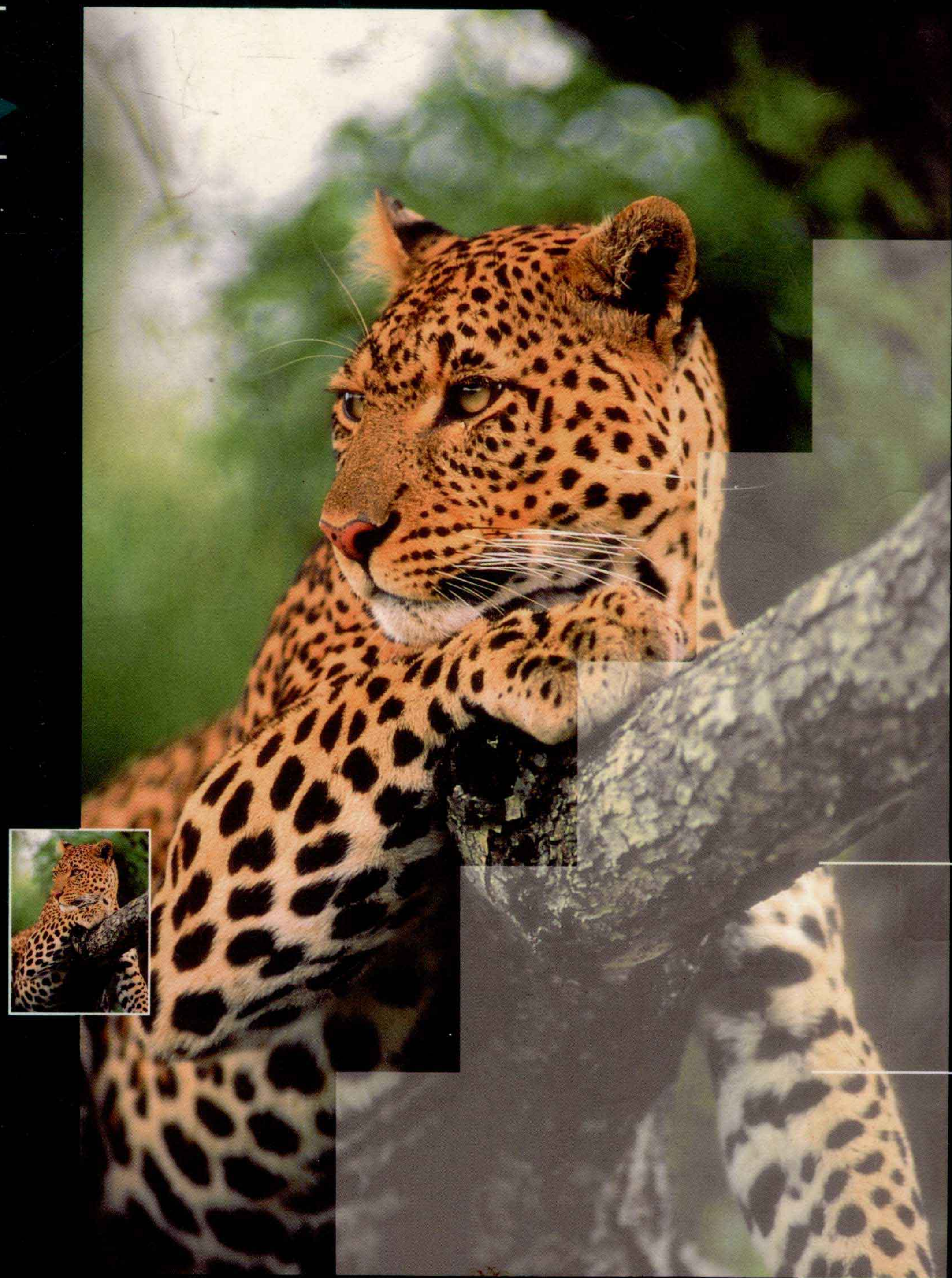
Central Concepts in Biology

CAMBRIDGE MODULAR SCIENCES



Central Concepts in Biology

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Introduction

This book is for A and AS level students who have already studied some of the basic elements of an advanced biology course, including cell structure, cell division, the molecular structure of proteins and the behaviour of enzymes.

Two very different subject areas are covered in this book. The first three chapters consider energy transfer within and between living organisms. The last three chapters cover genetic control within an organism, inheritance and evolution. These two areas are both fundamental to a study of biology.

Chapters 1 and 2 deal with the way in which living organisms obtain energy needed to keep them alive. In chapter 1 you will learn how plants transfer sunlight energy into chemical energy in organic compounds, in the reactions of photosynthesis. In chapter 2 you will see how the chemical energy in these organic compounds is released again by the reactions of respiration, usually producing ATP which is then used to provide energy for many different processes in living organisms.

While chapters 1 and 2 look in detail at the biochemistry of these energy-transferring processes, chapter 3 takes a wider view, considering how energy from sunlight is transferred through ecosystems. This chapter also looks at other aspects of ecosystems, describing two important nutrient cycles – those for carbon and nitrogen – and discussing how some human activities can affect the balance within these cycles.

Chapter 4 introduces DNA, explaining how its simple basic structure provides instructions for almost everything that takes place within a living organism. Chapter 5 shows how these instructions are passed on from parent to offspring. Chapter 6 provides a brief description of how natural selection acting on organisms with slightly different versions of DNA codes may lead to changes, or evolution, in the characteristics of the species, and even to the development of a completely new species.

Contents

Energy and photosynthesis

By the end of this chapter you should be able to:

1 outline the need for energy in living organisms;

2 describe the universal role of ATP as the energy 'currency' in all living organisms;

3 explain that photosynthesis traps light energy as chemical energy in organic molecules, and that respiration releases this energy in a form which can be used by living organisms;

4 explain the photoactivation of chlorophyll that results in the conversion of light energy into chemical energy of ATP and reduction of NADP;

5 describe in outline the Calvin cycle involving the light-independent fixation of carbon dioxide by combination with a five-carbon compound (RuBP) to yield a three-carbon compound, GP (PGA), and the subsequent conversion of this compound into carbohydrates, amino acids and lipids;

6 describe the structure of a dicotyledonous leaf, a palisade cell and a chloroplast and relate these structures to their roles in photosynthesis;

7 discuss limiting factors in photosynthesis.

The need for energy in living organisms

All living organisms require a continuous supply of energy to stay alive, either from the absorption of light energy or from chemical potential energy. The process of photosynthesis transfers light energy to chemical potential energy and so almost all life on Earth depends on photosynthesis, either directly or indirectly. Photosynthesis supplies living organisms with two essential requirements: an energy supply and usable carbon compounds.

All biological macromolecules, such as carbohydrates, lipids, proteins and nucleic acids, contain carbon. All living organisms therefore need a source of carbon. Organisms which can use an inorganic carbon source in the form of carbon dioxide are called **autotrophs**. Those needing a ready-made organic supply of carbon are **heterotrophs**. (An *organic* molecule is a compound including carbon and hydrogen. The term originally meant a molecule derived from an organism, but now includes all compounds of carbon and hydrogen even if they do not occur naturally.)

Organic molecules can be used by living organisms in two ways. They can serve as 'building bricks' for making other organic molecules that are essential to the organism, and they can represent chemical potential energy which can be released by breaking down the molecules in respiration (page 15). This energy can then be used for all forms of work. Heterotrophs depend on autotrophs for both materials and energy *(figure 1.1)*.

