Ecology of Tropical Plants

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with a chapter by
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Preface

This textbook is an adaptation, for tropical regions, of the established book by R. F. Daubenmire, *Plants and Environment – A textbook of Autecology*, 3rd edition, John Wiley and Sons Inc., 1974. The arrangement follows that of Daubenmire in that each facet of the physical and organic environment of plants is treated separately, starting with soil and ending with the influence of man. However, the text concentrates exclusively on the tropical environment and its influence on plants. The book contains much new and updated material, including a chapter devoted to practical aspects of the subject contributed by Dr. J. Hall.

Ecology is now firmly established as a discipline in its own right and its importance to the future well-being of mankind is fully recognized. Tropical ecosystems are both complex and highly vulnerable to interference by man. It is only through the study of such systems by ecologists and biogeographers that the effects of this interference can be predicted and, hopefully, steps taken to minimize the irreversible destruction which is now taking place in many areas of the tropics. During my ten-year residence in tropical Africa I was able to witness at first hand the disastrous effects on the environment of forest clearance, overcultivation, and overgrazing.

The tropical region encompasses four continents – Asia, Africa, South America, and Australasia. Although many environmental characteristics are common to all tropical regions, there are variations. This is especially true of the occurrence of individual plant species. While some are pantropical, others are much more restricted in their distribution. Thus in this book examples of individual species have been kept to a minimum and only quoted when some specific point needed illustrating. It is hoped that lecturers in the tropics using this book will expand the text by including examples of local plant species.

Finally, I would like to thank Dr. Hall for his contribution, 'Investigating the Environment'. This is a most valuable addition to the book, as it is only by carrying out field work that the principles of ecology can be fully appreciated by students.

Margaret L. Vickery

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Chapter 1

Introduction

Organisms cannot live in isolation and the study of their continual interaction with their environment, known as *ecology*, is an important facet of biology. The term *ecology* is derived from the Greek word for house and translates as the study of all members of a household. If *habitat* is substituted for household, then ecology can be scientifically defined as the study of habitats.

All organisms are affected by their environment, both living (other organisms) and non-living (soil, climate, etc.), the total influence of these environmental factors making up the habitat in which the organism lives. For animals that move around, a habitat can be a large area (for man it can cover the entire world), but for plants habitats can be quite small.

The basic functional unit of ecology is the *ecosystem*. An ecosystem is a functional, interacting entity which includes all the living organisms, termed a *community*, and the non-living environment of a particular area (fig. 1.1). All the earth's ecosystems taken together make up the *biosphere* (fig. 1.2).

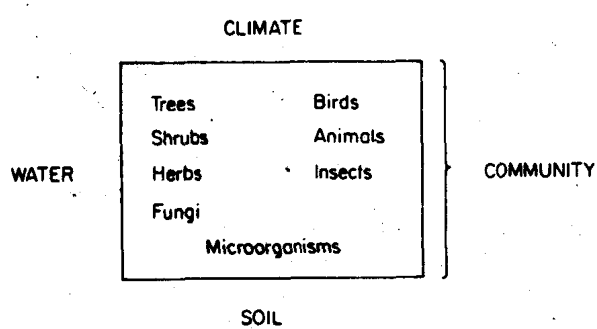

Fig. 1.1
The constituents of an ecosystem

Large, characteristic areas of vegetation, such as deserts, tropical rain forest, temperate grasslands, etc. are termed *biomes*. The tropical biomes are shown in fig. 1.3. Although dominated by one type of ecosystem, biomes can contain other types. For example, the tropical rain forest can include marshes, clearings, etc.

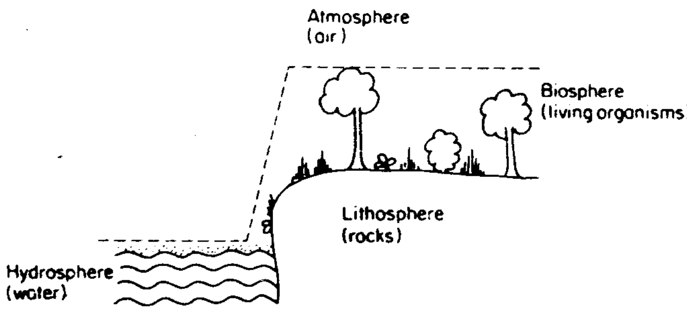

Fig. 1.2
The biosphere in relation to its environment

Within an ecosystem there are various *levels of organization* (fig. 1.4). A community can be broken down into *populations* of particular species and further into individual *organisms*. The study of an individual organism and its constituent parts is usually termed biology, while ecology studies populations and communities. Ecology and biology overlap, however, at the level of the individual organism, its relationship with its environment being termed *auto-ecology*.

