

# Biology

for the IB Diploma

**COURSEBOOK** 

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Third edition

**Digital Access** 



## > How to use this book

Throughout this book, you will find lots of different features that will help your learning. These are explained below.

#### UNIT INTRODUCTION

A unit is made up of a number of chapters. The key concepts for all the chapters covered in a unit are summarised in the unit opening chapter as the introduction.

#### LEARNING OBJECTIVES

Each chapter in the book begins with a list of learning objectives. These set the scene for each chapter, help with navigation through the coursebook and indicate the important concepts in each topic. A bulleted list at the beginning of each section clearly shows the learning objectives for the section.

#### **GUIDING QUESTIONS**

This feature contains questions and activities on subject knowledge you will need before starting this chapter.

The content in this book is divided into Standard and Higher Level material. A vertical line runs down the margin of all Higher Level material, allowing you to easily identify Higher Level from Standard material.

### Links

These are a mix of questions and explanation that refer to other chapters or sections of the book.

Key terms are highlighted in **orange bold** font at their first appearance in the book so you can immediately recognise them. At the end of the book, there is a glossary that defines all the key terms.

#### **KEY POINTS**

This feature contains important key learning points (facts) to reinforce your understanding and engagement.

#### **EXAM TIPS**

These short hints contain useful information that will help you tackle the tasks in the exam.

#### **SCIENCE IN CONTEXT**

This feature presents real-world examples and applications of the content in a chapter, encouraging you to look further into topics. You will note that some of these features end with questions intended to stimulate further thinking prompting you to consider some of the benefits and problems of these applications.

#### **NATURE OF SCIENCE**

Nature of Science is an overarching theme of the IB Biology Diploma course. The theme examines the processes and concepts that are central to scientific endeavour, and how science serves and connects with the wider community. Throughout the book, there are 'Nature of Science' features that discuss particular concepts or discoveries from the point of view of one or more aspects of Nature of Science.

#### THEORY OF KNOWLEDGE

This section stimulates thought about critical thinking and how we can say we know what we claim to know. You will note that some of these feature end with questions intended to get you thinking and discussing these important Theory of Knowledge issues.

#### INTERNATIONAL MINDEDNESS

Throughout this Biology for the IB Diploma course, the international mindedness feature highlights international concerns. Science is a truly international endeavour, being practised across all continents, frequently in international or even global partnerships. Many problems that science aims to solve are international and will require globally implemented solutions.

#### **TEST YOUR UNDERSTANDING**

These questions appear within each chapter and help you develop your understanding. The questions can be used as the basis for class discussions or homework assignments. If you can answer these questions, it means you have understood the important points of a section.

#### WORKED EXAMPLE

Many worked examples appear throughout the text to help you understand how to tackle different types of questions.

#### **REFLECTION**

These questions appear at the end of each chapter. The purpose is for you as a learner to reflect on the development of your skills proficiency and your progress against the objectives. The reflection questions are intended to encourage your critical thinking and inquiry-based learning.

#### **EXAM-STYLE QUESTIONS**

Exam-style questions at the end of each chapter provide essential practice and self-assessment. These are signposted in the print coursebook and can be found in the digital version of the coursebook.

#### SELF-ASSESSMENT CHECKLIST

These appear at the end of each chapter/section as a series of statements. You might find it helpful to rate how confident you are for each of these statements when you are revising. You should revisit any topics that you rated 'Needs more work' or 'Almost there'.