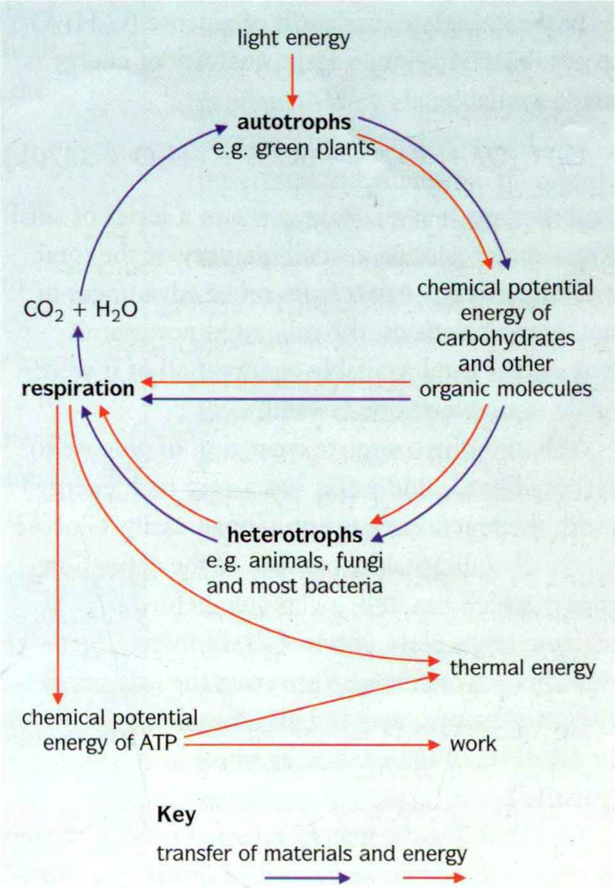


Figure 1.1 Transfer of materials and energy in an ecosystem.

Work

Work in a living organism includes:

- the synthesis of complex substances from simpler ones;
- the active transport of substances against a diffusion gradient;
- mechanical work such as muscle contraction and other cellular movements, for example the movement of cilia and flagella, amoeboid movement and the movement of vesicles through cytoplasm;
- in a few organisms, bioluminescence and electrical discharge.

Energy may also be used to maintain the body temperature. Two of these forms of work, active transport and muscle contraction, will be looked at in more detail later *(boxes 1A* and *1B)*.

For a living organism to do work, energy-requiring reactions must be linked to those that yield energy.

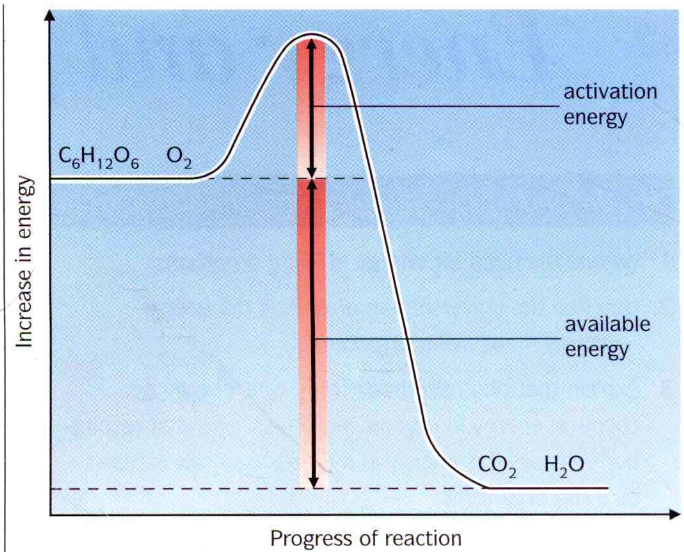
In the complete oxidation of glucose ($C_6H_{12}O_6$) in aerobic conditions a large quantity of energy is made available:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + 2870\,kJ$$

Reactions such as this take place in a series of small steps, each releasing a small quantity of the total available energy. Apart from other advantages of multi-step reactions, the cell could not usefully harness the total available energy if all of it were made available at one instant.

Although the complete oxidation of glucose to carbon dioxide and water has a very high energy yield, the reaction does not happen easily. Glucose is actually quite stable, because of the **activation energy** which has to be overcome before any reaction takes place *(figure 1.2)*. In living organisms this is overcome by lowering the activation energy using enzymes and also by raising the energy level of the glucose by phosphorylation (page 15).

Theoretically, the energy released from each step of respiration could be harnessed directly to some form of work in the cell. However a much more flexible system actually occurs in which energy-



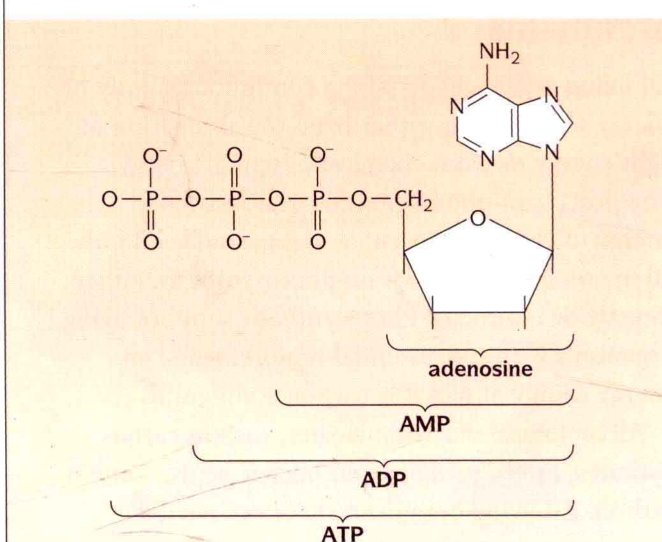
● ***Figure 1.2*** Oxidation of glucose.

yielding reactions are linked to the production of an intermediary molecule, **ATP** (adenosine triphosphate).

ATP

ATP as energy 'currency'

The structure of adenosine triphosphate (ATP) is shown in *figure 1.3*. It consists of adenine (an organic base) and ribose (a pentose sugar), which together make adenosine (a nucleoside). This is combined with three phosphate groups to make ATP. ATP is therefore a nucleotide (page 41). ATP



● ***Figure 1.3*** Structure of ATP.

is a small, water-soluble molecule. This allows it to be easily transported around the cell.

When a phosphate group is removed from ATP, adenosine diphosphate (ADP) is formed and $30.6\,\text{kJ mol}^{-1}$ of energy is released. Removal of a second phosphate produces adenosine monophosphate (AMP, *figure 4.5*) and $30.6\,\text{kJ mol}^{-1}$ of energy is again released. Removal of the last phosphate, leaving adenosine, releases only $13.8\,\text{kJ mol}^{-1}$ (*figure 1.4*). In the past, the bonds attaching the two outer phosphate groups have been called 'high energy bonds', because more energy is released when they are broken than when the last phosphate is removed. This is misleading and should be avoided since the energy does not come simply from breaking those bonds, but rather from changes in chemical potential energy of all the parts of the system.

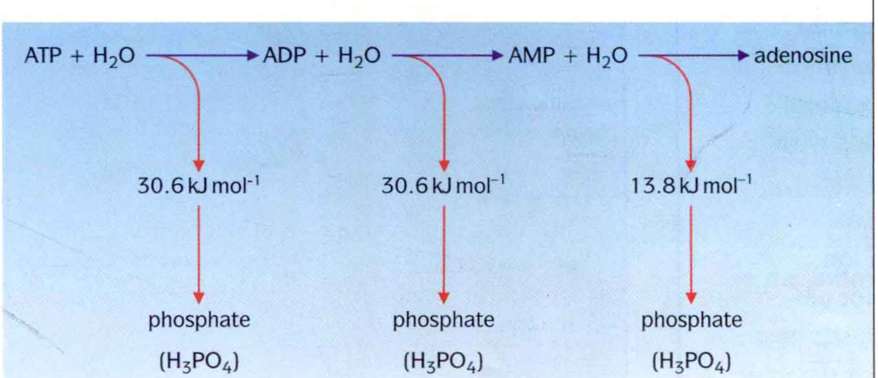
These reactions are all reversible and it is the interconversion of ATP and ADP that is all-important in providing energy for the cell:

$$\text{ATP} + H_2O \rightleftharpoons \text{ADP} + H_3PO_4 \pm 30.6\,\text{kJ}$$

The rate of interconversion, or turnover, is enormous. It is estimated that a resting human uses about 40 kg of ATP in 24 h, but at any one time contains only about 5 g of ATP. During strenuous exercise, ATP breakdown may be as much as 0.5 kg per minute.

