THREE

MAJOR NATURAL ECOSYSTEMS

Despite the undoubted complexity of the workings of the natural environment in detail, over large areas of the world ecosystem structure and functioning are broadly similar throughout, and we can use this as a basis for recognising several major types of natural ecosystem.

A fundamental distinction can obviously be made at this global scale between the marine ecosystem on the one hand and terrestrial ecosystem types on the other. The **marine** ecosystem is basically a much larger and more complicated version of the freshwater pond system described earlier (Chapter Nineteen). In both cases, depth of water presents an important control on the forms of life present. However, whereas large plants are common in pond systems, they are almost totally absent from oceans. The structure of the marine ecosystem is very similar for all oceans and it can be considered as one unit, but in the case of terrestrial ecosystems, a threefold division needs to be made.

Forest ecosystems have a complicated layered structure in which the dominant plants are tall and create a variety of ecological niches beneath them. **Grassland** ecosystems have a simpler and more uniform structure, although intermittent trees may occur, as in savanna. In cold or warm **biological deserts**, vegetation is low-growing, and the plants and animals have to tolerate extreme conditions. Despite the link between terrestrial ecosystem types and climate, it is very difficult to ascribe precise climatic limits to them, and for this reason they have not been used as a basis for the identification of climatic zones (Chapter Fifteen). Edaphic and anthropogenic factors are sometimes equally as important as climate in creating these 'natural' systems.

Forest Ecosystems

Forest is the ultimate vegetation type which results from the process of succession on land areas, unless local conditions such as climate, soil or biotic factors arrest development at an earlier seral stage (Chapter Nineteen). When the situation is favourable for the growth of trees, they become the dominant plants of the community for two main reasons. First, trees grow taller than other plants and their canopy establishes a micro-climate which has great influence on the plants and animals living beneath. Second, trees live for a long time and therefore the conditions they impose are maintained throughout the life-span of other organisms. However, although the longevity of trees enables them to outlive everything else, they have great problems in regenerating their own kind. The germination and growth of seedlings is precarious as they often have very narrow tolerance ranges and take a long time to mature: for example, pines take about twenty years and beech trees take as long as forty years.

Once the forest is established, it forms a complex ecosystem with a large standing crop. Much of this is made up of the wood of the trees themselves, which is non-productive but represents energy stored in the system as biomass. The productive part of the trees—the leaves—forms an extensive surface area for photosynthesis, so that a lot of food will be available from the primary level. The amounts of food produced and the paths the energy contained in the food take through the ecosystem, will vary with such factors as the species of the dominant trees and the climate. Generally, however, the food webs are complex, the detrital food chains being responsible for the majority of energy flow taking place. The nutrient cycling patterns will also vary with the ecosystem structure and the climate. The presence of a large standing crop means that many nutrients will be locked within organic material: trees immobilise nutrients for much longer periods than annuals or short-lived perennials.

Trees can be divided into the two main types: **evergreen**, which always have leaves, and **deciduous**, which have no leaves at all at some stage, usually in the winter or dry season. Both evergreen and deciduous trees vary greatly in their ecological tolerances, and so have many habitat possibilities. It is estimated that two thirds of the world's land area is still covered in forest, occupying many different climatic zones; not surprisingly, there are significant contrasts within the ecosystem type. Many naturalists have devised differing classifications of forests in relation to climatic zones, but there is general agreement in distinguishing **boreal, temperate deciduous** and **tropical rain forests.**

Boreal Forest

The boreal forest formation is a vast expanse of coniferous, evergreen forest extending across North America and Eurasia on the southern margins of the tundra zone, in a belt of approximately five hundred miles breadth from north to south (Fig. 23.1a). The area occupied by this formation has been subjected to severe glacial or periglacial activity and has much subdued relief and surface water. The conditions for life are harsh because of the adverse climate. The growing season is only of three or four months' duration and even during this time, the energy input from solar radiation is small because of the high latitude. Temperatures are low throughout the year, although the average temperature of the warmest month of the year is higher than 10° C. In the winter the temperatures fall to many degrees below freezing and permafrost frequently extends into the northern edge of the forest. Precipitation ranges from 400 to 700 mm per annum, mostly falling as snow, the weight of which may cause mechanical damage to the trees. Despite the climate, coniferous trees form a dense canopy which intercepts a great amount of light and precipitation so that conditions beneath are dark and dry. Consequently there is little opportunity for undergrowth to develop and very few other plants are associated with the coniferous trees.

The trees themselves show very little variety across the formation; species of pine, fir and spruce tend to be dominant throughout. As these are all evergreen they have their photosynthetic equipment ready for use as soon as conditions allow it. This partly compensates for the short growing season, but the primary productivity is still low compared to that of other types of forest. This is not only evident from the slow accumulation of biomass when regrowth occurs, but is also apparent in the ecosystem structure. The low primary productivity means that only a limited amount of energy is available for use at the secondary levels, and typically there is a very small amount of animal biomass as well as a lack of diversity. At the herbivore level the invertebrates are predominant, the vertebrate herbivores only becoming numerous in seral areas where foliage is thicker. Carnivores, such as the wolf and lynx, and the large omnivores, such as the black and grizzly bears, which need a lot of food to maintain themselves, are scarce. Studies conducted in the boreal zone indicate that the populations of animals inhabiting them oscillate markedly. Many ecologists interpret this as a sign of instability.

