Chapter 4

Ecosystem structure: site factors, soil and vegetation

Terrestrial ecosystems are characterised by their structure. The environmental factors – site factors – shape the vegetation and soil. In this chapter we will describe the coarse features of vegetation and soils. The interactions between vegetation, climate and soil material lead to the formation of biomes and soil types on global and regional scales. This chapter includes also some basic soil physics and chemistry.

Terrestrial ecosystems and site factors

Terrestrial ecosystems are shaped and governed by a number of interacting factors – site factors. These can be summarised in the following expression (Jenny 1941, Amundson & Jenny 1997):

$$E = f(c, o, r, p, t \ldots) \qquad (4.1)$$

where E = ecosystem; c = climate; o = organisms; r = topography; p = parent material or bedrock, which gradually changes into soil and t = time.

Site factors shape land ecosystems

This expression and Figure 4.1 show in a simplified way how these major factors affect a terrestrial ecosystem and resulting effects. We have grouped the factors according to their way of working. Of prime importance for the organisms and the ecosystem is the climate, in terms of its physical and chemical components. Light as a component of the physical climate is necessary for organisms, in particular plants. Further, the energy coming from light and expressed in temperature or heat is fundamental as a rate regulator of all biological activities (Chapters 5–7). A part of the physical climate is also water, with its double importance through its physiological action and its function as a carrier of substances in the plants, as well as in the whole ecosystem (Chapter 5). There is also a chemical dimension to the climate. The air contains not only gases such as oxygen, carbon dioxide and nitrogen, but also acids such as carbonic and sulfuric acid. The soil contains mineral or nutrient elements essential to the organisms. Over time there are also changes as a consequence of Man's actions or from natural causes (Chapters 9, 11, 12, 14 and 15). The topography or slope determines the incoming radiation to the ecosystems and also affects the ways water passes through the ecosystem. In addition, there are mechanical factors acting in and

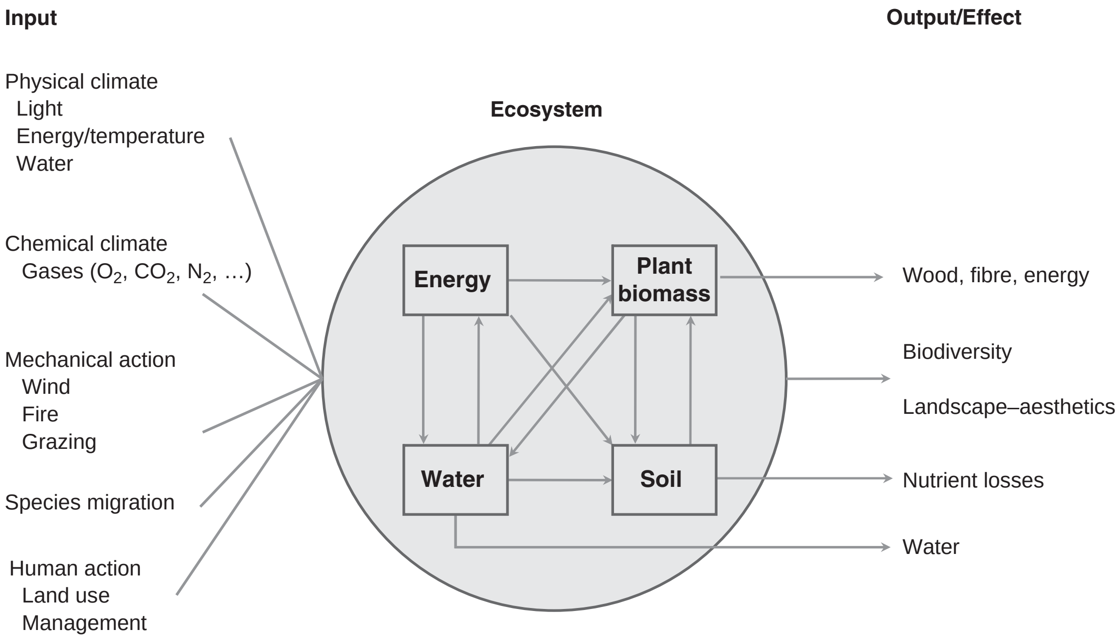


Figure 4.1 Factors shaping terrestrial ecosystems.

on the ecosystem: wind, fire, grazing and Man's activities, such as harvesting in fields and forests (Chapter 13). Finally, time is an essential factor, sometimes forgotten. It is always a question of the time perspective in which different factors should be considered – short term vs. long term.

The soil has a key role in terrestrial ecosystems as its properties determine the type of species and ecosystem that can and will develop under specific climatic regimes. To understand what shapes the structure of terrestrial ecosystems we need some insight into and understanding of basic soil properties and processes.

Soil physics and chemistry

The soil in an ecosystem context

What is soil?

The word soil is ambiguous as it used in many meanings. We use *soil* or *the soil*, *soils* and *soil type* with the following understanding:

> ***soil*** and *the soil* – refers to the material itself; its organic and inorganic composition
>
> ***soil*** or *soils* – refer to a natural body with a specific composition such as sandy clay
>
> ***soil*** *type* – refers to a soil, such as a spodosol, produced by a specific set of soil-forming factors.

A prime function of the soil is to support growth of higher plants. It is the medium for plant roots, offering physical support, transporting air, gases and water, buffering against extreme temperatures and other extreme weather conditions, providing protection from toxins and last but not least delivering mineral nutrients.

Plant roots need energy, which is gained through respiration and requires oxygen, which for most plants is taken up by the roots from the soil environment, and yields carbon dioxide. The soil must thus be ventilated or aerated in order to let oxygen enter and carbon dioxide escape. This requires a system or network of pores in the soil. The pore system is also essential for infiltration of water to the soil as plants and soil organisms more or less continuously need water for their life processes, such as photosynthesis, cell turgor, nutrient transport and heat balance. The capacity of a soil to hold water is important for the plants to withstand periods without precipitation (Chapter 5). Water, with its high specific heat and the high latent heat of fusion of ice, is also important for the thermal properties of the soil.