I can	Needs more work	Confident to move on

## Free online material

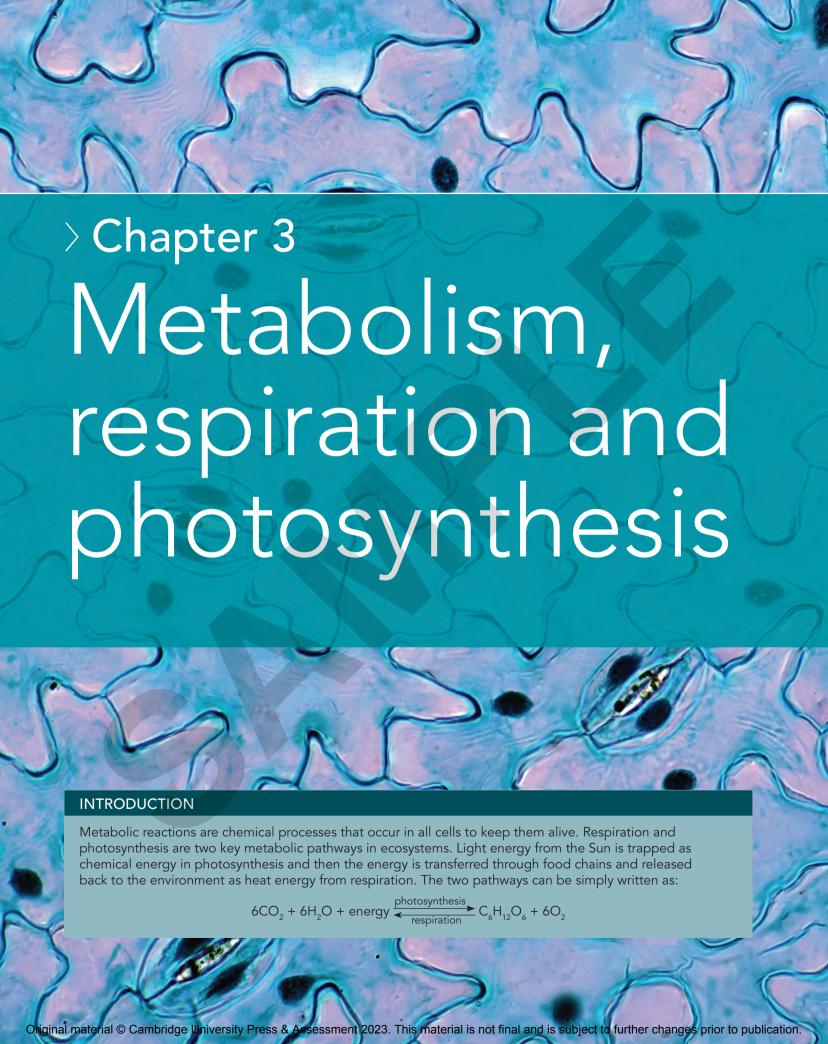
Additional material to support the Biology for the IB Diploma course is available online.

This includes Assessment guidance – a dedicated chapter in the digital coursebook helps teachers and

students unpack the new assessment and model exam specimen papers. Additionally, answers to the Test your understanding and Exam-style questions are also available.

Visit Cambridge GO and register to access these resources.





## 3.1 Metabolism

#### **LEARNING OBJECTIVES**

In this section you will:

- learn that metabolic pathways are made up of chains and cycles of enzymecatalysed reactions
- understand that metabolic processes can be anabolic or catabolic
- learn that enzymes are globular proteins that act as catalysts
- understand that enzymes have an area on their molecule, known as the active site, to which specific substrates bind
- learn that during enzyme-catalysed reactions molecules move about, and substrate molecules collide with the active sites on enzyme molecules
- discover how the rate of enzyme activity is influenced by temperature, pH and substrate concentration
- learn how enzyme molecules can be denatured
- understand how enzymes lower the activation energy of chemical reactions
- learn that enzyme inhibitors can be competitive or non-competitive
- understand how end-product inhibition can control metabolic pathways
- learn how co-enzymes and co-factors promote enzyme activity.

#### **GUIDING QUESTIONS**

- How are molecules transformed by metabolism?
- What is the role of enzymes in metabolic processes?
- What factors affect enzyme activity?

## 3.1.1 Metabolic pathways

Metabolic pathways consist of chains or cycles of reactions that are catalysed by enzymes. Metabolism includes all the chemical activities that keep organisms alive. Metabolic pathways may be very complex, but most consist of a series of steps, each controlled by an enzyme. Simple linear pathways involve the conversion of substrates to a final product:

#### **KEY POINTS**

anabolism a series of metabolic pathways that build molecules from smaller subunits. These reactions require energy.

catabolism a series of metabolic pathways that break down molecules into smaller units.

metabolism the sum of the chemical reactions that occur within living organisms.