The combination of coniferous dominants which are low in nutrient demand, the lack of diversity, and the climatic conditions, results in slow, impoverished nutrient cycles. Few nutrients will be taken into the plants and few will be returned to the soil in the leaf litter. However, there will be a continual return as the leaves fall from the evergreen trees throughout the year. Most decomposition is fungal since bacterial activity will be slow in these conditions, and the resulting humus is the mor type. Characteristically the boreal forest is found growing on podzols which tend to become highly acidic.

Temperate Deciduous Forest

This type of forest, dominated by broad-leaved deciduous trees, had a great extent in the past when it covered most of the temperate areas of Europe, eastern North America, eastern Asia and small parts of South America and Australia (see Fig. 23.1b). The temperate deciduous forest has probably been more modified by human activity than any other type of ecosystem. Most of it has been destroyed in historic times but we can attempt to reconstruct its main characteristics from evidence provided by pollen analysis and by studying the few remaining areas.

The climatic zone it occupies is less extreme than that of the boreal forest. There is a longer growing season, higher light intensity and a moderate amount of precipitation of between 500 and 1500 mm per annum. The temperature regime is also characterised by lack of extremes but there is still a marked cold season which plants and animals must endure.

The dominant trees are more varied than in the boreal forest: for example, in Europe there are twelve main dominant species including different sorts of oak, beech and ash, and in North America, which is richer in flora, there are at least sixty dominant species, notably several sorts of chestnut, maple and hemlock. The deciduous habit and the lighter shade cast by these trees compared to the conifers, allows sufficient light to reach beneath the canopy so that understorey vegetation can develop. This will vary dramatically with the tree species present. Beech casts quite a dark shade and consequently few plants grow below it, but oak and ash cast light shades and layers of shrubs and herbaceous plants may develop producing a species-rich community. Some undergrowth plants, such as the bluebell, are adapted to use the light available before the leaves grow on the trees in the spring. As soon as the temperature becomes warm enough these plants have a quick spurt of growth, flower and reproduce using the light energy prevailing in the absence of the canopy, then exist vegetatively for the rest of the year.

The primary productivity of the temperate deciduous forest is much greater than that of the boreal forest. There are larger amounts of biomass at the autotroph level and consequently a larger standing crop can be supported at the heterotroph level. The amount and rate of energy flow through the system is much more than in the boreal forest, and this in turn allows the development of diversity. There are more possible habitats and specialised ecological niches. The food chains are complex and long, and the system seems to exhibit more stability in its animal populations than the boreal forest.

Most of the deciduous trees are nutrient-demanding and therefore the nutrient cycling patterns also show marked contrasts with the boreal situation.