The soil is also a habitat for soil organisms, everything from soil-dwelling higher fauna to insects, fungi and microbes. The soils provide a huge variation in chemical and physical environment from basic to acid, from well aerated to anoxic. This explains the high diversity of organisms found in soils. The organisms act as consumers and decomposers and are responsible for the recycling of nutrients. Seen in a landscape perspective the soil also regulates, not only quantity, but also quality of groundwater with contributions to larger water bodies. The physically and biologically functioning soil can protect plant roots from harmful substances such as gases by good ventilation, and decompose or adsorb organic compounds, as well as suppress the formation of toxins; finally the soil provides plants with essential mineral nutrients originating from weathered bedrock or recycled from the organic matter formed in the ecosystem. The soil has a major role in the gas exchange between the ecosystem and the atmosphere. Some gases are released, such as carbon dioxide and nitrogen oxides, others are absorbed, such as oxygen, and some, like methane, can, depending upon specific conditions, be either released or absorbed.

We will now consider in some detail the physical and chemical properties of soils and their importance in ecosystem functioning; the biological part of the soil is dealt with in later chapters (Chapters 7–9).

Soil physical properties

A soil is a three-dimensional system composed of minerals, organic matter, air, water and organisms (Figure 4.2)

There are two major types of soil depending on the material: *mineral soil* and *organic soil*. The mineral soils originate from bedrocks of different chemical compositions and are composed of different fractions, such as rock fragments, stones, gravel, sand, silt and clay. The smaller the particles are, the more important they are for the ecological properties of the soil (Table 4.1). The organic soils consist of

Table 4.1 General properties of sand, silt and clay

Property	Sand	Silt	Clay
Diameter (mm)	2.0–0.05	0.05–0.002	< 0.002
Means of observation	Naked eye	Microscope	Electron microscope
Dominant minerals	Primary	Primary and secondary	Secondary
Attraction of particles for each other	Low	Medium	High
Attraction of particles for water	Low	Medium	High
Ability to hold chemicals and nutrients in plant-available form	Very low	Low	High
Water-holding capacity	Low	Medium to high	High
Aeration	Good	Medium	Poor
Soil organic matter level	Low	Medium to high	Medium to high
Decomposition of organic matter	Rapid	Medium	Slow
Warm-up in spring	Rapid	Medium	Slow
Pollutant leaching potential	High	Medium	Low/High
Resistance to pH change	Low	Medium	High

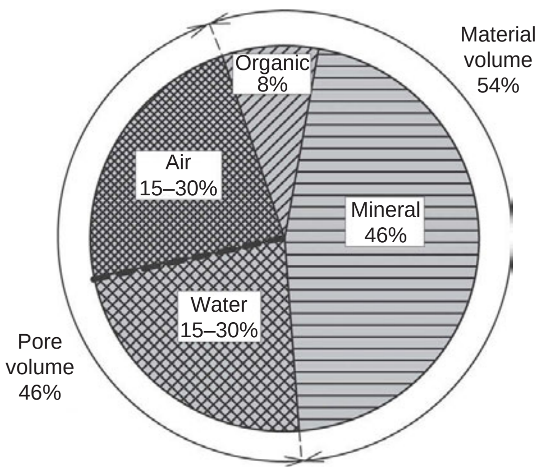


Figure 4.2 The composition of a soil from a deciduous forest: material and pore volume in volume %. The average composition of a soil favouring plant growth usually has 50% occupied by soil solids and 50% by air/gases and water. The latter fluctuates with weather conditions. Data from Andersson (1970a).

less decomposed plant material and more decomposed material – *humus*. The distinction between mineral and organic soils is not always clear, as mineral soils contain varying amounts of organic matter and minerals are mixed into organic soils.

More fine particles – better structure, more nutrients and water in the soil but less oxygen

The distribution of particle sizes in the mineral soil – the *texture* – as well as the content of organic matter determine many soil properties. The conventional classification of particles into size classes is: sand, silt and clay (Table 4.1). A gradual change in the mineral particles occurs through *physical* and *chemical weathering* processes, where *primary minerals* are changed into *secondary minerals*. The latter are of a colloidal size, < 0.001 mm. The distribution of particle sizes is important because the surface area per unit mass increases rapidly as the proportion of small particles increases. The surfaces of the colloids (both mineral and organic – clay–humus complexes) are electrically charged and therefore attract ions, positively or negatively charged, depending upon the type of mineral and pH of the soil, as well as water content. This fine fraction plays a key role for most soil chemical and physical processes.

Soil structure is another important physical property of the soil. The structure of the soil consists of a system of pores of different sizes and determines the volume of pores in the soil or the *porosity* (Box 4.1). This is the available volume for air and water. It determines the behaviour of gases and water in the soil and influences that of the plant roots. The soil structure depends on the ability of the soil to form aggregates, as well as their size and form. The aggregates can take different forms: spheroidal (granular, crumb), platelike, blocklike (angular, sub-angular) and prismalike (columnar, prismatic). The form

Box 4.1 | Soil texture, soil structure and water content

The *soil texture* or particle size composition can be crudely determined in field tests by 'feeling' in the hand. Different fractions such as sand, silt and clay have different characteristics. More detailed analyses are done on soil samples where the organic matter has been removed by oxidation. Coarse fractions are first sieved away. Finer fractions can then be determined in a water suspension because large particles fall faster than small ones (Stoke's law). Using the percentages of clay, silt and sand in a triangular diagram the (mineral) soil is then assigned to a texture class (Figure 4.3).

The *soil structure* is visible to the eye. The distribution of pore sizes is determined on volume-based samples saturated with water subjected to different pressures or suctions. The rate at which water is extracted can then be related to pore size.

