

Chapter 1

Photosynthesis and ATP synthesis

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

- a** describe the structure of a dicotyledonous leaf, a palisade cell and a chloroplast, relating these structures to their roles in the process of photosynthesis;
- b** make drawings from prepared slides of a transverse section of a dicotyledonous leaf and a palisade cell;
- c** explain the process of photophosphorylation;
- d** outline the essential stages of the Calvin cycle involving the light-independent fixation of carbon dioxide;
- e** discuss the concept of limiting factors in photosynthesis;
- f** discuss the extent to which knowledge of limiting factors can be used to improve plant productivity.

Humans, like all animals and fungi, are **heterotrophs**. This means that we need to eat food containing organic molecules, especially carbohydrates, fats and proteins. These organic molecules are our only source of energy.

Plants, however, do not need to take in any organic molecules at all. They obtain their energy from sunlight. They can use this energy to build their own organic molecules for themselves, using simple inorganic substances. They first produce carbohydrates from carbon dioxide and water, by **photosynthesis**. They can then use these carbohydrates, plus inorganic ions such as nitrate, phosphate and magnesium, to manufacture all the organic molecules that they need. Organisms that feed in this way – self-sufficient, not needing any organic molecules that another organism has made – are **autotrophs**.

So heterotrophs depend on autotrophs for the supply of organic molecules on which they feed. Some heterotrophs feed directly on plants, while others feed further along a food chain. But eventually all of an animal's or fungus's food can be traced back to plants, and the energy of sunlight.

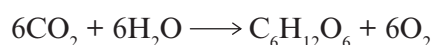
In this chapter, we will look in detail at how plants transfer energy from sunlight to chemical energy in organic molecules. In Chapter 2, we will see how all living organisms can then release the

trapped energy from these molecules and convert it into a form that their cells can use. This process is called **respiration**, and it involves oxidation of the energy-containing organic substances, forming another energy-containing substance called **ATP**. Every cell has to make its own ATP. You can find out more about ATP in Chapter 2.

An overview of photosynthesis

Photosynthesis happens in several different kinds of organisms, not only plants. There are many kinds of bacteria that can photosynthesise. Photosynthesis also takes place in **phytoplankton**, tiny organisms that float in the upper layers of the sea and lakes. Here, though, we will concentrate on photosynthesis in green plants, which takes place in the chloroplasts of several plant tissues, especially the palisade mesophyll and spongy mesophyll tissues of leaves (Figure 1.1). This photosynthesis is the ultimate source of almost all of our food.

The overall equation for photosynthesis is:



The xylem tissues of roots, stems and leaf vascular bundles bring water to the photosynthesising cells of the leaf. The carbon dioxide diffuses into the leaf through stomata, the tiny holes usually found in the lower epidermis of the leaf. It then

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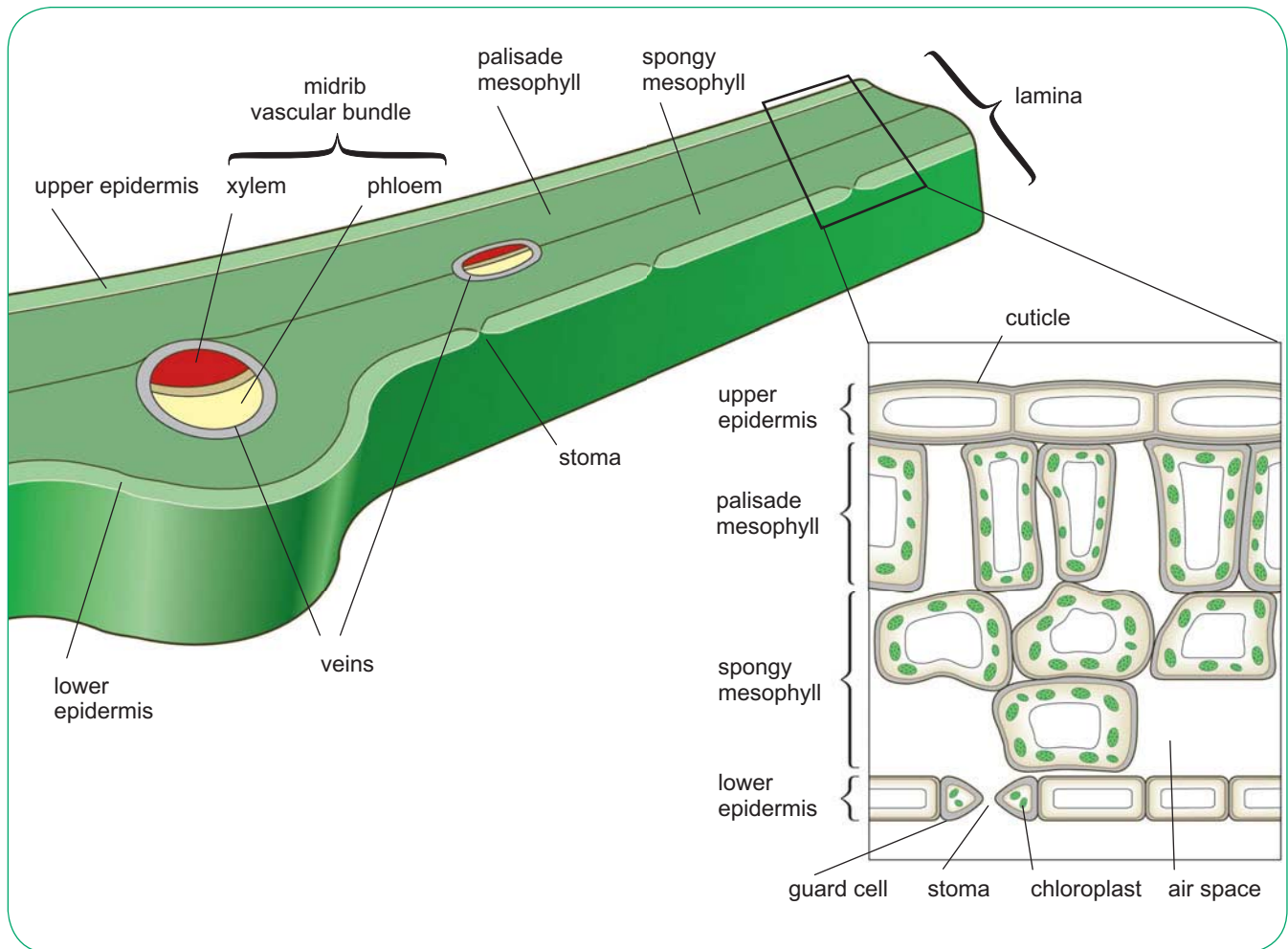