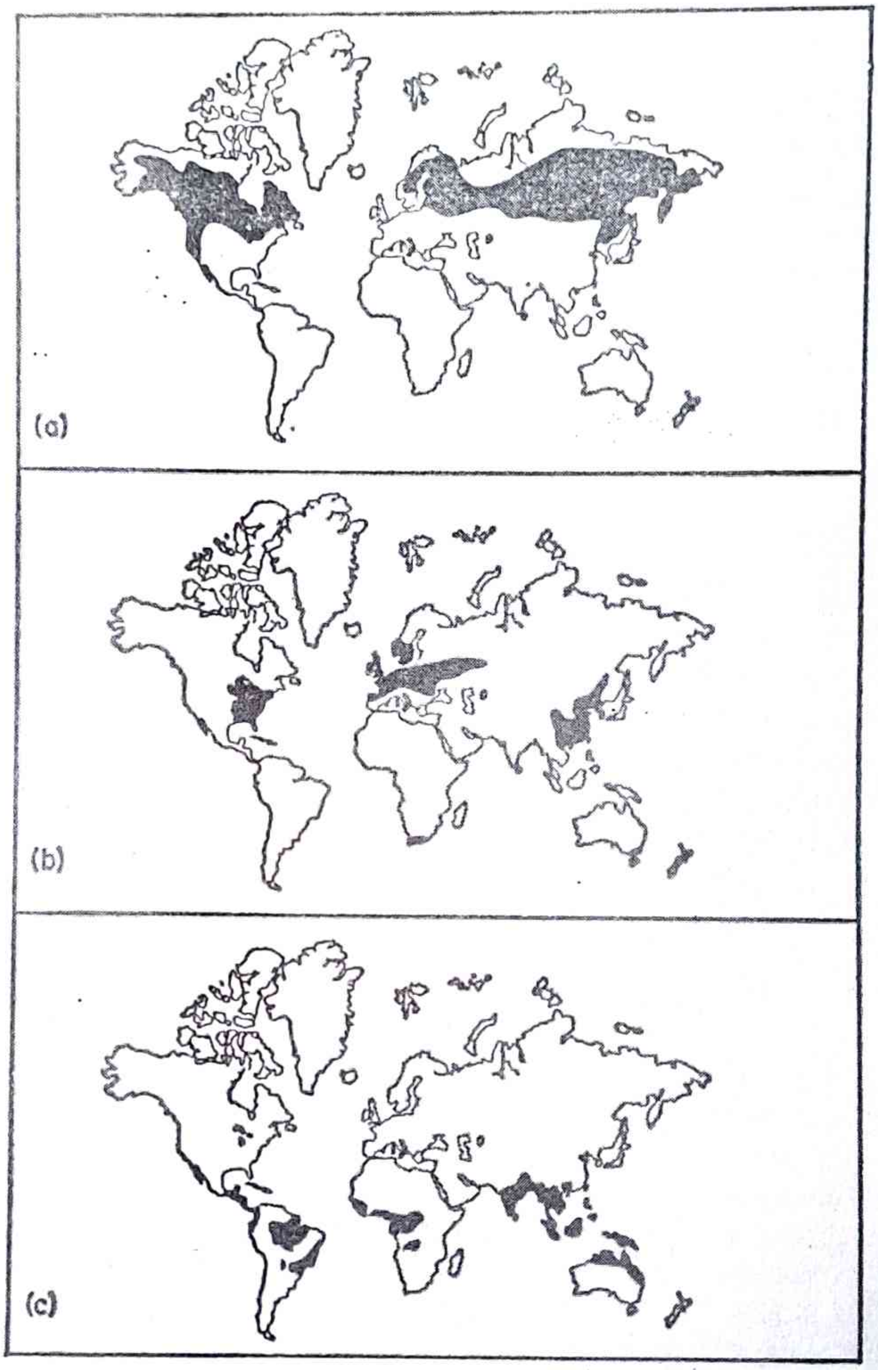

Fig. 23.1. Distribution of forest ecosystem types: (a) boreal forest; (b) temperate deciduous forest; (c) tropical rain forest.

(Reproduced from Cox, Healey and Moore: *Biogeography: An Ecological and Evolutionary Approach*, 2nd edition, 1976, by permission of Blackwell Scientific Publications)

Larger amounts of nutrients are used and their movement is more rapid. There is a bulk return of nutrients from the trees with the leaf fall of autumn. Characteristically the leaf litter is nutrient-rich and decays by the action of bacteria to form mull humus. The soils associated with the temperate deciduous forest are varied but on the whole they are brown earths.

Tropical Rain-forest

The tropical rain-forest occupies low-altitude areas near the equator in South America, Central and West Africa, and in the Indo-Malay peninsula and New Guinea regions (see Fig. 23.1c). Although these areas are physically isolated, the forest growing in them shows great similarity of structure and function. It is a broad-leaved evergreen forest of dense, prolific growth and an extremely diverse fauna and flora. The hot, wet tropical climate is highly conducive to plant growth and there is very little seasonality which means that the growing period extends throughout the year. This, combined with the large energy input to the system from solar radiation in the low-latitude areas, results in high rates of primary productivity, and a large standing crop of vegetation, which can support a great deal of animal biomass. In these conditions there will be severe competition for survival, leading to specialisation of roles and the predominance of narrow ecological niches. All green plants strive to reach the light so that they either become very tall, or adopt a climbing habit or live as **epiphytes** (plants living on other plants but not deriving food from them). Beneath the tree canopy, which may itself consist of two layers, there is usually a well-developed layering of understorey vegetation, which is so dense that hardly any light reaches ground level.

The dominant trees are extremely varied in species but have similar appearances, typically characterised by buttress roots, dark leaves and a thin bark. The leaves possess thick cuticles for protection against the strong sunlight, and drip tips whose probable function is to shed water rapidly, thereby aiding transpiration. The heterotrophs also show similarities in their general characteristics. Many snakes and mammals are adapted to live in the trees because this is where the bulk of the foliage exists.

Providing the tropical rain-forest is undisturbed it is the most diverse and productive type of forest ecosystem, but if the canopy is depleted the soils soon become infertile. Nutrient cycling is rapid, as the vegetation is demanding, and decomposition is accomplished quickly by bacterial action. Very few nutrients are stored in the soil and the system exists in a precarious state of balance which can easily be upset.

Grassland Ecosystems

The grass family (Graminaceae) exhibits a remarkable range of tolerance to habitat factors, and although most species are found in temperate or tropical regions, it has a world-wide distribution. Grasses can be annual, biennial or perennial in habit. Despite a variation in species height from a few centimetres to several metres, all grasses have a similar life form and all are herbaceous (non-woody), with the exception of the bamboos. The principal taxonomic feature of the family is that all species have sheath-like leaves produced alternately from nodes on the stem. Another important characteristic is that grasses grow from their base; consequently they can tolerate grazing or burning better than most plants. They also have extensive root systems, which, coupled with their efficient reproduction and dispersal capabilities, means that once a grass sward has formed, it is very difficult for other species to invade it.

Grassland ecosystems contrast with forest ecosystems in several ways. They have a much smaller biomass, of which a large percentage is made up of roots. In the part above ground, the simple growth form precludes any obvious structural layering. A ground layer of small plants with 'rosette' forms, mosses and lichens is one of the more consistent features. Similarly, there is not a great deal of micro-climatic variation within a sward, except in tropical grasslands, where a discontinuous layer of trees or shrubs may diversify the structure. However, a grass sward as a whole usually has a higher albedo than a tree canopy and protects the soil from direct heat. Grasses are probably not as effective at precipitation interception as trees, except for the period of maximum growth. The grass form facilitates stem flow, and surface run-off is greater from grass-covered than from forested slopes.