The cell's energy-yielding reactions are linked to ATP synthesis. The ATP is then used by the cell in all forms of work. ATP is the standard intermediary molecule between energy-yielding and energy-requiring reactions. In other words, ATP is the 'energy currency' of the cell. The cell 'trades' in ATP rather than making use of a number of different intermediates.

Energy transfers are inefficient. Some energy is converted to thermal energy whenever energy is transferred. At the different stages in a multi-step reaction, such as respiration, the energy made available may not perfectly correspond with the energy needed to synthesise ATP. Any 'excess' energy is converted to thermal energy. Also, many energy-requiring reactions in the cells use less energy than that released by hydrolysis of ATP to ADP. Again any extra energy will be released as thermal energy (page 24).



● ***Figure 1.4*** Hydrolysis of ATP.

Be careful to distinguish between molecules used as energy currency and as energy storage. An energy currency molecule acts as the immediate donor of energy to the cell's energy-requiring reactions. An energy storage molecule is a short-term (glucose or sucrose) or long-term (glycogen or starch) store of chemical potential energy.

Synthesis of ATP

Energy for ATP synthesis can become available in two ways. In respiration, energy released by reorganising chemical bonds (chemical potential energy) during glycolysis and the Krebs cycle (page 17) is used to make some ATP. However, most ATP in cells is generated using electrical potential energy. This energy is stored as a difference in hydrogen ion concentration across some phospholipid membranes in mitochondria and chloroplasts which are essentially impermeable to hydrogen ions. Hydrogen ions are then allowed to flow down their concentration gradient through a protein which spans the phospholipid bilayer. Part of this protein acts as an enzyme which synthesises ATP, and is called ATP synthetase. The transfer of three hydrogen ions allows the production of one ATP molecule. This process occurs in both chloroplasts (page 12) and mitochondria (page 18) and is summarised in *figure 1.5*. The process was first proposed by Peter Mitchell in 1961 and is called chemiosmosis.

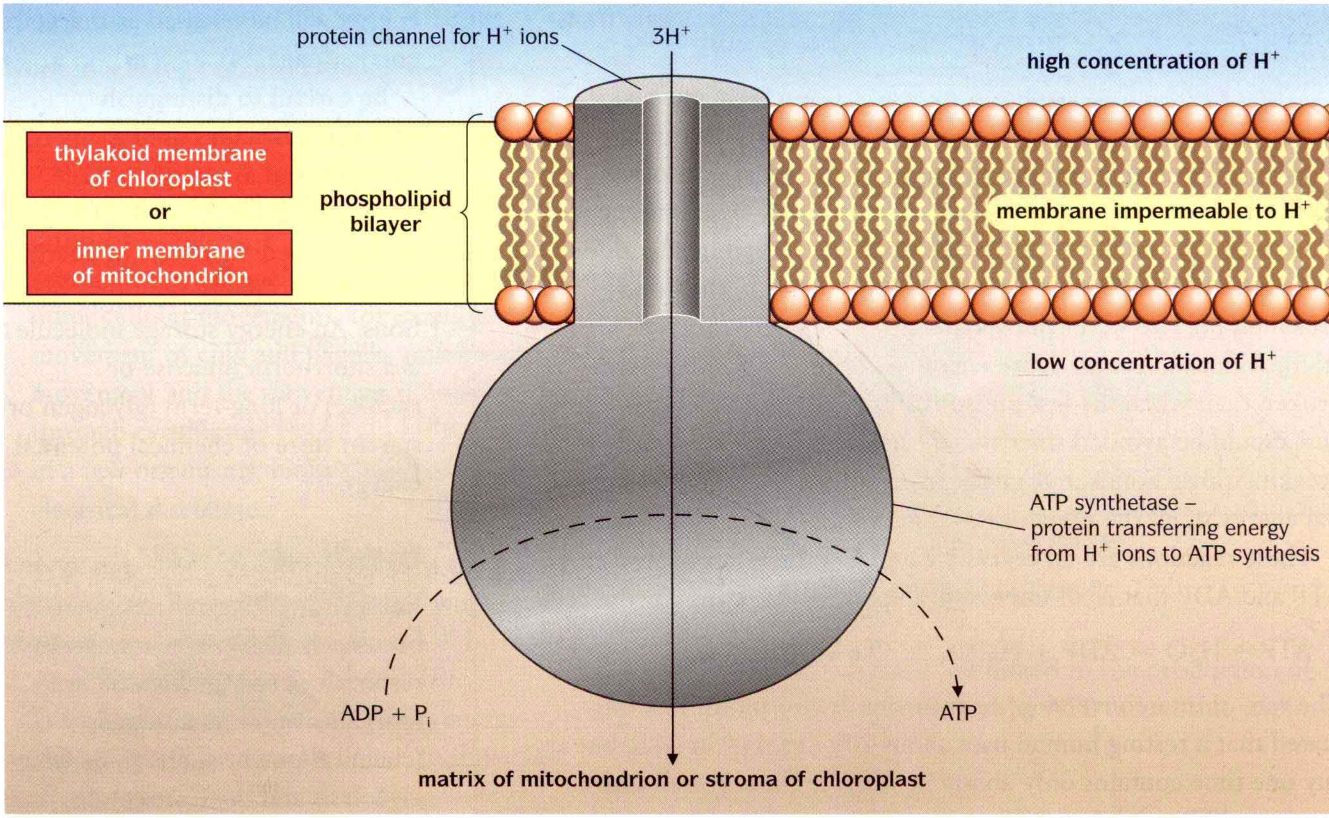


Figure 1.5 ATP synthesis.

The role of ATP in active transport

Active transport is the movement of molecules or ions across a differentially permeable membrane against a concentration gradient. Energy is needed, in the form of ATP, to counteract the tendency of these particles to move by diffusion down the gradient.

All cells show differences in concentration of ions, in particular sodium and potassium ions, inside the cell with respect to the surrounding solution. Most cells seem to have sodium pumps in the cell surface membrane which pump sodium ions out of the cell. This is usually coupled with the ability to pump potassium ions from the surrounding solution into the cell *(box 1A)*.

The importance of active transport in ion movement into and out of cells should not be underestimated. About 50% of the ATP used by a resting mammal is devoted to maintaining the ionic content of cells.

