

PHYSIOLOGY AND BEHAVIOUR OF PLANTS

Peter Scott

University of Sussex



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*This book is dedicated
to Helen and Edmund Scott,
whose love and support through
many plant hunts made this work possible.*

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Preface

We live in an age where we are more dependent upon our understanding of plants than ever before. With the world human population exceeding 6 billion, never has it been more important to be able to feed reliably so many people. Yet, paradoxically, it is an age when interest in plant biology is at an all-time low. The plant biology content of GCSE and A level biology in the UK has become minimal as more and more human biology is added to the curriculum. Funding of plant science research has become minuscule compared to that commanded by the medical sciences. As a consequence, universities employ fewer plant biologists and as a knock-on effect plant biology is scarcely offered as part of a biology degree any longer. Where plant biology is offered, the lecture material can be badly handled and few students are prepared to study it into their final year. But plant biology has to be one of the most interesting subjects in the whole of biology. Plants are central to life and play a crucial role in dictating the diversity of life we currently enjoy on this planet.

To address this problem, what is not needed is another plant physiology textbook. There are many volumes which do the job of teaching plant form and function very well. But what often comes across in these texts is that plants are stale and irrelevant. Somewhere, the interest, appeal and relevance to the real world has been lost in the detail. If you don't think this is true, then look no further than the most amazing enzyme of plants, RUBISCO. Most books dive into the sub-unit arrangement and its

carboxylase/oxygenase properties, but there is nothing to impress the reader that we are discussing the enzyme that supports virtually all of life currently on this planet! RUBISCO is the marvel enzyme of the universe, and yet most students never realize this. Then consider photosystem II, a complex enzyme which splits water to provide an electron donor for a chlorophyll molecule and allows non-cyclical photophosphorylation – but the fact that it generates all of the oxygen we need to breathe and supports the only other known biological autotrophic pathways known in bacteria is lost. So what is, on the face of it, merely a tricky biochemical pathway, suddenly becomes a vital component of our everyday life. Plant biology is amazing in so many ways that this book barely scratches the surface. Having said that, the most interesting and remarkable topics on plant biology have been hand-picked to give students the best chance possible to study plants in all of their glory. The book deliberately steers clear of in-depth discussion of molecular biology and the explosion of knowledge this is providing. This is because much of this knowledge is incomplete and as yet does not give an interesting insight into the mechanisms of plant life. Where molecular mechanisms are discussed, they are always related to the whole plant function, as this is primarily what the text is concerned with – plants.

Peter Scott
July 2007

1

Introducing plants

In this chapter, we look at how plants originated, what floral diversity there is today and the make-up of the plant and its ultrastructure.

The beginning: the evolution of plants and the major divisions

In the beginning, it is most probable that plants evolved from photosynthetic bacteria. From these bacteria the red and green algae evolved; and from freshwater-dwelling green algae the simple lower plants, such as mosses and ferns, evolved; and so on, up to the higher plants. A phylogenetic tree is shown in Figure 1.1 and Table 1.1 to demonstrate the relationship between the members of the plant kingdom and their relative abundance through the history of the planet.

Conquering the land

The origin of plants was in water, where both photosynthetic bacteria and then algae originated. Light penetration of water reduces with depth, and on average only 1% of incident light reaches to a depth of over 15 m. As a consequence, there is a body of water at the surface known as the photic zone, where all of the photosynthetic activity in oceans occurs. A great deal of this photosynthetic activity still occurs at the shores of the oceans, where more complex algae have evolved; as a group these are commonly referred to as seaweeds. Algae are restricted to the oceans and freshwater bodies since, as part of the life cycle of algae, gametes (sex cells) that swim through water are required for sexual reproduction. This is thought to have been a major hindrance to plants attempting to colonize the land surface of the Earth and to overcome this, new reproductive systems needed to evolve.

For the colonization of the land, methods of gamete transfer that were independent of water needed to evolve. Bryophytes (the mosses and liverworts), the first land-dwelling plants, still depend on moisture to complete their reproductive cycle (Figure 1.2). Sperm is released from haploid male gametophytes (a gamete-producing individual involved in the life cycle of bryophytes) which must swim to fuse with the egg cell of the haploid female gametophyte. This fusion yields a diploid zygote that divides to form a stalked cup-like structure, which releases haploid spores. These spores then form haploid male and female gametophytes. As a direct consequence of this life cycle and its requirement for water, mosses and liverworts are restricted to growing in moist habitats. In addition, these plants have no waterproof cuticle or vascular tissue, and are therefore very limited in their ability to transport water and carbohydrate made during photosynthesis to the rest of the plant. This makes it necessary for these plants to have a prostrate growth habit (rarely exceeding 2 cm in height), colonizing banks near to areas of water. Bryophytes do possess root-like structures known as rhizoids, but these are thought to have a function of anchorage rather than for transporting water to the aerial tissues. As a result of their inability to regulate water in the plant, bryophytes are poikilohydric; therefore, if the moisture declines in their habitat it also begins to decrease in their tissues. Some mosses can survive drying out but others need to be kept wet to survive. However, the ability to tolerate temporary drying of a habitat is a first step to colonizing dry land.

The mosses exhibit little ability to control water loss and if plants were ever to colonize a greater area of the land, the non-vascular plants needed to evolve solutions to this problem by developing a water transport system and a means of regulating water loss from the plant surface. The hornworts possess stomata on their leaf surfaces and therefore took the first steps to regulating water loss while maintaining gaseous exchange, which is essential for photosynthesis. These structures are absent in the mosses

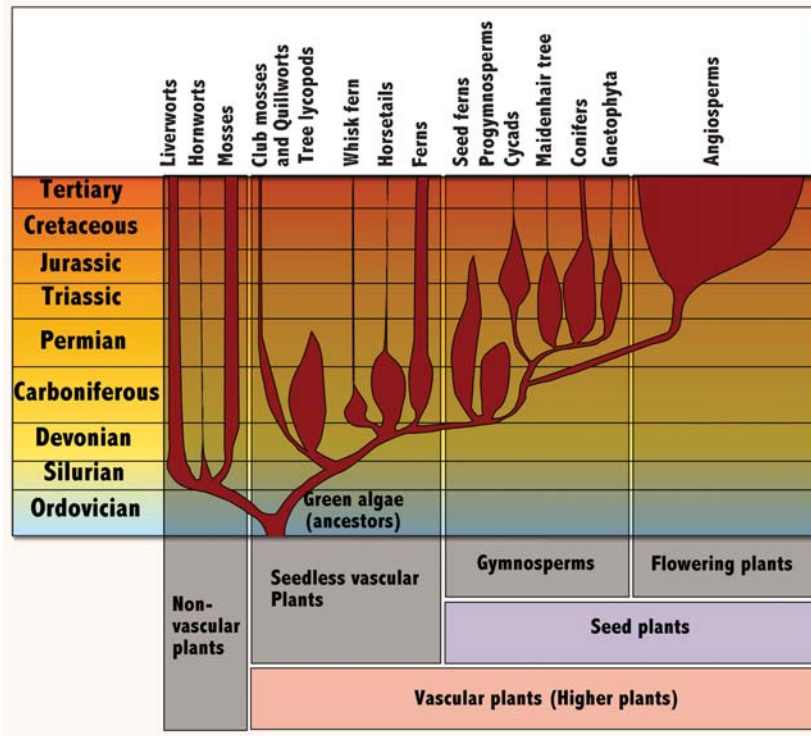


Figure 1.1 Schematic diagram of the phylogeny of plants. The diagram shows the evolutionary relationship between the different species and the relative abundance in terms of species numbers (shown by the width of the dark red lineage tree). On the y axis the different time periods of the evolutionary history of plants are shown. The diagram is based on that presented by Ridge 2002.

Table 1.1 Estimates of numbers of species occurring in plant divisions.

<i>Plant division</i>	<i>Common name</i>	<i>Approximate number of species</i>
Hepatophyta	Liverworts	6000
Anthoceroophyta	Hornworts	100
Bryophyta	Mosses	10 000
Lycophyta	Club mosses and quillworts	1000
Tree lycopods		Extinct
<i>Psilotum</i>	Whisk fern	3
<i>Equisetum</i>	Horsetail	15
Pterophyta	Ferns	11 000
Peltasperms	Seed ferns	Extinct
Progymnosperms		Extinct
Cycadophyta	Cycads	140
Ginkophyta	Maidenhair tree	1
Coniferophyta	Conifers	550
Gnetophyta	Vessel-bearing gymnosperms	70
Angiosperms	Flowering plants	235 000

These estimates are based on there being around 260 000 different species of plant in the world. Species of plants based on data from Ridge 2002.