It is often useful to talk about the total weight of living organisms in an ecosystem. This is termed the *biomass* and is defined as the weight of organisms per unit area.

A complete study of ecology covers not only such natural ecosystems as forests, deserts, etc., but man-made ecosystems, including cities, towns, dams and cultivated land. The majority of the ecosystems described in this book are natural, the influence of man on such ecosystems being covered in Chapter 9.

The components of an ecosystem can be divided into four main categories – *abiotic* (rocks, soil, water, climate); *autotrophs* (producers); *heterotrophs* (consumers), and *decomposers* (fungi, bacteria etc.). Autotroph means self-feeding and autotrophs are the plants and microorganisms which can convert inorganic substances into organic compounds utilizing the energy from the sun. Most autotrophs contain chlorophyll and convert carbon dioxide and water into sugars. Heterotrophs (other-feeders) have to obtain their food by eating other organisms. The *primary consumers* or herbivores eat plants, while the *secondary consumers* or carnivores eat herbivores. The decomposers obtain their food from dead material. A *food chain* can be constructed linking the various components of the living element of an ecosystem, as shown in fig. 1.5.

The food chain also illustrates the *energy flow* within an ecosystem, as energy from the sun is converted to chemical energy by the autotrophs and then passed along the chain to the decomposers. However, at every stage of the chain energy is lost, mainly as heat, and thus energy flow is a one-way process (fig. 1.5), unlike the cycling of nutrients.