Box 1A The sodium–potassium pump

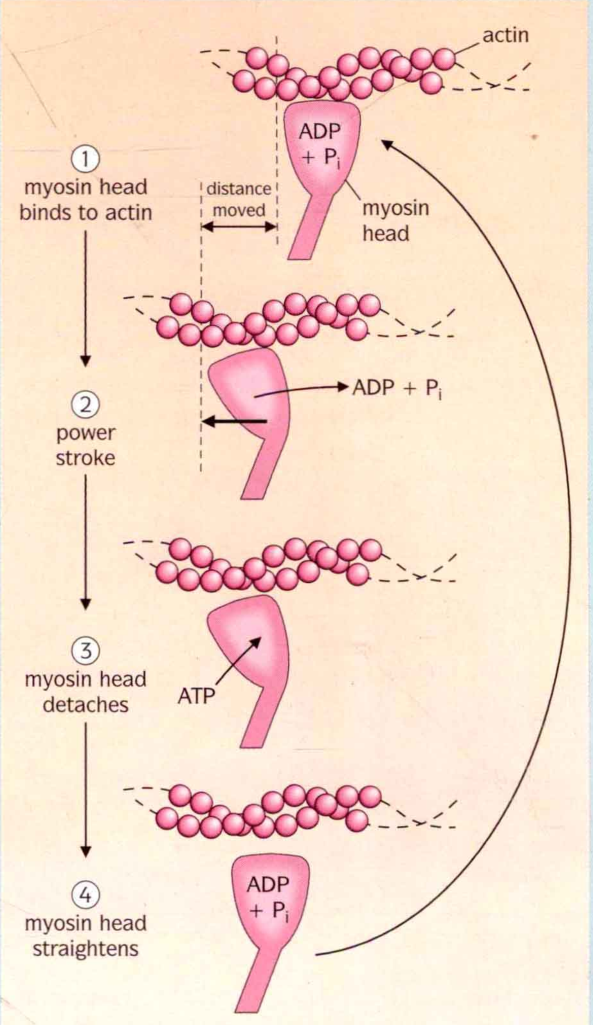
The sodium–potassium pump is a protein which spans the cell surface membrane. It has binding sites for sodium ions (Na^+) and for ATP on the inner side, and for potassium ions (K^+) on the outer side. The protein acts as an ATPase, and catalyses the hydrolysis of ATP to ADP and inorganic phosphate releasing energy to drive the pump. Changes in the shape of the protein move sodium and potassium ions across the membrane in opposite directions. For each ATP used, two potassium ions move into the cell and three sodium ions move out of the cell. Since only two potassium ions are added to the cell contents for every three sodium ions removed, a potential difference is created across the membrane which is negative inside with respect to outside. Both sodium and potassium ions leak back across the membrane, down their diffusion gradients. However cell surface membranes are much less permeable to sodium ions than potassium ions so this diffusion actually increases the potential difference across the membrane.

This potential difference is most clearly seen as the resting potential of a nerve cell (see *Foundation Biology* in this series). One of the specialisations of a nerve cell is an exaggeration of the potential difference across the cell surface membrane as a result of the activity of the sodium–potassium pump.

Box 1B Muscle contraction

A sarcomere contracts by sliding the thin **actin** filaments over the thick **myosin** filaments. When the muscle is activated by a nerve impulse, calcium ions are released from the **sarcoplasmic reticulum** (specialised endoplasmic reticulum). This allows the myosin heads to bind to the actin filaments. Myosin heads are ATPases and hydrolyse ATP to ADP and P_i which remain bound to the myosin heads. When myosin binds to actin, the shape of the head changes and the ADP and P_i are released. The myosin molecule then changes shape, moving the head with its attached thin actin filament to produce contraction of that part of the muscle cell. This is the 'power stroke'. Then another ATP binds, allowing the actin and myosin to separate. The ATP is hydrolysed and the cycle repeats. Note that the hydrolysis of ATP and the 'power stroke' do not occur at the same time.

When excitation ceases, ATP is again needed to pump calcium ions back into the sarcoplasmic reticulum.



● ***Figure 1.6*** The action of ATP in muscle contraction.

The role of ATP in the contraction of muscle

The energy for muscle contraction comes from the hydrolysis of ATP to ADP and inorganic phosphate. In resting muscle there is only a small concentration of ATP, and although this supplies the energy which is turned into muscular work, its concentration is about the same in resting and contracting muscle. During contraction the ATP is continually regenerated by a system which involves phosphocreatine (PCr). A resting muscle may contain around 20 mmol kg^{-1} of PCr compared with 6 mmol kg^{-1} of ATP.

The ADP produced during muscle contraction is reconverted to ATP by transferring a phosphate group from phosphocreatine, leaving creatine (Cr).

$$ADP + PCr \longrightarrow ATP + Cr$$

However, there is a limited supply of phosphocreatine. It is adequate for a sudden, short sprint lasting a few seconds. After this the phosphocreatine must be replenished via ATP from respiration. If the muscle is very active, the oxygen supply will be insufficient to maintain aerobic respiration in the cells. Then the lactate pathway is used to allow formation of ATP and the muscle cells incur an oxygen debt (see page 20).

Photosynthesis

An outline of the process

Photosynthesis is the trapping (fixation) of carbon dioxide and its subsequent reduction to carbohydrate, using hydrogen from water.

An overall equation for photosynthesis in green plants is:

$$\underset{\text{carbon dioxide}}{nCO_2} + \underset{\text{water}}{nH_2O} \xrightarrow[\text{in the presence of chlorophyll}]{\text{light energy}} \underset{\text{carbohydrate}}{(CH_2O)n} + \underset{\text{oxygen}}{nO_2}$$

Hexose sugars and starch are commonly formed, so the following equation is often used:

$$6CO_2 + 6H_2O \xrightarrow[\text{in the presence of chlorophyll}]{\text{light energy}} \underset{\text{glucose}}{C_6H_{12}O_6} + 6H_2O$$

Two sets of reactions are involved. These are the **light-dependent reactions**, for which light energy is necessary, and the **light-independent reactions**, for which light energy is not needed. The light-dependent reactions only take place in the presence of suitable pigments which absorb certain wavelengths of light. Light energy is necessary for the splitting of water into hydrogen and oxygen; oxygen is a waste product. Light energy is also needed to provide chemical energy (ATP) for the reduction of carbon dioxide to carbohydrate in the light-independent reactions.

Trapping light energy

Light energy is trapped by photosynthetic pigments. Different pigments absorb different wavelengths of light. The photosynthetic pigments of higher plants form two groups: the **chlorophylls** and the **carotenoids** *(table 1.1)*. Chlorophylls absorb mainly in the red and blue-violet regions of the light spectrum. They reflect green light, which is why plants look green. The structure of chlorophyll *a* is shown in *figure 1.7*. The carotenoids absorb mainly in the blue-violet region of the spectrum.

An **absorption spectrum** is a graph of the absorbance of different wavelengths of light by a pigment. The absorption spectra of chlorophyll *a* and *b*, and of the carotenoids can be seen in *figure 1.8a*.

An **action spectrum** is a graph of the rate of photosynthesis at different wavelengths of light *(figure 1.8b)*. This shows the effectiveness of the different wavelengths, which is, of course, related to their absorption and to their energy content. The shorter the wavelength, the greater the energy it contains.

Pigment		Colour
Chlorophylls:	chlorophyll *a*	yellow-green
	chlorophyll *b*	blue-green
Carotenoids:	β carotene	orange
	xanthophyll	yellow

Table 1.1 The colours of the commonly occurring photosynthetic pigments

In the process of photosynthesis, the light energy absorbed by the photosynthetic pigments is converted to chemical energy. The absorbed light energy excites electrons in the pigment molecules. If you illuminate a solution of chlorophyll *a* or *b* with ultraviolet light, you will see a red fluorescence. (In the absence of a safe ultraviolet light, you can illuminate the pigment with a standard fluorescent tube.) The ultraviolet light is absorbed and electrons are excited but, in a solution which only contains extracted pigment, the absorbed energy cannot usefully be passed on to do work. The electrons return to their unexcited state and the absorbed energy is transferred to the surroundings as thermal energy and as light at a longer (less energetic) wavelength than that which was