The annual primary productivity of a grassland ecosystem is only about an eighth or ninth of an adjacent forest area. The smaller standing crop also means that there are more limited nutrient reservoirs in grassland. Turnover of nutrients is relatively rapid. Since much of the plant food occurs in the soil, a large soil fauna, notably made up of decomposers, is a characteristic feature of the ecosystem type. Surface animal species are frequently large: herbivores (bison, antelope, horse) adapt their behaviour to the relatively open and unprotected habitat by congregating in herds and being fleet of foot. Smaller mammals, such as mice, voles and rabbits live below but feed above ground.

The ecological status of grasslands has given rise to much debate. Early workers thought that all extensive grasslands were too dry for trees and therefore represented a climatic climax. More recently, increased study of the fauna and the use of pollen analysis has led to the conclusion that fire and human activity are important elements in these ecosystems, even though we normally refer to them as 'natural'.

The most extensive natural grasslands occur in sub-humid or semi-arid areas which have a low variable rainfall with a marked spring or summer maximum. They attain their widest extent in continental areas of low relief, forming extensive plainlands. Two main types of grassland are normally distinguished (see Fig. 23.2a): temperate grasslands, in which woody growth is absent or negligible, and tropical grassland (savanna) in which scattered trees are much more common.

Temperate Grasslands

These include the prairies of North America, the steppes of Eurasia, the pampas of South America, and the veldt of South Africa. Smaller tracts occur in Australia and New Zealand. Precipitation in these areas ranges from 250 to 1000 mm per annum, and the grasslands extend over a wide range of soil conditions. Trees only occur on steep slopes or near water. The geographica isolation of these areas from each other has led to some species differentiation, but most other features are similar.

The prairies have been the most closely studied. They exhibit a gradual transition of character from east to west, partly related to climate. Areas of so-called 'true' prairie, composed of grass two or three metres high, were originally widespread in the wetter east in Michigan and Illinois, but have now almost completely vanished under extensive cultivation. Remaining remnants merge westward into mixed prairie, about one metre high, which itself is replaced by short-grass prairie on the high plains. Here, grasses are only ten to fifteen centimetres high, and in the lee of the Rockies, become mixed with cactus and sagebrush. Short-grass prairie, formerly attributed solely to the increasing westwards aridity, is now thought to be partly a function of grazing pressure: if this is eliminated, medium grasses reappear and become dominant. Soils within the prairie belt include deep and fertile chernozems, prairie soils and chestnut soils (Chapter Eighteen).