Each arrow represents the specific enzyme needed to catalyse the conversion of one substrate to the next. An example of a linear pathway is the breakdown of glucose in the glycolysis pathway (Section 3.2, Respiration) and the digestion of starch to maltose and glucose in the digestive system:

Other metabolic pathways, such as photosynthesis or respiration, involve both chains of reactions and cycles of reactions. Two examples of cyclical pathways are the Krebs cycle in aerobic respiration and the Calvin cycle in photosynthesis (Sections 3.2 and 3.3). Both of these cycles have many enzyme-catalysed steps.

Some metabolic reactions, such as protein synthesis, take place inside cells and are said to be intracellular, while others, such as digestion, occur outside cells and are known as extracellular reactions.

There are two types of metabolic process: anabolic reactions which build new molecules and catabolic reactions which break down large molecules.

#### **NATURE OF SCIENCE**

## How does scientific understanding change and develop over time?

What affects longevity: metabolic rate or size? In 1926 an American biologist, Raymond Pearl, proposed the *rate of living hypothesis*. It suggested that a key factor determining how long a species lives is the speed of their resting metabolism. His evidence came from his observations that bigger animals tend to live longer and have lower heart, breathing and metabolic rates. He proposed that longevity is inversely related to basal (resting) metabolic rate.

The rate of living hypothesis was a well accepted theory for nearly 50 years. But over time, other scientists have made observations that have cast doubt on it. For example, rats and bats have similar metabolic rates, but a bat lives several times longer than a rat. Modern statistical methods that correct for the effects of body size and species group do not support the theory. They show that metabolic rate does not correlate with longevity in either mammal or bird groups.

Another newer model to explore body size, metabolism and ageing looked at how these are linked within the same species. Some of the results support the original rate of living theory and others do not. Scientists allowed some animals to expend more energy than others which were kept inactive and found that the amount of energy used does affect lifespan within a species. But the results were confused by the discovery that in some species smaller

individuals with higher rates of metabolism live longer than slower, larger members of the same species.

A free radical theory of ageing proposed in the twenty-first century provided a new way of linking metabolism to ageing. Oxygen free radicals are formed during cell respiration in mitochondria. They can damage cells and contribute to ageing. The free radical theory suggested that more or faster respiration could make organisms' lives shorter. But today, scientists believe that free radical damage from metabolism on its own cannot be the cause of ageing. The accumulation of other defects and imperfections must also be important. It seems that free radical theory has served its purpose in our understanding of the ageing process. More investigations and newer theories are needed to advance our knowledge of how we grow old. Only recently, experimental tools, such as sequencing of DNA and profiling of proteomes and metabolites, have been developed and these may be used to begin assessing the many types of damage that cause cells and bodies to age.

#### To consider:

- 1 Scientific knowledge is provisional and theories must be modified in the light of new observations and evidence.
- Which areas of biology do you think will be important in understanding the ageing process?
- 3 How has modern technology helped scientists gather data for new theories?

Two examples of anabolic reactions are protein synthesis, when amino acid monomers are linked by condensation reactions (Section 2.4), and photosynthesis (Section 3.3), which builds glucose molecules from carbon dioxide and water.

Catabolic reactions include the hydrolysis of large molecules, such as carbohydrates into glucose monomers during digestion, and respiration, which breaks down glucose to release energy.

## 3.1.2 Enzymes and active sites

An enzyme is a biological catalyst. Like all catalysts, enzymes speed up biochemical reactions, such as digestion and respiration, but they remain unchanged at

the end of the process. All enzymes are proteins with long polypeptide chains that are folded into three-dimensional shapes. The arrangement of these shapes is very precise and gives each enzyme the ability to catalyse one specific reaction. If the three-dimensional shape of an enzyme is destroyed or damaged, it can no longer function and is said to have undergone denaturation. Extremes of temperature and heavy metals and, in some cases, pH changes can cause permanent changes in an enzyme.

