularly important, and even less so the summertime (rainy season) differences in temperature: in the subtropics most (at least 4) of the rainy months have mean temperatures of $\geq 18\,^{\circ}\mathrm{C}$ and are thus similarly warm. The amount of insolation is also just as high as in the wet/dry tropics.

Correspondingly – assuming similar hygric conditions – many identical plant and animal species are found on both sides of the tropical boundary, and the same annual "tropical" crops may be cultivated. The only restrictions on growth are generated by the more or less long dry periods, and they are the same whether on the equatorward or poleward side of the "frost boundary".

In fact, the general environmental conditions do not undergo any fundamental change (in a poleward direction) until the point is reached where either (1) winter rain takes the place of summer rain, and the growing season thus falls within the cool season of the year (Mediterranean-Type Subtropics); (2) precipitation falls all the year round (Humid Subtropics), (3) the precipitation decreases to such an extent that a dry season prevails all the year round or almost all the year round (Tropical/Subtropical Arid Lands); or (4) the summer warming remains relatively insignificant (less than 4 months with $tm \geq 18\,^{\circ}\mathrm{C}$) and the period of winter dormancy is brought on not by drought, but by low temperatures (Humid Mid-Latitudes).

Thus the savanna-steppe-problem does not arise if *hygric demarcation criteria* (instead of thermal criteria) are emphasized and used to exclude all those regions in which a lack of water has a limiting effect all the year round, i.e. even during the rainy season. In the tropics, this is usually the case at annual precipitations from < 500 mm onwards, and in the terrain it can be recognized from the fact that xeromorphic growth forms predominate in the natural vegetation and rain-fed agriculture is no longer possible or is highly risky (for further criteria see Chap. 3.4.1). In this type of evaluation, not only the tropical Sahel-type thornscrubs (thorn savannas) but also the subtropical "steppes", with – at most – 5 rainy summer months are moved to the Tropical/Subtropical Arid Lands. The more humid of the subtropical steppes receiving summer rains during more than 5 months can be assigned without any major restriction to the Humid Subtropics because they receive moderate amounts of precipitation even during the "dry seasons" (see Chap. 3.8.1).

This hygric demarcation will be adopted in the present book, i.e. *only moist and dry savannas will be included in the Seasonal Tropics (sensu stricto)*. As a result, the outer (poleward) boundary of the Seasonal Tropics is shifted clearly into the thermally delimited region of the tropics, however not for thermal but for hygric reasons. The entire area is then calculated to cover 24.4 million km^2, which is equal to 16.3% of the mainland area of the earth. The term savanna (region) is used as a synonym for the Seasonal Tropics which are delimited in this way, and it thus does not include the *thorn savanna regions*, a term sometimes applied to the Sahel-type thornscrubs.

Major *large-scale differences* in the savanna regions are linked with differences in humidity resulting from annual rainy periods of unequal length. Using this criterion, the *dry savannas* mentioned above, which have about 4.5–7 rainy months can be differentiated from the *moist savannas*, which have approximately 7–9.5 rainy months (Troll and Paffen 1964). Numerically similar ranges are obtained when the duration of the "humid" season is used instead of the rainy months. Deviations due to different methods of determining humidity (e.g. Penmann 1948; Lauer 1952; Thornthwaite and Mather 1955; Walter 1955; Jätzold 1984) are all so slight that they are insignificant as far as the subdivision into ecozones is concerned.

3.7.2 Climate

Within the planetary air pressure belts at sea level, the Seasonal Tropics occupy a position between the equatorial low pressure trough and the subtropical/tropical belts of high pressure cells (see Chap. 3.5.2). The pressure gradient towards the equator corresponds to an easterly air flow extending high into the atmosphere (= upper or primary trades, zone of equatorial easterlies), which is deflected towards the equator in the lower strata of the troposphere, due to the effect of ground friction, and thus becomes the *NE trade wind* in the Northern Hemisphere and the *SE trade wind* in the Southern Hemisphere. This deflection increases, the closer one gets to the equator, because of the decline in the Coriolis force. The equatorial low pressure trough and the subtropical/tropical high pressure belts are fairly stable pressure phenomena and as a result the trade winds which they generate are very constant.

In the course of the year *these pressure structures and wind systems are displaced as the height of the sun changes* and the high pressure belt is broken up in the respective summer hemisphere by continental thermal lows (Fig. 152). As the high pressure cells advance towards the equatorial low pressure trough in the winter, the pressure gradient increases and with it also the strength of the trade winds. As a result, the descending movement of the air in the trade winds, which always tends to be present because of the *divergence in area* (the zones on either sides of the meridians become larger towards the equator), is at the same time intensified. This results in an extraordinarily stable stratification of the air masses which, in a typical case, includes an inversion (trade wind inversion) at an altitude of several 100 metres (in the outer tropics) up to almost 2000 m (in the inner tropics). Convection clouds (cumulus clouds) may form up to but never beyond this trade wind inversion, i.e. they never extend high into the sky. Periods when strong trade winds are blowing are therefore periods low in or totally devoid of precipitation, i.e. *dry periods* (= trade wind-related dry periods in the months when the sun is at a low angle or during the "winter"). In the

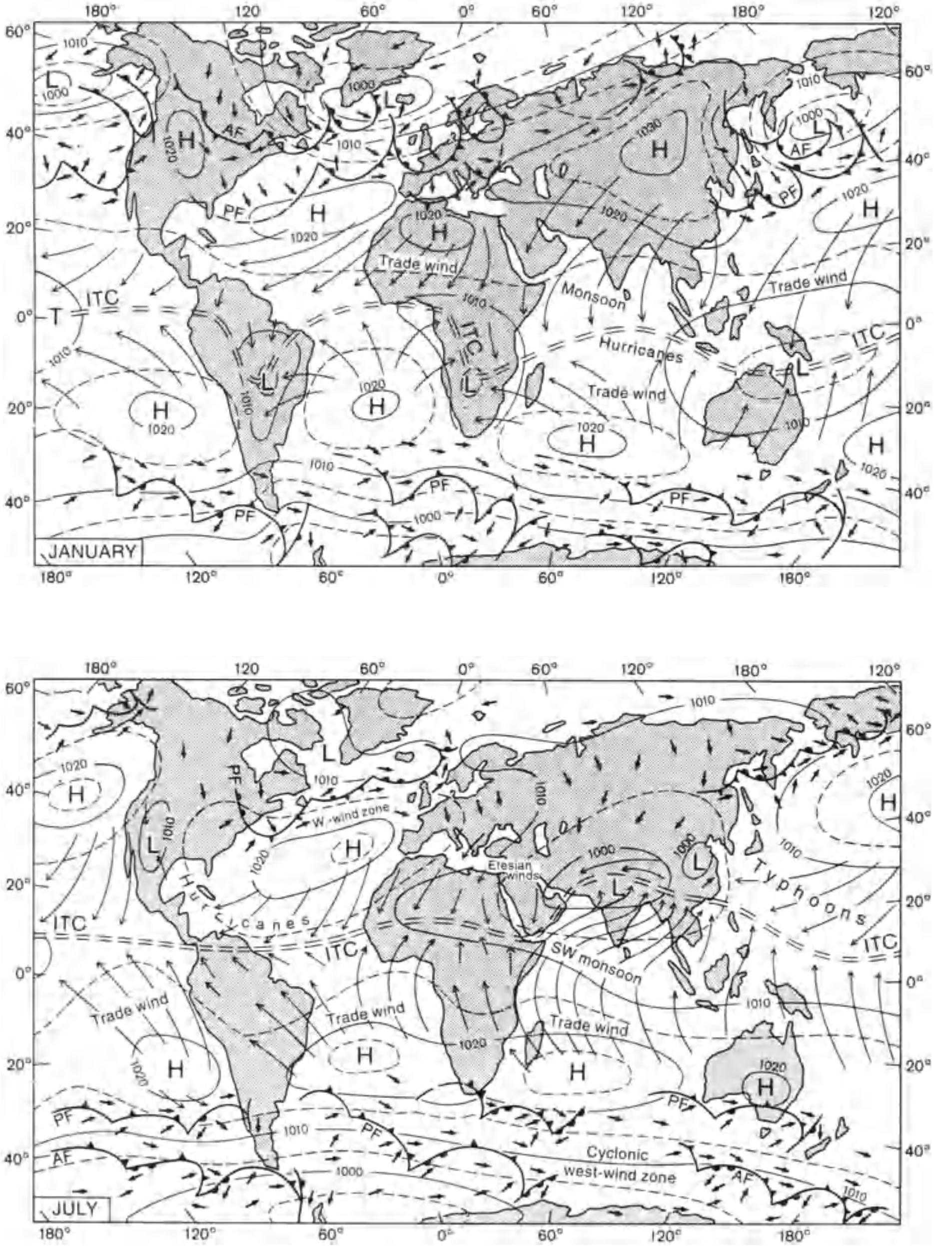


Fig. 152. Global atmospheric pressure and circulation pattern near sea level, in January and July. (Weischet 1983)

range of the Seasonal Tropics, these periods last by definition for at least 2.5 up to a maximum of 7.5 months (see Chap. 3.7.1).

Conditions deviate where the trade wind flows come into contact with mountains and are forced to ascend above the inversion. Copious year-round *orographic precipitation*, with pronounced maxima occurring in the winter months may be the result, e.g. in the Caribbean and on the eastern coasts of Brazil and Madagascar.

As the height of the sun increases during the summer months, the distance between the subtropical/tropical high pressure zones and the equatorial low pressure trough increases once more. In addition, in the area of the high pressure belt, thermal lows form above all the continents (the telluric influence causes the subtropical/tropical high pressure belt to break up into separate anticyclones with core regions over the oceans). As a result, the pressure gradient towards the equatorial low pressure trough decreases significantly, the trade winds die down and greatly modified circulation patterns can result over the continents. These include, in particular, high-reaching convective air movements which generate strong rain showers (zenithal rain during the period of the maximum declination of the sun, solstitial rain).

Near the equator, these precipitations are distributed between two maxima in the spring and in the autumn (*double rainy season*: e.g. in Ethiopia and in the Llanos of Venezuela), according to the two zenithal positions of the sun which occur a long time apart here. With increasing distance from the equator, the rain maxima come closer and closer together, as the time between the maximum declinations of the sun decreases, to form a twin-peaked and finally a *single rainy season* which alternates with a rainless dry season (single rainy season of the outer tropics). At the same time, the period of precipitation becomes shorter and less rain falls. During the rainy season of the moist savannas, which lasts 7–9.5 (9) months, approximately 1000–1500 mm of rain falls per annum, while barely 500 mm of precipitation occurs in the dry savannas at the edge of the Tropical/Subtropical Arid Lands, where the rainy season lasts only 4.5 (5) months. With decreasing precipitation, the variability increases: the percentage fluctuations in the annual amounts of precipitation are increased and the distribution of the rainfall over the rainy season becomes more irregular.

The circulation conditions are slightly different in the Southern and Southeast Asian region of the Seasonal Tropics. In this region, the SE trade winds, which spill over everywhere into the Northern Hemisphere during the northern summer months, are led particularly far northwards under the effect of a powerful thermal low (monsoonal low) which forms during the summer over southern Asia and whose air pressure is much lower than that of the equatorial low pressure trough; and as a result of Coriolis force they assume a south westerly flow. This air flow, which is then referred to as a *SW monsoon*, no longer possesses the stable stratification which it had during its initial trade wind phase, because as it flows towards the pole it is subjected to the effect of surface convergence. The resulting convective processes (instead of descending processes, as in the case of the trade winds blowing towards the equator) as well as orographically induced vertical movements lead to rainfall in India and in the Indo-Chinese peninsula (monsoon rains). Monsoonal phenomena also occur in West Africa and northern Australia.

When they are strongly formed, the trade winds in the Northern and Southern Hemispheres can meet together in a narrow zone 100 to 200 km wide, which is known as the *intertropical convergence* (ITC). This convergence of the air flows results in an upward movement in the air masses, which breaks through the trade wind inversion. As a result, a high-reaching thermal convection can become established, leading to the creation of cumulonimbus clouds rising to a height of up to 16 km, with thunderstorms and strong rain showers. The ITCZ (intertropical convergence zone) is thus a region of increased thermal convection in which more precipitation falls than is otherwise the case in the runout zones of the trade winds.

The ITCZ is not a stable element in tropical air circulation. It can suddenly change its position by several hundred kilometres, disappear completely for a certain period of time, and reappear at a completely different location. Because of these rapid swings, the related weather phenomena, cloud formation and precipitation are spread over a relatively wide zone.

This wider zone changes position as the mean position of the ITCZ changes periodically over the course of the year with the declination of the sun. Above the oceans the mean change in latitudes is small; it varies between 0° in January and 8–10° North in July. Much larger changes occur over the continents; from the observed annual precipitation cycles it is assumed (Weischet 1983, p. 133) that in the Southern Hemisphere they extend in January to about 15° and in the Northern Hemisphere in July they extend as far as or – in the case of India – even beyond the Tropic of Cancer. During the equinoxes, the ITC is largely lacking.

The *radiation budget* is positive all year round, although it is significantly weaker in the winter season. The lengths of the days deviate in the course of the year by no more than 1 h from the 12-h day. This fact and the rain distribution pattern lead to a moderately balanced temperature cycle with mean seasonal temperature differences which are lower than the daily differences: at sea level, all the monthly averages are above +18 °C; the maximum temperatures are attained immediately before the start of the rainy seasons; a somewhat stronger drop in temperature occurs at the start of the dry season. Frost does not occur, at least not during the rainy season, but freezing temperatures may occasionally be recorded in higher-lying plateau regions during the dry seasons. Frost-sensitive species of crop which have a perennial growth cycle can therefore not be cultivated everywhere. Restrictions also apply to crops from higher latitudes which possess long-day photoperiodism.

3.7.3 Relief and Hydrology

Strong *chemical weathering processes* (probably in most cases hydrolysis), which occur in the usually permanently wet subsoil all year round (i.e. also during the dry season), are characteristic of this ecozone [this is an important distinction between it and the semi-arid (Sahel-type) thorn savanna regions which follow towards the pole; see Chap. 3.5.3]. As a result, a deep clay-rich soil develops and the underlying rock is decomposed to a considerable depth, i.e. a relatively thick zone of rotted rock (saprolite) forms. However, the depth of this saprolite and of the overlying regolith (disintegrated loose rock waste and soil) is usually less than in tropical rain forest regions (see Chap. 3.9.3).

In many savanna regions a (quartz) stone-rich layer, known as a *stone line*, forms at various depths (in large exposures, e.g. road cuttings, it looks like an irregular undulating band). Various interpretations of the origin have been given (cf. Spőnemann 1974). For example, it has been claimed that the line is made up of residual weathering products formed from quartz bands in the parent rock. The activity of termites is used to explain the fact that the stone lines do not occur at the surface but regularly at a depth of about 50–200 cm: the fine-grained material transported upwards by these animals is said to cause the stone lines to appear at a relatively lower depth. At the same time, this explains why the stone lines are found particularly frequently in the tropics – i.e. in the distribution ranges of the termites. However, this theory is contradicted by the fact that stone lines also occur elsewhere.

The so-called *laterites* (ironstone) are another phenomenon which is widespread in the wet/dry tropical soils. Laterites are irreversibly hardened soil horizons consisting of an iron-rich substrate (ferricretes) which appear at the surface (duricrusts): most of them probably only came to the surface after the topsoil had been eroded away (see Chap. 3.9.4). They are capable of "cementing" sheet erosion surfaces and may form piedmont steps or step-like structures on mountain slopes (Fig. 153).

According to Büdel (1981), the Seasonal Tropics constitute a "zone of excessive planation"; according to Hagedorn and Poser (1974), they form, together with the thorn scrub regions, areas of predominant planation or – with respect to the moist savanna regions – areas of further planation.

The process of planation is brought about by morphologically extremely effective *sheet wash* (sheet erosion) during the rainy seasons (this is an important difference compared with the rain forest regions which follow towards the equator; see Chap. 3.9.3), with which the linear-fluvial processes hardly keep pace. As a consequence, only washed basin floors (Spülmulden) and shallow saucer-shaped valleys (Flachmuldentäler) with broad and flat river beds are formed by fluvial action.

The great effectiveness of overland flows in the wet-dry tropics is correlated with the *high intensity of the precipitation*. For example, values of more than 25 mm h^{-1}, which can be attained for several minutes at a stretch, are not infrequent. Ahnert (1982), describing the situation at Machakos in southern Kenya, states that on average per annum 12 × daily precipitation totals of at least 25 mm, 4 × totals of at least 40 mm and 1 × total of at least 65 mm occur, and that daily totals in excess of 90 mm are exceeded once every 5 years (Fig. 154). Astonishingly, the mean amount of precipitation per rainy day is higher in dry regions

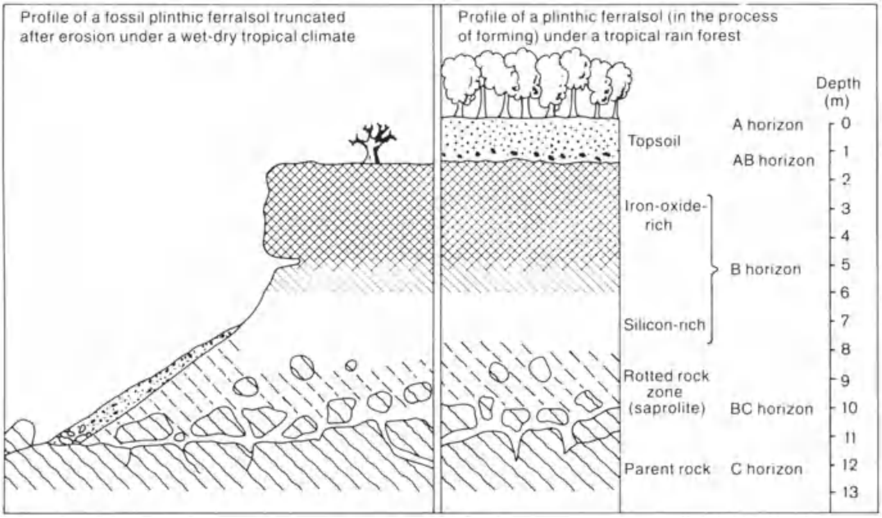


Fig. 153. After erosion of the topsoil and repeated drying out of the B horizon, the iron-oxide-rich layer (plinthite) becomes irreversibly hardened into ironstone (laterite). (After Thomas 1974). The hard laterite crusts can "cement" sheet erosion surfaces and form step-like structures on mountain slopes

at 12 mm (given an annual amount of precipitation of 500 mm) than in wetter regions, where it attains only 9.3 mm (given 1000 mm of annual precipitation).

On days of heavy rainfall, the *permeability* of most soils is not sufficient to absorb the precipitation at the rate at which it is supplied, i.e. even on gently inclined slopes some of the rainwater runs off (storm runoff). Ahnert (1982) quotes a daily precipitation value of 25 mm (given about 2 h of rain) as the probable threshold value at which surface runoff occurs.

As a general rule, the permeability of the soil, and thus the *rate of infiltration of rainwater*, declines with the duration of a precipitation event, i.e. an increasingly large amount of the rain reaching the ground flows off at the surface. The reason for the deterioration in permeability is the progressive silting up of soil pores, animal burrows and interstices (puddle erosion). Swelling processes may also be involved in the sealing of the soil (e.g. in smectite-rich soils). The danger of silting up is particularly great when the surface of the soil is insufficiently protected by vegetation cover and some of the rain drops can therefore impact with full force on the soil, thereby dislodging particles of the soil (splash erosion). This is what happens in the wet-dry tropics generally at the start of the rainy seasons (it never happens in tropical rain forests).

Figure 155 illustrates the *change in the rate of infiltration with the duration of a precipitation event.* Surface runoff (by sheet flows) occurs only when the intensity of the precipitation exceeds the infiltration rate. The precipitation intensity at which this happens, and after what duration of rainfall, depends essentially

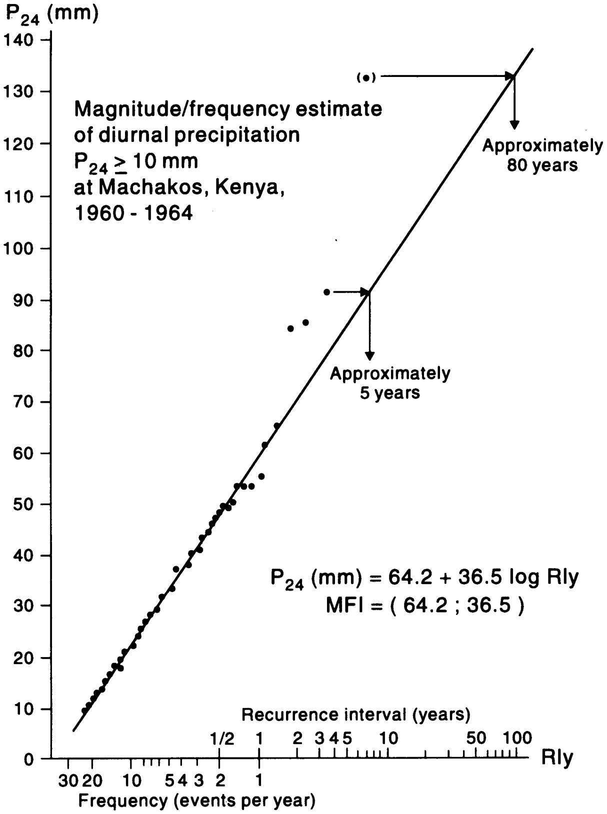


Fig. 154. Magnitude/frequency analysis of precipitation at Machakos, Kenya. (Ahnert 1987). See text for explanations (on the method, see Chap. 2.3)

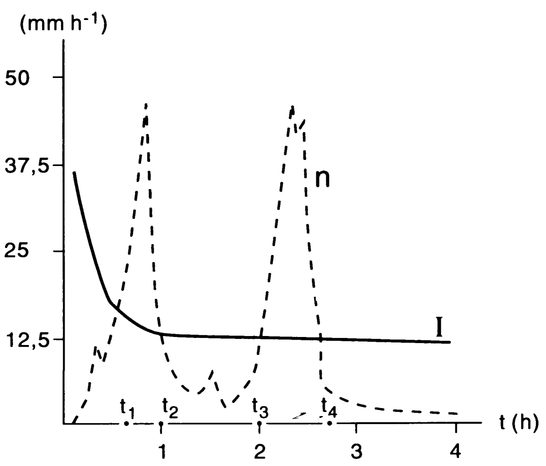


Fig. 155. The change in the infiltration rate with the duration of rainfall and the build-up of surface runoff in the period from t_1 to t_2 and t_3 to t_4. (Herrmann 1977). The surface runoff commences as soon as the intensity of the precipitation (*n, broken line*) is greater than the rate of infiltration (*I*)

on the type of soil and vegetation. Table 38 gives, by way of example, the *minimum infiltration* rates for certain soils, i.e. the values which the infiltration rates asymptotically approach after long periods of rainfall. According to Table 38, the rates in the Seasonal Tropics finally decline to approximately 1 to 7 mm h^{-1}; in the semi-arid thorn savannas and steppes they remain above that value, apart from clay-rich pans (e.g. Jackson 1958). The explanation for this difference is that most soils in the arid lands tend to be more coarsely textured.

The correlations between sheet flows, type of soil, and vegetation cover explain why the *percentage of surface runoff (on slopes) in the total runoff* can vary widely in the tropics, both according to season and region. In general, it increases – as less protection is provided by the vegetation – from rain forest (here the surface runoff is very low) via moist and dry savannas through to thorn savannas; the groundwater runoff decreases in the same sequence, and in the thorn savanna it is practically zero. On the other hand, the annual amounts of precipitation rise in the direction of the rain forest and, parallel to this, the number of rainy days increases on which, for example, the above-mentioned limit of 25 mm of precipitation is exceeded. The largest amount of surface runoff in absolute terms therefore probably occurs in the wetter regions of the dry savanna.

The *erosive effect of sheet flows* depends fundamentally not only on slope angle and flow resistance (again affected, for example, by the density of the vegetation), but also on whether transportable substrate material is present. In the Seasonal Tropics (and certainly in the Humid Tropics) such a substrate exists in the form of a thick layer of fine-grained, clay-rich unconsolidated material formed by intensive chemical weathering processes (whereas in thorn savannas the often similarly thick layers of unconsolidated material are coarser due to prevailing mechanical fragmentation). The largest amounts of sheet erosion are therefore likely to occur in the dry savannas, and the next largest amounts in the thorn savannas; moderate surface erosion takes place in the moist savannas, while minimal erosion is measured under rain forest.

Depending on the angle of slope, surface roughness, and other factors, the slope wash takes the form of *sheet erosion* or of *rill erosion* and over a long period of time results in a relatively constant lowering and planation of the surface.

Table 38. Minimum infiltration rates for some types of soil and rocks. (Musgrave 1955, taken from Herrmann 1977)

Soils	Infiltration rate (mm h^{-1})
1. Sand, loess, silt, well-structured	11–7
2. Shallow loess, sandy loam	7–4
3. Clayey loam, shallow sandy loam, soils with a low content of organic components soils with a large clay fraction	4–1
4. Easily swelling soils (alkali soils)	< 1

However, if a sufficiently deep layer of coherent fine material exists, the erosion may start out linearly by forming deep gullies (gully erosion) which extend down to the more resistant rock disintegration zone. As erosion continues, the walls of the gullies move gradually further apart, and flat and increasingly wide gully floors are formed at surface of the saprolite. Finally, if these processes continue, the last ridges of soil between the gully walls are eliminated and the erosion process is then concluded for a long period of time (at least until a new cover of weathered material forms) (Fig. 156). This type of rather abrupt downcutting of a slope occurs frequently in those areas where the natural vegetation cover has been destroyed, for example by overgrazing, and trampling by animals has resulted in compaction of the soil. The first signs of erosive action are usually linked with such compacted areas (trample paths).

In areas where severe sheet erosion occurs, large amounts of material are washed into the rivers. The energy needed to *transport this load* is correspondingly high and thus the rate of downcutting is low. The typical valley form is therefore that of the *broad, shallow valley* (saucer-shaped valley) whose flanks are so gently sloping that they can scarcely be perceived with the naked eye (Fig. 157). The watershed areas between these valleys are frequently lowered by sheet erosion to form broad *interfluves*, so that overall an almost flat land surface (gently undulating plain) forms. This is referred to as a *peneplain* (*pediplain*) and the morphodynamic processes which form it are collectively known as pediplana-

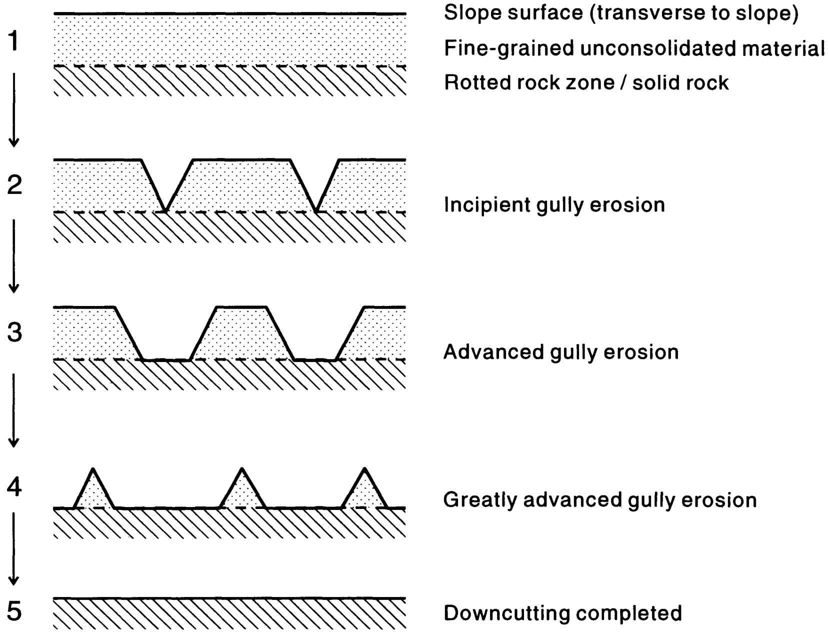


Fig. 156. Downcutting of a surface by progressive gully erosion

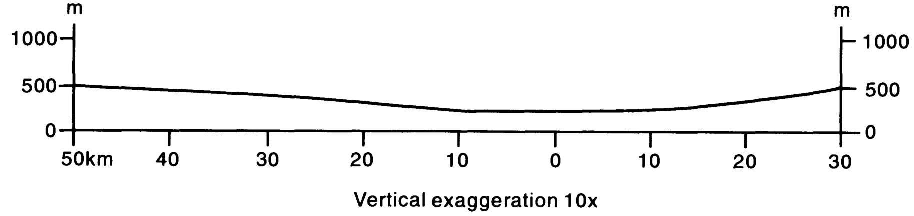


Fig. 157. Transverse profile through the broad shallow (saucer-shaped) valley (Flachmuldental) of the Ruvuma (Tanzania) 200 km upstream from its mouth. (Louis 1967). The valley slopes rise just a few metres, or at most tens of metres, vertically over horizontal distances of several kilometres

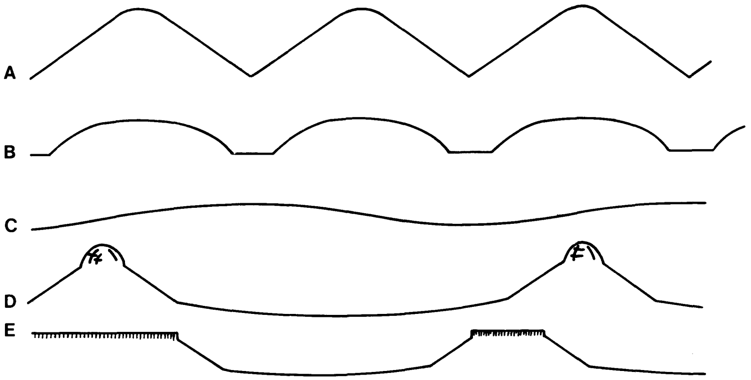


Fig. 158. Typical relief forms found in the tropics. (Young 1976). *A* Rain forest zone: ridge and ravine relief; *B* rain forest zone: "demi-orange" relief; *C* savanna zone: peneplain; *D* inselbergs with pediments; *E* plateau and mesa relief

tion – in contrast to the basically similar process of pedimentation, which gives rise to the formation of gently sloping rock surfaces (pediments) at the foot of mountains/mountainous areas (see Chap. 3.4.3). Peneplains easily overcome differences in rock types and may extend over many hundreds of kilometres (Fig. 158). They constitute the most obvious landform in the Seasonal Tropics.

The *beds of the rivers* flowing in the shallow saucer-shaped valleys, or the beds of the channels below pediments, are broad and flat (the maximum depth of the channels is just enough to cope with floodwater levels) and they carry very few pebbles; instead, their transported load consists mainly of sandy material (their own or colluvial sediments). The river beds are frequently relocated during (episodic/periodic) floodwater events. Normally, there are no river terraces (in contrast to the Humid Mid-Latitudes) because the old valley floors are always eaten up by the subsequent process of pedimentation (Rohdenburg 1971, p. 90).

In contrast to the thorn and dry savanna regions, the *width-to-depth ratio of the rivers* in the moist savanna regions is smaller and the relocation of the river beds occurs less frequently; here – and particularly in the permanently Humid

Tropics – the rivers may have cut their way down to the level of the solid rock. Further downcutting takes place only slowly thereafter because the rivers do not carry any coarse pebble material, and the chemical weathering of the river bed is much less significant than that occuring under a continuous soil cover.

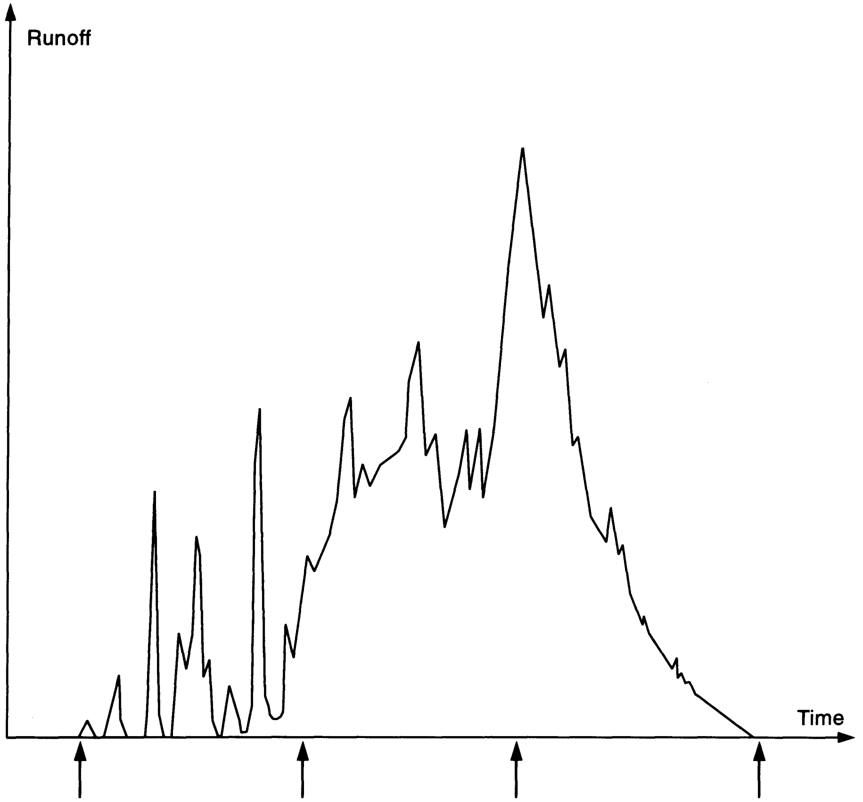
The *runoff* in the rivers is usually restricted to certain periods of the year. After that, the river beds dry up. The runoff in the rivers is linked not only with the seasonal alternation of rainy and dry periods, but also with the more or less high percentage of *surface* runoff (sheet flow) within their catchment areas. As already described, this surface runoff is particularly high at the start of the rainy season when little or no soil protection from vegetation is available. The runoff of the rivers around this time is correspondingly marked by extreme fluctuation. As the vegetation develops during the rainy season, the amount of rainwater percolating into the soil increases, i.e. the amount of water held in the soil gradually builds up until it finally exceeds the field capacity. At that point, groundwater runoff commences and supplies the rivers with a much more constant flow of water than the surface runoff; the discharge of the rivers as a result becomes more balanced. The runoff may still continue to increase after rainfall and it may temporarily decline following dry periods within the rainy seasons, but these fluctuations tend to be moderate; the extreme peaks and minimum values of the early period are lacking. At the end of the rainy season the runoff declines steadily to zero (Fig. 159).