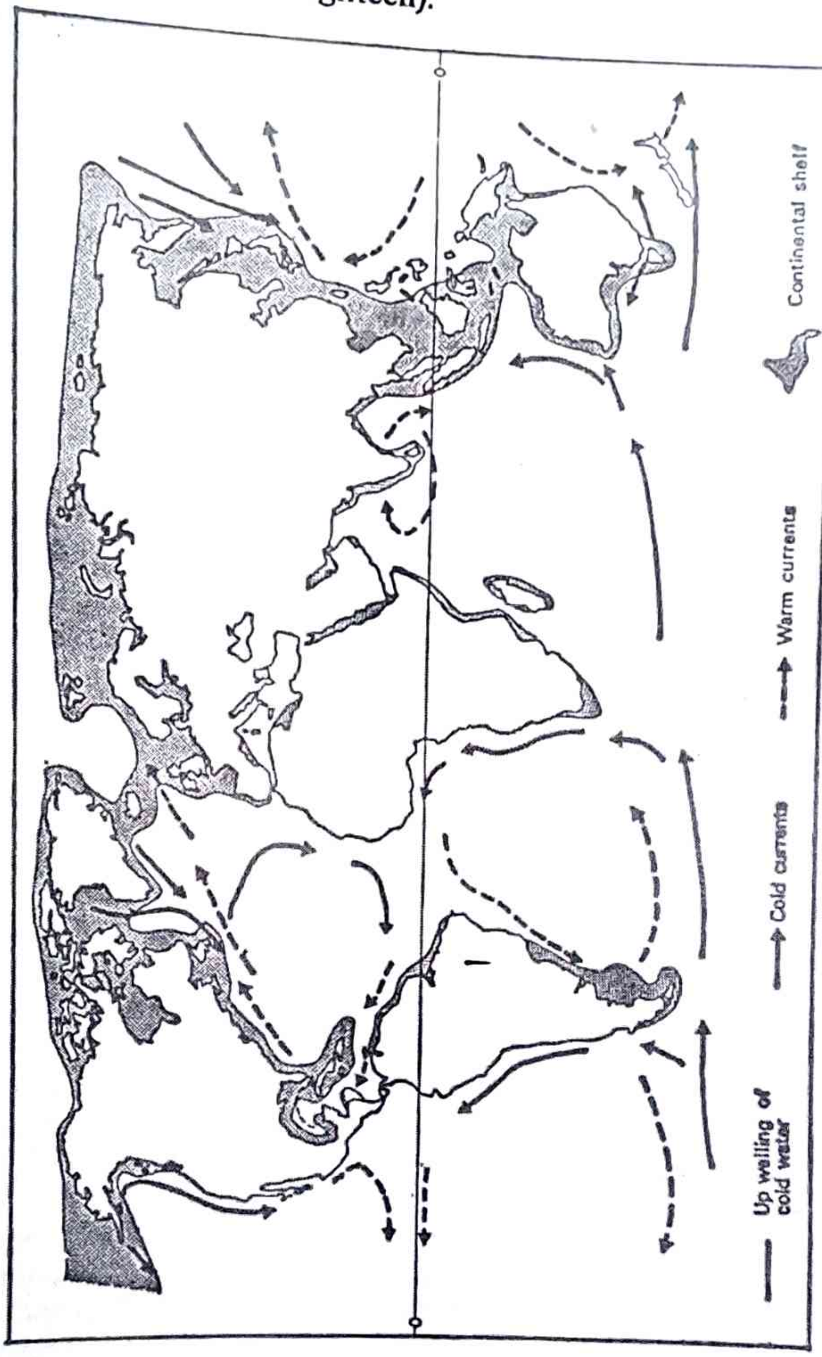

Fig. 23.2. Distribution of (a) temperate grasslands (*light shading*) and tropical savanna (*dark shading*), (b) tundra, and (c) arid areas.

(Reproduced from Cox, Healey and Moore: *Biogeography: An Ecological and Evolutionary Approach*, 2nd edition, 1976, by permission of Blackwell Scientific Publications)

Although the boundaries of the prairies seem to have fluctuated in the geological past, one of the most interesting features is the sharpness of the prairie edge, and the lack of an ecotone or transitional area with adjacent forests. The factors which have created this situation are difficult to isolate, but most authorities would include grazing and fire. Large herds of bison once roamed the prairies; it is estimated that in 1600 there were as many as forty-five million, an important force in maintaining the general uniformity of the whole habitat. The American ecologist Carl Sauer particularly favours fire as a necessary condition of prairie maintenance: forest remnants can be shown to exist only where steep slopes form a natural fire-break. Early white settlers noted that the Plains Indian frequently used fire as a means of herding bison. Sauer has suggested that the prairies are essentially a product of post-glacial times, but others relate the development of large herbivorous animals in the Tertiary to the presence of open grassland habitats. One possible conclusion is that the prairies, and other similar grasslands, may originally have been of a climatic origin, but they have been maintained and extended by other factors.

Tropical Grasslands (Savannas)

The savanna lands of Africa, South America and Australia (see Fig. 23.2a) are essentially open, and ecologically dominated by a herbaceous stratum in which grasses and sedges are the principal components. However, the much greater diversity of tropical as opposed to temperate grasslands is often a function of the added variety afforded by wooded plants. In some cases the tree cover may be as much as 50 per cent; in others it may be nil. All types experience a climate of marked seasonal drought, and many of the plants, both grasses and woody species, exhibit xerophytic features. The ferralsolic soils of savanna areas frequently include near-surface lateritic crusts, creating an impermeable surface soil layer in which nutrients, especially phosphates and nitrates, are markedly lacking. It has been suggested that these edaphic factors, as much as climatic controls, favour the xerophytic tendencies of savanna species. Marked contrasts exist in the appearance of the savanna during the year: the brown and withered short grasses of the dry season give way rapidly to tall lush growth with the arrival of the summer rains.

As in the case of prairies, tropical grasslands tend to show little ecotone development, especially on margins adjacent to tropical rain-forest. Overall, savanna boundaries on all continents reveal only poor correlation with precipitation amounts or the duration of the rainy season. Botanists such as A. Schimper, who tried to correlate savanna as a climax type with climate, found this impossible. Again, this strongly suggests that factors of soil, fire and grazing are important in maintaining the character of tropical grasslands. Many of the tree species appear to be fire-resistant. Although human occupation of the African savanna may extend over hundreds of thousands of years, fire and grazing are not necessarily always man-induced. The great variety of herbivores and carnivores in these areas indicates that the ecosystem is of considerable antiquity. It has been proposed that tropical grasslands have evolved over a long period of time which has been accompanied by progressive soil degradation. If so, savannas are now **edaphic climaxes**, depleted further in many areas by burning and grazing to treeless grasslands. Thus they persist in many areas where the climatic conditions are suitable for tree growth.

Biological Deserts

Very few areas of the world, apart from ice-sheets, are absolute deserts, devoid of any form of life. On the other hand, there are extensive regions where biomass and organic productivity are very low. The largest areas where