Figure 1.1 The structure of a leaf.

diffuses through air spaces and into mesophyll cells and finally into chloroplasts, where photosynthesis takes place.

Leaf structure and function

The leaf has a broad, thin lamina, a midrib and a network of veins.

It may also have a leaf stalk (petiole). Figure 1.2 is a photomicrograph of a section of a typical leaf from a mesophyte – that is, a plant adapted for normal terrestrial conditions (it is adapted neither 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;

- be able to 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 and thinness of the lamina allows it to absorb a lot of light. Its thinness minimises the length of 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 preventing water loss other than through the stomata, which can be closed in dry

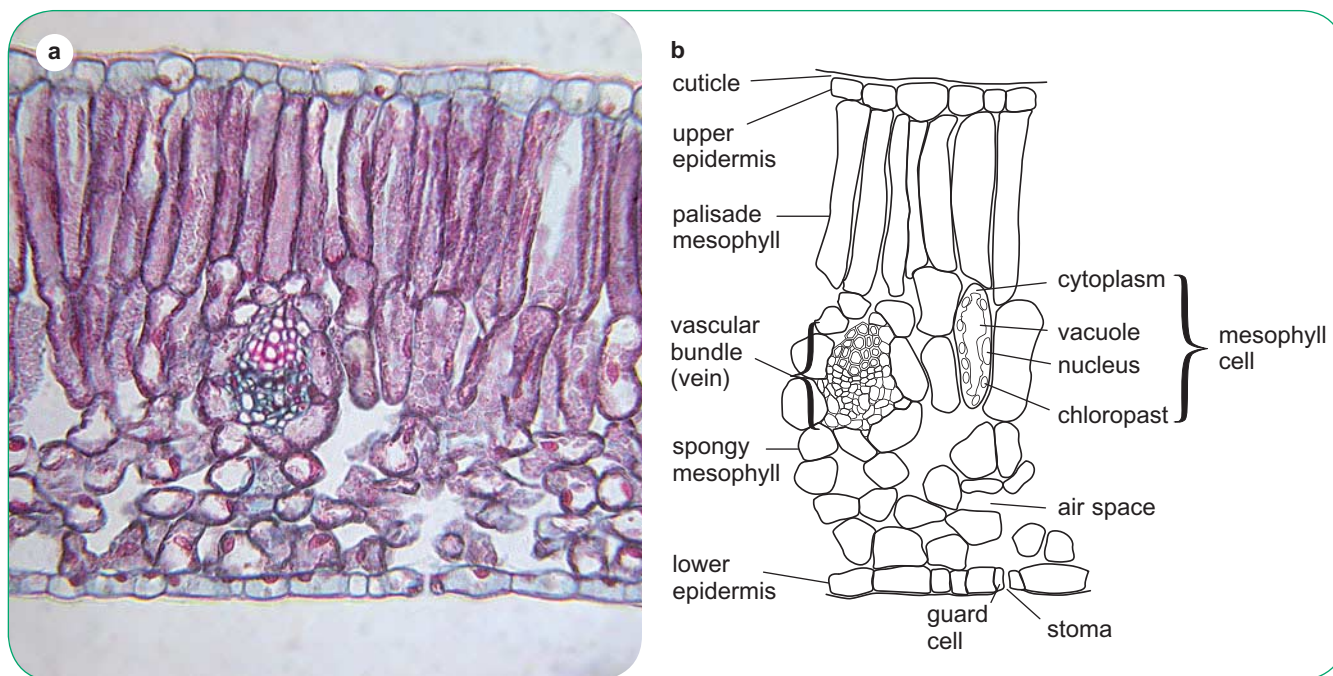


Figure 1.2 a Photomicrograph of a TS of a leaf ($\times 300$), b drawing of part of a.

conditions. The cuticle and epidermis together form a protective layer against microorganisms and some insects.

