K1 PHYSICAL FACTORS AND PLANT DISTRIBUTION

Key Notes

The requirements for plant life

All plants have the same basic requirements for solar energy, water and nutrients. Their distribution is determined by adaptations to withstand environmental stress and their ability to spread, along with biotic interactions.

Temperature

The number of plant species in a community increases with increasing temperature, given sufficient water. Frost is a barrier for many plants and requires adaptations to prevent tissues from freezing. The distribution of some plants follows isotherms.

Water

In most parts of the world water is limiting at some time of year and plants must resist drought. In waterlogged conditions plants may be limited by the availability of air, though aquatic plants may derive dissolved gases from the water. High rainfall and humidity on tropical mountains leads to reduced transpiration and stunted growth. Bryophytes dominate in some wet environments. Very few flowering plants occur in the sea.

Nutrients and ions

The overall and relative quantities of elements in soils varies greatly, both with underlying geology and age and thickness of the soil. Many are essential and some toxic, and plants differ in their requirements and abilities to withstand toxicity; communities differ under different conditions. Plants tolerant to sea salt occur around all coastlines.

Disasters

Periodic or occasional disasters such as fire, hurricanes or landslides can dominate plant communities. Fire may occur frequently in savannahs and less than one per century in conifer forests, but still have an overriding influence.

Plant geography

Some plants have good seed dispersal and colonize easily but many do not and barriers of unsuitable habitat preclude colonization or migration. Globally, the world is divided into several phytogeographic regions, these regions reflecting the current distribution of the continents and their drift over the past 120 million years or so.

Glaciation and plant migration

Over the last million years, glaciers have expanded and contracted over the northern hemisphere making many of these areas suitable only for tundra-like vegetation. The plants have migrated differentially leading to a flexible community structure. In the tropics, glacial periods are dry and rainforests were more fragmented. There is good evidence from plant fossils, mainly pollen, of post-glacial changes.

Related topics

Plants and water (I1)
Plant communities (K2)
Uptake of mineral nutrients by plants (I4)

The requirements for plant life

Plants are dependent on external **temperature** and **solar radiation**, **water** supplies, and **nutrients**, normally in the soil, for their survival (Topics I4 and I5). The basic requirements are the same for all plants. No plant can survive when its growing temperature remains below 0°C all the year round (plants frequently have a higher internal temperature than the ambient air temperature) or in the driest of deserts where the soil is often unstable. The overall geographical distribution of plants is partly determined by their relative abilities to withstand different climates and soil conditions. These major differences across the world give rise to different **biomes**, i.e. groups of plant communities dominated by plants of similar form, such as tropical rainforest or temperate grassland, which may have a totally different species composition in different areas but look similar and function in similar ways (*Fig. 1*).

For many plants, dispersal across unfavorable environments, such as the sea or a desert, is limited, giving rise to different plant **communities** in different regions of similar climate and frequently a different flora on islands from continental areas. Interactions between plants, such as competition, and interactions with other organisms, have an overriding influence on the distribution of a species within one geographical region and can affect major distribution patterns (Topics K3 and K4, and Sections L and M).

Temperature

Temperature and incoming solar radiation have a profound influence on the distribution of plant communities. In general, given sufficient water, the number of plant species present increases with increasing temperature. One of the major limits is **frost**; many plants cannot tolerate the presence of frost at any time of year. Frost limits not just species but whole biomes. **Temperate** and **boreal** (northern, between temperate and arctic) environments are characterized by more or less frequent frosts in one season of the year and during this period the plants become dormant, having developed mechanisms to stop their tissues from freezing. These mechanisms include becoming deciduous, dying down completely or concentrating their cell contents.

Many plants appear to be limited in their distribution by temperature at a particular time of year, following the line of a maximum or minimum **isotherm**, though the reasons for this are not clear. Many plants are able to live outside their observed natural distribution in cultivation. The reasons are probably competition with other plants or other biotic interactions.

Water

On land, the quantity and distribution of **rainfall** or other sources of water such as **fog** or **snowmelt** have a major influence on overall plant distribution. In most parts of the world water is limited at some season, either by a dry period in the seasonal tropics or a dry summer or frosty winter outside the tropics. In **deserts** and **steppes** it is limited most of the time. In all these environments there are specialized plants that have adaptations to limit water loss during the dry periods and most plants become partially or totally dormant during the dry periods.

At the other extreme, in permanently waterlogged conditions and in **aquatic** environments, **aeration** is often the limiting factor for plant growth and only plants specialized to withstand waterlogging can survive, although there are aquatic plants with submerged leaves that derive all their photosynthate and nutrients from the water. On tropical mountains there is frequently a high rainfall and frequent fog and high humidity, low solar radiation and cool temperatures. These conditions lead to a stunted forest, since transpiration, and

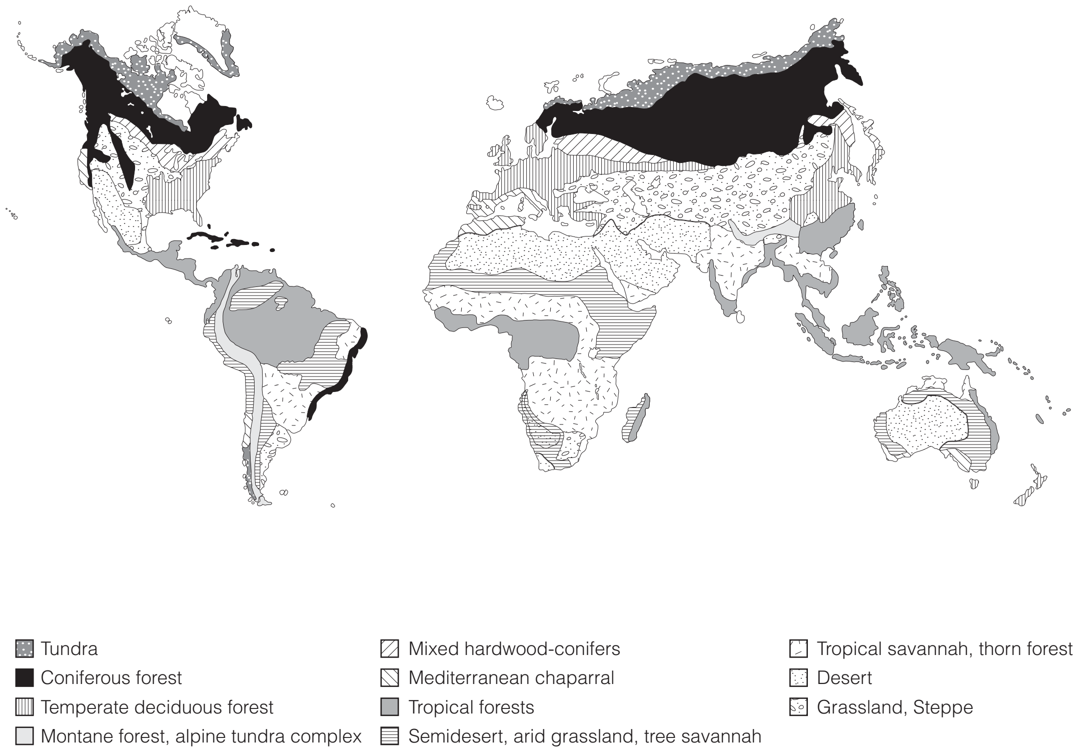

Fig. 1. Distribution of the major biomes of the world. (Redrawn from A. Mackenzie et al. *(1998),* Instant Notes in Ecology, *BIOS Scientific Publishers Ltd.)*