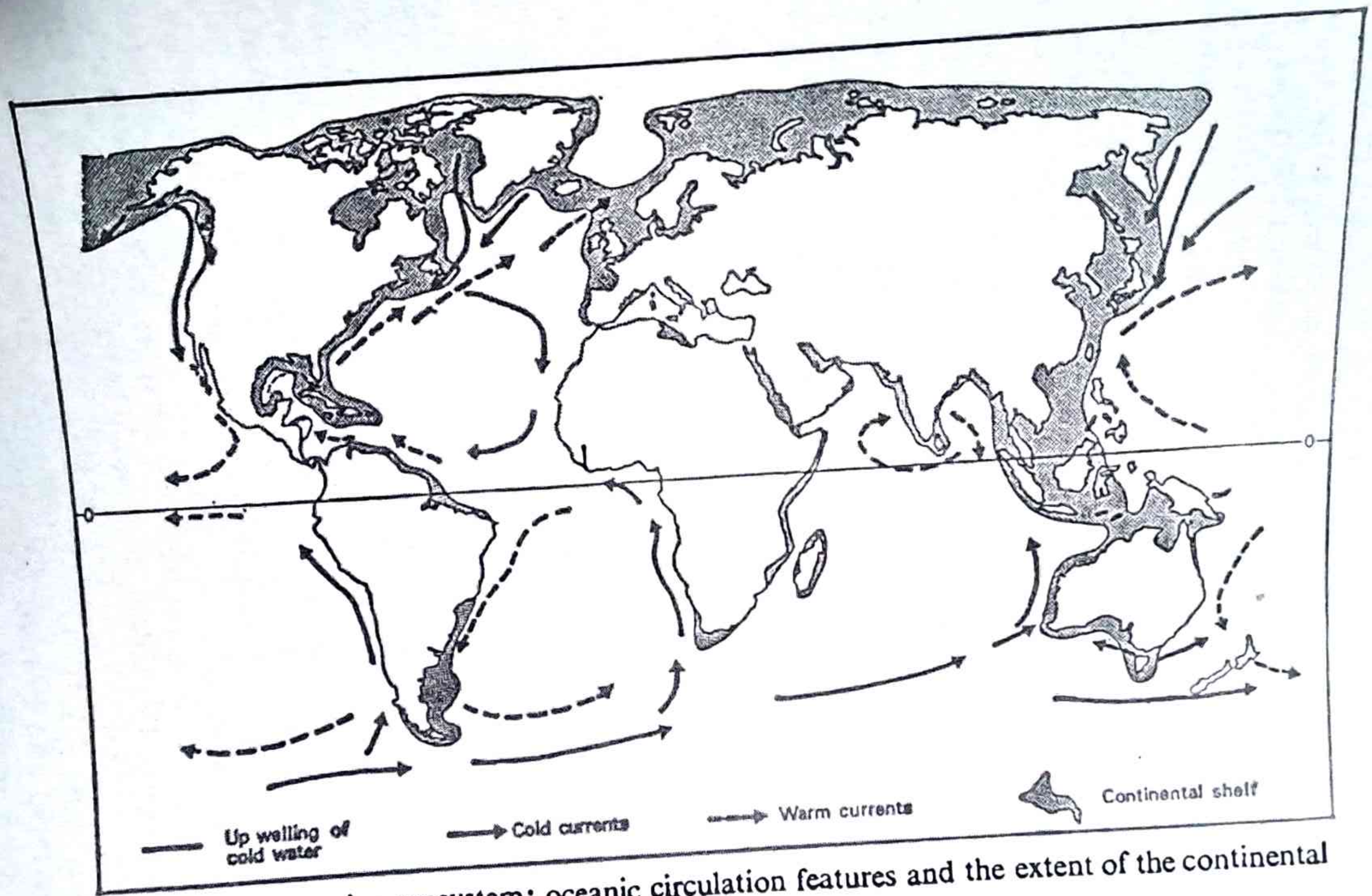

Fig. 23.3. The marine ecosystem: oceanic circulation features and the extent of the continental shelf.

this is the case are climatically conditioned, either by a lack of water as in ho deserts, or by extreme cold as in tundra regions (polar or cold deserts).

Despite the obvious climatic and geomorphological differences between arid and cold deserts, they have certain basic ecological characteristics in common. In both, the environment is harsh, requiring a high degree of tolerance or adaptation in the organisms present. Plants and animals of biological deserts tend to show less species variety than other ecosystems, but more specialisation. The physical conditions, often unstable because of high rates of wind deflation, frost heave and other processes, exert a greater ecological influence on the composition and form of the vegetation in biological deserts than elsewhere. As a result, the diversity of physical habitats in these regions is reflected in the mosaic of small communities, especially in the more hilly regions.

The virtual absence of trees is a marked visual feature of biological deserts. With the exception of giant cacti, they are characterised by plants of low growth of which much of the organism is below ground. The communities themselves have a simple structure and a lack of stratification, and frequently form only a discontinuous ground cover. Inevitably, the lack of plant food restricts the number of heterotrophs that can be supported. The close interrelationship between the lack of vegetation cover and the unstable geomorphological environment gives biological deserts a character of delicate instability in which they are particularly susceptible to disruption by man (Chapter Twenty-Four).

Tundra

The tundra is taken here to include all types of vegetation found in high latitudes between the limits of tree growth and the polar ice-caps (see Fig. 23.2b). In effect, this virtually confines us to the northern hemisphere. Some of the ground conditions and geomorphological processes operating in the tundra were outlined in Chapter Six. There is a considerable variation in surface processes depending on lithology, moisture availability and slope gradient, but solifluction over permafrost is common over large areas. The climate of the tundra roughly corresponds to that of the sub-polar zone described in Chapter Fifteen. In broad terms, climates range from a continental type of extremely cold winters and little snow precipitation, as in Siberia and northern Canada, to the raw maritime conditions of southern Greenland, northern Norway and Alaska.

