Energy transformation

Unit 5

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5.2 How do plants harness light energy in photosynthesis? (page 170)	• Draw, label and describe a chloroplast. • Locate where light-dependent and -independent processes occur in the chloroplast. • Name the products of the light-dependent and -independent processes. • Explain how the structure of a photosystem is related to its function. • Explain what is meant by a photosynthetic unit. • Describe how glucose is synthesised in the light-independent reactions of photosynthesis. • Describe the factors that affect the rate of photosynthesis and explain why they affect the rate. • Separate photosynthetic pigments by paper chromatography. • Explain photorespiration and how it is related to higher temperatures. • Distinguish between C3 and C4 plants and give at least three examples of each. • Appreciate the importance of C4 plants in Ethiopia. • Describe the CAM photosynthetic pathway and explain why this brings added benefits to plants living in desert conditions.

5.1 Respiration

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

- Describe the structure of ATP and its role in cellular metabolism.
- Explain how ATP is adapted to its role as an energy transfer molecule within a cell.
- Describe how ATP is produced in a cell.
- Locate where the different processes of cellular respiration occur in the cell.
- Explain the role of electron donors and acceptors.
- Describe in detail each stage of aerobic respiration.
- Draw and label the structure of a mitochondrion.
- Explain the processes of alcoholic fermentation and lactate production.
- Appreciate the importance of lactate production during running and other sports.
- Summarise the metabolism of proteins, polysaccharides and lipids.

What is the ATP molecule like?

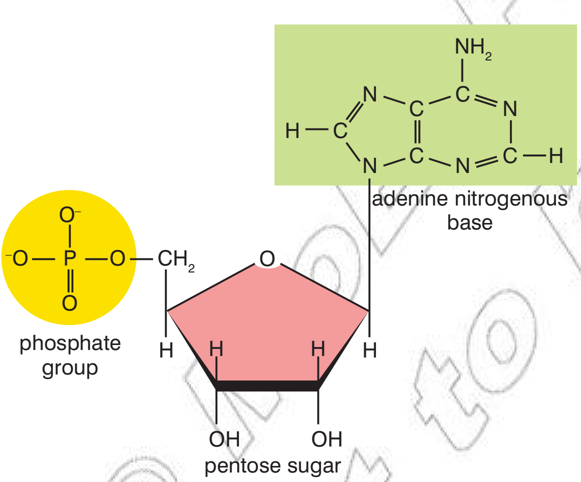


Figure 5.1 A nucleotide containing the nitrogenous base adenine

The full name for ATP is **A**denosine **T**ri-**P**hosphate – but you will not need to use this name, all biologists always refer to it as ATP. So why bother telling you? Well, it helps to understand about the structure of the molecule.

In unit 2, we learned that nucleic acids are built from nucleotides, like the one shown in figure 5.1.

All nucleotides contain:

- a nitrogenous base (this one contains adenine)
- a pentose sugar
- a phosphate group

The ATP molecule is based on this nucleotide. ATP is sometimes described as a **phosphorylated nucleotide**. If you look at figure 5.2, you can perhaps work out why. When you 'phosphorylate' a molecule, you add one or more phosphate groups to it. ATP is essentially the adenine nucleotide with two extra phosphate groups added on – making three in all. Adding the extra phosphates requires energy, particularly when the third phosphate is added. As a result, energy is stored in the ATP molecule and when the bonds that hold this third phosphate in place are broken, the energy is released again. When the third phosphate is removed from ATP, we are still left with a phosphorylated nucleotide, but this one only has two nucleotides. It is **Adenosine Di-Phosphate** – or **ADP**.

The phosphate group that is split off is usually written as P_i as a kind of shorthand to save writing out the full formula.

The inter-conversion of ADP and ATP is shown in figure 5.3. Notice that the diagram says that the energy to form ATP can come from 'sunlight or from food'. This is because ATP is formed in both photosynthesis and in cellular respiration.

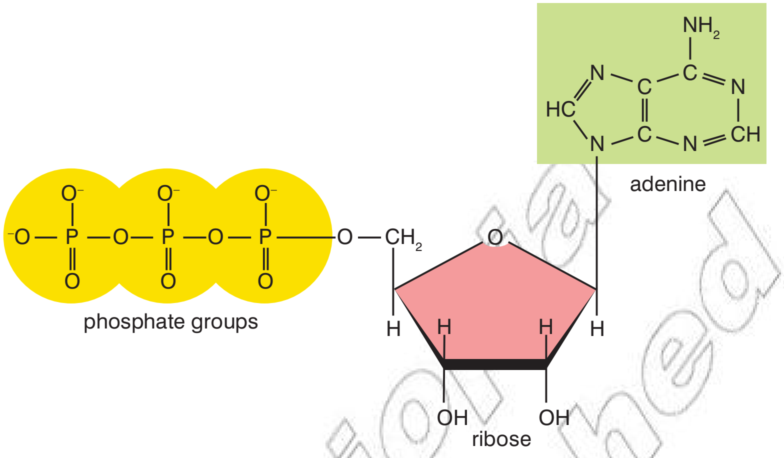


***Figure 5.2** The structure of the ATP molecule*

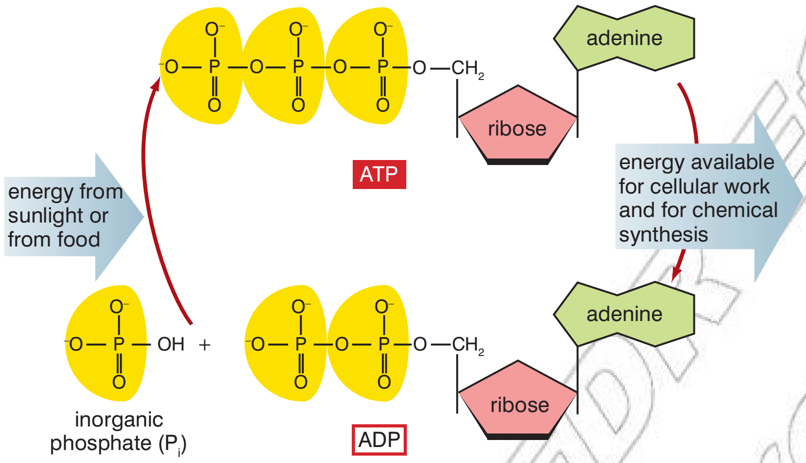


***Figure 5.3** The inter-conversion of ADP and ATP*

How is ATP adapted to its role as an energy transfer molecule in cells?

First, we must explain what we mean by an energy transfer molecule. Sunlight energy cannot be used directly by plants (and certainly not by other organisms) to 'drive' the synthesis of proteins – or any other molecules. The same applies to the energy held in a glucose molecule. These two energy sources must be used to produce ATP, which is used to transfer the energy to the relevant cellular process. We say that it is coupled to these processes.

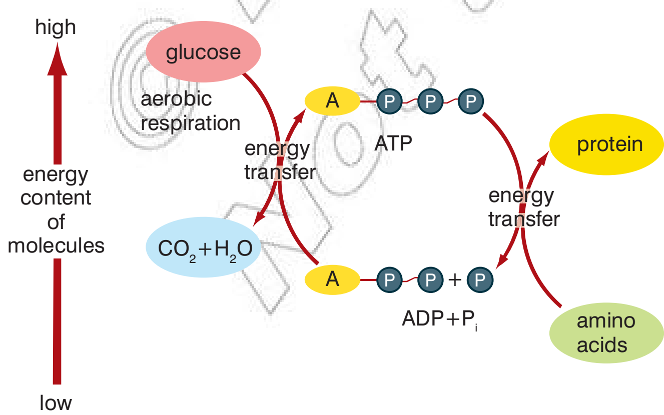


***Figure 5.4** Coupled reactions transfer energy in cells*

KEY WORDS

phosphorylated nucleotide *the adding of one or more phosphate groups to a molecule*

adenosine di-phosphate *removing the third phosphate from ATP leaves a phosphorylated nucleotide with two nucleotides*

DID YOU KNOW?

All living cells respire all the time to produce the ATP they need. There are no exceptions.

KEY WORD

ATP synthase *enzyme involved in the formation of ATP*

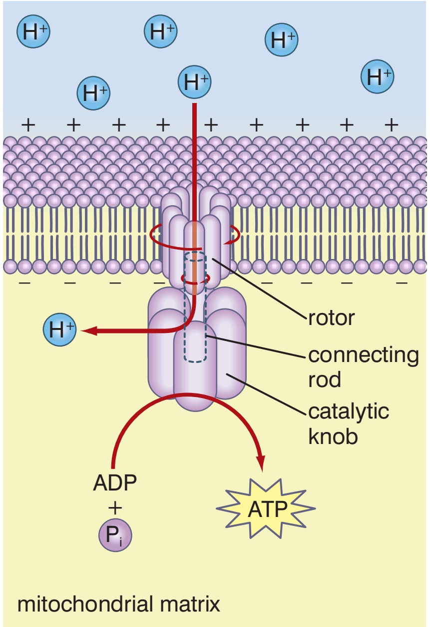


***Figure 5.5** The structure of ATP synthase*

DID YOU KNOW?

About the ADP/ATP inter-conversion

More than one eminent biologist has said 'the whole biological world turns on the coupling and uncoupling of the third phosphate of ATP'. This is because this process is virtually the only way in which energy can be harnessed and then released to drive metabolic processes in cells.

ATP is adapted to this role because it:

- releases energy in relatively small amounts that are closely matched to the amounts of energy required in many biological processes occurring inside cells
- releases energy in a single-step hydrolysis reaction, so the energy can be released quickly
- is able to move around the cell easily, but cannot escape from the cell

The following processes are examples of processes that require energy from ATP:

- the synthesis of macromolecules – such as proteins
- active transport across a plasma membrane (see unit 4 for details)
- muscle contraction
- conduction of nerve impulses
- the initial reactions of respiration (the later reactions release energy from glucose to form more ATP)

How is ATP produced in a cell?

Almost all the ATP produced in cells is formed in the same way. It obviously involves ADP and P_i joining to form ATP and this requires an input of energy. What we need to look at is just how it is made to happen.

The formation of ATP involves an enzyme called **ATP synthase**. Figure 5.5 shows the structure of the ATP synthase molecule. The ATP synthase in this diagram is in one of the membranes of a mitochondrion, but it could be in a membrane in a chloroplast.

To understand how it works, you should think of it as a kind of molecular 'water wheel'. When the rotor is made to spin by hydrogen ions passing through it, the energy of the spinning is used to activate sites in the catalytic knob that convert ADP and P_i to ATP.

In both photosynthesis and aerobic respiration, many of the reactions generate the hydrogen ions that will pass through the ATP synthase to produce ATP.

How is ATP produced in respiration?

There are two main pathways by which respiration can produce ATP:

- the aerobic pathway (aerobic respiration) – this requires the presence of oxygen, and
- the anaerobic pathway (anaerobic respiration and fermentation) – this can take place in the absence of oxygen.

How is ATP produced in aerobic respiration?

A small amount of ATP is produced in a way that does not involve the ATP synthase molecule; this method is called **substrate level phosphorylation**. In this process, another molecule such as phosphoenol pyruvate (the *substrate*) is able to transfer a phosphate group directly to ADP. There is no ATP synthase involved and no P_i. The process is still catalysed by an enzyme, it is just not ATP synthase.

Figure 5.6 shows how substrate level phosphorylation works. As already mentioned, this process only produces a relatively small amount of the ATP produced in aerobic respiration – in fact it produces about 10% of the total ATP produced in aerobic respiration.

As about 90% of the ATP produced in aerobic respiration is produced by ATP synthase, many of the reactions of this process are geared to producing the hydrogen ions that will spin the rotor of the ATP synthase molecule.

Many different organic molecules can be respired – they are called **respiratory substrates**. However, glucose is the most commonly respired substrate and so we will begin by looking at how this molecule is respired.

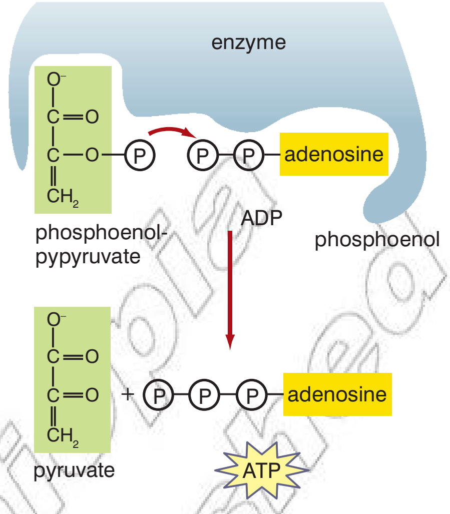


***Figure 5.6** Substrate level phosphorylation*

How are hydrogen ions transferred from glucose to ATP synthase?

Two molecules are important in this transfer process:

- Nicotinamide Adenine Dinucleotide (NAD)
- Flavine Adenine Dinucleotide (FAD)

Both are coenzymes and are capable of accepting hydrogen ions. When this happens, we say that the molecules have been **reduced**. We write the reduced forms of the molecules as NADH and FADH or NAD(reduced) and FAD(reduced).

These molecules can release their hydrogen ions and become **oxidised** again. The hydrogen ions can then be used to turn the rotor of ATP synthase.

What are the stages of aerobic respiration of glucose?

There are four stages in the aerobic respiration of glucose. These are:

- glycolysis
- the link reaction
- Krebs cycle
- electron transport and chemiosmosis

KEY WORDS

substrate level phosphorylation *when another molecule (substrate) is able to transfer a phosphate group directly to ADP*

respiratory substrates *organic molecules that can be respired*

reduce *decrease the oxidation state of a substance*

oxidise *increase the oxidation state of a substance*

Activity 5.1

Make a simple model of ATP which you can use to demonstrate how it is converted to ADP and back again by the removal or addition of a phosphate group.

DID YOU KNOW?

Oxidation and reduction

Reduction is the opposite of oxidation, in which particles accept oxygen, lose hydrogen or lose electrons. In reduction, a particle loses oxygen, gains hydrogen or gains electrons. When a particle of compound A is oxidised by (say) losing electrons, the electrons have to go somewhere. A particle of compound B accepts the electrons and is reduced. The two processes always happen together and the reactions in which they are involved are called redox (reduction and oxidation) reactions. Figure 5.7 shows this.

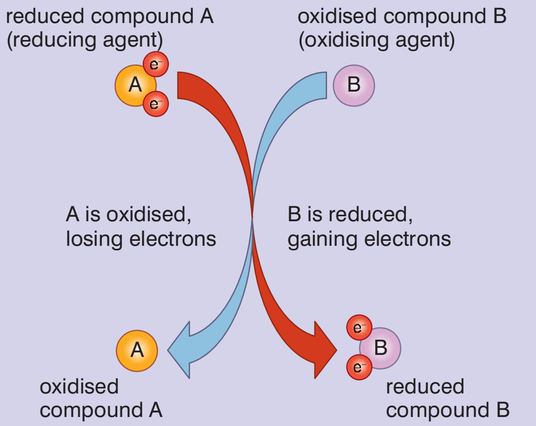


***Figure 5.7** A redox reaction*

Activity 5.2

Draw and label a simple diagram of a mitochondrion which shows where the various parts of cellular respiration takes place and demonstrates the importance of the mitochondrial membranes.

The first stage, glycolysis, takes place in the cytoplasm. It does not take place inside the mitochondria because:

- the glucose molecule cannot diffuse through the mitochondrial membranes (it is a medium-sized molecule and is not lipid soluble), and
- there are no carrier proteins to transport the glucose molecule across the membranes.

Glycolysis (literally 'glucose splitting') results in glucose being converted into a smaller molecule containing only three carbon atoms – pyruvate. Pyruvate can enter the mitochondria and so all the other stages take place inside the mitochondrion. Figure 5.8 shows where the stages of aerobic respiration take place.

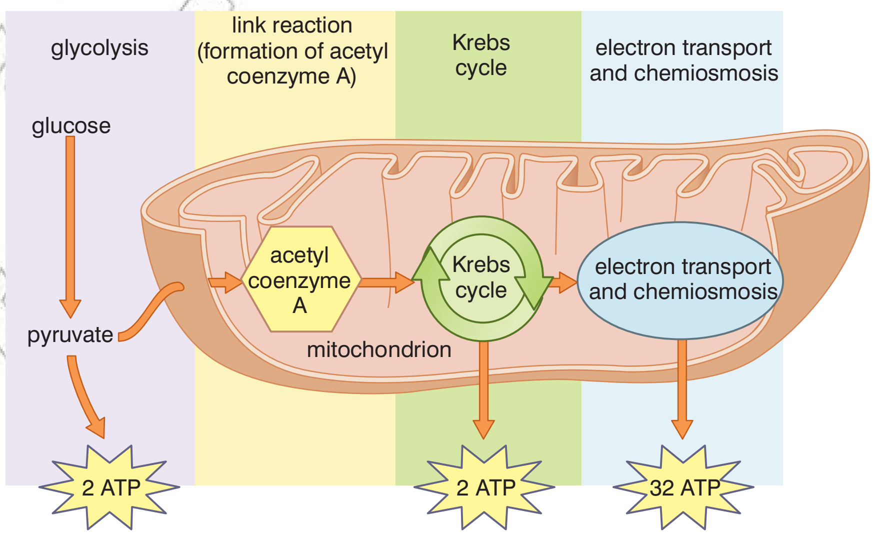


***Figure 5.8** The stages of aerobic respiration*

In the link reaction, pyruvate is then converted into a two-carbon compound that enters into a cycle of reactions – the Krebs cycle (named after Sir Hans Krebs who discovered the reactions involved). Both these stages take place in the fluid **matrix** of a mitochondrion.