A seasonal runoff which is largely independent of individual precipitation events, because it is fed by groundwater, is referred to as a *periodic runoff* in contrast to an *episodic runoff*, which is fed by surface inflows following heavy precipitation and lasts for only a short period of time. While – as already described – it is characteristic of the Seasonal Tropics that the runoff is episodic at the start of the rainy season and later is periodic in character, in the arid lands (ecozones 4 and 5) it is always only episodic.

Many peneplains contain small, shallow depressions no more than a few km^2 in size. They are roundish to elongated in outline and frequently form the beginnings or widenings of shallow valleys; during the rainy season they tend to become waterlogged or flooded for some time. The soils they contain are either vertisols or in the moist savannas, gleysols; the vegetation is (mostly) treeless grassland. In Zambia such depressions are known as *Dambos* and in Tanzania as *Mbugas* (Ackermann 1936; Louis 1964; Mäckel 1974).

Many of the vertisols exhibit at their surface a microrelief known as *gilgai* consisting of a series of gentle undulations. This surface feature is caused by *hydroturbation* (see Chap. 3.7.4).

The peneplains may be broken up by individual mountains or multipeaked groups of mountains (ranges) which bear the name *inselbergs or inselberg groups*, because of their isolated position in the middle of broad plains. They rise up rather abruptly and steeply (usually with a significant knickpoint) from the surrounding land, even though at the foot they are usually encircled by (compared with the rest of the terrain) slightly steeper sloping pediments (Fig. 158). "As a rule, the smaller the mountain, ... the greater the mean slope angle. Thus, inselbergs



Start of the rainy season: at first episodic runoff with extreme peaks and interruptions in the runoff

Soil water content charged up to field capacity; from this point onwards: periodic runoff, fluctuations in runoff less distinct than before

End of the rainy season: from this point on, continuous decline in runoff

End of the periodic runoff: from this point on, the river bed remains dry until the start of the next rainy season

Fig. 159. Hydrograph of the annual runoff cycle of rivers in the Seasonal Tropics

behave in the opposite way to fluvially sculpted surfaces in the middle latitudes, where the mean slope angle usually increases with the relief" (Ahnert 1982, p. 44).

The *slopes of the inselbergs* may be formed in the solid rock. But in most cases they are covered by layers of soil which may contain large amounts of fine-sized material (clay), as well as sometimes large quantities of rock debris. The rock slopes are attacked by salt cracking and hydrolysis. As a result, block disintegration occurs (due to weathering along joints in the rock), as well as superficial scaling (flaking) and exfoliation (spalling) along pressure-relief jointing.

The unconsolidated material, from block to grus size, in which hydrolysis is the predominant effective type of weathering, is subjected to sheet erosion, and in the case of large groups of inselbergs fluvial erosion forming V-shaped valleys occurs.

Compared with the unconsolidated material on the slopes of the inselbergs, the *hill wash sediments (possibly fluvial sediments) at the foot of the inselbergs* are characterized by a higher and certainly longer-lasting moisture content. In most cases, at some depth, the moisture probably lasts all year round instead of – as on the slopes – only during the rainy season, provided that the sediments are thick enough. Given the generally high temperatures, these conditions go together with significantly higher rates of (in this case mainly chemical) weathering. The material formed in the process is finer-grained than the material formed further up the slope (mainly by mechanical weathering) and it may be relatively rapidly transported away by the sheet flood (the amount of water increases as it comes down the slope and is therefore greater at the foot of the inselberg than on its slopes). The gradient and sharp knickpoint at the base are thus retained and the backwearing of the inselberg slope corresponds to a widening of the pediments.

There are various, not always clear causes or complexes of causes behind the *formation of inselbergs*. For example, inselbergs may be due to tectonically formed elevations (which were perhaps cut up into individual mountains by fluvial action); or they may be harder sections of rock surrounded by less resistant rock (monadnocks); the relatively large distance from the drainage *network* (interfluvial location, outliers) may be another cause; or they may be primarily traced back to hummocks (Grundhöcker) formed as a result of selective weathering processes at the surface of the bedrock, at varying depths below the original surface of the soil (Rohdenburg 1971). The latter interpretation is based on the observation that, once rock has been exposed, it is less severely affected by weathering and erosion than bedrock which is covered by soil. Therefore, as soon as they come to the surface (due to a general lowering of the area around them), hummocks which were originally formed by weathering beneath the soil in the bedrock must gain relatively in height (rise up) as the general erosion of the surface continues. The formation of the knickpoint between mountain slope and adjoining pediment, which is characteristic for inselbergs, might be explained by the unequal (divergent) rates of weathering and erosion, as described above, which apply to these two sites in the wet/dry tropics.

In many cases, the peneplains have formed at different levels and are separated by highly eroded and dissected *step surfaces*. The higher planation surfaces are classified as older formations and the lower surfaces are associated with recent crustal movements (uplifts). The step surfaces are usually cut up into *zonal inselbergs* and thus recede.

3.7.4 Soils

Tropical Soils – General

The boundary between the Tropical/Subtropical Arid Lands and the Seasonal Tropics is formed by the equatorward limit of the pedocals (for the poleward limit of the pedocals, see Chap. 3.4.4): above precipitation totals of 500–600 mm per annum, leaching processes again predominate over accumulation processes and thus soils in the *pedalfer* group predominate, i.e. most soils (on freely draining sites) exhibit an acid reaction, that is to say they are low in exchangeable nutrient ions; free carbonates and salts are lacking; illuvial clay accumulation in the subsoil is widespread.

Compared with the pedalfers of the higher latitudes, those in the tropics exhibit some peculiar features in the mineral structures of their clay fractions. Most important, under the humid-hot climatic conditions, mainly *two-layered (1:1) clay minerals* (mostly kaolinite, but also halloysite) are formed instead of three-layered (2:1) minerals (e.g. illite) which predominate in temperate-humid climates[25]. Secondly, the extent of *oxide formation* (free, finely distributed oxides and hydroxides of Fe, Al and Mn = sesquioxides) is much higher in the tropics. It generally increases with the intensity and duration of the humid-hot conditions and reaches its peak when the silicon released by the weathering is removed (desilication). When the iron (which is contained in many rock minerals) is oxidized, not only yellow-brown goethite, which predominates in cooler climates, is formed, but also red *hematite*. This is what causes the widespread red coloration of tropical/subtropical soils. Thirdly, due to extremely intensive chemical weathering processes, most tropical soils contain only small amounts of weatherable silicates, or none at all, in their fine earth fractions. Mineral nutrients are resupplied essentially through the decomposition of organic wastes in the soil, i.e. nutrient reserves are concentrated in the topsoil.

The composition of the clay fraction is of great importance for the fertility of the soil: 1:1 clay minerals and sesquioxides are extremely *weakly sorptive*, 2:1 minerals have higher, in many cases much higher exchange capacities. Therefore, data on the clay *content* are by themselves not a measure of the quality of a soil as a site for plant growth; the experience which we have gained in the mid-latitudes (e.g. a loamy soil is regarded as more fertile than a sandy soil) cannot easily be transferred to the tropics: tropical clays almost always have low to very low contents of nutrients available to plants.

Soils with clay fractions consisting largely or exclusively of weakly sorptive kaolinites and sesquioxides [CEC $< 24\,\mathrm{cmol(+)\,kg^{-1}}$ clay, at pH 7] are grouped together as *LAC (= Low Activity Clay) soils* (the others are then referred to

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[25] In contrast to the illitic clay minerals, which are formed chiefly through conversion (as transformation products) from phyllosilicates (mostly mica), kaolinitic clay minerals are synthesized from weathering solutions.

as HAC soils = High Activity Clay soils). The LAC soils include all the important zonal soils of the humid tropics, i.e. in particular the ferralsols, plinthosols, acrisols, alisols and lixisols; nitisols are a borderline case.

The *charge characteristics* of Low Activity Clays (LACs) *are dependent on pH* to a significantly higher degree (expressed in percent) than High Activity Clays (HACs). At low pH values, the negative charge of kaolinitic clay minerals and thus their CEC are low but increase as the pH value rises; vice versa, with declining pH, the positive charge of sesquioxides rises and thus the AEC (anion exchange capacity) of the soil. The total of exchangeable ions, depending on the respective pH of the soil, is referred to as the effective or EC_{eff} (or CEC_{eff}), while the total determined at pH 7 is referred to as the potential or EC_{pot} (or CEC_{pot}). The difference between the two totals increases in direct proportion to the acidity of the soil (Fig. 160)[26]. *Some important consequences arise from the relationships between exchange capacity and pH:*

- As a result of the high AEC in sesquioxide-rich acid soils (in particular the acrisols and ferralsols), the absorption of the phosphorus which occurs in the soil as a PO_4 anion may be irreversible. This gives rise to the unfavourable *phosphorus fixation* (as Fe-phosphates and Al-phosphates) which is frequently described.
- As a result of the CEC, which declines with increasing soil acidity, an aluminium dynamic results, i.e. Al ions are released from the exchangers, and thus the Al concentration in the soil solution is increased to a level which is toxic for many species of plants (*aluminium toxicity*). Also, below pH 5, Al compounds are increasingly likely to go into solution.

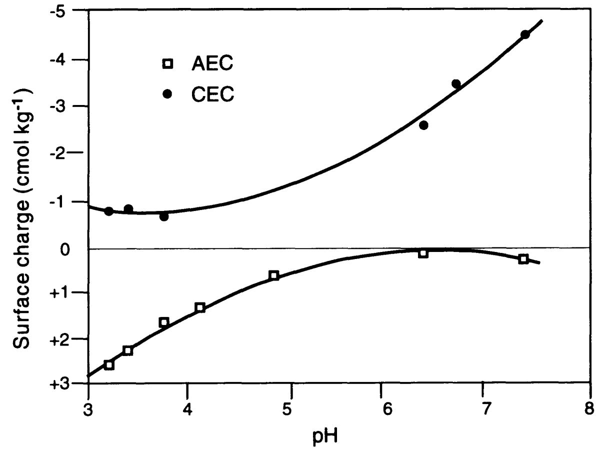

Fig. 160. The variations of charges (anion and cation exchange properties) as a function of pH, shown by the example of a ferralic B horizon (ferralsol). (Van Wambeke 1992, p. 148)

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[26] Large differences between EC_{pot} and EC_{eff} may occur even in acid HAC soils (e.g. in podzols; dystric cambisols). However, these are mainly linked with the high percentage of pH-dependent charges of organic substances in the Ah horizon.

- *Raising the pH*, e.g. by liming, brings about a strong (up to 50%) increase in the CEC. This improves the efficiency of fertilizer applications, and the disadvantages arising from phosphorus fixation and aluminium toxicity decline or disappear entirely. Admittedly, one disadvantage of liming is that the rate of decomposition of the humus is at the same time increased.

The Most Important Soil Units in the Seasonal Tropics

The most frequent zonal soil units in the Seasonal and Humid Tropics/Subtropics are acrisols, alisols, ferralsols, plinthosols, lixisols and nitisols. The more frequent substrate-bound or relief-bound soil types include the ferralic arenosols and vertisols, as well as the gleysols and fluvisols, which occur all over the world under conditions of waterlogging or temporary flooding respectively.

The distribution of these soil types is *decisively determined* not only by the climatic and edaphic differences, but also *by the amount of time which was available for pedogenesis.* For example, ferralsols occur not only in the Humid Tropics, where they are particularly characteristic types, but also in moist savanna climates, as long as the period of pedogenesis lasts long enough (as is the case, for example, on many old land surfaces). On the other hand, ferralsols are lacking even in the Humid Tropics, wherever erosion forces are effective or the development of the soil started at a relatively late date; these conditions are found, for example, in mountainous regions or on recent volcanic aggradations.

The great importance of the time factor (age of the soil) explains why it is particularly difficult in the Seasonal and Humid Tropics/Subtropics to assign individual soil units or soil associations to specific ecozones (which are delimited according to recent functional structures). Most of those soil units mentioned above occur in all the zones in question, although the individual areas which they cover are very unequal.

The soil units are in each case described in connection with those ecozones in which they are most widely distributed, i.e. the nitisols, lixisols and vertisols are described in the present chapter, while the acrisols and alisols are described in Chapter 3.8, on the Humid Subtropics, and the ferralsols, plinthosols and ferralic arenosols are described in Chapter 3.9, on the Humid Tropics. The gleysols and fluvisols will not be discussed again (on this topic, see Chap. 3.3.4).

Nitisols (Formerly Nitosols). These are red to reddish brown soils which, like the acrisols formed under (extreme, but not excessively so) humid-warm climatic conditions; however, in contrast to the latter soils, they developed on silicate-rich (= basic) rock (e.g. basalt, micaceous schist) and, based on the duration of their period of pedogenesis, they must be classified as having formed at a later date (Early to Middle Pleistocene compared to early Pleistocene and older in the case of the acrisols). While it is true that, also in their case, the primary (rock) minerals are highly weathered, and mainly kaolinite (as well as small amounts of 2:1 clay minerals) evolved as a result of the secondary clay formation, there are nevertheless still vestiges of weatherable minerals in the sand and silt size range. In addition to this, the effective moisture storage capacity is high, and favourable phosphate sorption/desorption properties exist. All of this forms the basis for the relatively high *production potential* of the nitisols.

The cation exchange capacity remains as a rule below 24 cmol(+) kg^{-1} clay; only at higher humus contents may it also be significantly higher (Schmidt-Lorenz 1986, p. 85). The base saturation (at pH 7) is more than 50% in the case of the *eutric* nitisols and less than 50% in the case of the *dystric* nitisols. In the revised FAO legend both subdivisions are substituted by *haplic* and *rhodic nitisols* which are distinguished by a red to dusky red argic B horizon in case of the latter subunit.

Like the acrisols, the nitisols also exhibit an illuvial accumulation of the clay in the B horizon (Bt: argic B horizon); in contrast to the acrisols, the clay contents decline by less than 20% from their maximum in the upper Bt horizon down to a depth of 150 cm (in the case of the acrisols the decline is more than 20%); also, the topsoils contain large amounts of clay – at least 35% and not infrequently more than 60%.

Despite the clay accumulation, the physical properties are regarded as favourable. The angular blocky structure is characterized by stable aggregates whose shiny ped surfaces (either thin clay coatings or pressure faces) were the source of the name for these soils (Latin nitidus = shiny). The porosity of these soils is such that rapid infiltration of rainwater (*low susceptibility to erosion*), the storage of a large amount of plant available soil water (*large useful water capacity*) and good aeration are guaranteed. These characteristics also distinguish the nitisols clearly from the less favourable acrisols and lixisols as far as plant production is concerned. They are thus among the best tropical/subtropical soils and can be permanently used for traditional agriculture, i.e. without lying fallow for several years, which is otherwise a very widespread practice. However, they are far less broadly distributed than the other tropical/subtropical soils. Frequently, only small isolated occurrences are found within the regions predominantly occupied by acrisols and lixisols (covering at most one-fifth of the amount of area taken up by these other two soils mentioned).

Lixisols (Latin *lixivia* = Washing). This newly created soil unit was split out from the former (more broadly defined) luvisol group and comprises all those (tropical) luvisols from the first classification having a low cation exchange capacity [less than 24 cmol(+) kg^{-1} clay in at least some part of the B horizon]. Like the HAC luvisols of the non-tropical regions, the lixisols also form an argic B horizon and have a high base saturation (by definition at least 50%). Therefore, despite the predominance of kaolinitic clays and low humus contents, they have a moderately high yield potential.

Vertisols . These are dark grey to black (in the case of *chromic vertisols*: brown), clay-rich (at least 30%, frequently > 50% clay) soils of the humid-dry tropics and subtropics (at least 200–300 mm precipitation per annum and 3 to 9 dry months). Generally, they occupy (originally) grass-covered, poorly drained plains and depressions consisting of clay-rich (mainly $CaCO_3$-containing) weathering products or sediments. During the rainy season they have a dense (low porous) viscous-plastic consistency, and during the dry season shrinkage cracks (up to more than 10 cm in width and 50–150 cm in depth) develop and divide up the soil mass into wedge-shaped or parallelepiped structural aggregates.

The cracks may be filled up by soil material falling into them, blown into them, trampled into them by animals, or washed in by the first rainfalls following the dry season. Under such conditions, the *swelling processes* which take place during the following wetting phase commence in the subsoil at an elevated dry volume. With increasing water uptake, correspondingly high swelling pressures are generated (see Chap. 3.7.3). As a result, movements occur (hydroturbation, peloturbation) which lead to deep-reaching mixing and homogenization of the soil material and thus to the formation of an often more than 1 m thick Ah horizon. It is these mixing processes from which the name vertisol in the FAO system is derived (Latin *vertere* = turn over). Older names for the same soils are regurs, black cotton soils, tirs. Evidence of the movements can be seen in the soil structure in the form of shiny sliding and shear surfaces on the soil aggregates (parallel oriented clay minerals = slickensides, stress cutans); at the surface of the soil they are evident in the so-called gilgai relief (see Chap. 3.7.3).

The pronounced swelling/shrinkage phenomena are linked with the generally high percentage of swellable clay minerals (above all smectites). These clay minerals have a high cation exchange capacity and that of the soil is also correspondingly very high at approximately 40–80 cmol(+) kg^{-1}. The reaction is neutral to alkaline. Carbonate precipitations (sometimes concretions) may occur in the profile. Despite the dark colour of the soil, the humus content is less than 3%. The humus substances occur in stable clay-humus complexes, and the C/N ratio is around 15.

Because of their considerable content of nutrient substances, vertisols have a very *high production potential.* The large amount of clay, on the other hand, brings some problems with it, e.g. the (potentially large) water storage is available only to a very limited extent to the plants (high permanent wilting points), it is very difficult to work the soil both in the wet (viscous-sticky) as well as in the dry (rock hard) state, the root systems of the plants may be impaired by hydroturbate movements, and there may be a risk of erosion. Many vertisol regions are therefore used as (natural or near-natural) grazing land. Among other crops, cotton, sugar cane and wheat are suitable for cultivation.

3.7.5 Vegetation and Animal Life

3.7.5.1 Structural Characteristics

Ecological-Physiognomical Characteristics

The savannas, as defined in this book (see Chap. 3.7.1), include such different (according to flora and physiognomy) vegetation types as, for example, the campos in Brazil (e.g. campo cerrado), llanos on the Orinoco, monsoon forests in

SE Asia (e.g. teak forests), miombo and mopane forests in Central and Eastern Africa or eucalyptus savanna forests in Australia. Behind all the obvious diversity there is, however, one important common feature which, apart from the thorn savannas, is not found in any other zonal plant formation in the world: in each case, the formation consists of *mixed combinations of trees and grasses.* The regional differences are based essentially on the *varying degrees of cover provided by the trees* which may extend from (almost) totally treeless grassland all the way up to closure of the canopy of the tree stands. Independently of this, the *grass cover is always closed.* The predominant species of grasses belong to the *C_4 plants* (see Chap. 3.4.5.2), which are regarded as more efficient than C_3 plants under the conditions of strong solar radiation, high temperatures and high evaporation rates which are characteristic of the Seasonal Tropics.

The density and height of the tree stand are often lower in drier regions with richer accumulations of nutrients in the soils (arid eutrophic savannas) than in wetter regions with lower nutrient contents in the soils (moist dystrophic savannas) (Huntley and Walker 1982; Cole 1986). Therefore, in the former type, low-growth tree and shrub savannas predominate, and in the latter type tall-growth savanna woodlands or dry or even semi-evergreen forests are the rule (Fig. 161). However, this relationship is by no means unambiguous. More evident correlations to natural environmental conditions may exist with the *growth height of the grass.* For example, the species of grass predominating in the moist savannas (frequently Andropogoneae and Paniceae) grow taller ($>$ 1 m) (*tall-grass savannas*) than those in the dry or even thorn savannas (frequently Eragrostidae, Aristidae and Chloridae). Figure 162 shows a recent attempt to classify the savannas of the earth according to physiognomic and floristic criteria in dependance of climatic and edaphic environmental conditions.

Any further subdivision is scarcely possible because most savannas have been severely modified by the effects of fire (mostly caused by humans), grazing, clearcutting, etc. In many cases, the anthropogenic influence is difficult to estimate and accordingly the question of what is natural under the given circumstances (i.e. how would the potentially natural vegetation look) cannot always be clearly answered.

Long-term observations conducted on test areas (e.g. Vuattoux 1976; Menaut 1977) which were protected from human influence have been conducted in many savanna regions. As a rule, they have shown that the *tree stand* increases in density, height and number of species with the duration of protection (Fig. 163). In particular, in moist savanna regions, it is probable that woodlands, and sometimes also closed forest formations (dry forests), originally occupied much larger areas of land and that the grassland which is now largely dominant here did not start to expand until the process of human-induced *savannification* commenced.

Nevertheless, there can be no doubt that *open grasslands* also formed part of the *natural* plant formations, and the only question is how far their present extent can be regarded as natural.

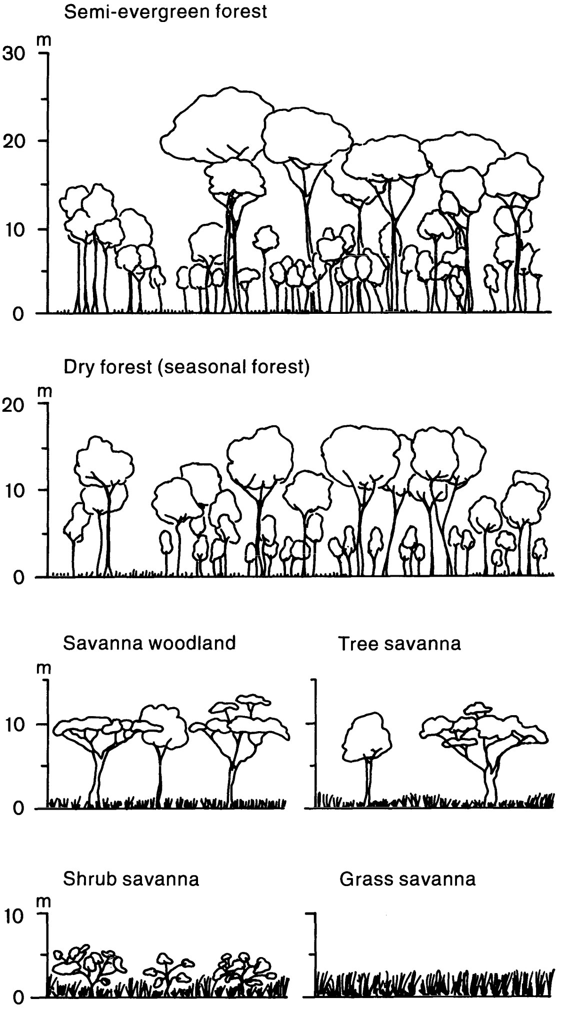

Fig. 161. Physiognomic savanna types. (Harris 1980). Grass growth may be missing or discontinuous in places (in the shadow of dense tree stands) in the dry forests and – more frequently – in the semi-evergreen forests. The assignment here to savannas is doubtful. The majority of the semi-evergreen forests (moist forests) can certainly be better classified as a transitional form between moist savannas and rain forests

The Seasonality of Plant Growth

The *dry season*, which lasts approximately 3 to 7 months each year, is the most important limiting factor for plant growth. As a rule, the trees react to the stress of drought by casting their leaves (except in Australia), and the grasses and herbaceous plants react by allowing their above-ground shoots to die off; i.e. rain-green (dry-deciduous) tropophytes and hemicryptophytes, and to a lesser extent also cryptophytes, are the dominant life forms, and the photosynthetic performance of the plant cover drops to zero during the dry season.

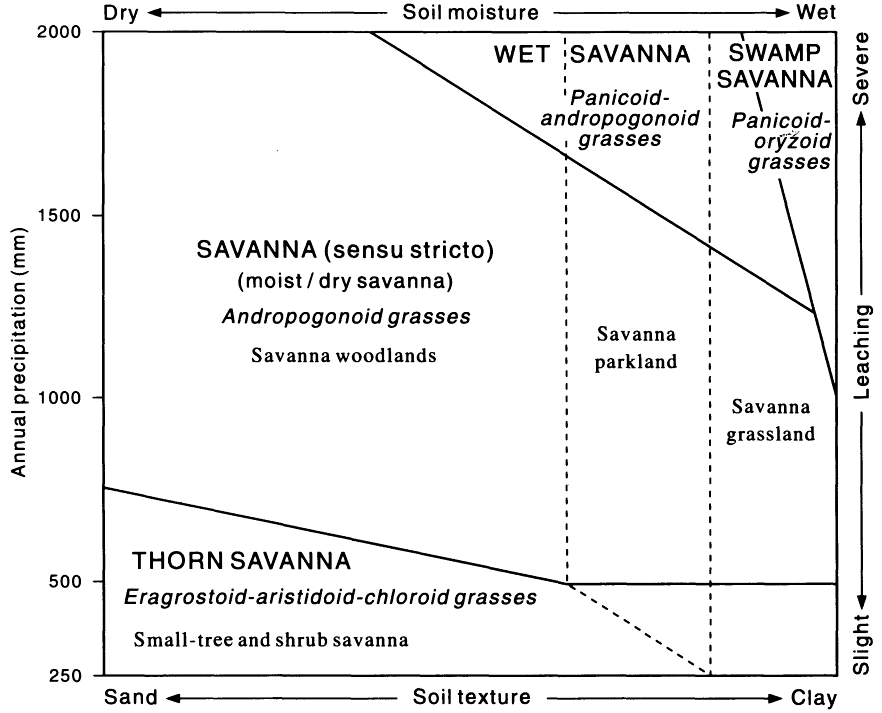

Fig. 162. Classification of the world's savannas. (After Johnson and Tothill 1985, with slight modifications). The andropogonoid grasses (e.g. *Andropogon*, *Bothriochloa*, *Chrysopogon*, *Cymbopogon*, *Dichanthium*, *Eulalia*, *Heteropogon*, *Hyparrhenia*, *Loudetia*, *Sehima*, *Sorghum*, *Themeda*, *Trachypogon*) are characteristic of all the world's moist and (at least the wetter of the) dry savannas (core savannas, savannas sensu stricto). On sandy soils with low water-retention capacity they still occur at precipitation values up to 2000 mm a^{-1} (instead of the rain forests which otherwise occur – on loamy fertile soils – under such humid conditions), whereas on clay-rich soils with high water-retention capacity they occur already at precipitation values of 500 mm a^{-1}, and up to 1000 mm a^{-1}. The tree growth differs essentially according to the edaphic conditions: on light (sandy) well-drained soils, more or less continuous and tall tree cover is obtained (savanna woodlands); the trees thin out wherever loamy to clayey soils are present (savanna parklands); on heavy clay soils, tree growth is usually entirely missing (savanna grassland).

Wherever large amounts of precipitation ($>$ 1500 mm a^{-1}) temporarily give rise to waterlogging or flooding, because of impermeable soils, wet savannas replace the moist savannas. Many of the grass species which predominate here belong to the panicoid group (e.g. *Echinochloa*, *Hygrochloa*, *Hymenachne*, *Leptocoryphium*, *Mesosetum*, *Panicum*, *Paspalum*). Under conditions of year-round waterlogging and long-term flooding, swamp savannas form in which panicoids but also oryzoids (e.g. Cyperaceae, *Leersia*, *Oryza*, *Phragmites*) occur.

For the thorn savannas, which receive $<$ 500 mm, and for dry savannas on sandy grounds with $<$ 750 mm of annual precipitation, short grasses of the eragrostoid-aristidoid-chloroid group (e.g. *Aristida*, *Chloris*, *Ctenium*, *Eragrostis*, *Plectrachne*, *Trichoneura*, *Triodia*), as well as small trees and shrubs, are the characteristic vegetation. The panicoid grass *Cenchrus* may also be common. Since the grass cover is not continuous, the thorn savannas do not strictly speaking belong any more to the savannas (see text). The exclusion of the thorn savanna regions (Sahel-type scrublands) from the ecozone of the Seasonal Tropics, which was undertaken at the beginning of this chapter (3.7.1) for other reasons, is therefore also confirmed by biogeographical criteria. Another, again

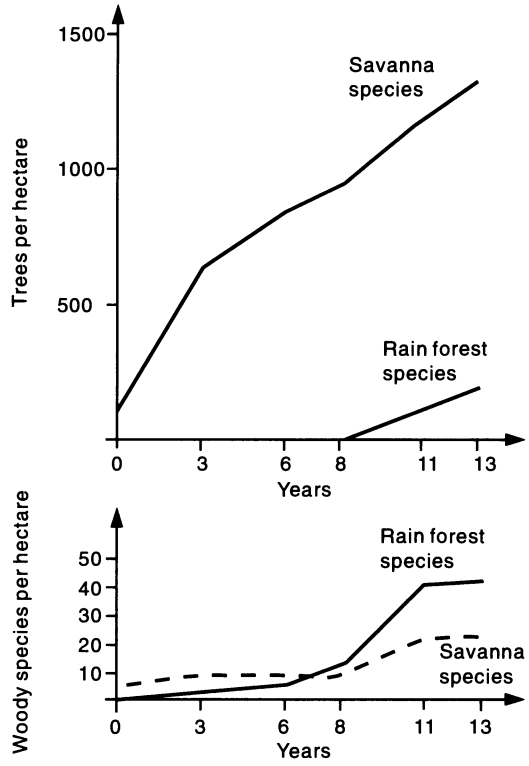

Fig. 163. The changes in the tree stand, following complete protection from burning, according to density (*1*) and number of woody species (*2*) in a moist savanna at Lamto, Ivory Coast. (Menault 1977, taken from Gillon 1983)

During the *rainy season*, infiltrating water – in contrast to what happens in the thorn savannas – considerably increases the soil water content down to a great depth; in the process, the field capacity is exceeded, at least temporarily, thus permitting groundwater discharge to occur. Consequently, a great deal of water is still available to the savanna vegetation even after the end of the rainy season, and the growing season is correspondingly extended into the dry season (Fig. 164). How long this lasts depends on the amount of available water contained in the soil, the depth of root growth and the transpiration ratio of the plants. In most loamy soils the amount of plant-available water stored can be as much as 15–20% of the soil volume, namely 15–20 mm (or 15–20 $\mathrm{l\,m^{-2}}$) for every 10 cm in depth of the root zone.

In the case of the grass species *Cynodon dactylon*, Russel (1966) found near Nairobi that the plant put down roots to a depth of 3 m and withdrew 400 mm of water from the soil in the post-rainy season. The mat of ***Pennisetum clandestinum***

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biogeographical, distinction can be made on the predominating C-pathway: most C_4 grasses of the thorn savannas belong to the aspartate-formers, while those of the savanna sensu stricto belong to the malate-formers. In the former, aspartate is the primary photosynthetic CO_2-fixing product (the CO_2 antenna), while in the latter it is malate which assumes this role

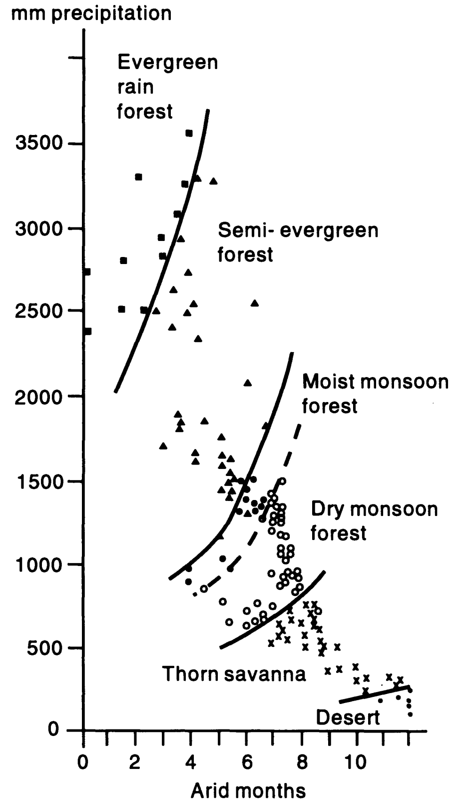


Fig. 164. The distribution of some tropical vegetation types in relation to annual precipitation levels (*ordinate*) and the lengths of dry seasons (*abscissa*) in India. (Walter 1979). Higher amounts of precipitation during the rainy seasons create larger reserves of water in the root horizon of the trees; this allows the hygric growing season to extend far into the climato-ecologically arid season of the year

growing nearby had roots extending 120 cm deep and withdrew 180–200 mm of water; given a daily transpiration rate of 4–5 mm d^{-1}, these plants were able to continue growing for 6 weeks beyond the end of the rainy season.