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 the pores in the epidermis through which diffusion of gases occurs, including carbon dioxide. Each stoma is bounded by two sausage-shaped guard cells (Figure 1.3). Changes in the

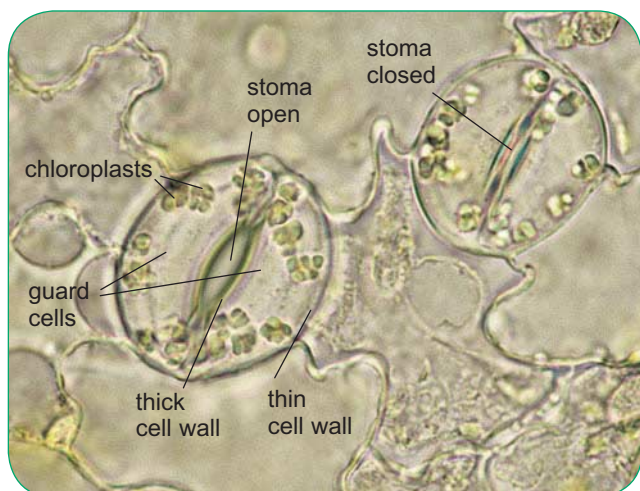


Figure 1.3 Photomicrograph of stomata and guard cells in *Tradescantia* leaf epidermis ($\times 2000$).

turgidity of these guard cells cause them to change shape so that they open and close the pore. When the guard cells gain water, 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 each guard cell and, 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 is achieved by the active removal of hydrogen ions, using energy from ATP, and then intake of potassium ions (indirect active transport).

An electron micrograph and a drawing of a palisade cell is shown in Unit 1 on page 41. Figure 1.4 shows a photomicrograph of palisade cells. The palisade mesophyll is the main site of photosynthesis, as there are more chloroplasts per cell than in the spongy mesophyll.

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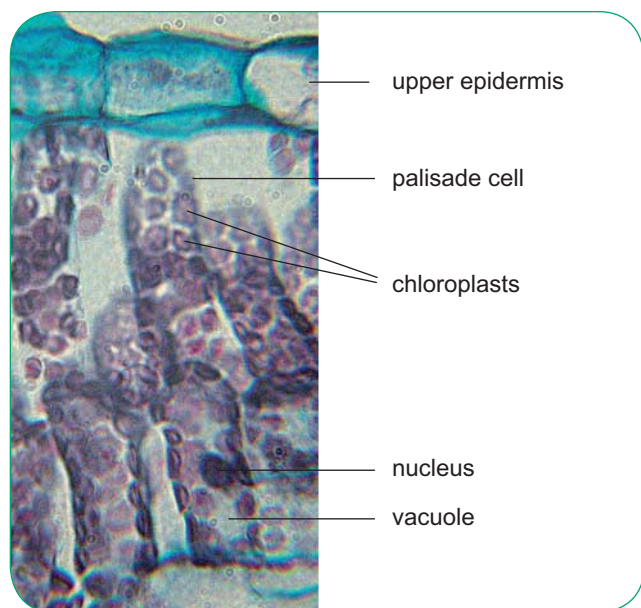


Figure 1.4 Photomicrograph of palisade cells ($\times 600$).

Palisade 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, as 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.

Chloroplast structure and function

The equation on page 1 is a simplification of photosynthesis. In reality photosynthesis is a complex **metabolic pathway** – a series of reactions linked to each other in numerous steps, many of which are catalysed by enzymes. These reactions take place in two stages. The first is the **light-dependent stage**, and this is followed by the **light-independent stage**. Both of these stages take place inside chloroplasts within cells of the leaves and often stems of plants (Figure 1.5).

Figure 1.6 shows the structure of a typical chloroplast. Each cell in a photosynthesising tissue may have ten or even 100 chloroplasts inside it.

A chloroplast is surrounded by two membranes, forming an **envelope**. There are more membranes inside the chloroplast, which are arranged so that they enclose fluid-filled sacs between them. The membranes are called **lamellae** and the fluid-

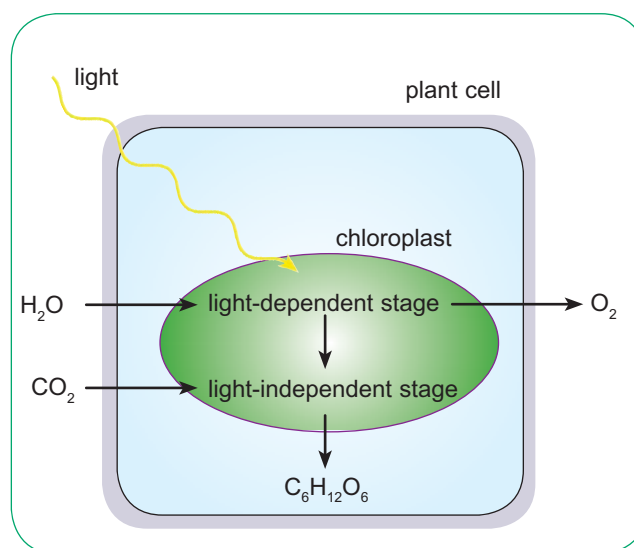


Figure 1.5 The stages of photosynthesis.