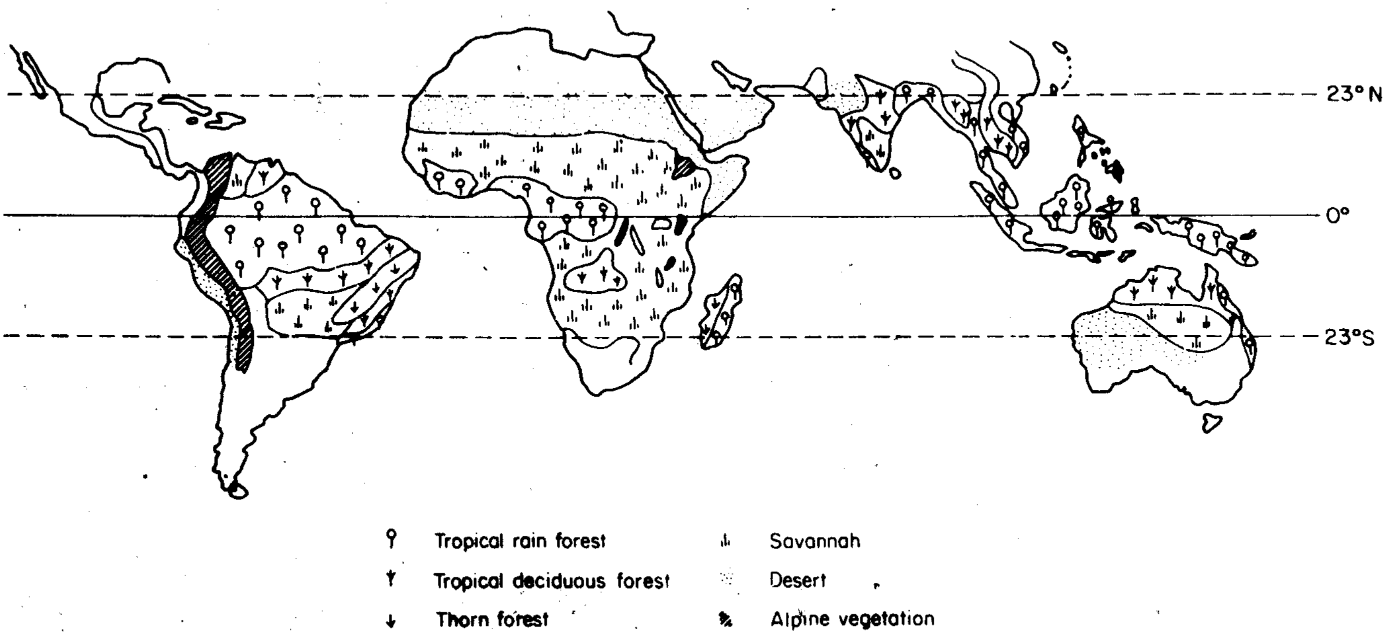

Fig. 1.3
Tropical biomes

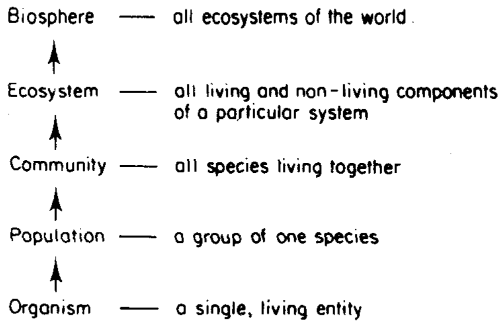

Fig. 1.4
Levels of organization

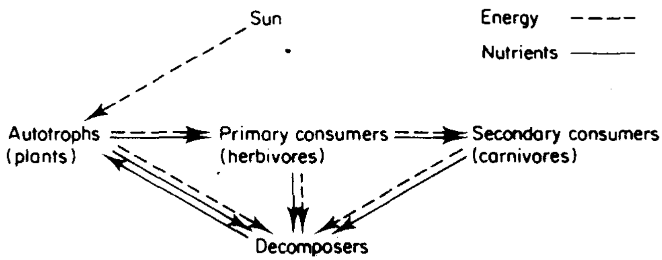

Fig. 1.5
The energy flow and cycling of nutrients within an ecosystem

Productivity

Only a small portion of the solar energy entering an ecosystem is actually captured by photosynthesizing organisms (autotrophs) and converted to chemical energy. The rate at which solar energy is converted to chemical energy is known as the *gross primary productivity*. As this energy is locked up in the bonds of organic compounds it can be equated with the production of dry matter by autotrophs.

Dry matter is broken down and energy released during the process of respiration, which takes place in all living organisms. Thus, though accumulating dry matter through photosynthesis, autotrophs also lose it through respiration. The difference between the gross primary productivity and the energy/dry matter lost through respiration of autotrophs is known as the *net primary productivity* of an ecosystem.

$$NPP = GPP - E_r$$

where NPP = net primary productivity
GPP = gross primary productivity
E_r = energy/dry matter lost through respiration of autotrophs

Net primary productivity is of great importance to an ecosystem as it represents the energy available to members further along the food chain. Ecosystems with small NPPs support fewer heterotrophs than those with high NPPs. In the tropics NPP can be roughly correlated with the amount of rain an area receives, although there are exceptions. Evergreen rain forests have much higher NPPs than savannas, as shown in Table 1.1.

Table 1
The net primary productivities of some tropical ecosystems

Tropical ecosystem	Average net primary productivity/g m^{-2} y^{-1}
Rain forest	2000–2200
Deciduous forest	1600
Savanna	700–900
Desert	100

The Biogeochemical Cycles

Two types of biogeochemical cycle occur – those such as the carbon and nitrogen cycles which contain a gas as the major constituent, and those, the sedimentary cycles, in which the major constituent is an insoluble compound. The gaseous cycles can be considered global, carbon dioxide and nitrogen being mobile and able to diffuse throughout the atmosphere. Thus, although there may be local pockets where nitrogen-containing compounds are over-abundant or in short supply, on a world-wide scale the concentration of nitrogen in the atmosphere and that locked up in organic and inorganic compounds remains fairly constant. The hydrological cycle, discussed in Chapter 3, also has a major gaseous constituent in the form of water vapour and can thus be considered global, despite the occurrence of oceans and deserts.