Despite the conspicuous seasonality of the moisture conditions, the individual *development phases of the savanna plants* are by no means always synchronous. For example, many trees blossom in the late dry season, shortly before or simultaneously with the development of foliage, which also usually starts before the new rainy season. The impulse triggering these events, which commence in a phase of minimal water supply, is probably not hygroperiodic in nature. Instead, it seems more likely that correlations exist with the radiation and temperature conditions (Sarmiento and Monasterio 1983): the last dry months preceding the rainy season are the hottest season of the year with the largest diurnal temperature fluctuations; this period is immediately preceded by the coolest season (first part of the dry season) with the shortest days of the year.

In the case of plants which bloom during the rainy season, the reproductive phases may occur at the beginning, in the middle of, or at the end of the humid period.

With the onset of the dry season, the grasses and herbaceous plants (all of which possess only minimal transpiration protection) die off within a few weeks. In the case of the perennial species, only the above-ground shoots dry out. These then cover the vegetative cones at the surface of the soil and thus protect them from further drying.

The date of *shedding* obviously depends on the reserves of water available in the soil (see above). Since deeper-rooted woody plants have access to such reserves for longer periods than grasses and herbaceous plants, the leaf fall usually occurs several weeks after the herbaceous plants have dried out. If, exceptionally, the soil water reserves extend throughout the entire dry season (due to above-average amounts of precipitation during the preceding rainy season or an unusually late end to the rainfall), then many of the otherwise deciduous trees retain their foliage. Thus in their case, shedding the foliage is a facultative process. In many species, the leaf fall is preceded by a change in colour (which is only moderate compared with what happens in autumn with summer-green tropophytes in the Humid Mid-Latitudes).

In the moist savanna zone, evergreen tree and shrub species can gradually increase in number and thus *semi-evergreen forests* are formed. The leaves of these evergreen woody plants exhibit a scleromorphic structure (see Chap. 3.6.5.1). Their assimilation during the dry season is usually low. Evergreen forests frequently occur along rivers and are known as *gallery forests.*

Tree Layer – Grass Layer

The shade created by the tree layer influences the grass layer in various ways (Koechlin et al. 1979): in the *wetter areas* the shade from the trees impedes grass growth. Therefore, in these areas, mostly shade-tolerant, low-production herbaceous plants occur in the place of grasses, and the conditions for young trees to grow are favourable. When protection from fire and grazing is available, the coverage by woody plants rapidly increases.

In *drier regions,* on the other hand, the shade from the trees can favour mesophytic, highly productive grass growth. For example, in the Sudan zone, Koechlin found that the shoot masses of the grass layer at sunny sites were 0.7–2.5 t dry matter per hectare (depending on the quality of the soil), but rose to more than 3 $\mathrm{t\,ha^{-1}}$ at shady sites; in the even drier Sahel belt, the differences were as much as 2.5 times in favour of the shady sites. The grass growth profits from the tree layer, because the transpiration stress is lower in the cooling shade from the trees (in the moist savannas this advantage is of no significance because the plants suffer much less frequently from drought stress). The protection from the hot sun is particularly important for grasses because most of them are virtually unable to limit their transpiration, when the water supplies are low (in contrast to the trees, which are able to very finely regulate their transpiration losses via their stomata). Tracts of grass therefore "burn" very easily, i.e. previously green areas dry out and become yellow within a few days (Walter and Breckle 1984, p. 125).

A further advantage which is offered by the growth sites beneath the tree canopies is that the layers of soil close to the surface are supplied via the leaf fall with large amounts of organic material, and thus also with nutrients which the trees have in some cases brought up from deeper soil levels out of reach of the roots of the grasses. The humus content, which is demonstrably higher below the trees, may also be related to the fact that the rate of decomposition is lower in the shade of the trees than in the open grasslands.

Animal Life

A rich insect and arachnoid fauna is characteristic of this ecozone. Almost everywhere, the most important primary consumers are grasshoppers (also locusts) and – during the rainy seasons – caterpillars. Among the secondary consumers, spiders and ants occupy a dominant position. Many arthropods survive the dry season in the form of drought-resistant eggs, pupae, etc.

The *macrofauna* of the savanna zone has developed in very different ways on the individual continents. Not only are there fundamental differences in the species which are represented (which is not surprising because the savanna regions belong to several animal kingdoms), but also the density of the animal population, the life forms represented and their functions in the savanna ecosystem deviate considerably from region to region.

Many of the African savannas are extraordinarily rich in game (originally they all were); their animal populations include, among others, the herbivorous antelopes, gazelles, elephants, giraffes, hippopotami, rhinoceroses, warthogs and ostriches, as well as the carnivorous lions, leopards and hyenas. In East Africa, the mass of the large mammals in some moist savannas attains values of 0.1 to 0.3 $\mathrm{t\,ha^{-1}}$ (mostly elephants and hippopotami), while in the dry savannas, still considerable values of 0.06 to 0.1 $\mathrm{t\,ha^{-1}}$ are recorded.

The animal populations of the Indian savannas were originally similar to those found in Africa, but they have always contained fewer species. On the other hand, South America possesses hardly any large herbivorous mammals. Various marsupials are found in Australia as primary consumers. Many of them occupy similar *niches* to those filled by certain species of mammal in other continents, and to a certain extent therefore they are *equivalent in position.*

Many savanna-dwelling animals are highly gregarious, a characteristic which is also found in the two other open zonobiomes of the steppes and the tundras. In addition to grasses and forbs, many species of shrub and tree serve as important sources of food to wild animals, especially during the dry season when the grass is burnt. Some ungulates (e.g. the white-bearded gnus in East Africa) migrate with the rain.

In general, only a minor part of the phytomass consumed by animals (ingestion, consumption = C) is assimilated (assimilation = A), a larger amount is egested again – more or less unchanged – with the feces (egestion). This organic matter is then – like the non-consumed phytomass – available for consumption by other organisms, particularly detrivores.

The *digestion or assimilation efficiency (A/C)* of the herbivores can fluctuate within wide limits from animal to animal (also in single individuals, depending on age and diet); frequently, it is in the range from 30 to 60% (in the case of mammals it tends to be in the upper part of this range, sometimes even higher) and thus it is significantly lower than in the case of most carnivores, but much higher than what is achieved by the detrivores (Table 39).

Of the assimilated energy, the herbivorous mammals put 1–5% into produc-

Table 39. Energy conversion parameters, at population level, for some savanna animals. (Lamotte and Bourliere 1983). For explanations, see text

	Assimilation efficiency A/C	Net production efficiency P/A	Gross production efficiency P/C	Turnover rate P/B
Herbivores				
Grasshoppers				
Burkea savanna various spp	32	19	6	
Acacia savanna various spp	32	21	7	
Orthochtha brachycnemis	20	42	9	9.6
Caterpillars				
Cirina forda	43	15	6	
Herbivorous termites				
Trinervitermes geminatus			9	10.4
Ancistotermes cavithorax (fungus-cultivating)			2	9.7
Hodotermes mossambicus	61			
Ungulates				
Uganda kob (*Kobus kob*)	84	1	1	0.27
Impala (*Aepyceros melampus*)	59	4	2	
Domestic cattle (*Bos taurus*) Transvaal	57	5	2	
African elephant (*Loxodonta africana*)	30	2	0.5	
Carnivores				
Spiders				
Orinocosa celerierae	95	53	50	
Detrivores				
Earthworms				
Millsonia anomala	9	4	0.6	2

tion (P), i.e. into growth or reproduction. A significantly higher *net production efficiency (P/A)* is achieved by the majority of poikilothermic animals. Most of these put more than 10%, and a few of them more than 50%, of the assimilated energy into their own production (however, see below the remarks on the Lamto savanna).

The *gross production efficiency* (also called *ecological efficiency*), i.e. the growth and reproduction of animals in relation to their food intake (P/C) can be determined from the efficiencies of assimilation and net production. In the case of the savanna-dwelling animals mentioned in Table 39, this fluctuates between 0.5% for elephants and 50% for a species of spider, i.e. in the case of elephants only 0.5% of the food intake goes into production (including reproduction), whereas in the case of the species of spider, half the food intake is used. For the majority of animals the P/C values are between 1 and 10%, and the warm-blooded animals fall clearly in the lower part of this range.

In the last column of Table 39, the *turnover rate* of populations is calculated by correlating the annual production of a population (P) with its (mean) size (B). Assuming a population which (on average) remains constant over a long period of time, this rate increases in direct proportion to the number of generations that follow each other every year.

The foregoing indices permit the ecological status of individuals and of populations to be determined at a certain point in time. Admittedly, this is no more than a first step towards understanding secondary production in a savanna ecosystem. A complete picture can only be obtained by collecting the data for all the animal populations involved and by taking account of the pronounced seasonal differences. So far, this has not been accomplished.

Many studies have confirmed that the grazing of the savannas by wild animals or cattle, i.e. the removal of living phytomass from the system, in no way damages the primary production, but on the contrary stimulates increased production output. However, it is necessary that the consumption by the animals should be kept within limits, i.e. should be spread over the growing season, and the plants should not be excessively weakened (it is generally agreed that 30–45% of the above-ground PP_N is a *tolerable amount of fodder to remove*). Walter and Breckle (1983, p. 43) report a test in which the grazing was simulated by repeatedly cutting, in each case, 70% of the grass. This stimulated the regeneration processes to such an extent that the primary production increased by 40–74% over the non-mown or ungrazed comparative surfaces. On these, in contrast, the production declined over the course of the years as more and more dead plant material accumulated in them.

3.7.5.2 Savanna Fires

Dry-season grass fires, which occasionally also spread into the shrub and tree layer, are extremely characteristic of all savannas. Probably not one single area of savanna is left untouched by such fires over the course of several years (cf. San José and Medina 1975; Coutinho 1982; Huntley 1982; Trollope 1982, 1984; Gillon 1983; Cass et al. 1984; Griffith and Friedel 1984; Frost and Robinson 1987).

In principle, grass and bush fires can only develop where a continuous grass cover with a minimum amount of dry matter (approximately 1 $\mathrm{t\,ha^{-1}}$) exists; therefore, such fires do not occur in semi-deserts and thorn savannas or, if they occur at all, then it is only after periods of exceptionally copious rainfall resulting in far above-average development of biomass.

Fires may be caused (at the start of the rainy seasons) by lightning strikes; however, they are much more frequently set by human beings. The custom of setting fires, as practised by the inhabitants of the savannas, goes back many ten thousands of years in the Paleotropical region, and is at least several thousand years old in the Neotropical region. In many regions, the regular burning of the grass, and to some extent also of the woody plants, is an entrenched tradition. It is done for several reasons: (1) to maintain and improve pastureland, (2) to clear land for cultivation and to provide ash as a fertilizer, (3) to keep wild animals away, (4) to destroy vermin (snakes).

The grass and bush fires have far-reaching *effects on the savanna ecosystem.* For example, they are important selection factors for the flora and fauna; they determine to a large extent the vegetation structures; they influence the heat and water budgets of the soils, of the plant cover and of the layer of air close to the ground; and they modify the energy and material turnovers in the system. Various *degradation* or *succession stages* occur, depending on the frequency with which individual areas are burnt, the dates (whether early or late in the dry seasons) when this occurs, and the intervals which have elapsed since the last fires occurred or which are normally left between deliberately set fires. The different seral stages join together to form a mosaic of vegetation, the individual parts of which may be replaced as time goes by, but the complex structure is retained in similar fashion for long periods of time. This mosaic can therefore be regarded as a *fire climax formation*, and changes do not occur until the savanna fires are prevented (see above).

As a result of the frequent fires, the species of trees which have asserted themselves are generally those having a certain amount of fire resistance, and are accordingly referred to as *pyrophytes*; but there are also many species of woody plants which are remarkably sensitive to fire, at least in the early growth stages.

The *intensity of the fires* depends on the amount and type (e.g. moisture content) of the combustible material and also on the climatic conditions. The amount of easily flammable material increases, the air temperature rises, and the atmospheric humidity decreases, in direct proportion to the length of the dry season; as a result, fires occurring late in the dry season are always more intensive than those occurring at the start of the dry season. If a strong fire develops, the trees may also be damaged, particularly if their flowers have opened and their foliage has developed at the time of the fires. Young trees are also particularly affected when their young shoots are engulfed within the flames and the cambium is afforded very little protection by the thin layer of bark. The intensity of the fires occurring late in the dry season is at its highest where grass – which is always the most important fuel at the start of a fire – grows in large quantities (density and height) and a large amount of dry material (standing dead, litter) has collected because of the long periods of time which have elapsed between fires. Under these conditions, large trees can also burn and (even in savanna woodlands where trees are plentiful) up to 90% of the above-ground phytomass may be destroyed.

Normally, however, much less is burnt. According to data compiled from various authors by Frost and Robertson (1987) for African savannas, only about 70–90% of the grass layer and grass litter, 20–50% of the litter from trees, 12–58% of the twigs, bark and woody parts, and up to 20% of the standing dead of the tree layer are burnt in individual fire events.

The *reduction of the litter* and – secondarily – (see below) also of the humus in the soil by fire is minimal when compared with areas which have not been exposed to fire. For example, in the miombo woodland of Zambia, Trapnell et al. (1976) found everywhere that the amounts of dead organic substance on and in the soil were only small, regardless of whether fires had occurred early, late or not at all. The explanation that they give for this is that large populations of termites rapidly process the litter if this is not burnt.

The savanna fires spread along *fire lines*, which can run for hundreds of metres or even many kilometres, at a rate of several metres per minute (with a following wind and other favourable conditions the fires can also move at several metres per second), leaving behind them surfaces covered with black ash. They usually end after travelling a few kilometres, for example when they come to roads, animal tracks, rivers, wet areas, or when the wind drops or turns. The individual burnt areas are several hectares to several square kilometres in extent and have a typical irregular and bizarre outline which can still be clearly identified many years later, for example on aerial photographs.

When the fire passes through, high *temperature* occur for short periods of time (usually just a few seconds, and at the most for a few minutes) (Fig. 165). At the surface of the ground the temperatures can attain 100–500 °C (within tufts of grass the temperatures are much lower) – depending on the combustible material – and at a height of 50 cm above the ground they can reach as much as 500–600 °C (max. 800 °C) for a few seconds; from that level up to about 3 m (approximately the average height of the flames), temperatures of several hundred degrees still prevail. In contrast, only slight increases in temperature occur within the soil itself. Up to 50 °C is measured immediately beneath the surface of the soil, but below that the warming process declines rapidly; below a depth of about 5 cm, no increase at all in temperature is detectable. This explains why both the soil fauna and flora as well as the below-ground organs of the savanna plants are very little affected by the fires. The only places where the soil may be heated to a greater depth are found where broken-down trees continue to smoulder for long periods of time (up to several days).

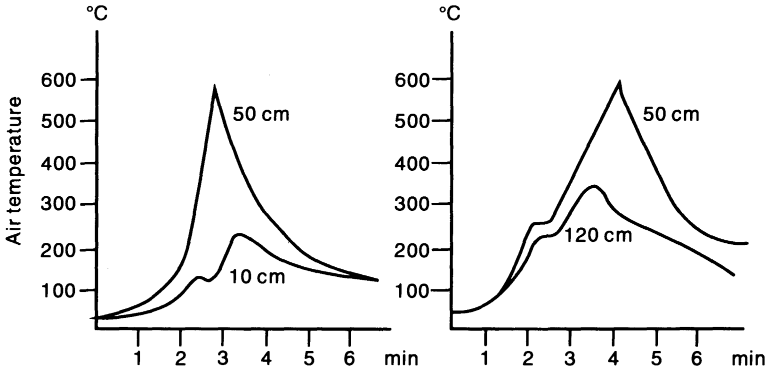


Fig. 165. The rise in temperature at various heights (10, 50 and 120 cm) above the ground when a grass fire passes through. (Gillon 1983). The two measurements were taken in a moist savanna (height of grass: 70 cm) at Lamto, Ivory Coast

However, savanna fires have a series of *indirect effects on the soil.* For example, in the long term, they modify:

- The *heat budget*: more solar radiation is absorbed by the unprotected and blackened burnt ground, and the temperatures in those areas rise correspondingly during the daytime hours. This accelerates the drying out of the uppermost layer of soil and the breakdown of the humus substances.
- The *water budget*: once the layer of litter has been burnt, the rate of evaporation increases. It was also noted (Cass et al. 1984) that the rate of infiltration declines on areas which have been repeatedly exposed to fire, and thus more rainwater runs off at the surface. This probably happens because of the progressive breakdown of humus and the compaction of the soil which accompanies this process. Thus, frequent fires put a stress on the soil water budget by increasing both the evaporative losses and the runoff losses.
- The *susceptibility to erosion*: both the fact that freshly burnt areas are totally unprotected, and their reduced permeability, in principle increase the risk of soil erosion by sheet flow or rill wash. The mineral-rich ash lying loose on the surface of the soil is particularly likely to be washed away.
- The *supply of mineral nutrients*: when phytomass and litter are burnt, the minerals contained in them are released and are thus made available again to the plants unless, like nitrogen and to some extent also sulphur and phosphorus, they are volatile. Losses caused by the ash being relocated by wind and water, may handicap certain areas, but will add correspondingly to the nutrient supplies in others. Therefore, fires normally increase the reserves of available K, Ca, Mg and other minerals in the soil and – together with this – bring about a short-term increase in the base saturation and the pH value. These positive effects are frequently greater in dry savannas than in moist savannas where accelerated leaching can be expected to occur (see Chap. 3.9.5).

Once the burning has stopped, new grass shoots spring up almost immediately (especially in the moist savannas) regardless of whether rain falls or not. Obviously, a *growth impulse* is triggered by the heat shock or by the exposure of the innovation buds at the surface of the soil (the number of these buds is frequently increased after fire). The young grass finds more favourable conditions for net photosynthesis than beforehand, since more light can reach the ground, the daytime air temperatures are higher (both of these factors are advantageous in particular for the C_4 plants which generally predominate), and the nighttime temperatures are lower (thus reducing the respiration losses). In addition, the burning puts a great deal of minerals back into the soil.

For cattle, the young grass growing back on the burnt areas is particularly valuable during the dry season, when normally very little forage is available. Therefore, in many cases it is the cattle herders who set fire to the grass in order to obtain fresh forage for their animals. However, this practice is ecologically at least questionable when the burning takes place right at the start of the dry season, because the resorption (internal translocation) of minerals from the shoots into the roots, which takes place as the shoots dry out, has not yet been completed and the new grass growth faces a long period of time without rain. The risk of damage increases when this young grass is grazed. These circumstances also militate against the often propagated *controlled use of fire at the start of dry seasons* for the purpose of protecting the tree layer from the danger of more severe fires in the latter part of the dry season.

Instead, as far as grass growth is concerned, *fires occurring late in the dry season* must be regarded as more favourable – especially when grazing by cattle or other animals is an important factor. Many observations confirm that such fires do not adversely affect the grass layer; on the contrary, they generally increase the PP_N and the phytomass compared with that of unburnt areas, and the fires may possibly also favour perennial species of grasses over annual species (Afolayan 1978).

The *regeneration of the woody plants* usually takes place vegetatively, for example through the formation of adventitious buds on stems which have been damaged by fire, by coppice growth from tree stumps, or suckers from roots. Young trees have particularly high root/shoot ratios. This increases their chances of survival in savanna fires because the loss of their above-ground parts (which are particularly endangered by fire compared with larger trees) is not so significant, and more mass is available for renewal via sprouting from roots.

The grasses and woody plants of the savannas in general have a high *regeneration capability* (which is much more characteristic of the savanna plants than fire resistance); thus the conditions for restoring the pre-fire status are fundamentally satisfied. What actually develops depends to a large extent on external conditions (Frost and Robertson 1987). Sometimes tree growth and sometimes grass growth gains the upper hand, depending on whether the fire is followed by long periods of drought which impede the process of regeneration, or rain falls soon and promotes the new growth, or animal browsing hampers the growth of new trees and also restricts the development of grasses, thereby reducing the possible effectiveness of later fires etc. Once established, trees as well as grasses generate a certain self-reinforcing (stabilizing) effect, on the one hand by producing shade or on the other by suppressing the development of tree seedlings.

3.7.5.3 Stand Reserves, Material and Energy Turnovers, Ecosystems

Phytomass and Primary Production

The magnitude of the phytomass is determined primarily by the density and height of the tree stand. Since both, as already described, tend to be anthropogenically rather than naturally determined in most savannas, any data on the total phytomass are of little ecological value. Instead, it makes more sense to provide data exclusively related to the grass (forb) layer because, as long as the tree stand is not excessively dense and thus suppresses the grass growth, the production of these grasses and forbs approximately reflects the natural production potential (see below).

Rather like in the steppes, the *above-ground grass mass* is characterized by extremely wide seasonal variation. In the savannas, where the grass burns off during the dry season, the mass ranges in the extreme case from zero (immediately following the passage of the fire) up to the amount of the PP_N. In general, however, the amplitude is much smaller because not all the grass burns during the savanna fires and some of the new growth dies off, drops off or is consumed by herbivores before the growing season is over. As a result, the maximum above-ground mass of herbaceous plants is reached not at the end of the growing season but earlier (Fig. 166).

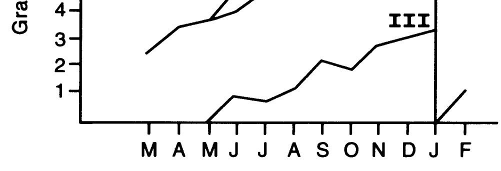


Fig. 166. The seasonal variations in above-ground grass matter in the moist savanna at Lamto, Ivory Coast. (César and Menaut 1974, from Gillon 1983) The maximum standing crop (*I*) and (live) phytomass (*II*) is attained before the end of the growing season, which extends almost to the end of the year. *III* Standing dead

In addition to the seasonal variations, considerable fluctuations also occur from year to year because the production of grass mass is much higher during periods of heavy rainfall than at times of low precipitation. For example, Braun (1973), in two successive years at the same sites in the Serengeti/Tanzania, once measured 1.5–4 t ha^{-1}, and on the second occasion 6–11.5 t ha^{-1}, i.e. amounts which in the first case are typical of a dry savanna and in the second case are more typical of a moist savanna. This shows clearly that single measurements are not really able to provide representative results and that various measurements taken at different sites and times cannot be compared with one another unless precise data can be given on the respective circumstances, such as the mean and actual amounts of precipitation, the slope of the terrain, the water-retention capacity of the soil and the composition of the plant stand (by species and life form).

Figure 167 shows the maximum (above-ground) phytomasses and primary production values which were found in various areas of Western and Central Africa having different mean amounts of annual precipitation. On the whole, a linear correlation exists, similar to that found in the steppes and thorn savannas. However, in each case this correlation depends on the respective composition of species in the grass stands (Fig. 168) as well as on some further production conditions, such as the quality of the soil and the length of the rainy season. In general, the correlation is less distinct at high levels of precipitation.

Compared with the temperate steppes and the semi-arid thorn savannas, a large amount of the primary production goes into the above-ground phytomass; at least in the moist savannas, it is more than 50% of the total PP_N.

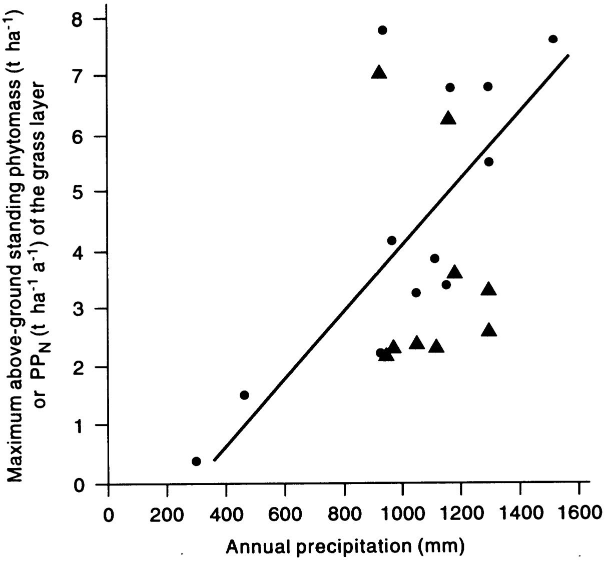


Fig. 167. Relationship between mean annual precipitation, maximum grass phytomass (*circles*) and above-ground primary production (*triangles*) of the grass layer in Central and West African savannas. (Ohiagu and Wood 1979)

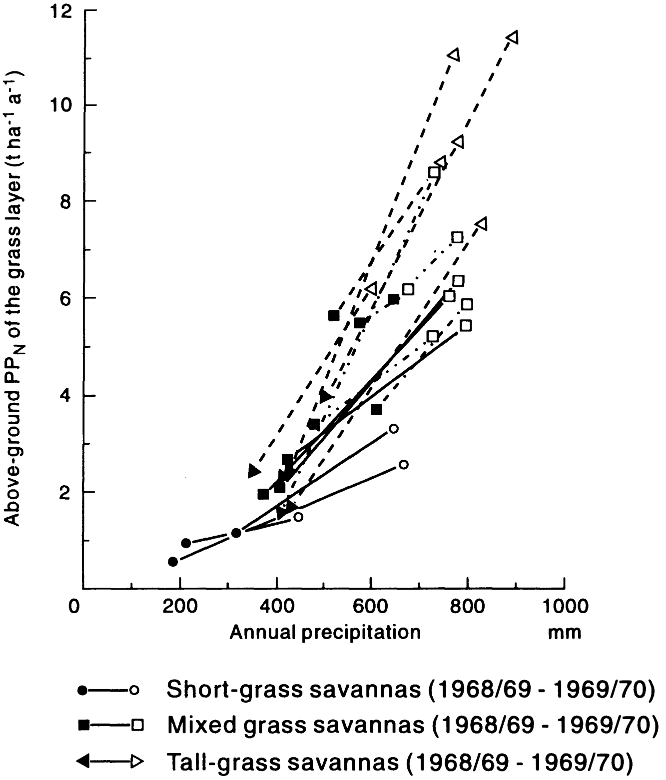


Fig. 168. Grass production in the Serengeti/Tanzania as a function of precipitation and plant stands. (Braun 1973). All the savanna stands reacted to the increased amounts of precipitation during the 1969/70 rainy season, as compared with the 1968/69 rainy season, by an increase in PP_N, although there was great variation in the individual amounts

Mineral Reserves and Turnovers, Decomposition of the Litter

The *nutrient supply in the soils* is generally poor. For the plants, it is therefore particularly important to maintain and make optimal use of the stock of nutrients present in the system. The grasses do this by forming high root/shoot ratios and through their dense ('intensive') root systems, which are closely linked with microorganisms, such as the N_2-fixing azospirillum and the mycorrhizas. Investigations conducted in several African and South American savannas have shown that azospirillum binds on average 10–37 g N ha^{-1} per day and a maximum (together with the N_2-fixing blue-green algae living free in the soil) of up to 100 g N ha^{-1} per day (Medina 1987). It is assumed that the mycorrhizas significantly increase the availability of P.

As far as is known, the biological fixing of N_2 and the amounts of nitrogen input with the rainwater equal the losses caused by nitrate leaching and – in particular – by volatilization when organic substances are burnt (Table 40). Also,

Table 40. Nitrogen balances (in kg ha^{-1} a^{-1} in two moist savannas). (Medina 1987)

	Lamto (Ivory Coast)	Venezuela (Trachypogon Sav.)
Inputs through rainwater	19 (Inorganic 4.5)	2.6
Biological N_2 fixing		
Blue-green algae	–	0.7
Microorganisms in the root zone (rhizosphere)	9–12	6.7
Losses due to fire	17–23	8.5
Leaching	5.6	0.5
Balance	+3.9	+1.0

in the case of the partially volatile phosphates, fire does not result in deficits (Medina 1987).

The rapid *decomposition of dead organic matter*, which is characteristic of all savanna regions and is evident from the low percentage of standing dead in the phytomass and the almost total lack of litter layers, is advantageous in view of the low reserves of nutrients in the soil. The material is broken down, if not by fire then in particular by termites. Most herbivores, from grasshoppers to the large mammals, can make at best only inadequate use of dead grasses/leaves. They contribute to the turnovers of matter and energy essentially by consuming living plants and, in the case of large mammals, also by trampling (mechanical size reduction) (Ruess 1987).

Termites are a characteristic component of all savanna ecosystems. Many species build above-ground structures for their nests (*termitaria*). These may be a few decimetres to several metres tall; they may be slender or broad (hill-like) in shape and they may appear singly or in dense clusters (occupying up to about 5% of the surface area). In almost every case, they are striking features in the landscape, sometimes by themselves, and sometimes because they are covered with a shrub and tree vegetation which is different and frequently denser than that in the surrounding countryside (termitaria savanna).

The species of termites which build above-ground structures fetch the necessary soil material from depths down to 150 cm. They transport frequently small grain sizes (usually clays and fine sands, maximum grain size = approximately 2–3 mm) to the surface (there are no mound-building termites on low-clay substrates). As a rule, termite mounds are therefore characterized by more finely textured material than their surroundings. Also, they have higher cation exchange capacities, higher base saturations (in particular high Ca percentages) and higher humus and nitrogen contents.

The amount of *soil moved (displaced) by termites* can be considerable. For example, calculations in western Nigeria and Zaire revealed that, if all the mounds were flattened, the surface of the soil would be covered with a layer of material between 20 and 30 cm thick (Nye 1955; Meyer 1960). According to other studies, the amount of material transported to the surface by termites over a period of 100–1000 years is equivalent to a soil layer 1 cm thick (Young 1976).

Most species of termites live exclusively on dead organic material. They are capable of utilizing cellulose with the help of the protozoans and bacteria which live in their digestive tracts; others culture fungi to help them digest the litter and dead wood, or they consume only microbially processed wastes (so-called humus eaters). Under comparable soil conditions, the *termite density* increases with the amount of organic substance which is available to them. The density is therefore higher in the rainier, and thus more productive, savannas than in the drier ones: in the former, more than 100 million termites per hectare occur, while in the latter "only" a few million are counted. In each case, the termites play a considerable role in helping to break down organic wastes. As long as fire is not responsible for most of the decomposition, it can be anticipated that at least one quarter, but usually more than 50%, of all the wastes pass through the "stomachs" of the termites.

The activity of the termites, like that of other groups of soil-dwelling fauna, facilitates the microbial breakdown of the plant wastes by mechanically (and partially also chemically) comminuting them, and by mixing them with the mineral soil.

On the other hand, many soil-dwelling organisms also profit from the microbes because they cannot utilize the waste materials until the latter have been decomposed to varying degrees. The excrements of these organisms are then processed again by the microbes. These animals thus occupy an intermediate position in the biological chain of decomposition.

Depending on their food specialization (see above), termites can appear either at the beginning of the food chain or, as described for other soil dwellers, at a later stage in the chain. As in the Humid Mid-Latitudes, the microbial decomposers include fungi, actinomyctes and bacteria. They are the actual mineralizers in this system, i.e. it is through their activity that most of the organically bound minerals are finally released in simple inorganic form and thus become available to the plants once more. On average, this *recycling period* (time taken to mineralize the wastes) is completed in less than 1 year. Since humification processes are relatively insignificant, this means that the humus contents of the savanna soils are in all cases low.

Correspondingly, the reserves of nitrogen and phosphorus are also low, and not infrequently inadequate, and thus a limiting factor as far as plant production is concerned (San José and Medina 1976; Mott et al. 1985).

Ecosystems

The savanna ecosystems differ considerably from each other – as regards reserves and turnover rates – depending on the humidity conditions (moist or dry savannas), tree density (dry forests, semi-evergreen humid forests, tree savannas, grass savannas), the significance of animal browsing (ungulates) or other forms of herbivory (insects) and fire (frequency, intensity etc.). Therefore, it is not possible to present an ecosystem model which is representative of all savannas or even of only the more frequent types of savanna.

The following remarks are restricted essentially to reporting the results which were achieved in two thoroughly studied African savannas. The first of these is a moist savanna near Lamto on the Ivory Coast (Lamotte 1975, 1978; Menaut and César 1982; Lamotte and Bourlière 1983), and the second is the dry savanna of the Serengeti in Tanzania (Sinclair 1975; Lamprey 1979; Sinclair and Norton-Griffith 1979). Detailed ecological studies are also available for the Nylsvley savanna in Transvaal/South Africa (Huntley and Walker 1982, inter alia) and from the grasslands of Varanasi in India (Singh 1985, inter alia).

The *Lamto savanna* consists of a grass layer 1.50–2.50 m tall (consisting of *Andropogon* spp., *Hyparrhenia* spp., *Loudetia simplex* and others) and sometimes open, sometimes dense, stands of trees (including many Borassus palms) and shrubs. Various types of savanna can be identified on the basis of the prevailing stands of plant species, and their distribution is linked with different soil conditions. The climate is characterized by large amounts of annual precipitation (on average 1250 mm, fluctuating between 900 and 1700 mm annually), a short dry season from December to February (maximum from November to March) and high air temperatures of 24–30 °C on a year-round basis. In climatic terms, the Lamto savanna belongs therefore to the Humid Tropics. In keeping with the favourable humidity conditions, the PP_N is very high at more than 27 $t\,ha^{-1}\,a^{-1}$ (Table 41). The most important producers are the grasses. About 0.8% of the global radiation is utilized.