with it nutrient supply, becomes limiting (Topic I1). In these environments, **bryophytes** become particularly common since they absorb water from the atmosphere and have no internal conduction system (Topic P3). In ever-wet cool or cold conditions on seaboards in temperate zones, in mountains and in sub-polar conditions, bryophytes, notably *Sphagnum* mosses, dominate and dead plant material does not decay fully, forming peat.

Where water, aeration and temperature are not limiting factors, as in parts of the tropics, **rain forests** grow. The tropical rainforests are among the most diverse terrestrial environments in plant species and life form. In these environments biotic interactions play an important role in limiting plant distribution (Topic K2).

In the sea there are very few highly specialized flowering plants, such as eel-grasses (*Zostera* spp.), the great majority of photosynthesis being done by unicellular algal plankton and, inshore, by large algae (Topic P2).

Nutrients and ions

The nutrient and ion status of soils is variable, with different elements limiting in different places and some elements being toxic (Topic I4). In many soils, **nitrogen** is one of the main limiting nutrients although some plants, notably legumes, have nodules in their roots filled with nitrogen-fixing bacteria (Topic M2). In many soils more than one nutrient may be in short supply and plants compete for them. The ion status of a soil will depend in part on the underlying

geology and certain elements, such as calcium, are most common in alkaline conditions, but in these soils iron may be limiting. Likewise in many acid soils, many nutrients are in limited supply but aluminum becomes available and is a toxic element for many plants. These and other differences between soils lead to quite different plant species and communities occurring on different soils. In places rich in **heavy metals**, many of which are toxic (e.g. lead), only certain specialized plants can grow. As a soil ages, elements will gradually leach away and it will become poorer in nutrients. In these conditions the presence of animal dung or carcases, ant nests or other plants can lead to great variation in nutrient status on a small scale within the community.

Areas dominated by **saline** conditions occur around all coastlines and estuaries. The great majority of flowering plants cannot grow in the presence of salt in concentrations found in sea water, with its high osmotic potential. Specialized plants with adaptations for excluding or excreting salt occur, mostly succulent and low-growing (Topic I5). Tidal estuaries which are inundated for part of each day with brackish water are often rich in other nutrients and can be highly productive for those plants that can tolerate the conditions: specialized mangrove trees in tropical estuaries; herbs and low shrubs in temperate saltmarshes.

Disasters

Some parts of the world are prone to periodic or occasional destructive forces that can dominate a plant community. **Fire** is the most common, started naturally by lightning, but in many places becoming more frequent with human influence. In some savannahs the grass which dominates the ground layer is burned most years but regrows when rain returns. This maintains the savannah community. In other places, such as coniferous woodland and heathland, fires are less frequent, even as few as one per century or less, but still are one of the overriding influences on the composition of the plant community.

High winds are frequent near many coasts and on mountains, and tall-growing trees frequently cannot grow through mechanical instability. Periodic or infrequent storms or **hurricanes**, developing over the sea, can cause havoc in restricted areas, usually near coasts. Though each hurricane ploughs a different path, certain parts of the world, such as the Caribbean and the Philippines, are hurricane-prone. Some plants resist these winds better than others and in these places communities can be dominated by occasional hurricanes.

Tsunamis (tidal waves), **volcanic activity** or **landslides** can also devastate communities, sometimes maintaining them as permanent pioneer communities.

Plant geography

The dispersal of plants is normally dependent on seeds. In those plants with light, wind-dispersed seeds and some of those with seeds dispersed by birds or other means, dispersal can cover long distances over unfavorable habitat and the plants can colonize new places. Other plants are much more restricted (Topic L2) so the spread of species across the world is limited. If a plant is restricted to a particular environment which has a discontinuous distribution, e.g. mountain ranges, dispersal between one range and another may be impossible, restricting a plant's distribution and resulting in different species occurring on each range.

Most plants cannot disperse from one continent to another and there are differences in the floras of the major continents at the genus and family level. The major **phytogeographic regions** of the world are given in *Fig. 2*. The distribution of these regions is a reflection not only of the existing configuration of the continents, but of their histories. It is inferred from geological and fossil

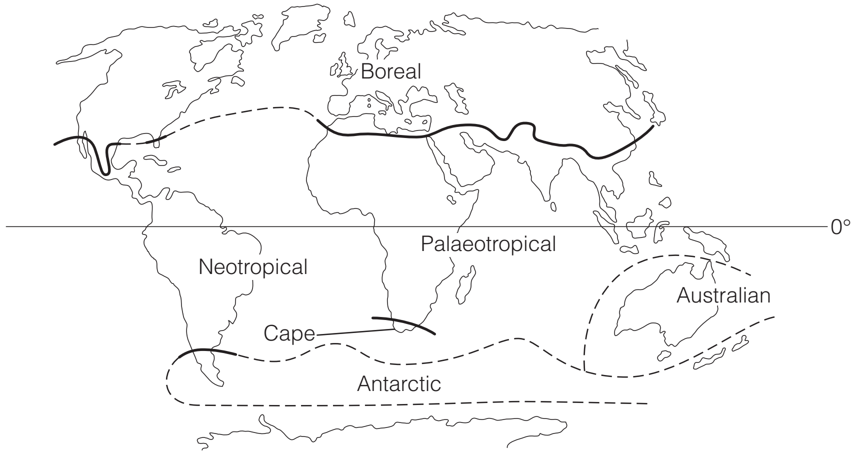

Fig. 2. Phytogeographic regions of the world.

evidence that about 120 million years ago there were only two continents and the first flowering plants were appearing. The subsequent evolution of flowering plants has been dramatically affected by the shifts in continents that have occurred since, and consequent isolation or joining together of, large land masses. The regions are mainly similar to vertebrate geographical regions but are less well defined owing to the fact that flowering plants evolved before modern vertebrate groups and migrated across the world earlier, maintaining affinities across regions. They differ particularly in the southern temperate zone.