The sedimentary cycles, however, are localized and consist of many interwoven cycles, the reservoir of nutrient generally being locked up as an insoluble constituent of rocks and not mobile. The cycles of all mineral plant nutrients are sedimentary.

The carbon cycle

The carbon cycle (fig. 1.6) can be considered the most important of all the biogeochemical cycles, as ultimately all life on earth depends on its continued functioning. Primarily, the carbon (or carbon dioxide) cycle consists of two parts – the conversion of inorganic carbon dioxide to organic carbon compounds with the simultaneous storage of energy from sunlight, and the degradation of these compounds back to carbon dioxide with the release of this energy. The carbon cycle operates over land and water wherever green plants are to be found. Although small variations in carbon dioxide concentration are found locally, winds and the buffering effect of oceans which dissolve excess of the gas, ensure that globally carbon dioxide concentration in the atmosphere remains constant.

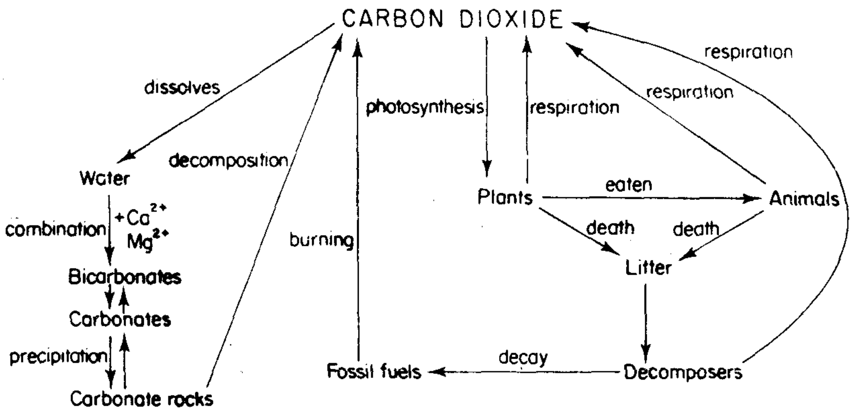

Fig. 1.6
The carbon cycle

The nitrogen cycle

Although some atmospheric nitrogen is fixed as oxides by electric discharges occurring during thunder storms, the conversion of the gas to inorganic nitrogen compounds is mainly carried out by nitrogen-fixing microorganisms (see Chapter 7). However, only a relatively small amount of nitrogen is locked up in organic and inorganic compounds at any one time and the cycle (fig. 1.7) depends on the efficiency of nitrifying and denitrifying microorganisms.

The phosphorus cycle

The phosphorus and other sedimentary cycles lack large, mobile reserves of elements and are therefore easily upset by natural processes or human interference. The phosphorus cycle (fig. 1.8) contains two main storage pools of the element – inorganic phosphorus compounds locked up in rocks and insoluble