Determination of pore volume. A soil sample with known volume is taken. We then calculate:

$$\text{Pore volume in } \% = \left(1 - \frac{\text{Bulk density}}{\text{Particle density}}\right)100 \tag{4.2}$$

where

$$\text{Bulk density} = \frac{\text{Dry weight of sample at } 105^{\circ}\text{C}}{\text{Volume of sample}} \tag{4.3}$$

and particle density is the density of the mineral particles, typically 2.65 Mg m^{-3}.

The *water content* of a soil is determined by collecting soil samples from different levels of a soil profile. The fresh/wet weight as well as dry weight after drying at 105 °C to constant weight is determined. The volume % of water can now be calculated as well as the total amount of water. Water considered as non-available for organisms is determined as what remains after suction, usually at 15 atm.

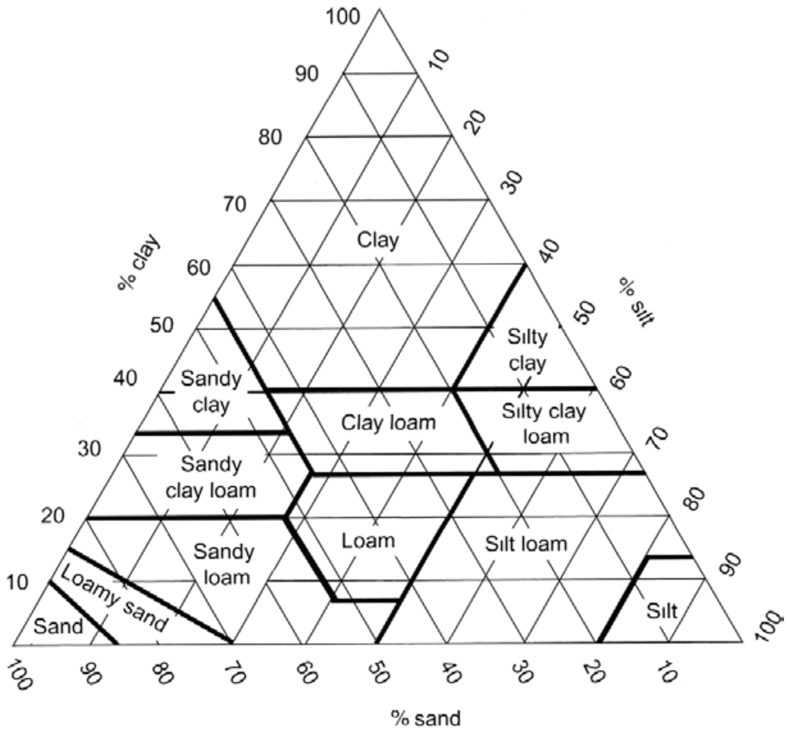


Figure 4.3 Triangle diagram for determination of texture classes.

is determined by the forces active in the soil and depends on processes such as freeze–thaw, wet–dry, shrink–swell, penetration of roots and burrowing soil animals like earthworms, as well as activity of other organisms such as fungi and bacteria.

Soil air

The soil air is essential for the biological and chemical processes in the soil. The distribution of root systems, root respiration and nutrient uptake, as well as the presence of soil organisms, are directly related to the amount and composition of the soil air. The composition of the soil air is mainly determined by the activity of soil organisms and the intensity of the exchange between soil air and atmosphere. Because the soil processes consume oxygen and yield carbon dioxide the quotient CO_2/O_2 is therefore higher in the soil air than in the atmosphere; the soil air can have more than 10 times higher concentrations of CO_2 than the atmosphere. The exchange between soil and atmosphere takes place by gaseous diffusion. As a result of the distribution of the biological activity and the diffusion process, the CO_2 concentrations will generally have its maximum at 20–30 cm depth, but with considerable variability between ecosystem and season. If the soil air falls below 10 volume %, root functioning begins to be disturbed. There are, however, plants which have special morphological adaptations to these situations.

Soil water

Availability of water determines the level of productivity of plants and is a function of climate. If there is a surplus of water, i.e. precipitation is higher than evapotranspiration, there is a downward water movement, when the opposite prevails there is an upward water movement. This is fundamental to the formation of soil types.

The soil water contains dissolved organic and inorganic constituents. It is a *soil solution* or a nutrient solution where the plant roots can take up plant nutrients such as calcium, potassium, nitrogen and phosphorus. The soil solution is also in balance with elements or nutrients adsorbed to surfaces of soil particles – clay–humus complexes. There is a constant exchange of cations and anions between the soil solution and particles. Because of this exchange the soil solution has the ability to withstand changes. It buffers in particular its contents of acid (H^+) and basic (OH^-) components.

Soil chemical properties, mineral nutrients and plants

Plant nutrients originate from the bedrock

The chemical properties of the material from which minerals essential to plant and soil reactions are derived depend on the underlying bedrock. There are three basic types of rocks: igneous, metamorphic and sedimentary. Igneous rock is a result of volcanic activity. Metamorphic bedrock consists of igneous rocks which have been transformed. From igneous and metamorphic bedrock, weathered material is transported to deep valleys and set under pressure, which leads to the formation of sedimentary bedrock. A rule of thumb is that dark-coloured igneous and metamorphic bedrocks have a more basic composition than light-coloured ones. Sedimentary bedrock is often more soft and light-coloured than igneous and metamorphic bedrock and contains generally more basic elements.

The bedrock changes gradually through physical and chemical processes – weathering. The physical processes lead to disintegration of the rock into primary minerals. The rate depends on the property of the minerals, resistant or less resistant. The main forces behind the physical weathering are changes in temperature and the rate of abrasion by water, ice and wind. In addition, roots, with their mycorrhiza, and animals may also have a physical impact. The primary minerals in the bedrock can be categorised into five classes depending on their ability to be weathered (Table 4.2). Class 1 is easily weathered and class 5 is the most resistant.