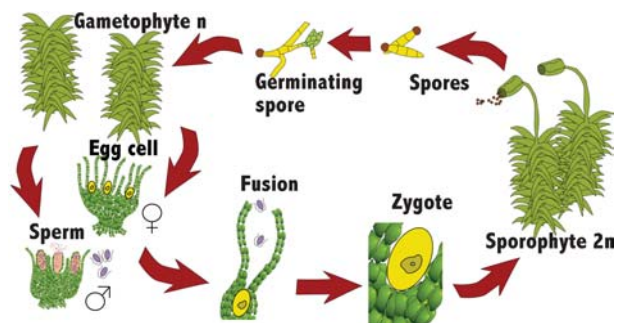


Figure 1.2 The life cycle of a bryophyte (mosses). There are around 10 000 different bryophyte species. The life cycle of bryophytes occurs in two phases, the sporophytic phase and the gametophytic phase. In the sporophytic phase the plant is diploid and develops as sporophyte. This releases spores which form gametophytes that are haploid. These form into separate sex gametophytes. The male gametophyte releases sperm, which is motile and swims towards the archegonium on the female gametophytes that bears the egg cells. These fuse to yield a zygote that then forms the sporophyte.

but present in more advanced plants. The prostrate growth of the mosses does not use light effectively and makes the damp habitat very competitive. As a consequence, there must have been a great selective pressure for structures to evolve in plants which raised the plants off the ground, which will have led to the evolution of a limited upright shoot in the bryophytes.

The evolution of the pteridophytes (ferns) marked the development of a simple vascular tissue, allowing long-distance transport of water and carbohydrate around the plant. It also permitted the evolution of the upright shoot, thereby making taller plants possible. Ferns use a method for sexual reproduction similar to that of mosses (Figure 1.3). The adult fern plant is diploid and releases haploid spores, which divide and form male and female gametophytes. The male releases haploid mobile gametes, which swim and fuse with the female gametes to form diploid zygotes, which then divide to form the adult ferns. Pteridophytes possess distinct leaves, which enhance their ability to photosynthesize. Although the pteridophytes possess a water-resistant cuticle, they exhibit poor control of water loss from their leaves and in most instances are still restricted to moist habitats. The spores released by the adult ferns are tolerant of desiccation but movement of the male gamete still requires water. The ferns were the first plants to evolve lignin as a defence and support structure (see later). Plants that contain vascular tissue are frequently referred to as 'higher plants'.

A small number of ferns and lycophytes exhibit heterospory (separate sex spores). In bryophytes and

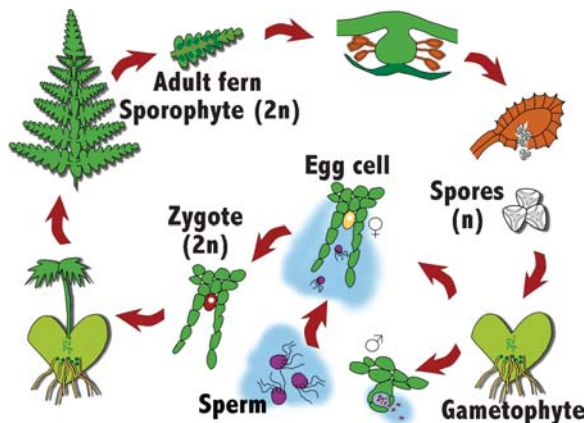


Figure 1.3 The life cycle of a pteridophyte (ferns). The adult fern, or sporophyte, is diploid and on maturity releases spores from sori on the underside of leaves. These spores fall to the soil and germinate and form a gametophyte, also known as a thallus. This matures and forms an archegonium (where egg cells form) and an antheridium (where the sperm develops). The sperm are released and swim to the egg cells, with which they fuse to form diploid zygotes. The zygote then develops into an adult fern.

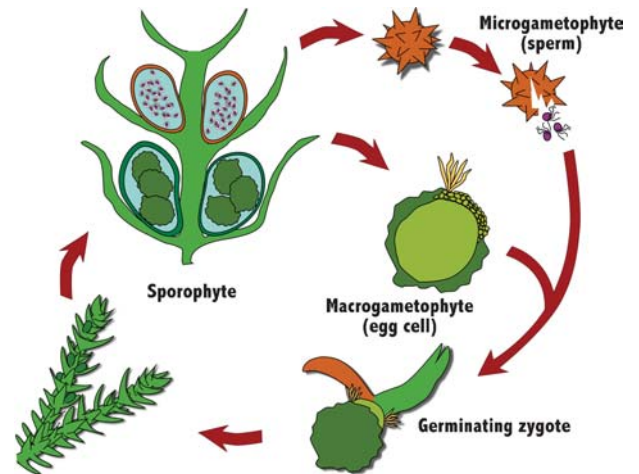


Figure 1.4 The life cycle of a heterosporous pteridophyte. In a small number of instances species of ferns are heterosporous and this is thought to be a crucial evolutionary step in the formation of the flowering plants. In Figure 1.3 the egg cell and the sperm are the same size, but in heterosporous pteridophytes, the female gamete (macrogametophyte) is much larger than the male gamete (microgametophyte).

pteridophytes discussed so far, the spores are all identical. However, with heterosporous species the male sperm are formed from a microgametophyte and the female gamete from a macrogametophyte (Figure 1.4). The formation of separate sex gametophytes is considered to be one of the major steps towards the formation of plants that bear seeds.

The habitat range of plants on land was widened considerably with the evolution of plants that produce seeds. The transition from being wholly aquatic to wholly terrestrial is considered complete in such plants. The seed-bearing plants are divided into two divisions, the gymnosperms (Pinophyta) and the angiosperms (flowering plants, Magnoliophyta). The angiosperms form the largest and most diverse plant division. Angiosperms produce reproductive structures in specialized organs called flowers, where the ovary and the ovule are enclosed in other tissues. The gymnosperms do not form a flower and the reproductive structures are in the form of cones, in which the ovule is not enclosed at pollination. On formation of a seed, the embryo is covered by a specialized scale leaf rather than the ovary and this gives rise to the name 'gymnosperm', which means 'naked seed'. Gymnosperms were widespread in the Jurassic and Cretaceous periods of the Earth's history but there are now fewer than 800 different species. They occupy a range of different habitats from temperate forests to more arid habitats. Most of the species are trees and shrubs, which are adapted very well to temperate areas of the world, where water availability is limited over extensive periods of the year (due to ground frosts).

Species such as pines are well adapted to cold climates through features such as small needle-shaped leaves (which hold little snow and are resistant to weather damage), sunken stomata (which reduce water loss) and a thick waxy cuticle. There are a few examples of gymnosperms which live in desert habitats, such as *Welwitschia*, and in tropical habitats, such as the cycads, but these species are limited in number.

The gymnosperms were once the dominant division of plants on Earth, but in the Cretaceous period there was a huge expansion in the number of angiosperms, which led to the steady decline of gymnosperms. The failure of gymnosperms to maintain the dominant position appears to be the result of improvements in reproductive biology in the angiosperms. Gymnosperms use wind as a means of transferring pollen from the male cones to the female cones (Figures 1.5 and 1.6). The use of air currents for pollination will be discussed in greater detail in Chapter 9, but suffice it to say here that this process is inefficient and wasteful of

resources. Moreover, gymnosperms rely mainly on the scale leaf around the seed to disperse it, with a few species such as yews using primitive fruits to attract animals. Angiosperms, however, evolved a huge range of different methods for attracting insects and animals for flower pollination and for the subsequent seed dispersal. The evolution of broader leaves may have been a disadvantage in colder climates, but everywhere else this allowed increases in efficiency of photosynthesis and hence growth rates.