#### **KEY POINT**

**enzyme** a globular protein that functions as a biological catalyst of chemical reactions.

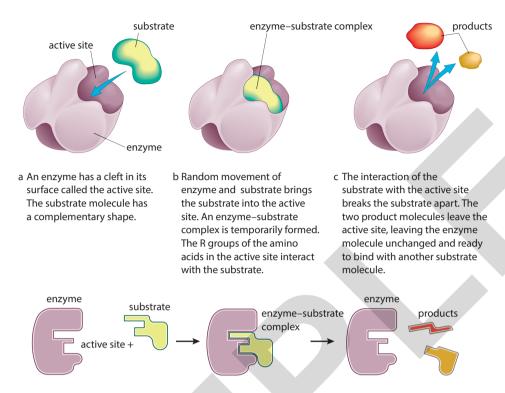


Figure 3.1.1: How an enzyme catalyses the breakdown of a substrate molecule into two product molecules.

The three-dimensional shape of an enzyme is crucial to the way it works. In the structure of every enzyme is a specially shaped region known as an active site (Figure 3.1.1). It is here that the substrate and enzyme bind together. The substrates are the chemicals involved in the reaction catalysed by the enzyme. The shapes of the enzyme and substrate are complementary, so that they fit together perfectly like a key fits into a lock. The 'lock-and-key hypothesis' is a way of explaining how each enzyme can be so specific. To unlock a door requires just one special key. To catalyse a reaction requires one special enzyme. Just as only one key fits perfectly into the lock, only one substrate fits perfectly into the active site of an enzyme.

Enzyme and substrate molecules move freely in solution and in most cases will eventually collide with one another. When a substrate molecule collides with the active site of an enzyme it will bind with it to form an enzyme–substrate complex. Once in place in an active site, substrates may be bonded together to form a new substance or they may be broken apart in processes such as digestion and respiration. For example, one type of enzyme bonds amino acids together to form a

polypeptide, while very different enzymes are involved in digesting them.

### Induced-fit model of enzyme action

In 1958, research published by Daniel Koshland (1920–2007) proposed a theory to explain how enzymes and substrates bind together. It is known as the induced-fit model of enzyme action. We know that substrates require a specific enzyme to catalyse their reactions and the model explains how only the correct substrate is able to bind to an enzyme.

#### **KEY POINTS**

active site a region on the surface of an enzyme molecule where a substrate molecule binds and which catalyses a reaction involving the substrate.

induced-fit model a model of enzyme action in which the shape of the active site alters when an enzyme binds to its substrate so that a reaction can take place.

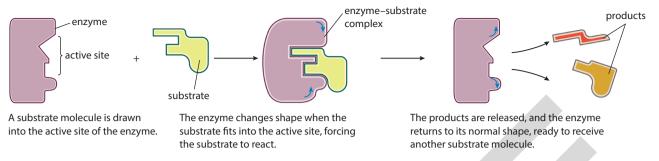


Figure 3.1.2: The induced-fit model of enzyme action.

As a specific substrate approaches an enzyme it induces the correct alignment of substrate and active site so that catalysis can take place. The specificity is a molecular recognition mechanism and it acts so that enzyme and substrate complement each other perfectly. Only the proper substrate is capable of inducing the proper alignment of the active site that will enable the enzyme to perform its catalytic function. The model also suggests that the active site continues to change until the substrate is completely bound to it.

Figure 3.1.2 shows how the substrate causes or induces a slight change in the shape of the active site so it can fit perfectly. As the enzyme changes shape, the substrate molecule is activated so that it can react and the resulting product or products are released. The enzyme is left to return to its normal shape, ready to receive another substrate molecule.

### Factors affecting enzyme action

Enzymes work in many different places in living organisms and they require special conditions to work at their greatest, or optimum, efficiency. Temperature, pH and the concentration of the substrates involved all affect the rate at which enzymes operate and produce their products.

#### **Temperature**

Enzymes and their substrates usually meet as a result of random collisions between their molecules, which move freely in body fluids or cytoplasm. In the human body, most reactions proceed at their greatest rate at a temperature of about 37 °C and deviations from this optimum temperature affect the reaction rate, as the graph in Figure 3.1.3 shows.

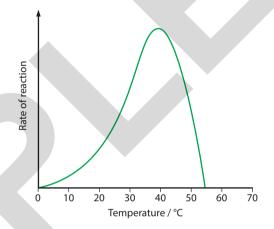


Figure 3.1.3: The effect of temperature on the rate of an enzyme-controlled reaction. An enzyme works most efficiently at its optimum temperature.