Plants in the tundra adapt to these unfavourable conditions in several ways. The main problems are posed by the low temperatures and the short growing season. Adaption to sub-zero temperatures would appear to be both physiological and morphological. Physiological protection entails changes in the cell sap and protoplasm, so that in some species cellular ice does not form until temperatures drop below −30°C. Other plants, such as lichens, never freeze and can adjust to rapid and extreme temperature changes. The low growth form of tundra plants represents a morphological adaptation which takes advantage of slightly higher temperatures near the ground and avoids extreme wind exposure.

The shortness of the growing season—less than three months—is to some extent offset by long day length in summer. Nevertheless, the growing season poses major problems for productivity and reproduction, and plants must complete their development cycle in the time available. Photosynthesis in most tundra plants starts immediately soil temperatures rise above 0°C, particularly in evergreen shrubs. Deciduous plants may possess partly developed leaves, formed in the previous autumn, which allow the plant to take advantage of the whole of the new growing season. Some reproduction in tundra plants takes place vegetatively, some by seed production, which may need two or three seasons to be completed. Flowers, often vivid, are formed in one season, and seed maturation occurs in the next. In still other plants, germination commences before the seed is dispersed. However, not surprisingly, annuals are rare.

The importance of these limiting factors means that the principal regional variations in tundra vegetation are related to the northward reduction of the duration and warmth of the growing season, combined with increasing winter severity. Where undisturbed, the southern parts of the tundra are characterised by stands of dwarf willow, birch and alder, sometimes up to two metres in height. Further north, these give way to heaths of cowberry or crowberry or to intermittent swards dominated by rushes and sedges over peat. Under the severest conditions, all plants but mosses and lichens are eliminated, and large areas of bare rubble or rock are to be found. Superimposed on this broad framework are communities of vegetation dependent on local conditions. In particular, relief variations affect the depth and duration of snow cover, as well as soil mobility, and these factors in turn produce local vegetation sequences, or **catenas**, related to altitude and slope angle.

Animals in the tundra are limited in number and variety by the lack of plant food and the intense cold. The difficulty of finding shelter is compounded by the impossibility of underground refuge where permafrost exists. Warm-blooded animals must either be protected from the surface cold by such adaptions as woolly coats and low surface area to body volume ratios, as in the polar bear, or they must migrate. Cold-blooded animals, of which the insects are by far the most numerous, can survive in larval form throughout the winter. The main herbivores include caribou, reindeer, musk ox, lemmings and the Arctic hare; predators, both carnivores and omnivores, include the Arctic fox, the wolf and bears. The total animal biomass is relatively small and undergoes marked seasonal fluctuations in volume. The lack of animal diversity is reflected in the small number of trophic levels, although food webs are often made complex by the relatively high proportion of omnivores in the system.

Some authorities are of the opinion that the simplicity of the tundra ecosystem renders it inherently unstable. One possible manifestation of this instability is the great periodic fluctuations that occur in the population of such species as lemming or Arctic fox. Because the types of prey at any particular trophic level are so few, any variation in numbers has major repercussions on those of the next higher level. It is difficult to decide whether the lack of diversity in the ecosystem is entirely a result of the rigour of the climatic conditions, or whether it also reflects the shortage of time in which the system has been able to develop. The tundra in its present geographical position can only date from the recession of the ice-sheets after the last glaciation, although tundra as an ecosystem type may have first appeared in the late Tertiary.

Arid Areas

Up to a third of the world's land surface can be described as arid (see Fig. 23.2c), characterised from a biological point of view by a lack of water availability rather than a complete absence of water. The ecosystem type described here refers mainly to the hot arid zones of the world, such as the Sahara and Australian deserts. Cooler deserts—for example, those of the Gobi and Patagonia—have been relatively little studied, but possess some of the limiting factors of both the hot deserts and the tundra. Hot deserts occur in the subtropical dry zone of the global atmospheric circulation system (Chapter Fifteen). The majority of accounts of the plant and animal life of these areas have been largely descriptive; much less is known about ecosystem functioning.

With one or two notable exceptions, such as the creosote bush (south-west USA), desert plants capable of withstanding extreme desiccation of their tissues or very high temperatures are in fact relatively few. Up to 60 per cent of desert floras are made up of annual or ephemeral species which evade the drought by completing their life cycles within a few weeks of the onset of any rain, their seeds remaining quiescent throughout the succeeding dry period. Perennials, on the other hand, are faced with the year-round conflicting problem of avoiding desiccation and keeping cool at the same time. One of the most important ways of avoiding water loss is to close the leaf stomata, particularly during the hottest period of the day, yet the stomata need to be kept at least partly open to maintain transpiration and cool the leaves. Some plants only open their stomata at night. Succulents, such as cacti, combat the water problem with the aid of well-developed water storage organs and small surface area to volume ratios.

In addition to the problems of physical drought and great heat, many arid zone plants have to tolerate the physiological drought set up by saline ground conditions. An evasion of the worst effects of high salt concentrations may be achieved by the synchronisation of life cycles with rain periods sufficiently wet to leach temporarily the upper soil layers. Thus besides their xerophytic characteristics, many plants need also to be halophytic.