The whole **north temperate zone** is regarded as a single region, the **boreal**. The north Atlantic formed about 50 million years ago and North America and Eurasia have periodically been joined at the Bering Strait. The whole region has had great climatic changes in the last million years through **glaciations**, probably extinguishing many species so that only adaptable plants with good dispersal powers remain. In the tropics there are three regions: **South America** with central America; tropical and subtropical **Africa** with tropical **Asia** forming the palaeotropical region; and **Australia**. The **Cape** region of South Africa is a separate and exceptionally diverse small region and the **Antarctic** region comprises southern South America and New Zealand.

There are strong affinities between all the tropical floras; New Guinea and north-eastern Australia have a similar flora to Asia. The southern super-continent, **Gondwana**, split up about 100 million years ago to form the southern continents of today and all drifted north except for Antarctica. The Antarctic region retains a remnant flora of what was once widespread across Gondwana, and the Cape and Australian regions have rather different Gondwanan floras of drier Mediterranean-climate and semi-desert floras that have evolved separately. They have not been subject to the major glaciations and climatic shifts of the northern hemisphere. Minor phytogeographic regions are formed by some **oceanic islands**, particularly in the Pacific.

Glaciation and plant migration

Over the last million years, periodic cooling and warming of the world has led to glaciers spreading and retreating in the northern hemisphere and the tropics becoming drier during glacial periods and wetter during interglacials. These fluctuations have led to major changes in the range of plant communities in the northern hemisphere with large areas of Europe and North America containing temperate broad-leaved forest as its natural community dominated by Arctic-like **tundra**. In the tropics, rainforest became more restricted and fragmented during the drier glacial periods. There were many extinctions during these glacial times. The spread and retreat of the glaciers affected plant distribution throughout the north temperate, plants with good colonizing ability surviving better than others and some tundra plants reaching their current disjunct distributions, i.e. distributions consisting of several quite separate areas, through their retreat northwards and into mountains as the glaciers retreated.

In post-glacial times (the last 10 000 years or so) we have a better record than for any previous time from the analysis of pollen and other fossil fragments preserved mainly in **peat** and lake **sediments**. These show that plants have spread at different speeds north and often west as well, following the ameliorating climate, and that the plant communities in the northern hemisphere have changed markedly in extent and composition throughout this time.

K2 PLANT COMMUNITIES

Key Notes

Plant communities of the world

Plants define the biological communities of the world. Within one biome, communities vary greatly and different communities are found in swamps, on mountains and on particular soils. Within one biome, species richness and composition differs greatly and oceanic islands are frequently poor in species. People have modified many habitats, particularly through removal of trees.

Succession

When colonizing bare ground there is a primary succession of plants from pioneers through one or more transitional stages to a climax community. Secondary succession of similar nature happens within more mature communities after disturbance. Succession is often not orderly, can be deflected and end points may differ. Within all communities plants differ in their ability to colonize and pioneer plants are a feature of all plant communities.

Dominance and diversity

Some communities are dominated by one or a few plant species, something expected on the principle of competitive exclusion, particularly for plants of similar life form, but many are not. Dominance occurs in high nutrient conditions where competition may be intense and on certain soils, but many communities have numerous coexisting species.

α, β and γ diversity

Diversity can be divided into α diversity, species living in the same habitat, β diversity, species occupying separate habitats and γ diversity, species occupying separate geographical areas. β diversity can be explained easily although habitat distinctions may be small and subtle; γ diversity varies from region to region depending on the topography and history of the land. α diversity is much harder to explain within one life form. The critical stage of a plant's life cycle is the stage from germination to establishment, often not seen in a mature community, but the conditions at this stage may affect which species establish. Pioneer species may persist for decades. Herbivores and diseases can kill mainly the young stages, preventing dominance. The climate fluctuates and plants are migrating continuously, leaving many communities in a state of permanent transition.

Community definitions

In some places, particularly where modified by people, communities are well defined and have been classified. In others there is continuous variation. Classification is mainly useful within a small well-defined region.

Related topics

Physical factors and plant distribution (K1)

Ecology of different growth forms (K3)

Plant communities of the world

Plants define the world's natural communities, providing the habitat for all its other inhabitants as well as providing the great majority of the biomass. A general picture of the distribution of **biomes** is given in Topic K1 but there are many different plant communities within each biome. For instance, across the northern hemisphere in the boreal and temperate zones there is a patchwork of deciduous broad-leaved and coniferous forest, often with a single species dominant in any one place, and with more broad-leaved forest as one moves south. In the Mediterranean climate regions of the world (in both hemispheres), there is a rich mixture of, mainly evergreen, tree and shrub communities extending to grasslands in the center of the main continents where the climate is drier at similar latitudes. In the seasonal subtropics and tropics there is a range of savannah communities dominated by grasses with increasing numbers of trees as the climate gets wetter.

Within all these places there are patches of other communities and specialist communities in swamps, on mountains, near the sea and in response to particular soil conditions. Different continents differ in their plant communities, and species richness can vary greatly between communities within one biome. Oceanic islands are usually much poorer in species than continental areas. People have modified many communities and, in particular, removed trees to replace them with grassland or other open communities for pasture and agricultural communities and dwellings.

Succession

One of the best known ecological theories is that of succession which is seen to occur in places such as sand dunes and marshes, on abandoned fields and by retreating glaciers. Certain fast-growing **pioneer** plant species with good seed dispersal **colonize** when the new habitat is first available. These species modify the conditions both in the soil and in the biotic environment that allows other species to colonize. There may be a period of open herbaceous vegetation followed by shrubs or pioneer trees, eventually in many places leading to a community dominated by trees as the **climax** vegetation. The pioneer species are usually outcompeted by later colonizers, although some communities are halted at one point in this succession, e.g. by grazing animals. This description applies to a primary succession but, in a gap in a mature community, there is secondary succession involving new colonization by pioneer species. This is followed by changes in the plant community, though with less change in the soil conditions. This classic view of succession is simplistic, in that very often the climax community species are present early on, particularly in secondary succession. There is a large role of chance in how the succession progresses, and the end point may not always be the same or there may not be an end point as such. It does provide a clear illustration of some of the differences between plants in their ecology and an insight into the formation of plant communities.

Plants differ in their abilities to colonize and in their speed of growth and response to light and nutrients. There are plants which are specialist colonizers and do not persist in any one place but move around in a community. Secondary succession is happening continuously as trees or other dominant plants die or are blown over, or herbivorous mammals graze or uproot certain plants, creating gaps. In any gap some form of succession can take place and this will take a different form depending on the size and nature of the gap and the presence of any animals. There are pioneer species in all plant communities colonizing these gaps and any 'climax' plant community is in a dynamic state.