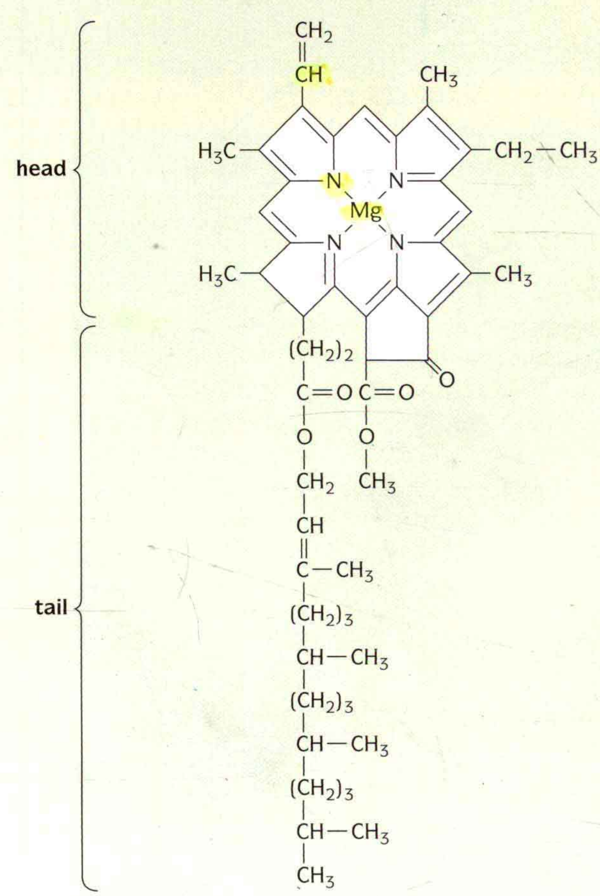
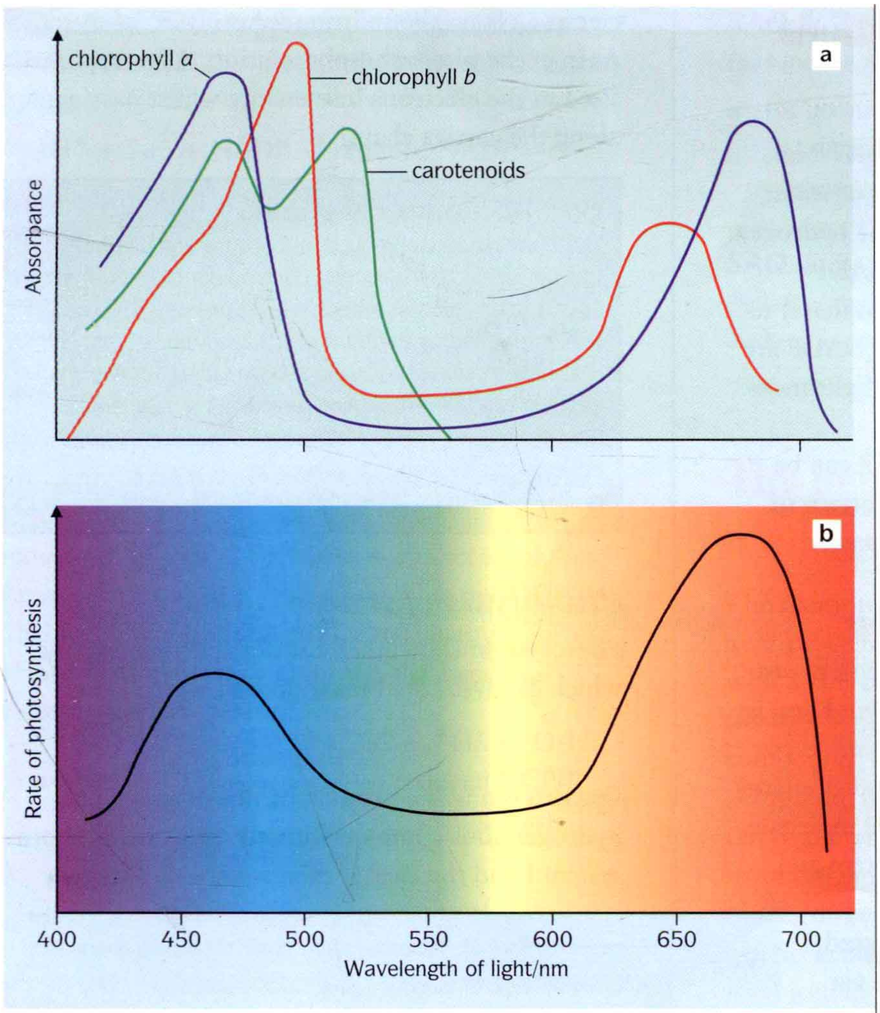


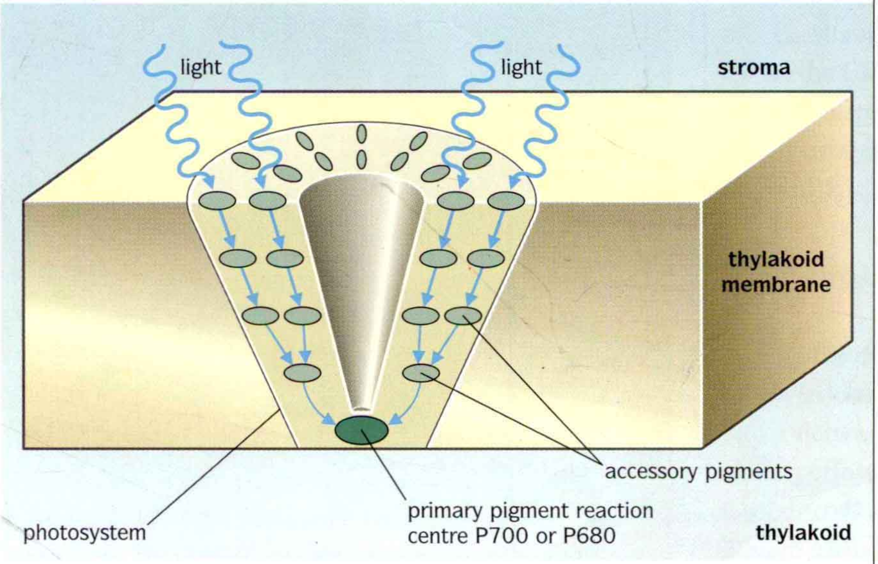
Figure 1.7 Structure of chlorophyll *a*.



● ***Figure 1.8***

a Absorption spectra of chlorophyll *a*, *b* and carotenoid pigments.

b Photosynthetic action spectrum.



● ***Figure 1.9*** A photosystem: a light-harvesting cluster of photosynthetic pigments. Only a few of the pigment molecules are shown.

absorbed, and is seen as the red fluorescence. In the functioning photosynthetic system it is this energy that drives the process of photosynthesis.

The photosynthetic pigments fall into two categories: **primary pigments** and **accessory pigments.** The primary pigments are two forms of chlorophyll *a* with slightly different absorption peaks. The accessory pigments include other forms of chlorophyll *a*, chlorophyll *b* and the carotenoids. The pigments are arranged in light-harvesting clusters called **photosystems.** In a photosystem, several hundred accessory pigment molecules surround a primary pigment molecule and the energy of the light absorbed by the different pigments is passed to the primary pigment *(figure 1.9)*. The primary pigments are said to act as **reaction centres.** **Photosystem I** is arranged around a molecule of chlorophyll *a* with a peak absorption at 700 nm. The reaction centre of photosystem I is therefore known as **P700.** **Photosystem II** is based on a molecule of chlorophyll *a* with a peak absorption of 680 nm. The reaction centre of photosystem II is therefore known as **P680.**

SAQ 1.1

Compare the absorption spectra shown in *figure 1.8a* with the action spectrum shown in *figure 1.8b*.

a Identify and explain any similarities in the absorption and action spectra.

b Identify and explain any differences between the absorption and action spectra.

The light-dependent reactions of photosynthesis

These reactions include the synthesis of ATP in **photophosphorylation** and the splitting of water by **photolysis** to give hydrogen ions. The hydrogen ions combine with a carrier molecule **NADP** (nicotinamide adenine dinucleotide phosphate) to make reduced NADP. ATP and reduced NADP are passed from the light-dependent to the light-independent reactions.

Photophosphorylation of ADP to ATP can be **cyclic** or **non-cyclic** depending on the pattern of electron flow in one or both photosystems.

Cyclic photophosphorylation

Cyclic photophosphorylation only involves photosystem I. Light is absorbed by photosystem I and is passed to chlorophyll *a* (P700). An electron in the chlorophyll *a* molecule is excited to a higher energy level and is emitted from the chlorophyll molecule. Instead of falling back into the photosystem and losing its energy as fluorescence, it is captured by an **electron acceptor** and passed back to a chlorophyll *a* (P700) molecule via a chain of **electron carriers**. During this process enough energy is released to synthesise ATP from ADP and an inorganic phosphate group (P_i). The ATP then passes to the light-independent reactions.