Although gymnosperms are not as successful as angiosperms, they still have an important place in the ancestry of the flowering plants. Most of the structures thought of as typical in flowering plants can be found in individuals of the gymnosperms, but no species contains them all. The closest relative to the gymnosperms is thought to be the phylum Gnetophyta, which contains species such as *Welwitschia mirabilis* and *Ephedra viridis* (see Chapter 19). Angiosperms first appear in fossil records in the early

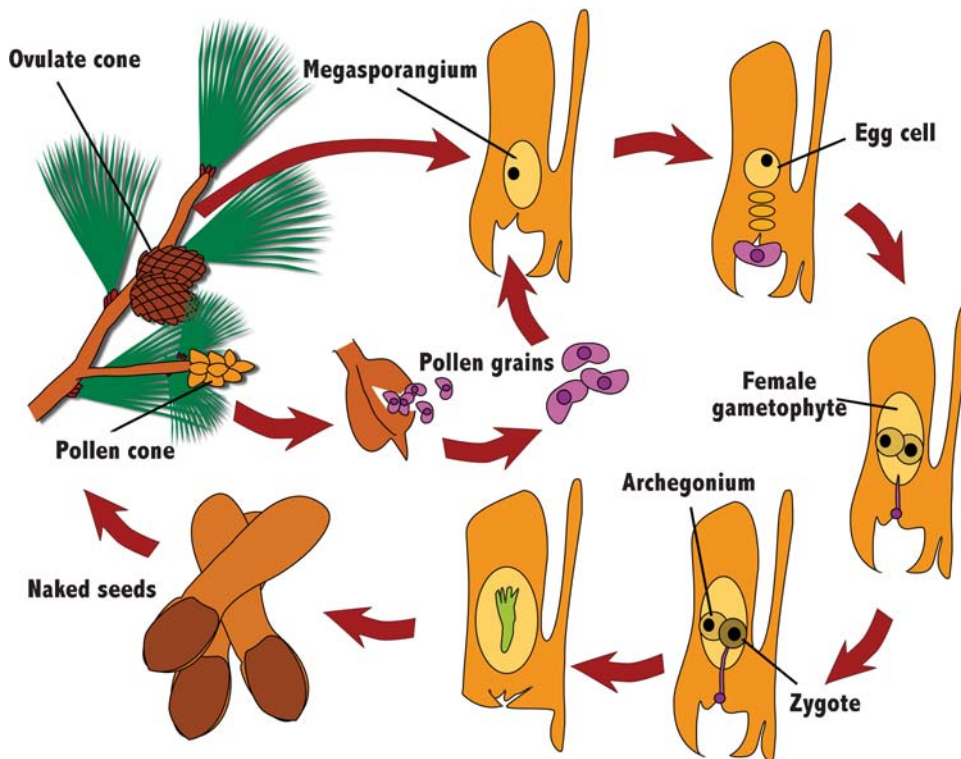


Figure 1.5 The life cycle of a gymnosperm. Mature gymnosperms such as conifers form two types of cones; the female cone is called the ovulate cone and the male cone is called the pollen cone. The female egg cell forms from a macrospore mother cell, which undergoes meiosis to form a tetrad of macrospores. Only a single one of these survives and undergoes many mitotic divisions to form ultimately the female gametophyte. An egg cell forms which can be up to 3 mm in diameter, making it the largest egg cell in the plant kingdom. The male gametes are released and are carried by air currents to the ovulate cones. The pollen germinates and fertilizes an egg cell. This goes on to develop into a zygote and ultimately a seed. This seed is not enclosed by an ovary, which gives the gymnosperms ('naked seeds') their name. There are four distinct divisions of the gymnosperms: Coniferophyta, Cycadophyta, Ginkgophyta and Gnetophyta. These are split into less than 800 different species recognized currently.

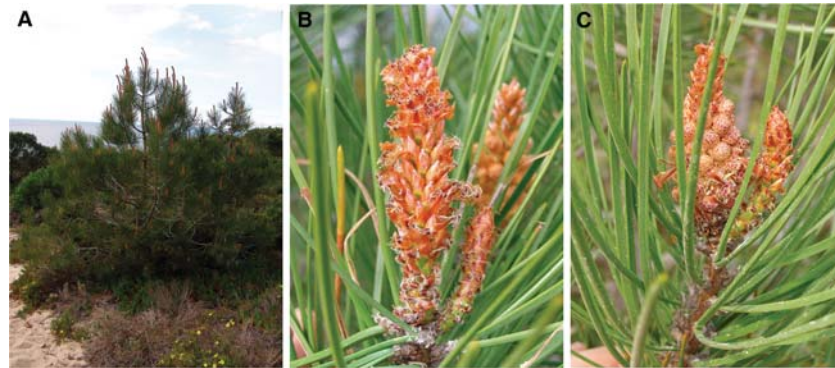


Figure 1.6 Gymnosperm cones. Here the male (B) and female cones (C) of the stone pine (*Pinus pinea*) are shown.

Cretaceous period, around 140 million years ago, but despite their late appearance they have been spectacularly successful (Willis and McElwain, 2002). The features that identify angiosperms are:

1. The presence of an enclosed ovary (covered by carpels and two layers of integument).
2. The formation of flowers.
3. The presence of specialized vascular tissues for nutrient and water movement.
4. The presence of double fertilization for the formation of the embryo and endosperm.

There are around 350 different families of flowering plant and 260 000 different species. The life cycle of a typical angiosperm is shown in Chapter 9. The angiosperm division is subdivided into two classes of plants, the

Magnoliopsida (dicotyledons, around 180 000 species) and the Liliopsida (monocotyledons, around 80 000 species, about 33% of these belonging to the family Orchidaceae). The principal characteristics that allow easy identification of these classes are shown in Table 1.2. Monocotyledons produce pollen with a single pore or furrow, which is the place where the pollen tube will emerge on the stigmatic surface upon germination. This means that if the pollen grain lands with this furrow facing away from the stigma, fertilization is more difficult to achieve. In dicotyledons there are three such furrows and this is thought to result in a furrow always being in contact with the surface of the stigma, therefore making fertilization easier (Endress, 1987). However, both classes are very successful in terms of land area covered and number of different species. From the earliest fossil records there is compelling evidence that the dicotyledons were the first angiosperms to evolve, with very few monocotyledon tissues being preserved as fossils at this time. However, many of the monocotyledon species known today are

Table 1.2 The usual distinguishing characteristics between monocotyledons and dicotyledons.

<i>Feature</i>	<i>Monocotyledons</i>	<i>Dicotyledons</i>
Flower structure	Petals and sepals in groups of three	Petals and sepals in groups of four or five
Pollen	Monocolpate (one pore or furrow)	Tricolpate (three pores or furrows)
Cotyledons	One	Two
Vascular tissue arrangement in leaves	Parallel	Net-like
Vascular bundles through stem	No apparent order in arrangement	Encircling the stem just under the epidermis of the stem
Secondary growth	Absent	Present

Redrawn from Raven *et al.* (1992) and Magallon *et al.* (1992). There are exceptions to these characteristics, but those listed are the common features that allow easy identification.

thought to have evolved from species originating in the early Cretaceous period. It is thought that the absence of monocotyledons from the fossil record may be a result of there being fewer monocotyledon species and the fact that they are generally herbaceous and do not possess woody tissues, which would make them less likely to be preserved as fossils.

The most recent evolutionary change to have occurred, judging from the plant fossil record, is the appearance of plants possessing modifications to the usual C3 pathway for photosynthesis, i.e. C4 and Crassulacean acid metabolism (CAM) plants. These plants are discussed in greater detail in Chapter 12.