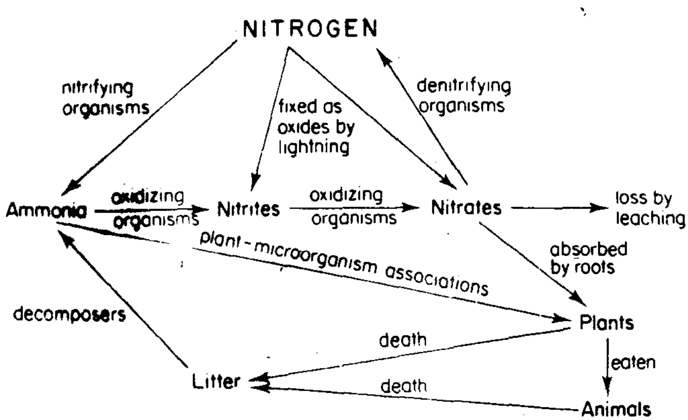

Fig. 1.7
The nitrogen cycle

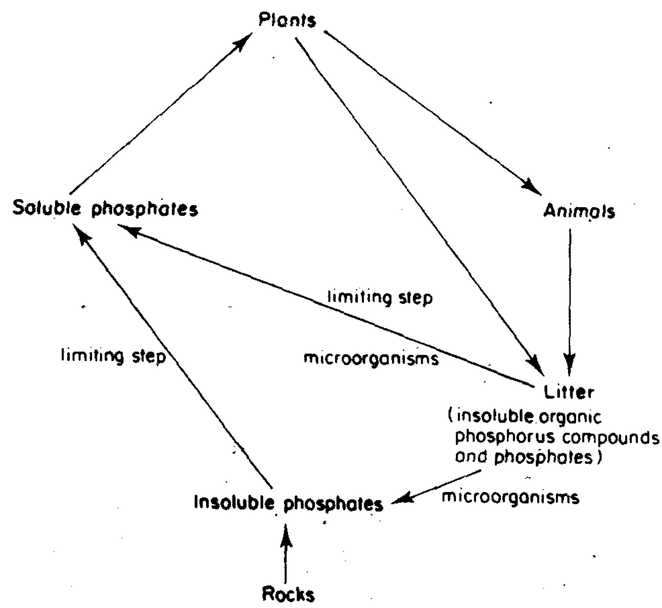

Fig. 1.8
The phosphorus cycle

organic compounds in litter. The solubility of inorganic phosphorus compounds and the degradation of litter by microorganisms are limiting steps in the cycle. Although little of the element is lost through leaching, erosion can cause serious depletion.

Succession

There are few ecosystems which are so stable that they show no appreciable change with time. Most are undergoing *succession* in which one set of species is replaced by another as the ecosystem develops. The colonization of bare rock, or new soil such as that resulting from a volcanic eruption or the deposit of windblown sand, are examples of *primary succession. Secondary succession* takes place on land which has supported vegetation in the past, such as abandoned fields, or the soil left behind after a forest fire or the death of a tree.

An ecosystem which has reached the stage where no more change takes place is said to be at its *climax*. Although no overall change of ecological significance takes place in an ecosystem at its climax, such a system is not static but is in dynamic equilibrium. Plants die and seeds germinate, old animals die and young animals are born, such processes taking place continuously in an ecosystem at its climax. A tropical rain forest is an example of primary succession at its climax, but within such forests secondary succession takes place whenever a tree dies and the area of soil once occupied by the tree is colonized by other species. The climax vegetation of secondary succession is often quite different from that of the previous climax.

Succession is the result of the modification of the environment by organisms occupying the habitat at any one time. Organisms which colonize an ecosystem during the first stages of its development are termed *colonizers* or *pioneer species*. Lichens colonizing bare rock, for example, are pioneer species which change the environment, making it suitable for the growth of other species. The fungal component of the lichen secretes chemical substances which dissolve some of the minerals contained in the rock. These dissolved nutrients are absorbed by the lichen, while the undissolved portion of rock forms pockets of soil in which small insects and microorganisms can live. Such organisms feed on dead organic matter and through their activities enrich the new soil, eventually converting it to a medium suitable for the growth of hardy, drought-tolerant plants (xerophytes). An increase in the depth of soil, and its enrichment through the death of pioneer species and the collection of wind-blown debris, eventually produces a medium which can hold sufficient water for the growth of less drought-tolerant species (mesophytes). Grasses are the most common of the pioneering mesophytes, and these, together with other species, form a *microclimate* at ground level, which is less extreme than that experienced by the xerophytes. The presence of such a microclimate enables shrub and eventually tree seedlings to develop. An example of the succession of an ecosystem is shown in fig. 1.9.

Each stage of succession changes the environment so that it becomes less suitable for the resident species and more suitable for invading species, until the climax is attained. Theoretically, the climax vegetation should remain in dynamic equilibrium forever, but in many instances it is upset by the activities of man or some natural catastrophe such as a hurricane, typhoon, or forest fire.

The environment of an ecosystem at its climax is quite different from that at the pioneer stage, as soil, temperature, humidity, light intensity, and windspeed are all affected by the vegetation within the ecosystem. The type of vegetation occurring at the climax depends on many factors, including climate, altitude, competition between species, soil type, and the activities of man. When the vegetation type depends only on the climate, the ecosystem is said to be at its *climatic climax*. Where factors such as soil determine the vegetation type, it is at an *edaphic climax*. Tropical rain forest is an example of a climatic climax, while marshland vegetation, which is the result of poor drainage, is an example of an edaphic climax.