The grass burns off each year. As a result, 6–8 t of dry matter is destroyed per hectare, i.e. about one half of the above-ground production or just under one third of the total PP_N. The remainder is for the most part consumed by *herbivores* or *saprovores*, the most important of which are the grasshoppers, termites and earthworms (usually Megascolecidae); rodents, caterpillars and ants may also play

Table 41. Phytomass and primary production in an open scrub savanna (*Andropogonea* open scrub savanna) at Lamto, Ivory Coast. (Menaut and César 1982)

	Grasses	Woody plants	Total
Phytomass (t ha^{-1})			
– Above-ground	7.0[a]	21.9[c]	28.9
– Below-ground	10.1[b]	9.2	19.3
– Total	17.1	31.1	48.2
Primary production (t ha^{-1})			
– Above-ground	12.8	1.33	14.1
– Below-ground	13.3	0.13	13.4
– Total	26.1	1.46	27.6

[a] Maximum standing crop. [b] Mean root mass. [c] Wood mass.

a certain role. Ungulates, which feature prominently elsewhere on the African savannas, are rare in the Lamto savanna.

Only an extremely small part of the food taken up by the primary consumers is assimilated (on average, barely 13%) (Fig. 169). Correspondingly, the secondary production by the primary consumers is remarkably low at only about 1% of the ingested food energy, although their respiration losses (because they are all poikilothermic animals) are relatively small. In particular, the earthworms have an extremely low *gross production efficiency* (P/C) (Table 42).

Most of the food intake is defecated again virtually unchanged (226×10^6 kJ ha^{-1} a^{-1}) and, together with the smaller amount of PP_N, which neither burns nor is consumed by animals (67×10^6 kJ ha^{-1} a^{-1}), it is therefore available to the *decomposers* (fungi, actinomycetes, bacteria) to be further broken down; this process accounts for no less than > 60% of the primary production. Accord-

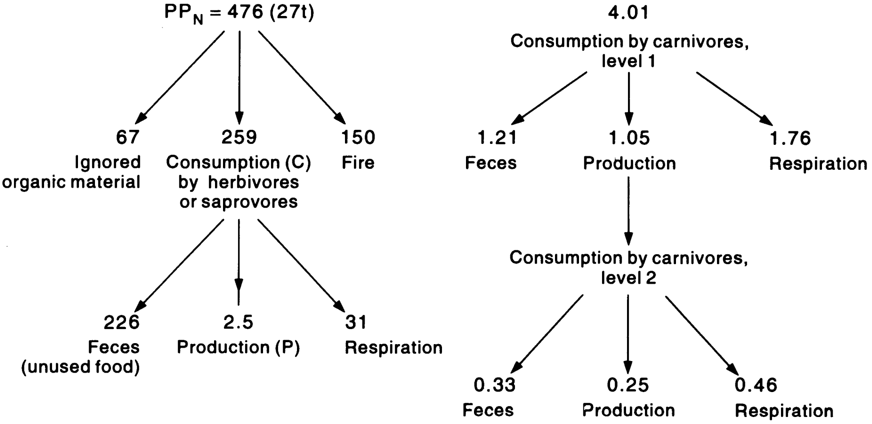


Fig. 169. Energy conversion by primary consumers (herbivores or saprovores) and secondary consumers (carnivores, at two levels) in the Lamto savanna. (Lamotte and Bourlière 1983). The energy flows (*arrows*) are given in 10^6 kJ ha^{-1} a^{-1}

Table 42. Average animal biomass, consumption and production (in 10^3 kJ ha^{-1} or 10^3 kJ ha^{-1} a^{-1}) and turnover efficiencies of some major groups of primary consumers in the Lamto savanna. (Lamotte 1982)

	Animal biomass	Consumption	Production	Turnover efficiencies		
	(B)	(C)	(P)	C/B	P/B	P/C
Rodents	7.3	730	14.6	100	2	0.02
Grasshoppers	12	1 300	83	108	7	0.06
Termites (fungus cultivators)	23	17 000	230	740	10	0.014
Earthworms	850	230 000	1500	270	1.8	0.007

ing to the measurements, it is probable that part of the standing dead, equivalent to 51×10^6 kJ ha^{-1} a^{-1}, is already broken down before it falls to the ground and becomes litter. Similar facts are also reported from steppe ecosystems (see Chap. 3.4.5.2).

In the case of the *secondary consumers* (carnivores), we can distinguish at least two trophic levels (food levels) on which the energy flows are distributed, as shown in Fig. 169. The fact that the energy taken up by the carnivores, namely 4.01×10^6 kJ ha^{-1} a^{-1}, is greater than the energy stored in the herbivores (2.5×10^6 kJ ha^{-1} a^{-1}), is probably because many of the secondary consumers feed partially on the feces (excrement) of the herbivores and also consume detrivores. The low respiration losses of the carnivores, which like the herbivores are mostly poikilothermic animals, as well as their high digestion (assimilation) efficiency, explain the high degree of *gross production efficiency* at both levels: in each case, about one quarter of the food intake goes into the production of the secondary consumers. In Lamto, the important secondary consumers include some species of birds, lizards, mantises (*Mantodea* e.g. praying mantises), spiders and ants.

The *Serengeti* differs from the Lamto savanna not only in that it belongs to the dry savanna type, but also because it has a large stock of game. The first of these two factors means that primary production is interrupted for many more months, with the result that (1) the annual growth is significantly less than that in Lamto, and (2) no green plant material (leaves of trees, fresh grass) is available for long periods of time. Ungulates and other herbivores are then forced to live partially on low grade forage, which they are barely able to assimilate, and partially on the reserves of fat which they built up during the previous rainy

Table 43. Grass production and off-take (in kg ha^{-1} a^{-1} and in %) by some major groups of herbivores and detrivores in dry savanna types of the Serengeti. (Sinclair 1975)

	Tall-grass savannas		Short-grass savannas		Kopjes (outcrop rocks)	
Above-ground grass production	5978	100.0	4703	100.0	5978	100.0
Herbivore consumption, total	1647	27.6	1795	38.2	865	14.4
– Ungulates	*1122*	*18.8*	*1597*	*34.0*	*122*	*2.0*
– Small mammals	*69*	*1.2*	*4*	*0.1*	*259*	*4.3*
– Grasshoppers	*456*	*7.6*	*194*	*4.1*	*484*	*8.1*
Removed by fire	3185	53.3	586	12.5	3430	57.4
Breakdown by detrivores	1146	19.2	2322	49.5	1683	28.2
Animal biomass (kg ha^{-1})						
– Ungulates	22.90		17.90		3.39	
– Small mammals	0.42		0.07		2.44	
– Grasshoppers	0.79		0.34		0.81	
– Detrivores	6.80		13.80		10.00	

season. For many of them, these reserves are insufficient, and as a result, the death rate climbs significantly during the dry season.

Table 43 shows the annual grass production of three types of savanna in the Serengeti, the utilization of this material by herbivores and detrivores, as well as their biomasses (Sinclair 1975). More than 50% of the grass production was burnt on the tall-grass savannas and on the kopjes (outcrop rocks). In the former, a further 28% was consumed by herbivores and 19% by detrivores; on the kopjes, however, the amounts consumed by the detrivores were higher, because there are fewer herbivores in those areas. In the short-grass savannas, where the losses due to fire were low, the herbivores consumed 38% of the grass production and the detrivores more than 50%. Termites were by far the most important of the detrivores.

3.7.6 Land Use

The Seasonal Tropics are the most densely populated and agriculturally utilized regions in the tropics (in SE Asia, some of the areas which were formerly covered by rain forest are the only other tropical places which have very high population). Compared with the Humid Tropics, which follow towards the equator, their superiority lies in the fact that,

- the soils, as a rule, are more fertile (or to put it the other way, less infertile);
- the "winter" drought makes it easier to clear the land by burning, if any dense tree growth exists at all;
- the continuous grass cover favours cattle herding;
- the high air temperatures, copious precipitation and large amounts of insolation which favour growth conditions in the Humid Tropics are available in equal quality in the savanna regions during the rainy season;
- many savanna crops, such as maize, sugar cane and cotton, whose ripening phase extends beyond the end of the rainy season, profit from the more sunny conditions at that time, as compared to a permanently humid climate.

The superiority of the Seasonal Tropics over the Tropical/Subtropical Arid Lands which follow towards the Tropics of Cancer and Capricorn requires no further explanation. It is lacking only in those areas where artificial irrigation can be carried out in the arid lands.

The length of the rainy season and the magnitude of the rainfall are sufficient everywhere in the Seasonal Tropics (although not every year) to support rain-fed cultivation of numerous species of crops, such as maize, sorghum, several small-grained species of millets, cotton, groundnuts, rice, various species of beans and sweet potatoes (batatas). On the other hand, the fact that a seasonal dry period lasting at least 3 months regularly occurs means that only annual species can be cultivated, unless additional artificial irrigation is provided (as is generally the case with sugar cane plantations), or relatively drought-resistant species are grown [e.g. cassava (manioc) and sisal]. Permanent plantations of crops having a greater need for moisture, such as coffee and tea, flourish only in high-altitude regions that profit from orographic rains or fogs during the "dry seasons".

Rain-fed agriculture is still carried on to this day, on a large scale, in its traditional form of *semi-permanent cultivation*, (land rotation, shifting cultivation sensu lato). In this land-use system, the fields are abandoned for several years after they have been cultivated for an equally long period of time, so that the fertility of the soil can regenerate itself. Land rotation is thus a land-use system which is adapted to the (moderately) difficult soil conditions in the Seasonal Tropics and to the generally low level of economic inputs (particularly fertilizers).

The temporal relationship between cultivation years and fallow periods, i.e. the *intensity of rotation*, can be expressed for any given farm, either in the form of a cultivation factor (Allen 1949) or by the symbol R (Joosten 1962; Schultz 1984, p. 93).

In the case of the *cultivation factor*, the entire period of rotation, i.e. the number of cultivation years plus the number of subsequent fallow years until cultivation starts up again, is divided by the number of cultivation years. The result shows how many fields are required to maintain a certain rotation. For example, if a 5-year cultivation period is followed by 5 years of fallow, then the cultivation factor is 2; i.e. altogether two fields having the same size (and same quality) are needed, one of which is undergoing regeneration at any one time.

In the case of the *symbol R*, the number of cultivation years is divided by the total period of rotation (i.e. the reciprocal of the cultivation factor), and the result is frequently expressed as a percentage. The advantage of this method of calculation is that it directly indicates the percentage area under cultivation, in relation to the total area available for arable farming. For instance, R in the above example works out to 0.5; the percentage of land which has just been cultivated therefore amounts to 50% of the total arable land, and the remaining 50% temporarily remain fallow.

We talk of land rotation when $R \geq 0.3 \leq 0.7$. The area required for a subsistence farm is then 1.5 to 3 times as large as that of a corresponding farm in which permanent cultivation is practised. It rises even higher (i.e. $R<0.3$) when extremely unfavourable soil conditions further shorten the possible length of cultivation and force longer periods of fallow to be imposed, in order to permit the soil fertility to be regenerated. This is the case in many moist savanna regions, and certainly even more in the Humid Tropics (see Chap. 3.9.6: slash-and-burn/shifting cultivation).

The rapid increase in population in all savanna regions (the population has approximately doubled over the last 25 years) has necessitated a considerable expansion of the area under cultivation. In many places, this has led to a shortage of land which no longer permits the original fallow system, with its great demands for land, to be maintained. The change to more intensive cropping systems has become possible because the introduction of mineral fertilizers offers a modern alternative means of regenerating the nutrient reserves of the soil. Therefore, *permanent cultivation systems* (without any fallow years) are more and more frequently replacing the earlier land rotation systems; at least, many farms are now practising permanent cultivation close to their farmyards, in so-called homegardens.

For mixed (agro-pastoral) land-use systems, the rotation with shrub and herbaceous legumes as forage plants (instead of vegetation growing wild on the traditional fallow areas) offers another way of intensifying land use. Species such as *Cajanus*, *Centrosema*, *Leucaena* and *Stylosanthes*, which place little stress on the soil and for the most part exhibit high forage values, are possible choices here. In addition, they increase the nitrogen content in the soil, and this is of benefit for the subsequent crops. When moderate amounts of phosphorus fertilizers are applied, the yields of the plants can also be increased.

Irrigation of the fields is not necessary in the case of annual crops, but it can increase the yields, and possibly allows a larger number of harvests per year. Therefore, irrigation farming is widespread in particularly densely populated areas, such as South and Southeast Asia, in the form of paddy rice cultivation. Irrigation farming also permits crops such as wheat and various types of vegetables, which suffer from a high instance of disease and pest infestation during the rainy season, to be cultivated during the dry season. Finally, irrigation is used to supplement rainfall in the case of permanent crops, such as coffee, tea, sugar cane, plantain (bananas), citrus fruits, oil palms and pineapples.

Characteristics of the farms: in general, the farms are small in size and grow a wide variety of crops. Part, or sometimes even all, of the produce from the farm is used to support the farmer and his family. Simple implements, e.g. hoes and ox-drawn ploughs, are widely used, and productivity per worker is correspondingly low. Apart from the irrigated crops, the productivity per unit area is also low. Most farms keep livestock, frequently cattle. The link between crop growing and animal husbandry is weak. In many regions (e.g. Africa), only recently has it been strengthened slightly as increasing use has been made of draft animals to pull the ploughs, and the dung of these animals has been spread on the fields to improve the soil. Practically no forage crops for the animals are grown anywhere. However, the livestock can graze on the harvest residues and the fallow areas. Otherwise, the cattle, sheep and goats are driven into areas of the savanna which are not used for crop growing and therefore are available to everybody as (natural) grazing areas.

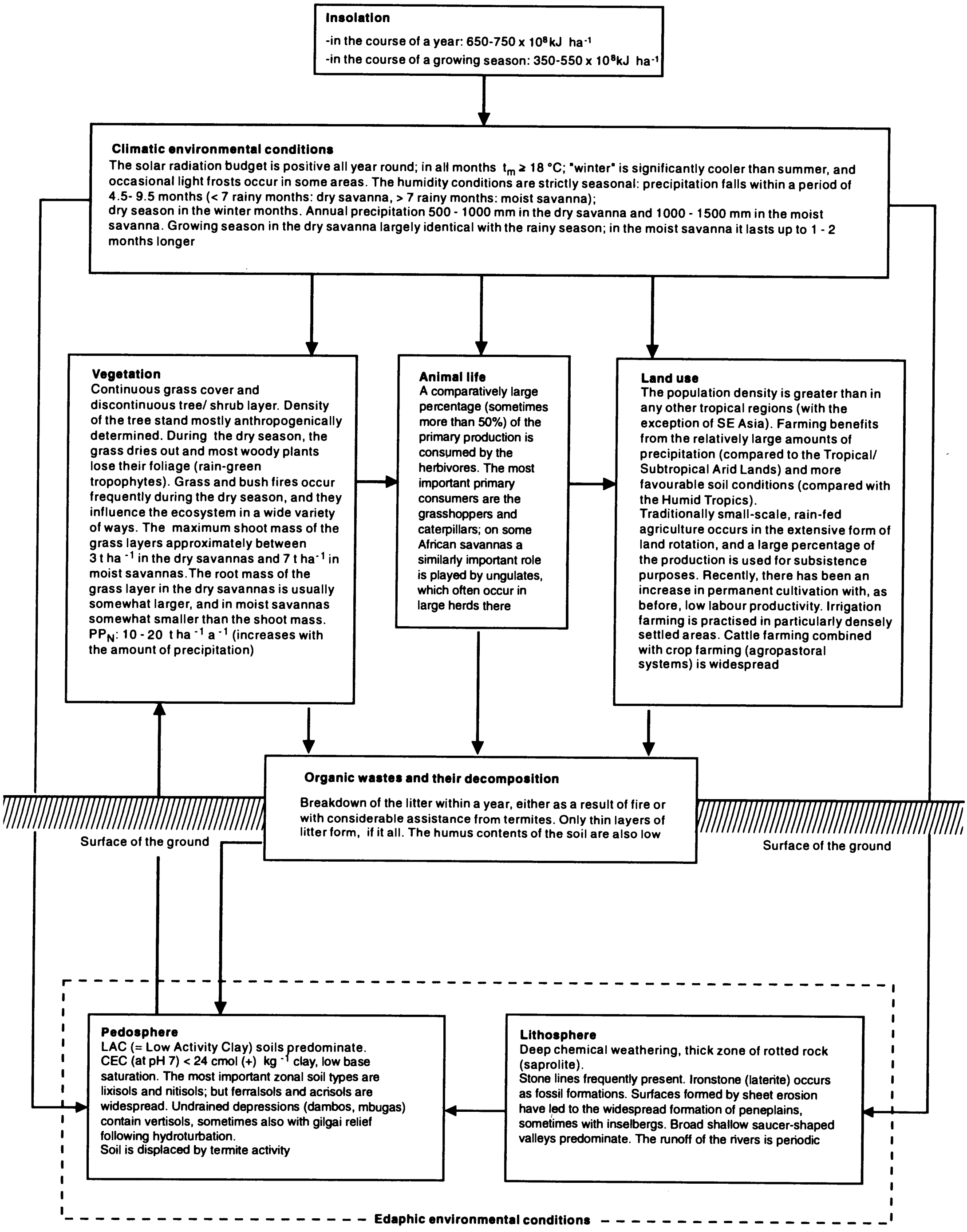
In Africa, the use of the savanna for grazing cattle runs into difficulties where the *tsetse flies* occur in large numbers, because they transmit *Nagana disease* (trypanosomiasis). By and large, this problem exists wherever dense tree stands, particularly in the dry and moist forests, offer adequate shade to the flies, which are sensitive to transpiration losses. The progressive deforestation which goes together with increasing settlement of the land, and the conversion of these formations and of the forested savannas into open grassland, therefore has the positive effect of eradicating the tsetse (*tsetse clearings*).

Overgrazing occurred in many regions, as the population increased rapidly and the number of animals kept per household grew even faster. Table 44 shows the *approximate numbers of animals that can be supported* by natural pastures in the three zonal savanna formations. If the stocking density is increased beyond

Table 44. Estimates of livestock-carrying capacity in savannas, as a function of the moisture conditions. (Koechlin and Menaut 1979). For comparison, the data for the respective stocks of wild animals in East Africa are also given. (Lamprey 1983)

	Above-ground grass/ forb production ($t\ ha^{-1}a^{-1}$)	Livestock-carrying capacity (kg live weight $ha^{-1}a^{-1}$)	Minimum grazing area (in ha per livestock unit = 500 kg live weight)	Mean wildlife biomass (kg live weight $ha^{-1}a^{-1}$)
Moist savanna $> 1200\ mm\,a^{-1}$	6–20	150 (up to 500 during the growing season)	3.3	100
Dry savanna 500–1200 mm a^{-1}	1–8	80–125[a] (160–250 during the growing season)	4–6.25	66
Thorn savanna $< 500\ mm\,a^{-1}$	0.2–5	50	10	28.2

[a] The ability to support livestock is considerably reduced if fires *early* in the dry season destroy the grass: although the grass loses most of its nutritional value as a result of becoming dried out, it still helps to reduce the forage deficits during the dry season. On the other hand, fires *late* in the dry season are advantageous (see Chap 3.7.5.2).



Insolation

-in the course of a year: 650-750 x 10^8 kJ ha^{-1}
-in the course of a growing season: 350-550 x 10^8 kJ ha^{-1}

Climatic environmental conditions

The solar radiation budget is positive all year round; in all months $t_m \geq 18$ °C; "winter" is significantly cooler than summer, and occasional light frosts occur in some areas. The humidity conditions are strictly seasonal: precipitation falls within a period of 4.5- 9.5 months (< 7 rainy months: dry savanna, > 7 rainy months: moist savanna); dry season in the winter months. Annual precipitation 500 - 1000 mm in the dry savanna and 1000 - 1500 mm in the moist savanna. Growing season in the dry savanna largely identical with the rainy season; in the moist savanna it lasts up to 1 - 2 months longer

Vegetation

Continuous grass cover and discontinuous tree/ shrub layer. Density of the tree stand mostly anthropogenically determined. During the dry season, the grass dries out and most woody plants lose their foliage (rain-green tropophytes). Grass and bush fires occur frequently during the dry season, and they influence the ecosystem in a wide variety of ways. The maximum shoot mass of the grass layers approximately between 3 t ha^{-1} in the dry savannas and 7 t ha^{-1} in moist savannas. The root mass of the grass layer in the dry savannas is usually somewhat larger, and in moist savannas somewhat smaller than the shoot mass. PP_N: 10 - 20 t ha^{-1} a^{-1} (increases with the amount of precipitation)

Animal life

A comparatively large percentage (sometimes more than 50%) of the primary production is consumed by the herbivores. The most important primary consumers are the grasshoppers and caterpillars; on some African savannas a similarly important role is played by ungulates, which often occur in large herds there

Land use

The population density is greater than in any other tropical regions (with the exception of SE Asia). Farming benefits from the relatively large amounts of precipitation (compared to the Tropical/ Subtropical Arid Lands) and more favourable soil conditions (compared with the Humid Tropics).
Traditionally small-scale, rain-fed agriculture occurs in the extensive form of land rotation, and a large percentage of the production is used for subsistence purposes. Recently, there has been an increase in permanent cultivation with, as before, low labour productivity. Irrigation farming is practised in particularly densely settled areas. Cattle farming combined with crop farming (agropastoral systems) is widespread

Organic wastes and their decomposition

Breakdown of the litter within a year, either as a result of fire or with considerable assistance from termites. Only thin layers of litter form, if it all. The humus contents of the soil are also low

Pedosphere

LAC (= Low Activity Clay) soils predominate.
CEC (at pH 7) < 24 cmol (+) kg^{-1} clay, low base saturation. The most important zonal soil types are lixisols and nitisols; but ferralsols and acrisols are widespread. Undrained depressions (dambos, mbugas) contain vertisols, sometimes also with gilgai relief following hydroturbation.
Soil is displaced by termite activity

Lithosphere

Deep chemical weathering, thick zone of rotted rock (saprolite).
Stone lines frequently present. Ironstone (laterite) occurs as fossil formations. Surfaces formed by sheet erosion have led to the widespread formation of peneplains, sometimes with inselbergs. Broad shallow saucer-shaped valleys predominate. The runoff of the rivers is periodic

Edaphic environmental conditions

Fig. 170. Synoptic diagram of the Seasonal Tropics

these limits, the grass cover is damaged and thus grass production is reduced; in addition, bushes may spread over the grazing areas, and on sloping land the soil may be destroyed by erosion (see Chap. 3.7.3).

It is a matter of dispute whether grazing animals gradually shift the composition of the grass layer towards inedible species. The studies conducted by Dye (1983), Mathews (1984) and Walker (1987) revealed that it was, in fact, the distribution of rainfall in the individual years that decided which species of grass or forb would predominate, regardless of whether there was any grazing or not.

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Chapter 3.7: Seasonal Tropics

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3.8 Humid Subtropics

3.8.1 Distribution

The distribution of the Humid Subtropics is just as fragmented as that of the Mediterranean-Type Subtropics: the individual regions are also distributed among five continents (Fig. 171), but they are located slightly closer to the equator (in the latitude range of 25–35°), and one major difference is that they occur strictly on the *eastern sides of the continental land masses*. The individual regions making up the Humid Subtropics have a total combined area of 6.1 million km^2, i.e. they account for 4.1% of the continental land mass.

Towards the equator, the Humid Subtropics border either on the Humid or the Seasonal Tropics, and towards the pole they adjoin the Humid Mid-Latitudes. In all three cases, *thermal* criteria may be used to define the boundaries. The threshold value between the Humid Subtropics and the Humid and Seasonal Tropics is taken to be the absolute frost boundary or the +18 °C isotherm of the coldest month, in each case in the lowlands. The boundary with the Humid Mid-Latitudes

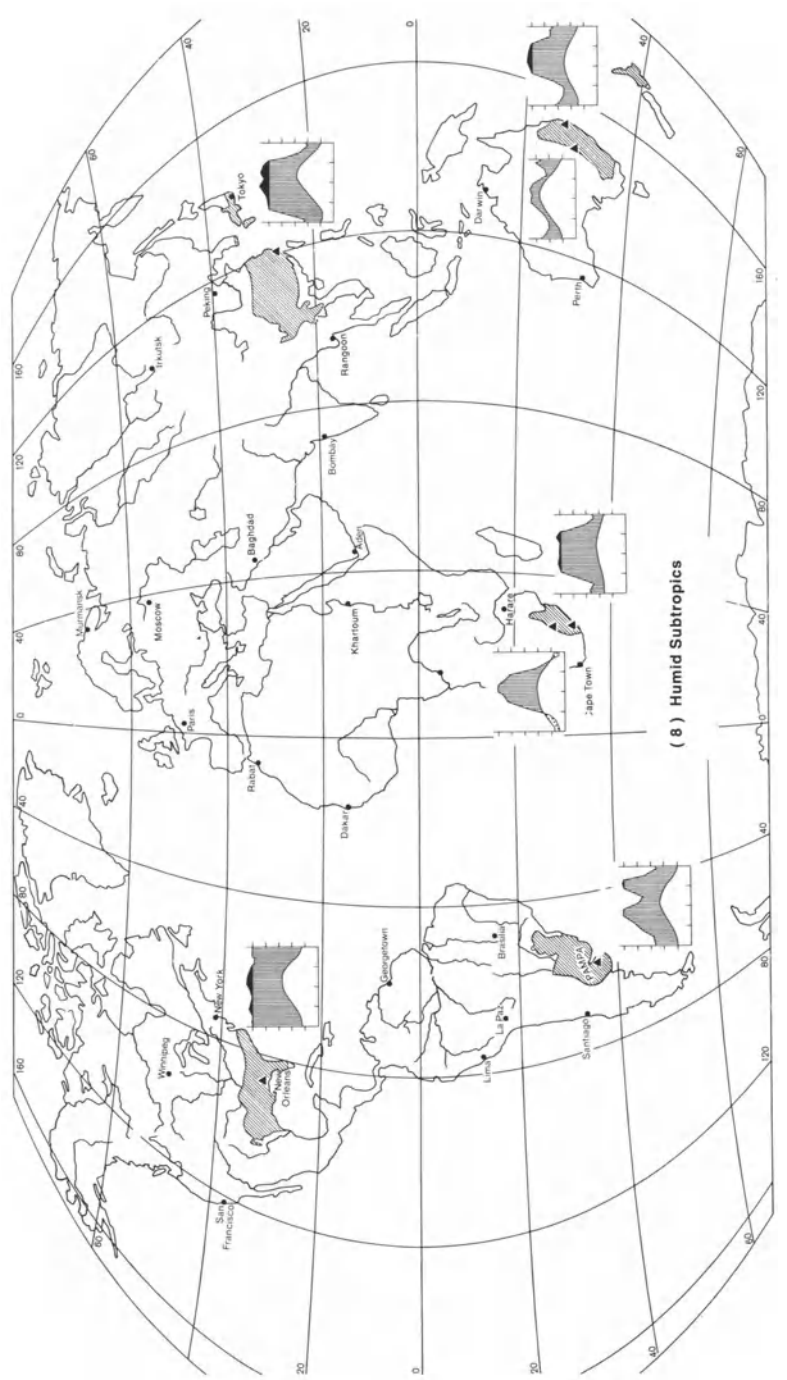


Fig. 171. Humid Subtropics. In both hemispheres, the individual regions are located on the eastern sides of the continents, in each case approximately between latitude 25 and 35°

runs approximately along the line where the summer warming attains mean temperatures of +18 °C in fewer than 4 months and the mean temperature of the coldest month is less than +5 °C, and in some (continental) regions less than +2 °C. In contrast to the Humid Tropics, the periodicity of plant growth is thermally restricted, but this is less pronounced than in most regions of the Humid Mid-Latitudes.

To the west, i.e. towards the inland areas of the continents, the Tropical/Subtropical Arid Lands are preceded by a *transitional zone* which is frequently several hundred kilometres wide. This transitional zone is characterized by a continuous decline not only in the amount of precipitation (to a level which increasingly limits plant growth), but also in the length of the humid period (as calculated according to the customary humidity indices), which is at first limited to the summer season of the year, then to fewer and fewer summer months until finally desert climates take over.

In this transitional zone, the boundary between the Humid Subtropics and the Tropical/Subtropical Arid Lands has been very arbitrarily drawn where the number of humid months is less than 5 and the vegetation is formed by thorn steppes. This is justifiable because the more humid summer-rain regions also receive moderate amounts of precipitation during the "dry season" (in the climatic diagrams, the precipitation curves run just below the temperature curves during the "dry months"; Figs. 171 and 172), i.e. there is no true (i.e. rainless) dry season, but instead subhumid or semi-arid periods alternate with the humid periods. Many drought-adapted species of plant are able to grow all the year round under these conditions and for them the climate is within certain limits continuously humid.

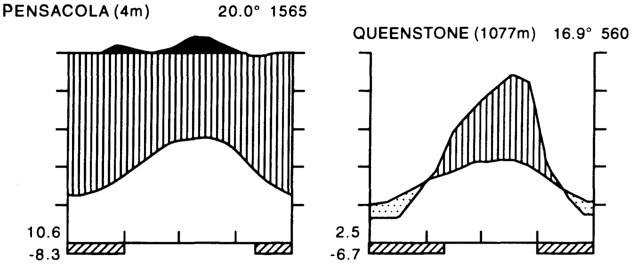


Fig. 172. Climatic diagrams from two stations in the Humid Subtropics. The diagram for Pensacola in the southeastern USA (approximately 31° N and 87° W) shows the conditions which prevail in the Humid Subtropics, sensu stricto: the precipitation is high all year round with a maximum in the summer; the air temperatures decline significantly in the winter months (this is the most striking difference compared with the Humid Tropics), but they remain more or less high above +5 °C (although frosts may temporarily occur in several months). In contrast, the diagram for Queenstown in South Africa, which is located about 150 km inland from the east coast, represents the transitional regions which adjoin the Humid Subtropics, sensu stricto, to the west; the humid period comprises the summer months, while the winter months are subhumid

The Humid Subtropics as defined in this manner include the following regions:

- The whole of the southeastern part of the USA, approximately up to 35° N and extending in the west as far as the mesquite tall-grass prairie of Texas.
- The whole of central China to approximately 32° N (north of the Yangtze), and in the west as far as the forest steppes and the sclerophyllous monsoon forests of Yunnan.
- The southern coastal lowland of Korea.
- The southern half of Japan (in the North up to about 37° N), including the Riukiu Islands.
- The southern states of Brazil (São Paulo, Paraná, Santa Catarina and Rio Grande do Sul), the eastern pampa of Argentina and Uruguay and – as a semi-arid transitional region to the arid lands following to the west – the western pampa of Argentina.
- The southeastern part of South Africa (Natal, Transkei, eastern Cape Province).
- The coastal zone and Great Dividing Range of eastern Australia, approximately between 23° and 37° S.
- The North Island of New Zealand.

3.8.2 Climate

Contrary to the rule which normally applies in the tropics/subtropics, i.e. the precipitation declines from the equator towards the Tropics of Cancer and Capricorn respectively, so that the equatorial rain forest belt is followed first by savanna belts and then by desert belts (see Chap. 3.7.2), the amounts of rainfall on the eastern sides of the continents remain high all the year round. Therefore, in those regions, rain forests can flourish in a latitudinal zone in which otherwise only savannas, deserts or – on the western sides of the continents – sclerophyllous plant formations occur.

This *west-east asymmetry* is linked with monsoonal effects. In the summer months in the respective hemispheres, thermal lows (monsoonal lows) form over the continents bringing oceanic air masses containing water vapour inland from the east. Then, convective events over the continents permit heavy rain showers to occur. As a result, the maximum rainfall occurs in the summer. With increasing distance from the coastal regions, the air masses dry out and the amount of precipitation activity declines. This explains why the latitudinal sequence of *humidity and vegetation parameters* which normally prevails in the tropics/subtropics is replaced by an *east-west sequence.*

The *winter rainfalls* occur in conjunction with inflows of cold air which, in the Northern Hemisphere, come from the low-temperature highs building up over central Asia and central North America. Occasionally, the precipitation falls as snow. The temperatures then drop more sharply than at the same time on the western sides of the continents (nevertheless, the mean monthly temperatures usually remain above +5 °C). Plant growth is therefore more severely restricted by winter cold than in the Mediterranean-Type Subtropics, but most species do not undergo any genuine cold-induced dormancy period of significant duration. However, the occasional frost or sometimes also somewhat longer periods of frost make it impossible to cultivate frost-sensitive species of crops during the winter months. On the other hand, the summers are hot, with large amounts of insolation being received, and are comparable to those of the Seasonal Tropics and to the year-round conditions in the Humid Tropics (Fig. 172).

3.8.3 Relief and Hydrology

According to the morphodynamics, the Humid Subtropics are not an independent zone; instead, in keeping with the hygrothermal conditions, they tend to occupy a middle position between the Humid Tropics and the Humid Mid-Latitudes. For this position it is characteristic that deep chemical weathering occurs; however, not as far advanced as in the Humid Tropics (instead of ferralsols there are only acrisols; see Chap. 3.8.4 Soils); and the subtropical rain forest, which is less luxuriant and less highly developed than the tropical rain forest, offers less protection against erosion; therefore, rilling and gullying of the slopes occur more frequently.