The evolution of lignin

Lignin is a complex polymer of phenylpropane units, containing very variable bonding, bound to cellulose to

make the cell wall of plants (Figure 1.7). The structure is very rigid and forms a strong support or defence structure in various plant tissues. The evolution of lignin synthesis in plants was essential for the transition from prostrate plants to upright plants. In order to move water through tissues, osmosis can be relied on for short distances, but if the plant is to become upright, reinforced transport vessels are needed in the form of the xylem (see Chapter 4). It has been proposed that plants could not grow taller than a few centimetres in height without the evolution of lignin (Niklas, 1997). Lignin is thought to have evolved around 430 million years ago and the key to its appearance has been proposed to be the high oxygen levels present in the atmosphere at that time (Willis and McElwain, 2002). Lignin played a central role in the evolution of plants because it permits the support of upright plants, which optimized the use of light levels. It allowed the evolution of the upright ferns and ultimately the first trees. The evolution of upright plants also permitted the movement

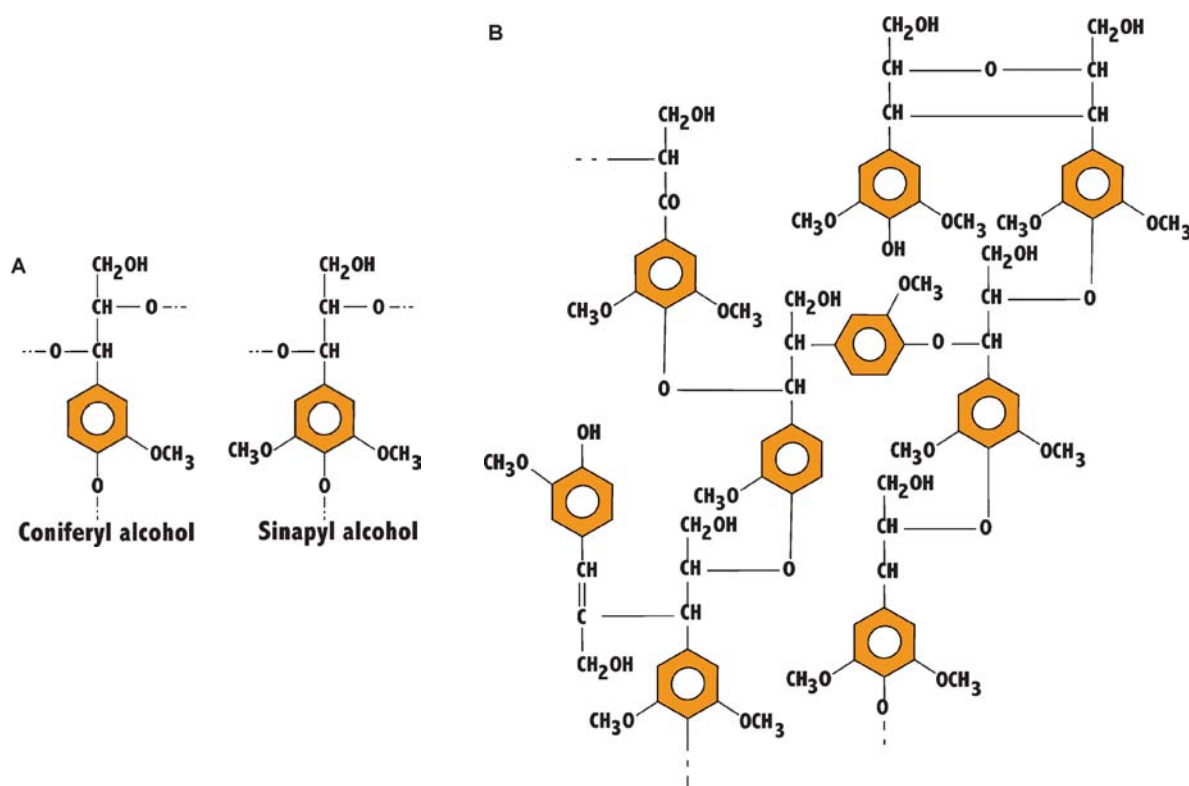


Figure 1.7 The structure of lignin. The group of compounds known as lignin are among the most abundant organic chemicals on earth. Lignin makes around one-third of the dry weight of wood and is especially used by plants to reinforce the xylem for support. It is also a very effective defensive compound, being very difficult to break down and metabolize. It is a biopolymer made up of several different monomers, two of which are shown, coniferyl and sinapyl alcohol (A). These monomers are polymerized to make the complex structure of lignin, an example of which is shown in (B).

of plants into a wider range of habitats and hence allowed plants to conquer the land. In addition, lignin is not easily broken down by other organisms; it was therefore an excellent defence compound. As a consequence of this, large amounts of plant material could not be degraded and gradually became buried in the earth, yielding what we now know as oil and coal. These reserves provided a huge sink for taking CO₂ out of the atmosphere and storing it in an organic form. This supported a fall in global CO₂ levels, which in turn influenced evolution of all the other organisms on the planet. It is only in the present day that this stored CO₂ is being re-released into the atmosphere through the actions of humankind, with the knock-on effect of potential global warming.

Plants and mass extinction

Over the course of the Earth's history, there are five recognized periods of mass extinction in the marine fauna records. These are times when 20–85% of all living marine fauna species are recorded to have disappeared in the fossil record. The most well-known of these events is at the boundary between the Cretaceous and Tertiary periods, when all the dinosaurs are thought to have become extinct. At this point, around 80% of all animal species became extinct. How did plants fare at this time? There is a marked reduction in the abundance and range of species represented in the fossil record at this point in time (Saito *et al.*, 1986). There was then a striking, but temporary, rise in the abundance of fern spores, which was followed by a major reduction in the diversity of fossil plants compared with that prior to the boundary event. It is thought that this may represent major destruction of much of the vegetation, followed by a rapid process of revegetation. However, different areas of the world seem to have been affected in different ways, such that in some regions the vegetation cover appears scarcely to have changed. The extinction rate of plants at this time has been estimated as 5–10% (Halstead, 1990). This period was therefore one in which a great deal of the Earth's biomass was lost, but there were no mass extinctions, as observed with the fauna species. Similar observations were made at the other points of mass extinction noted in the fauna fossil records.

Why did mass extinctions not occur in the plant kingdom? The answer to this question reveals something about the versatility of plants and why they are so successful. Most animal species are very mobile and if their habitat becomes less amenable to survival, they can simply move to a new region. However, if the changes are far-reaching, it may not be within the organism's capacity to move

beyond the stressed habitat and death or extinction is likely. These major extinction events are all likely to have been global catastrophes resulting in major changes in the world's climate, therefore escape would have been impossible. Plants, however, have always had to tolerate the inconvenience of not being able to move: therefore they have evolved to be adaptable to survive local catastrophes. These survival mechanisms appear to have been so effective that even after global catastrophes plants appear to have bounced back very rapidly. Put simply, shooting all the white rhinoceros in Africa will cause the species to become extinct since animals cannot regenerate or give birth to young once dead; however, cut down all the *Acacia* trees in Africa and they will resprout and grow again within a season. If all the plants were ripped out of the ground, they could rely upon the bank of seeds in and on the soil surface to regenerate the population. Seeds, as discussed in Chapter 14, can be very resistant to environmental stresses, such as long-term drought, high temperatures, darkness and other adverse conditions. In consequence, plants are much more difficult to eradicate than animals, as any gardener struggling with bindweed or ground elder can testify! It is estimated that around 1% of the angiosperm species that have ever existed are still alive today. This is a difficult figure to estimate from the fossil record but nevertheless this is a very high percentage compared with the survival of animal species, and is testimony to the resilience of plants in the face of adversity.

The majority of plants are angiosperms and therefore most of the discussion in this book will be restricted to the higher plants, and mainly the angiosperms.

Floristic kingdoms, biogeography and biomes

As plants evolved and time passed, the continents of the Earth shifted. It is therefore logical that certain later-evolving plants will be located only in specific regions of the world, whereas other species, which were particularly successful and evolved at an early stage in the Earth's history, will be found over many regions of the world. For example, the sundew *Drosera rotundifolia* is found over a wide area of the Northern Hemisphere, from the Far East to North America (Figure 1.8). This species is extraordinarily successful and is probably the most widespread of all of the *Drosera* species. The logical explanation for its distribution is that it evolved at a time when Asia, Europe and North America were contiguous. However, another carnivorous plant, *Sarracenia*, has a very wide range on the eastern side of North



Figure 1.8 Global distribution of the round-leaved sundew, *Drosera rotundifolia*. The distribution map emphasizes that this species of sundew is found extensively in the temperate regions of the northern hemisphere, but is completely absent from the southern hemisphere. This genus is therefore highly likely to have evolved prior to the major continental drift had occurred, which isolated the Sarraceniaceae.

America but is found nowhere else in the world (Figure 1.9). These species are also very successful and in trial planting in the UK certain species have proved to be very invasive. Thus, there are many potential habitats across the world in which *Sarracenia* could thrive, and yet it is restricted to North America. The most likely reason for this failure to spread is that this genus evolved in North America after the continents separated, and thus never had the opportunity to colonize Europe.