In all three stages (glycolysis, the link reaction and Krebs cycle), hydrogen atoms are transferred to NAD to produce reduced NAD. The Krebs cycle also produces reduced FAD. These molecules later release their hydrogen atoms as protons (hydrogen ions) and electrons in the final stage of aerobic respiration. The electrons pass along a series of molecules called an **electron transport chain**. The protons are used in the chemiosmotic synthesis of ATP as they spin the rotor of the ATP synthase enzyme located in the inner membrane of the mitochondrion. Eventually, the protons (hydrogen ions) and electrons will combine with oxygen to form water.

Without the oxygen, this cannot happen as there is nothing at the end of the electron transport chain to accept the electrons. The electron transport chain grinds to a halt and so does the production of ATP by ATP synthase. Because it is oxygen-dependent, this method of production of ATP is called **oxidative phosphorylation**.

The link reaction, Krebs cycle and the reactions of the electron transport chain all depend on the presence of oxygen. None of these occurs in anaerobic respiration. Glycolysis can take place in the absence of oxygen and is the only energy-releasing process in anaerobic respiration.

KEY WORDS

matrix *fluid in the mitochondrion in which the reactions of the Krebs cycle take place*

electron transport chain *a series of molecules along which electrons travel*

oxidative phosphorylation *oxygen-dependent production of ATP*

What happens in glycolysis?

The reactions of glycolysis take place in the cytoplasm. The following reactions take place in glycolosis:

- two molecules of ATP are used to 'phosphorylate' each molecule of glucose. This makes the glucose more reactive
- in the phosphorylation process, it is converted to another six-carbon sugar (fructose 1,6-bisphosphate)
- the fructose 1,6-bisphosphate is split into two molecules of the three-carbon sugar glyceraldehyde-3 phosphate (GP)
- each molecule of GP is then converted into pyruvate, with the production of two molecules of ATP (by substrate level phosphorylation) and one molecule of reduced NAD

The main reactions of glycolysis are shown in figure 5.9. Note:

- the figures in brackets give the number of carbon atoms in that molecule, so (6C) means six carbon atoms per molecule
- two molecules of pyruvate are produced from one molecule of glucose

At the end of glycolysis, there is a net gain of two ATP molecules per molecule of glucose (two molecules are used initially and then four are produced). Two molecules of reduced NAD are also produced (per molecule of glucose). The molecules of pyruvate pass into the mitochondria through carrier molecules in the mitochondrial membrane.

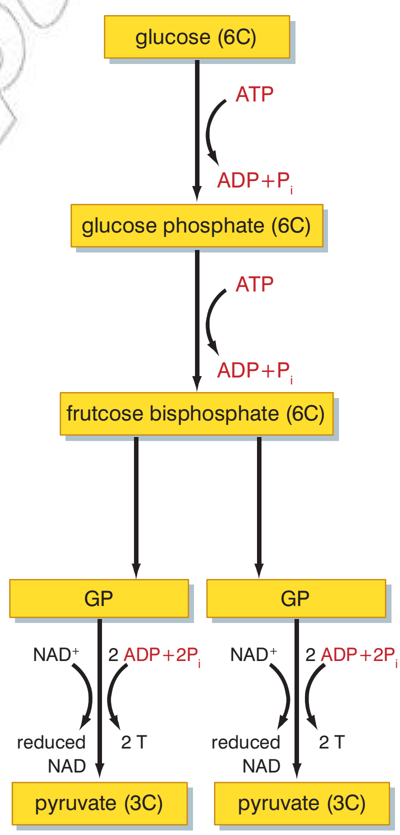


Figure 5.9 *The main stages of glycolysis*

A summary of the overall reaction of glycolosis:

$$C_6H_{12}0_6 + 2ATP + 4ADP + 2P_i + 2NAD \rightarrow 2C_3H_60_3 + 2ADP + 4ATP + 2NAD \text{ reduced} + 2H^+ + 2H_20$$

Two ideas to keep in mind

1. The idea of net gain of ATP is like the profit a business makes. It invests money in materials, advertising and staff. It sells its product and the extra money is profit – net gain. Glycolysis 'invests' two molecules of ATP to make the glucose reactive, then, later, produces four molecules of ATP – a net gain of two molecules of ATP.
2. There are two molecules of pyruvate made from each molecule of glucose. So all the gains of ATP and reduced NAD and reduced FAD that accrue from each pyruvate must be doubled to give the gain from each molecule of glucose.

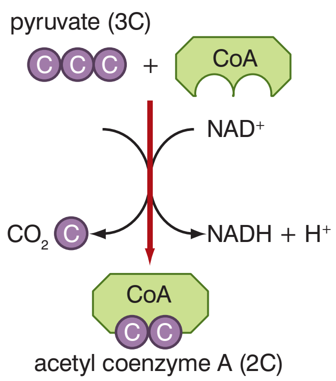


***Figure 5.10** The link reaction*

Both of these stages of respiration take place in the fluid matrix of the mitochondrion.

In the link reaction, a molecule of pyruvate reacts with a molecule of **coenzyme A** (CoA) to form a molecule of **acetyl coenzyme A** (acetyl CoA). In the reaction:

- hydrogen is lost and reduced NAD is formed; removing hydrogen from a molecule is **dehydrogenation**
- a carbon atom is lost to form carbon dioxide; removing carbon from a molecule is **decarboxylation**.

The acetyl coenzyme A then reacts with a C4 molecule (a molecule containing four carbon atoms) called oxaloacetate. In the reaction, acetyl CoA breaks down into:

- a two-carbon 'acetyl' group, which reacts with the C4 compound oxaloacetate to form a C6 compound, and
- the original coenzyme A molecule, which is reused in further reactions with other molecules of pyruvate.

This is the first reaction of the Krebs cycle.

What happens in the Krebs cycle?

- the two-carbon group from acetyl coenzyme A reacts with the four-carbon compound **oxaloacetate** to form a six-carbon compound called **citrate**
- citrate then loses a carbon atom (is decarboxylated) to form a five-carbon compound and CO_2 is produced
- the five-carbon compound is then further decarboxylated to form a four-carbon compound and CO_2 is again produced; a molecule of ATP is also produced by substrate level phosphorylation
- the four-carbon compound undergoes several molecular transformations to regenerate the original four-carbon compound (oxaloacetate) and the cycle is complete and can begin again with oxaloacetate reacting with another molecule of acetyl CoA

KEY WORDS

coenzyme A *coenzyme derived from pantothenic acid needed for respiration*

acetyl coenzyme A *produced by the reaction of coenzyme A with a molecule of pyruvate*

dehydrogenation *removing hydrogen from a molecule*

decarboxylation *removing carbon from a molecule*

- in several reactions in the cycle, reduced NAD is produced and, in just one reaction, reduced FAD is produced

The reactions of the Krebs cycle are summarised in figure 5.12.

A summary of the overall reaction of the Krebs cycle:

$CH_3CO.CoA + 3NAD + FAD + C_4H_2O_5^{2-} \rightarrow 2CO_2 + 3NAD$ reduced + FAD reduced + CoA + $C_4H_2O_5^{2-}$

What happens in the electron transport chain and chemiosmosis?

The electron transport chain and chemiosmosis together make up the process of oxidative phosphorylation.

Whereas the reactions of the link reaction and Krebs cycle take place in the fluid matrix of the mitochondrion, the reactions of the electron transport chain and chemiosmosis take place on the inner mitochondrial membrane. Figure 5.13 shows an electron-micrograph of a mitochondrion.

On the cristae, the following events take place:

- the hydrogen atoms carried by reduced NAD and reduced FAD are released and split into protons (hydrogen ions) and electrons
- the electrons pass along a series of electron carriers that form the transport chain; they lose energy as they pass from one carrier to the next
- three of the electron carriers are proton pumps that move protons from the matrix of the mitochondrion to the inter-membrane space
- as the electrons are transferred through these three proton pumps, the energy they lose powers the pumps which move the protons into the inter-membrane space
- electrons from reduced NAD make this happen at all three pumps

The molecules that act as electron carriers in the electron transport chain are:

- reduced NAD dehydrogenase (also a proton pump)
- ubiquinone (also a proton pump), and
- a number of carriers called cytochromes (these are proteins that contain iron); two of them form a complex that acts as the third proton pump.

KEY WORDS

oxaloacetate *an ester of oxaloacetic acid*

citrate *an ester of citric acid*

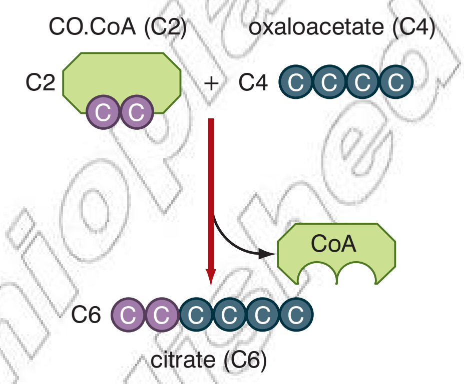


Figure 5.11 *The first reaction of the Krebs cycle*

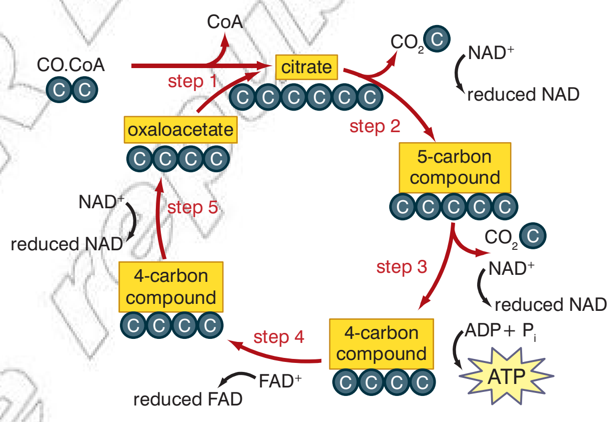


Figure 5.12 *The main stages of the Krebs cycle*

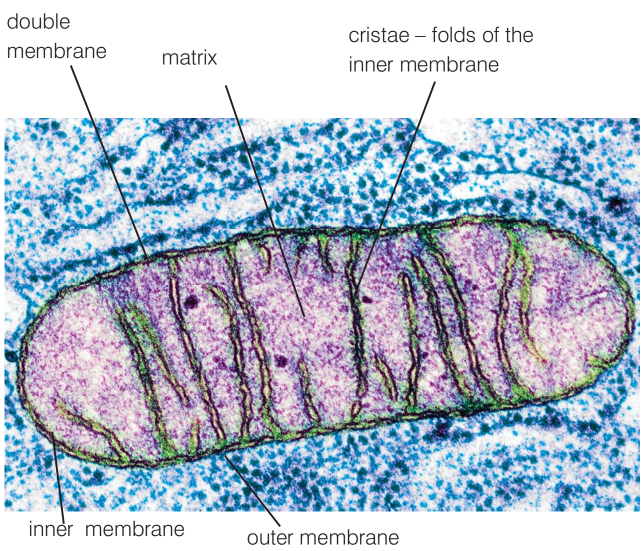


Figure 5.13 *An electron-micrograph of a mitochondrion*

The arrangement of these molecules is shown in figure 5.14.

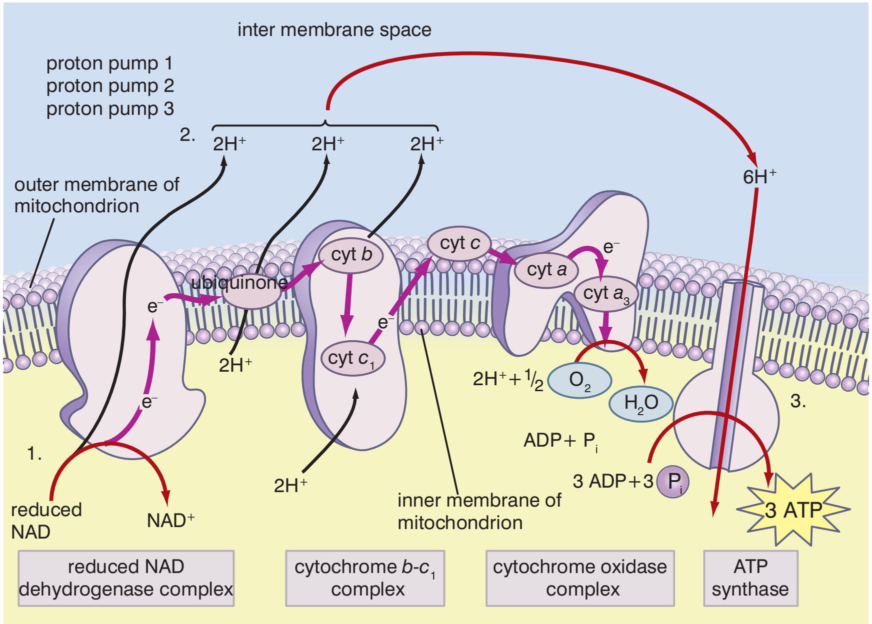


***Figure 5.14** The carrier molecules in the electron transport chain on the inner membrane of a mitochondrion*

At the end of the electron transport chain, the electrons combine with protons and with oxygen to form molecules of water. Because of this, oxygen is known as the **terminal electron acceptor**.

Whereas reduced NAD is dehydrogenated by the NAD dehydrogenase complex, reduced FAD is dehydrogenated by ubiquinone. So electrons from reduced FAD only operate two of the three proton pumps.

Because of the action of the proton pumps, protons accumulate in the inter-membrane space creating a higher concentration there than in the matrix (on the other side of the membrane). This proton gradient results in protons diffusing through the ATP synthase molecule (down the concentration gradient) making the synthase rotor 'spin' and produce ATP from ADP and P_i. The diffusion of hydrogen ions through the ATP synthase is chemiosmosis.

The oxidation of one molecule of reduced NAD results in six protons passing through ATP synthase and so leads to the synthesis of three molecules of ATP.

The oxidation of one molecule of reduced FAD results in four protons passing through ATP synthase and so leads to the synthesis of just two molecules of ATP.

By adding up the number of molecules of ATP produced, the model of aerobic respiration we have discussed predicts that there will be a net yield of 38 molecules of ATP per molecule of glucose.

KEY WORD

terminal electron acceptor *the final molecule at the end of the electron transport chain to accept an electron*

A summary of the overall reaction of the electron transport system:

6 reduced NAD (from Krebs' cycle) + 2 reduced NAD (from glycolysis) + 2 reduced FAD (from Krebs' cycle) + 30 ADP + 30 Pi – 2ATP (used in proton pumps) ➞ 36 ATP + 8 NAD + 2FAD

In practice, this is not achieved because some energy (the equivalent of just over two molecules of ATP) is used to drive the proton pumps. The actual yield is about 36 molecules of ATP per molecule of glucose.

Figure 5.15 summarises the production of ATP in aerobic respiration.

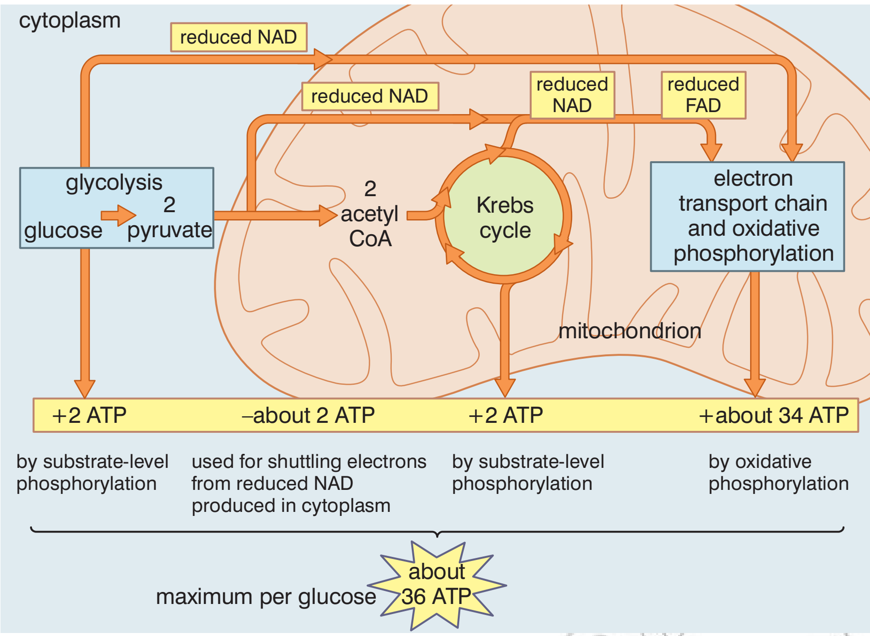


***Figure 5.15** The production of ATP during the aerobic respiration of glucose*

The summary equation for aerobic respiration is:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 + \text{energy released}$$

Respirometers

Respirometers come in several different forms, but they all work on the principle that oxygen is used in aerobic respiration and carbon dioxide is produced.

The overall summary equation for the aerobic respiration of glucose is:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 36ATP$$

This equation predicts that the volume of oxygen used ($6O_2$) is equal to the volume of carbon dioxide produced ($6CO_2$). This is the basis of how respirometers work.

Figure 5.16 overleaf shows a basic respirometer. For every molecule of oxygen the organism uses, a molecule of carbon dioxide will be produced, but, the carbon dioxide will be absorbed by the potassium hydroxide (KOH). So, over time, there will be a reduction in volume inside the respirometer.

Activity 5.3

Make a large annotated wall chart showing glycolysis and Krebs cycle and how they are linked together. Make sure you show the different compounds and where ATP is formed. This should be as accurate as possible so it can form the basis of your revision of this complex topic.