At less than 37 °C, molecules in solution move more slowly so the likelihood of collision between them is reduced. This slows down the production of products. At very low temperatures, enzymes hardly work at all and the rate of reaction is very low. As the temperature rises, molecular collisions are more frequent and energetic, and therefore the rate of the enzyme-controlled reaction increases.

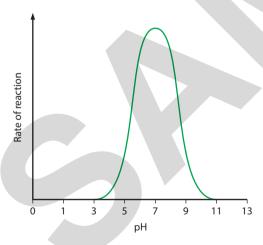
As the temperature rises above the optimum, the enzyme and substrate molecules move faster, but atoms in the enzyme molecule itself also move more energetically, straining the bonds holding it together. Eventually, these bonds may be stressed or broken to such an extent that the enzyme loses its three-dimensional shape and the active site can no longer receive substrate molecules. At these high temperatures, the structure is permanently destroyed: the enzyme is denatured and can no longer catalyse the reaction.

#### pН

pH is a measure of the relative numbers of  $H^+$  and  $OH^-$  ions in a solution. A solution with a low pH value has many free  $H^+$  ions and is acidic, whereas a high pH value indicates more  $OH^-$  ions and a basic solution. Pure water is neutral and has a pH value of 7, indicating that the number of  $OH^-$  and  $H^+$  ions is equal.

Enzyme action is influenced by pH because the amino acids that make up an enzyme molecule contain many positive and negative regions, some of which are around the active site. An excess of H<sup>+</sup> ions in an acidic solution can lead to bonding between the H<sup>+</sup> ions and negative charges in the active site or other parts of the enzyme. These interactions can inhibit the matching process between the enzyme and its substrate, and slow down or even prevent enzyme activity. A similar effect occurs if a solution becomes too basic: the excess of negative ions upsets the enzyme in the same way. At extremes of pH, the enzyme may even lose its shape and be denatured. The changes are usually, though not always, permanent.

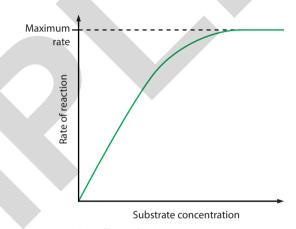
Not all enzymes have the same optimum pH. Proteases (protein-digesting enzymes) in the stomach have an optimum pH of 2 and work well in the acidic conditions there, but proteases in the small intestine have an optimum of pH 8. Most enzymes that work in the cytoplasm of body cells have an optimum pH of about 7. The graph in Figure 3.1.4 shows how reaction rate varies with pH for this type of enzyme.



**Figure 3.1.4:** The effect of pH on the rate of an enzyme-controlled reaction. Changing pH affects the charges on the amino acid molecules in the enzyme. The shape of the enzyme and its active site changes, reducing the rate of reaction

#### **Concentration of substrate**

If there is a set concentration of enzyme present in a reaction mixture, and the concentration of substrate increases, the rate of production of the products will increase because of the greater chance of collisions between substrate and enzyme molecules. More collisions mean that the enzyme is able to process or 'turn over' more substrate molecules. But there is a limit to this increase in reaction rate. If the concentration of substrate increases too much, it will exceed the maximum rate at which the enzyme can work. When this happens, at any one moment all the active sites are occupied by substrate or product molecules, and so adding further substrate has no effect. The rate reaches its limit; you can see this as the plateau in the graph in Figure 3.1.5.



**Figure 3.1.5:** The effect of substrate concentration on the rate of an enzyme-catalysed reaction.

#### **TEST YOUR UNDERSTANDING**

- 1 Define the term metabolism.
- 2 Explain the difference between an anabolic and a catabolic reaction.
- **3** Complete this sentence:

Enzymes are ...... proteins that act as ..... in metabolic reactions.

- 4 Describe why temperature tends to speed up the rate of enzyme activity using the terms 'molecular motion' and 'collision'.
- Why does increasing the substrate concentration in a enzyme-controlled reaction produce a graph that levels off after a certain concentration is reached?