Chemical weathering is a biogeochemical process. It is more intensive in areas with warm and wet conditions. Presence of water and oxygen enhances the weathering rate as well as the activity of soil organisms, in particular fungi and other microorganisms. These organisms can accelerate the weathering process by exuding organic acids. Depending upon the substrate and the environmental conditions there are different processes acting in chemical weathering: hydration,

Table 4.2 | Weathering classes of minerals

Weathering class	Primary mineral	Contains
1	Carbonate of lime, dolomite, gypsum	Ca, Mg, C, O, S
2	Apatite	Ca, P, O
3	Dark mica (biotite), hornblende, pyroxene, plagioclase	Ca, K, Fe, Mg, Al, Si, O, H
4	Light mica (muscovite), plagioclase, feldspar	Ca, K, Na, Fe, Al, Si, O
5	Quartz, kaoline	Si, O

hydrolysis, dissolution, acid reaction, oxidation–reduction and complexation (see Glossary).

Soil reactions and availability of mineral nutrients

Uptake mechanism are: root interception, diffusion and mass flow

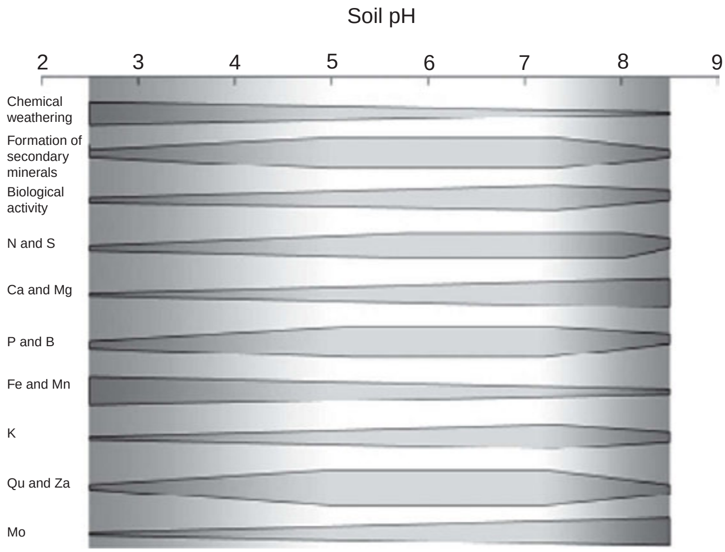
Mineral nutrients come in a range of availabilities to plants. The primary minerals and organic matter provide very low availability. The clay–humus complexes offer low availability and the adsorbed fractions on the colloidal surfaces give moderate availability. Finally, the dissolved fraction in ionic form in the soil solution is freely available for uptake by plant roots. The roots can actively penetrate the soil – *root interception* – and find the mineral nutrients, whereas *diffusion* and *mass flow* are mechanisms transporting the nutrients to the roots (see Chapter 6). Roots can respond to concentration differences in the soil such that root growth is directed towards regions of high nutrient availability. Uptake of nutrients creates in itself a nutrient gradient that sustains the flow of nutrients to the roots. When the mass flow caused by transpiration is higher than the uptake capacity of the roots, there can be a build-up of nutrients around the roots and the concentration gradient will be away from the root.

Soil pH regulates intensity of soil processes and availability of plant nutrients

The *acid–base status* of the soil affects almost all chemical and biological processes in the soil, as well as the availability of mineral elements to plants (Figure 4.4). A pH between 5.5 and 7 is most favourable for nutrient availability and thus also production, which is why farmlands are kept in this pH range. Going up or down from this pH range will increase the availability of some elements, but decrease others making it difficult to maintain the nutrient balance required by plants (Chapter 6). However, functioning natural, less human-influenced ecosystems exist well outside this range. For northern conditions with acid soils the pH values are commonly lower.

The acid–base status (Box 4.2) is commonly used to describe the chemical properties of the soil. The acid–base status is fundamental to the activity of biological processes in the ecosystem. Low acid–base status corresponds to low productivity and vice versa. Several processes contribute to the acid–base status by producing and consuming hydrogen ions (Table 4.3). It should be noted that the form in which nitrogen is taken up (NO_3^- or NH_4^+) affects the acid–base status of the soil.

Figure 4.4 Soil pH and availability of some important nutrients to plants, as well as some ecological and pedological processes. In the pH interval 5–7 the availability of all essential nutrients is good.



Box 4.2 | Acid–base status of a soil

Two different expressions describe the acid–base status of a soil: pH and degree of base saturation, or just base saturation (BS).

They are determined as follows:

pH

A soil sample, fresh or dry, is put in suspension with distilled water, shaken and left for sedimentation. The relation between soil and water by volume is standardised, usually 1:2. The pH is measured in the suspension.

Solutions of neutral salts such as $CaCl_2$ or KCl are also used for the suspension; $CaCl_2$ with a concentration of 0.01 M and KCl with a concentration of 0.2 or 1 M. The cations replace hydrogen ions on the surfaces of the mineral and humus colloids. As a result the measured pH is lower than in the water extracts, usually 0.5–1 pH units. pH determined from dry samples gives 0.1–0.2 pH unit lower values than from fresh samples. Fresh samples are therefore preferred.