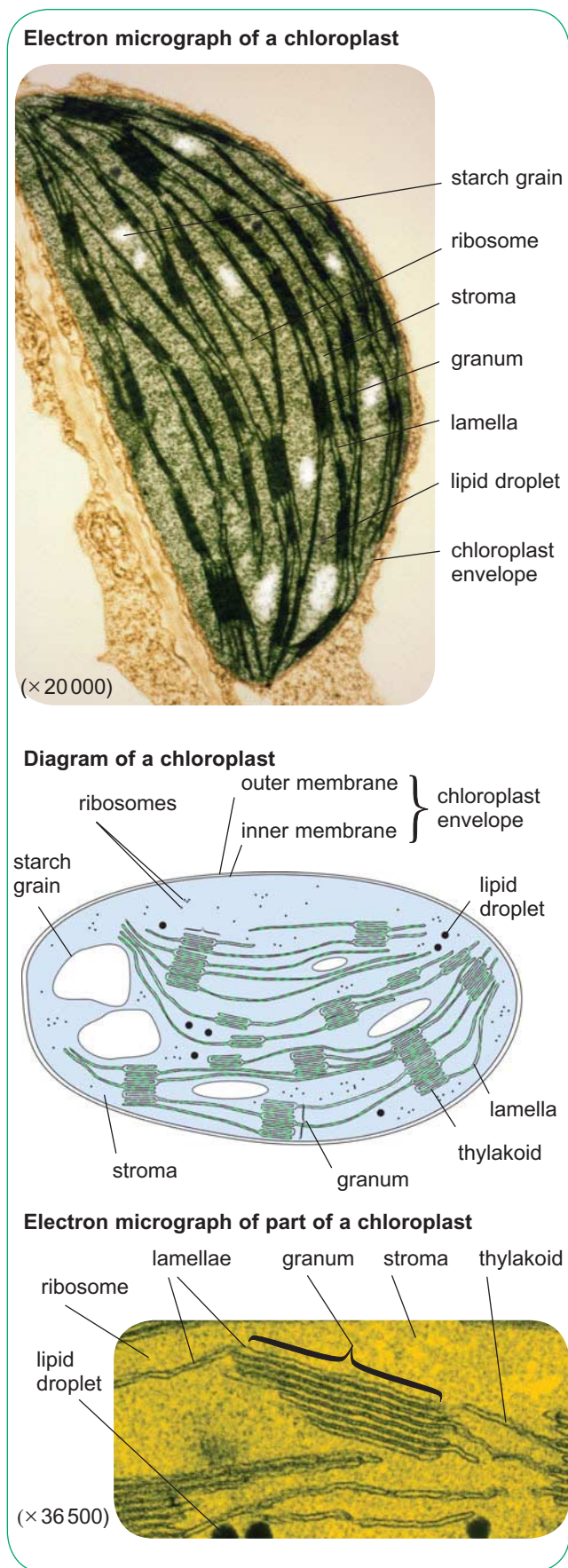


Figure 1.6 The structure of a chloroplast.

filled sacs are **thylakoids**. In some parts of the chloroplasts, the thylakoids are stacked up like a pile of pancakes, and these stacks are called **grana**. The ‘background material’ inside the chloroplast is called the **stroma**.

Embedded tightly in the membranes inside the chloroplast are several different kinds of **photosynthetic pigments**. These are coloured substances that absorb energy from certain wavelengths (colours) of light. The most abundant pigment is **chlorophyll**, which comes in two forms, **chlorophyll a** and **chlorophyll b**.

The stacked membranes have a large surface area and so their photosynthetic pigments can capture light very efficiently. The transformation of light energy into chemical energy is carried out by other chemicals in the membranes closely associated with the photosynthetic pigments. The membranes not only hold chemicals allowing them to function correctly, but also create the thylakoid spaces. The space inside each thylakoid, the thylakoid lumen, is needed for the accumulation of hydrogen ions, H^+ , used in the production of ATP (see page 7 and Chapter 2).

Chloroplasts often contain **starch grains**, because starch is the form in which plants store the carbohydrate that they make by photosynthesis. They also contain **ribosomes** and their own small circular strand of **DNA**. (You may remember that chloroplasts are thought to have evolved from bacteria that first invaded eukaryotic cells over a thousand million years ago.)

SAQ

- 1 List the features of a chloroplast that aid photosynthesis.

Photosynthetic pigments

A pigment is a substance whose molecules absorb some wavelengths (colours) of light, but not others. The wavelengths it does not absorb are either reflected or transmitted through the substance. These unabsorbed wavelengths reach our eyes, so we see the pigment in these colours.

The majority of the pigments in a chloroplast are chlorophyll *a* and chlorophyll *b* (Figure 1.7).

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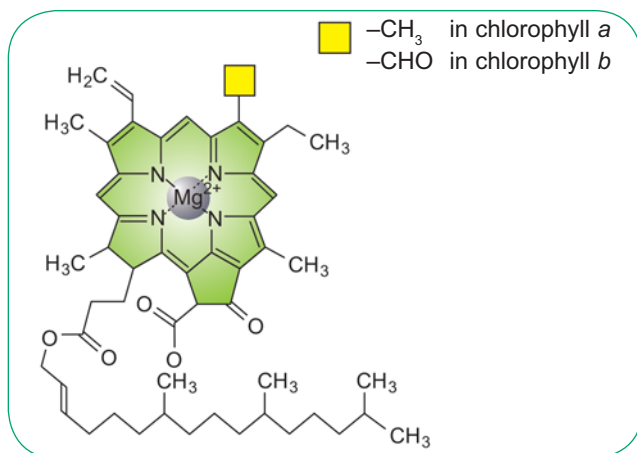


Figure 1.7 A chlorophyll molecule.

These are the primary pigments. Both types of chlorophyll absorb similar wavelengths of light, but chlorophyll *a* absorbs slightly longer wavelengths than chlorophyll *b*. This can be shown in a graph called an **absorption spectrum** (Figure 1.8).