## 3.1.3 Activation energy

Enzymes work by lowering the activation energy of the substrate or substrates. For a metabolic reaction to occur, the substrate has to reach an unstable, highenergy 'transition state' where the chemical bonds are destabilised, and this requires an input of energy, which is called the activation energy. When the substrate reaches this transition stage, it can then immediately form the product. Enzymes can make reactions occur more quickly because they reduce the activation energy of reactions they catalyse to bring about a chemical change (Figure 3.1.6).

#### **KEY POINT**

**Enzymes** do not change the quantity of product that is formed, only the rate at which the product is formed.

Metabolic reactions that occur in living organisms have to occur at the body temperature of the organism, which is never high enough to bring substrates to their transition state. The active site of an enzyme is very important because it can lower the amount of energy needed to reach a transition state, so the reaction can occur at the temperature of the organism.

## Key 1 = activation energy without catalyst 2 = activation energy with catalyst uncatalysed reaction catalysed energy reaction change

Course of reaction

Figure 3.1.6: Graph to show activation energy for an exothermic reaction with and without a catalyst.

## 3.1.4 Competitive and non-competitive inhibition

Enzyme inhibitors are substances that reduce or prevent an enzyme's activity. Some inhibitors are competitive and others non-competitive.

#### **KEY POINT**

Enzymes can be affected by the presence of other molecules that temporarily bind to them, either at the active site or at an allosteric site, a region on the surface of an enzyme to which an allosteric, effector molecule binds.

Inhibition by a molecule whose structure is similar to that of the substrate molecule that normally binds to the active site is an example of **competitive inhibition**. Competitive inhibitors compete with the substrate to occupy the active site of the enzyme, and prevent the substrate molecules from binding (Figure 3.1.7, left-hand side). These inhibitors are not affected by the enzyme and do not form products. The rate of reaction of the enzyme is lower because substrate molecules cannot enter the active site of the enzyme molecules that are blocked by an inhibitor. At low concentrations of substrate, competitive inhibitors have a more significant effect than at higher concentrations, when the substrate can outcompete the inhibitor (Figure 3.1.8). A competitive inhibitor occupies the active site temporarily, so the inhibition is reversible.

Permanent binding of an inhibitor to the active site or to another part of an enzyme is known as noncompetitive inhibition. Inhibitors may bind at part of the enzyme molecule where they partly block access of the substrate to the active site, or they may cause a change in the shape of the enzyme so that the substrate cannot enter the active site (Figure 3.1.7, right-hand side). Increasing the concentration of substrate in the presence of a non-competitive inhibitor does not overcome inhibition (Figure 3.1.8).

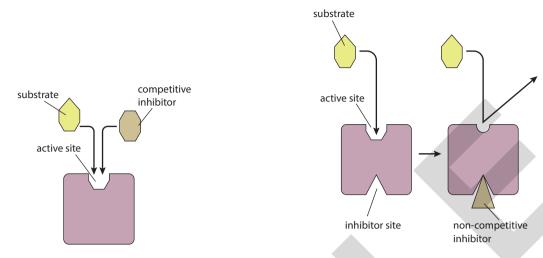
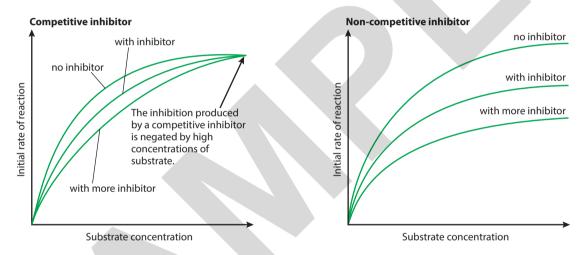


Figure 3.1.7: (Left) Competitive inhibition and (right) non-competitive inhibition.



**Figure 3.1.8:** Graphs to show the effects of competitive and non-competitive inhibitors on reaction rate, as substrate concentration increases.

Table 3.1.1 compares the nature and effects of competitive and non-competitive inhibitors.

## Using non-competitive inhibition by penicillin to inhibit bacteria

Penicillin is an antibacterial medicine that works by inhibiting the formation of bacterial cell walls. Penicillin is most effective against Gram-positive bacteria such as staphylococci and streptococci (Chapter 5). These bacteria have thick cell walls built of many linked peptidoglycan molecules. Penicillin is an irreversible inhibitor that covalently binds to the bacterial enzyme transpeptidase. Transpeptidase catalyses the

formation of cross-links between the long polymers of peptidoglycan in the bacterial cell wall. The walls are left weakened and, when the bacteria divide, their new walls are not properly formed so that the cells burst and die.