Base saturation

Base saturation (BS) is defined as the percentage of exchangeable base cations (EBC) in total cation exchange capacity (CEC), the sum of EBC and exchangeable acidity (EA) or exchangeable acid cations (EAC):

$$\mathrm{EBC} = \mathrm{Na}^{+} + \mathrm{K}^{+} + \mathrm{Mg}^{2+} + \mathrm{Ca}^{2+} \tag{4.4}$$

$$\mathrm{EA} = \text{titratable acidity} \tag{4.5}$$

$$\mathrm{EAC} = \mathrm{Al}^{3+} + \mathrm{H}^{+} + \mathrm{Fe}^{2+} + \mathrm{Mn}^{2+} \tag{4.6}$$

$$\mathrm{CEC} = \mathrm{EBC} + \mathrm{EA} \tag{4.7}$$

A soil sample (fresh or dry) is extracted with 0.01 M $BaCl_2$. One fraction of the extract is titrated with NaOH to pH 7.8 and the EA is calculated. The acidity can also be calculated by measuring Al^{3+}, H^+, $Fe^{2+}$and Mn^{2+} in the extract and calculating the sum of the acid cations. Another fraction of the extract is determined on its content of base cations (Na^+, K^+, Mg^{2+} and Ca^{2+}). The EBC is calculated as the sum of the base cations.

Table 4.3 Processes producing and consuming hydrogen ions (H^+) in soils

Acidifying processes	Alkalinising processess
Deposition of acid sulfur and nitrogen compounds	Deposition of basic compounds, e.g. $CaCO_3$
Accumulation of cations by plants	Accumulation of anions by plants
Accumulation of cations in litter and humus	Decomposition and mineralisation of organic material
Leaching of metallic cations	Leaching of H^+ and Al^{3+} ions
Oxidation of nitrogen and sulfur	Reduction of nitrogen and sulfur
Desorption of sulfur compounds in the soil	Adsorption of sulfur compounds in the soil
Acid reaction of weak acids	Weathering of minerals

Soil types

Soil type – an interaction between climate, soil and vegetation

Climate is the major force behind the formation of soil types through weathering of the bedrock. An example of silicate weathering is the fate of the primary mineral potassium feldspar or orthoclase ($KAlO_2\ (SiO_2)_3$). In cold, humid areas the weathering is slow and the following happens:

$$\begin{aligned}&\text{feldspar} + \text{water} \rightarrow \\ &\text{potassium ions} + \text{silicic acid} + \text{kaolinite (clay mineral)}\end{aligned} \tag{4.8}$$

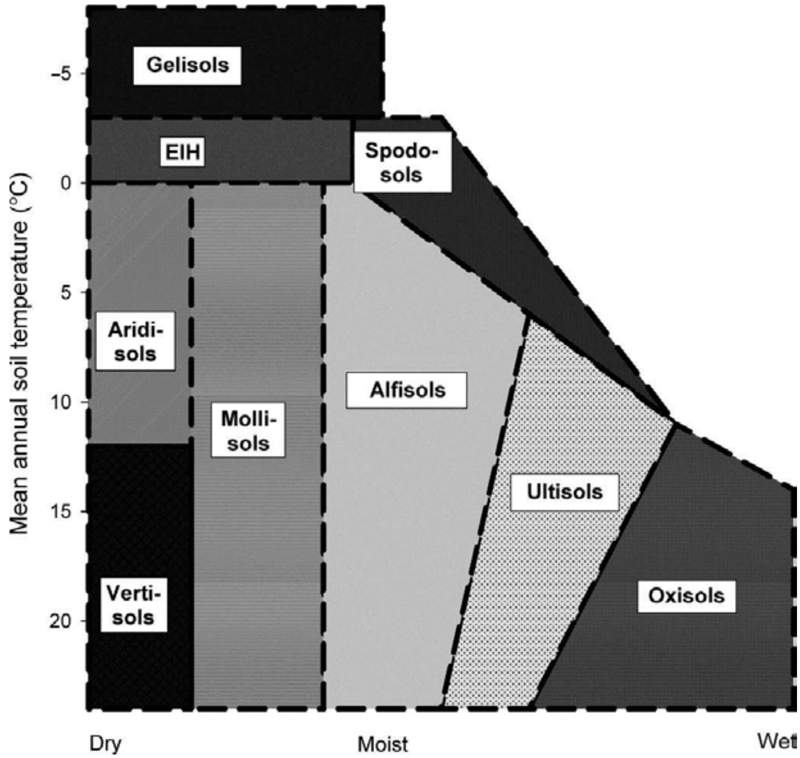
Potassium ions are released, together with silicic acid (a family of compounds with the generic formula $[SiO_x(OH)_{4-2x}]_n$, quartz) and aluminium hydroxide. Some silicic acid and aluminium hydroxide join and form a clay mineral (kaolinite $Si_4Al_4O_{10}(OH)_8$. This, often together with iron compounds, is then transported downwards, meets higher pH and is precipitated. Left is silicic acid, which forms a white horizon (the bleached or ash layer), while the aluminium and iron oxides form a reddish-coloured horizon below the bleached layer. In this way a *spodosol* is formed.

Water movements together with weathering lead to four major soil type-forming processes:

Podsolisation: Podsolisation is typical for cool, moist and acid areas. Iron, aluminium and organic matter are leached and quartz is left in the A horizon. The formation of secondary clay minerals is low. The B horizon is rich in accumulated aluminium and iron oxides. This is a typical *spodosol* (also named *podsol*). The O horizon is well developed. Productivity is low.

Laterisation: In hot and moist areas the silicic acid is weathered rapidly and leached out from the soil. Iron and aluminium oxides are precipitated in the B horizon, leading to a typical red tropical and sub-tropical soil type – *oxisol* – known as *laterite*. High productivity and rapid turnover of organic matter are associated with this

Figure 4.5 Main soil orders according to the US system in relation to soil temperature and soil moisture. EIH represents the soil orders of entisols, inceptisols and histosols. Andisols are not restricted to any particular climate. Global maps of the distribution of soil orders can be found at www.usda.gov. Modified from Brady & Weil (2007).



soil type. One form of laterisation is deposits of bauxite, which is used as a source for production of aluminium.

Lessivage and *Melanisation*: In temperate areas with fine, well-textured mineral soil and less acidic conditions the clay fraction tends to move to the B horizon – lessivage. In the A horizon humus material and mineral soil are well mixed due the activity of soil organisms. The A horizon is dark-coloured from humus material – melanisation.