Dominance and diversity

Some plant communities are dominated by a single species, some by a small number and some appear to have no dominant species at all. The principle of **competitive exclusion**, developed in relation to microorganisms, states that if two species occupy the same ecological **niche**, defined as the total of all a species' requirements, one will outcompete the other; if they coexist some aspect of their lives, i.e. their niches, must differ. The definition of a plant's niche is not well worked out, but the life forms of plants (Topic M2) will, clearly, allow many species to coexist by occupying different parts of a community and, within each life form, there are many different requirements, e.g. for light-demanding and shade-tolerant trees. Despite this, by applying the competitive exclusion principle, one would expect most plant communities to have a dominant species within each major life form present, but this is only true under certain limited conditions. It is true for some communities on soils rich in nutrients, particularly in temperate zones. Although many plants thrive best under high nutrient conditions, competition is intense and one species may become dominant through faster growth or stronger competitive ability. Dominant plant species also occur in places subjected to an environmental stress, such as waterlogging or the presence of a normally toxic element. In most places, however, there is a diversity of species within each life form, this diversity increasing towards the tropics until, in many tropical rainforests, there are numerous species all apparently with similar requirements growing in the same plant community.

α, β and γ diversity

Diversity can be divided into three categories: α **diversity**, the diversity within one habitat or microhabitat; β **diversity**, that between habitats; and γ **diversity**, that between different geographical areas within one overall area, e.g. two mountains within one range. β diversity may include differences in subtle features such as particular nutrient rich patches in a poor soil, e.g. in an animal dung heap, or a small change in gradient, but it is easily comprehensible and, given sensitive equipment, straightforward to explain. γ diversity varies greatly, with some areas such as the Cape region of South Africa having a particularly high γ diversity and many species with a narrowly restricted distribution, probably owing to a combination of its varied topography and history. Other places, such as northern Europe, have low γ diversity.

α diversity is much harder to explain, beyond the differences in life form already mentioned. It probably arises from a combination of many factors. One of the most significant details is that, in many species, we rarely see the most vulnerable stage in a plant's life cycle, the period between germination and establishment. Plants can live for many years, some many centuries, so the existence of a group of individuals of one species may reflect conditions that applied several decades or centuries earlier. Communities are periodically disturbed, e.g. by freak weather conditions or by large animals, and germination conditions for any one species may only occur infrequently. Gap formation in any plant community is significant for the germination of most plants and which species establishes will depend on the size of the gap and how frequently gaps are formed as well as precise soil conditions. There must also be seeds of that species in position when favorable conditions appear, so chance must play a part. Plants are vulnerable to attack from herbivores, particularly insects, and diseases and pathogens such as fungi (Topics M3 and M4). This is well known in crop monocultures and will affect mostly abundant or dominant plants, and mostly at the young stages. Attack is likely to be periodic and may not be seen in a limited study period, but it will reduce the dominance by any one species.

A plant community will always be subject to change. The climate has changed markedly over the last million years with periodic glaciations of greater or lesser extent and more minor climatic fluctuations in any one area over a shorter time scale. These have given rise not just to cool and warm periods but, in the tropics, drier periods during glacial times and the rising and falling of sea level and, over a time scale of centuries, dry or wet periods and cool or warm ones. Plants have migrated north and south and across tropical land masses in response to the large changes and with smaller changes in community boundaries and local invasions and extinctions with the smaller changes. If we consider this with the long generation time of many of the dominant plants in a community, it suggests that many communities may be in a state of continuous succession, with the persistence of pioneer species for decades or centuries and the whole community not reaching any equilibrium.

All of the above factors probably affect the structure of a plant community to a greater or lesser extent and contribute to an explanation of the α diversity. In the most diverse environments in the world such as some tropical rainforests, there is high α, β and γ diversity.

Community definitions

Certain plants tend to grow together and form a community and these communities can be well defined, with clear boundaries in places. This is mainly true where people have modified the vegetation or where there are abrupt changes in soil conditions, e.g. at the edge of a woodland and pasture, or where limestone intrudes among acidic rocks. This has led to a classification of plant communities, particularly in Europe where these transitions are most clear. In many places there are gradual transitions from one community to another. These are best regarded as collections of species that happen to be able to exist under certain conditions but have different limits; the community as a whole is not a precise entity and its composition is changing continuously across its extent. All communities vary like this and classification is most useful within one limited geographical region. In most parts of the world the communities have not been classified except in broad terms.

K3 ECOLOGY OF DIFFERENT GROWTH FORMS

Key Notes

Variety of form	Plants can be mechanically independent and woody, i.e. trees or shrubs, or herbaceous. Mechanically dependent plants are climbers, epiphytes or stranglers. There are also parasites and saprophytes.
Ecology of woody plants	Trees dominate many terrestrial habitats where there is sufficient rain and a warm temperature for at least part of the year. These are mainly dicotyledons and conifers. Shrubs dominate heathlands and extend to the tundra as dwarf shrubs.
Herbaceous plants	These dominate the ground layer in many habitats, and grasslands are entirely dominated by them. Many in seasonal environments die down in the dry season or winter and some are short-lived.
Mechanically dependent plants	All these are most common in tropical rainforests and they depend mainly on trees for their support. Climbers include woody and non-woody forms. Epiphytes include some specialist families and are much less common in seasonal environments with only bryophytes occurring as common epiphytes in temperate climates.

Related topics Physical factors and plant distribution (K1); Plant communities (K2); Parasites and saprophytes (M6)

Variety of form

There is a great variety of growth forms of plants but they can be classified into a few main categories with different ecological characteristics. Most plants grow without any mechanical support and these may be **woody**, forming **trees** or **shrubs**, or they may be **herbaceous** without any woody parts. Trees and woody shrubs range from giants of over 100 m height to many-stemmed shrubs and some undershrubs that remain prostrate on the ground but retain their woody stems. Tree ferns, cycads and most palms have a single trunk with one enormous bud and leaf rosette at their tip, while other trees have a few branches, sometimes dichotomous (Topic Q1). A majority of the larger **mechanically independent** woody plants have a single main stem with side branches, though often flattening out to a domed crown in which there is no one dominant stem. Some woody plants, particularly shrubs, have underground rhizomes from which several woody stems grow, forming thickets.

Herbaceous plants are low-growing without lignified stems. Frequently, the above-ground stems are ephemeral and many in seasonal regions lose their above-ground parts during the dormant season. Some are short-lived (Topic K4). Many have rhizomes or stolons and spread vegetatively.

Mechanically dependent plants include **climbers** which can reach the tops of tall trees and may have woody stems. Other climbers persist without much secondary thickening and some in seasonal climates grow like herbaceous plants and die back each dormant season. **Epiphytes** grow attached to other plants, usually trees, by their roots or stems but not extracting nutrients directly from the supporting tree. These are light-demanding plants that obtain water and nutrients directly from rain and run-off along branches. **Stranglers** start life as epiphytes but send some roots to the ground to become partially or totally independent. **Heterotrophic** plants depend on other plants or fungi for all or part of their nutrients (Topics M6 and M7).