Devastating cyclones occur occasionally on some islands and in certain coastal areas; this is a typical phenomenon, for example, in the American intercontinental sea (hurricanes) and in the southeast part of eastern Asia (typhoons). These cyclones are characterized by storms with extremely high wind velocities (frequently far exceeding 150 km h^{-1}) and extremely intense rainfall (several 100 mm h^{-1}). Even if these cyclones occur only relatively infrequently in the areas in question, they can nevertheless be expected to have a highly destructive effect, sometimes extending far inland in the form of soil erosion, flooding and storm damage. The inner tropics close to the equator, i.e. most parts of the Humid Tropics, are free from tropical cyclones.

3.8.4 Soils

On this topic, see also Chapter 3.7.4 Tropical Soils – General.

The zonal soil type which is characteristic of the Humid Subtropics is the *acrisol*. It is characterized by the fact that the illuvial accumulation of clay (like in the case of luvisols) has resulted in an *argic B horizon* (B_t), which has (in contrast to the luvisols) a cation exchange capacity of less than 24 cmol(+) kg^{-1} clay and a base saturation of less than 50%, at least in some parts of the B_t within 125 cm of the surface. This latter phenomenon is to be seen as the result of the hot-humid climate under which most acrisols occur. The name of the soil (Latin acer = acid) refers to the strong degree of acidification which goes together with the deep weathering and leaching of bases.

The clay fraction contains predominately *low activity clays* (kaolinite), but small amounts of 2 : 1 clay minerals may also occur (in contrast to the ferralsols). Those soils formerly classified as acrisols, having on the one hand atypically *high activity clays* and (correspondingly) a CEC of at least 24 cmol(+) kg^{-1} clay, but showing on the other hand still typically low base saturations due to high exchangeable aluminium contents, are now listed as a separate type of soil having the designation *alisol* (Latin: aluminium). Such soils are frequent in the southeastern part of the USA and in South America.

In both soil units, finely distributed Fe oxides and hydroxides may account for more than 10% of the fine soil. Gibbsite (Al hydroxide) is frequently present. The content of silicate silt is very low; the sand fraction is dominated by quartzes. Weatherable minerals (silicates) are present at most in moderate amounts, but usually not at all. The humus content of the topsoil is generally low (ochric A-horizon), or of low base saturation (umbric A-horizon).

Like the ferralsols, the acrisols form low-nutrient sites – although not always such extreme ones – which require regular fertilizing if they are to be permanently cultivated. Then, however, and when further tending is carried out, they can achieve *high yields*; otherwise, like the ferralsols, they can be used only by means of shifting cultivation, but with shorter periods of fallow than in that case, if significant residual amounts of minerals are still present. Compared with the ferralsols, the *usable (for plants) water-retention capacity* is also more favourable, but on the other hand their greater susceptibility to erosion is more disadvantageous.

Acrisols are by far the most frequent soils in the Humid Tropics and the moist savanna climates (= high-precipitation regions of the Seasonal Tropics). They are particularly frequently present in the subtropical-humid region of the southeastern USA and southeastern China, as well as in tropical southeast Asia.

3.8.5 Vegetation

3.8.5.1 Structural Characteristics

In the regions close to the coast and on the windward side of mountain slopes, where large amounts of precipitation fall all the year round, the potentially natural vegetation consists of luxuriant rain forests; these are initially followed farther inland (towards the west), as the amounts of precipitation decline, by semi-evergreen moist forests or evergreen laurel forests and then by deciduous monsoon or dry forests. Instead of forests, tall-grass meadows can also occur. The rain forests, and in particular the mountain rain forests, may be very similar to those in the tropics. On the other hand, the *laurel forests* are significantly less tall, contain fewer species and have at most two-layer canopies. Tree ferns and epiphytic ferns are frequently present, lianas are rare. The laurel-type leaf shape from which the name of these forests is derived is relatively large (magnolia type) and only moderately scleromorphic – compared with the scleromorphic leaves of mediterranean woody plants.

It is no longer possible today to determine to what extent this *East-West sequence of different plant formations* occurred in all the individual regions of the Humid Subtropics. Especially in the regions located in the Northern Hemisphere, the anthropogenic influences have progressed to such an extent that it is almost impossible to reconstruct the original character of the vegetation. The problem is aggravated by the fact that the three regions in the Southern Hemisphere belong to different floral kingdoms (Neotropical, Paleotropical, Australian kingdoms) and, although they belong to a common floral kingdom (Holarctica), the two regions in the Northern Hemisphere are extremely far apart and have had no connection with one another since at the latest the Pleistocene; i.e. significantly dissimilar flora occur in all regions. Given these facts, it is quite likely that even in its original state, the vegetation exhibited significant regional deviations (quite apart from edaphic factors which individually may have exerted a major influence; see below: pampa). The present situation in the individual regions is as follows:

In *southeastern North America* evergreen broadleaved forests nowadays only occur in small, scattered stands; pine forests are by far the dominant form. In many cases, the evergreen broadleaved trees are mixed with deciduous broadleaved trees and evergreen conifers, and the respective percentages of these three different life forms can vary widely. Often, the evergreen hardwoods form the undergrowth. The evergreen hardwood species include (Olson 1983, p. 103): *Gordonia lasianthus*, *Ilex* spp., *Magnolia grandiflora*, *M. virginiana*, *Myrica cerifera*, *Persea borbonia* and several species of oak (*Quercus* spp.).

As a rule, the percentages of evergreen trees (both leaf and needle species) are higher wherever there is an unfavourable supply of calcium, potassium and phosphorus and a low amount of water available to plants in the soil (Monk 1966). The evergreen species are possibly superior here to the deciduous species because in their case the return of plant nutrients to the soil via crown leaching and leaf fall takes place continuously over the entire year, i.e. the release of the nutrients corresponds to the ongoing needs (of the trees) and therefore leaching losses from the soil occur less easily.

Nowadays, due to human interference, the *east Asian distribution areas* are almost totally lacking in forests. The original vegetation probably consisted of broadleaved, laurel-type forests and sometimes, perhaps, also of sclerophyllous woody plants mixed with deciduous elements (Schmithüsen 1968). To the south, the laurel forests merged into subtropical rain forests. In remote mountain regions of Japan, for example, the vestiges of the original forest vegetation contain large percentages of evergreen Fagaceae (especially *Castanopsis cuspidata*, *Cyclobalanopsis* spp. and *Quercus* spp.) and Lauraceae (including *Cinnamonum* spp., *Machilus* spp.). Other evergreen hardwood species present are *Camellia japonica*, *Distylium racemosum* and *Myrica rubra*; coniferous trees are represented by several species of *Podocarpus*, *Pinus*, *Abies* and *Tsuga* (Satoo 1983). The large number of species and age classes per unit area of forest is a characteristic phenomena. The leaf area index is around 8 $m^2 m^{-2}$. According to Satoo (1983), primary production in a young forest of *Castanopsis cuspidata* is 17.8 $\mathrm{t\,ha^{-1}\,a^{-1}}$ and in a mature forest of *Cinnamonum camphora* it is 15.27 $\mathrm{t\,ha^{-1}\,a^{-1}}$.

In *South America*, large areas of subtropical humid forests still exist. In the mountainous areas of Brazil, their character is determined partly by laurel-type vegetation (*Ilex paraguayensis*) and partly by conifers (*Araucaria angustifolia*) (Schmithüsen 1968). According to the climatic conditions, the eastern pampa is also part of the Humid Subtropics. It has not been clarified whether this area, which is nowadays for the most part used for agricultural purposes, was originally forested land or grass steppe.

In *South Africa*, rain forests flourish along the southern and eastern coasts, from eastern Cape Province to Swaziland. These forests are about 20 m tall (with individual trees reaching 30 m high); they contain a large number of species, and they usually possess two tree/shrub storeys below their canopies as well as a forb layer on the floor of the forest. Common tree species are those of the conifer genus *Podocarpus* (usually *P. latifolius*) and, in many cases the most frequent in the canopy, *Olea capensis*. Epiphytes (mostly mosses, ferns, orchids) and lianas are present in large numbers.

The evergreen humid forests of *Australia*, extending over a width of 150–600 km, almost totally cover the eastern slope of the Great Dividing Range from about 25 °S to Victoria, and they differ from the aforementioned forests in that trees of the genus *Eucalyptus* are almost exclusively dominant in the tree layer (Ovington and Pryor 1983). They grow on low-nutrient soils. Most of the minerals circulating in the system are contained in the organic matter of the plant cover and the litter.

In contrast to the humid forests of eastern Australia, the subtropical forests of the North Island of *New Zealand* are dominated by Podocarpaceae. The genera most frequently found are *Podocarpus, Dacrycarpus, Dacrydium* and *Phyllocladus* (Wardle et al. 1983). Numerous evergreen broadleaf trees are present in the multilayered undergrowth.

3.8.5.2 Stand Reserves and Turnovers of Organic Matter and of Mineral Nutrients in a Semi-Evergreen Oak Forest in the Southeastern USA

The description given here is based on the research results provided by Monk and Day (1988); minor discrepancies in the numerical data contained in that publication unfortunately had to be included here as well. The forest which was studied is located in the southern Appalachians (Coweeta Basin, North Carolina), i.e. in the region bordering on the Humid Mid-Latitudes. Summer-green oaks predominate in the tree stand. The proportion of *evergreen* species of trees and shrubs is estimated – on the basis of their contribution to the leaf production of the forest – at 20–35%. The *leaf area index* is 6.2 $\mathrm{m^2\,m^{-2}}$. The soil is an acrisol with the following characteristics (Swank and Crossley 1988, p. 16):

Depth of soil cm	pH	Cation exchange capacity cmol(+) kg^{-1}	Base saturation %
0–10	4.74	11.6	17.2
20–30	5.02	6.8	19.1

The above-ground phytomass (standing crop) is relatively small at 139.9 t ha^{-1}, whereas the amount of below-ground phytomass is high at 51.4 t ha^{-1} (Fig. 173). The explanation for this is presumably that the above-ground tree layer was decimated by felling (at the start of the century) and the chestnut trees which were formerly dominant have been almost entirely eliminated by disease (in the 1930s). Altogether, the primary production amounts to 14.4 t ha^{-1} a^{-1} (of this amount 8.4 t is above ground). 4.4 t ha^{-1} a^{-1} of the above-ground phytomass are lost as wastes and 0.2 t ha^{-1} a^{-1} is eaten by herbivorous arthropods.

The difference between both sources of loss and the PP$_{\text{N(tree layer)}}$ constitutes the above-ground stand increment (Δ_{GROWTH}), i.e. 4 t ha^{-1} a^{-1}. The forest which

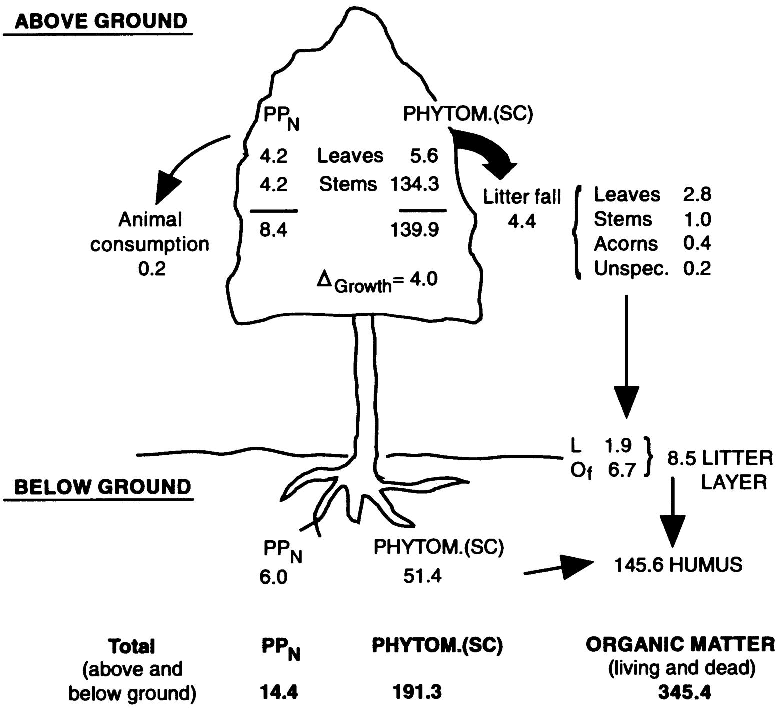


Fig. 173. Stand reserves (t ha^{-1}) and turnovers (t ha^{-1} a^{-1}) of organic matter in a semi-evergreen oak forest in the Coweeta Basin of North Carolina, USA. (Monk and Day 1988); *SC* Standing crop

was investigated is thus in a productive rejuvenation or optimal (mature) phase (Fig. 10).

The differences between (the standing crop of the) leaf mass (5.6 t ha^{-1}) and leaf production (4.2 t ha^{-1} a^{-1}), as well as between leaf production and leaf fall (2.8 t ha^{-1} a^{-1}), in both cases 1.4 t, reveal the major importance of *evergreen* woody plant species. A direct comparison of leaf mass and leaf fall also brings this out clearly; the latter is only one half of the leaf mass.

The *accumulation of litter* on the forest floor attains 8.5 t ha^{-1}. Given a litter input of 4.4 t ha^{-1} a^{-1}, this means that the duration of decomposition of the litter layer is just under two years (decomposition rate 52%). At 64% the leaves account for the largest proportion of the litter fall.

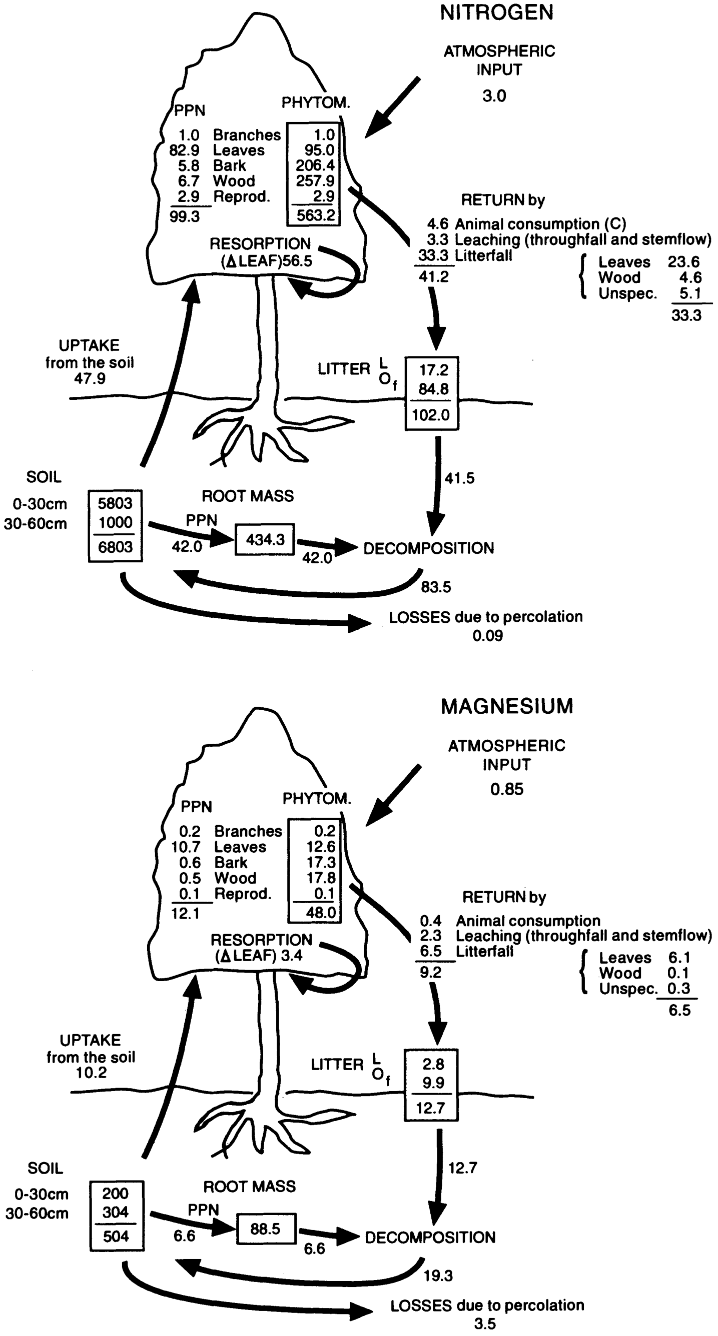
Much larger amounts of dead organic substances are found in the form of *humus*; they are estimated at 145.6 t ha^{-1}. Phytomass (191.3 t ha^{-1}), litter accumulation (8.5 t ha^{-1}) and humus add up to a total of 345.4 t ha^{-1}. Since the animal biomass is not a significant quantity, this figure at the same time represents the entire organic matter content of the system.

In the case of K, Ca and P, the *amounts of minerals bound up in the phytomass* are significantly higher than those available in solution in the soil or in exchangeable form; only in the case of N and Mg are the amounts contained in mineral form (or in the case of N, also organically bound) in the soil higher than in the phytomass (Fig. 174). The high percentages of minerals contained in the vegetation, compared with the total amounts present in the overall mineral cycle, are characteristic for many subtropical rain forests and moist forests.

Of the nutrient elements measured (N, K, Ca, Mg and P), 1.2–7.6% are contained in the litter. In the case of Mg and K, the residence time in the litter is 1.4 and 1.5 years respectively and thus shorter than the mean turnover period of the litter itself (1.9 years), whereas in the case of N, Ca and P the residence time is somewhat longer at 2.2, 2.6 and 2.9 years respectively.

The *minerals required* for primary production are supplied to a considerable extent by resorption from the leaves ($N_{\Delta LEAF}$) before they are cast. The contribution of this internal translocation can be estimated (see also Box 8) from the difference of the mineral contents of $N_{PPN\ (leaves)}$ and $N_{Waste\ (leaves)}$, minus the leaching losses (N_R). It amounts (annually and per hectare) to 56.5 kg N, 13.5 kg K, 3.4 kg Mg and 3.1 kg P; Ca is not resorbed. If these values are compared with the uptake of minerals from the soil, then the contributions made by resorption to the mineral requirements are as follows: 54% in the case of N, 26% in the case of P, 25% in the case of Mg and 21% in the case of K.

The *mineral contents of the annual stand increment* (above ground: 4 t dry matter ha^{-1} a^{-1}) can be calculated from the difference between the mineral uptake and the mineral return. It is seen that only 6–9% of the amounts of N, Mg, Ca and K required for PP_N go into the increment, and only P attains a value of close to 25%. This shows clearly how “wastefully” the minerals are consumed in forming the relatively short-lived leaves and how “sparingly” they are used, on the other hand, for the production of wood.



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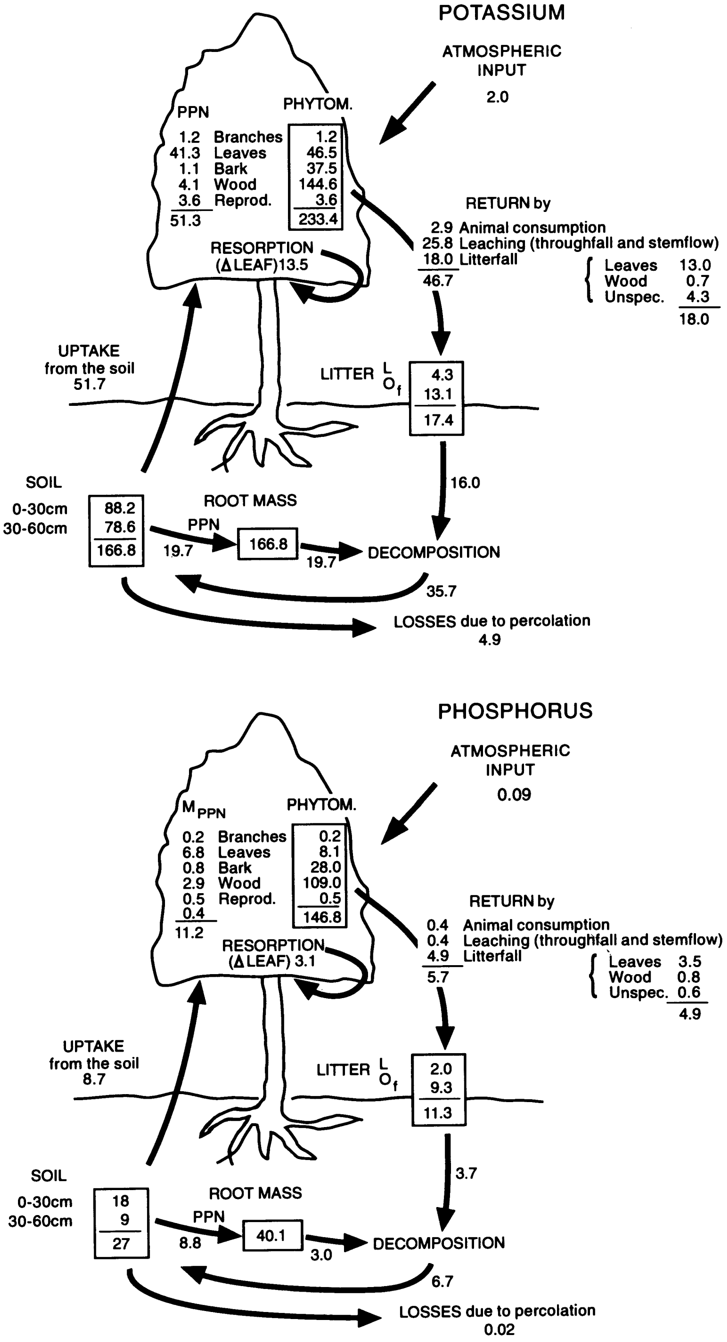

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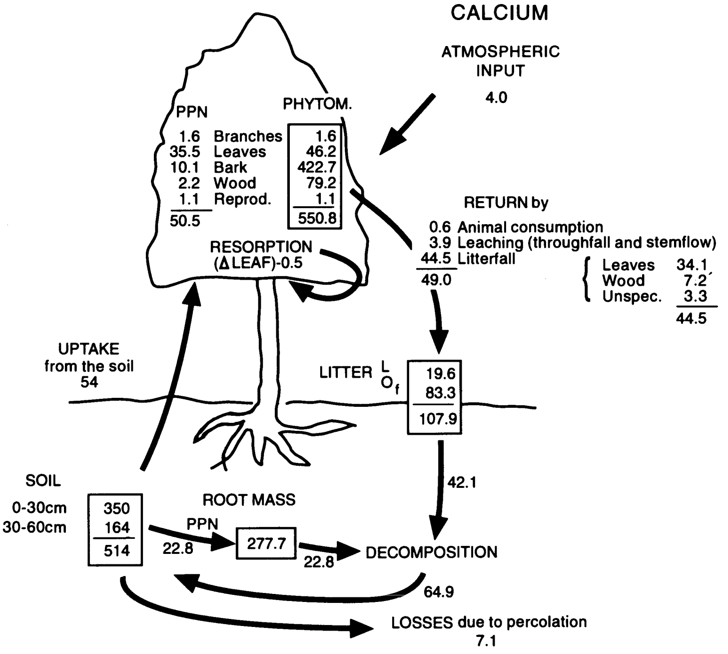
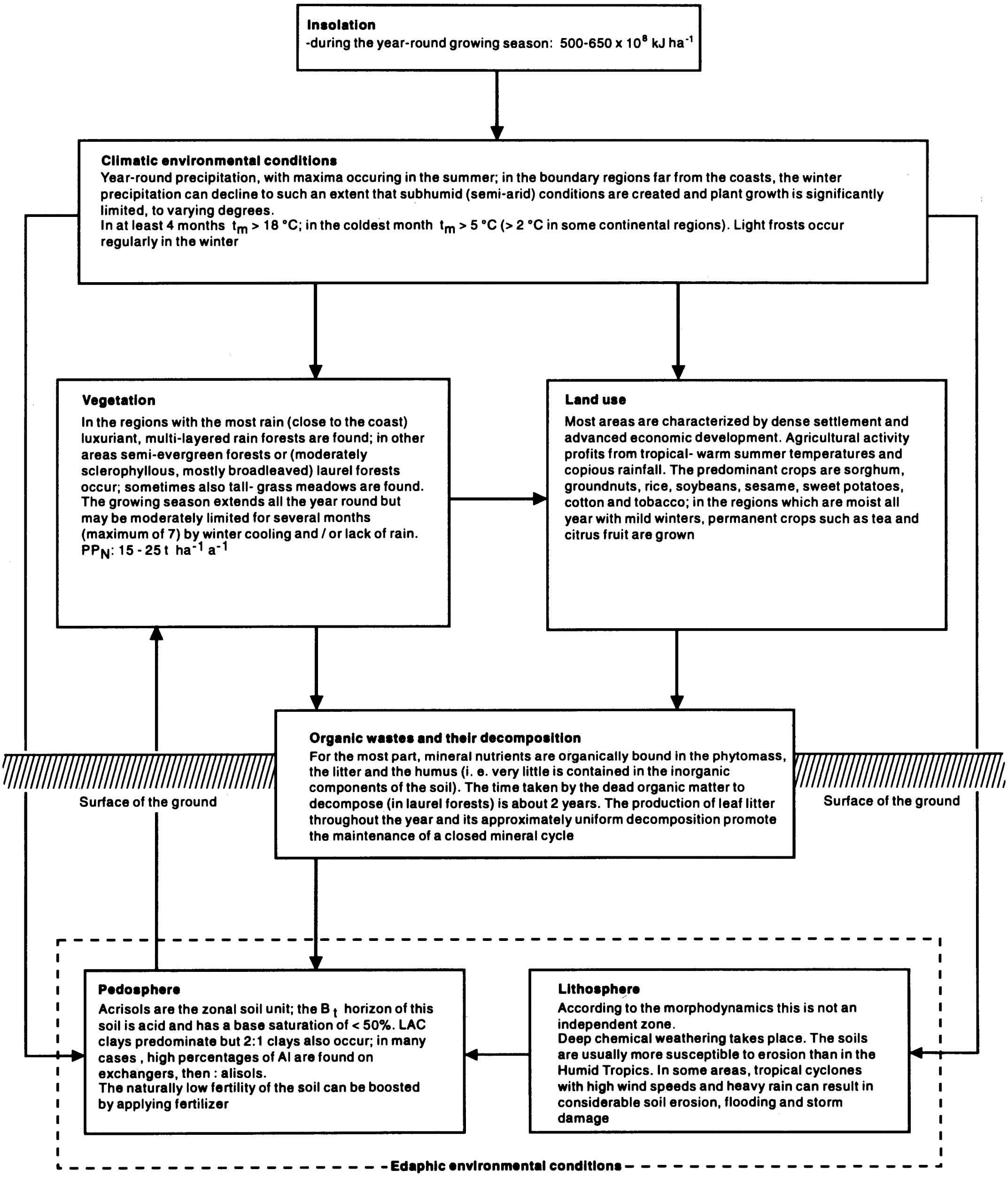


Fig. 174. Mineral reserves (kg ha^{-1}) and turnovers (kg ha^{-1} a^{-1}) in a semi-evergreen oak forest in the Coweeta Basin of North Carolina, USA. (Monk and Day 1988). The numbers for the mineral contents in the soil relate to the easily available minerals, i.e. those in solution or adsorbed onto exchangers; only in the case of nitrogen are the reserves bound in the organic soil matter also included in the figures. *Phytom.* Standing crop. For further explanations see the text

The amount of minerals in the stand increment corresponds to an equal reduction in the soil mineral reserves. Assuming constant rates of increment, it is possible to calculate how long a given reserve in the soil will last. In the case described, Ca would last 138 years, K 95 years, Mg 517 years, P 12.5 years and N 1031 years. The annual amounts of minerals returned via plant wastes and leaching last for more than 8 years of stand increment at a constant rate.

3.8.6 Land Use

Almost all individual regions of the Humid Subtropics belong to the densely populated and economically highly developed parts of the world. Consequently, the natural vegetation has been severely displaced throughout the ecozone (see above) and replaced by a cultural landscape. This occurred, however, to a greatly varying extent, depending on the specific cultural traditions and economic developments found in the individual regions of the ecozone.



Insolation

-during the year-round growing season: 500-650 x 10^8 kJ ha^{-1}

Climatic environmental conditions

Year-round precipitation, with maxima occuring in the summer; in the boundary regions far from the coasts, the winter precipitation can decline to such an extent that subhumid (semi-arid) conditions are created and plant growth is significantly limited, to varying degrees.

In at least 4 months $t_m > 18$ °C; in the coldest month $t_m > 5$ °C (> 2 °C in some continental regions). Light frosts occur regularly in the winter

Vegetation

In the regions with the most rain (close to the coast) luxuriant, multi-layered rain forests are found; in other areas semi-evergreen forests or (moderately sclerophyllous, mostly broadleaved) laurel forests occur; sometimes also tall- grass meadows are found. The growing season extends all the year round but may be moderately limited for several months (maximum of 7) by winter cooling and / or lack of rain. PP_N: 15 - 25 t ha^{-1} a^{-1}

Land use

Most areas are characterized by dense settlement and advanced economic development. Agricultural activity profits from tropical- warm summer temperatures and copious rainfall. The predominant crops are sorghum, groundnuts, rice, soybeans, sesame, sweet potatoes, cotton and tobacco; in the regions which are moist all year with mild winters, permanent crops such as tea and citrus fruit are grown

Organic wastes and their decomposition

For the most part, mineral nutrients are organically bound in the phytomass, the litter and the humus (i. e. very little is contained in the inorganic components of the soil). The time taken by the dead organic matter to decompose (in laurel forests) is about 2 years. The production of leaf litter throughout the year and its approximately uniform decomposition promote the maintenance of a closed mineral cycle

Pedosphere

Acrisols are the zonal soil unit; the B_t horizon of this soil is acid and has a base saturation of < 50%. LAC clays predominate but 2:1 clays also occur; in many cases , high percentages of Al are found on exchangers, then : alisols.

The naturally low fertility of the soil can be boosted by applying fertilizer

Lithosphere

According to the morphodynamics this is not an independent zone.

Deep chemical weathering takes place. The soils are usually more susceptible to erosion than in the Humid Tropics. In some areas, tropical cyclones with high wind speeds and heavy rain can result in considerable soil erosion, flooding and storm damage

Fig. 175. Synoptic diagram of the Humid Subtropics

For agricultural purposes, it is particularly advantageous that "tropical" temperatures predominate during the summers, thus permitting the cultivation of many crops which prefer warm temperatures, and that at the same time adequate precipitation is available for rain-fed agriculture (in contrast to the Mediterranean-Type Subtropics on the western sides of the continents where, in addition, the temperatures in the summer are usually not as warm). Most regions have mild winters with only occasionally light frosts.

Under these conditions, even *perennial thermophilous crops* (such as citrus and tea) can flourish as long as they are not highly susceptible to frost. *Annual* thermophilous crops commonly cultivated, include sorghum, groundnuts, rice, soybeans, sesame, sweet potatoes, cotton and tobacco. Sometimes, annual crops from the mid-latitudes are cultivated additionally during the winter months. Where this is practised, two and occasionally as many as three harvests per year can be obtained.

The unfavourable soil conditions (see above) do not as a rule impede the cultivation of plants, provided that the soil is properly tended.

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Chapter 3.8: Humid Subtropics

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Werger MJA (ed) (1978) see Chapter 3.7

3.9 Humid Tropics

3.9.1 Distribution

Most of the areas which belong to the Humid Tropics occur within a latitudinal range from 10° N to 10° S, the distribution is thus mainly equatorial. In some regions, such as in Central America, at the eastern edge of the Cordilleras, in southeastern Brazil, eastern Madagascar and South East Asia, the range extends to about 20 °N and 20 °S, and in extreme cases to nearly 30° N and 30° S. There are no humid tropical regions in eastern equatorial Africa. The total area amounts to 12.5 million km^2, i.e. 8.3% of the total land mass.

The outer boundary is drawn wherever a dry season of more than 2.5 to 3 months occurs. The moist savanna regions in the adjoining Seasonal Tropics have a few features in common with the Humid Tropics, such as in the fields of soils, morphogenesis, vegetation and land use. As a result, it is the common practice to group rain forest and moist savanna climates together into one spatial unit known as the *moist tropics*. The distribution map (Fig. 176) shows not only the Humid Tropics but also these wet-dry transitional regions.

3.9.2 Climate

The climate is uniquely *uniform throughout the year*. This means that the Humid Tropics, in particular those regions close to the equator, form a *zone without any (strikingly different) seasons*. As a result, given that the period of daylight remains almost unchanged at 12 h[27] throughout the year, and given also that the radiation balance remains strongly positive all year round, the mean daily temperatures stay within the narrow range of approximately 25–27 °C. The daily amplitudes, with maximum values of approximately 6–11 °C, are considerably larger than the annual fluctuations which occur (Fig. 177).

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[27] Since the sun disappears almost vertically below the horizon in the evening and rises almost vertically above it in the morning, the periods of twilight are extremely short.