At each stage of succession the biomass increases, as does the diversity of species, although the latter can decline in the final stages. The types of species found at any one time change rapidly during the first stages of succession but more slowly as the climax is approached.

Dominance

Generally, at each stage of succession there are some species which are more common than others and which are important in determining the nature of the ecosystem. Such species are termed *dominants*, and their removal radically

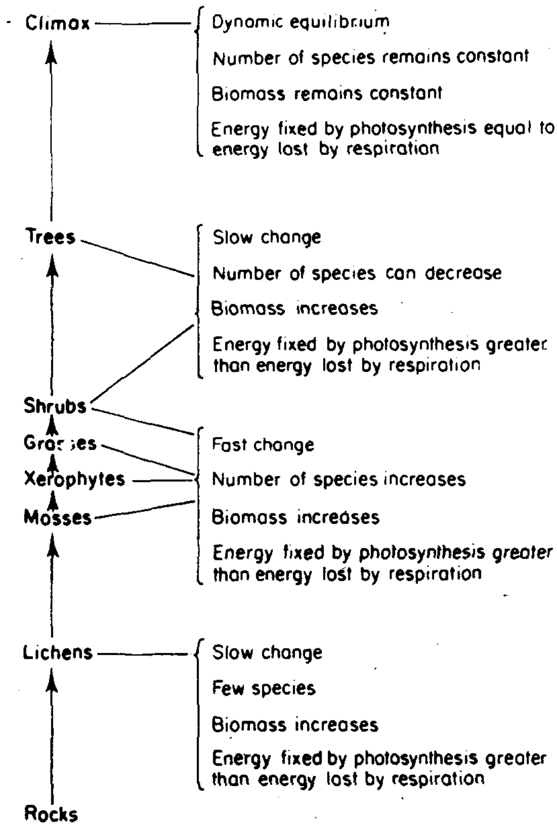

Fig. 1.9
Succession in an ecosystem

alters the ecosystem. The number of dominants in an ecosystem can vary widely. A typical tropical rain forest has a high diversity of species and can contain a dozen or more trees which are more plentiful than other species and can therefore be said to be dominant. Forest vegetation on an island, however, may be dominated by only one species, such as *Mora excelsa* in the West Indies.

Ecological Niche

Each organism within an ecosystem plays its own particular role within the overall scheme, this role being known as the *ecological niche* of the organism. The roles played by individual species are many and varied, but each is important to the overall success of the ecosystem. Green plants are producers and their main role is to convert energy from the sun into chemical energy which can be used to support other members of the community. Fungi, however, are the decomposers and their task is to release nutrients from dead organic matter for the use of green plants. Some insects are important as pollinators of flowers, ensuring future generations of plants, while others, such as termites, are decomposers which help to break down plant matter. Animals are also important as pollinators or seed dispersal agents. Today, the role of man is probably the most important of all, as his activities can determine the very nature of the ecosystem.

The kinds of organisms found in any ecosystem depend on geography and environment. Tree species found in the tropical rain forests of Asia are different from those found in similar forests in South America, but they occupy the same ecological niche. Thus ecologically equivalent species have evolved in different parts of the world with similar climates.

Species occupying different ecological niches in the same ecosystem live together quite happily, but those occupying the same niche are in competition with one another. Sometimes such competition leads to the extinction of one of the species from that particular ecosystem. By introducing or removing species man can influence the occupancy of an ecological niche.

The most successful species are those which can adapt to occupy different niches under varying sets of environmental conditions. Many plants have spread throughout the world, as they have been able to adapt to local habitats. Other species, unable to adapt, are found only in one specific type of environment. Many tropical plants, for example, are unable to adapt to low temperatures and are thus unable to grow in temperate climates. Often a species which cannot compete successfully for a niche under one set of environmental conditions adapts to a less favourable environment and thus occupies a different niche. Many plants which flourish on soils with a high calcium content (calcicoles) are unable to compete with other species on more neutral soils.