These growth forms have no direct relationship with plant classification, though some plant families are specialized to one particular form. Some growth forms include plants from widely different families and some plants are intermediate. Some individual species can adopt a different growth form in different conditions.

Ecology of woody plants

Trees dominate most ecosystems where the climate is warm and moist for at least part of the year. They cease to dominate where the soil is too thin for their roots, where it is too dry in deserts, where there is permafrost in tundra regions, in permanently waterlogged places, places dominated by salt or heavy metals and in many environments modified by people. They can live for a few years or decades to as long as a few thousand years setting seed most years, or only for a few years. The majority of woodland and forest ecosystems are dominated by **dicotyledonous angiosperms** except for the great **coniferous** forests of the northern hemisphere. Tree ferns, cycads and monocotyledonous trees may be common but are rarely dominant except occasionally in swamps or in colonizing situations. In many forests the trees form **strata**. They have a **canopy** layer, with taller **emergent** trees projecting through it in some rainforests, and **understorey** trees and shrubs often with more than one layer. Different species of tree are frequently involved, with the shade-tolerant species forming the understorey and faster growing canopy trees being more light-demanding, though there is overlap, with saplings of larger trees present in the lower layers. At the edges of forests and where there is a gap, other **pioneer**, fast-growing species grow.

Shrubs and smaller woody plants occur at the edges of many forests and dominate ecosystems in the arctic regions and in some deserts where the environment is too harsh for trees. **Heathland** is dominated by low-growing shrubs mostly less than 1 m high as well as some arctic shrubs, such as willows (*Salix* spp.), rising no more than 1 cm above ground level having all their woody parts below ground.

Herbaceous plants

Many herbaceous plants in seasonal environments die down at the end of each growing season leaving only their roots and sometimes leaves to survive until the following season. These plants, along with small shrubs, form the **ground layer** in many habitats, and dominate in **savannahs**, **temperate woodlands** and **grasslands** throughout the world. Some herbaceous plants persist above ground, particularly in less seasonal areas but these mostly remain less than about 3 m tall. Those that live for less than a year are the quick colonizers of newly opened areas or take advantage of the rare rains in deserts to grow quickly to set seed before unsuitable conditions return.

Grasses are all herbaceous, except for the bamboo group, and they are particularly well adapted to withstand grazing pressure since they have growing meristems at nodes rather than at the tip, and produce stems above these nodes. They frequently dominate in places with intense grazing pressure, and those that have meristems below the soil surface can withstand fire.

Mechanically dependent plants

Climbers, epiphytes and stranglers all require the presence of other plants, normally trees, for their growth and all are much more abundant in tropical rainforests than elsewhere. Climbers occur throughout woodland habitats with many woody climbers (**lianas**) in **tropical forests**. Many fewer occur outside tropical rainforests but most temperate woodlands have some, e.g. *Clematis* spp. Herbaceous climbers can be small and occur throughout the world, some persisting in grasslands. In tropical rainforests, some of the tallest climbers do not produce woody stems, or only a little secondary thickening, e.g. members of the arum family, Araceae.

Epiphytes are dependent on a high rainfall since they only get water from it and run-off along branches. They are abundant in tropical forests. Many ferns and members of certain families, notably the orchids, Orchidaceae, and bromeliads, Bromeliaceae, are specialist epiphytes but many other families are represented. Tropical mountains have a particularly abundant epiphyte flora. Epiphytes are common in parts of the seasonal tropics but become much rarer and less diverse in drier climates. In temperate regions epiphytic flowering plants only occasionally occur, although there are a few ferns. Bryophytes are abundant epiphytes in the wet tropics, even occurring on the leaves of rainforest trees. They are the only common epiphytes in temperate woodlands, along with lichens. In tropical rainforests some epiphytes are shrubby, producing woody stems and some of these develop roots which reach the ground to become independent. The figs (*Ficus* spp.), are the most prominent of these **stranglers** and can become self-supporting, killing the tree on which they started life.

The mistletoes (two families, Loranthaceae and Viscaceae) and a few other plants are epiphytic in growth form but are partial parasites, penetrating their hosts and extracting nutrients and sugars. They are considered with other heterotrophic plants in Topic M6.

K4 Populations

Key Notes

Plant life cycles

Plants may live for a few weeks to thousands of years; reproduce once and die or reproduce many times. Semelparous plants reproduce just once, after a few weeks (ephemerals) or over a year (biennials) to many years (semelparous perennials). Iteroparous plants reproduce many times and some of these produce rhizomes and spread clonally.

Ecology of ephemeral plants

These occur everywhere but are common in temperate climates and deserts. Many have seeds that can remain dormant for many years and their numbers often fluctuate markedly between years. Many temperate species have small self-fertilizing flowers.

Biennials and semelparous perennials

Biennials are opportunist plants, often with seeds that can be dormant, living in successional habitats mainly in the temperate zone. They produce showy flowers. Life cycles are flexible and they live longer if damaged. Semelparous perennials live in conditions where growth is slow or where swamping seed predators is important.

Iteroparous perennials

These range from short-lived herbaceous species similar to ephemerals to long-lived trees. They dominate most stable habitats and, in any one place, the dominants often have individuals all of similar age owing to cyclical changes in the plant community. Some spread clonally, particularly herbaceous plants on woodland floors and in wetlands.

Timing of reproduction

Early reproduction is often an advantage but iteroparous perennials are at an advantage if there is high seedling mortality.

Population dynamics

There are many hazards in a plant's life cycle, but all populations have the potential to increase exponentially, the rates depending on birth rate, death rate, immigration and emigration. If plants grow above a certain density, over time density-dependent mortality occurs, known as self-thinning. This can be described mathematically with the –3/2 power law which is constant for many plants. There is often great variation in size within a population and small plants die first.

Populations of clonal plants

A 'population' of a clonal plant can be one genetic individual. Clonal plants can regulate their own shoot density although sometimes shoots compete. Growth behavior differs in different environments and they can exploit rich patches effectively while crossing less favorable ones. The disadvantage of clonal growth is mainly disease susceptibility.