## Using competitive inhibition to treat poisoning

Another example of an enzyme inhibitor that is used in medicine is fomepizole. Fomepizole is a competitive inhibitor of the enzyme alcohol dehydrogenase, which usually catalyses the oxidation of ethanol (alcohol) to acetaldehyde. Acetaldehyde is converted to harmless products in the liver and so it does not harm the body.

Competitive inhibitors	Non-competitive inhibitors		
structurally similar to the substrate molecule	structurally unlike the substrate molecule		
occupy and block the active site	bind at a site away from the active site, reducing access to it		
if concentration of inhibitor is low, increasing the concentration of substrate will reduce the inhibition	if concentration of substrate is low, increasing the concentration of substrate has no effect on binding of the inhibitor so inhibition stays high		
examples include:	examples include:		
oxygen, which competes with carbon dioxide for the active site of ribulose bisphosphate carboxylase in photosynthesis	cyanide and carbon monoxide, which block cytochrome oxidase in aerobic respiration, leading to death		
disulfiram, which competes with acetaldehyde for the active site of aldehyde dehydrogenase	penicillin, which blocks the active site of an enzyme that synthesises the cell walls of some bacteria		
ethanol, which can be used in preventing antifreeze poisoning because it is a competitive inhibitor of the enzyme alcohol dehydrogenase (refer to section 'Using competitive inhibition to treat poisoning')			

Table 3.1.1: Comparing competitive and non-competitive inhibitors.

But alcohol dehydrogenase also catalyses steps in the metabolism of ethylene glycol (antifreeze) to toxic metabolites that cause severe damage to the kidneys. If ethylene glycol is accidentally ingested, an injection of fomepizole blocks alcohol dehydrogenase so that toxic metabolites are not produced and the kidneys are not harmed.

## 3.1.5 Controlling metabolic pathways

### **End-product inhibition**

End-product inhibition occurs when an enzyme in a metabolic pathway is inhibited by the product of that pathway. This prevents a cell over-producing a substance it does not need at the time. Many products may be needed by a cell at specific times or in specific amounts and over-production not only wastes energy but may also become toxic if the product accumulates.

In an assembly-line reaction, such as those described in Figure 3.1.9, each step is controlled by a different enzyme. If the end product begins to accumulate because it is not being used, it inhibits an enzyme earlier in the pathway to switch off the assembly line. In most cases, the inhibiting effect is on the

first enzyme in a process, but in other cases it can act at a branch point to divert the reaction along another pathway.

When the end product starts to be used up, its inhibiting effect reduces, the inhibited enzyme is reactivated and production begins again. This is an example of negative feedback.

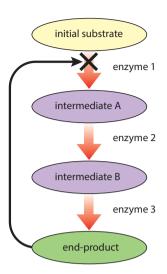
#### **KEY POINTS**

end-product inhibition control of a metabolic pathway by a product in or at the end of that pathway; the product inhibits an enzyme found earlier in the pathway.

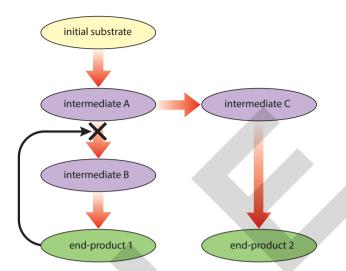
**negative feedback** a regulating mechanism in which a change in a sensed variable results in a correction that opposes the change.

#### **EXTENSION**

Negative feedback is also important in the control of several physiological processes including regulation of blood sugar levels and reproductive cycles.

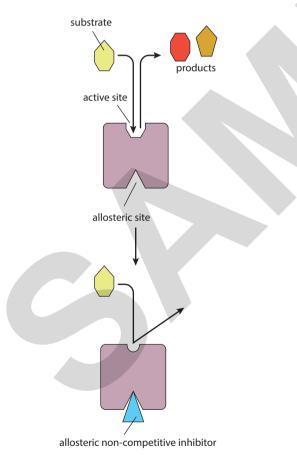


The end-product inhibits the enzyme catalysing the first reaction in the series, so all the subsequent reactions stop.