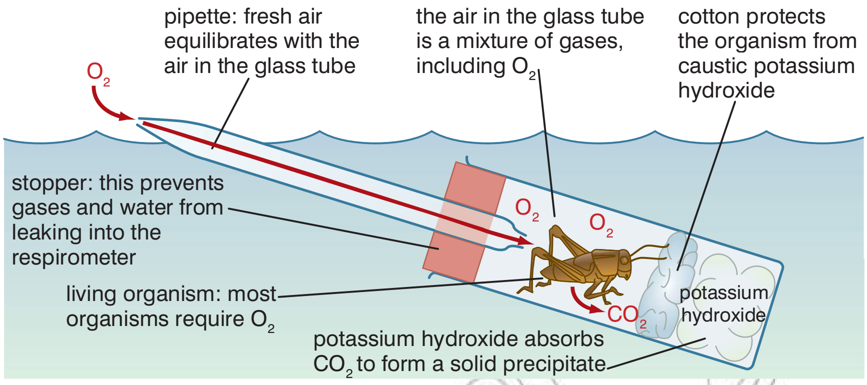


Figure 5.16 *A basic respirometer*

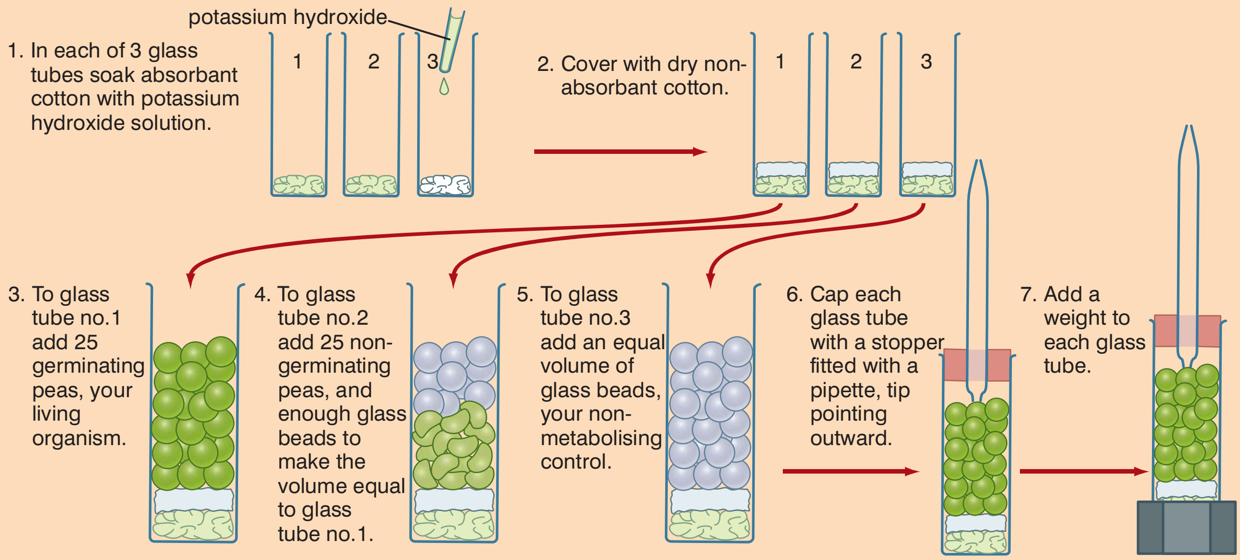
Figure 5.16 shows the respirometer placed under water. As the volume inside the respirometer decreases, water will enter the pipette. The volume of water entering is equal to the volume of oxygen being used up. We can use this to measure the rate of respiration by measuring how much oxygen is used in a set period of time (say 10 minutes) then working out a rate per minute.

Activity 5.4: Measuring the rate of respiration of pea seeds

You will need

- 3 respirometers, set up as in figure 5.17
- 3 water baths

Figure 5.17 *How to assemble a respirometer*



Method

1. Place the three respirometers in a water bath at 20 °C with the tips of the pipettes out of the water, resting on a sling of tape. Leave them for five minutes to equilibrate.
2. Lower the tips of each pipette into the water and immediately:
   - take a reading from each
   - start a timer
3. Take a reading from each respirometer every two minutes for 20 minutes.
4. Repeat the investigation at 30 °C and at 40 °C.

The volume of oxygen used is the same as the volume of water that has entered the pipette.

There are several aspects of this experiment you should consider:

- Why did we use tubes containing non-germinating peas and glass beads as well as the tube with the germinating peas?
- Why does the water move into the pipette during the investigation ?
- What was the purpose of leaving the tubes for five minutes before starting each investigation?
- How could you investigate temperatures lower than 20 °C?

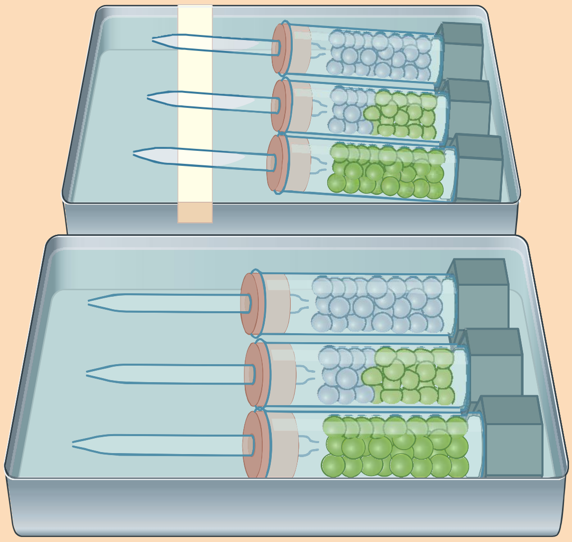


***Figure 5.18** Carrying out the experiment*

A different design of respirometer removes the need to set up three at the same time. This is shown in Figure 5.19.

In this design, the tap on tube A is left open for five minutes at the start of the investigation and the levels of the coloured oil in the U-tube are equalised with the syringe.

When the investigation starts, the tap is closed and the coloured oil moves towards the organisms (tube B). The distance it moves per minute is a measure of the rate of respiration.

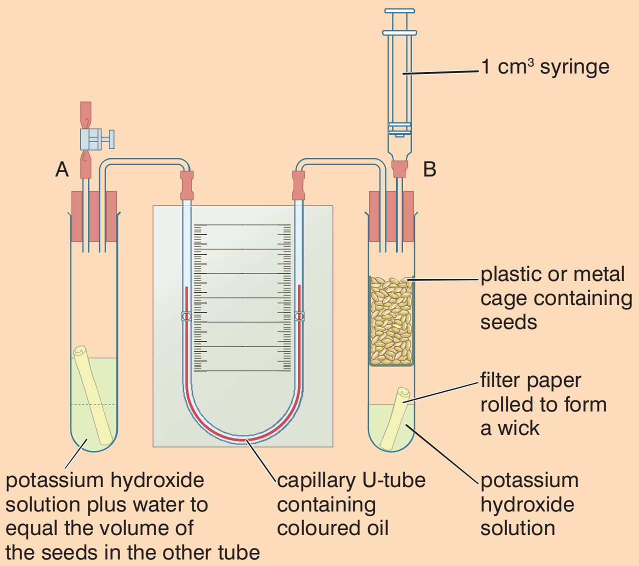


***Figure 5.19** A more sophisticated respirometer*

Once one investigation is complete, the tap can be reopened and the levels reset using the syringe ready for a repeat or another investigation at a different temperature. In this design of respirometer, tube A acts as a control tube and so another set of apparatus with glass beads or non-germinating seeds is not necessary. Figure 5.20 shows how this respirometer can be used to investigate the rate of respiration at different temperatures.

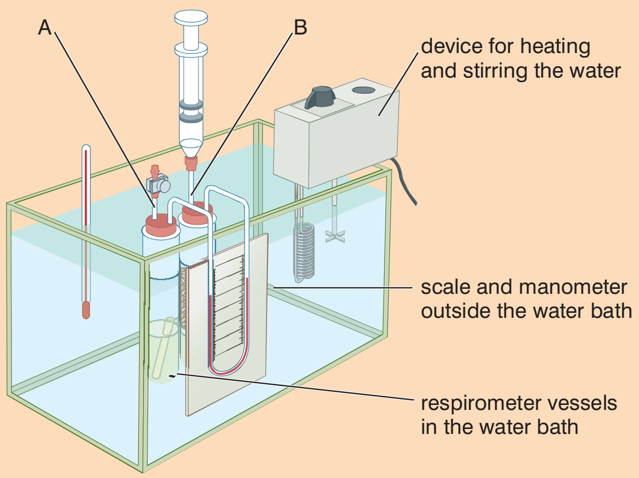


***Figure 5.20** Using the respirometer in a water bath*

What happens in the anaerobic pathway?

If there is no oxygen present, the final reaction of oxidative phosphorylation, where electrons and protons react with oxygen to form water, cannot take place. As a result, the electron transport chain comes to a halt. No protons are pumped and the action of ATP synthase also stops.

There is a further 'knock-on' effect. If the electron transport chain does not function, NAD is not regenerated from reduced NAD and FAD is not regenerated from reduced FAD. Very quickly, the Krebs cycle and the link reaction come to a halt as both NAD and FAD are required in their oxidised forms for the Krebs cycle to function. NAD is also required in the link reaction and so this comes to a halt also.

However, glycolysis *can* continue even though it also requires NAD. This is because the reduced NAD formed during glycolysis can be regenerated under anaerobic conditions by converting the pyruvate into another product in a reduction reaction. Reduced NAD supplies the hydrogen for this reduction and becomes oxidised itself. It is therefore regenerated and can be used again in glycolysis.

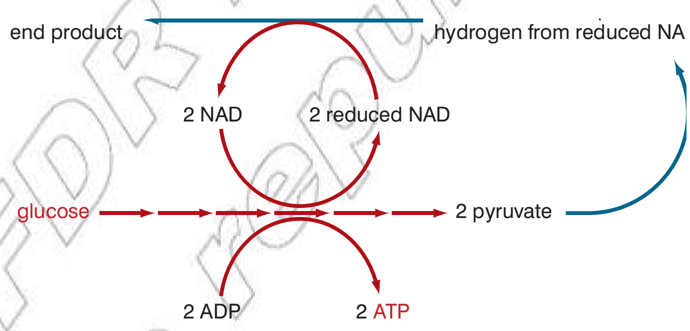


***Figure 5.21** How NAD is regenerated in fermentation*

Different organisms produce different fermentation end products. Animal cells produce lactate (lactic acid) when they ferment glucose. Yeast cells produce ethanol (ethyl alcohol). But both only produce two molecules of ATP per molecule of glucose.

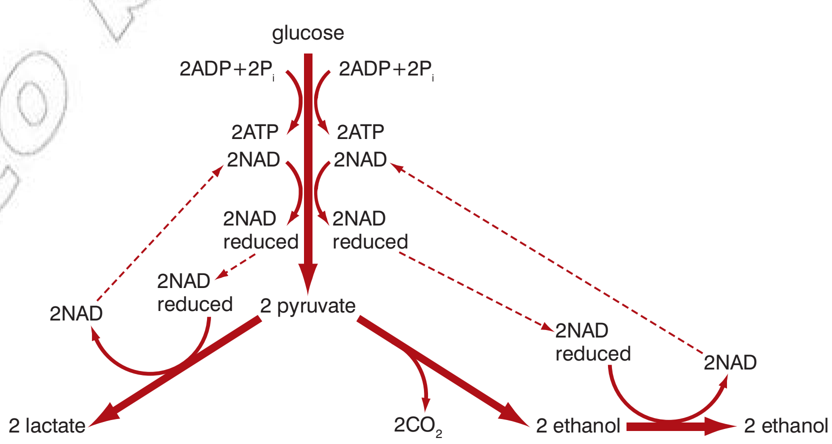


***Figure 5.22** The fermentation processes in animal cells and yeast*

A summary of anaerobic respiration in yeast cells

$$\underset{\text{Glucose}}{C_6H_{12}O_6} \longrightarrow \underset{\text{Ethanol (alcohol)}}{2C_2H_5OH} + \underset{\text{carbon dioxide}}{2CO_2} + 2ATP$$

A summary of anaerobic respiration in animal cells

$$\underset{\text{Glucose}}{C_6H_{12}O_6} \longrightarrow \underset{\text{Lactate (lactic acid)}}{2C_3H_6O_3} + 2ATP$$

KEY IDEA

Lactate formation during exercise

During exercise, the energy demand of muscle cells increases greatly. More glucose is respired to meet the demand. However, sometimes, aerobic respiration is insufficient to meet this energy demand. Fermentation of glucose supplies the extra energy. But it also forms lactate and as this accumulates, it leads to muscle fatigue. Also, fermentation only yields 2 molecules of ATP per molecule of glucose whereas aerobic respiration yields 38. However, fermentation is a much faster process and can produce a lot of ATP quickly, over a short period of time. The ATP used in sprints and short-distance runs is nearly all generated anaerobically.

But, due to muscle fatigue, this cannot be sustained. Longer races must be run slower to allow aerobic respiration to produce the ATP at its slower rate.

Lactate, once formed, can be used to regenerate glucose or be metabolised as an energy source by the liver. Figure 5.23 shows how the Cori cycle makes this happen.

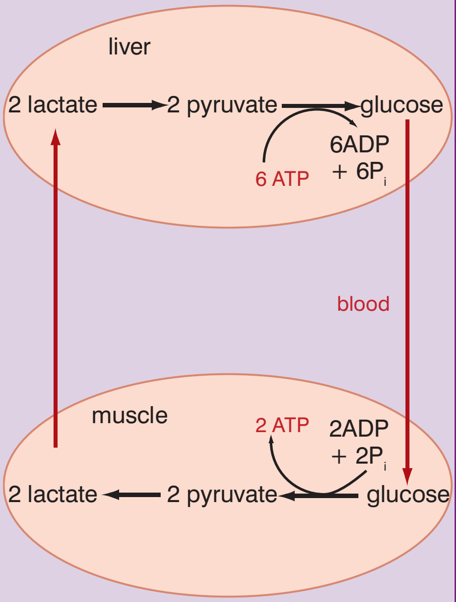


Figure 5.23 *The Cori cycle*

Other organisms produce other fermentation products, many of which are made use of in different industries. Figure 5.24 shows some of these.

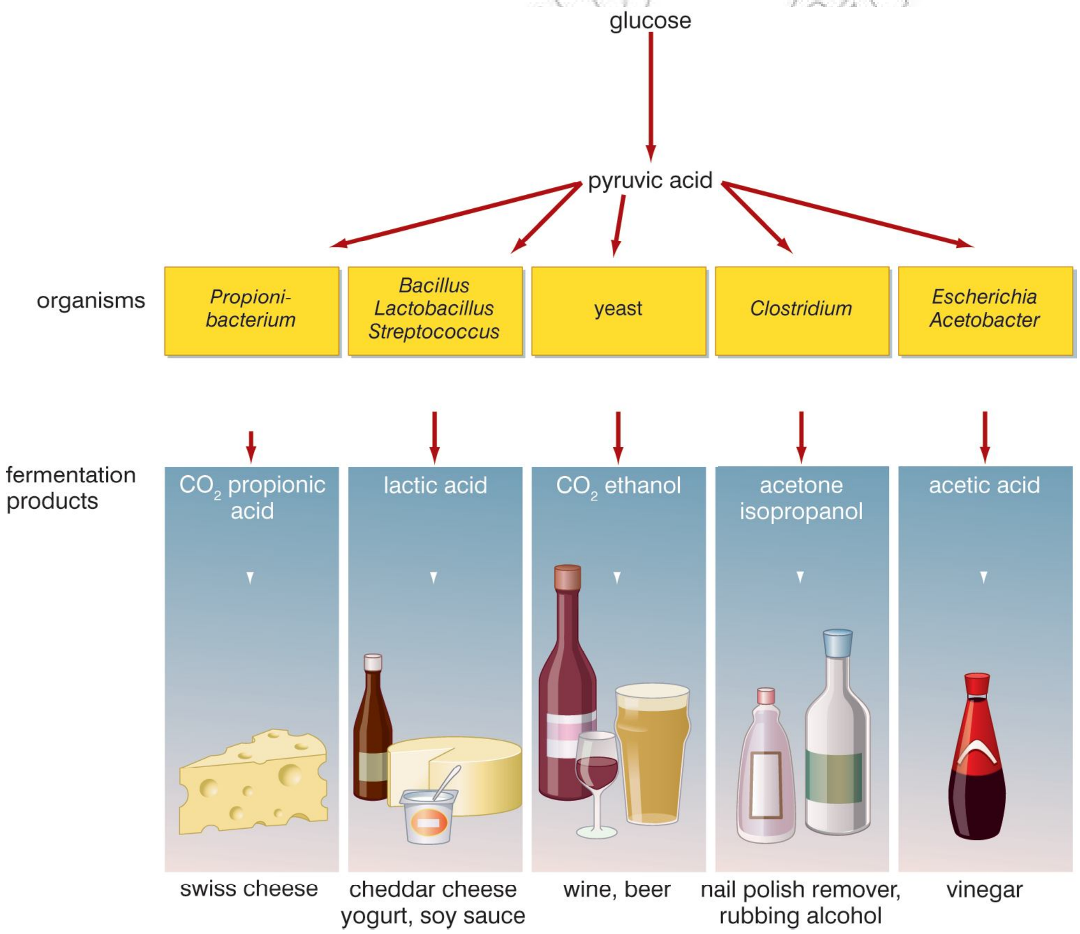


Figure 5.24 *Some uses of fermentation in industry*

Activity 5.5: Investigating the rate of fermentation in yeast

There are many different ways of carrying out this investigation, ranging from those using only basic equipment to sophisticated electronically monitored fermenters. Figure 5.25 shows just about the simplest way of investigating this. The test tube containing the yeast and glucose can be held in a water bath at the desired temperature and the number of bubbles collected per minute recorded. However, rate of bubbling is not the most accurate way of measuring rate of respiration. Are you sure that all the bubbles are the same volume? The method is improved if the test tube of water is replaced by a gas syringe.