Related topics

Regeneration and establishment (L3)

Polymorphisms and population genetics (L4)

Plant life cycles

A complete life cycle of a plant, from germination through its reproductive life to death, varies from about 3 weeks to several thousand years. Plants may be divided into those that flower and set seed once in their lives, known as **semelparous** or **monocarpic**, and those that reproduce more than once, known as **iteroparous** or **polycarpic**. Semelparous plants may live for a few weeks or for many years. Short-lived ones are known as **ephemerals** or, commonly, **annuals**, although most complete their life cycle in much less than a year, and the shortest-lived, such as *Boerhavia* spp. (Nyctaginaceae) may complete their life-cycle in less than 4 weeks. Those that live longer than a year are mostly known as **biennials**. These normally grow as a leaf rosette in their first year, flowering and dying in their second. Longer-lived semelparous plants are rarer but some of these have leaf rosettes of ever increasing size over several years, such as the century plants, *Agave* spp. (Agavaceae), which usually live for 15–70 years rather than a century. Some are woody, notably some bamboos which can flower after 120 years, and the royal palm, *Roystonea*, which can live for 80 years and reach 30 m before flowering and dying. Those that live for more than about 3 years are known as **semelparous perennials**.

Iteroparous plants range from those that live for just a few years and normally flower less than five times to some of the longest-lived of all organisms such as the huon pine, *Dacrydium franklinii*, in Tasmania and the bristlecone pine, *Pinus aristata*, in Arizona, both of which can live for over 4000 years. Living creosote bushes, *Larrea tridentata* (Zygophyllaceae), of the deserts of western USA may be even older, over 11 000-years-old, spreading clonally from a central source. Nearly all woody plants are iteroparous.

All plants have meristems and if shoots remain vegetative they have indeterminate growth, i.e. continue to grow throughout their lives, remaining 'forever young'. Many have developed underground rhizomes or stolons which grow continuously and can form large patches or grow a long way from where they first germinated. These produce roots as they grow and the plant can then be split to form independent physiological units. These clones, or parts of them, can live for many centuries and the definition of an individual becomes obscured since a genetic individual and a physiological individual become different. Clonal spread is frequent among herbaceous perennials, less so among woody plants.

Ecology of ephemeral plants

These occur in most plant communities but are common in deserts, regions with a Mediterranean climate of cool wet winters and hot dry summers, agricultural and disturbed land and places with unstable soils like sand dunes. In mature plant communities such as woodlands and permanent grasslands they are mainly associated with disturbed areas, e.g. from animal digging or tree falls. Some will germinate at almost any time of year and desert ephemerals germinate in response to a substantial fall of rain. There is a group of 'winter annuals' in temperate climates that germinate in the fall and flower and set seed in the spring before the summer drought. In many ephemerals, generations of adult plants do not overlap, but they may have seeds that can remain dormant for a long period so seeds from different years may germinate together. Some appear to rely on each year's seed crop and have limited dormancy. Many ephemerals in temperate zones are small plants with small flowers that can self-fertilize, but among desert ephemerals there is great variation and many have large colorful flowers. Most populations of ephemeral plants fluctuate markedly from year to year.

Biennials and semelparous perennials

Biennials are opportunist plants, like the ephemerals, and many have long-lived dormant seeds. They occur in early successional stages where a mature habitat such as a woodland or grassland has been disturbed from tree falls for example, or at the edges of grasslands, mainly in temperate climates. They do not occur on agricultural land in general. Frequently the life cycle is flexible and a normally biennial plant can perennate (i.e. live for longer and flower a second time) if its flowers or fruits are eaten or damaged. Frequently the flowers are produced in showy inflorescences attractive to flower-visiting animals, this being especially true for those plants that live for longer than a year before flowering. By the time they flower, the place they are occupying is often not suitable for the next generation so the seeds must disperse or lie dormant.

Some semelparous perennials are associated with regions where growth is restricted such as deserts or tropical mountains; others such as the bamboos are thought to reproduce once so that the huge numbers of seeds produced will swamp any potential predators. Frequently in these species all the plants in an area will flower synchronously.

Iteroparous perennials

These range from short-lived pioneers that behave in a similar way to ephemeral and biennial species through to long-lived species with much more stable populations. The dominant species in most communities are long-lived non-clonal species, such as most trees and many of the dominant plants of open areas. The adult plants of the dominant species in some communities are of similar age where there is some kind of cyclical change and the main germination is at a time when the area is more open, through a natural disaster. Understorey trees and other plants in a woodland, by contrast, normally have a wide range of ages including many seedlings and saplings often with smaller numbers of adults.

Clonal species dominate certain habitats, particularly wetlands and woodland floor habitats, and one genetic individual can cover a large area, even an entire habitat. The vegetative branches, or **ramets**, can utilize the resources of the mother plant as they grow and this gives them a huge advantage in establishing themselves over non-clonal plants that rely on new seedlings.

Timing of reproduction

In general, it will be selectively advantageous for a plant to reproduce as early as possible. This will often lead to maximal population growth, e.g. if a plant produces 10 seeds after 1 year and then dies, the following year each of those 10 seeds can grow and produce 10 seeds, so any plant that delays reproduction until the second year will need to produce 100 seeds to equal the potential output of one reproducing in its first year. Although this does not take into account mortality at any stage, which is likely to be different for seeds and established plants, the potential advantage of reproducing early is clear and ephemerals are thought to be among the most advanced of plants. Ephemeral plants put most of their resources into reproduction, but an iteroparous perennial needs to retain some resources for its own survival so seed production is likely to be less. To determine which is at an advantage the survival of seedlings (pre-reproductive) and of adults must be taken into account. We can say that for an ephemeral plant:

$$\lambda_e = cm_e$$

where λ_e is the rate of increase, c is the seedling survival and m_e is the mean seed production.

For an iteroparous perennial:

$$\lambda_p = cm_p + p$$

where p is the adult survival.

We can derive from this that an ephemeral plant will reproduce faster if $m_e > m_p + p/c$. This indicates that one of the important terms is the ratio between adult survival and seedling survival (p/c): if there is good seedling survival it will be advantageous to be ephemeral; if seedling survival is poor an iteroparous perennial will be at an advantage. Studies have confirmed that this is largely true.

Population dynamics

There is often high mortality of the seeds, and there may be many natural hazards before they can germinate, such as seed-eating animals, rain and wind. After germination, the main competition occurs during active growth to flowering, and this is likely to involve competition with associated plants as well as members of the same species. After this an established plant faces many fewer hazards, so the greatest selection is likely to be in the seedling stage. In general, plants live in populations in the same way as animals, with birth rates, death rates, immigration and emigration. Any change in that population must take these into account and this can be expressed by this **basic equation** of population change:

$$N_{t+1} = N_t + B - D + I - E$$

where N_t is the number at time t, B is number of births, D number of deaths, I is immigration, E is emigration. When $B + I = D + E$ the population is stable, but when $B + I > D + E$ the population will increase **exponentially**, i.e. increasing by the same factor each year, giving a logarithmic growth curve (*Fig. 1*). This has been recorded when a plant is colonizing a new area. Clearly this rate of increase can only continue for a short period after which the population will be regulated by some finite resource such as germination sites or nutrient availability.