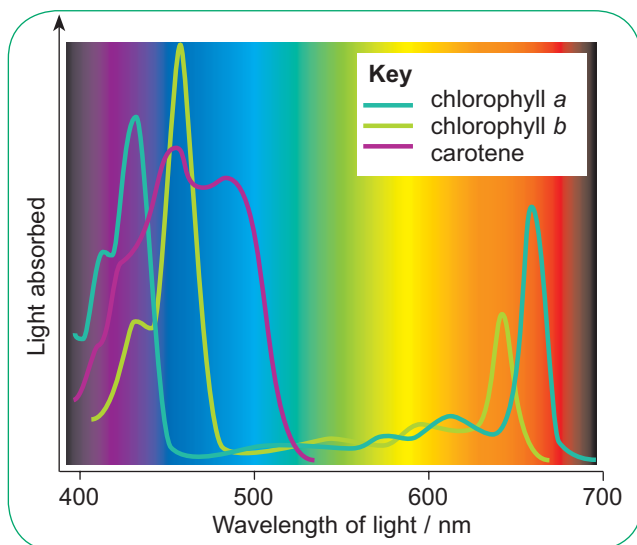


Figure 1.8 Absorption spectra for chlorophyll and carotene.

Other pigments found in chloroplasts include **carotenoids**, such as carotene and xanthophylls. These absorb a wide range of short wavelength light, including more blue-green light than the chlorophylls. They are **accessory pigments**. They help by absorbing wavelengths of light that would otherwise not be used by the plant. They pass on some of this energy to chlorophyll. They probably also help to protect chlorophyll from damage by very intense light.

SAQ

- 2 a** Use Figure 1.8 to explain why chlorophyll looks green.
b What colour are carotenoids?

The light-dependent stage

This stage of photosynthesis takes place on the thylakoids inside the chloroplast. It involves the absorption of light energy by chlorophyll, and the use of that energy and the products from splitting water to make ATP and reduced NADP.

Photosystems

The chlorophyll molecules are arranged in clusters called **photosystems** in the thylakoid membranes (Figure 1.9). Each photosystem spans the membrane, and contains protein molecules and pigment molecules. Energy is captured from

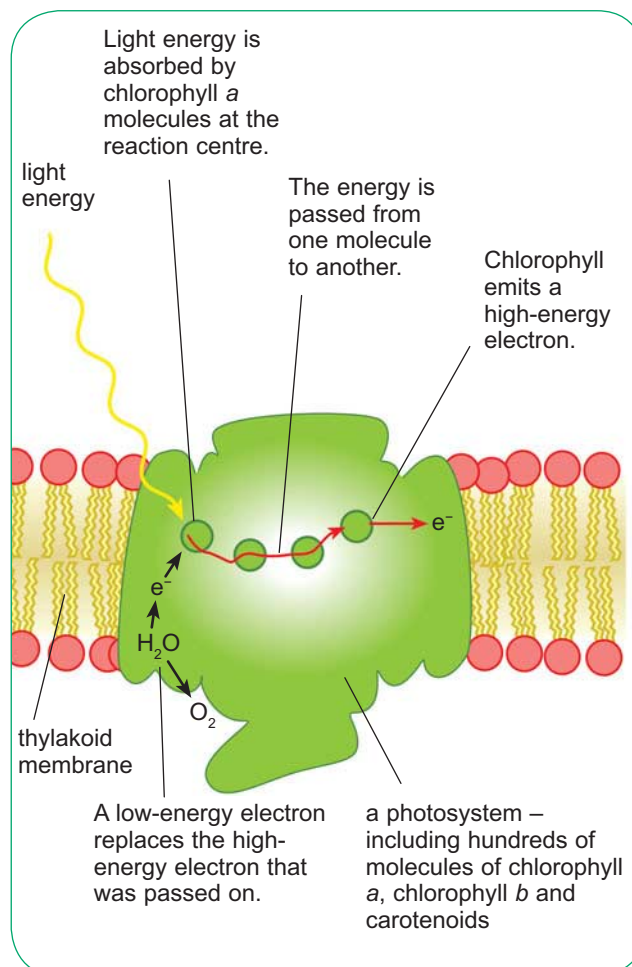


Figure 1.9 A photosystem in a thylakoid membrane showing photoactivation of chlorophyll.

photons of light that hit the photosystem, and is funnelled down to a pair of molecules at the **reaction centre** of the photosystem complex.

There are two different sorts of photosystem, **PSI** and **PSII**, both with a small number of molecules of chlorophyll *a* at the reaction centre.

Photophosphorylation

Photophosphorylation means ‘phosphorylation using light’. It refers to the production of ATP, by combining a phosphate group with ADP, using energy that originally came from light:



Photophosphorylation happens when an electron is passed along a series of **electron carriers**, forming an **electron transport chain** in the thylakoid membranes. The electron starts off with a lot of energy, and it gradually loses some of it as it moves from one carrier to the next. The energy is used to cause a phosphate group to react with ADP.

Cyclic photophosphorylation

This process involves only PSI, not PSII. It results in the formation of ATP, but not reduced NADP (Figure 1.10).