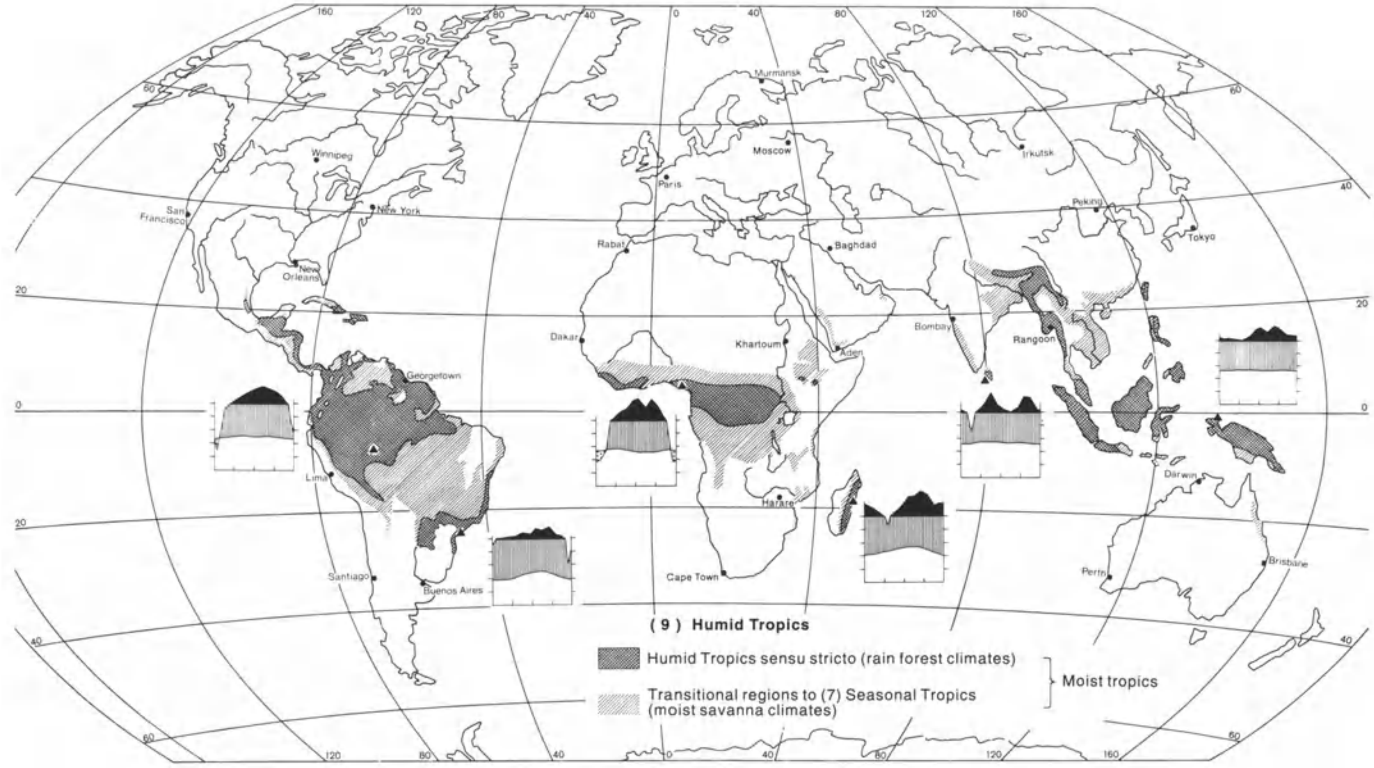

Fig. 176. Humid Tropics. The distribution is equatorial, but where the summer zenithal rainfall is supplemented by winter trade wind or summer monsoon rainfall (both frequently assisted orographically) the range of this ecozone extends further polewards. In extreme cases it may even extend beyond 20° N and 20° S

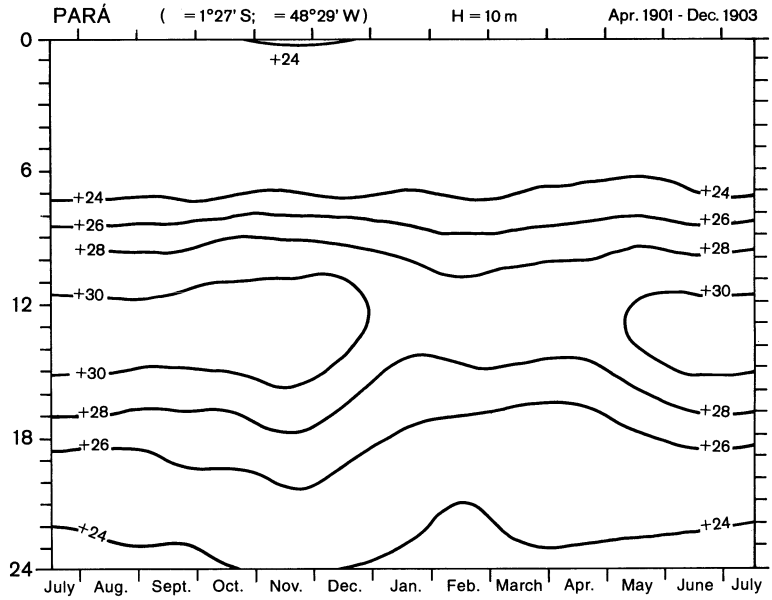

Fig. 177. Thermoisopleths for Pará (Belem), Brazil. (Troll and Paffen 1964). The temperatures remain similar throughout the year, as indicated by approximately the same mean daily maxima and minima in each month (29–31 °C and 24 °C respectively). The diurnal differences (5–7 °C) are thus significantly higher than the seasonal differences

As elsewhere in the tropics, the *precipitation* falls as zenithal rain, i.e. the seasonal maxima follow – with a slight delay – the highest positions of the sun. In keeping with this, there are always two seasonal peaks in the rainfall near the equator (*double rainy season*), each occurring shortly after the two equinoxes in the year (*equinoctial rain*) i.e. in April and October. The decline between these two peaks usually remains at a high level for most months; there are nowhere more than 2.5 (3) months with rainfall lower than potential evapotranspiration. Therefore, plant growth can continue all year round without being interrupted by drought, although temporary periods or even regular seasons of restriction may occur. In the latter case, many species subsequently respond by going through striking phenological phases such as changing their foliage or blossoming.

As in the Seasonal Tropics, the precipitation falls mainly in conjunction with convectional processes (i.e. from cumuliform clouds, frequently cumulonimbus), in particular in the sphere of influence of the Intertropical Convergence Zone (ITCZ) (see Chap. 3.7.2). In addition, equatorial west winds, which are probably formed by trade winds blowing across the equator, bring rain with them (e.g. monsoon in West Africa). The relatively balanced annual march of precipitation is connected with the fact that the Humid Tropics remain all year round within the sphere of influence of the ITCZ, or of a broader runout zone of the trade winds, where very weak pressure gradients and consequently thermal convection prevail.

The annual amounts of precipitation are as a result very high and frequently attain values of 2000–3000 mm.

When the temperatures and amounts of precipitation remain constantly high, this generally gives rise to high atmospheric moisture contents (tropical sultriness) and unstable air conditions. The individual precipitation events are correspondingly very intense (frequently short and violent thundershowers), and the daily totals may exceed 100 mm.

The high degree of cloudiness and the high atmospheric humidity explain why the amount of *diffuse atmospheric radiation* (skylight and cloudlight) contained in the global radiation is up to around 40%. By far the largest amount of the solar radiation received (global radiation approximately 500–650 × 10^8 kJ $\mathrm{ha}^{-1}\,\mathrm{a}^{-1}$) is consumed in the process of evaporating water, i.e. it is transferred in the form of latent heat of evaporation (in the Amazonian rain forest near Manaus, for example, 87.3% of the radiation balance goes into this transfer) (see Galoux et al. 1981, p. 180). More than 1000 mm, up to a maximum of approximately 1500 mm, of water are evaporated/transpired per annum; this is significantly more than in any other ecozone. The amount of rainwater which infiltrates into the soil and flows into the rivers as groundwater is reduced by this amount of water, which equals approximately 50% of the precipitation (*runoff coefficient* 0.5–0.6, Fig. 5). Without the high degree of evapotranspiration, the danger of soil leaching would be very much higher than it already is.

On the eastern sides of (near) equatorial South America and Africa (NE Brazil and Somalia respectively) the Humid Tropics cover only a narrow coastal band, or they are missing altogether. The reason for this is that trade winds of more continental origin exert a strong influence here and suppress the precipitation activity for long periods of time so that convective showers, rather like in the Seasonal Tropics, can only occur during periods when the sun is at its highest level.

In contrast, where maritime tropical air masses, abundantly supplied with moisture, are brought by the tropical easterlies, or the trade winds, from oceanic subtropical highs to eastern coasts and where these unstable air masses are forced to rise on mountain slopes, heavy orographic precipitation results. This, together with convectional (zenithal) rains during high-sun solstice periods, creates (generally narrow bands of) tropical rainfall climates even far north and far south of the equator, as is, for instance, the case on the eastern sides of Central America and Brazil, on the eastern slope of the Andes, on the east coast of Africa and Madagascar, as well as on the east coasts of southern China and northern Australia.

3.9.3 Relief and Hydrology

Within the *regolith* extremely intense *chemical weathering processes* (mainly hydrolysis) take place under the following prevailing conditions: high soil moisture content all the year round, consistently high temperatures (which, because of the heat released in the decomposition of humus, may be a few degrees higher in the soil than the mean air temperature) and usually high soil acidity. On the other hand, since physical types of weathering are totally insignificant and rock disintegration only occurs in connection with pressure release, the chemical weathering processes lack support from mechanical rock destruction, as is the case in the wet-dry tropics and (even more so) in the non-tropical regions.

This means that bare *rock surfaces* undergo practically no breakdown, particularly where the rock face is steep and unfissured: the frequent, but only temporary, wetting of the rock with rainwater obviously does not permit severe chemical weathering.

According to Rohdenburg (1971) the same also applies in the case of rocky river beds. Since the process of corrasion is also weak here, because of the low or totally lacking gravel load (as a consequence of intense chemical weathering), the rate at which the rivers cut down into the terrain is relatively low (lower than for rivers outside the tropical regions, but higher than for rivers in the wet-dry tropics). Consequently, many inner tropical rivers have, on average, a relatively steep slope gradient (Rohdenburg 1971, p. 183), or waterfalls are interposed between less steeply inclined stretches of river bed.

On the other hand, solution rill lapiés may develop on granitic and calcarous rocks over which the highly acidic soil solution flows, and blocks can be formed in rocky river beds without any previous "weathering", when the water flow "tears" pieces out of a rock narrowly dissected by fissures, and in this way creates a pebble load.

In particular in those areas where it has acted over long periods of time, such as on old land surfaces, the strong chemical weathering has created deep soil layers extending to a depth unattained elsewhere, and below these soils come *zones of decomposed rock (saprolite) many metres thick* before the intact rock is reached, perhaps as much as 100 m below the surface (for comparison: in the Humid Mid-Latitudes the rock decomposition zones are nowhere more than 1 m thick). In addition, the deep chemical weathering has meant that practically no silicates from the parent rock have been preserved in the upper soil horizons and mainly kaolinite, gibbsite, hematite and goethite have formed as secondary products. Fresh rock crops out only in steep relief (e.g. of cratonic margins; not of young folded mountains) as rock walls, rock needles, and rocky river beds etc. (see above).

Fluvial processes are of great importance in shaping the relief. In no other zone of the earth does so much water run off per unit area, and is the stream density so high as in this ecozone (scarcely any locality is situated more than 400 m away from the nearest river – Young 1976, p. 30). Therefore, assuming adequate slope gradients (e.g. in young folded mountains), highly linear *V-shaped valleys* and steep-flanked, narrow-crested ridges are cut into the terrain over geological periods of time. In flatter terrain, where downcutting erosion gives way to lateral erosion, broad and almost level valley floors (usually flooded for long periods of time each year) develop. The flanks of these valleys may be inclined at all angles from very steep to gentle (in contrast to the wet-dry tropics, where extremely shallow valleys prevail; Fig. 158).

Despite very frequent occurrences of high intensity rainfall, there is no *slope erosion* under natural conditions: the densely layered canopy of the rain forest (see below) at first intercepts the rain and some time elapses before a fraction of the water (frequently only 5–50%) penetrates, usually in the form of throughfall; the amount of stemflow is small (Grimm and Fassbender 1981; Edwards 1982) but increases during major precipitation events and, if there is an accumulation of such events (i.e. in particularly rainy regions), may cause a considerable redistribution of the rainwater in the soil (Landsberg 1984).

About 98 to 99% of the rainwater reaching the ground percolates into the soil (Tricart and Cailleux 1972, p. 252) and – unless taken up by the roots of the plants – runs into the rivers as groundwater. The suspended load of these rivers is as a result extremely low and consists almost exclusively of kaolinites and sesquioxides. The water is clear, but it may be black in colour (black water) because of dissolved fulvic acids.

Planation processes in outcropping rock, even "partial" planation (Büdel 1971), are therefore not typical, nor are there any buildups of large alluvial fans.

Because of the process of desilication which is characteristic for the Humid Tropics (see below), *silica* accounts for a strikingly large percentage of the dissolved products which are transported by rivers (in generally very low concentrations). For example, Bruijnzeel (1982) found the following amounts (in kg ha^{-1}) of dissolved substances in the Mondo river system of central Java (from Walter and Breckle 1984):

	Ca	Mg	Na	K	SiO_2	Runoff (mm)
1977:	21.7	22.9	19.6	16.0	393.8	2501

Soil creep is probably also not a significant phenomenon because the dense root formation, particularly in the near-surface zone (see below), to a very large extent stabilizes the soil substrate; only after deforestation can soil creep increase considerably.

Much more significant for the creation of landforms (especially in young folded mountains), even under undisturbed conditions, are two other kinds of mass movements under the influence of gravity, i.e. *earth flows* (e.g. mud avalanches) and *landslides*. Both are promoted by the thick layers of loamy, water-saturated material which results from the intense chemical weathering and high rainfall. Even if both types of soil movement occur only at widely spaced and irregular intervals, they are nevertheless the most important agents of slope denudation occurring in tropical rain forest regions. Over long periods of time, they probably affect virtually all the steeper slopes, and the process repeats itself when thick accumulations of unconsolidated material build up once more. Therefore, in the long term, they have a major morphological impact (in contrast to the minimal slope degradation caused by sheet erosion). Earth flows and landslides can have catastrophic effects after forest has been cleared.

After landslides have taken place, the suspended load transported by the rivers can temporarily undergo a sharp increase and the percentage of primary rock particles in the suspended load can also increase significantly. Such waters change to milky colour (then named white waters) and may create large sediment terraces further downstreams.

3.9.4 Soils

See also Chapter 3.7.4 Tropical Soils – General

The characteristic zonal soil type in the Humid Tropics is the *ferralsol* (Latin ferrum = iron; al comes from aluminium); this is identical with the oxisol in the US Soil Taxonomy (1975); other, fundamentally identical designations are (non-leached) sols ferrallitiques of the French CPCS classification; less accurately: latosols, lateritic soils.

Ferralsols formed over very long periods of time (dating at least from the Early Pleistocene, sometimes as early as the Miocene, or even earlier) from various parent rocks, in continuous warm-humid conditions under forest (moist tropics). They are typical of old land surfaces.

As a consequence of deep chemical weathering, the profile is very uniform in colour (from bright yellow to deep red), in texture, and in several other properties throughout its entire depth. The following are the typical properties of the *ferralic B horizon* (formerly: oxic B horizon; diagnostic horizon for ferralsols):

- extremely deep development: 20–50 m (similar thicknesses are otherwise only found in some acrisols); according to the definition, the minimum thickness is 30 cm;
- no clay illuvation and thus no clay skins (immobility of clay is a characteristic feature of ferralsols);
- at most, only trace amounts of weatherable silicates remain; according to definition: less than 10% weatherable minerals in the 50–200 µm fraction; if there are any more, the soils become ferralic cambisols;
- the texture is sandy loam or finer and has at least 8% clay in the fine earth fraction; if coarser, the soils are ferralic arenosols;
- the clay fraction consists almost entirely of kaolinite, iron oxides and aluminium oxides, while the sand and silt fraction consists almost entirely of quartz;
- a high silt content is atypical; the silt-clay ratio is at the most 0.2;
- the cation exchange capacity of the mineral soil is low to extremely low [$\mathrm{CEC_{pot}} \leq 16\,\mathrm{cmol(+)\,kg^{-1}}$ clay, $\mathrm{CEC_{eff}} \leq 12\,\mathrm{cmol(+)\,kg^{-1}}$ clay], the base saturation is also low and the soil reaction is correspondingly acid to very acid.

The soil processes which result in ferralic B horizons are grouped together under the term *ferralitization*. The process of mobilizing and removing silicon (with drainage water), i.e. *desilication*, takes place parallel to this (since the residual enrichment of kaolinite and sesquioxides is not possible without this leaching of silicon, the desilication may also be regarded as a subprocess of ferralitization).

Particularly intensive desilication occurs under permanently humid-hot conditions, when at the same time the soil reaction is highly acidic. This is very much the situation which exists practically everywhere under tropical rain forests with their high litter production and fast decomposition processes, which are coupled with the release of considerable amounts of *respiratory carbon dioxide* (on average five times more than in the temperate forests). Besides carbonic acids, other inorganic acids play a relatively minor role (Johnson et al. 1977). Even organic acids (humic acids) are remarkably insignificant, which becomes understandable from the fact that the decomposition of organic matter (apart from marshy sites, see below) is directed towards achieving rapid mineralization (Jordan 1984, p. 7); this contrasts to many soils in other humid ecozones (e.g. to podzols of the Boreal Zone in whose genesis and dynamics fulvic acids play an important role; see Chap. 3.2.4).

Fe- and Al-oxides tend to form stable aggregates in the millimetre to centimetre size range, creating what is known as *pseudosand*. Therefore, even clay-rich ferralsols contain large numbers of stable (intergranular) coarse pores. They are correspondingly easily infiltrated and drained (making them relatively unsusceptible to erosion, and easy to walk on or cultivate after heavy rainfall). However, since they contain a large percentage of dead water (locked inside the pseudosand particles), on the one hand, and rapid-draining pores on the other, they tend to have a low plant-available water-retention capacity, and even under perhumid conditions, this can lead to drought stress for shallow-rooted plants during rainless periods (Schmidt-Lorenz 1986, p. 86).

In the *plinthic ferralsols*, the (upper) B horizon consists of an iron-rich, humus-poor mixture of clay (kaolinite, sesquioxides) with quartz, known altogether as *plinthite*. The Fe-concentrations are formed as residual enrichments. As a rule, they take the form of red mottles, usually in platy, polygonal or reticulate patterns. In the moist state, the consistency is firm but spadable, combined with low permeability. Therefore, elevated runoff rates are measured on slopes having plinthic ferralsols, and in flat areas flooding is frequent. After being repeatedly dried out (as can happen more easily on fields after the topsoil has been washed away) the plinthite may become irreversibly hardened in the form of a crust or irregular aggregates. In the FAO classification, the hardened material is referred to as a petroferric or skeletic phase; otherwise it is also known as *ironstone*, while in the non-pedological literature the name *laterite* is widely used (see Chap. 3.7.3). In general (in this latter type of literature) the danger of lateritic hardpans forming is exaggerated. The major soil problems in the Humid Tropics are caused by other characteristics, such as the extremely low or lacking residual content of weatherable minerals, the low CEC and base saturation, as well as the rapid decomposition of humus following clearing of the forests.

In the recently revised FAO classification (1988), all the plinthic ferralsols which have at least 25% plinthite by volume in a horizon that is at least 15 cm thick and within 50 cm of the surface, are given the rank of an independent soil unit which bears the name *plinthosol* (Greek plinthos = brick).

Two other types of soil which are occasionally encountered in the Humid Tropics are the ferralic cambisols and the ferralic arenosols. The latter are also present in the wet-dry tropics and subtropics.

The *ferralic cambisols* are interpreted as young stages of ferralitic weathering. In contrast to the ferralsols they still contain weatherable silicates, and the CEC is higher (although it is lower than in the other cambisol units). This explains why they are regarded as relatively fertile soils. In West Africa, they occur in hilly or mountainous regions (frequently together with leptosols) where slope degradation permits only early stages of pedogenesis. They account for only an insignificant percentage of the area covered by tropical/subtropical soils.

Ferralic arenosols (see also Chap. 3.5.4): the ferralic arenosols are characterized by the dominant presence of kaolinitic clay minerals (= ferralic properties). In the moist tropics they formed probably on (sub-)recent, relocated material originating from highly weathered soil formations (i.e. from ferralsols or acrisols). The occurrences of ferralic arenosols in semi-arid regions (e.g. in large parts of Central Australia) are probably due to deposits of Tertiary soil material formed under more humid conditions.

Ferralic arenosols are unfavourable sites for plant growth, not only because of their low silicate content and their low CEC, but also because of their low water-retention capacity (their field capacity is often only about 10 vol%). This means that, even in the moist tropics, the occurrences of arenosols are (edaphically) dry, and as far as agriculture is concerned, drought-threatened sites. In response to the drought stress, the vegetation which grows naturally on these soils exhibits a larger number of xeromorphic characteristics than is otherwise the case under the same precipitation conditions; the choice of crop therefore tends to be cassava, which is not very demanding.

3.9.5 Vegetation and Animal Life

3.9.5.1 Structural Characteristics

Tropical Rain Forest

The *zonal vegetation* of the Humid Tropics is the *evergreen tropical lowland rain forest* (also called Hylea). Clearing activity, in particular during the last 20 years, has reduced this forest to less than half its original extent. It is to be feared that the destruction of the forest will continue in the future as well, although so far very few major benefits of any kind (if at all) have been obtained for mankind. At present, it is estimated that about 20 million hectares of forest per annum are being cleared. Despite this ongoing massive destruction, there are still larger percentages of primeval forest than in any other ecozone, in which forests form the potentially natural vegetation.

All tropical rain forests share a large number of common structural characteristics, although there are also many regional differences. The common features (according to, inter alia, Unesco 1978; Vareschi 1980; Golley 1983; Seibert 1984; Walter and Breckle 1984; Roth 1986) include the following:

Often more than 70% of all the species are trees. Practically all of them are evergreen and, like the herbaceous plants, exhibit a wide range of conspicuous adaptations to the constantly high humidity, i.e. they are *hygrophytes* (moisture-loving plants). Only the canopy trees in the uppermost layer of the forest, and many epiphytes, should instead be classified as *mesophytes*.

Luxuriance of the vegetation: the product of the height and density of the plant stand is the highest found in any plant formation, and the (above-ground) phytomass per unit area is correspondingly greater than anywhere else. The *tree density* (number of trees per hectare having a diameter at breast height of at least 10 cm) ranges from several hundred to a maximum of approx. 1000 (e.g. Lamprecht 1972, p. 271; Burgess 1981, p. 10; Hall and Swaine 1981 p. 42). Most stems belong to trees in the middle and lower storeys of the forest (see below). The sum of all the *basal areas* (total cross-sectional area at breast height) is at least 25, but usually 30–40 $m^2 ha^{-1}$.

The *height of the canopy* attains 30–40 m, with some tree crowns extending far above this height (frequently up to 50–60 m, more rarely up to 70–80 m); the surface of the canopy is remarkably "uneven". In all other zonal forest formations, the trees forming the canopy are usually of similar height.

Under the uppermost canopy there is a dense undergrowth of less tall trees whose crowns (or maximum leaf masses) sometimes (but certainly not always) concentrate within certain height ranges so that (about three to five) **storeys** can be distinguished. Each of these storeys is characterized by a sudden decline in the amount of light available compared with the overlying storey. As a result, this creates significantly different living conditions, not only for the plants, but also for the animals (Fig. 178). In addition, it is important for the plants that the percentage of photosynthetically active radiation (PAR) declines in inverse proportion to height, e.g. in Costa Rica – as measured by Chazdon and Fetcher 1984 – from 53% (measured in a clearing) to 18% measured in the shade of the forest.

Since only about 0.1–0.5% (1%) of the solar radiation reaching the canopy can penetrate through to the forest floor, it is virtually impossible for a layer of *herbaceous plants* to develop; contrary to what is frequently assumed, there is no "impenetrable" mass of plants on the forest floor. The layer of herbaceous plants may be denser for short periods where trees have fallen over and, temporarily, more sunshine can reach the floor of the forest. Many tree seedlings also make use of this brief opportunity. The survival of the young plants depends decisively on how quickly they succeed in gaining height and thus derive more benefit from the incident light than their competitors. The ability to grow rapidly in length (bamboo shoots, for example, can grow at the rate of 0.5 m per day) is therefore characteristic of many species, whether herbaceous or young woody plants.

The high growth rates are usually achieved by incorporating large amounts

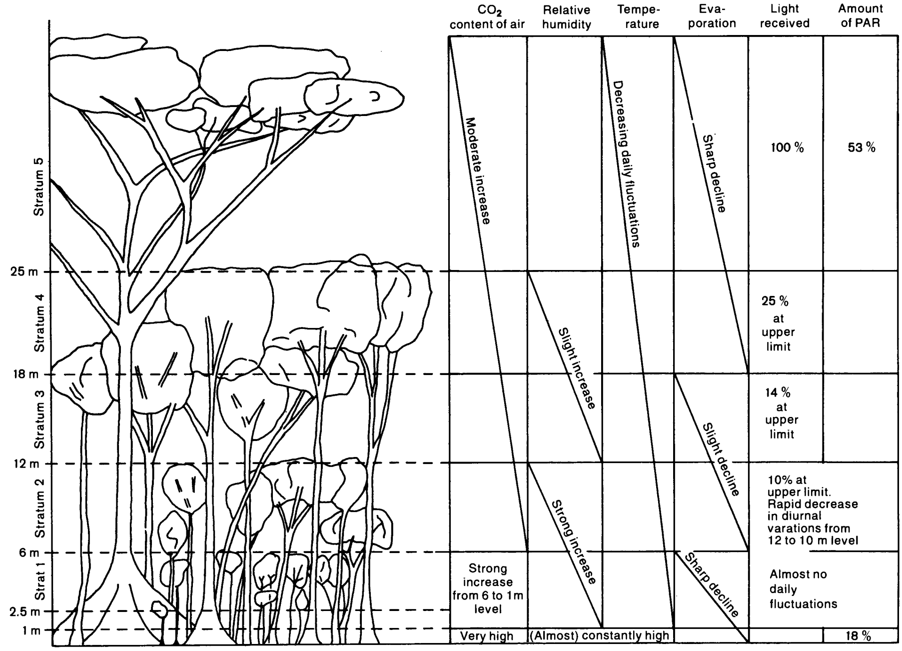

Fig. 178. The layers (strata) in a tropical rain forest and associated ecological conditions, taking a rain forest in the Ivory Coast as an example. (After Bourgeron 1983, slightly modified). See text for explanations

of water into the cell vacuoles, thereby stretching small cells to more than 100 times their original size; supporting tissue, which consumes greater quantities of organic matter, is not formed until later. In this way, even herbaceous plants can attain unusual heights (6 m and more) in a short time (giant herbaceous perennials).

As a result of the attenuation of light in the interior of the forest, different *air temperatures* and different *atmospheric humidity levels* exist for the individual layers. In the area of the uppermost canopy, the daytime temperature may be as much as 10–12 °C higher than the nighttime temperature (i.e. it may climb to about 40 °C), and the relative humidity then drops to about 30–40%, so that considerable saturation deficits exist[28]. The diurnal fluctuations are not as large in the lower storeys of the forest. At the floor of the forest they are barely

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[28] Walter and Breckle (1984) point out that 50% atmospheric humidity at 32.2 °C gives a saturation deficit of 18.3 mm Hg. This is a value characteristic of semi-arid steppe regions. However, in the Humid Tropics this saturation deficit occurs (if at all) for no more than a few hours in the morning and during the midday period. At least at night the air is saturated everywhere. This means that, in the canopy as well, the transpiration rates per unit leaf area are low for most of the time, while they are always low in the stem region.

noticeable: Here the temperature of the air, both by day and night, is around 25–27 °C (i.e. the same as the mean annual temperature), and the relative humidity is 90–100%.

The uniformity of the climate described in Chapter 3.9.2 applies primarily to the interior of the forest, in particular close to the ground. In the area of the canopy, significant diurnal as well as annual deviations may occur.

Different strengths of *air movements* are another distinguishing features of forest storeys. By the time they penetrate to the interior of the forest, the fury of the sometimes violent thunderstorms is abated and their effects are rarely, if ever, felt in the layer of air close to the ground. For this reason (and also because photosynthetic processes do not play a major role in this layer), the large amounts of carbon dioxide released by the decomposition processes taking place within the litter layer and the soil itself (soil respiration) can accumulate to a maximum of approximately double the values normally found in the open atmosphere.

The multilayered structure of the forests explains why the *leaf area index* is very high at 8–12 $m^2 m^{-2}$ (higher than in any other zonal plant formation).

The *species diversity*, i.e. the number of species per unit area, is extremely high. The *number of tree species* per hectare alone can reach over 100 (often only 2–3 specimens of the most frequent species occur). For comparison: in Venezuela, the number of species in a deciduous moist forest was 60, in a deciduous dry forest 36, and in a thorn shrubland 11 (Lamprecht 1972; in each case only trees with a diameter at breast height of > 20 cm were counted); the numbers for temperate forests are usually between 10 and 20, those for the taiga are even lower.

In the course of floristic surveys conducted in rain forest regions, it has always been found that sometimes up to 50% of the species discovered had not been previously taxonomically recorded (Bourgeron 1983). Here, far more than in any other zone, it must be expected that many new species (including animal species) will be discovered in the future.

Many of the *large trees* form *slender to columnar stems*; disregarding their basal sections, which are frequently broadened by the formation of *buttress roots* (Fig. 179), these stems do not taper very much as they grow taller, and branches are not formed until great heights have been reached; the bark is thin, smooth and light-coloured. *Annual growth rings* are at best indistinctly formed, and it is therefore not possible (or is at least difficult) to determine the age of the trees by counting these rings, which is the common method used in non-tropical trees[29]. The *root systems* spread out usually just below the surface, which is optimal for the uptake of nutrients (see below), but in the case of many trees these root systems alone do not provide sufficient anchorage, and instead must be reinforced by buttress roots (Henwood 1973).

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[29] Annual rings may form wherever short periods of drought or flooding result in periodical annual restrictions in growth. Usually they are at best weakly developed and can only be detected by using sophisticated methods (e.g. X-ray densitometers or isotopic analyses.)

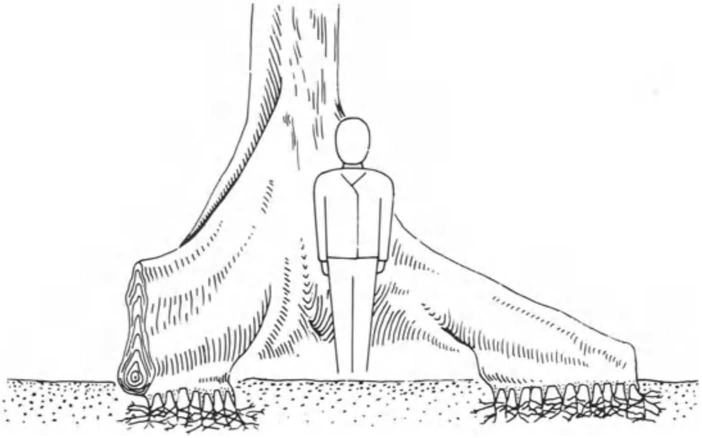
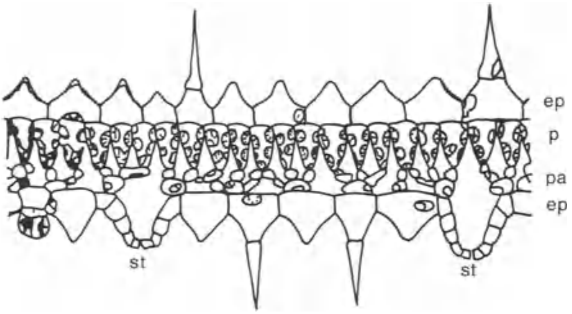


Fig. 179. Buttress roots on a tree in a tropical rain forest. (Vareschi 1980; Klink and Mayer 1983). The "buttresses" do not extend below the surface but instead form a comb-like row of smaller roots which penetrate the soil

Another, perhaps more important function of the buttress roots may be to support respiration processes (for even further possible explanations see Smith 1972). Many tree species form *aerial roots* for this purpose. Such auxiliary devices are required because the root respiration within the soil is severely impeded by frequent waterlogging (i.e. the filling of all pores with water), high oxygen consumption of decomposers, and – as described – low gas exchange with the outer atmosphere.

Usually smaller, laurel-like *leaf forms* (see Chap. 3.8.5.1), with facilities for reducing transpiration losses (e.g. thick cuticle, wax layer), predominate in the upper canopy region where the leaves may be exposed to several hours of direct sunlight and strong wind each day, so that for a while considerable drought stress may exist (xeromorphic sun leaves) (Givnish and Vermej 1976; Roth 1980; Givnish 1984). In the much more protected stem region, on the other hand, the leaves are softer, larger and darker green in colour (hygromorphic shade leaves), and no bud scales are developed. The large leaf surfaces favour photosynthesis in conditions of dim light. Problems arising from the vapour saturation of air for the plant transpiration are quite commonly solved with the help of *hydathodes* (water pores), through which water (water droplets) can be actively excreted. Sometimes the stomata are raised above the leaf surface in order to facilitate transpiration (Fig. 180).