A traveller around the globe would encounter very different plant species in different continents. This led Ronald



Figure 1.9 Global distribution of the North American pitcher plant, genus *Sarracenia*. The distribution map emphasizes that this genus is only found on the continent of North America. Therefore this genus is highly likely to have evolved once this continent had split from other continents.



Figure 1.10 Floral kingdoms of the world. Ronald Good (1947) proposed a means of dividing the globe into six floristic kingdoms, based on the distribution areas of unrelated taxa. The location and extent of these kingdoms are shown on the map; they have since been subdivided into subkingdoms or provinces and then into regions.

Good (1947) to divide the world into six floristic kingdoms (Figure 1.10), based on the distribution areas of unrelated taxa. These kingdoms were subdivided into subkingdoms or provinces and then into regions (Table 1.3). Despite an unfortunate use of the word 'kingdom', Good had defined a very useful way of looking at the flora of the planet. The significance of this work meant that our hypothetical traveller could move westwards from China all the way to Alaska and encounter very similar species of flora (the Boreal kingdom). For example, the orchid genus *Cypripedium* can be found over just that range. Many other species could also be detailed in a similar way. However, if

Table 1.3 Proportions of flowering plant species found in the different floral kingdoms.

Floristic kingdom	Proportion of world species (%)	Location
Boreal (Holarctic)	42	North America, Europe, Central Asia
Paleotropical	35	Central Africa
Neotropical	14	South America
Australian	8	Australia, Tasmania, and New Zealand
Antarctic (Holantarctic)	1	Southern tip of South America
Cape (Fynbos)	0.04	Western Cape within South Africa

The densest area for flora in the world is the Fynbos (1300 species/10 000 km²); the next densest is the Neotropical Kingdom (400 species/10 000 km²).

our traveller moved southwards towards South America the vegetation would gradually change to that of the Neotropical kingdom. There have been many further attempts to redefine the floristic kingdoms into biogeographical areas (Takhtajan, (1986)) or into biomes (major regional ecosystems, e.g. desert, characterized by dominant forms of plant life and the prevailing climate) but the underlying message is the same. Over certain areas of the world specific plant species are endemic.

One particular feature that stands out in Good's floristic kingdoms is the presence of the Fynbos region in South Africa. This is the smallest of the floristic kingdoms, measuring only 90 000 km² and yet possessing over 8600 different plant species, around 5800 (68%) of them being endemic (Cowling and Hilton-Taylor, 1994). Consequently, in terms of flora, this is the most biologically diverse area in the world. Table Mountain above Cape Town has more different plant species growing on its hillsides than are found in the whole of the UK! The main vegetation of the Fynbos region is hard-leaved evergreen shrubland, which is prone to frequent fires. Many of the species present in the region use fire as a cue to trigger germination of the seeds (see Chapter 14). The main species are members of the families Restionaceae (Cape reeds), Ericaceae (heathers and their relatives), Fabaceae (pea family), Proteaceae (the largest shrubs in the area) and Iridaceae (bulb plants) (Figure 1.11). The other remarkable feature of the area is that more than 10 of the genera are represented by more than 100 different species, which is very diverse indeed. Many of the plants that are frequently found in gardens across the world were originally from this area, e.g. *Gladiolus*, *Freesia*, *Pelargonium*, *Ixia* and *Sparaxis*, to name but a few. Nowhere else on Earth can such floral diversity be seen.

What makes a plant?

Structure of the whole plant

What makes plants so remarkable and why are they any different from animals? To appreciate this, we need to look at the overall general structure of a plant and then at the ultrastructure of the plant cell.

The general structure of a plant is shown in Figure 1.12. Plants possess a root system for anchorage, water uptake and mineral ion uptake. The role of the root system in plants is discussed in more detail in Chapter 4. At the tip of the root is an apical meristem, which generates further root axis and controls the development of root growth. As mentioned earlier, the acquisition of a root system was crucial for supporting the movement of plants onto dry

land. Water is essential for the functioning of a living cell and therefore an efficient mechanism for moving water from the soil to all of the cells of a plant is necessary for the transition to drier habitats. But roots should be seen as a support tissue and, as mosses have been successful for millions of years with just a rudimentary rhizoid system for water and mineral uptake, they are obviously not essential in damp habitats. It is the presence of the root system which dictates that plants are fixed in position. For an efficient root system, there needs to be considerable branching through the soil; this makes withdrawal of the root system from the soil impossible and hence plants can never be mobile. This factor steers the rest of the evolution of plants, because they need to be able to deal with anything their environment can throw at them or they will die.

Connected to the roots is the stem, which in some plants is so short that it is barely visible without dissection. However, this is a result of internode lengths. Along the stem, leaves are attached at nodes and the stem spacing between the nodes is known as an internode. Short internodes yield a plant which is short and produces a rosette of leaves. Longer internodes yield a plant which is tall and can take advantage of light at several different levels. Which habit a plant adopts is dependent upon what the plant has evolved to compete with. A tall plant may optimize light usage but also risks damage. In addition, height does not necessarily mean that light levels are optimized. Measurements from my own laboratory show that the tongue orchid (*Serapias lingua*) is tall to compete with tall grasses in its habitat. However, it is slower-growing and less efficient at producing a tuber at the end of a growth season than the rosette-forming green winged orchid (*Anacamptis morio*), which competes with lower-growing grasses (Figure 1.13). Height may therefore be an advantage, or it may just be a necessity of competition.

Leaves are attached at the nodes along the stem. At each leaf attachment point there is frequently an axillary bud. The leaves form the major sites on most plants for photosynthesis. The first land plants possessed mainly photosynthetic stems, but upright structures are inefficient at absorbing the available light and leaves evolved to form a structure perfectly adapted to capturing light while minimizing water loss. Leaves come in so many varying shapes and forms that there is apparently no specific leaf shape which is optimal for photosynthesis.

At the tip of the stem is the apical meristem, which generates further aerial plant structures, such as new stem, leaves, flowers and fruits. The axillary buds are usually dormant until the apical meristem has grown a sufficient distance away from the axillary bud; however, if