Non-cyclic photophosphorylation

Non-cyclic photophosphorylation involves *both* photosystems in the so-called 'Z-scheme' of electron flow *(figure 1.10)*. Light is absorbed by both photosystems and excited electrons are emitted from the primary pigments of both reaction centres (P680 and P700). These electrons are absorbed by electron acceptors and pass along chains of electron carriers leaving the photosystems positively charged. The P700 of photosystem I absorbs electrons from photosystem II. P680 receives replacement electrons from the splitting (photolysis) of water. As in cyclic photophosphorylation, ATP is synthesised as the electrons lose energy whilst passing along the carrier chain.

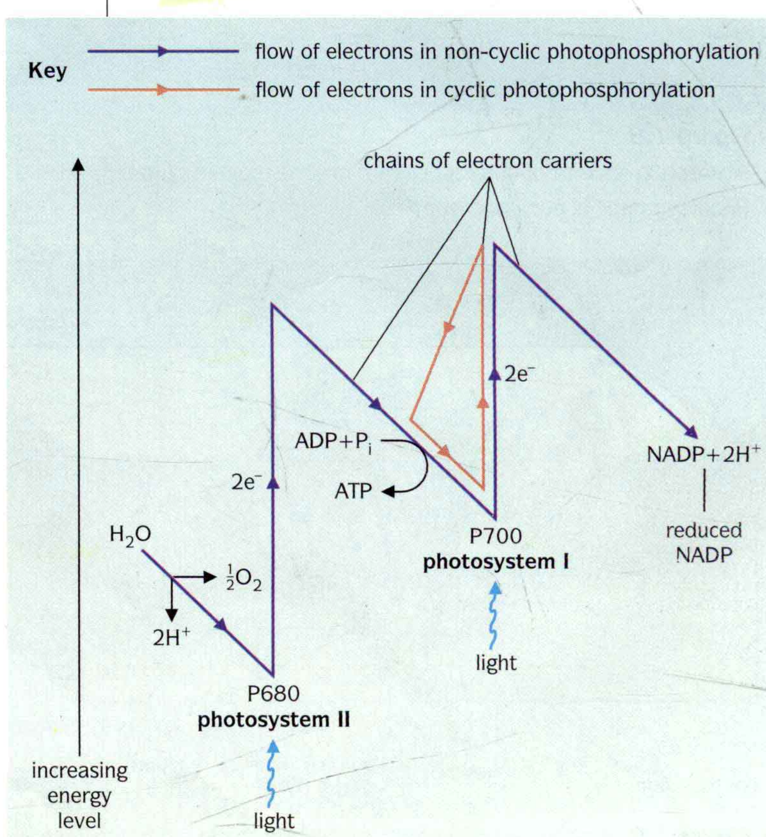
> **Box 1C Redox reactions**
>
> These are oxidation–reduction reactions and involve the transfer of electrons from an electron donor (reducing agent) to an electron acceptor (oxidising agent). Sometimes hydrogen atoms are transferred, so that dehydrogenation is equivalent to oxidation. Chains of electron carriers involve electrons passing via redox reactions from one carrier to the next. Such chains occur in both chloroplasts and mitochondria. During their passage, electrons fall from higher to lower energy states.

Photolysis of water

Photosystem II includes a water-splitting enzyme which catalyses the breakdown of water:

$$H_2O \rightarrow 2H^+ + 2e^- + \tfrac{1}{2}O_2$$

Oxygen is a waste product of this process. The hydrogen ions combine with electrons from photosystem I and the carrier molecule NADP to give



● *Figure 1.10* The 'Z' scheme of electron flow in photophosphorylation.

reduced NADP. This passes to the light independent reactions and is used in the synthesis of carbohydrate.

$$2H^+ + 2e^- + NADP \rightarrow \text{reduced NADP}$$

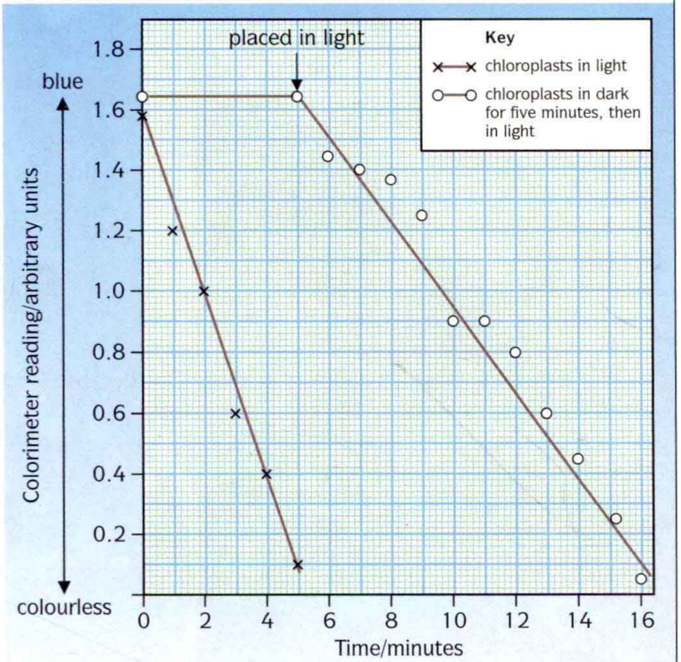
The photolysis of water can be demonstrated by the Hill reaction.

The Hill reaction

In 1939, Robert Hill showed that isolated chloroplasts had 'reducing power', and liberated oxygen from water in the presence of an oxidising agent. The 'reducing power' was demonstrated by using a redox agent *(box 1C)* which changed colour on reduction. Hill used Fe^{3+} ions as his acceptor, but various redox agents, such as the blue dye DCPIP (dichlorophenolindophenol), can substitute for the plant's NADP in this system. DCPIP becomes colourless when reduced.

$$\underset{\text{(blue)}}{\text{oxidised DCPIP}} \xrightarrow[H_2O \;\rightarrow\; \frac{1}{2}O_2]{\text{chloroplasts in light}} \underset{\text{(colourless)}}{\text{reduced DCPIP}}$$

Figure 1.11 shows classroom results of this reaction.



● ***Figure 1.11*** The Hill reaction. Chloroplasts were extracted from lettuce and placed in buffer with DCPIP. The colorimeter reading is proportional to the amount of DCPIP remaining unreduced.

SAQ 1.2

Examine the two curves shown in *figure 1.11* and explain:

a the downward trend of the two curves;

b the differences between the two curves.

SAQ 1.3

Explain what contribution the discovery of the Hill reaction made to an understanding of the process of photosynthesis.

The light-independent reactions of photosynthesis

The fixation of carbon dioxide is a light-independent process in which carbon dioxide combines with a five-carbon sugar, **ribulose bisphosphate (RuBP)**, to give two molecules of a three-carbon compound, **glycerate 3-phosphate (GP)**. (This compound is also sometimes known as PGA.) GP, in the presence of ATP and reduced NADP from the light stages, is reduced to triose phosphate (three-carbon sugar).

This is the point at which carbohydrate is produced in photosynthesis. Some of these triose phosphates condense to form hexose phosphates, sucrose, starch and cellulose or are used to make amino acids and lipids. Others regenerate RuBP. This cycle of events was worked out by Calvin, Benson and Bassham between 1946 and 1953, and is usually called the **Calvin cycle** *(figure 1.12)*. The enzyme ribulose bisphosphate carboxylase (RuBISCO), which catalyses the combination of carbon dioxide and RuBP, is the most common enzyme in the world.

Leaf structure and function

The leaf is the main photosynthetic organ in dicotyledons. It has a broad, thin **lamina**, a **midrib** and a **network of veins**. It may also have a leaf stalk (**petiole**). *Figure 1.13* is a photomicrograph of a section of a typical leaf from a mesophyte, that is a plant adapted for 'middling' terrestrial conditions (it is not adapted for living in water nor for withstanding excessive drought).