Many species of rain forest tree have leaves with long drawn-out *drip tips*. In some regions, e.g. Borneo, Sri Lanka and Nigeria, more than 90% of the species have leaves of this type. It is unclear whether the drip tips offer any ecological advantage. The argument that they accelerate the runoff of rainwater and thus facilitate the gas exchange required for photosynthesis and respiration is by no means correct in all cases; many "drip tips" are in fact turned upwards.



ep = Epidermis of upper and lower leaf surface
st = Raised stomata
p = Hill-shaped palisade cells
pa = Spongy parenchyma

Fig. 180. Cross section through the leaf of the tropical shade plant *Ruellia portellae* (Acanthaceae). (Strasburger 1983, p. 191)

Also, such tips are lacking where one would least expect, namely in many of the wettest forests (Vareschi 1980, p. 85f.).

Growth flushes of foliage are a widespread phenomenon in many of the tree species and involve the rapid growth of long shoots bearing many leaves. Since the formation of supporting tissue and chlorophyll cannot keep pace with the rapid longitudinal growth (up to 20–30 cm per day), the shoots formed in this way are at first whitish or (through the presence of anthocyanins) reddish in colour, and pendulous.

Cauliflory, i.e. the growth of flowers and fruits (caulicarpy) on leafless stems (e.g. found in the case of the cacao tree, *Theobroma cacao*), is not a common phenomenon, but much more frequent than in any other ecozone.

After trees, the next most important *life forms* are the *lianas* (climbing phanerophytes) and (macro-)*epiphytes* (mosses, ferns, orchids, and other flowering plants, including even woody plants such as various species of *Ficus*). About 90% of all recent lianas are indigenous to the tropical rain forests. Their superiority over other life forms lies in the fact that they can grow to great heights, with only a relatively low need to produce their own tissue (because they support themselves on other plants). This means that their contribution to the basal areas remains very low even when they are present in large numbers and their contribution to canopy layers is high.

A further step in the process of adaptation is exhibited by epiphytes, whose entire development cycle takes place high in the forest on "support plants". Epiphytes are especially common in mountain forests (cloud forests). Their importance here, as well as in lowland rain forests, is discussed in Benzing 1984. The epiphytes adhering to leaves, commonly lichen, algae and bacteria, are referred to as *epiphylls*. They also include nitrogen-binding bacteria, e.g. *Azotobacter*, *Beijerinckia*.

The *annual periodicity* of foliation, flowering, fruiting etc., which is very conspicious in all other zonal plant formations, is lacking in the plants of the tropical rain forest (some species have an endigenous periodicity) or it is at least not as obvious. In most species the different development phases occur at varying times; temporal deviations may occur even among the members of the same species, and occasionally even in the individual branches of one and the same tree. Therefore, *seasonal (phenological) changes* are totally lacking in the tropical rain forests.

Figure 181 depicts some of the more striking differences between tropical rain forests and winter-deciduous forests of the Humid Mid-Latitudes.

Regional differences of tropical rain forests are related to climate, affinity to floral kingdom, altitude above sea level, soil fertility and soil water budget. In the case of regular flooding, it plays a role in the development of the forest, whether the water is rich in dissolved solids and suspended sediments, (*white water*) or low in such substances (*clear water*; in case of high contents of organic

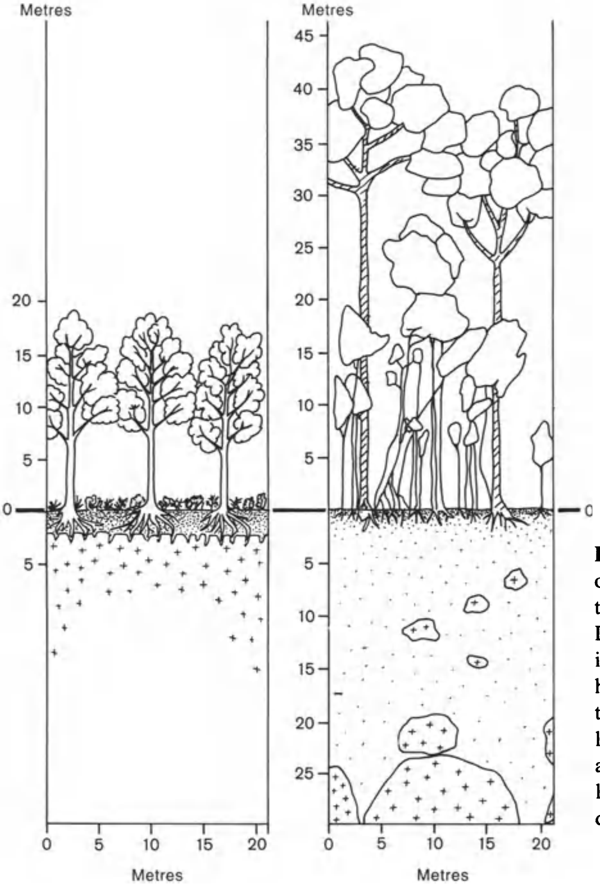
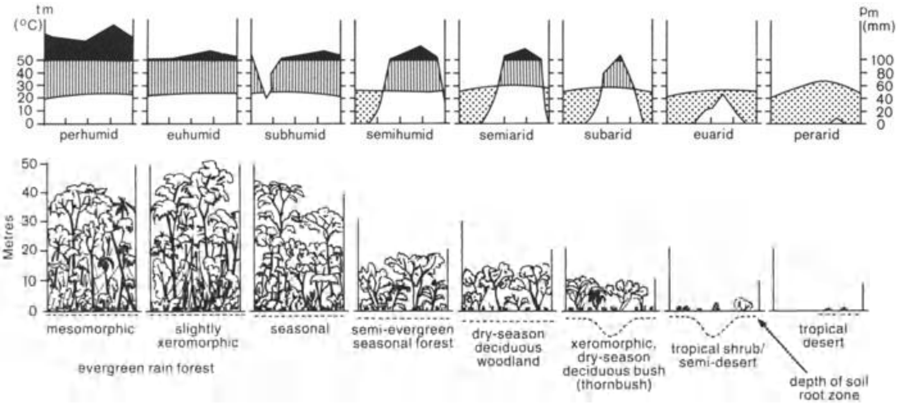


Fig. 181. Diagrammatic profile of a tropical rain forest and of a temperate deciduous forest. (After Douglas 1977). The rain forest is characterized by taller growth height, the multilayered structure, the less prominent herbaceous layer, the shallower rooting depth and the development of a deep layer of soil over a thick zone of decomposed rock (saprolite)

colloids: *black water*). The development is usually particularly luxuriant when annual precipitation levels are high, but not extremely high, and are distributed uniformly throughout the year, and no extended periods of flooding occur. The first three diagrams of Fig. 182 show the correlation with different degrees of climatic "humidity" (the others illustrate the situation all the way through to desert conditions). *Termite mounds* are usually present in large numbers (although not always in noticeable hill form, Fig. 183) and may cause differences in the soil



t_m = mean monthly temperature p_m = mean monthly rainfall

Fig. 182. Sequence of climatic conditions and plant formations in the tropical zone, from the humid to the arid regions (example taken from the foreland of the Andes in Peru). (Strasburger 1983, p. 1036)

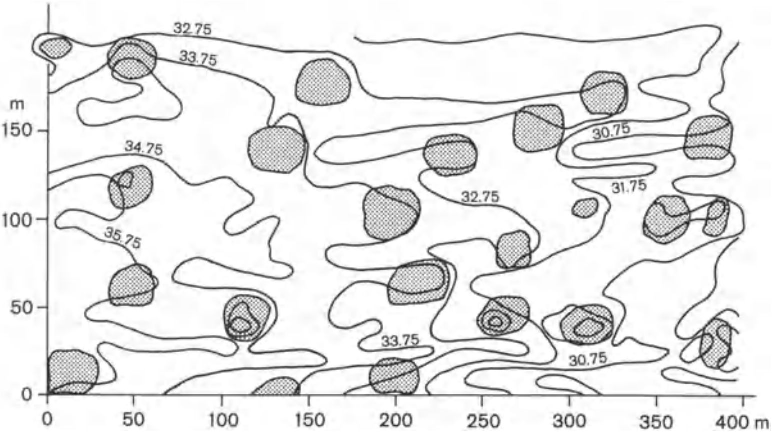


Fig. 183. Termite mounds (*shaded areas*) on a cleared area of forest near Yangambi in the Congo Basin. (Walter and Breckle 1984). They cover about 20% of the total area. The *contour lines* are spaced 1 m apart. Only a few termite mounds are hill-shaped

over short distances which could be relevant to the composition of the forest; but no reliable data exist on this point.

Besides site-specific differences, there are others which are related to the varying *age of the stand.* Trees which fall to the ground for reasons of age create gaps in the forest that are only gradually closed by the new trees. In the long term, there is nowhere in the forest that is not affected at some time or another by such sudden and, at first, destructive events, initiating the rejuvenation of forest stands. Therefore, each forest is composed of a tight mosaic of variously old and thus physiognomically and floristically different stands. In mountain regions, and in regions far from the equator, such as in the Philippines, landslides and tropical cyclones respectively can create wider clearings in the forest and thus initiate new growth cycles over large areas.

Animal Life

It is characteristic of tropical rain forests that animals are barely seen or heard. The luxuriant phytomass absorbs all noise, and the forest appears uninhabited. The fact that the fauna of the rain forest is made up of the largest number of species anywhere in the world is not at variance with this statement. Most species of animals are represented by just a few individuals which are distributed among a large number of different ecological niches; and many of these are in the upper storeys of the forest, because the sparse ground flora offers an adequate food base to only a few herbivores. Ground-dwelling mammals are rare, and they are shy. Some of them, even large species, were therefore not discovered until a relatively late date, like, for example, the okapi, which was found in Central Africa at the start of this century; other species are known only from the footprints which they leave behind or from the descriptions given of them by natives; e.g. the rhinoceroses which inhabit Borneo. Better-known large mammals include elephants in Africa and in Sri Lanka, the giant wild pig of the forests in the Congo Basin, tapirs in South America and South East Asia as well as manatees in the Amazon and Congo rivers.

The animal groups which contain particularly large numbers of species include the (poikilothermic) reptiles and amphibians; in their case, the consistently warm-humid environment creates uniformly favourable internal conditions which they are themselves unable to control. The permanently wet (sticky) conditions permit many other animals, which otherwise live only in water, to exist also out of the water, e.g. many species of leech. A large number of animals are active at night or during the twilight hours. Those which are active at night have in many cases reduced eyes, but this handicap is compensated by highly developed chemical sensory organs or other orienteering aids; this applies, for example, to many tree frogs, geckos, tree snakes and bats. The animals which are active at dusk have particularly large eyes, for example tarsiers, night monkeys, and some species of frogs.

In the same way that many herbaceous plants penetrate into the higher levels of the forest as epiphytes, many species of animals also establish their habitats there. Therefore, the multilayered structure of the forest also corresponds to a stratification of the fauna (e.g. Boulière 1983). The various animals living in the canopy layers include termites (which build their nests in the trees), ants, wasps, bees, beetles, spiders, butterflies, frogs, chameleons, snakes, birds and numerous species of mammal (monkeys, sloths, loirs etc.). For many species of plants, certain groups of animals play an important role in pollination (e.g. hummingbirds in South America for the flowers of fuchsia plants, bats for many cauliflorous plants) and they help distribute the seeds [e.g. flying foxes (bats) distribute the fruits of many caulicarpous trees].

3.9.5.2 Stand Reserves, Material and Energy Turnovers, Ecosystems

Phytomass and Primary Production

The Humid Tropics are superior to all other ecozones with regard to several climatic factors. These include high levels of solar radiation, high temperatures, high levels of atmospheric humidity and copious amounts of precipitation, all of which are rather evenly distributed over the year. There is no other natural terrestrial habitat on this planet which can claim a similarly favourable overall constellation of these environmental factors. This explains why a uniquely luxuriant forest with a high productivity potential is able to develop, despite the widespread unfavourable soil conditions (Schultz 1982).

Estimates and measurements of the *phytomass* have become available from a large number of forests. Most of them are in the order of 300 and 650 $\mathrm{t\,ha^{-1}}$; the average value is just below 500 $\mathrm{t\,ha^{-1}}$ (Bruenig 1983 p. 68; Golley 1983 p. 105; et al.). There is not always a correlation between the magnitude of the phytomass and the fertility of the soil (here = nutrient supply from exchangers) (Hase and Fölster 1982; Proctor 1983).

In each case, between 75 and 90% of the phytomasses are above ground, and 90% of this amount occurs in the form of the wood of living trees. Only about 2–3% is accounted for by the leaf mass of the trees. The root mass is located for the most part (in many cases more than 90%) in the upper 20–30 cm of the soil. The rooting depth is thus exceptionally shallow (Fig. 182).

There is general agreement that the *primary production* of the tropical rain forest exceeds that of other zonal plant formations (Rodin and Bazilevich 1967; Golley and Lieth 1972; Lugo et al. 1973; Murphy 1975; Whittaker and Likens 1975; et al.). Most of the values which were estimated or calculated on the basis of partial measurement (e.g. of annual litter fall) are within or close to the range of 20–30 $\mathrm{t\,ha^{-1}\,a^{-1}}$. However, some people take the view that the productivity is no higher than that of temperate forests (e.g. Leigh 1975; Jordan 1983; Whitmore 1984b). It is difficult to prove either claim, partly because the lack of annual growth rings makes it hard or impossible to determine the annual above-ground increment of wood. Special problems also arise because of the enormous number of species with possibly different growth rates which make it necessary to take a great many measurements; also the higher storeys of the forest, in which presumably the maximum amount of production takes place, are difficult to access.

There is no dispute that the *gross primary production* is everywhere very high, and the PP_N is probably only about 25% of this production. The high respiratory losses (i.e. about 75% compared with only 50% in the forests of the Humid Mid-Latitudes) are partially explained by the high percentages of photosynthetically non-active, i.e. only respiring, stems and branches (together with the roots = about 98% of the phytomass of the trees; in our forests the percentage is even less favourable, Table 4). The main reason, however, is that the temperatures are high even at night, and respiration is therefore fundamentally more intense than under the conditions of nighttime cooling.

Although the external conditions permit year-round primary production, most plants produce only for part of this time, i.e. they interpose growth pauses.

Animal Biomass and Consumption by Animals

Because of the large species diversity coupled with low population densities, the food chains are extremely complicated. Tracing them is further complicated by the fact that many species of animal are difficult to find. So far, studies have been carried out for only a few species or groups of animals, e.g. for sloths (Montgomery and Sunquist 1975) and leafcutter ants (Haines 1975), in both cases in the rain forests of Panama, as well as for birds (Karr 1975) in several forest regions. Somewhat more frequent attempts have been made to quantify the entire animal biomass. The following table presents the findings in two South American rain forest regions (in kg ha^{-1}):

	Herbivores	Carnivores	Soil fauna	Ratio of phytomass to animal biomass	Reference
Amazon	30	15	165	2252	Fittkau and Klinge (1973)
Puerto Rico	25	10	80	3594	Odum and Pigeon (1970)

One is struck by the fact that the figure for the animal biomass is extremely small. This is still the case even if one bears in mind that the figures given for the forests on Puerto Rico are too low compared with the actual values. Therefore, the quantitative importance of consumers in the energy and material turnovers in the rain forest ecosystem must be regarded as insignificant; the substances circulate almost exclusively in the form of a "short" cycle, i.e. directly between primary producers and decomposers. Owen (1983), however, feels it is possible that herbivorous insects play a larger role than the previous study results would lead one to believe (cf. also Dirzo 1984; Morrow 1984). According to Golley (1983, p. 147), the amounts of material which these insects consume, rather like in many non-tropical forests, are between approximately 8 and 10% of the total leaf surface. The frequent assertion that the animals of the tropical rain forest are more important for their regulatory effects on the reserves and cycles in the forest ecosystem than for their direct involvement in the turnover process is probably more of an assumption than a hard fact.

Accumulation and Decomposition of Litter

In the tropical rain forest, the litter fall is evenly distributed over the entire year. Since the losses due to animal consumption are (most likely) insignificant, it is at the level of the above-ground PP_N (i.e. probably about 15–25 $t\,ha^{-1}\,a^{-1}$), averaged over the long term. The *leaf* fall accounts for approximately 7 $t\,ha^{-1}\,a^{-1}$ of this amount, i.e. about 80% of the total leaf mass; that is to say, the average longevity of the so-called evergreen leaves exceeds 1 year only by a few months[30].

The values quoted in the research studies for "litter fall" in tropical rain forests are usually lower; e.g. the figures compiled by Jordan (1983, p. 124) are for the most part between 8 and 12 $t\,ha^{-1}\,a^{-1}$. It is however likely and somehow supported by the figures quoted by Proctor (1983, p. 427f.) for the "small litter fall", that in most cases the former values also refer only to part of the litter fall, chiefly the *leaf fall*; woody wastes, e.g. fallen trees, were obviously not included in the count.

The figures quoted by Procter at the same time confirm the thesis put forward by Jordan and Herrera (1981) that there is no close correlation between the amount of small litter fall and the soil fertility (supply of nutrients). This clashes with another thesis, according to which the perennial nature of the leaves can be regarded as a protective measure when nutrients are in short supply (e.g. Monk 1966; Monk and Day 1988), i.e. the leaf fall of a forest would be reduced in direct proportion to the decline in nutritional content of the soil substrate on which the trees grow.

Despite the considerable supply of litter, as a rule the forest floor is not covered by an unbroken *layer of litter*. According to the values compiled by Klinge (1976, p. 61) for seven rain forest regions in South America, Africa, and South East Asia, the amount of litter is only between 2.3 and 14.2 $t\,ha^{-1}$.

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[30] According to Medina (1984), the leaves of evergreen rain forest trees have an average life time of only 12–13 months. This means that as much as approximately 95% of the leaf mass would be renewed each year.

The thin and fragmentary litter accumulation is due, among other things, to the fact that wastes from the upper storeys of the forest get caught up in the lower layers of the canopy (Golley 1983, p. 142), where they are available to epiphytes. However, a much more important reason is that the wastes are very quickly decomposed on the ground, on average in less than 1 year. Leaf litter may be decomposed within just a few months ($k > 1$; cf. Table 10).

In addition to termites, leaf cutter ants and (to a much lesser extent) earthworms, it is mainly fungi which play the major role in the *breakdown of litter.* The termites are chiefly responsible for decomposing dead wood mass. With their help, dead trees and branches are broken down within just a few years (Table 45).

The decay is fast because the *constantly humid-warm conditions* in the soil are highly favourable to biological-chemical decomposition processes. However, the bacterial activities can be restricted to a greater or lesser extent by a highly acid soil reaction. On those sites where oxygen deficits aggravate the situation, as in swamp forests, even peat may form (e.g. Amazon region, Sarawak). It is therefore not necessarily true that high decomposition rates exist everywhere (Anderson et al. 1983).

The activity of decomposers can be estimated by measuring the *soil respiration* and deducting the amounts of root respiration and the respiration of soil animals not involved in the decomposition process. Allowing for these deductions, 1 g of soil respiratory CO_2 corresponds approximately to the decomposition of 0.65 g of dry organic matter. Since the decomposition process in the tropical rain forest takes place extremely uniformly throughout the year, relatively few measurements are needed to determine the annual amount of *substances broken down in the soil.*

The results obtained in this way are to a large extent equal to the amount of annual leaf fall and below-ground waste. Compared with the total volume of decomposition processes actually taking place, they are too low, because the breakdown of dead wood is for the most part unrecorded since it takes place

Table 45. The decomposition (disappearance) of dead wood in tropical rain forests (from western Malaysia). (Abe 1978, from Golley 1983)

Tree species	Diameter of wood (cm)	Decomposed portion after 1.5 years (in %)
Shorea parvifolia		
Stem wood	30–50	14.5
Large branches	13–20	49.8
Medium-sized branches	6–13	60.0
Small branches	3–6	80.8
Ixonanthes icosandra		
Medium-sized branches	6–13	24.2
Small branches	3–6	37.1

essentially *above ground.* Therefore, the amounts of decomposition determined via measurements of the soil respiration may not be equated with the PP_N, instead they are more a measure equivalent to the annual leaf and root production.

The contents of *soil organic matter* which are found in the soil under tropical rain forests are in the order of 1% to more than 3% (approx. 50–150 t ha^{-1}) and thus are somewhat lower than in the soils below temperate forests (Sanchez and Buol 1975; Sanchez 1976; Schlesinger 1977). As in the case of litter, fungi are also the most important agents of decomposition in the soil. Many of these live in symbiotic relationships with the roots of higher plants, which are referred to as mycorrhizas.

Practically every tree in a rain forest possesses some form of mycorrhizas. The most frequent forms are the *vesicular-arbuscular (VA) mycorrhizas*, which belong to the group of the *endomycorrhizas* (cf. for example Janos 1984). In this group the fungal hyphae penetrate into the cortical cells of the roots (intracellular growth), while the hyphae of the *ectomycorrhizas* merely grow between the cells in the root cortex (intercellular growth). In the rhizosphere, the hyphae form a dense tangle (mycelium) which is in contact with almost all the roots.

For the trees, the mycorrhizas are advantageous because the fungal hyphae take up, store and transmit nutrients, and thus take over the *function of root hairs.* The surface of their water- and nutrient-absorbing root parts is thus considerably expanded.

Another very important aspect of the fungi is that they open up the humus, i.e. they release (mineralize) the nutrient elements bound in the dead organic matter and thus make them available again to the trees. In the Humid Tropics it is probable that the nutrient ions which are released by mycorrhizal activities do not enter into the soil solution (as is the case with non-symbiontic fungi) but are fed via the intracellular hyphae directly to the host plants (Went and Stark 1968), i.e. an *extremely short mineral cycle* exists, which provides optimal protection against leaching losses.

In addition, the VA mycorrhizas are said to have the advantage that they help the higher plants gain access to the iron and aluminium phosphates frequently present in the soil, but in insoluble form (cf. phosphorus fixation above) and thus not utilizable under normal circumstances. As a result, the trees are able to bridge any possible bottlenecks which might otherwise occur due to the widespread lack of available phosphorus (also because of excessive leaching).

Nutrient Reserves and Turnovers

Nutrient Reserves. It is known that relatively large (sometimes the largest) portions of the mineral nutrients circulating in the rain forest ecosystem are found in the biomass and not in the soil, as is often the case in temperate forest ecosystems. This is confirmed by all relevant studies on the subject. However, there are considerable differences between the individual rain forest regions (Proctor 1983): by no means all the forests are located on severely depleted soils of the type often described as the norm (e.g. Weischet 1980). For example, according to the figures compiled in Table 46, usually more than 80% of the total nitrogen and phosphorus are contained in the soil matter, and exchangeable Ca and Mg in the mineral soil make up at least 25% and in some cases more than 50% of the total reserves. K seems to be available in the smallest amounts in the soil; its content varies roughly between 10 and 35%[31]. Many pedological studies have in the meantime also confirmed that it is inaccurate to describe moist tropical soils as generally infertile (e.g. Proctor et al. 1983).

Nutrient Turnovers. It is characteristic of the rain forest ecosystem that the nutrient turnovers take place within a largely *closed cycle*. This is a necessary assumption to be made a priori because otherwise the extremely luxuriant development of vegetation on many of the highly nutrient-deficient soils could not be explained. A clear indication of the existence of a closed cycle is that the water in the rivers usually contains very low concentrations of dissolved and suspended matter, and in many cases the fertility of the soil declines rapidly once the forests have been cleared and the resupply of nutrients is thus terminated (this is particularly so when the humus substances are also broken down).

Admittedly, all natural ecosystems possess mechanisms by means of which they can maintain their nutrient stocks, but those in the tropical rain forests appear to be particularly efficient. The special ability of the rain forest system to keep leaching losses to a minimum is based on the extremely dense formation of roots in the topsoil (sometimes mats of roots are formed at the surface of the soil, i.e. in direct contact with the litter) and on their link with an even more dense entanglement of mycorrhizas. As a result of this combined root-hyphae network, not only are the nutrients supplied by precipitation and crown wash/stemflow to a large extent captured, but also the uptake of nutrients released from organic wastes is most guaranteed by minimizing the distances between the location of decomposition and root, or even by creating direct transfer paths (see above).

Although the soils have everywhere developed to great depths and therefore offer plenty of space for root growth, the roots are highly concentrated in the

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[31] It is fundamentally difficult to determine the mineral contents of forest stands. In the case of tropical rain forests the problems are particularly large because, as individual analyses have shown, the different species of trees possess very different mineral contents. Therefore, a floristic survey of the stand must precede the chemical analyses. Only then can be decided on which samples to be taken and how to weigh them for per hectare calculations. Since the species diversity is consistently very high, it is necessary to carry out a very large number of analyses before an adequately accurate statement on the overall stand reserves can be made.

In addition, it is necessary to take account of those differences which generally exist between the different plant organs. As elsewhere, the leaves contain higher concentrations of minerals than the stalks (stems) and the roots. Since no definite correlation exists which would permit conversions to be made, it is not possible from the leaf analyses alone to draw any conclusions about the mineral reserves of the whole plant or even the whole forest stand.

In the surveys which have been conducted so far, the "variables" mentioned have not always been adequately taken into account, and for that reason the results should be interpreted with a great deal of caution. This also applies in the case of the values listed in Table 46.

Table 46. The nutrient contents of the phytomasses of tropical rain forests in percent of the total nutrient reserves (i.e. in vegetation and soil); for comparison, the corresponding data are listed for two dry-deciduous forests in the Seasonal Tropics and two winter-deciduous mixed forests in the Humid Mid-Latitudes. (Proctor 1983)

		Phytomass		Soil depth surveyed (cm)	Nutrient contents of the phytomass in % of total ecosystem reserves[b]					Authors
		Above ground ($t\ ha^{-1}$)	Below ground ($t\ ha^{-1}$)		N	K	Ca	Mg	P	
New Guinea	Lower montane	310	40	0–30	*4*	66	29	26	63	Edwards und Grubb 1982
Puerto Rico	Lower montane	197	78	0–50	*10*	81	40	48	54	
Colombia	Lowland (river terrace)	185	–	0–50	*11*	65	78	65	*9*	Fölster, De Las Salas und
Colombia	Slope	326	–	0–50	*15*	65	30	50	*15*	Khanna 1976
Colombia	16-year-old secondary	203	–	0–30	*9*	81	75	63	*19*	
Panama	Lowland (river terrace)	316	11	0–30	–	*89*	*16*	*14*	*87*	Golley et al. 1975
Venezuela	Montane	348	56	0–40	*18*	76	53	57	*9*	Grimm und Fassbender 1981
Venezuela[a]	Lowland (river terrace)	398	–	0–50	*33*	81	65	43	*11*	Hase und Fölster 1982
Brazil	Lowland (river terrace)	406	67	0–30	*40*	*88*	*100*	*91*	*47*	Klinge 1976
Ghana	Lowland (river terrace)	233	54	0–30	*29*	56	46	52	80	Nye 1961
India	Dry deciduous	78	22	0–30	*19*	55	–	–	31	Singh und Misra 1978
India	Dry deciduous	71	19	0–30	*20*	53	–	–	28	
Belgium	Mixed oakwood	121	35	–	–	65	8	39	–	Duvigneaud und
		–	–	–	*11*	*1*	*1*	*2*	*5*	Denaeyer-De-Smet 1971
England	Mixed oakwood	128	75	–	–	58	43	61	55	Satchell 1971
		–	–	–	*11*	*2*	*33*	*1*	*5*	

[a] The mineral contents of the below-ground phytomasses were not included.

[b] The mineral contents of the soils were calculated as follows: In most cases only those nutrients present in the exchangeable (cation) or (in the case of phosphorus) soluble soil fractions were measured; where the calculation was based on the *total* quantities (i.e. including the mineral-bound or organically bound nutrients, as always in the case of N) the percentages are printed *in italics*.

upper 20–30 cm of the soil where the three above-mentioned nutrient inputs occur. This shows clearly once more the overwhelming importance which the recycled minerals and the minerals supplied via precipitation play in the nutrient turnovers compared with the minerals available on exchangers in mineral soil.

Amounts and percentages of the nutrient elements supplied to the soil are shown in Tables 47 and 48, taking as examples rain forests in the Ivory Coast and in New Guinea. In all cases (and as confirmed elsewhere) the inputs through precipitation are extremely significant. They compensate for the losses which occur via leaching, despite all the safety mechanisms (Klinge 1976; Proctor 1983).

Table 47. The annual amounts of nutrients supplied to the soil under tropical rain forests by precipitation, crown wash (including stemflow) and litter fall, taking as examples two forest stands in the Ivory Coast. (Bernhard-Reversat 1975).

Study areas	Supply of nutrients to the soil	N	K	Ca	Mg	P
Plateau	Total (kg ha^{-1} a^{-1})	258	85	97	91	9.8
	of which (in %) from					
	– Precipitation	9	6	22	4	14
	– Crown wash	25	61	15	40	4
	– Litter fall	66	33	63	56	82
Thalweg	Total (kg ha^{-1} a^{-1})	246	264	135	90	24
	of which (in %) from					
	– Precipitation	10	2	16	4	6
	– Crown wash	26	67	21	56	38
	– Litter fall	64	31	63	40	56

Table 48. Nutrient reserves and turnovers in montane rain forests in New Guinea. (Edwards 1982; Edwards and Grubb 1982, from Walter and Breckle 1984). Mean values from all sites studied. Reserves in kg ha^{-1}, turnovers in kg ha^{-1}a^{-1}

Reserves and turnovers	Organic matter	N	K	Ca	Mg	P
Phytomass						
– Above ground	310 000	683	668	1270	187	37
– Below ground	40 000	137	186	333	61	6.4
Litter layer	6 460	91	11.5	96	14.5	4.8
Organic matter in the soil	415 000	19 200	403	3750	682	2560[a]
Nutrients supplied to the soil						
– Total		121	99	114	30	7.6
– Precipitation		6.5	7.5	3.6	1.3	0.5
– Crown wash and steam flow		23.5	63.5	15.4	9.7	2.0
– Litter fall	7 550	91	28	95	19	5.1

[a] Fluoride-soluble P: 16 kg ha^{-1}.

However, the major inputs occur via the two (most important) pathways of *nutrient recycling*, namely via plant wastes and crown wash/stemflow (throughfall). The latter in particular is extremely important for the supply of potassium: twice as much of this nutrient element is returned to the soil via throughfall than via litter fall. Potassium thus circulates much faster than, for example, calcium. Throughfall also plays a major role in the return of magnesium. For all other nutrient elements, litter fall is more important.

In the case of litter fall, the leaf litter is of particular importance. Although it comprises only about 50% of the total amount of litter produced, its contribution to nutrient return – due to its greater nutrient contents and despite leaching losses and nutrient transfers into the twigs prior to abscission – is much higher. Since the tropical rain forests have much larger leaf masses than the winter-deciduous forests of the Humid Mid-Latitudes, the absolute amounts of nutrients returned via the leaf litter (as well as in total) are much higher than in the latter forests (cf. Fig. 85 and Table 27). This also holds true when considering that only about

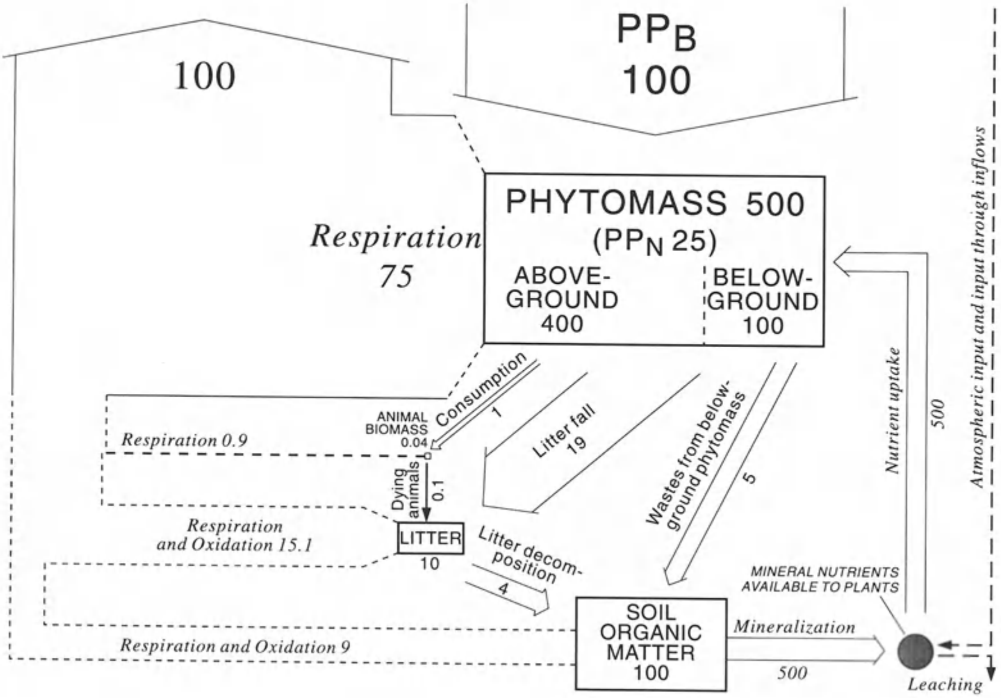


Fig. 184. Simplified ecosystem model of a tropical rain forest. (Compiled from data provided by Golley and Medina 1975; Murphy 1975; Klinge 1976; UNESCO 1978; Golley 1983; Proctor 1985; Jordan 1986). With regard to the layout of the model, see Chapter 2.5.2.5. Notice the large amount of phytomass and the (by comparison, strikingly) small amount of litter and organic matter in the soil; other typical features are the high turnovers of energy and minerals as well as the – in many cases – extremely low amounts of the exchangeable nutrients in the soil

80–90% of leaf mass is shed annually in tropical rain forest, whereas this amounts to 100% in temperate broadleaved forests.