Calcification and *Salinisation*: In arid areas where there is upward water movement, soluble compounds such as calcium carbonate or lime, sodium chloride and other salts remain in the soil. The upper part of the soil column may be leached to some extent during episodes of precipitation.

These processes lead to characteristic soil types. For larger regions they are grouped into soil orders (US Soil Taxonomy 1999); in addition to this US classification system the FAO/UNESCO system is often used (FAO 1998). The relations between temperature and precipitation, and soil orders are shown in Figure 4.5. Major characteristics of soil orders and their typical occurrence are seen in Table 4.4. There are also European soil systems, e.g. a German system which influences the terminology in other countries.

Table 4.4 | Names of the soil orders in the US soil taxonomy and their characteristics and typical location. The soil orders go from no development to highly developed. From Chapin *et al.* (2002) with kind permission from Springer Media + Business

Soil order	Area (% of ice-free land)	Major characteristics	Typical occurrence
Entisols	16.3	No well-developed horizons	Sand deposits, ploughed fields
Inceptisols	9.9	Weakly developed soil	Young or eroded soils
Histosols	1.2	Highly organic, low oxygen	Peatlands, bogs
Gelisols	8.6	Presence of permafrost	Tundra, boreal forests
Andisols	0.7	From volcanic ejecta, moderately developed horizons	Recent volcanic areas
Aridisols	12.1	Dry soils with little leaching	Arid areas
Mollisols	6.9	Deep dark-coloured A horizon with >50% base saturation	Grasslands, some deciduous forests
Vertisols	2.4	High content (>30%) of swelling clays, crack deeply when dry	Grasslands with distinct wet and dry seasons
Alfisols	9.7	Sufficient precipitation to leach clays into a B horizon, >50% base saturation	Humid forests, shrublands
Spodosols	2.6	Sandy leached (E) horizon, acidic B horizon, surface organic accumulation	Cold, wet climates, usually beneath conifer forests
Ultisols	8.5	Clay-rich B horizon, low base saturation	Wet tropical or sub-tropical climate, forest or savanna
Oxisols	7.6	Highly leached horizon with low clay, highly weathered on old landforms	Hot, humid tropics beneath forests
Rock and sand	14.1		

Ecosystem layering

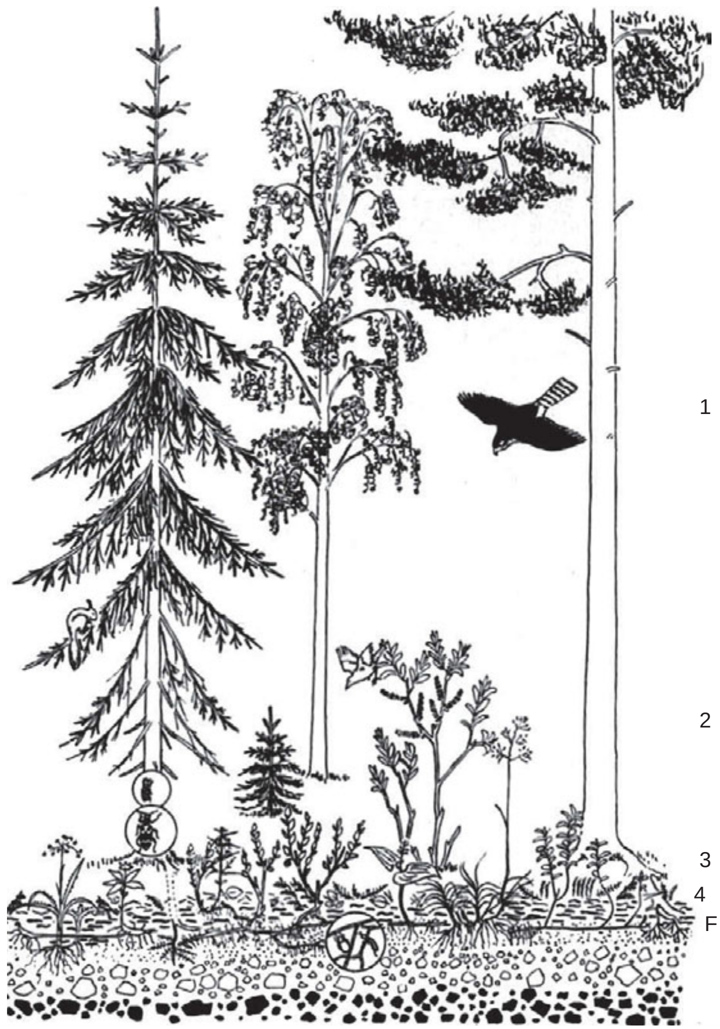
Ecosystems have characteristic layers in vegetation and soil

Although an ecosystem should be homogeneous with respect to site factors, some of them will still vary within the ecosystem. A characteristic feature of the forces exerted by site factors is that layers are formed in the vegetation as well as the soil, here exemplified by a boreal forest (Figure 4.6). The aboveground layering of the vegetation is to a great extent a result of the distribution of light, which means that different species have different light conditions, and even the same species or individual can have a great variation in light as well as temperature conditions (see also Figure 6.6). The most complicated vegetation layering is found in forests, in particular tropical rain forests, with up to five tree layers, a shrub layer, a field layer with grasses and herbs, and a bottom or ground layer with mosses and lichens.

In the soil the interactions between climate (water movements), roots and other soil organisms cause stratification with often clearly visible soil horizons (or layers). The following horizons are found in many soils:

O – Accumulation of litter and partially decomposed plant parts on top of the mineral soil. Often sub-divided into litter (S or L and F) and humus (H) horizons. This horizon consists mostly

Figure 4.6 A boreal forest ecosystem with characteristic layering in vegetation and soil. From Sjörs (1967) with kind permission from the Hugo Sjörs family.



of organic matter. In forest soils, this horizon is often called forest floor.