Light is absorbed by PSI and the energy passed on to electrons in the chlorophyll *a* molecules at the reaction centre. In each chlorophyll *a* molecule, one of the electrons becomes so energetic that it

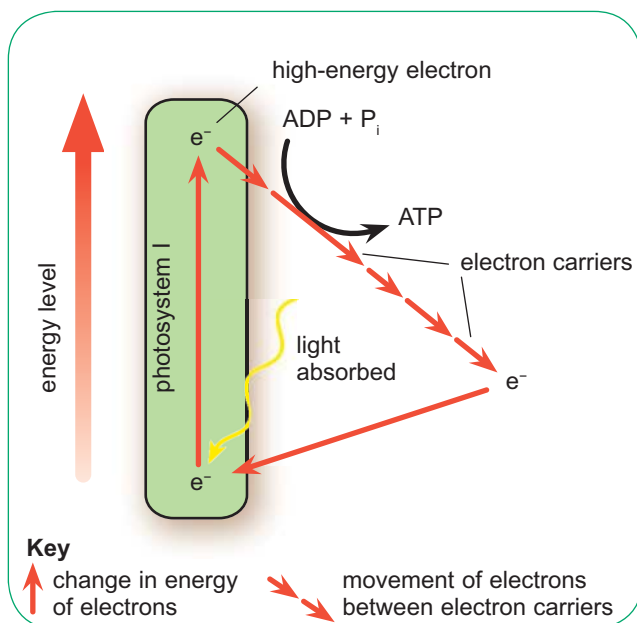


Figure 1.10 Cyclic photophosphorylation.

leaves the chlorophyll molecules completely. The electron is then passed along the chain of electron carriers. The energy from the electron is used to make ATP. The electron, now having lost its extra energy, eventually returns to chlorophyll *a* in PSI.

Non-cyclic photophosphorylation

This process involves both kinds of photosystem. It results not only in the production of ATP, but also of reduced NADP.

Light hitting either PSI or PSII causes electrons to be emitted. The electrons from PSII pass down the electron carrier chain, generating ATP by photophosphorylation. However, instead of going back to PSII, the electrons instead replace the electrons lost from PSI.

The phosphorylation of ADP to ATP involves the movement of H^+ across the thylakoid membrane. This process also occurs in respiration and is described in detail in Chapter 2.

The electrons emitted from PSI are not used to make ATP. Instead, they help to reduce NADP.

For this to happen, hydrogen ions are required. These come from another event that happens when light hits PSII. PSII contains an enzyme that splits water when it is activated by light. The reaction is called **photolysis**:



The hydrogen ions are taken up by NADP, forming reduced NADP. The electrons replace the ones that were emitted from PSII when light hit it. The oxygen diffuses out of the chloroplast and eventually out of the leaf, as an excretory product.

The Z-scheme

The **Z-scheme** is simply a way of summarising what happens to electrons during the light-dependent reactions. It is a kind of graph, with the *y*-axis indicating the ‘energy level’ of the electron (Figure 1.11).

Start at the bottom left, where light hits photosystem II. The red vertical line going up shows the increase in the energy level of electrons as they are emitted from this photosystem. You can also see where these electrons came from – the splitting of water molecules. (In fact, it probably isn’t the same electrons – but the electrons from the

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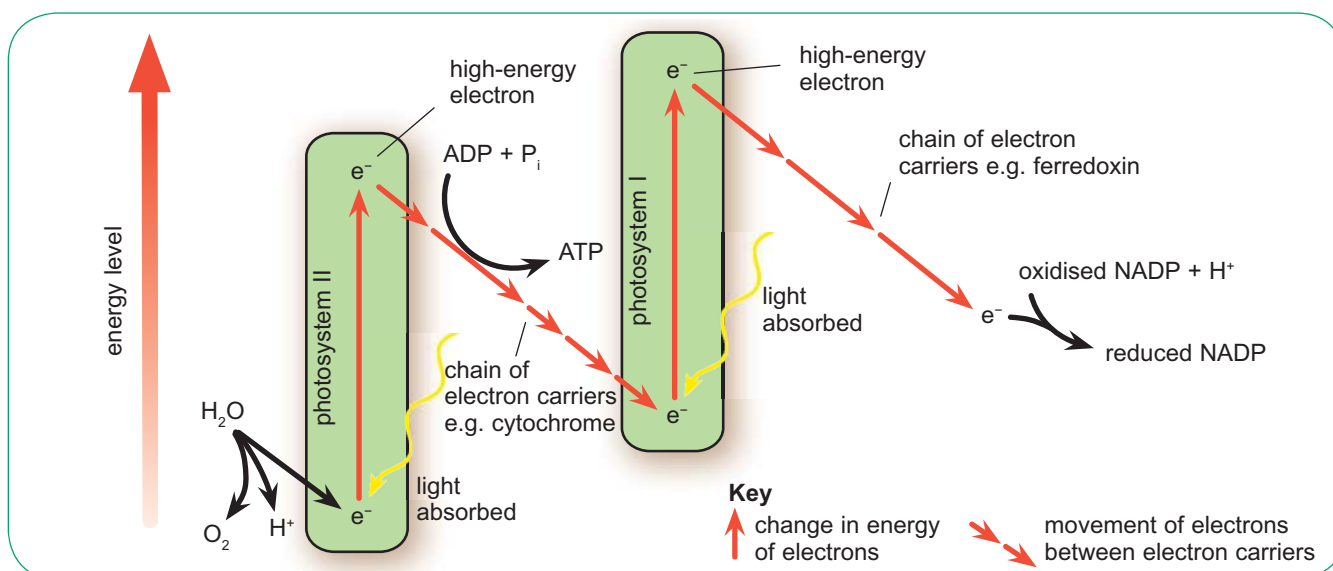


Figure 1.11 The Z-scheme, summarising non-cyclic photophosphorylation.

water replace the ones that are emitted from the photosystem.)