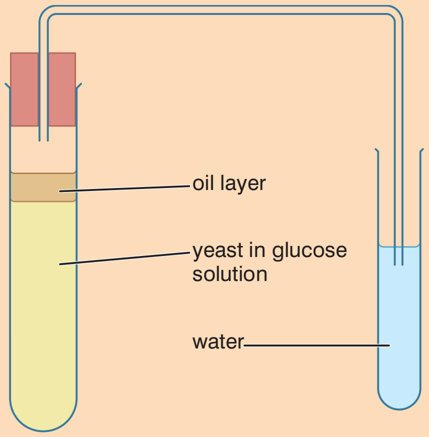


Figure 5.25 A simple way of investigating the rate of fermentation in yeast

Using this basic equipment, can you devise experiments to investigate:

- the effect of temperature on the rate of fermentation
- the effect of different substrates (different sugars) on the rate of fermentation
- the effect of substrate concentration on the rate of fermentation

In your plans, you should make clear:

- the independent variable
- the dependent variable
- other variables that you intend to control as well as:
  - why you need to control them, and
  - how you intend to control them.

Figure 5.26 A fermenter that monitors changes electronically

More sophisticated fermenters (such as that shown in figure 5.26) control all the conditions inside the fermenter and monitor the changes in the concentration of oxygen, carbon dioxide and ethanol. Other sensors could also monitor the concentration of the sugar being fermented.

Figure 5.27 shows the output from one such fermenter.

Can you explain the changes in the concentrations of the various substances as fermentation proceeds?

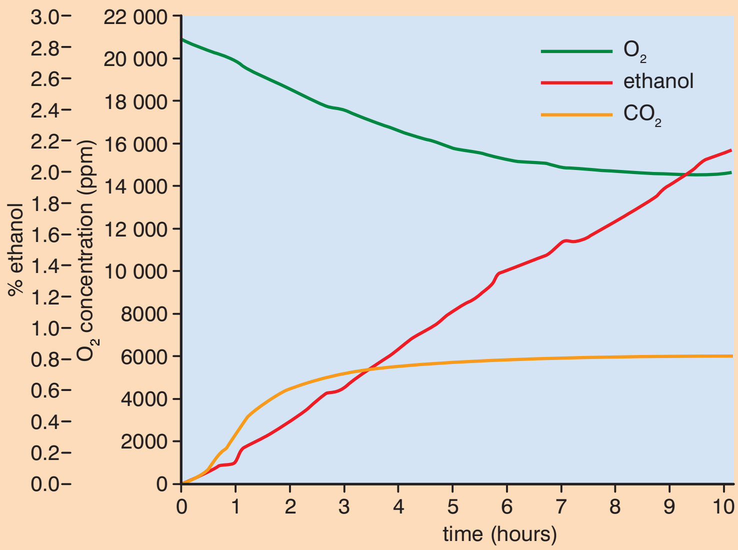


Figure 5.27 Output from a fermenter

What substances can be used as energy sources?

We have so far concentrated on the respiration and fermentation of glucose. But lipids and proteins can also be used as respiratory substrates. Figure 5.28 shows how lipids and proteins are converted into substances that can enter the aerobic respiration pathway at some point. The metabolism of proteins, lipids and carbohydrates 'converges' on the Krebs cycle.

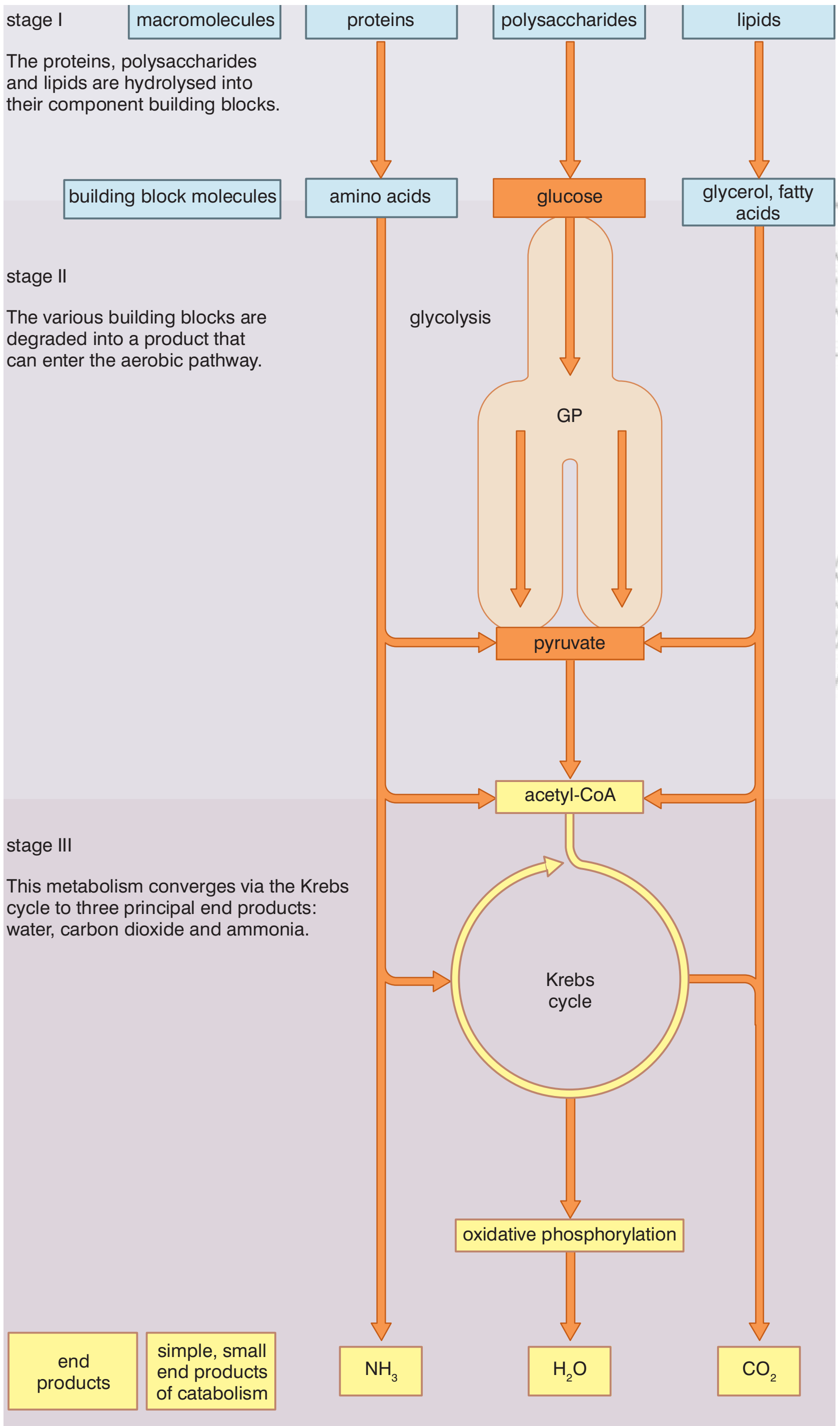


Figure 5.28 *The metabolic pathways by which carbohydrates, lipids and proteins are respired*

Activity 5.6

Plan a simple demonstration of anaerobic respiration in the muscles. Several students work together. You are going to investigate how quickly anaerobic respiration sets in by repeating a simple action until the muscles begin to ache. This action could be stepping on and off a step or box, and repeatedly lifting a book from the surface of the desk to the shoulder. All start the action together and time how long it takes for the muscle aching which indicates a build up of lactic acid to develop. Explain exactly what is happening in the muscles and discuss what individuals can do to change their physiology and maintain aerobic respiration in their muscles for as long as possible.

Activity 5.7

The Krebs cycle was worked out by Hans Krebs. He was awarded a Nobel Prize for his work. Find out as much as you can about Krebs and how he came to discover the chemistry of aerobic respiration in the cell. You can look in encyclopaedias, in other text books and online, e.g.

http://www.nobel-winners.com/Medicine/hans_adolf_krebs.html

http://nobelprize.org/nobel_prizes/medicine/laureates/1953/krebs-bio.html

http://en.wikipedia.org/wiki/Hans_Adolf_Krebs

Review questions

Choose the correct answer from A to D.

1. The ATP molecule is sometimes described as:
   A a phosphorylated nitrogenous base
   B a phosphorylated nucleotide
   C a glycosated nucleotide
   D a glycosated nitrogenous base
2. ATP is formed from:
   A AMP and P_i
   B ADP and AMP
   C ADP and P_i
   D AMP and A
3. Examples of processes requiring ATP include:
   A simple diffusion and active transport
   B active transport and facilitated diffusion
   C conduction of nerve impulses and osmosis
   D active transport and protein synthesis
4. The ATP synthase molecule produces ATP when:
   A electrons turn the rotor to activate sites in the catalytic knob
   B hydrogen ions spin the catalytic knob
   C electrons spin the catalytic knob
   D hydrogen ions turn the rotor to activate sites in the catalytic knob
5. ATP is an ideal energy transfer molecule in cells because it:
   A releases energy in small amounts
   B releases energy quickly
   C can move freely in, but not escape from, the cell
   D all of the above
6. Which of the following does not take place during the Krebs cycle?
   A oxidative phosphorylation
   B substrate-level phosphorylation
   C electron transport
   D the link reaction
7. In fermentation:
   A oxidative phosphorylation does not take place
   B substrate-level phosphorylation does take place
   C NAD is reduced in glycolysis
   D all of the above

8. Which of the following statements about mitochondria is NOT true?
   A the carrier molecules of the electron transfer chain are found on the inner mitochondrial membranes
   B the reactions of the Krebs cycle take place inside the mitochondria
   C all of the ATP needed by the cell is made in the mitochondria
   D much of the ATP needed by the cell is made in the mitochondria
9. In the electron transport chain, electrons are passed:
   A from the lumen of the mitochondrion to the inter-membrane space
   B from the inter-membrane space to the lumen of the mitochondrion
   C through ATP synthase
   D along a series of electron carriers
10. Oxidative phosphorylation includes:
   A the electron transport chain and chemiosmosis
   B the electron transport chain and the Krebs cycle
   C the Krebs cycle and chemiosmosis
   D none of these
11. In the Krebs cycle:
   A some ATP is made by oxidative phosphorylation
   B the four-carbon compound oxaloacetate is regenerated
   C ATP is used
   D the six-carbon compound citrate is split into two three-carbon compounds
12. When compared with aerobic respiration, fermentation of glucose by yeast:
   A yields less ATP per molecule of glucose
   B produces lactate
   C produces more CO_2
   D none of the above
13. Which of the following statements about aerobic respiration is correct?
   A Glycolysis takes place in the matrix of the mitochondrion.
   B Carrier molecules of the electron transport chain exist on the outer membrane of the mitochondrion.
   C A high concentration of hydrogen ions builds up in the matrix of the mitochondrion.
   D The Krebs cycle takes place in the matrix of the mitochondrion.

Activity 5.8

Work as a whole class with your teacher. Before you begin to study photosynthesis, brainstorm everything you know about photosynthesis from your studies in the lower grades. Your teacher will put all your ideas together into a big spider diagram and keep it until the end of this topic. Then you can look back and see how much you have learned.

14. In a respirometer…
    - A the amount of oxygen used by the organism is replaced with an equal amount of carbon dioxide
    - B the carbon dioxide given off is absorbed by potassium hydroxide
    - C the breathing rate of an organism is measured
    - D we measure the uptake of oxygen by an organism
15. Which of the following occur in both aerobic respiration and fermentation in mammals:
    - A substrate-level phosphorylation
    - B chemiosmosis
    - C link reaction
    - D decarboxylation

5.2 How do plants harness light energy in photosynthesis?

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

- Draw, label and describe a chloroplast.
- Locate where light-dependent and -independent processes occur in the chloroplast.
- Name the products of the light-dependent and -independent processes.
- Explain how the structure of a photosystem is related to its function.
- Explain what is meant by a photosynthetic unit.
- Describe how glucose is synthesised in the light-independent reactions of photosynthesis.
- Describe the factors that affect the rate of photosynthesis and explain why they affect the rate.
- Separate photosynthetic pigments by paper chromatography.
- Explain photorespiration and how it is related to higher temperatures.
- Distinguish between C3 and C4 plants and give at least three examples of each.
- Appreciate the importance of C4 plants in Ethiopia.
- Describe the CAM photosynthetic pathway and explain why this brings added benefits to plants living in desert conditions.

Photosynthesis

In photosynthesis, light energy is used in a series of reactions that lead to the synthesis of a range of organic molecules. The energy that entered the system as light is now held in the organic molecules produced. It is now chemical energy. When energy is changed from one form to another, we say it has been **transduced**. This takes place in a series of reactions called the **light-dependent reactions**. Light energy is absorbed by special **photosensitive pigments** such as **chlorophyll** in the chloroplasts. The light-dependent reactions take place in the membranes of the **thylakoids** in the chloroplasts. The liquid stroma is the site of the light-independent reactions, in which carbohydrates are synthesised. Chemical reactions like these take place most effectively in solution, rather than if some were fixed in membranes.

How is the structure of a chloroplast suited to its function?

The chlorophyll and other photosensitive pigment molecules are arranged in special **photosystems** that are linked to electron transport chains (ETCs). The molecules of the photosystems and the electron transport chains are fixed in the membranes of the thylakoids. This makes the process much more efficient than if they were just floating around in a solution.

There are two different photosystems, each sensitive to light of a different wavelength and linked to a different electron transport chain. These are called **photosystem I** and **photosystem II**.

KEY WORDS

transduced *conversion of energy from one form to another*

light-dependent reactions *reactions of photosynthesis dependent on light*

photosensitive pigments *pigments having a response to light*

chlorophyll *green pigment that absorbs blue and red light*

thylakoids *flattened sacs inside a chloroplast on which light-dependent reactions of photosynthesis take place*

photosystems *biochemical mechanism by which chlorophyll absorbs light energy*

photosystem I *photosystem in photosynthetic light reactions. Discovered before* **photosystem II**

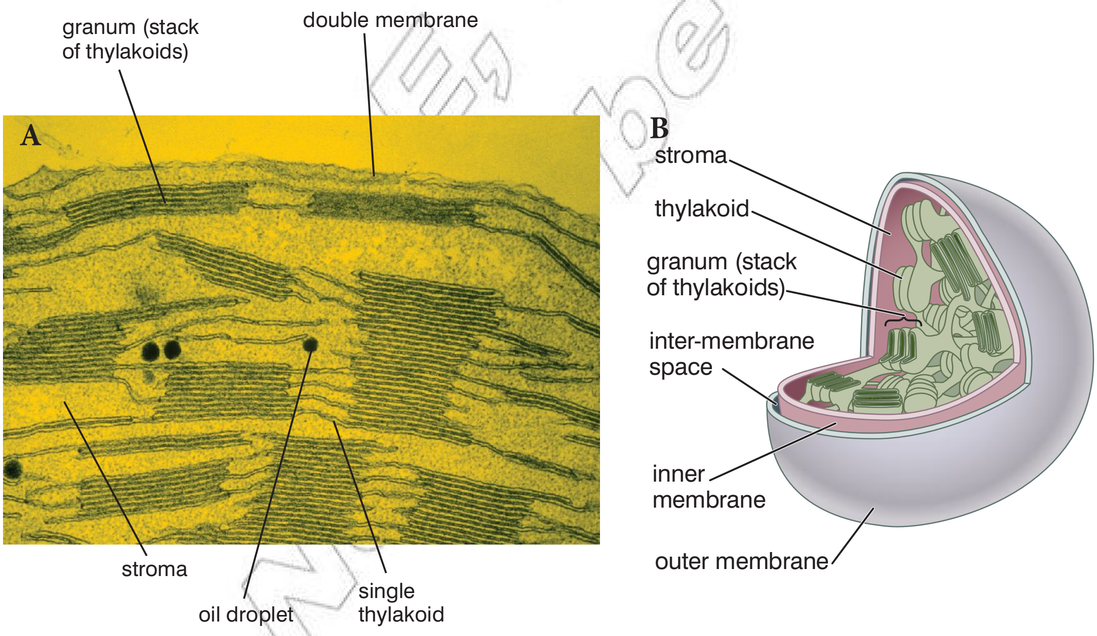


Figure 5.29 *The structure of a chloroplast:* ***A*** *A transmission electron micrograph of a section through a chloroplast;* ***B*** *A three-dimensional representation of the structure of a chloroplast*

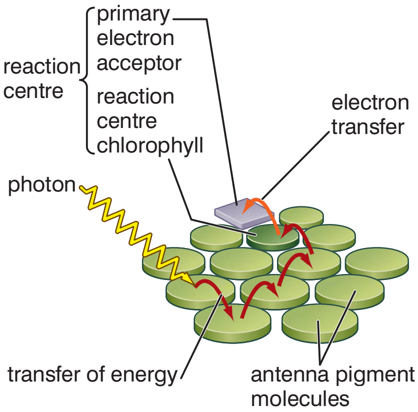


Figure 5.30 The structure of a photosystem

What is the structure of a photosystem?

A photosystem consists of a number of pigment molecules all clustered around one particular chlorophyll molecule called the reaction centre molecule. This cluster of pigment molecules is called an antenna complex. Only the reaction centre molecule is positioned next to the electron transport chain. Energy absorbed by other molecules in the photosystem is transferred to the **reaction centre molecule**, where the light-dependent reactions begin. Different pigment molecules in the **antenna complex** can absorb different wavelengths of light, making the whole system more efficient. The pigments in the antenna complex include chlorophyll a, chlorophyll b and carotenoids. The reaction centre molecule is always chlorophyll a. The range of wavelengths each molecule absorbs is its **absorption spectrum**. Figure 5.31A shows the absorption spectrum of chlorophyll a, chlorophyll b and carotenoids. Figure 5.31B shows the **action spectrum** for different wavelengths of light. This shows how effective photosynthesis is at each wavelength.