A − Eluviation (leaching) horizon. Mineral soil horizon mixed with organic matter at different stages of decomposition (A_h) and a white-coloured or bleached horizon (A_e). Mineral soil horizon with intensive weathering and from which mineral elements and dissolved humus are leached.

B − Illuvial (accumulation) horizon. Mineral soil horizon mixed with accumulation of organic and some inorganic (Al and Fe) material leached from the A horizon.

C − Mineral horizon largely unaffected by soil development.

R − Bedrock.

Sometimes these horizons are further sub-divided. Alternative labelling is also used.

Figure 4.6 illustrates such layering in a boreal forest.

(1) Tree layer of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula*).
(2) Shrub layer of willow (*Salix caprea*) and young Norway spruce.
(3) Field layer of *Vaccinium myrtillus, V. vitis-idaea, Deschampsia flexuosa, Luzula pilosa, Trientalis europaea, Maianthemum bifolium* and *Melampyrum pratense*.
(4) Bottom layer with the mosses *Pleurozium schreberi, Hylocomium splendens* and *Dicranum scoparium*.

O horizon with:

S – S layer of litter and living material from plants

F – F layer with partly decomposed plant material.

H – H layer with partly decomposed and humified material. Densely rooted.

A – A horizon. Often a bleached layer overlaying humus mixed with inorganic material. Intensive weathering. Roots.

B – B horizon. Reddish of accumulated iron and aluminium compounds. Traces of humus.

C – C horizon beneath B. Mostly unweathered soil material and not affected by soil formation. Not shown in the figure.

Plants have their roots predominantly in the O and A horizons, where most of the available nutrients are found, but some roots extend down to the B horizon. The layering in the soil is also coupled to the gradual change in the proportions of organic and inorganic material.

Information on vegetation as species, biomass and production as well as chemical and physical properties of the soil and water is required for the analysis of the structure and function of the ecosystem – an ecosystem analysis (Box 4.3).

Box 4.3 | Steps in an ecosystem analysis

An ecosystem analysis is a representative investigation of vegetation and soil in order to determine stocks in a number of compartments and movements of elements between the compartments. There are three stages of the work: data collection, calculation and analyses or synthesis (Figure 4.7). A schematic illustration of an ecosystem analysis of a forest follows:

Data collection

Trees and shrubs

From a combination of non-destructive and destructive measurements a number of biomass fractions or compartments can be calculated. The standard non-destructive measurements are diameter and height. These data are collected from replicated sample areas of a given size, often at time intervals of 5 or 10 years. On the basis

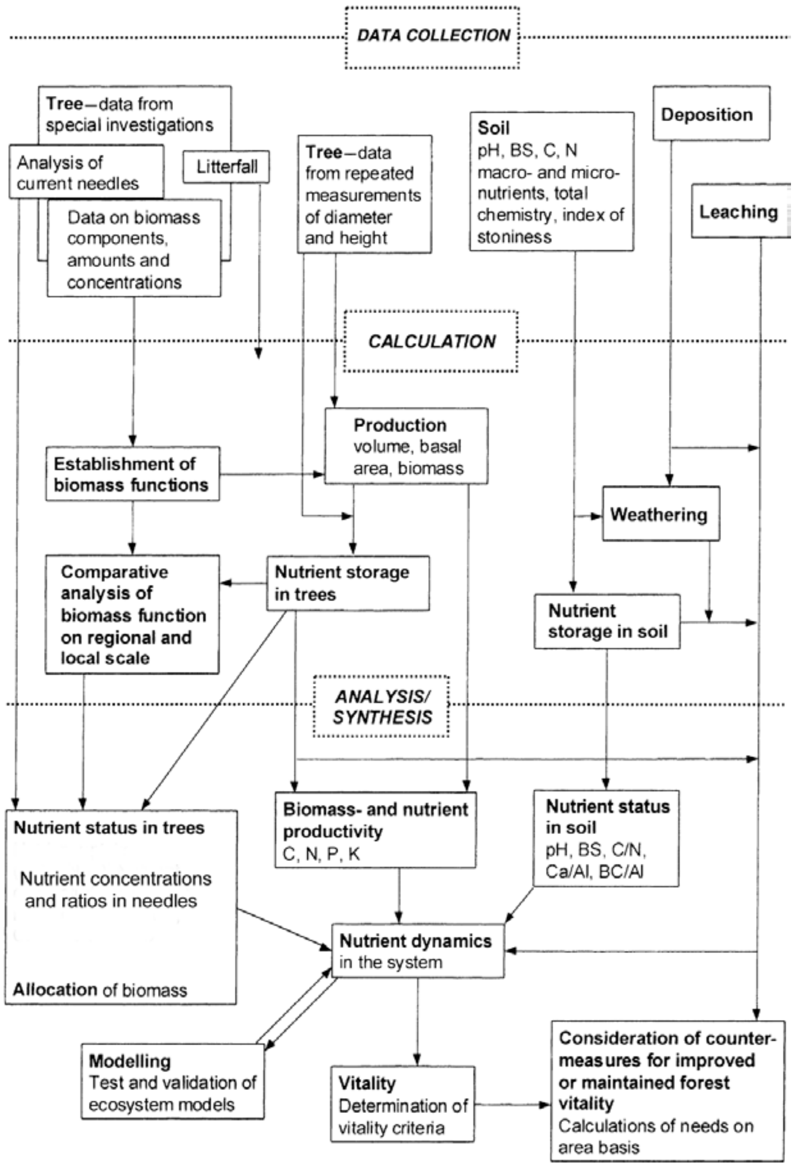


Figure 4.7 Illustration of the steps in an ecosystem analysis of a forest. Modified from Andersson *et al.* (2000) with kind permission from Elsevier.

of diameter and height distributions representative individuals are selected for destructive measurements, typically separated into stem with and without bark, branches, twigs, leaves, fruits, stump and roots in different diameter classes. *Fresh* and *dry weights* are determined. For further description of methods see, for example, Andersson (1970b) and Attiwill & Leeper (1987).