If you keep following the vertical line showing the increasing energy in the electrons, you arrive at a point where it starts a steep dive downwards. This shows the electrons losing their energy as they pass along the electron carrier chain. Eventually they arrive at photosystem I.

You can then track the movement of the electrons to a higher energy level when PSI is hit by light, before they fall back downwards as they lose energy and become part of a reduced NADP molecule.

The light-independent stage

Now the ATP and reduced NADP that have been formed in the light-dependent stage are used to help to produce carbohydrates from carbon dioxide. These events take place in the stroma of the chloroplast. The cyclic series of reactions is known as the Calvin cycle (Figure 1.12).

The chloroplast stroma contains an enzyme called **rubisco** (its full name is ribulose biphosphate carboxylase). This is thought to be the most abundant enzyme in the world. Its function is to catalyse the reaction in which carbon dioxide combines with a substance called **RuBP**

SAQ

3 Copy and complete the table to compare cyclic and non-cyclic photophosphorylation.

(If a box in a particular row is not applicable, write n/a.)

	Cyclic photophosphorylation	Non-cyclic photophosphorylation
Is PSI involved?		
Is PSII involved?		
Where does PSI obtain replacement electrons from?		
Where does PSII obtain replacement electrons from?		
Is ATP made?		
Is reduced NADP made?		

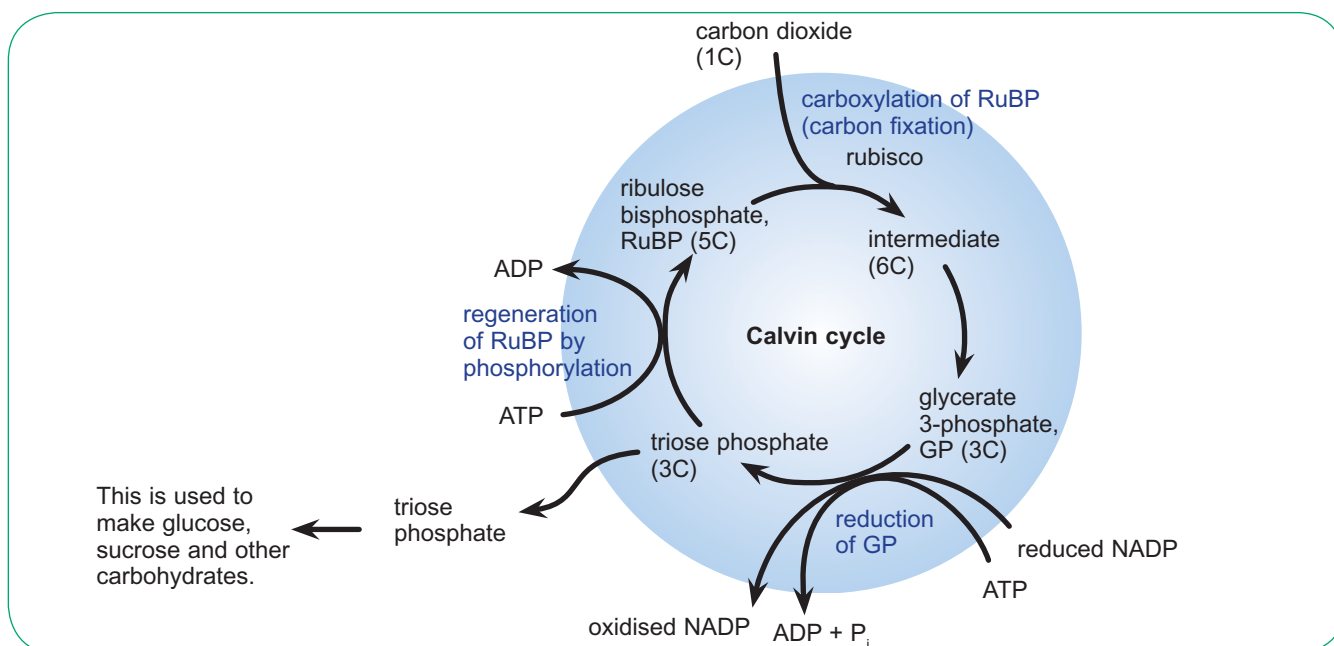


Figure 1.12 The Calvin cycle.

(ribulose biphosphate).

RuBP molecules each contain five atoms of carbon. The reaction with carbon dioxide therefore produces a six-carbon molecule, but this immediately splits to form two three-carbon molecules. This three-carbon substance is **glycerate 3-phosphate**, usually known as **GP**. An alternative name is phosphoglyceric acid (PGA).

Now the two products of the light-dependent stages come into play. The reduced NADP and the ATP are used to provide energy and phosphate groups, which change the GP into a three-carbon sugar called **triose phosphate (TP or GALP)**. This is the first carbohydrate that is made in photosynthesis.

There are many possible fates of the triose phosphate. Five-sixths of it are used to regenerate RuBP. The remainder can be converted into other carbohydrates. For example, two triose phosphates can combine to produce a hexose phosphate molecule. From these, glucose, fructose, sucrose, starch and cellulose can be formed.

The triose phosphate can also be used to make lipids and amino acids. For amino acid production, nitrogen needs to be added, which plants obtain from the soil in the form of nitrate ions or ammonium ions.

SAQ

- 4 Suggest what happens to the ADP, inorganic phosphate and NADP that are formed during the Calvin cycle.