The most noticeable visual characteristic of areas of desert vegetation is the discontinuous cover and the even spacing of individuals. This appears to be the result of extensive root development and competition. Vegetation is more discontinuous than in the tundra, but on the other hand it is more diverse in composition and form. Floras of discrete areas have tended to evolve in isolation from each other, whereas the tundra is more continuous. Related to varying degrees of aridity, desert vegetation includes low woody scrub formations, cacti communities, intermittent swards of perennial grass tufts, ephemeral or seasonal herbaceous vegetation, and 'accidental' vegetation in areas where rainfall may occur only once in several years. Under the most rigorous conditions a combination of a lack of precipitation, intensity of evaporation and high soil salinity or mobility (e.g. on dunes), may exclude vegetation entirely. These absolute biological deserts are, however, localised and limited in extent. In the particularly harsh conditions of the coastal deserts (see page 179), where the sole source of moisture is the sea mist, only halophytes or succulent epiphytes, absorbing moisture directly from the atmosphere, can survive.

As in the tundra, the animal species of deserts are fewer but more specialised than in humid environments. Protection against water loss and high levels of body heat pose similar problems as for plants. Morphological protection may be given by such features as an impermeable body covering, a small number of sweat glands and a light colouring. Camels and donkeys have in addition a physiological tolerance of high water losses and can survive a water reduction equal to more than 25 per cent of body weight. In smaller animals the burrowing habit is widely developed, especially among insects. The atmosphere of the deeper soil layers remains humid, and provides a more temperate climate than the soil surface or the free air above it. Nocturnal activity and summer dormancy are also common features.

The sparseness and marked seasonal variations of biomass at the autotroph level is reflected in the widely fluctuating populations of some of the animal species in both time and space. Synchronisation of breeding cycles with periods favourable to vegetation growth enhances the explosion of life that occurs in deserts within a few days of the onset of rain. A detrimental side-effect of this synchronisation occurs where man irrigates desert areas and provides an abundant source of food without predators. Spectacular locust plagues are one result of this. Desert ecosystems are as precariously balanced as that of the tundra.

Archaeological evidence suggests that desert margins have long been useful to man, either for grazing or, with irrigation, for crops. Irrigation tends to raise the water-table and can bring salts to the surface, ultimately rendering the ground sterile. This, coupled with widespread grazing, has created considerable areas of man-made desert. Although the desert ecosystem type can be said to have evolved because of climatic control, hardly anywhere today are its margins 'natural'.

The Marine Ecosystem

The basic functional mechanisms common to all ecosystems (Chapter Nineteen) apply as much to the sea as to the land, but major differences exist between the environmental conditions and life-forms in the marine ecosystem and those of the terrestrial types. Oceans cover 70 per cent of the surface area of the world, they are habitable throughout and support a total biomass probably as much as ten times that on land. In many ways, the marine environment is much more favourable to life than land areas; it is more equable, and the two most essential gases for life, oxygen and carbon dioxide, are readily available in water, provided it is not polluted. In addition, many of the nutrient minerals found in the Earth's crust are dissolved in the sea in varying amounts.

Environmental Conditions

The main environmental gradients in the sea are related to temperature, salinity, and light intensity. Salinity is caused by at least forty-five elements, the major two being sodium and chlorine. The most saline conditions occur where temperatures, and hence evaporation, are highest; the Red Sea has an average value of forty grams of salt per thousand of sea water (40‰). The lowest values occur near melting ice or near river mouths; the Baltic Sea has a salinity in summer months of barely 5‰. In the open water of the major oceans, the range is much less, from 37‰ in the tropics to 33‰ in polar seas. Many marine organisms have very narrow tolerance ranges to particular salinity concentrations, which may therefore localise them considerably in terms of depth or area.

Temperature variations in the sea are much less than those on land. The difference between the surface temperature of the warmest seas (32°C) and the coldest (−2°C) gives a range far less than that of land (about 90°C). Around the coasts of the British Isles, surface water temperatures vary annually from about 8°C to 17°C. Both vertical and horizontal ocean currents (Fig. 23.3) play a major role in equalising variations of temperature, salinity and dissolved gases in the oceans, as well as being important factors in the global energy budget.

The availability of light exercises as much fundamental control on the basic process of photosynthesis in the sea as it does on the land. The amount of light reaching the surface varies with latitude and with season; much is lost by reflection from the water surface in high latitudes and when the sea is rough. Absorption by the water increases very rapidly with depth; this rate is also affected by the amount of turbulence and suspended matter in the sea. The depth at which the compensation point occurs, i.e. the point at which the light is not sufficient to allow photosynthesis to proceed at a rate which compensates for the rate of respiration, varies considerably; it may be as little as ten metres in inshore waters, as much as a hundred metres in open water. The latter figure approximately separates the **euphotic** zone, in which there is enough light for photosynthesis, from the deeper **disphotic** zone lying between one and two hundred metres below the surface. Light penetrates into the latter zone but it is too dim for photosynthesis. It is noteworthy that the maximum depth of the euphotic zone roughly coincides with the average depth of the continental shelf.