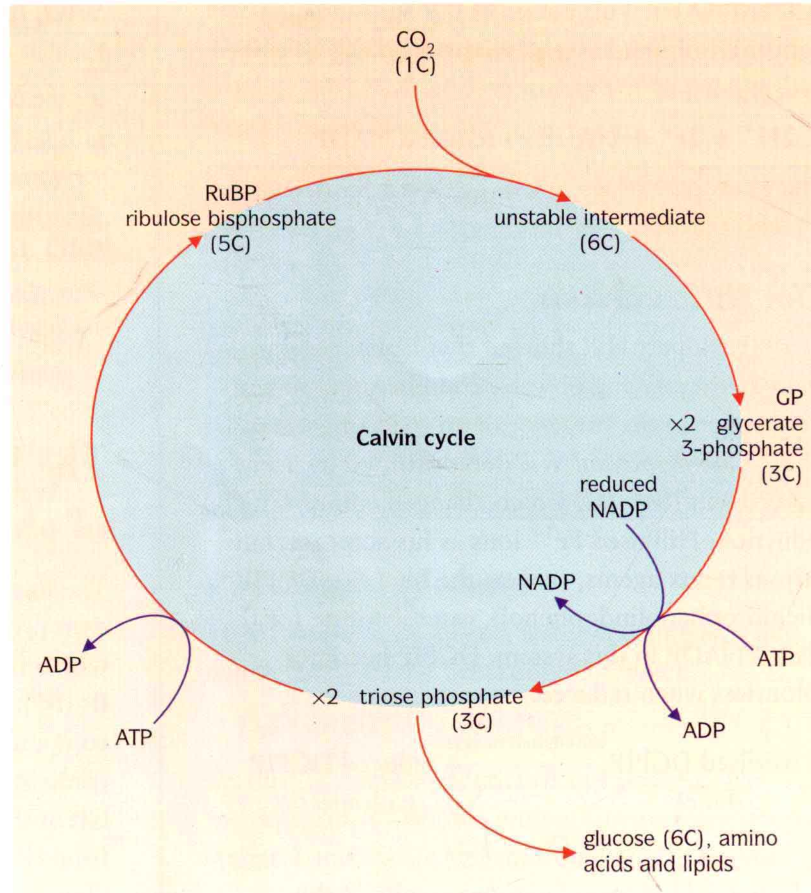
To perform its function the leaf must:

- contain chlorophyll and other photosynthetic pigments arranged in such a way that they can absorb light;
- absorb carbon dioxide and dispose of the waste product oxygen;
- have a water supply and be able to export manufactured carbohydrate to the rest of the plant.

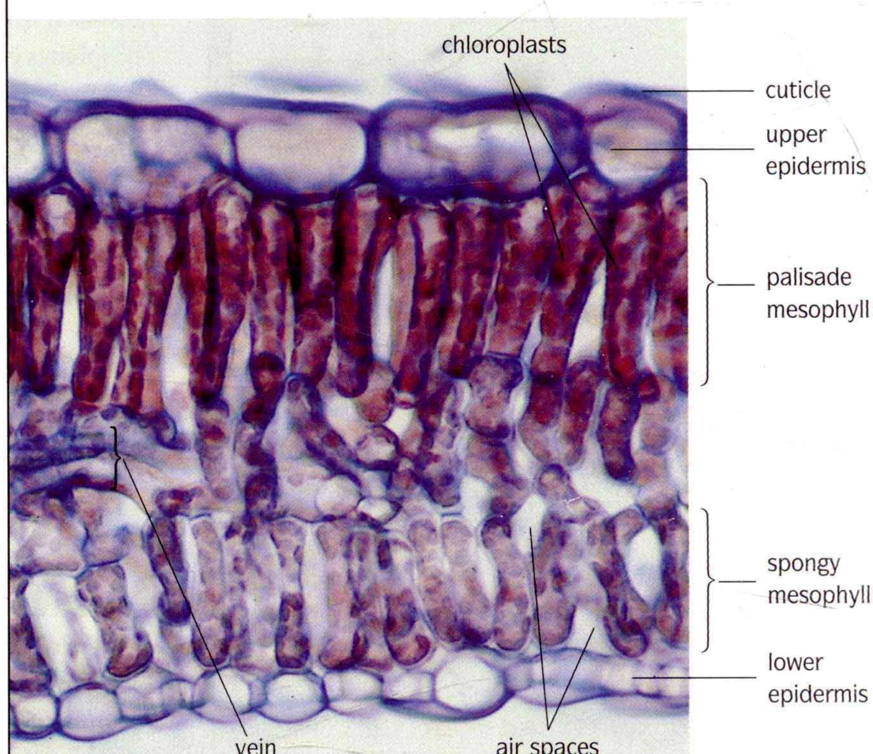
The large surface area of the lamina makes it easier to absorb light, and its thinness minimises the diffusion pathway for gaseous exchange. The arrangement of leaves on the plant (the leaf mosaic) helps the plant to absorb as much light as possible.

The upper **epidermis** is made of thin, flat, transparent cells which allow light through to the cells of the **mesophyll** below, where photosynthesis takes place. A waxy transparent **cuticle**, which is secreted by the epidermal cells, provides a watertight layer. The cuticle and epidermis together form a protective layer.

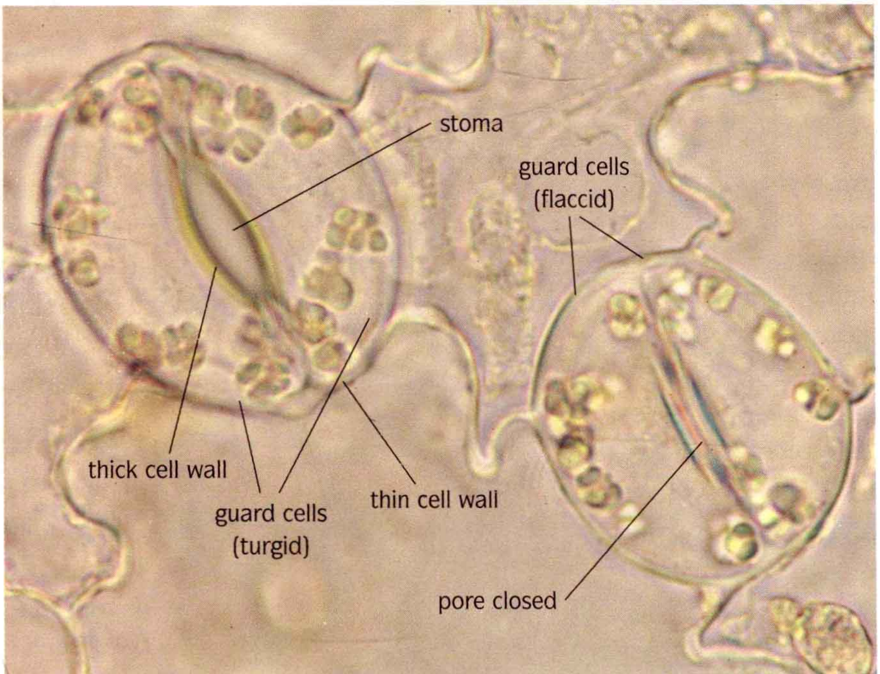
The structure of the lower epidermis is similar to that of the upper, except that most mesophytes have many **stomata** in the lower epidermis. (Some have a few stomata in the upper epidermis also.) Stomata are pores in the epidermis through which diffusion of gases occurs. Each stoma is bounded by two sausage-shaped **guard cells** (*figure 1.14*). Changes in the turgidity of these guard cells cause them to change shape so that they open and close the pore. When the guard cells gain water,