Factors affecting the rate of photosynthesis

Photosynthesis requires several inputs. It needs raw materials in the form of carbon dioxide and water, and energy in the form of sunlight. The light-independent stage also requires a reasonably high temperature, because the rates of reactions are affected by the kinetic energy of the molecules involved.

If any of these requirements is in short supply, it can limit the rate at which the reactions of photosynthesis are able to take place.

Light intensity

Light provides the energy that drives the light-dependent reactions, so it is obvious that when there is no light, there is no photosynthesis. If we provide a plant with more light, then it will photosynthesise faster.

However, this can only happen up to a point. We would eventually reach a light intensity where, if we give the plant more light, its rate

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of photosynthesis does not change. We can say that 'light saturation' has occurred. Some other factor, such as the availability of carbon dioxide or the quantity of chlorophyll in the plant's leaves, is preventing the rate of photosynthesis from continuing to increase.

This relationship is shown in Figure 1.13. Over the first part of the curve, we can see that rate of photosynthesis does indeed increase as light intensity increases. For these light intensities, light is a **limiting factor**. The light intensity is limiting the rate of photosynthesis. If we give the plant more light, then it will photosynthesise faster.

But, from point X onwards, increasing the light intensity has no effect on the rate of photosynthesis. Along this part of the curve, light is no longer a limiting factor. Something else is. It is most likely to be the carbon dioxide concentration.

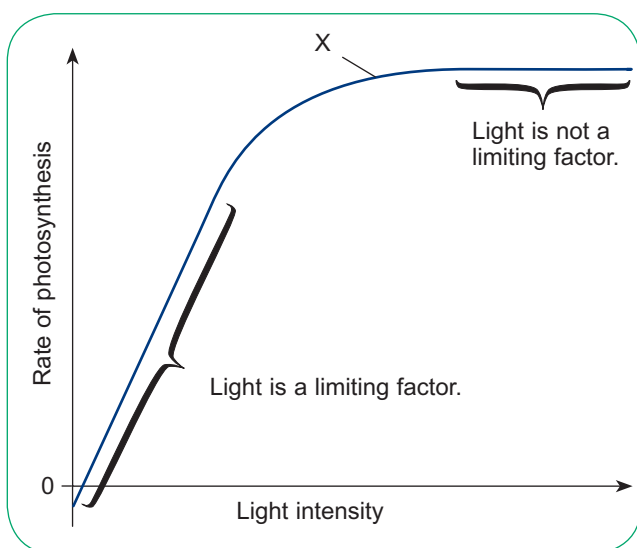


Figure 1.13 The effect of light intensity on the rate of photosynthesis.

Carbon dioxide concentration

The concentration of carbon dioxide in the air is very low, only about 0.04%. Yet this substance is needed for the formation of every organic molecule inside every living thing on Earth.

Plants absorb carbon dioxide into their leaves by diffusion through the stomata. During daylight, carbon dioxide is used in the Calvin cycle in the chloroplasts, so the concentration of carbon dioxide inside the leaf is even lower than in the air

outside, providing the diffusion gradient that keeps it moving into the leaf.

Carbon dioxide concentration is often a limiting factor for photosynthesis. If we give plants extra carbon dioxide, they can photosynthesise faster. Figure 1.14 shows the relationship between carbon dioxide concentration and rate of photosynthesis. Figure 1.15 shows the effect of carbon dioxide at different light intensities.

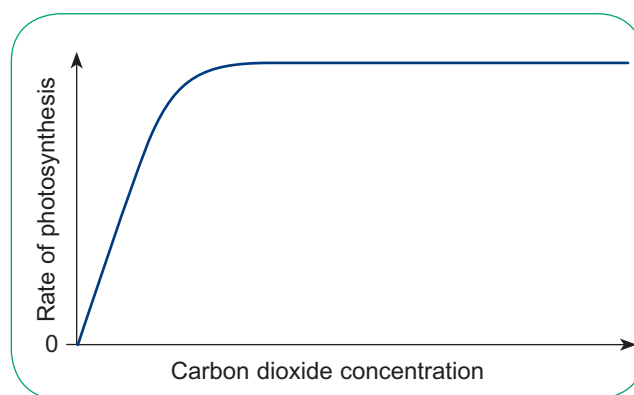


Figure 1.14 The effect of carbon dioxide on rate of photosynthesis.

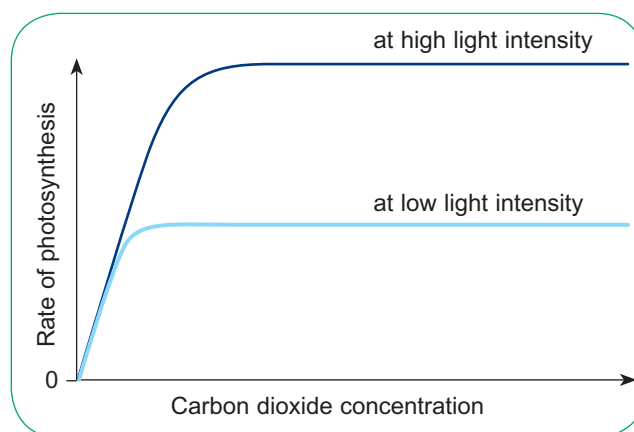


Figure 1.15 The effect of carbon dioxide concentration on the rate of photosynthesis at different light intensities.

SAQ

- 5 a Over which part of the curve in Figure 1.14 is carbon dioxide a limiting factor for photosynthesis?
- b Suggest why the curve flattens out at high levels of CO_2 .