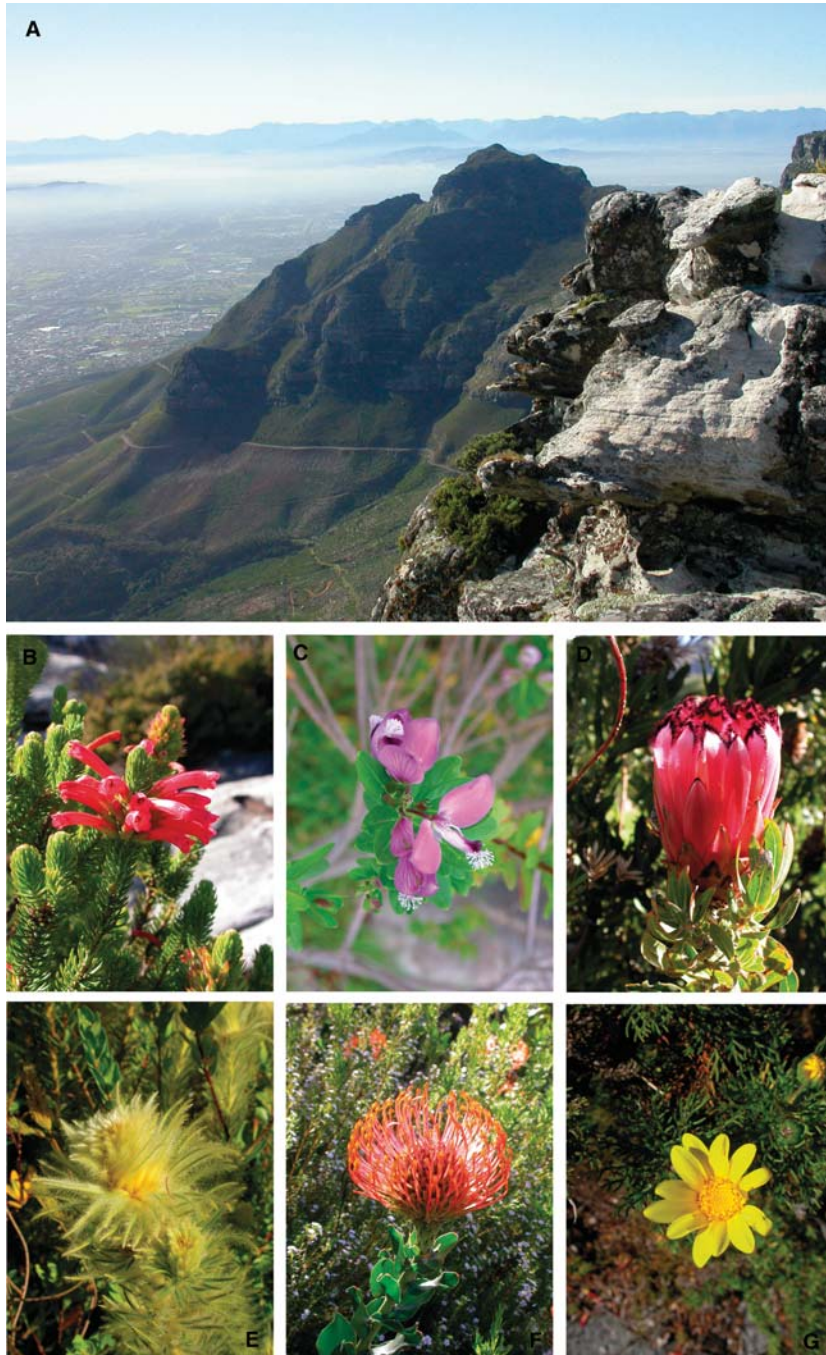


Figure 1.11 The smallest floral kingdom, the Fynbos region in South Africa, which covers 0.04% of the Earth's surface but possesses 3.4% of the recognized plant species, with around 68% of the species being endemic. To put this in context, the Fynbos region has 8500 different plant species with around 5700 endemics, whereas the UK only has 1500 different species with 20 endemics. This makes the Fynbos the most biologically diverse area on the planet. (A) A view from the top of Table Mountain, which is situated in the south-western corner of the Fynbos region. The other photographs show examples of some of the species which can be found in this region; (B) *Erica plukenetii*; (C) *Polygala myrtifolia*; (D) *Protea lepidocarpodendron*; (E) *Elegia capensis*; (F) *Leucospermum cordifolium*; (G) *Euryops abrotanifolius*.

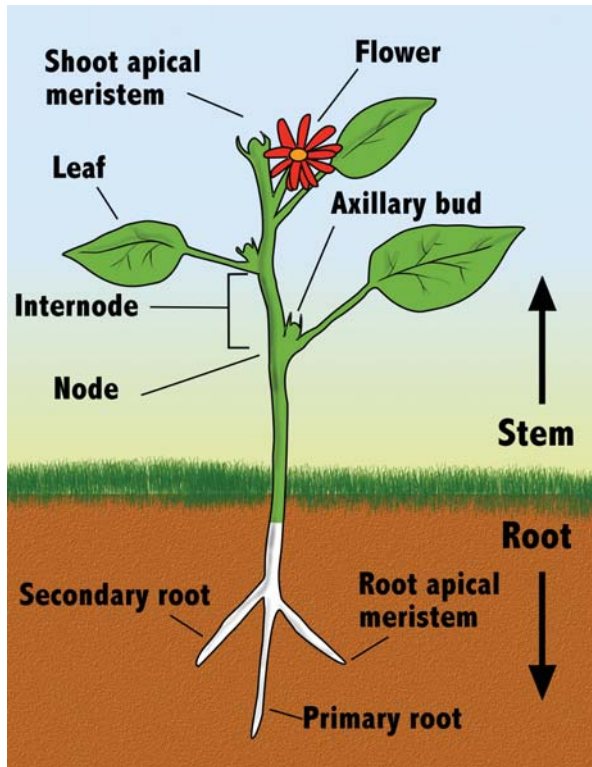


Figure 1.12 Schematic diagram of the general structure of a dicotyledonous plant, labelled with the major structures, which are referred to later in the text.

the apical meristem is damaged the apical dominance is released and the other buds on the stem can then begin to grow.

Structure of the plant cell

The plant cell displays numerous differences from an animal cell. Typical plant and animal cells are shown in Figure 1.14. The rest of the discussion here is limited to the structures specific to plants.

The most obvious difference is the degree of compartmentation in a plant cell. Plant cells contain more organelles and microbodies than animal cells. In addition, up to 95% of a plant cell can be devoted to a large membrane-bound space, the vacuole. All of these will be discussed in turn, but the most important difference between an animal cell and a plant cell is the presence of chloroplasts.

Chloroplasts and other plastids

Chloroplasts, like mitochondria, are around the same size as a bacterial cell. Both contain DNA, which is not arranged in the form of a chromosome but as a circular piece of DNA known as a plasmid (Figure 1.15). The gene sequences possess no introns and are controlled by

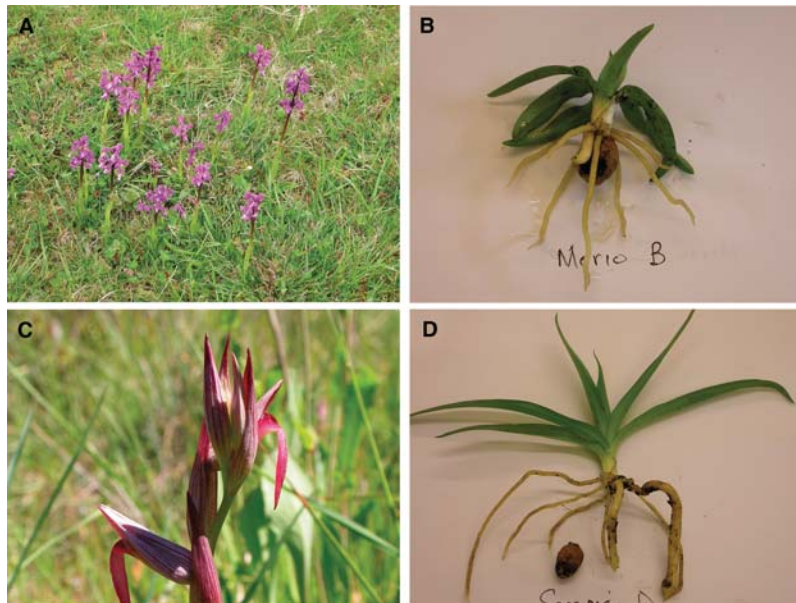


Figure 1.13 Growth habits of *Anacamptis morio* and *Serapias lingua*. (A) *A. morio* in its natural habitat at the Piddinghoe Reservoir, East Sussex, UK. (B) Isolated *A. morio* plant, showing the flattened leaves and short stem which is perfect for competing with short grasses. (C) *S. lingua* plant shown in its natural grassy habitat in Portugal. (D) Isolated *S. lingua* plant, showing the raised leaves and slightly longer stem. This allows the plant to compete with longer grasses, which is its preferred habitat.