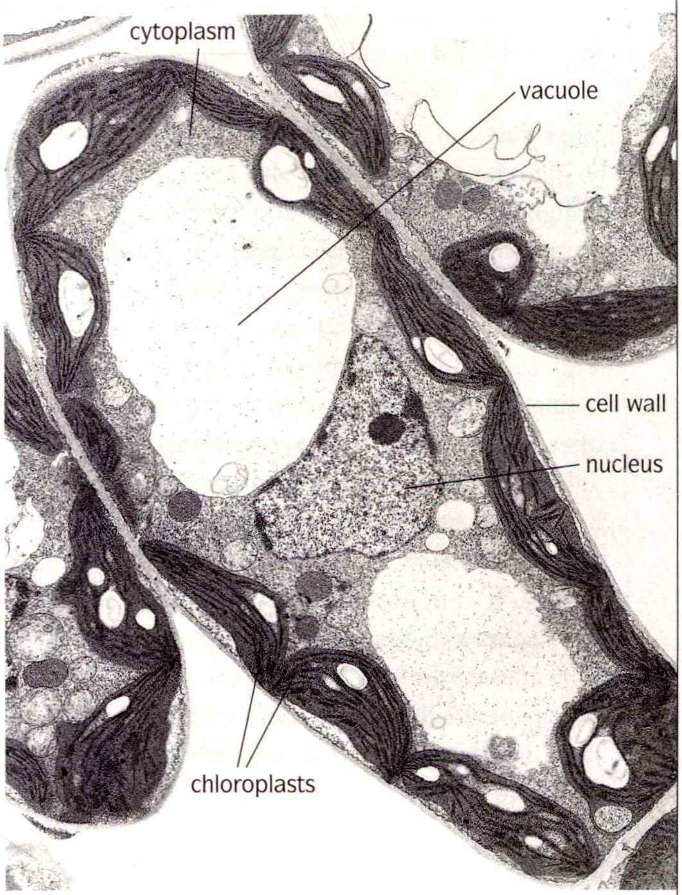
● ***Figure 1.12*** The Calvin cycle.



● ***Figure 1.13*** Photomicrograph of a TS of *Hypericum* leaf (× 1600).



● ***Figure 1.14*** Photomicrograph of stomata and guard cells in *Tradescantia* leaf epidermis (× 5000).



● ***Figure 1.15*** Transmission electron micrograph (TEM) of a palisade cell from soya bean leaf (× 6000).

the pore opens; as they lose water it closes. Guard cells have unevenly thickened cell walls. The wall adjacent to the pore is very thick, whilst the wall furthest from the pore is thin. Bundles of cellulose microfibrils are arranged as hoops around the cells so that, as the cell becomes turgid, these hoops ensure that the cell mostly increases in length and not diameter. Since the ends of the two guard cells are joined and the thin outer wall bends more readily than the thick inner one, the guard cells become curved. This makes the pore between the cells open.

Guard cells gain and lose water by osmosis. A decrease in water potential is needed before water can enter the cells by osmosis. This decrease is achieved by the active uptake of potassium ions into the guard cells, using energy from ATP.

The structure of a **palisade cell** is shown in *figure 1.15*. The palisade mesophyll is the main site of photosynthesis, as there are more chloroplasts per cell than in the spongy mesophyll. The cells show several adaptations for light absorption.

- They are long cylinders arranged at right-angles to the upper epidermis. This reduces the number of light-absorbing cross walls in the upper part of the leaf so that as much light as possible can reach the chloroplasts.
- The cells have a large vacuole with a thin peripheral layer of cytoplasm. This restricts the chloroplasts to a layer near the outside of the cell where light can reach them most easily.
- The chloroplasts can be moved (by proteins in the cytoplasm – they cannot move themselves) within the cells, to absorb the most light or to protect the chloroplasts from excessive light intensities.

The palisade cells also show adaptations for gaseous exchange.

- The cylindrical cells pack together with long, narrow air spaces between them. This gives a large surface area of contact between cell and air.

- The cell walls are thin, so that gases can diffuse through them more easily.

Spongy mesophyll is mainly adapted as a surface for the exchange of carbon dioxide and oxygen. The cells contain chloroplasts, but in smaller numbers than in palisade cells. Photosynthesis occurs in the spongy mesophyll only at high light intensities. The irregular packing of the cells and the large air spaces thus produced provide a large surface area of moist cell wall for gaseous exchange.

The veins in the leaf help to support the large surface area of the leaf. They contain xylem, which brings in the water necessary for photosynthesis and for cell turgor, and phloem, which takes the products of photosynthesis to other parts of the plant.

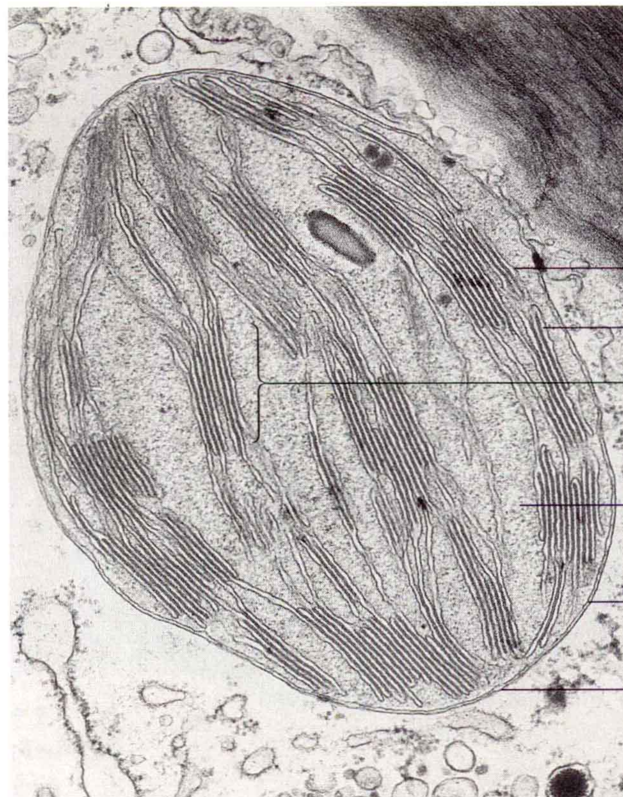


Figure 1.16 TEM of a chloroplast from *Potamogeton* leaf (× 27000)

Chloroplast structure and function

In eukaryotic organisms, the photosynthetic organelle is the chloroplast. In dicotyledons, chloroplasts can be seen with a light microscope and appear as biconvex discs about 3–10 μm in diameter. There may be only a few chloroplasts in a cell or as many as 100 in some palisade mesophyll cells.

The structure of a chloroplast is shown in *figure 1.16*. Each chloroplast is surrounded by an **envelope** of two phospholipid membranes. A system of membranes also runs through the ground substance, or **stroma**. The membrane system is the site of the light-dependent reactions of photosynthesis. It consists of a series of flattened fluid-filled sacs, or **thylakoids**, which in places form stacks, called **grana**, that are joined to one another by membranes. The membranes of the grana provide a large surface area which holds the pigments, enzymes and electron carriers needed for the light-dependent reactions. They make it possible for a large number of pigment molecules to be arranged so that they can absorb as much light as necessary. The pigment molecules are also arranged in particular light-harvesting clusters for efficient light absorption. In each photosystem the different pigments are arranged in the thylakoid in funnel-like structures (*figure 1.9*). Each pigment passes energy to the next member of the cluster, finally 'feeding' it to the chlorophyll *a* reaction centre (either P700 or P680). The membranes of the grana hold ATP synthetase and are the site of ATP synthesis by chemiosmosis (page 3).

The stroma is the site of the light-independent reactions. It contains the enzymes of the Calvin cycle, sugars and organic acids. It bathes the membranes of the grana and so can receive the products of the light-dependent reactions. Also within the stroma are small ribosomes, a loop of DNA, lipid droplets and starch grains. The loop of DNA codes for some of the chloroplast proteins, which are made by the chloroplast's ribosomes. However, other chloroplast proteins are coded for by the nuclear DNA.