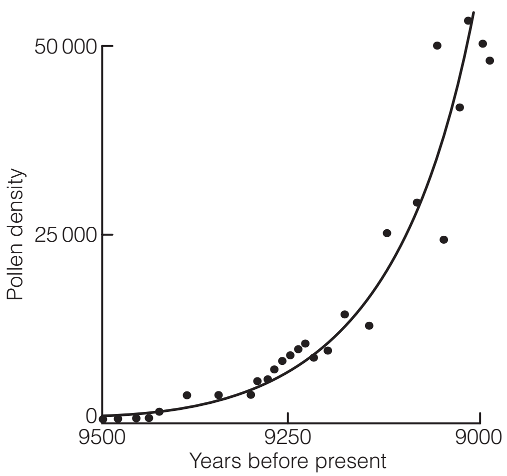

Fig. 1. Exponential increase in the population of the scots pine, Pinus sylvestris, *in Norfolk, UK, from pollen records in peat deposits (Redrawn with permission from Bennett, K.D.,* Nature *1983;* ***303****, 164–167. Copyright 1983 Macmillan Magazines Limited).*

As density increases the plants may start to interact with each other, limiting each others growth. This may be manifest in smaller plants and/or lower seed set, particularly in small ephemerals, but with longer lived plants some will die before reaching maturity. This is most obviously seen in trees where seedlings can cover the ground but there is fewer than one mature tree per 10 m^2. There is a process of **self-thinning**. The idea has been best developed in relation to crop plants and their yields since farmers will want to sow a crop to reach maximal yield while minimizing seed wastage. Experimentally, it was found that mortality started earlier, and at a smaller weight with denser sowings. If the relationship between sowing density and mean weight is plotted using a log scale on both axes the lines converge on a straight line (*Fig. 2*). This line has a slope of approximately –3/2 for many unrelated plants (including trees) and can be described by the equation:

$$\log w = c - 3/2 \log N$$

where w is mean plant weight, c is a constant, N is plant numbers. This is known as the **–3/2 power law**. In sparse populations interaction between individuals will be less and the slope of the line will flatten out, until it reaches 0 when there is no **density-dependent** interaction. Although this slope is remarkably constant across plants, the c value varies hugely. This is the intercept term on the y axis, i.e. the density at which there is no interaction between individuals, clearly totally different for a small ephemeral and a tree. There are other factors that influence numbers of plants that are dependent on the density of the population, such as disease and herbivore attack. Their effects are often intermittent and they are much harder to study than competition, but they can be equally or more important in determining population density (Topic O3).

If a population of a large plant such as a tree starts out at high density, over time there will arise a marked size difference between the largest and the smallest individuals, and the smallest will be the first to die in the self-thinning

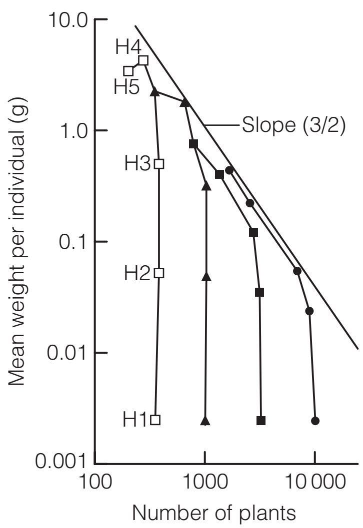

Fig. 2. Self-thinning in four populations of rye-grass, Lolium perenne, *planted at different densities. There were five successive harvests to give these lines (Redrawn from Kays S & Harper JL,* Journal of Ecology *1974:* ***62****, 97–105).*

process unless some other influence intervenes. Initial size difference may arise from slightly different germination times or genetic differences between individuals in their vigor of growth but this will be accentuated by competition once they start interacting.

In general, a plant population is affected by many processes that are **independent** of a plant's density such as frosts or floods at particular times and in density-dependent interactions with members of its own and other species.

Populations of clonal plants

Plants that spread **vegetatively** can regulate the density of their own shoots, although there can be competition between shoots as described for non-clonal species. An entire 'population' can be made up of just one genetic individual and this may be true of a hillside covered with bracken, *Pteridium aquilinum*, or a reed bed dominated by *Phragmites australis*. Clonal plants may grow densely to dominate an area or as long strands invading new places, and these invaders can tap the resources of the mother plant giving them a great advantage over seedling invaders. The invaders can change their '**behavior**' (in a plant, behavior means changes in growth form) in response to local conditions, growing densely where there are many nutrients, but sparsely between rich patches.

There appears superficially to be such a great advantage to clonal spread that it is surprising that, although it is common, more plants do not spread this way. The main disadvantage lies in the fact that clones are all identical genetically. This leaves them susceptible to insect attack or disease since, if a predator or pathogen can overcome the resistance of one member of the clone, all will be susceptible. This was shown graphically in Europe in the 1970s with the outbreak of elm disease attacking all the clonal elm species, e.g. *Ulmus procera*, but only some individuals of the mainly non-clonal *Ulmus glabra*. In agriculture, clonally produced crops require greater uses of pesticides.

K5 CONTRIBUTION TO CARBON BALANCE AND ATMOSPHERE

Key Notes

Global carbon dioxide	Carbon cycles between gaseous forms like CO_2 in the atmosphere and forms in which it is fixed, for instance in living organisms. Higher plants have a major role in removing carbon dioxide from the atmosphere. Global atmospheric CO_2 concentration was about 190 ppm at the end of the last ice age, but it has risen to 375 ppm today. Burning fossil fuels and widespread destruction of forests are responsible for this increase.
Global warming	Rising global atmospheric CO_2 concentration has resulted in increased mean surface temperatures on earth (about 0.5ºC over 50 years) as CO_2 absorbs some infra red radiation. Altered weather patterns are more significant to plants than small changes in average temperature.
Plants and rising carbon dioxide	C3 plants are limited by CO_2 levels, and growth rates in at least some species increase with increased CO_2. In natural communities, growth is limited by other factors such as nutrient availability. C4 species are not likely to show enhanced yields with rising CO_2, as they do not show photorespiration and have a much lower CO_2 compensation point. Plants reduce atmospheric CO_2 by fixing carbon; however this only decreases global atmospheric CO_2 concentrations if the plant material is not degraded to release CO_2 to the atmosphere.
Global climate and biodiversity	Altered weather conditions will affect sensitive biomes and species at the limit of their distribution. Unless a species can adapt to a changed environment or migrate to less hostile areas, it will become extinct. This is particularly likely to be true of long-lived tree species.
Related topics	Major reactions of photosynthesis (J2) C3 and C4 plants and CAM (J3)