Soil

Replicated soil samples are taken for identified soil horizons. A correction for stoniness may be necessary (Viro 1952). Fresh and dry weights are determined. Chemical analyses of exchangeable and total elements are done in the laboratory.

Calculations

The stem volume of trees is calculated from diameter and height data. Volume production can be obtained as a difference between repeated measurements. The data from destructive measurements of samples are used to establish biomass as well as biomass production regressions for the different fractions by combining them with the non-destructive measurements. For this purpose *allometric* regressions are often used:

$$Y = aX^b \tag{4.9}$$

where Y is biomass and X a variable or combination of variables such as diameter and height. These regressions are mostly calculated from the logarithmic form

$$\ln(Y) = \ln(a) + b\ln(X) \tag{4.10}$$

Nutrient storage in trees, other vegetation and soils are calculated from measured nutrient concentrations.

Synthesis

With the data obtained, a number of ecosystem properties can now be analysed, such as nutrient status of trees and soils. From a functional point of view biomass and nutrient productivities can be calculated and analysed. By combining these data with input data for atmospheric deposition and litter, as well as output data for losses through leaching and harvesting, it is possible to investigate the element dynamics of the ecosystem. The results will be used for understanding and predicting changes as consequences of different forms of utilisation of and environmental impact on the ecosystem.

Terrestrial biomes

Biomes are the result of the interaction between temperature and precipitation

Seen in a global perspective, the climate, through temperature and precipitation, is the most important site factor governing the development and distribution of vegetation and soils. In areas with similar climate and parent material, similar vegetation and soil types develop – *biomes*. The distribution of different biomes can be coupled to mean annual precipitation and mean annual temperature (Figure 4.8). A key feature is the extent to which precipitation exceeds evaporation and transpiration (evapotranspiration) in an area. Evapotranspiration is described by the *potential evapotranspiration* (PET), which is the water loss from a free water surface, and the *actual evapotranspiration* (AET), which is the actual loss of water to the atmosphere and where resistances to water transport through vegetation and soil are included (see further, Chapter 5). Areas where precipitation exceeds evapotranspiration have a humid climate and a downward water movement in the soils. When the opposite is prevailing the climate is arid and there will at times be an upward movement of water.

Vegetation

The broad classification of biomes on a world basis (Figure 4.6) can on the local level be taken further because plant species group together

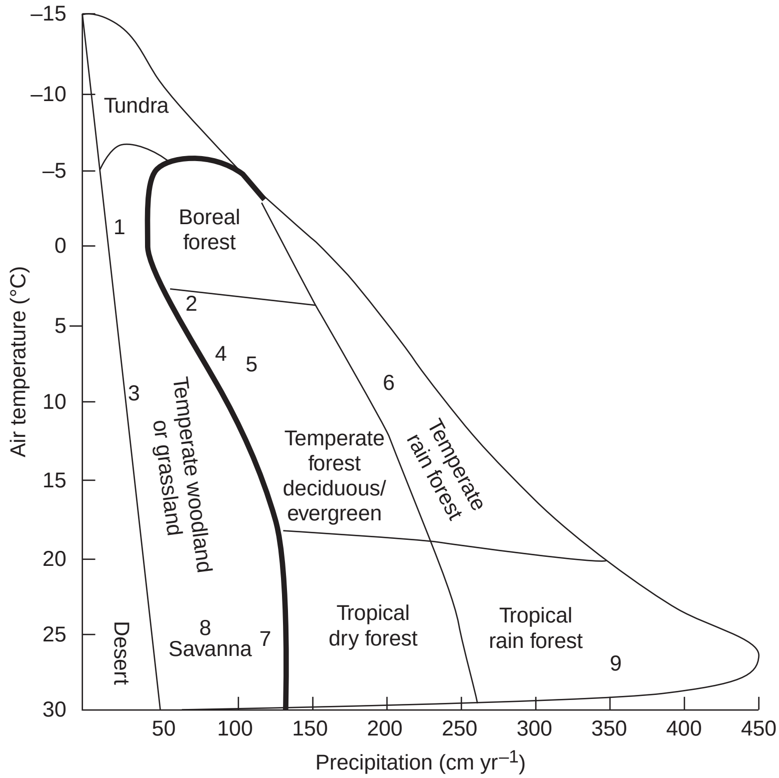


Figure 4.8 Approximate distribution of biomes as a function of temperature and precipitation. Some selected ecosystems indicated by numbers are described in detail in Figure 4.10. Note that forest ecosystems, separated by the thick line, require a certain threshold of precipitation. Modified from Whittaker (1975) with kind permission from Pearson Education, Inc.

in typical associations. The ecosystems can be identified by their dominating life forms and grouped along two gradients: acid–base (or nutrient poor–nutrient rich) and dry–wet gradients. In Norway and Sweden, which are dominated by boreal and temperate forests along with some tundra, the ecosystems fall into four series: heath, steppe, meadow and mire series (Figure 4.9). The heath series is dominated by dwarf shrubs, narrow-leafed grasses and a few herbs, as well as mosses. The steppe series has more herbs (different to the heath series) and other mosses and lichens. The meadow series is dominated by taller herbs and grasses. It is also more productive. The mire series is dominated by dwarf shrubs and graminoids as well as peat-mosses such as *Sphagnum*. The series can be represented by ground vegetation only, or with the tree layer included. The scheme can also be extended to a fifth series – the lake series, with oligotrophic and eutrophic lakes. The degree of human influence on the development of ecosystems also needs to be taken into consideration by grouping into natural and semi-natural ecosystems. (Figure 4.9a and b).

Features of terrestrial biomes and ecosystems

The broad distribution of terrestrial biomes is governed by climate – precipitation and temperature (Figures 4.8 and 4.11). Their extent,