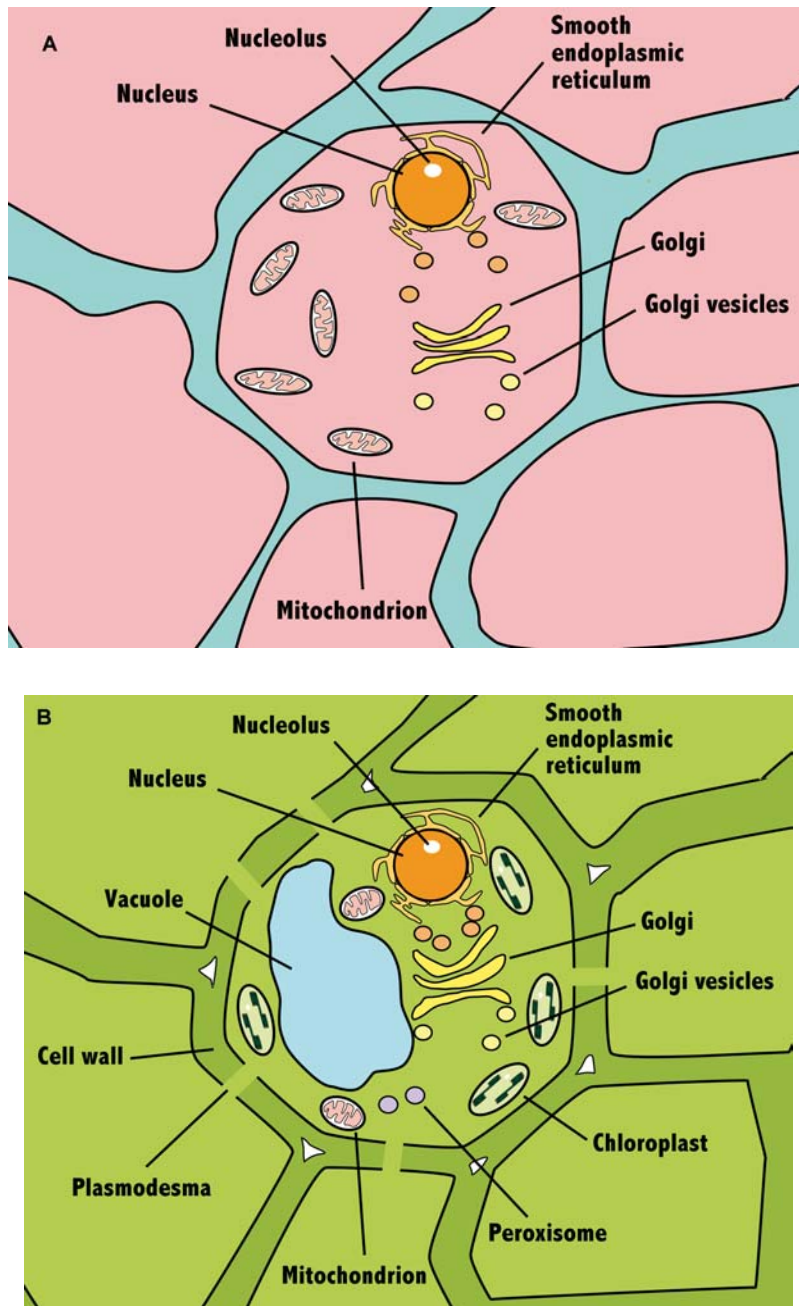


Figure 1.14 Schematic diagram of the general structure of an animal cell (A) and a plant cell (B). There are numerous differences, which are labelled.

promoter sequences which are very similar to those observed in bacteria. In addition, the ribosomes used by both of these organelles are smaller than those used for protein synthesis in the cytosol of plant cells and are again very similar to those used by bacteria. This compelling evidence has led to the suggestion that these organelles in animals and plants were once free bacteria, which at some

point in the evolution of life fused with some larger form of bacterium or eukaryote. During invagination into the larger bacterial cell, a second membrane covered the organelles to give the double-membrane-bound chloroplast (a photosynthetic bacterium) and mitochondrion (a non-photosynthetic bacterium). Animal cells never acquired chloroplasts. The photosynthetic system used by

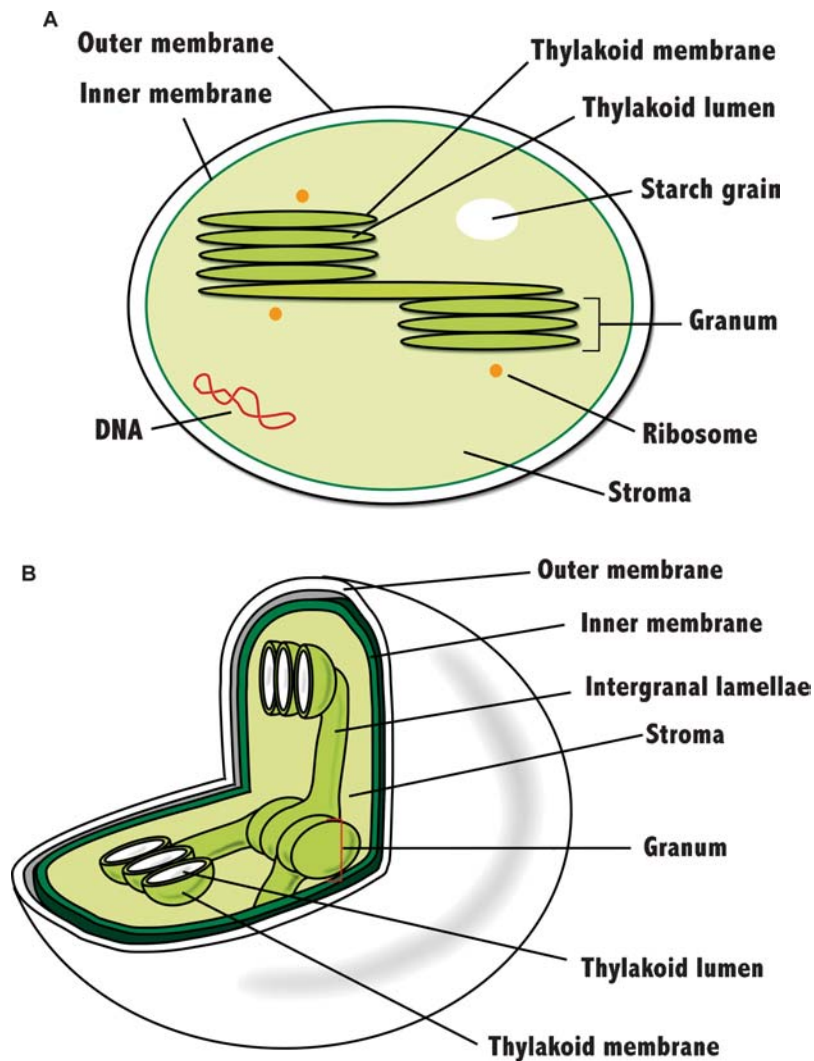


Figure 1.15 Detailed schematic diagram of a chloroplast, shown simply as a cross-section and as a three-dimensional representation.

plants is therefore essentially that of a bacterium which has evolved for millions of years within the plant cell and hence has changed with time. This accounts for why the photosynthetic mechanisms in cyanobacteria and plants are so similar. It is not known whether there was just a single union of a bacterium with a large bacterium or whether this occurred many times in the Earth's history.

The mechanism of photosynthesis and the ultrastructure of the chloroplast are discussed in greater detail in Chapter 2, but the chloroplast is just one of a family of organelles unique to plants, collectively known as plastids. In flowers there is a rearrangement of the internal thylakoid membrane to produce a wave effect, and in this membrane coloured pigments, such as carotenoids, are borne; these plastids are called chromoplasts and they give rise to colour in some flowers and other plant structures, e.g. the

colour of carrot roots is formed from carotenoids in the chromoplasts. In non-photosynthetic plant tissues the plastids are frequently used for the synthesis of starch, and these are known as leuco- or amyloplasts (see Chapter 3). The basic structure is the same in all of these plastids and in many instances they can transform from one to another, e.g. carrots can become green, and many flowers begin green but turn another colour as they mature. Many synthetic reactions occur in the plastids of plants cells, such as starch and lipid synthesis, and many amino acids are also synthesized in them. The presence of plastids in plant cells varies. In some cells, such as pollen cells, there are few plastids. In non-photosynthetic plant cells there can be 5–10 amyloplasts, whereas there can be several hundred chloroplasts in a photosynthetic cell in a leaf. They can occupy as much as 20% of the cell volume in

certain cells, which highlights their importance in metabolism.

The vacuole

Another obvious feature in the plant cell is the presence of a vacuole. The volume which this 'bag' occupies varies from cell to cell and species to species. The vacuole in a Crassulacean acid metabolism plant may occupy up to 98% of the cell volume, but a typical cell will have a vacuole which occupies 70–95% of the cell. The vacuole is bound by a single membrane, known as the tonoplast. In immature cells the vacuole is frequently divided into a number of smaller vacuoles but as the cell matures these tend to fuse to form one. The vacuole is a reserve for storing certain compounds but, more importantly, it is a means of generating cell volume without diluting the contents of the cytosol (the volume of cell outside the membrane-bound organelles, vacuole and microbodies in the cell). Through regulation of the solute concentration in the vacuole, a plant can regulate its volume. The vacuole can then be used to apply pressure on the cell wall of the plant cell, and thus in certain circumstances cause the cell to expand and in others allow the cell to maintain turgidity. This permits cell growth with little investment in *de novo* synthesis of new cellular materials. It also allows plant cells to be much larger than animal cells in general.

In many tissues, pigments such as anthocyanins are dissolved in the vacuole to give the cell a colour. This is used in some plants to give rise to flower or fruit colour. Mineral ions, sucrose and secondary metabolites are also stored in the vacuole.