Activity 5.9

Draw and label the structure of a chloroplast, showing where the light-dependent and the light-independent reactions take place.

Compare this diagram to the one you made earlier of a chloroplast and describe the similarities and differences between these two organelles.

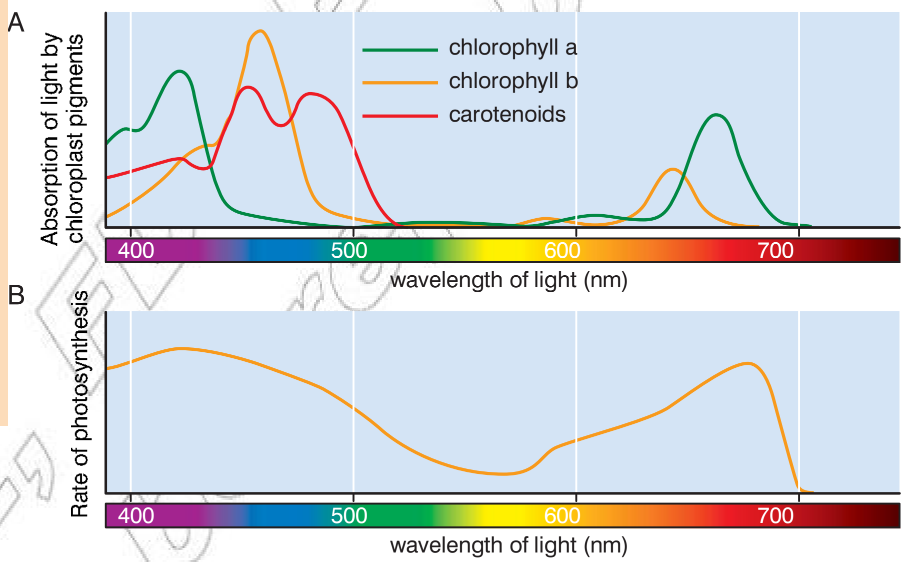


***Figure 5.31A** The absorption spectrum of chlorophyll a, chlorophyll b and carotenoids. Notice how between them they absorb most wavelengths of visible light – except 500 nm to 600 nm – green! Plants are green because these wavelengths are reflected, not absorbed;* ***B** The action spectrum for different wavelengths of light. Notice the dip in the 'green' region of the spectrum*

KEY WORDS

reaction centre molecule *where light-dependent reactions begin*

antenna complex *an array of protein and chlorophyll light-harvesting molecules embedded in the thylakoid membrane*

absorption spectrum *the range of wavelengths a molecule absorbs*

action spectrum *the photosynthesis effectiveness of each wavelength*

What happens in the light-dependent reactions?

The light-dependent reactions use light energy to 'drive' the synthesis of two molecules that will, in turn, drive the light-independent reactions. These two molecules are:

- ATP – this provides the energy for the reactions, and
- reduced NADP – this provides the hydrogen ions for a key reduction reaction.

NADP is very similar to NAD that is used in respiration and it has the same function – transporting hydrogen ions.

The main events in the light-dependent reactions are summarised in figure 5.32.

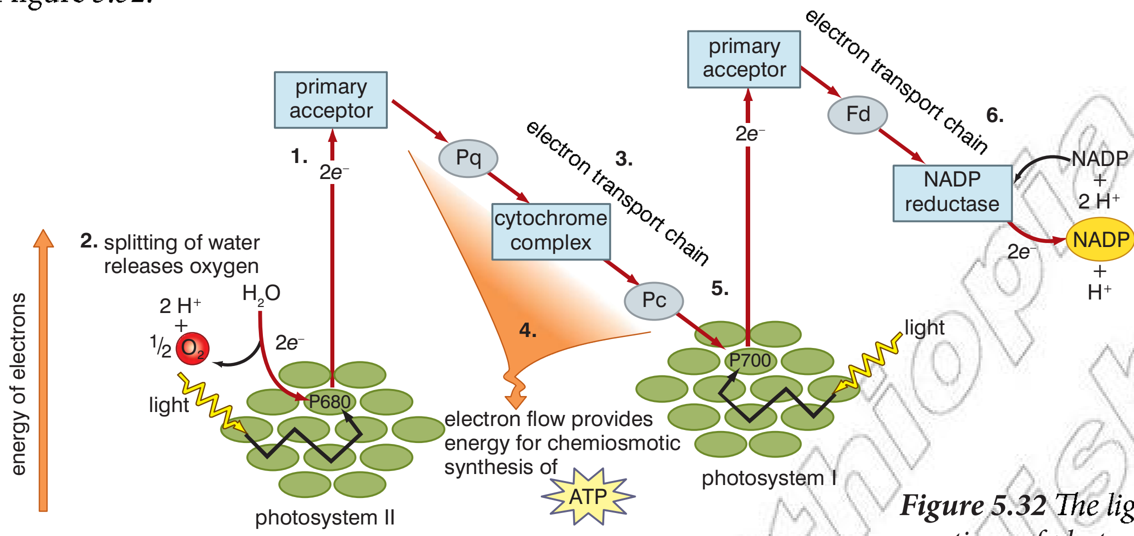


Figure 5.32 The light-dependent reactions of photosynthesis

Photosystem I and photosystem II

1. Electrons (e⁻) in chlorophyll molecules in photosystem II are excited by the energy in photons of light – they become more energetic. Because of the extra energy, they escape from the chlorophyll and pass to an electron acceptor (the **primary electron acceptor**).
2. The conditions created in the chloroplast cause the following reaction to occur:

   $2H_2O \rightarrow O_2 + 4H^+ + 4e^-$

   This light-dependent splitting of water is called **photolysis**. The electrons replace those lost from the chlorophyll molecule.
3. The primary electron acceptor passes the electrons to the next molecule in an electron transport chain (plastoquinone or 'Pq'). The electrons then pass along a series of cytochromes (similar to those in the mitochondrial electron transport chain) and finally to plastocyanin (Pc) – the last carrier in the chain. The electrons lose energy as they are passed from one carrier to the next.
4. One of the molecules in the cytochromes complex is a proton (hydrogen ion) pump. As electrons are transferred to and then transferred from this molecule, the energy they lose powers the pump which moves protons from the stroma of the chloroplast to the space inside the thylakoid. This leads to an accumulation of protons inside the thylakoid, which drives the chemiosmotic synthesis of ATP.
5. Electrons in chlorophyll molecules in photosystem I are excited (as this photosystem absorbs photons of light) and escape from the molecule. They are replaced by the electrons that have passed down the electron transport chain from photosystem II.
6. The electrons then pass along a second electron transport chain involving ferredoxin (Fd) and NADP reductase. At the end

DID YOU KNOW?

The chlorophyll a molecule in photosystem II is most active with light of wavelength of 680 nm (P680); that in photosystem I is most active with light of a wavelength of 700 nm (P700).

KEY WORDS

primary electron acceptor *the first molecule to accept the excited electron displaced from a chlorophyll molecule*

photolysis *light-dependent splitting of water*

KEY WORDS

photosynthetic unit *an arrangement of molecules capable of carrying out all the reactions in the light-dependent stage of photosynthesis.*

non-cyclic photophosphorylation *the formation of ATP via photosystem II*

cyclic photophosphorylation *use of only photosystem I to generate ATP*

of this electron transport chain, they can react with protons (hydrogen ions) and NADP in the stroma of the chloroplast to form reduced NADP.

Figure 5.32 is part graph and part flow chart showing how the reactions take place and in what sequence. But it doesn't show how the molecules are arranged in relation to each other to form what is called a **photosynthetic unit**. Figure 5.33 shows this arrangement.

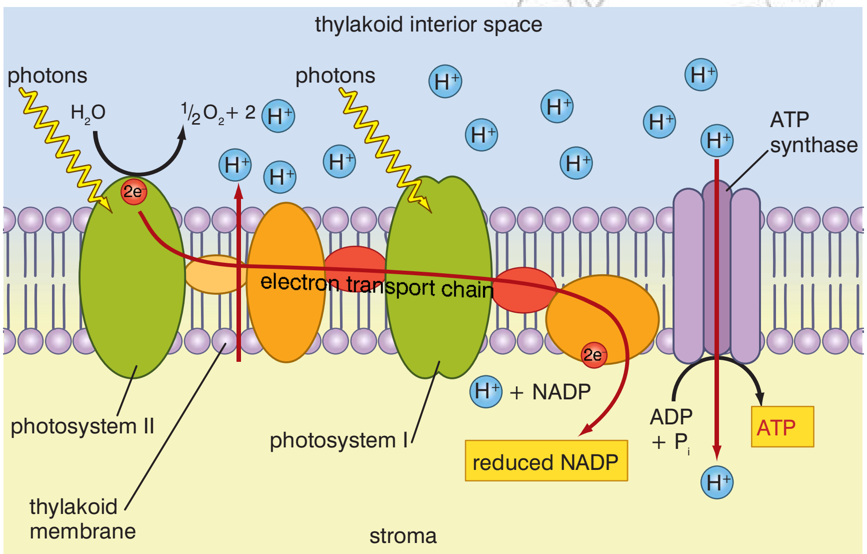


Figure 5.33 *How the molecules are arranged in a photosynthetic unit*

A photosynthetic unit is a unit of pigments, electron carriers and ATP synthase that is capable of carrying out all the reactions in the light-dependent stage of photosynthesis. The formation of ATP in the way described above is called **non-cyclic photophosphorylation**. This is because:

- the phosphorylation (formation of ATP) is light-dependent
- the electrons lost from the chlorophyll are not recycled in any way

Plants sometimes generate ATP by **cyclic photophosphorylation**. In cyclic photophosphorylation, only photosystem I is used. No oxygen and no reduced NADP are formed. Figure 5.34 shows this system. Here, you can see that electrons lost from the chlorophyll molecule are returned to it. Hence the name 'cyclic'. This process usually only happens when sugars cannot be synthesised for some reason – such as lack of carbon dioxide.

In cyclic and non-cyclic photophosphorylation, ATP is produced because:

- there is an accumulation of protons (hydrogen ions) in the interior of a thylakoid
- this creates a concentration gradient between the thylakoid interior and the stroma of the chloroplast
- protons move down this concentration gradient, through ATP synthase, causing the rotor to spin, just as in mitochondria during respiration

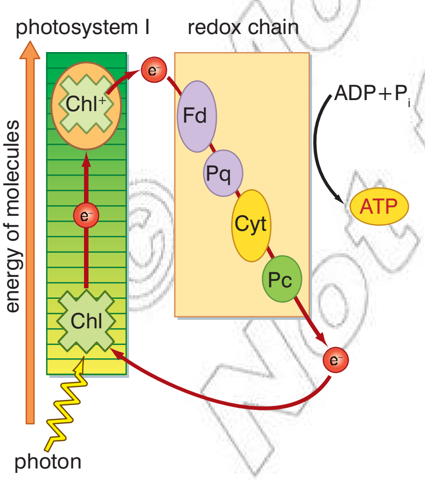


Figure 5.34 *Cyclic photophosphorylation*

A summary of the light-dependent reactions

Light energy is used to excite electrons which then:

- cause the transfer of protons to the inside of the thylakoid membrane as they pass along the first electron transport chain; this eventually leads to the formation of ATP, and
- react with hydrogen ions and NADP at the end of the second electron transport chain to form reduced NADP; this reaction could only happen because of the extra energy possessed by the electrons.

The ATP and reduced NADP are used to drive the synthesis of carbohydrates in the light-independent reactions of photosynthesis.

Activity 5.10: Separate the photosynthetic pigments in spinach leaves

You will need:

- spinach (or other) leaves
- pestle and mortar
- 80% acetone
- calcium carbonate
- filter funnel, beaker, measuring cylinder, glass jar with a tight cork
- no.1 filter paper, petroleum ether, acetone, hook, micropipette

Method

1. Take 50 g of fresh spinach leaves in a pestle and mortar. Grind them with 20 ml of 80% acetone.
2. Add a pinch of calcium carbonate and again crush.
3. Filter the extract. The deep-green-coloured filtrate contains the photosynthetic pigments (chlorophylls, carotenoids and xanthophylls).
4. Take a glass jar (about 45 cm high) with a tight cork fitted in it. The cork should have a hole in the centre.

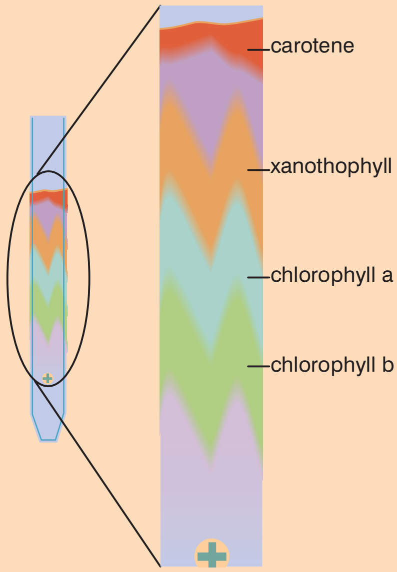


***Figure 5.35** A chromatogram of the pigments in spinach leaves*

5. Mix 25 cm^3 petroleum ether and 3 cm^3 acetone. Pour the solvent into the jar and allow the jar to become saturated.
6. Cut a strip of filter paper of the size which will fit in the jar.
7. Mark a pencil line about 3 cm from one end.
8. Place a small circular spot of pigment extract on the pencil line.
9. Allow the spot to dry and add another spot in the same place.
10. Repeat stages 8 and 9 several times until you have a concentrated spot – but do not let the spot 'spread' too far whilst you are preparing it.
11. Now hang the strip inside the jar (you could tape it to the base of the cork) and close the cork. DO NOT ALLOW THE SPOT TO DIP INTO THE SOLVENT.
12. Allow the chromatogram to run until the solvent has nearly reached the top of the filter paper. DO NOT LET THE SOLVENT RUN TO THE TOP OF THE FILTER PAPER.

You should see something like the distribution of pigments shown in figure 5.35.

KEY WORDS

ribulose bisphosphate *a five-carbon compound in the stroma*

DID YOU KNOW?

About Rubisco

The full name for the enzyme is ribulose bisphosphate carboxylase oxygenase. Notice that there are two '-ases' in the name. Rubisco can catalyse the addition of CO_2 or O_2 to ribulose bisphosphate. It is unusual for an enzyme to be able to catalyse two reactions involving different substrates. We shall see the importance of this when we study photorespiration later.

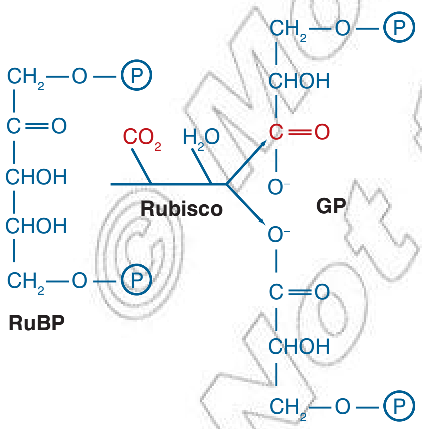


***Figure 5.36** The action of Rubisco*

How is carbohydrate synthesised in the light-independent reactions?

The light-independent reactions of photosynthesis occur in the stroma of the chloroplasts. They comprise a complex cycle of reactions that involves the addition of carbon dioxide to a pre-existing five-carbon molecule (a molecule containing five carbon atoms) within the chloroplast. The resulting molecules are modified to regenerate the original molecule whilst, at the same time, synthesising glucose. The sequence of reactions was discovered by Melvin Calvin, an American biologist. Because of his work, the light-independent reactions are also referred to as the Calvin cycle.

In the 1950s Melvin Calvin experimented with unicellular algae called *Chlorella* by exposing them to radioactive carbon dioxide.

After different periods of time, the algae were killed and the chemicals in the algae that contained radioactive carbon (which must have come from the carbon dioxide) were identified using two-dimensional chromatography.

As time passes more compounds contain the radioactive carbon. By refining the experiment and using shorter and shorter intervals, Calvin identified the first stable compound to be formed as a compound containing three carbon atoms called glycerate phosphate (GP).

The main stages of the light-independent reactions are:

- carbon dioxide reacts with **ribulose bisphosphate** (**RuBP**) – a five-carbon compound in the stroma; the reaction is catalysed by the enzyme **Rubisco**.
- two molecules of the three-carbon compound GP are formed from this reaction as figure 5.36 shows
- each molecule of GP is converted to TP (triose phosphate – another three-carbon compound); this is a reduction reaction using hydrogen ions from reduced NADP and energy from ATP
- some of the TP formed is used to regenerate the RuBP (ATP is again required) whilst some is used to form glucose and other useful organic compounds

Figure 5.37 summarises the light-independent reactions of photosynthesis. It shows how three 'turns of the cycle' result in an output of one molecule of TP. Six turns of the cycle would give an output of two molecules of TP – enough to make one molecule of glucose.

TP can also be converted to lipids, amino acids and from these into nucleotides and all the other organic molecules found in plants. TP is the basis for the synthesis of all organic molecules.