Figure 184 shows the characteristic stand reserves and turnovers of a tropical rain forest ecosystem according to the model scheme as already used for some other ecozones (cf. Chap. 3.1.5, 3.2.5, 3.3.5 and 3.4.5).

3.9.6 Land Use

The Humid Tropics are regions of the earth which to this day are still thinly populated. One reason which is occasionally given for this is that they are "ecologically disadvantaged" (Weischet 1980) as far as agrarian use is concerned, a thesis which was already established by Walter (1936) and Milne (1937) on the basis of studies conducted in East Africa, and by Hardy (1936) following studies in Trinidad. This is a reference to the following *unfavourable soil properties* such as occur in many ferralsols (see also chapter 3.9.4):

- The low content of weatherable silicates means that the soils do not have a reserve fraction from which nutrient elements could be mobilized in the long and medium term by weathering, i.e. the soils have no intrinsic regenerative ability.
- The predominance of weakly sorptive two-layered clay minerals of the kaolinite group and of sesquioxides gives rise to a low exchange capacity of the mineral fraction. Instead, plant nutrients and exchange capacity are to a large extent provided by the humus complex within the uppermost 20–30 cm of the soils.
- Once the rain forest has been cleared and crop husbandry has been commenced, there is a rapid decline in the amount of humus, because there is virtually no longer any supply of litter, and the higher soil temperature (heating by direct insolation) accelerates the decay of humus originally formed under forest cover; thus the main source of nutrient recycling is lost and the (total) exchange capacity of the soil drops more and more to the low level of the mineral components (= low activity clays).
- The base saturation is low, i.e. only a small part of the already low exchange capacity is available for the sorption of nutrients such as K^+, Ca^{2+}, and Mg^{2+}. Instead, there is an excess of H^+ and Al^{3+} in the cation layer of the exchangers and in the soil solution; the soil reaction is correspondingly very acid. As a result, problems are encountered with aluminium toxicity and phosphorus fixation.
- Unless special measures are taken to improve the soil, ferralsols having the described characteristics can be used for a maximum of just a few years only, because the yields decline rapidly.
- The attempt to compensate for the lack of naturally available nutrients by supplying them artificially i.e. in the form of fertilizers, has its limits – so it is claimed – due to the low exchange capacity of the soil. This restricts the maximum quantities which a soil may retain of these artificial fertilizers to a very low level. Anything supplied in addition to this amount passes through

the soil unused, together with the percolating water, and finally appears as undesired fertilizer in the rivers.

According to the large number of pedological and ecological studies of many subregions of the tropics which have been published until now, it is becoming increasingly evident that the above given view has to be revised. It is no longer true to generally classify moist tropical soils as infertile. In fact, the described disadvantages are not the norm, but instead they represent the most unfavourable case. For example, the supply of plant nutrients in the soils is often not all that bad (cf. also Chap. 3.9.5.2). The initial rapid losses of humus substances following clearing of the forest grow less severe, as the rate of decomposition falls from 10% in the first year to less than 1% after a long period of use (Young 1976, p. 115). The CEC can be considerably increased (see Chap. 3.7.4), toxic aluminium can be eliminated, and the availability of phosphorus can be boosted, by artificially adding organic matter (e.g. by mulching), by incomplete burning of the former forest (which then results in a near continuous nutrient supply for several yeras), and by raising the pH value (e.g. by liming). As is shown by the sometimes excellent production figures achieved by modern agricultural operations in all parts of the Humid Tropics, agricultural exploitation of the land can be extremely successful (also on a long-term basis) if suitable methods of exploitation are employed (see below). In many regions, no doubt, the potential land suitability of land for agricultural use and the *potential productivity*, i.e. the long-term or permanently achievable economic yield once all deficiencies have been eliminated, are definitely much higher than the *actual productivity* suggests.

Traditional Agricultural Systems

Slash-and-burn/shifting cultivation was and still is probably the most widely adopted of the traditional agricultural systems in the Humid Tropics (Fig. 91). In addition, *paddy rice farming* is very important in the South and South East Asian sub-region. All parts of the Humid Tropics contain more or less large numbers of farms growing tree crops. These may range from smallholdings all the way up to large plantations. Hunting and gathering which was practised in the past, e.g. by pygmies in the Congo Basin, some Indian tribes in the Amazon region, and Melanesians in Southeast Asia, never involved very many people but extended over large areas.

In the case of shifting cultivation (slash-and-burn), the cultivation activity is relocated after short periods of time (a few years) to new areas in the forest from which part of the vegetation (above all, lopped branches with foliage attached, but rarely whole trees) has been removed and burnt. The burning fertilizes the soil (with ash). The farmers have no choice but to relocate the fields after short periods of use because the yields rapidly decline. A previously cultivated area cannot be reworked with any prospects of success until a long rest period has elapsed (15–30 years).

The *reason generally given for the decline in production* as utilization continues is that the nutrients are withdrawn from the soil by the crops and also removed by leaching, thereby causing the fertility of the soil to decline to a level where it increasingly limits plant growth. This interpretation must probably be revised. For example, the *studies conducted between 1976 and 1983 in a rain forest region near San Carlos de Rio Negro in Southern Venezuela*, near the border with Colombia and Brazil (Jordan 1986), have shown that the reserves of important minerals in the soil do not decline during the 3-year period for which an area is usually farmed in that region, before it is abandoned due to a severe drop in yield; this is also confirmed by other, for the most part recent, studies performed in African and South East Asian rain forest regions (cf. literature references in Jordan). Therefore, the decline in production must be caused by some other factors. The following remarks refer to the study carried out in San Carlos.

The soil in the study area is a ferralsol. Its surface is covered by a layer of litter up to a few cm thick. This and the dead organic matter in the soil together total 60 $\mathrm{t\,ha^{-1}}$. The phytomass of the primary forest amounts to 324 $\mathrm{t\,ha^{-1}}$, of which 274 t is above-ground (9 t leaf mass, 265 t wood mass). The distribution of the mineral reserves in the forest ecosystem is shown by, in each case, the first columns (Column 1) in the sets of columns contained in Fig. 185. The largest amounts of K and Ca are found in the above-ground phytomass, whereas the largest amounts of N and P are contained in the soil. Of the phosphorus reserves in the soil, only about 2% (or about 5 $\mathrm{kg\,ha^{-1}}$) occur in solution or on exchangers. The remainder is fixed in the form of Al or Fe phosphates and is not available to the plants.

In shifting cultivation, as a rule, only the small branches with foliage are burnt by the *fires set to clear the land.* On the other hand, the tree stems and stumps are for the most part preserved. Thus, the fires release only some of the nutrients contained in the phytomass, and the rest are only gradually released from the organic matter as it breaks down biologically.

In the experiment conducted by Jordan over a period of 7 years, fire was used in a similar manner and the land was subsequently cultivated using the traditional methods. The results of the first 3 years of cultivation are given below.

The fires brought about a rapid change in the distribution of the minerals. The percentages contained in the above-ground phytomass declined roughly in proportion to the amount of phytomass that was burnt, and the percentages contained in the soil increased essentially to the same extent. Only nitrogen escaped in large quantities (Fig. 185, column 2 in each set of columns).

As the minerals were supplied to the soil, so the *leaching losses* increased steeply, as expected. K was particularly severely affected, while large amounts of Ca and Mg were adsorbed by the exchangers. P did not accumulate in the water of percolation; probably it was bound by iron and aluminium immediately after it was released.

The third columns in each set of Fig. 185 show what amounts of N, K, Ca and Mg were leached out altogether after 3 years of use (excesses of leaching over atmospheric inputs). At the same time, these columns show the cumulative losses which occurred as a result of harvesting during this period.

Despite this fact that, to some extent, considerable amounts of nutrient had

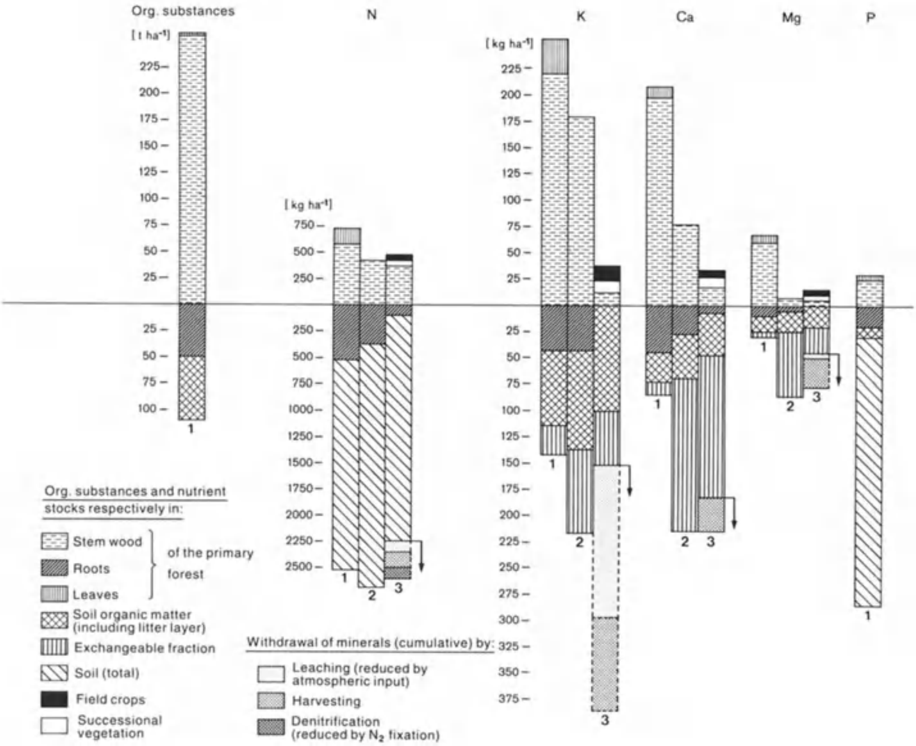


Fig. 185. The fractions of the organic substances and of the major mineral nutrients in an Amazonian rain forest ecosystem (*Columns 1*), and the nutrient dynamics, shortly after clearing of the forest (*Columns 2*), and after 3 years of agrarian use by the traditional method of shifting cultivation (*Columns 3*). (Compiled on the basis of research data obtained by Jordon 1986). See text for further explanations

been withdrawn, the mineral reserves in the soil as also shown (as the most striking result) in the third columns were still fairly *constant even after 3 years of exploitation.* None of the major nutrient elements had dropped below the pre-fire stage. Obviously, therefore, the minerals supplied with the ash and – as cropping continued – those supplied by the decomposition of litter and also of plants which had been killed off but not totally burnt by the fire, permanently exceeded the leaching losses to such an extent that even the withdrawal by the crops was still covered.

The supply of nutrients from the decomposition of dead organic substances declined after the third year of cultivation – the litter disappeared between the second and third year, the tree trunks and roots a couple of years later (see Figs. 2.3 and 2.4 in Jordan 1986) – and it was only then that a drop occurred in the soil nutrient status.

Nevertheless, the yields shrank already within the 3-year cultivation period, in the manner which is characteristic of all areas exploited by shifting cultivation in the moist tropics. Between the first and third years, the total PP_N of the crops declined from 5.3 t to 3.1 t $ha^{-1} a^{-1}$ and the yields of cassava, the most important field crop, dropped from 1.46 to 0.70 t $ha^{-1} a^{-1}$.

Jordan believes that the explanation for this discrepancy is to be found in the increasing fixation of phosphorus and the increasing amounts of toxic aluminium, with which the crops are faced when the pH values drop again in the course of land use: the initial increase in pH from 3.9 to 5.4 (Fig. 186) on the areas which had been cleared (as a result of the ash fertilizing effect) was at first associated with an increase in available P and a reduction in toxic Al; these positive changes were reversed again once the pH value dropped to 4.1, and later even to 3.8. According to this, the *main benefit of slash-and-burn* clearing would be that it raises the pH value, and less so that plant nutrients are released from their organic compounds and are thus made available for plant take-up (Sanchez 1976).

The *regrowth of the forest* once cultivation of the land is stopped *commences with a significantly lower (overall) stock of nutrients* (i.e. those in the soil and in the phytomass) than existed in the rain forest ecosystem prior to the forest being cleared (compare, for each of the chosen nutrients, columns 1 and 3 in Fig. 185). In the case of San Carlos, once the farming activity was terminated, further heavy losses continued to be incurred, probably because of surface erosion. This depressed, for example, the stocks of K, Ca and Mg to about one-quarter of the original reserves. Even if, perhaps, these extreme losses do not always occur, it is nevertheless certain that at least some deficits need to be made up in all areas, so that a forest of the original type (primary forest) can regenerate itself.

Since the soils are not capable of resupplying the missing nutrients from weatherable silicates, the only source can be *atmospheric input* (chiefly via precipitation). Only phosphorus is probably replenished from fixed reserves and nitrogen is partially supplied via biological N_2-fixation (Saldar-Riaga 1986).

It takes about a century or more before the original nutrient levels are restored and a primary forest replaces the secondary forest. Provided that approximately this time span is maintained between the abandonment and renewed cultivation

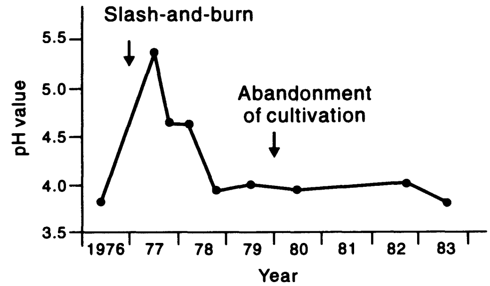


Fig. 186. The changes in the pH of the soil under an Amazonian rain forest after slash-and-burn clearing and three years of agrarian use by the traditional method of shifting cultivation. (Jordan 1986). The ash fertilizer quickly brings about a significant increase in the pH, with which is possibly linked a reduction in the phosphorus fixation and the aluminium toxicity. The reversal of this process could explain the rapid decline in agricultural yields; cf. also Fig. 185

of the land, shifting cultivation is a system of farming which in the long term can be practised without causing any irreversible damage to the rain forest, i.e. it an ecologically sustainable system.

This does not mean, however, that it is also the best possible system of cultivation. It is a disadvantage, for example, that the *land required by shifting cultivation* is many times larger than that needed by a farmer practising semi-permanent cultivation, whose land requirement in turn is greater than that of a farmer with permanent fields (in each case relative to the amount of farmland needed to meet the farmer's own requirements). In a shifting cultivation system in which the fields are farmed for 2 years, followed by 24 years of fallow, each farm requires an area 13 times larger (cultivation factor 13) than in the case of permanent-field systems; and only 8% of that area ($R = 0.08$) is under cultivation at any one time (see Chap. 3.7.6, Land Use). Areas in which shifting cultivation is practised can therefore support only very small populations per unit area (approximately two to five inhabitants per km^2).

In addition, shifting cultivation is labour-intensive (although less so than some traditional cultivation systems using shorter periods of fallow or employing permanent cultivation) and, despite the fertilizing with ash, the yields per unit area are low compared with the non-tropical zones. Therefore, people can do no more than provide for their own needs (subsistence) when they employ the methods of shifting cultivation, and even then they have to use vast areas of land and burn off enormous amounts of organically bound energy from which no benefits are derived.

It should also be remembered that, in practically every area, the population density has increased beyond the level at which shifting cultivation is ecologically acceptable, and the rain forest is thus deprived with increasing frequency of the chance to regenerate between the intervals of exploitation. From the modern standpoint, shifting cultivation must therefore be regarded as a highly unsatisfactory system of farming, both in economic and ecological terms.

Modern Land Use Systems

However, when looking for *new forms of exploitation*, use should be made of the centuries, if not thousands of years, of experience on which the system of shifting cultivation is based. In the long term, the only farming systems which will succeed are those which best satisfy the special ecological conditions of the moist tropics. Important *problems/dangers* against which precautionary measures must be taken, whatever kind of agrarian use is made of the land, include:

- Structural deterioration of the soils after being put under cultivation: soil compaction due to puddle erosion and/or the use of heavy machinery to clear and work the land, induration following drying of the soil, as well as a decrease in the humus content.
- Low usable water capacity of the soils.
- Soil leaching (especially of K) and erosion.

- Low effective CEC and base saturation.
- Soil acidity, phosphorus fixation and aluminium toxicity.
- Volatilization of nitrogen when fire is applied (especially serious when pasture land is repeatedly set on fire).
- Rapid spread of plant diseases, pests and parasites after the natural species diversity has been replaced by uniform crop stands.
- Overgrowth of weeds which are very difficult to bring under control.

Suitable *countermeasures* can include:

- Using high yield and disease-resistant species of crops with strong root development.
- Searching for genotypical variants (ecotypes) of crop plants which are particularly well adapted to unfavourable soil properties, for example high Al concentrations, and extreme soil acidity.
- Screening the surface of the soil by planting crops which create as far as possible a permanently closed canopy of leaves, preferably permanent crops (possibly supplemented by forest trees which are left standing).
- Selecting permanent crops with low nutrient requirements, for harvested parts (e.g. some tree crops; see below).
- Mulching with harvest residues, or with material of annual plants, which are cultivated quite frequently in tropical tree plantations as intermediate crops for subsistence and/or for soil protection, or with plant material supplied from outside the cultivated area; the rapid decomposition which this material undergoes in the hot wet climate is not a disadvantage: it provides the also desired rapid supply of minerals for the field crops (green fertilizer); it should not be a problem to renew the layer of mulch at frequent intervals, by making use of the high biomass production of the natural vegetation or also by establishing, for instance, elephant grass plantations specially for this purpose.
- Using nitrogen-binding field crops, trees or fodder plants such as *Erythrina, Leucaena leucocephala, Phaseolus lunatus, Psophocarpus tetragonolobus* and *Vigna unguiculata.*
- Raising the pH level by liming.
- Replacing nutrient losses by adding fertilizers adapted to the high risks of leaching, e.g. by top dressing and long-term dressing with organic fertilizer or depot fertilizer.
- Maintaining maximum possible diversity, e.g. by following a land use system that can be classified as *ecofarming*: planting mixed crops, using varied crop rotations, etc.
- Minimizing tillage.
- Controlling weed growth at early stages.

The most sensible solution seems to be to use *ecologically adapted cultivation methods* (ecofarming). This approach is concerned primarily with adapting the agrarian (and silvicultural) exploitation in the closest way possible to the natural site conditions (i.e. the goals are in principle the same as in many traditional cultivation systems, although in this case a higher degree of scientific and technical expertise is involved). By following the ecological approach, it will be possible to minimize the risks that generally occur when land is put under cultivation for the first time, e.g. the risks of soil depletion, crop diseases etc., and at the same time it will reduce the labour and material expenses required to support the agrarian or forested ecosystems, e.g. in the form of fertilizer applications and pest control measures. The following methods are directed more or less clearly towards achieving these goals:

- *Improved crop rotations*: for example by including in the crop rotation cycle (or also in mixed croppings) crops such as cassava, mountain rice, sweet potatoes and cowpeas, which are relatively undemanding and do not harm the humus (soil), and also by including legumes such as groundnuts and soybeans, which bind atmospheric nitrogen.
- *Maintenance of permanent plant cover*: for example by relay cropping, by planting intermediate and mixed crops in the fields, by undersowing in permanent crops or by providing protective (covering) plants (e.g. by planting shadow trees or by leaving certain trees from the original forest vegetation). Integration with tree plantations appears a particularly favourable solution. Besides soil protection, they have the advantage that the portions harvested are relatively small and the removal of mineral nutrients is correspondingly low. Also, the roots of the trees can bring up nutrients from deeper soil strata, and the soil can be more gently tilled. From an ecological standpoint, tree crops which are undercropped with the widest possible range of shrubby and herbaceous crop species, i.e. a multistorey mixed cropping, come closest in character to the natural forest (for example, a relatively closed nutrient cycle can develop in them) (Fig. 187).
- *Replacement of uncontrolled fallowing by a controlled profitable fallow*: e.g. by using fodder plants in conjunction with animal husbandry, or also by carrying out afforestation, for example with leguminous trees which at the same time can help improve the soil and also be used for timber production (agrosilviculture).

One example of successful ecofarming is described for the region of Tome-Assu, 150 km south of Bélem, Brazil (Jordan 1986); many other positive examples have been reported from Southeast Asia (Prinz 1986). As a rule, these farms also keep animals, and this activity is advantageously combined with their crop-growing operations (e.g. collection of dung, use of animal traction in the fields, grazing under permanent crops, fodder growing).

Even *permanent agriculture*, of the kind practised outside the tropics, seems to be successful under certain conditions. This is reasonably reliably confirmed by some experimental agricultural areas in Yurimagua, Peru, in the western part of the Amazon region (Sanchez et al. 1983). In that region, the soil is an acrisol with a high content of Al, deficiencies of P, K and most other nutrient elements, as well as a pH value of 4. By applying fertilizer and lime, also by adopting suitable crop rotations, the nutrient content and the pH value of the soil were noticeably increased, the amounts of Al were reduced and consistently high yields were achieved (Fig. 188).

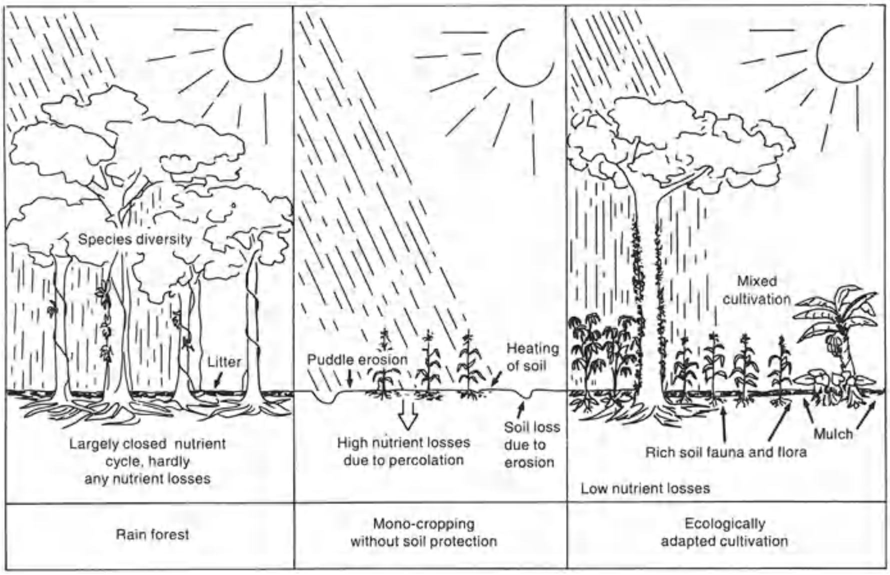


Fig. 187. Ecologically adapted multistorey cultivation compared with mono-cropping and primary forest. (Prinz 1986). *Left* Diagrammatic structure of the tropical rain forest with a largely closed nutrient cycle; *Centre* cultivation of an annual crop (maize) after clearing the forest, without protection against sun or heavy rain; *Right* ecologically adapted multilayered cultivation with mulching

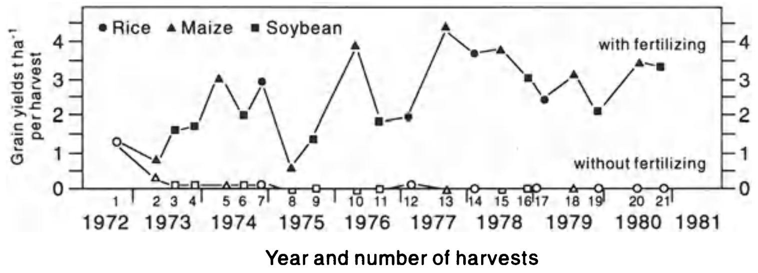
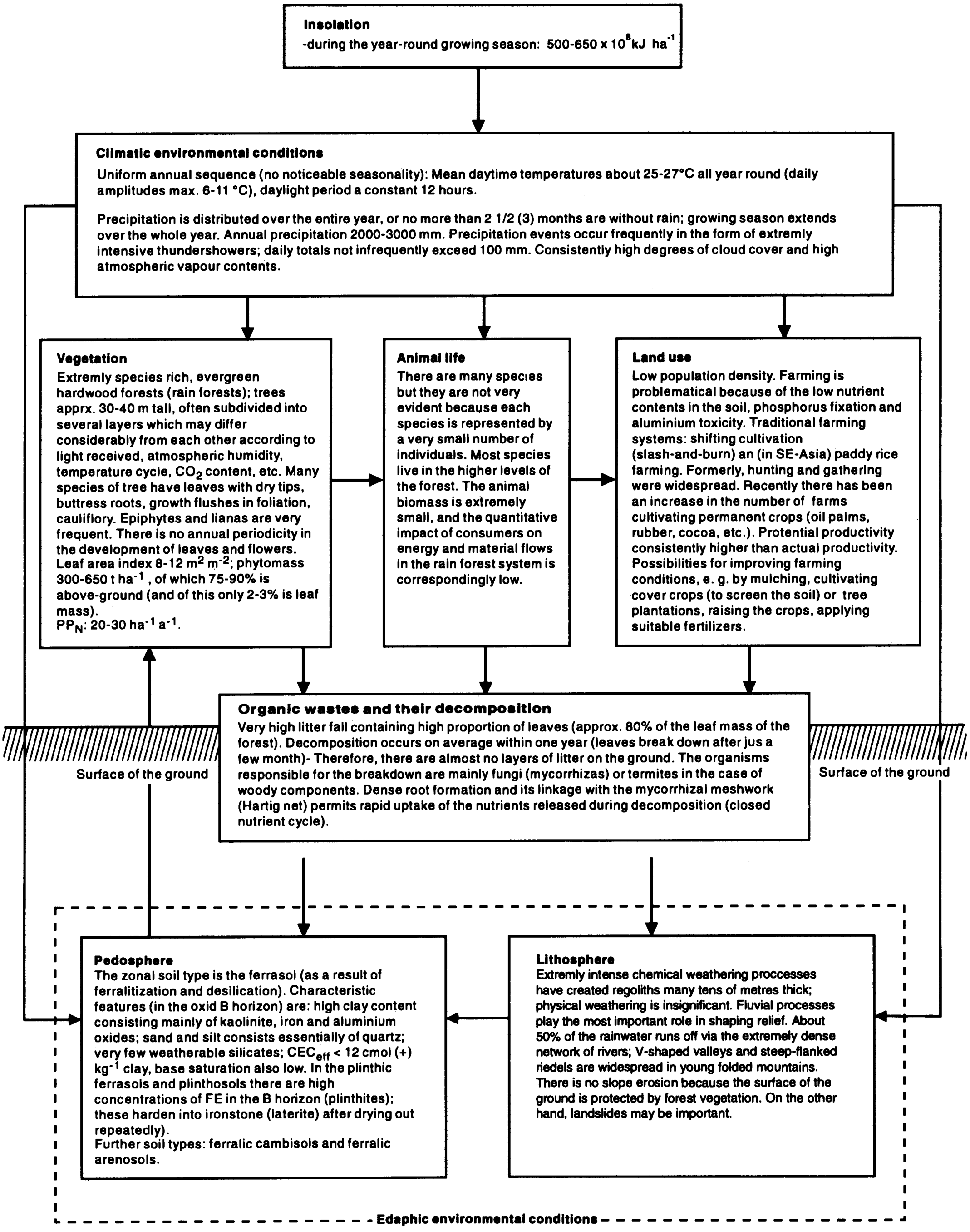


Fig. 188. Yield record of a continuously cultivated plot on an Amazonian acrisol in Yurimaguas, Peru. (Jordan 1986). In most years two and in some years three crops were sown and harvested. The *upper curve* shows the yields obtained with complete fertilization (initially 80–100–80 kg N–P–K per hectare, and lime to raise the pH to 5.5; then 100–26–80 kg N–P–K per hectare and field crop). The *lower curve* shows for comparison the development of production on unfertilized fields

In many places *plantations of perennial tree crops* such as rubber, cacao or oil palm, employing modern management methods, have been successfully developed. The yields are often extremely high. For example, one oil tree plantation in the Amazon region has for many years been producing a crop of 4 t of oil ha^{-1} per annum.



Insolation
-during the year-round growing season: 500-650 x 10^8kJ ha^{-1}

Climatic environmental conditions
Uniform annual sequence (no noticeable seasonality): Mean daytime temperatures about 25-27°C all year round (daily amplitudes max. 6-11 °C), daylight period a constant 12 hours.

Precipitation is distributed over the entire year, or no more than 2 1/2 (3) months are without rain; growing season extends over the whole year. Annual precipitation 2000-3000 mm. Precipitation events occur frequently in the form of extremly intensive thundershowers; daily totals not infrequently exceed 100 mm. Consistently high degrees of cloud cover and high atmospheric vapour contents.

Vegetation
Extremly species rich, evergreen hardwood forests (rain forests); trees apprx. 30-40 m tall, often subdivided into several layers which may differ considerably from each other according to light received, atmospheric humidity, temperature cycle, CO_2 content, etc. Many species of tree have leaves with dry tips, buttress roots, growth flushes in foliation, cauliflory. Epiphytes and lianas are very frequent. There is no annual periodicity in the development of leaves and flowers. Leaf area index 8-12 m^2 m^{-2}; phytomass 300-650 t ha^{-1}, of which 75-90% is above-ground (and of this only 2-3% is leaf mass).
PP_N: 20-30 ha^{-1} a^{-1}.

Animal life
There are many species but they are not very evident because each species is represented by a very small number of individuals. Most species live in the higher levels of the forest. The animal biomass is extremely small, and the quantitative impact of consumers on energy and material flows in the rain forest system is correspondingly low.

Land use
Low population density. Farming is problematical because of the low nutrient contents in the soil, phosphorus fixation and aluminium toxicity. Traditional farming systems: shifting cultivation (slash-and-burn) an (in SE-Asia) paddy rice farming. Formerly, hunting and gathering were widespread. Recently there has been an increase in the number of farms cultivating permanent crops (oil palms, rubber, cocoa, etc.). Potential productivity consistently higher than actual productivity. Possibilities for improving farming conditions, e. g. by mulching, cultivating cover crops (to screen the soil) or tree plantations, raising the crops, applying suitable fertilizers.

Organic wastes and their decomposition
Very high litter fall containing high proportion of leaves (approx. 80% of the leaf mass of the forest). Decomposition occurs on average within one year (leaves break down after jus a few month)- Therefore, there are almost no layers of litter on the ground. The organisms responsible for the breakdown are mainly fungi (mycorrhizas) or termites in the case of woody components. Dense root formation and its linkage with the mycorrhizal meshwork (Hartig net) permits rapid uptake of the nutrients released during decomposition (closed nutrient cycle).

Pedosphere
The zonal soil type is the ferrasol (as a result of ferralitization and desilication). Characteristic features (in the oxid B horizon) are: high clay content consisting mainly of kaolinite, iron and aluminium oxides; sand and silt consists essentially of quartz; very few weatherable silicates; CEC_{eff} < 12 cmol (+) kg^{-1} clay, base saturation also low. In the plinthic ferrasols and plinthosols there are high concentrations of FE in the B horizon (plinthites); these harden into ironstone (laterite) after drying out repeatedly).
Further soil types: ferralic cambisols and ferralic arenosols.

Lithosphere
Extremly intense chemical weathering proccesses have created regoliths many tens of metres thick; physical weathering is insignificant. Fluvial processes play the most important role in shaping relief. About 50% of the rainwater runs off via the extremely dense network of rivers; V-shaped valleys and steep-flanked riedels are widespread in young folded mountains. There is no slope erosion because the surface of the ground is protected by forest vegetation. On the other hand, landslides may be important.

Edaphic environmental conditions

Fig. 189. Synoptic diagram of the Humid Tropics

Instead of the formerly preferred softwood plantations (established, for example, by Daniel Ludwig in the Amazon region), many of which in the meantime have proved a failure, *aisle-planting (line-planting)* and *upgrading of the rain forest* seem to be better ways of practising agrosilviculture and forestry in these regions. In the first case, the crops are planted along parallel running aisles (swaths) cleared in the native forest. The partial clearing means that the strips of forest which are preserved can exercise a stabilizing effect and protect the new plantings from erosion, insect damage, etc. In the second case, the forest is upgraded by selectively felling and removing undesired species of tree, so that the proportion of useful species (e.g. oil palms, Brazil nuts, kapok trees) becomes relatively enriched.

The foregoing remarks relate to the more unfavourable sites in the Humid Tropics, such as large areas of the tierre firme in the Amazon region (see beginning of this chapter).

Far fewer problems are encountered where soils with better natural qualities exist. Better sites of this kind are found in more or less large numbers and varying sizes throughout the tropical regions. Carefully selecting the sites which are to be used can therefore help avoid problems at a later date (as well as prevent areas of forest being cleared for no good reason). Favourable sites are often formed by the alluvial soils on the valley floors of rivers when fertile sediments are deposited here during flooding, e.g. the Varzea sites in the Amazon region. There should be good prospects here, in particular for growing rice.

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Chapter 3.9: Humid Tropics

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