Global carbon dioxide

Figure 1 illustrates the global carbon cycle. Carbon cycles between 'fixed' forms (organic carbon and carbonates) and the atmosphere (e.g. as CO_2). Significant pools of carbon are present in the atmosphere, the oceans, soils and land plants. A very large amount also exists in carbonate rocks and in buried fossil fuels. Plants play a vital role in this cycle by fixing carbon from the atmosphere. At the end of the last ice age, about 18 000 years ago, the global atmospheric CO_2 concentration was about 190 ppm (parts per million). Since then it has risen, reaching about 250 ppm in the 1700s to 375 ppm today; and it continues to rise (*Fig. 2*). This rise has been largely attributed to the burning of fossil fuels and the destruction of forests. Carbon is removed from the atmosphere when living organisms die and are preserved in deposits of coal, oil, peat and other sediments. It is also deposited as calcium carbonate minerals, including the exoskeletons of living organisms. As large amounts of the world's carbon

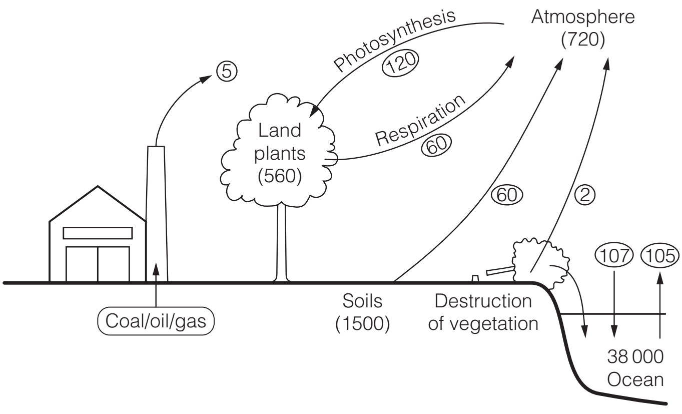

Fig. 1. A global carbon cycle. Pools of carbon are expressed as 10^{15} g of carbon and fluxes as 10^{15} g year^{-1} of carbon.

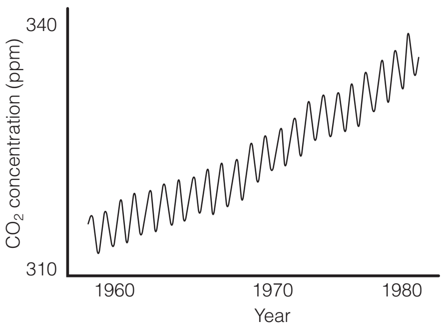

Fig. 2. Mean monthly atmospheric CO_2 concentrations measured at Muana Loa, Hawaii. (Data obtained from the National Oceanic and Atmospheric Administration (NOAA), Climate Monitoring and Diagnostic Laboratory (CMDL), Carbon Cyde-Greenhouse Gases, Boulder, CO, USA.)

deposits are extracted from the ground and burned, large amounts of CO_2 are released to the atmosphere. Destruction of forests reduces fixation of CO_2 and gives further CO_2 release.

Global warming

Rising global CO_2 levels have a number of consequences, the chief of which is a net rise in global temperature. Solar radiation travelling through the earth's atmosphere is partly reflected back into space by the earth's surface and clouds; however, CO_2 in the atmosphere absorbs some of the infra-red radiation which would escape. This makes the earth warmer; the degree of warming increasing with more CO_2. While it is very hard to estimate precisely the degree of warming experienced as a result of rising CO_2, and the presence of other greenhouse gases such as methane may be very significant, a rise of about 0.5ºC in global mean surface temperature has occurred over the last quarter century. Altered average temperatures have been accompanied by more extreme weather changes. These include earlier and later frosts and heavier rainfall in some areas and drought in others. With drought comes the possibility of fire and these have been widespread, particularly in the Asia/Pacific region. Rising sea level accompanied by melting ice-shelves in the Arctic and Antarctic are also consequences of global warming. World sea levels have risen by more than 10 cm in the last century and their continued rise will result in losses of coastal land and island communities.

Plants and rising carbon dioxide

At present, photosynthesis in C3 plants (Topic J2) is limited by CO_2 levels and growth rates in at least some species increase if CO_2 concentrations are increased. Growth rates may increase by 30–60% if CO_2 concentrations are doubled, but this may only be temporary as growth and development are regulated in other ways (Topic F1). In natural communities, growth is likely to be limited by other factors such as nutrient availability. Yields of some glasshouse crops, such as tomato, have been increased by enriching the air around them with CO_2. C4 species (Topic J3) are not likely to show enhanced yields with rising CO_2, as they do not show photorespiration and have a much lower CO_2 compensation point (Topic J3). *Figure 3* illustrates net photosynthetic rates of a C3 plant (e.g. wheat) and C4 plant (e.g. maize) at different CO_2 concentrations but otherwise optimal environments. While the C4 plant is more efficient at current global CO_2 concentrations of around 360 ppm, this efficiency advantage will diminish and eventually C3 species will exceed C4 in efficiency if CO_2 concentrations continue to rise.

While in the short term, plants reduce atmospheric CO_2 by fixing carbon, in the long term this only decreases global atmospheric CO_2 concentrations if the plant material is not burnt or rotted, processes which release CO_2 to the atmosphere (*Fig. 1*).

Global climate and biodiversity

Overall, the impact of changing climate is likely to be greater than direct effects of CO_2 concentration. While crop yields may increase in optimal environments, losses due to drought, flooding, sea level increases and disease will also increase. Plant communities will be changed as the competitive abilities of some species increase while others decline. Biomes likely to be sensitive to climate change include tundra (loss of permafrost); savannah and deciduous tropical forests (drought and fire) and deserts (rising temperatures). Other biomes, like tropical rain forests, are at risk from both human activity and drought. If a species is to survive, it must either adapt to its new surroundings or migrate through seed dispersal at a rate equal to that of climate change. For many long-lived species this may not be possible and they may become extinct.

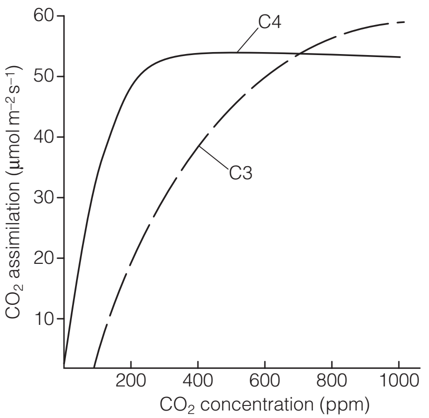

Fig. 3. Photosynthetic responses of a C3 plant and a C4 plant to rising CO_2 concentrations under experimental conditions. Atmospheric CO_2 concentrations are >360 ppm and increasing by about 10 ppm every 10 years.