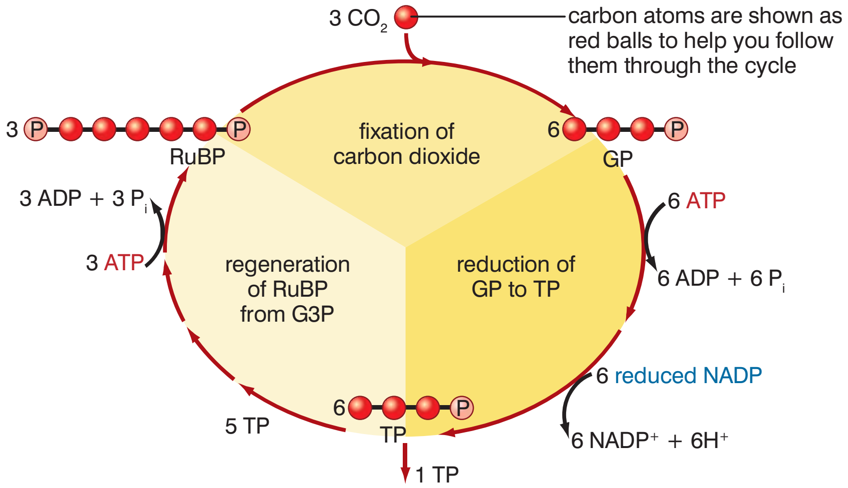


Figure 5.37 The light-independent reactions

DID YOU KNOW?

How the light-dependent and light-independent reactions are related

During the light-independent reactions, reduced NADP is reoxidised to NADP and ATP is hydrolysed to ADP and P_i. These are then reused in the light-dependent reactions to regenerate ATP and reduced NADP to be used again in the light-independent reactions … and so on. Figure 5.38 summarises the relationship between the light-dependent reactions and the light-independent reactions.

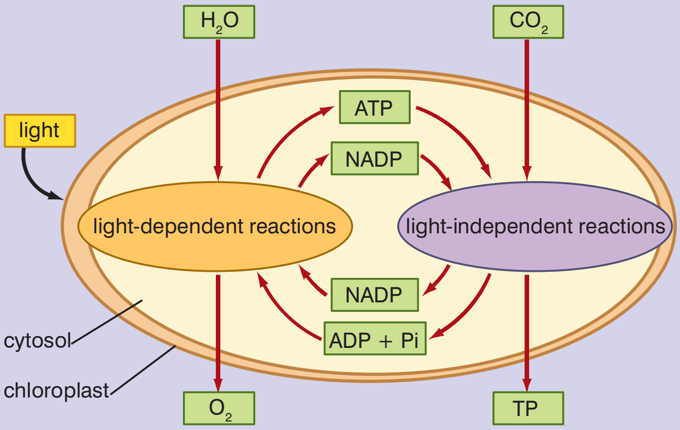


Figure 5.38 The relationship between the light-dependent and light-independent reactions

What factors affect the rate of photosynthesis?

Photosynthesis is dependent on a number of factors. The main ones, and their effects, are shown in the table below.

Table 5.1 Factors affecting the rate of photosynthesis

Factor	Effect on photosynthesis
Light intensity	Low light intensity can limit the light-dependent reactions by reducing the number of electrons in chlorophyll molecules that are photo-excited.
Carbon dioxide concentration	Can limit the light-independent reactions by influencing the rate of the initial reaction with RuBP.
Temperature	Can limit the rate of enzyme action, for example, ATP synthase (light-dependent reactions) and Rubisco (light-independent reactions).

DID YOU KNOW?

About the optimum temperatures of enzymes controlling photosynthesis

The actual optimum temperature for the enzymes of photosynthesis varies with the geographical location. The enzymes of plants that live within the Arctic Circle have a much lower optimum than those of plants found in the tropics.

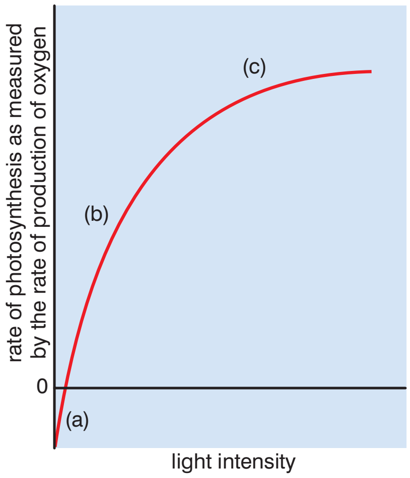


***Figure 5.39** The effect of light intensity on the rate of photosynthesis (measured by the rate of production of oxygen)*

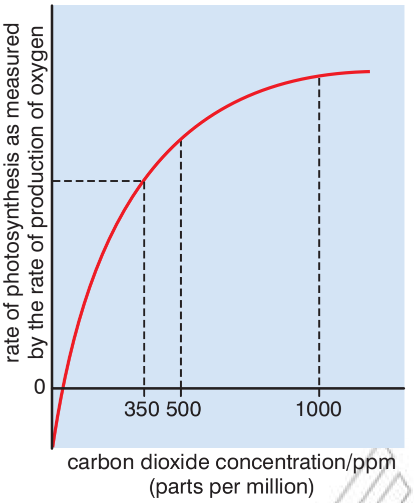


***Figure 5.40** The effect of carbon dioxide on the rate of photosynthesis*

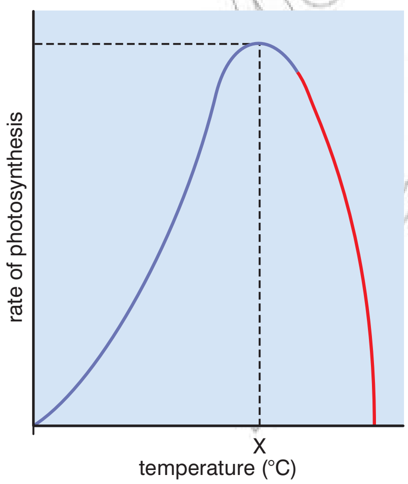


***Figure 5.41** The effect of temperature on the rate of photosynthesis*

In table 5.1, you can see that there is a reference to the factors 'limiting' the rate of photosynthesis when their presence is in short supply. But which factor actually limits the rate of photosynthesis? The answer to this question could well be different on different days. On a cold, bright day in an Arctic country, temperature is likely to hold back the rate of photosynthesis. On a warm, cloudy day in summer, light intensity is likely to limit the rate. On a warm, sunny day in summer, it could well be the concentration of carbon dioxide.

In general terms we can say that:

The rate of photosynthesis is limited by the factor that is present in a limiting quantity.

This is known as the **principle of limiting factors**.

What is the effect of light intensity on the rate of photosynthesis?

This is shown as a graph in figure 5.39. The graph is divided into three regions:

a) very low light intensities – respiration is still occurring and is taking in oxygen faster than photosynthesis is producing it

b) medium light intensities – photosynthesis is producing more oxygen than respiration uses, the rate of photosynthesis increases with increasing light intensity

c) very high light intensities – the rate of photosynthesis is beginning to level out, even though the light intensity is still increasing; some other factor is probably limiting the rate

What is the effect of the concentration of carbon dioxide on the rate of photosynthesis?

Again, it is convenient to show this as a graph (figure 5.40). The graph is similar to that in figure 5.39. At very low concentrations of carbon dioxide, little photosynthesis takes place, although respiration is still using up oxygen. As the carbon dioxide concentration increases, so does the rate of photosynthesis. Again, however, it begins to level off at higher concentrations. This may be due to some other factor, or it could be due to the saturation of Rubisco.

How does temperature affect the rate of photosynthesis?

Many of the reactions in both the light-dependent stage and the light-independent stage are controlled by enzymes, which are affected by temperature. Once the temperature exceeds the optimum, the enzyme denatures and the rate of photosynthesis decreases rapidly.

How can all the factors interact to influence the rate of photosynthesis?

Increasing the light intensity should increase the rate at which ATP and reduced NADP are produced in the light-dependent reactions and, as a result, increase the rate at which the Calvin cycle can take place. However, the rate at which the Calvin cycle can 'turn' could be limited by:

- a low temperature (limiting the rate at which enzymes such as Rubisco can operate)
- a low concentration of carbon dioxide

This limits the rate at which reduced NADP and ATP can be used, which, in turn, limits the amount of NADP and ADP + P_i that can be reused by the light-dependent reactions. The whole process is therefore limited, even though the light intensity continues to increase. This is shown in figure 5.42.

KEY WORD

principle of limiting factors *limitation by a factor that is present in a limiting quantity*

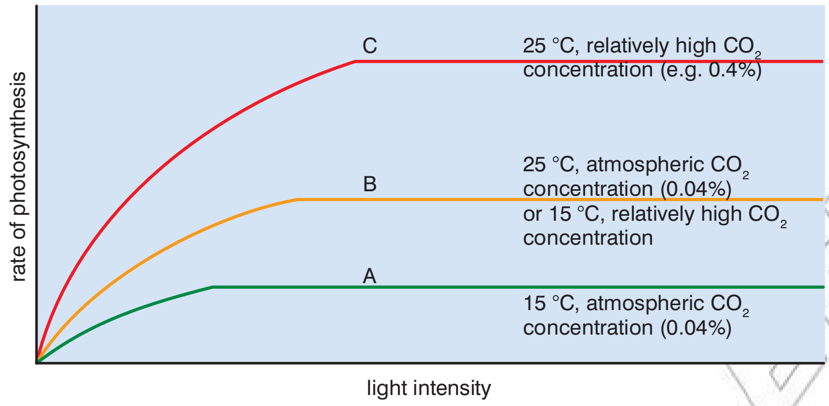


Figure 5.42 *The effect of several factors on the rate of photosynthesis*

In the region of the graphs where light is non-limiting (horizontal lines), the factors that are limiting are:

A – both temperature and carbon dioxide; increasing either produces an increase in the rate of photosynthesis to level B

B – temperature or carbon dioxide concentration (the factor that hasn't been increased from A); increasing the temperature increases the rate to level C

As well as the major factors discussed above, a number of other factors influence the rate of photosynthesis. These include:

- the wavelength of the light; photosynthesis takes place faster in 'red' and 'blue' wavelengths than in other wavelengths because these wavelengths are absorbed more efficiently than others; leaves are green because green wavelengths are reflected
- the amount of chlorophyll present

DID YOU KNOW?

That commercial growers make use of the law of limiting factors

Crops are often grown in large glass 'greenhouses' or in even larger 'polytunnels'.

In both cases the crops are effectively grown in an indoor, controlled environment covered in a transparent material to allow light to penetrate. Here, growers can apply knowledge of the principle of limiting factors to enhance photosynthesis and, therefore, the yield of the crop. Increasing the carbon dioxide concentration and increasing the temperature (up to a point) can increase both the rate of photosynthesis and, therefore, the yield of the crop.

Figure 5.43 *Crop plants being grown in a polytunnel*

Just enclosing the plants in a greenhouse or polytunnel will increase the temperature (because of the 'greenhouse effect') without any extra heating costs. However, this will only happen during daylight hours. At night, the greenhouse will cool down and growth processes other than photosynthesis will also slow down.

However, before investing in any equipment to maintain increased temperatures and carbon dioxide concentrations, the grower needs to be aware of the likely gains. He/she needs to ask what will be the extra yield:

- from increasing the concentration of carbon dioxide?
- from increasing the temperature?

And will the extra cost of this be offset by extra profits?

Activity 5.11: Investigating the rate of photosynthesis

The rate of photosynthesis can be measured in some aquatic plants by collecting the oxygen given off in a certain period of time. The diagram below shows a simple apparatus for collecting the oxygen produced by *Elodea* – a pond weed.

The lamp is to make sure that the plant is illuminated constantly for 24 hours. Carbon dioxide is supplied by dissolving sodium hydrogen carbonate in the water. In solution, the sodium hydrogen carbonate releases carbon dioxide over a period of time.

You can use this simple apparatus to plan investigations into:

- the effect of temperature on the rate of photosynthesis
- the effect of carbon dioxide concentration on the rate of photosynthesis
- the effect of light intensity on the rate of photosynthesis

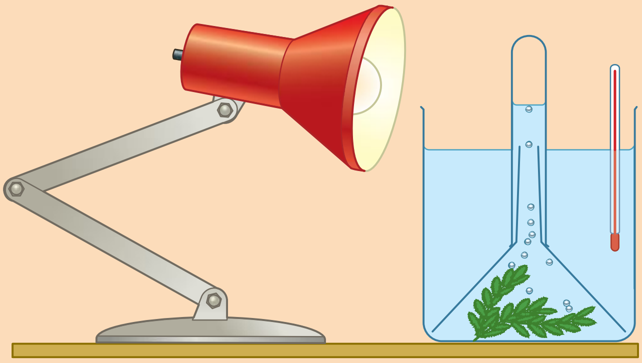


Figure 5.44 *Investigating the effect of light intensity on the rate of photosynthesis*

In your plans, you must make clear:

- how you will change the independent variable
- how you will measure the dependent variable
- how you will control other variables that might influence your results
- the steps you will take to ensure that your results are as reliable as possible

Are there any other ways of photosynthesising?

C3 photosynthesis and photorespiration

What we have just described is the method of photosynthesis that takes place in plants living in temperate environments, such as those found in Europe. It is called C3 photosynthesis – because the first compound formed in the light-independent reactions of the Calvin cycle is GP, which contains three carbon atoms. C3 plants have leaves that are adapted to this method of photosynthesis. These leaves are generally broad, to catch as much sunlight as possible.

The cells that contain most chloroplasts (the palisade cells) are nearest the upper surface of the leaf (to absorb as much light as possible). The stomata are mainly on the lower surface, to minimise water loss. During the day, the stomata are open for most of the time to allow the entry of carbon dioxide, but they can be closed if the water loss is too great on a hot day. The spongy mesophyll has air spaces that allow easy diffusion of carbon dioxide and oxygen between the palisade layer and the stomata. Figure 5.45 shows the structure of the leaf of a C3 plant.

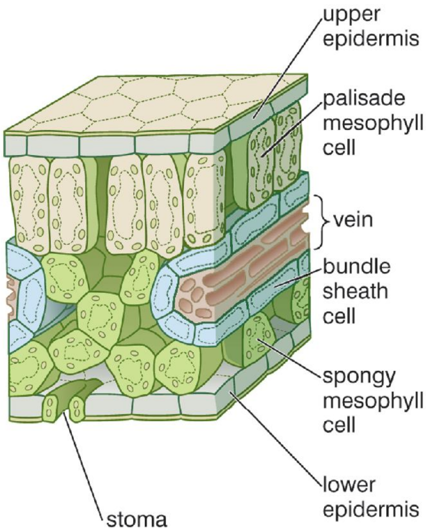


Figure 5.45 A leaf from a C3 plant

However, plants in the tropics have a problem. Here, it can be very hot and the leaves close their stomata to minimise water loss. When C3 plants do this, the concentration of carbon dioxide in the leaves falls and the enzyme Rubisco starts to behave in an unusual way. In the low concentrations of carbon dioxide, Rubisco binds with oxygen, not carbon dioxide. This means that RuBP is oxidised to one molecule of GP (not two) and a molecule of phosphoglycolate. In addition, carbon dioxide is produced in the process. The process is called **photorespiration** because it involves oxidation of carbon.

$$\text{Ribulose bisphosphate + oxygen} \xrightarrow{\text{Rubisco}} \text{GP + phosphoglycolate}$$

KEY WORD

photorespiration *process involving the oxidation of carbon*

The one molecule of GP formed in photorespiration can re-enter the Calvin cycle, but the phosphoglycolate must be converted into GP for use in the Calvin cycle by a complex series of reactions. These reactions (involving a chloroplast, an organelle called a peroxisome and a mitochondrion) are summarised in figure 5.46

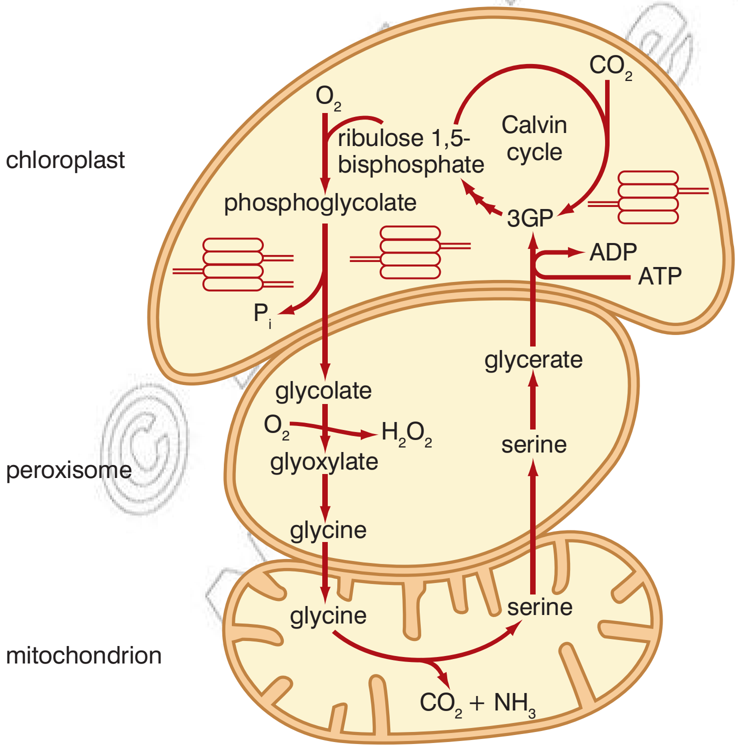


Figure 5.46 The reactions of photorespiration

DID YOU KNOW?

Why peroxisomes are named this way

It is because they produce and then break down hydrogen **perox**ide.

KEY WORD

C4 photosynthesis *light-dependent reactions are the same as in C3 photosynthesis but the first compound formed in the light-independent reactions contains four carbons, not three*

It is not necessary to try to remember all these reactions. Instead, think of the two phases of photorespiration:

1. Rubisco catalyses a reaction between oxygen and RuBP to form one molecule of GP (not two) and one molecule of phosphoglycolate.
2. The phosphoglycolate is converted to GP in reactions in the chloroplast, peroxisome and mitochondrion.

Photorespiration reduces the efficiency of photosynthesis for several reasons, including:

- the carbon is oxidised, which is the reverse of photosynthesis – the reduction of carbon to carbohydrate
- the ribulose bisphosphate must be resynthesised and the phosphoglycolate removed
- ATP is used in the resynthesis of RuBP.