Some species occupy a very precise ecological niche, such as those insects associated with one particular plant species, while others have wider niches. The specialists are the most successful at exploiting their resources, but more vulnerable to change. In the above example, should the plant become extinct then so would the insect. The wider the niche the more likely an organism is to survive a drastic change in its environment.

Suggestions for Further Reading

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Chapter 2

Plants and Soil

Introduction

Soil can be defined as the weathered layer of the earth's crust to which has been added the decomposition products of living and dead organisms. Mixed with the soil are air, water, and a multitude of living organisms, including algae, bacteria, fungi, the roots of plants, and many soil animals and insects. Soils are classified according to their *profiles*, which are obtained by cutting vertical sections through the soil from topsoil to underlying parent material. Such a section can be divided into *horizons*, the most important being the topsoil or A horizon, the subsoil or B horizon, and the weathered substratum or C horizon. A layer of litter usually covers the topsoil. The main features of a soil profile are shown in fig. 2.1. Often the A and B horizons are subdivided, while the litter layer on many tropical soils is thin, as high temperatures and humidity ensure that decomposition of this layer is rapid.

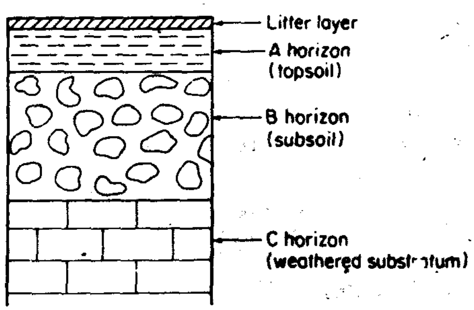

Fig. 2.1
The main features of a soil profile

The importance of soil to plants cannot be overstressed. Man may have devised the soilless method of cultivation known as hydroponics, but few plants grow naturally without soil. Parasites obtain their requirements from other plants and some lichens can grow directly on bare rock, but most plants need soil to grow to maturity. Seeds falling on bare rock or other soilless environments may germinate if water is present, but the young plants soon die. Soil provides nutrients, which are essential to growth, water, one of the basic requirements for photosynthesis, and air, which is needed by the roots for respiration. Soil also gives plants a medium in which roots can spread, thus anchoring the plant and increasing the available food supply. Plants growing in soils which hinder root penetration are poorly developed compared with those growing in soils in which the roots can easily spread. Because of the large surface area of the roots there is much contact between plant and soil. Not only does the soil affect the plant but the plant influences the soil, both physically and chemically. Penetration of the roots helps to break up large particles of soil, while roots secrete carbon dioxide and other substances which attack and break down minerals.

Because soil is such an important part of their environment plants have been classified according to the type of soil in which they naturally grow as shown in Table 2.1.

Table 2.1
Classification of plants according to soil type

Plants	Soil type
Oxylophytes	Acid soils
Calciphytes	Alkaline soils
Halophytes	Saline soils
Psammophytes	Sandy soils
Chasmophytes	Rock crevices
Lithophytes	Rock surfaces

A theoretical succession of plant types colonizing bare rock can be devised as shown in fig. 2.2, assuming that production of an acid soil is the final stage of succession.

Soils vary in the amounts of nutrients they contain and also in their ability to retain air and water. Despite the luxuriant vegetation of the tropical rain

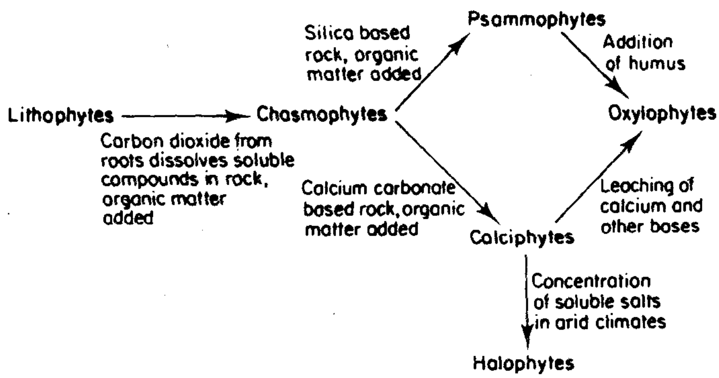

Fig. 2.2
Theoretical succession of plants colonizing bare rock