Microbodies

Microbodies are single-membrane bound organelles in the cytoplasm of plant cells. They are small in size, around 1 µm in diameter. They are often associated with activity of the endoplasmic reticulum but there are two very important microbodies found in plants, the peroxisome and the glyoxysome.

Peroxisomes are used mainly in the metabolism of hydrogen peroxide and most of the cellular reactions which generate this compound are carried out in this microbody. Hydrogen peroxide can be potentially very damaging to cells, as it is a powerful oxidizing agent. The peroxisome contains the enzyme catalase, which metabolizes this reagent to water. There is still some debate as to the function of the peroxisome, as certain reactions which generate hydrogen peroxide also occur in the cytosol.

However, the detoxification hypothesis is the best to date. The role of the peroxisome in photorespiration is discussed in Chapter 2.

The glyoxysome is found in tissues such as oil-bearing seeds which are metabolizing lipids and converting them to carbohydrate. They catalyse the breakdown of fatty acids to acetyl co-enzyme A (acetyl-Co A), which is exported from the microbody and used in respiration or the synthesis of sucrose. Glyoxysomes have rarely been observed to occur in animal cells and hence animals have great difficulty converting fats into carbohydrate.

The cell wall

Animal cells generally do not possess a rigid cell wall, but plant cells do. Rather than being like brick wall, the cell wall should be viewed as a molecular filter and a dynamic part of the cell. The cell wall occupies the space between neighbouring cells and is made up of complex polymers of cellulose, hemicellulose, pectin, lignin and proteins (Figure 1.16). In growing cells the primary cell wall is flexible and thin, but as the cells age a secondary cell wall develops, which is much more rigid and plays a major role in support of the whole plant. The primary cell wall is made up mainly of cellulose but the secondary cell wall contains a large proportion of lignin. As mentioned earlier, the evolution of lignin as a strengthening compound in plants played a major role in enabling plants to becoming upright (i.e. attaining the strength to hold aerial tissue off the ground) and therefore in vastly broadening the habitat range of plants. Lignin is resistant to degradation by other organisms and is very strong. The strength of lignin is best appreciated in the wood of trees. The trunk of a tree can support many tons in weight and strong winds, and lignin is probably one of the strongest natural materials. This is precisely why it has been so useful as a building material for most human cultures.

Plasmodesmata

Many plant cells possess links between cells known as plasmodesmata (singular: plasmodesma), which offer a continuum between the cytosol of one cell and that of a neighbouring cell (Figure 1.17). This allows the movement of solutes between the cells. The role of the plasmodesmata in sucrose movement within leaves and developing sink organs is discussed in detail in Chapter 3. The frequency of their occurrence between plant cells is usually an indication of the traffic between cells. There is some evidence that there is control of movement between cells through plasmodesmata, since they can be used to load the phloem

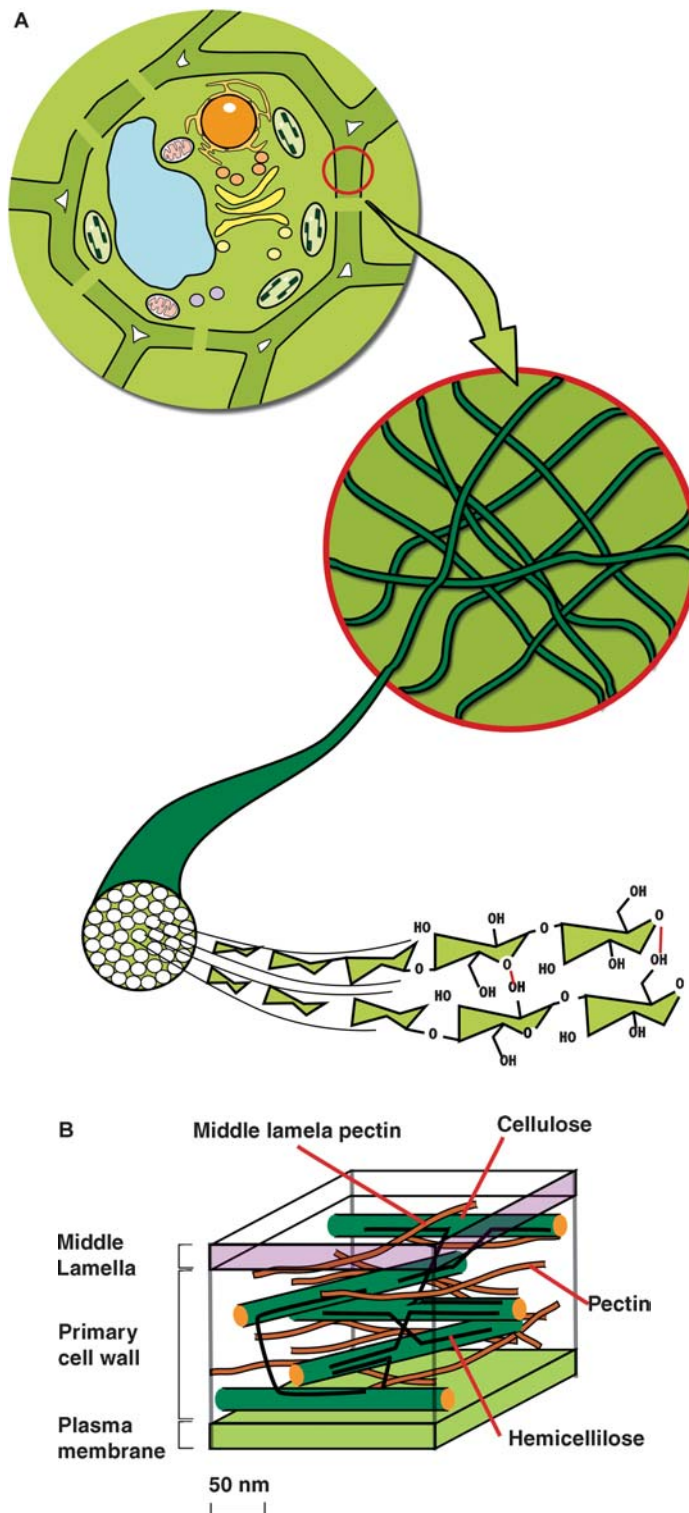


Figure 1.16 Detailed schematic diagram of the plant cell wall, shown as it relates to a plant cell in a leaf, showing a series of magnifications of the structure. The actual composition of the cell wall is also shown, and how the structure is layered around each plant cell.

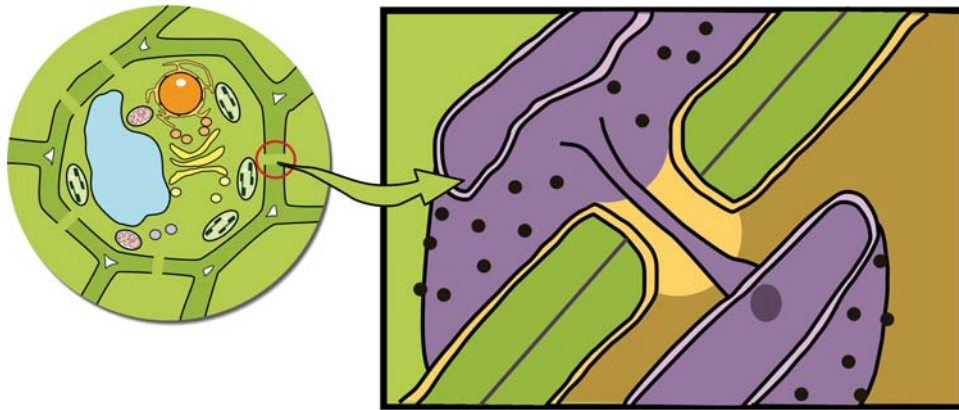


Figure 1.17 Detailed schematic diagram of an individual plasmodesma. The plasmodesma forms a symplastic link between two adjacent plant cells.

in certain plant species. Larger molecules, e.g. raffinose and stachyose, cannot get through plasmodesmata (see Chapter 3).

This chapter has outlined the evolution of plants, their types and distribution in different parts of the world and the basic structure of a plant and its cells, setting the scene for the following chapters. Plants dominate the planet – but how did they get to this position and what are the underlying physiological characteristics that allow them to be so successful?

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