C4 photosynthesis

To get round the problem of photorespiration reducing the efficiency of photosynthesis, plants that grow in tropical areas like Ethiopia (such as maize, crabgrass, sorghum and sugar cane) have evolved a different photosynthetic pathway called **C4 photosynthesis**.

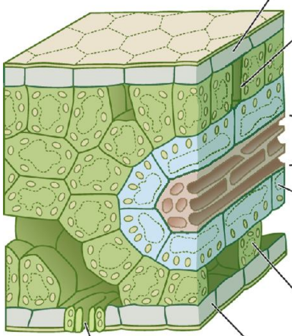


Figure 5.47 *The structure of a leaf from a C4 plant*

As the name suggests, the first compound formed in the light-independent reactions is a C4 compound (contains four carbon atoms) not GP (a C3 compound). The light-dependent reactions are the same as in the C3 plants, but there is a difference in how glucose is synthesised in the light-independent reactions. First, look at the structure of the leaf of a C4 plant in figure 5.47. The structure is essentially similar to that of a C3 plant, but there is one important difference. The cells of the bundle sheath contain chloroplasts, which they don't in C3 plants. Having no thylakoids means that the light-dependent reactions cannot occur here and so oxygen is not produced in these chloroplasts. This helps to prevent photorespiration and allows the Calvin cycle to take place in these cells.

Activity 5.12

List as many C4 plants that grow in Ethiopia as you can – you can use your textbook and the library, ask your teacher and use the internet if it is available to help you find as many as possible.

The light-dependent reactions in the C4 pathway also involve a set of reactions not found in C3 plants. These reactions take place in the mesophyll cells, which have chloroplasts with thylakoids and so can carry out the light-dependent reactions. However, they do not have the enzymes to catalyse the reactions of the Calvin cycle. Instead, the following reactions take place:

1. Carbon dioxide reacts with a C3 compound called PEP to form the C4 compound oxaloacetate. This is catalysed by the enzyme PEP carboxylase.
2. Oxaloacetate is converted into another C4 compound (malate), which then passes from the mesophyll cell into a bundle sheath cell.

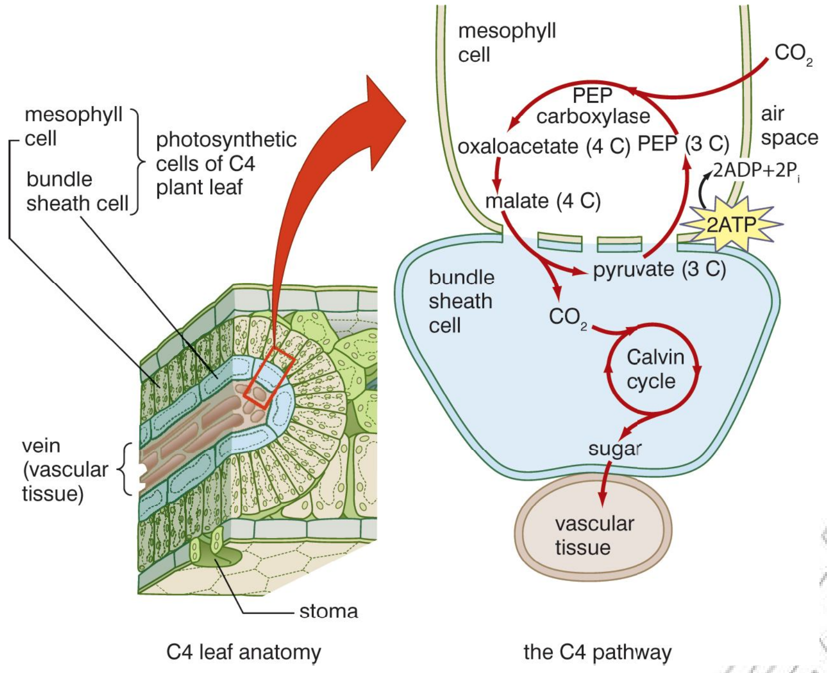


***Figure 5.48** The light-independent reactions of the C4 pathway of photosynthesis*

3. In the bundle sheath cell, malate is converted to pyruvate with the release of a molecule of carbon dioxide, which starts the reactions of the Calvin cycle by binding with RuBP.
4. The pyruvate is converted back to PEP; this reaction requires ATP. These reactions are summarised in figure 5.48.

Overall, the C4 cycle uses two more molecules of ATP to deliver a molecule of carbon dioxide to Rubisco than does the C3 cycle. During active photosynthesis in the tropics, this is not a problem, as the high light intensity generates much ATP from the light-dependent reactions.

C4 photosynthesis is most efficient in conditions of:

- low carbon dioxide concentration
- high light intensity
- high temperature

Figure 5.49 compares the efficiency of C3 and C4 photosynthesis under different concentrations of carbon dioxide.

DID YOU KNOW?

Why C4 plants experience a low concentration of carbon dioxide

This is not because the composition of air in tropical regions is any different from that in other regions. It is because C4 plants (grasses, maize) often grow very close together and so compete for the carbon dioxide in the air, reducing its concentration.

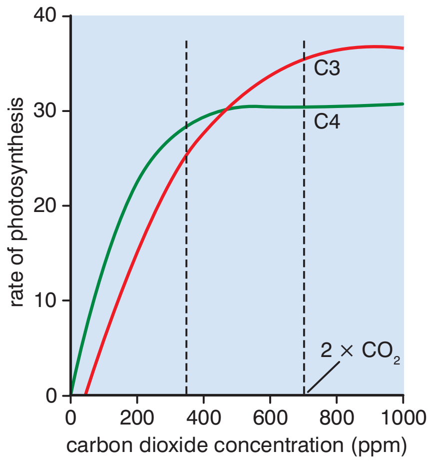


***Figure 5.49** The efficiency of C3 and C4 photosynthesis at different carbon dioxide concentrations*

DID YOU KNOW?

Cacti do it yet another way!

In the extreme heat of deserts, having stomata open during the day is a sure path to desiccation and death for the plants. But if they don't open their stomata, how will they get the carbon dioxide they need for photosynthesis? The answer is obvious really – open them at night when temperatures fall.

Cacti use what is essentially the same set of reactions as C4 plants, but they separate the two stages not by carrying them out in different cells, but by carrying them out at different times. The CAM photosynthesis cycle is as follows:

1. At night, the plants open their stomata to allow in CO_2, which then reacts with PEP in mesophyll cells to form oxaloacetate, and then malate just as in the C4 pathway.
2. The malate is then stored in the vacuoles of these cells overnight.
3. During the day, the light-dependent reactions generate ATP and reduced NADP so that the Calvin cycle can continue.
4. Malate is released from the vacuoles and is broken down to glycerate, releasing carbon dioxide for the reactions of the Calvin cycle.

Figure 5.50 compares the C4 pathway and the CAM pathway.

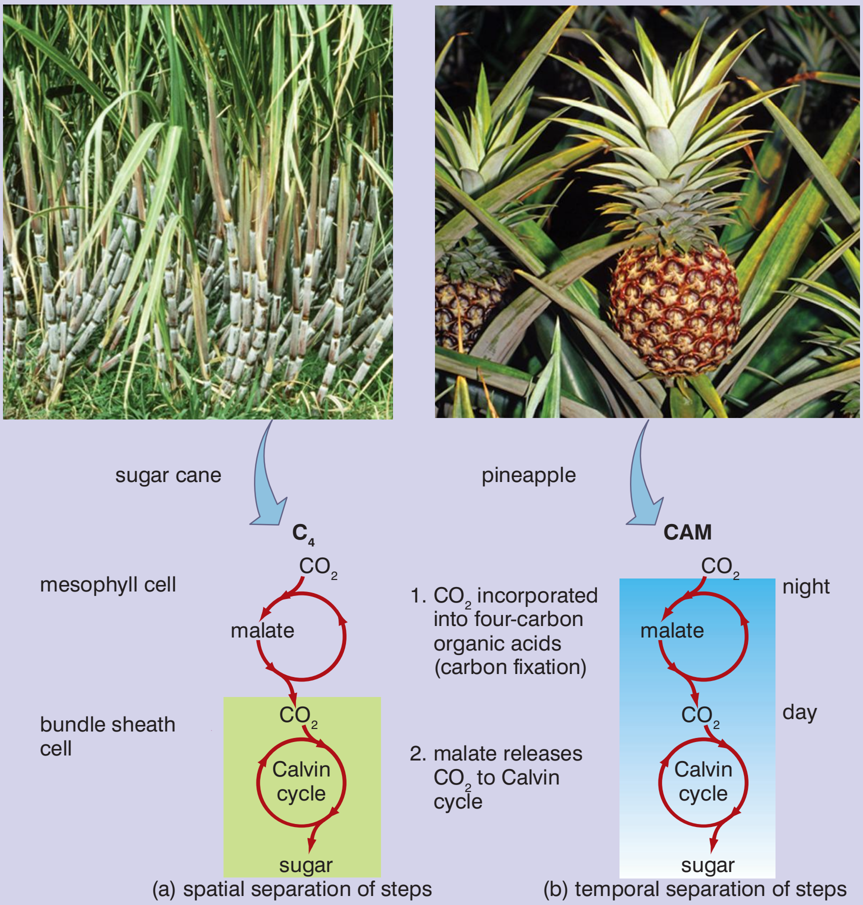


***Figure 5.50** The C4 and CAM photosynthetic pathways*

Table 5.2 compares several aspects of the two processes.

***Table 5.2** A comparison of C3 and C4 photosynthesis*

Feature	C3	C4
Bundle sheath cells	Lack chloroplasts	Have chloroplasts with no thylakoids
Enzyme used to fix CO_2	Rubisco	Pepco (PEP carboxylase)
Optimum temperature	15–25 °C	30–40 °C
Optimum CO_2 concentration	700 ppm	400 ppm
Fixation of CO_2	Mesophyll cells	Mesophyll cells
Calvin cycle	Mesophyll cells	Bundle sheath cells

The crop plants that are grown in Ethiopia (such as sorghum and wheat) are all C4 plants and are, therefore, well adapted to photosynthesise efficiently in the hot, bright days found in this country. Crop plants that are grown in temperate areas (such as peas and carrots) would not photosynthesise as efficiently, because they are C3 plants. They would, therefore, not produce high yields.

Activity 5.13: presentations on aspects of photosynthesis

In this activity, you will be divided into groups to prepare a presentation on some aspect of photosynthesis.

The main aspects that different groups will cover are:

- the light-harvesting complex of pigments
- the light dependent reactions
- the light independent reactions
- photorespiration
- C3 and C4 photosynthesis

Each group should:

- concentrate on the main features of their assigned task (it is important not to over-complicate your presentation)
- present these in a manner that will be easily recognised and easily understood by those members of the class who have not made a detailed study of your aspect of photosynthesis
- include visual material to break up any text that they present
- try to keep their presentation brief – keep to five minutes if possible

Review questions

Choose the correct answer from A to D.

1. In the light-dependent reactions of photosynthesis:
   - A NADP is reduced
   - B ATP is produced
   - C ADP is produced
   - D Light energy excites chlorophyll electrons

Figure 5.51 shows the effect of light intensity on the rate of photosynthesis at different concentrations of carbon dioxide and at different temperatures. Questions 2 and 3 relate to this graph.

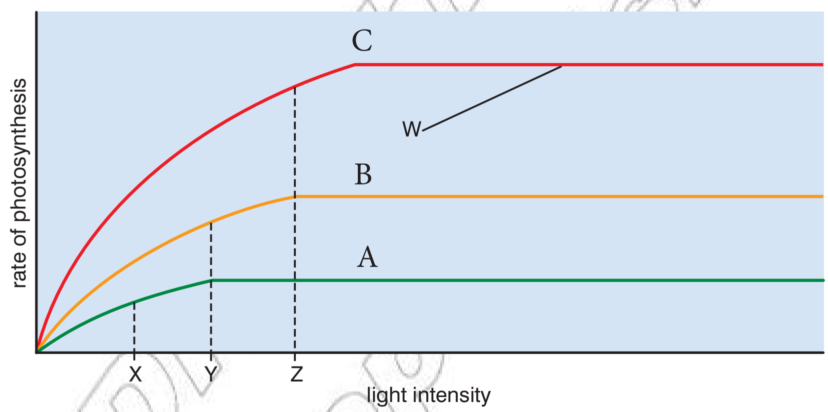


Figure 5.51

2. Line B could represent:
   - A low carbon dioxide concentration and high temperature
   - B low carbon dioxide and low temperature
   - C high carbon dioxide and high temperature
   - D any of the above
3. Which region of the graph, W, X, Y or Z, represents conditions in which light intensity is not limiting the rate of photosynthesis?
   - A W
   - B X
   - C Y
   - D Z
4. In the light-independent reactions of photosynthesis:
   - A ATP is used to convert GP into TP
   - B reduced NADP is used to convert GP into TP
   - C ATP is produced
   - D carbohydrates are produced

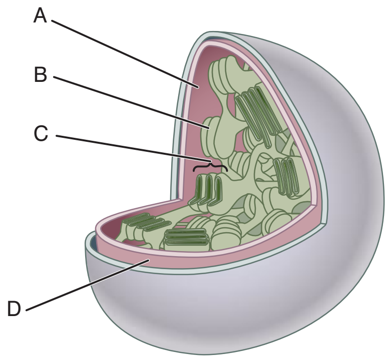


Figure 5.52 *Structure of a chloroplast*

Figure 5.42 shows the structure of a chloroplast. Questions 5 and 6 relate to this diagram.

5. During the light-dependent reactions of photosynthesis, ATP is produced in the regions labelled:
   A A
   B B
   C C
   D D
6. NADP moves from:
   A A to B
   B B to A
   C B to C
   D C to A
7. Cyclic photophosphorylation produces:
   A oxygen and ATP
   B reduced NADP and ATP
   C oxygen only
   D ATP only
8. In the light-independent reactions, reduced NADP is used to:
   A oxidise GP to TP
   B oxidise TP to GP
   C reduce TP to GP
   D reduce GP to TP
9. A photosynthetic unit can carry out:
   A photolysis
   B the synthesis of ATP
   C the synthesis of reduced NADP
   D all of the above
10. A photosystem consists of:
    A a reaction centre molecule and an electron transport chain
    B a reaction centre molecule and an antenna complex
    C an accessory pigment and an antenna complex
    D an accessory pigment and an electron transport chain

Activity 5.14

Make a big poster to show the Calvin cycle in photosynthesis. Have an inset area to show cyclic and non-cyclic photophosphorylation and how it fits in with the production of sugars.

11. In photorespiration:
    A low oxygen concentrations cause Rubisco to form more GP than usual
    B low oxygen concentrations cause Rubisco to form less GP than usual
    C low carbon dioxide concentrations cause Rubisco to form less GP than usual
    D low carbon dioxide concentrations cause Rubisco to form more GP than usual
12. In the C4 pathway:
    A PEP carboxylase catalyses the reaction of carbon dioxide with RuBP in the mesophyll cells
    B PEP carboxylase catalyses the reaction of carbon dioxide with RuBP in the bundle sheath cells
    C PEP carboxylase catalyses the reaction of carbon dioxide with PEP in the mesophyll cells
    D PEP carboxylase catalyses the reaction of carbon dioxide with PEP in the bundle sheath cells
13. C4 photosynthesis is more efficient than C3 photosynthesis in conditions of:
    A high light intensity and high carbon dioxide concentrations
    B low light intensity and high carbon dioxide concentrations
    C high light intensity and low carbon dioxide concentrations
    D low light intensity and low carbon dioxide concentrations
14. The chloroplasts in the bundle sheath cells of C4 plants are an adaptation to this pathway because:
    A they contain no Calvin cycle enzymes
    B they contain no thylakoids
    C they have a large surface area
    D they produce large amounts of oxygen
15. Which of the following statements about C4 and CAM photosynthesis is true?
    A In CAM photosynthesis, the C4 stage and the Calvin cycle are separated in time.
    B In CAM photosynthesis, the C4 stage and the Calvin cycle are separated in space.
    C In C4 photosynthesis, the C4 stage and the Calvin cycle are separated in time.
    D In C4 photosynthesis, the C4 stage and the Calvin cycle both occur in the same cell.

Summary

In this unit you have learnt that:

- ATP is an ideal energy-storage molecule in a cell because:
  - energy is released from the molecule quickly, in a single-step hydrolysis reaction
  - energy is released in small amounts (that are closely matched to the amounts needed for cellular reactions)
  - the molecule is easily moved around within the cell but cannot leave the cell
- The main stages of aerobic respiration are: glycolysis, the link reaction, the Krebs cycle, the electron transport chain and the chemiosmotic synthesis of ATP.
- In glycolysis, glucose (C6) is converted to pyruvate (C3) with the net gain of two molecules of ATP and two molecules of reduced NAD.
- In the link reaction, pyruvate is converted to acetyl coenzyme A (C2) with the loss of carbon dioxide and the production of two molecules of reduced NAD.
- In the Krebs cycle, acetyl coenzyme A combines with oxaloacetate (C4) to form citrate (C6), which is then decarboxylated to a C5 compound and then to a C4 compound, which is then converted into oxaloacetate; the cycle produces six molecules of reduced NAD, 2 molecules of reduced FAD and two molecules of ATP (by substrate level phosphorylation).
- As electrons from reduced NAD and reduced FAD pass along the electron transport chain they lose energy, which is used to pump protons from the matrix to the inter-membrane space.
- Protons then pass down an electrochemical gradient back into the mitochondrion through molecules of ATP synthase; each proton that passes through the enzyme causes one molecule of ATP to be synthesised.
- In fermentation (the anaerobic pathway):
  - the reactions of the electron transport chain, Krebs cycle and the link reaction cannot occur as, without oxygen as the terminal electron acceptor, NAD and FAD cannot be regenerated from reduced NAD and reduced FAD
  - glycolysis still occurs in anaerobic conditions as the NAD needed can be regenerated from reduced NAD by reducing pyruvate to lactate (animal cells) or ethanol (plant cells and yeast cells)
- Chloroplasts are well adapted to carry out photosynthesis because:
  - the grana provide a large surface area for the arrangement of chlorophyll molecules and the associated electron

  transport systems of the light-dependent reactions
  - the stroma provides a fluid medium for the reactions of the light-independent reactions
- The light-dependent reactions produce ATP and reduced NADP that are needed in the light-independent reactions.
- In the light-independent reactions:
  - CO_2 combines with RuBP (C5) to form two molecules of GP
  - GP is reduced to TP; reduced NADP supplies the hydrogen ions and ATP supplies the energy; the NADP and ADP + P_i are recycled to the light-dependent reactions
  - some TP is used to synthesise useful carbohydrates (such as glucose)
  - most TP is used to regenerate the RuBP so that the cycle of reactions can begin again
- The rate of photosynthesis is influenced by light intensity, concentration of carbon dioxide and temperature.
- The factor present in the lowest quantity will limit the rate of photosynthesis.
- When carbon dioxide concentrations fall, photorespiration can occur because oxygen then outcompetes carbon dioxide for the active site of Rubisco.
- Photorespiration reduces the efficiency of photosynthesis because:
  - only one molecule of GP is produced from RuBP
  - phosphoglycolate is produced which must be reconverted to RuBP, using up ATP
- C4 photosynthesis has evolved in plants in the tropics as a way of preventing photorespiration.
- In this process, the reactions of the Calvin cycle only take place in chloroplasts in bundle sheath cells.
- The bundle sheath cells can carry out the reactions of the Calvin cycle efficiently because:
  - they have no grana, so produce no oxygen to compete with carbon dioxide for the active site of Rubisco
  - there is a high concentration of carbon dioxide due to the decomposition of malate
- C4 photosynthesis is more efficient than C3 photosynthesis in conditions of high light intensity, high temperature and low carbon dioxide concentrations.
- CAM photosynthesis is effective in desert plants because it separates the light-dependent and light-independent stages in time; the leaves only open their stomata to allow the light-independent reactions to take place during the night, saving precious water.

End of unit questions

1. a) Describe how the structure of a chloroplast is suited to its function.

   b) Describe *two* ways in which chloroplasts and mitochondria are:

   (i) similar

   (ii) different

2. a) Describe *three* ways in which the ATP molecule is suited to its function of energy carrier in a cell.

   b) Describe how ATP is formed by:

   (i) substrate-level phosphorylation

   (ii) chemiosmosis

3. Figure 5.53 shows the structure of a chloroplast from a mesophyll cell of a C3 plant.

   a) Name the parts labelled A, B, C and D.

   b) Describe how the chloroplasts from a bundle sheath cell of a C4 plant would be different from this chloroplast. Explain the benefit to the plant of this difference.

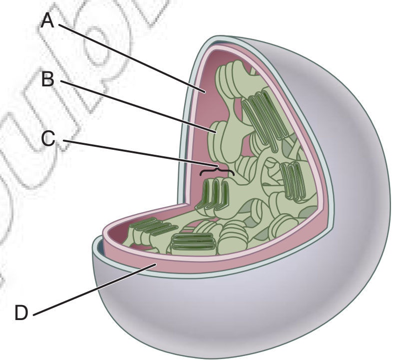


Figure 5.53

4. a) Make a drawing of apparatus you could use to measure the rate of fermentation of glucose by yeast.

   b) Describe how you could use your apparatus to investigate the effect of temperature on the rate of fermentation in yeast. You must make clear in your account:

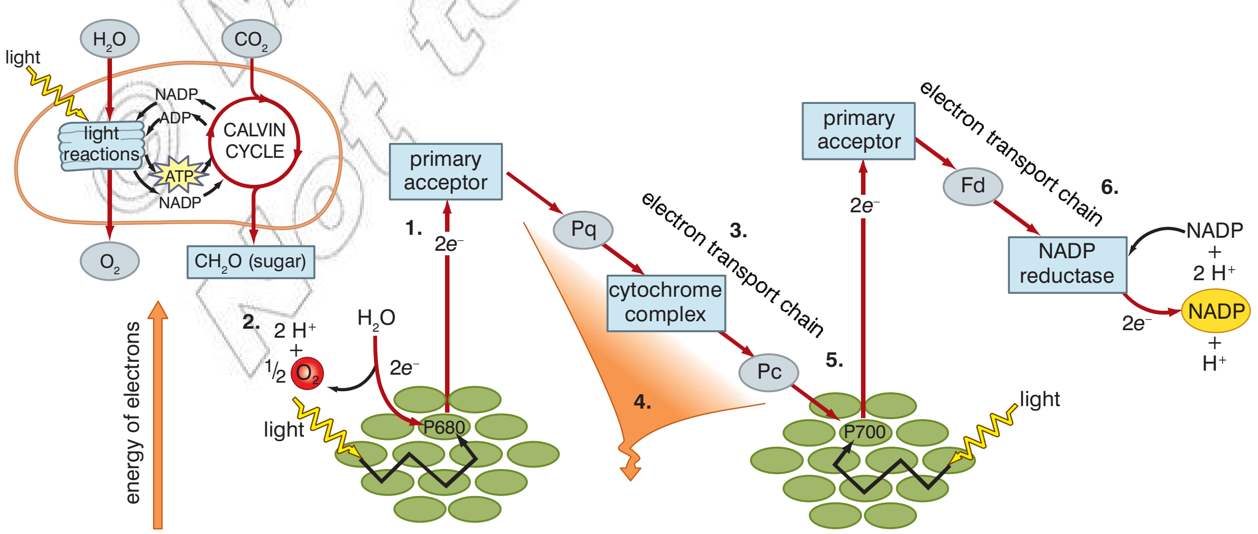
   – how you will change the temperature

   – how you will measure the rate of fermentation

   – how you will control other factors that might influence the results

5. Figure 5.54 shows the light-dependent reactions of photosynthesis. Explain what is happening at each of the stages 1–6.

Figure 5.54



6. Figure 5.55 summarises the Krebs cycle.

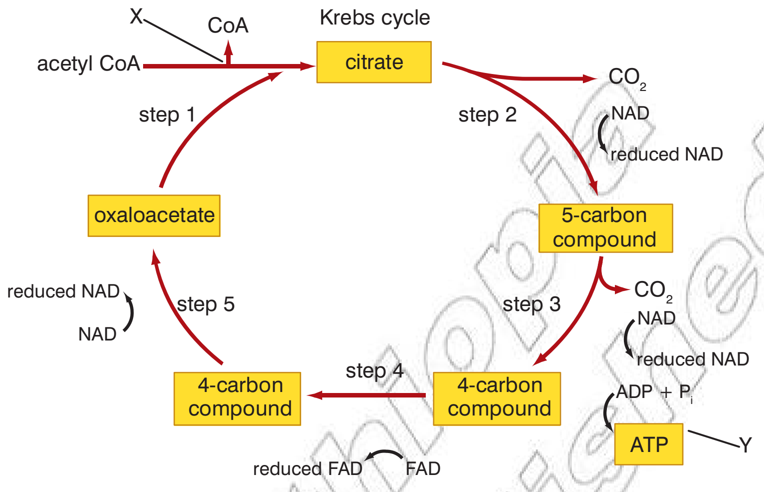


Figure 5.55

a) (i) Name, and briefly describe, the processes labelled X and Y.

(ii) Describe one other occasion during aerobic respiration where the process labelled Y takes place.

b) In the absence of oxygen, the Krebs cycle cannot take place, even though its reactions do not use oxygen. Explain why.

c) Reduced NAD is also produced during glycolysis. Explain what becomes of this reduced NAD in animal cells under:

(i) aerobic conditions

(ii) anaerobic conditions

7. The graph in figure 5.56 shows the influence of temperature, carbon dioxide and light intensity on the rate of photosynthesis.

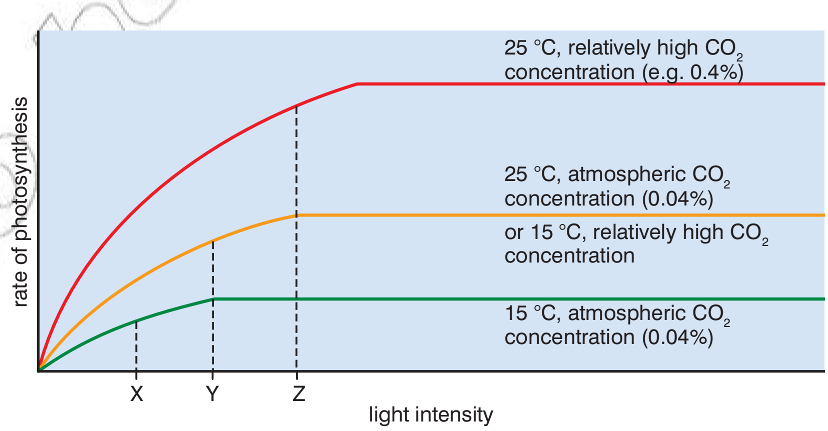


Figure 5.56

a) In the regions labelled X, Y and Z, is light a limiting or a non-limiting factor? Give reasons for your answer.

b) Describe and explain fully the difference between the three lines on the graph.

8. Figure 5.57 shows some of the reactions of the Calvin cycle.

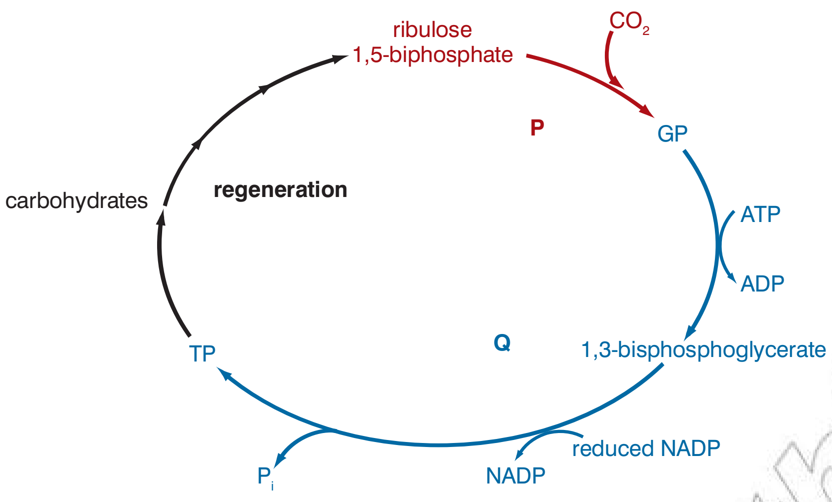


Figure 5.57

a) Describe three possible fates of the TP formed in these reactions.

b) Describe the processes occurring at P and at Q.

c) The graph in figure 5.58 shows the changes in the levels of GP and RuBP in a chloroplast when the light source is removed.

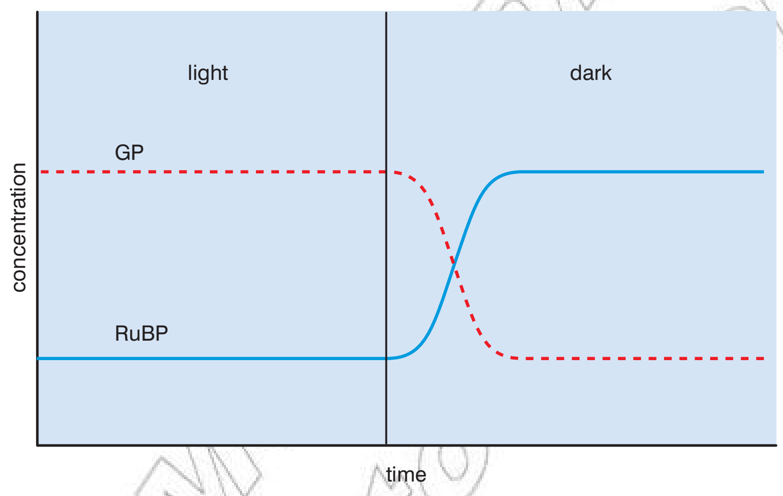
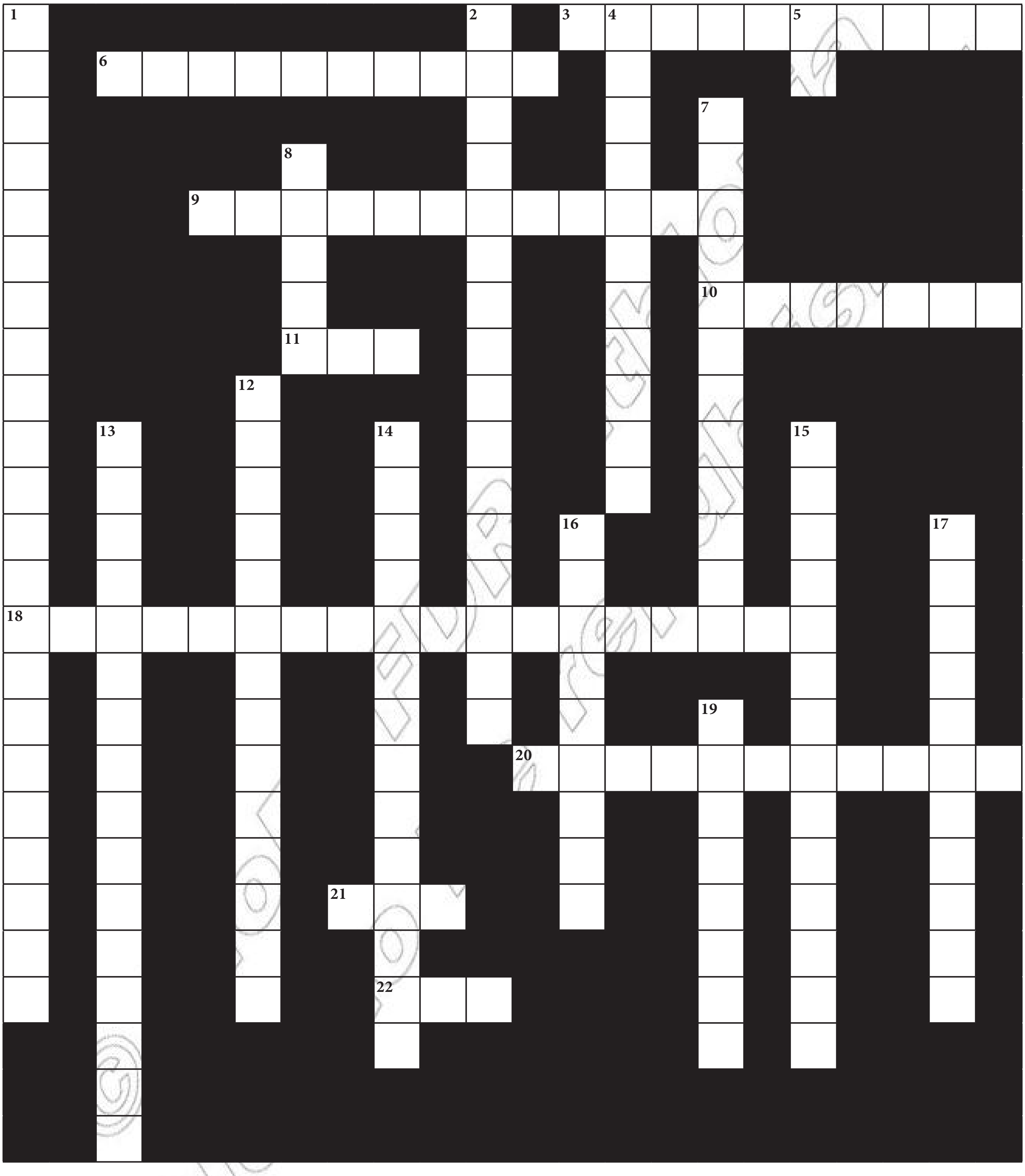


Figure 5.58

Use the graph to explain the changes in the levels of GP and RuBP when the light source is removed.

Copy the crossword puzzle below into your exercise book (or your teacher may give you a photocopy) and solve the numbered clues to complete it.



Across

3. Cycle of reactions that converts citrate to oxaloacetate (5, 5)
6. First stage of aerobic respiration (10)
9. Way in which ATP is produced by yeast when no oxygen is available (12)
10. Enzyme that catalyses the reaction between RuBP and carbon dioxide (7)
11. The main energy transfer molecule in a cell (3)
18. Smallest structure that can carry out all the reactions of the light-dependent stage of photosynthesis (14, 4)
20. Enzyme that catalyses the formation of ATP (3, 8)
21. Molecule that combines with P_i to produce ATP (3)
22. Nicotinamide adenine dinucleotide (3)

Down

1. Chain of molecules on cristae of mitochondria that moves electrons (8, 9, 5)
2. Reactions of photosynthesis that use ATP and reduced NADP to synthesise glucose (5, 11)
4. Process that releases energy from organic molecules (11)
5. Type of photosynthesis found in many tropical plants (2)
7. Stage of aerobic respiration in which pyruvate is converted to acetyl CoA (4, 8)
8. Stacks of thylakoids (5)
12. Process using light energy to drive the synthesis of carbohydrate (14)
13. Process in which RuBP combines with oxygen rather than carbon dioxide (16)
14. Reactions of photosynthesis that require light energy to produce ATP and reduced NADP (5, 9)
15. Type of phosphorylation in which a phosphate group is transferred to ADP from another substance (9, 5)
16. Type of phosphorylation that occurs at the end of the electron transport chain (9)
17. Cluster of photosynthetic pigments on a thylakoid membrane (11)
19. End-product of glycolysis (8)