The end-product inhibits an enzyme in the pathway, which causes a different enzyme to come into play and the pathway is diverted down a different route.

Figure 3.1.9: End-product inhibition.

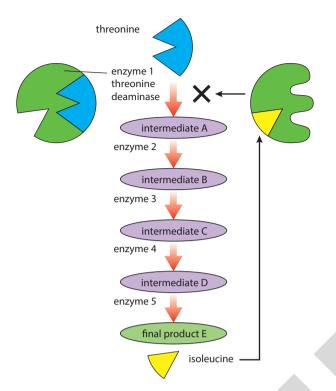


**Figure 3.1.10:** Allosteric control. Allosteric inhibitors prevent the active site functioning.

End-product inhibition may be competitive or non-competitive. Competitive inhibition will only work if the product is a similar shape to the normal substrate and there can be an induced fit of the product or inhibitor onto the enzyme. In most cases, the product will be a different shape and therefore there has to be non-competitive inhibition. In this case, the enzyme is known as an allosteric enzyme, the product is called an allosteric inhibitor and the place where it binds to the enzyme is called the allosteric site (Figure 3.1.10).

## An example of end-product inhibition

Threonine is converted to isoleucine in series of five enzyme-controlled stages. Isoleucine is important in the immune system and also in the synthesis of proteins including hemoglobin. Isoleucine, as the end product of threonine metabolism, can inhibit threonine deaminase, the first of the five enzymes in the process (Figure 3.1.11). Isoleucine inhibits the enzyme by binding on the molecule at a site away from the active site. When it is attached, the active site of the enzyme is changed so that no further substrate can bind to it. As isoleucine concentration increases, more and more isoleucine molecules attach to this inhibition site on enzyme molecules and therefore inhibit further production of isoleucine. As their concentration falls, isoleucine molecules detach from the threonine deaminase enzyme molecules and are used in the cell. Once the inhibitor has been removed, the active site can bind new substrate and the pathway is reactivated.



**Figure 3.1.11:** The pathway that converts threonine to isoleucine – a specific example of end-product inhibition.

This mechanism makes the metabolic pathway selfregulating so that there is always sufficient isoleucine present in the cell.

## 3.1.6 Co-enzymes and co-factors

A co-enzyme is an organic, non-protein molecule that binds to an enzyme to allow it to catalyse a reaction. Co-enzymes cannot work alone, but they can be reused several times with an enzyme. Many co-enzymes are vitamins or are derived from vitamins. For example, pantothenic acid (also called vitamin B5) is needed for the synthesis of co-enzyme A, which is essential for fatty acid metabolism and in the link reaction of aerobic respiration (Section 3.2).

Co-factors are inorganic substances. Many metal ions are co-factors. For example, cupric ions are co-factors

#### **KEY POINT**

Co-enzymes and co-factors both promote enzyme activity. Co-enzymes are organic molecules; co-factors are inorganic.

needed to promote cytochrome oxidase activity and zinc is a co-factor in nearly 300 enzymes involved in metabolism. Chloride ions are allosteric activators for human amylases. As one chloride ion binds to amylase, it induces activation of the enzyme and increases the rate of reaction of the hydrolysis of starch.

#### TEST YOUR UNDERSTANDING

- 6 Outline what is meant by activation energy.
- 7 Explain how an enzyme pathway can be switched off by an accumulation of the end product of the pathway.
- 8 Outline the way in which penicillin leads to the death of bacteria.
- **9** List three differences between competitive and non-competitive enzyme inhibitors.

#### THEORY OF KNOWLEDGE

#### Studying metabolic pathways

Metabolic pathways have been studied for centuries but one of the most significant advances was made by Eduard Buchner (1860–1917), who discovered enzymes at the start of the 20th century. At first, studies of whole animals were made, but more recently it has been possible to analyse metabolic pathways and their component reactions using modern techniques such as chromatography, X-ray diffraction, spectroscopy and radioactive isotopes. In the mid-20th century, the Krebs cycle (often called the citric acid cycle; see Section 3.2) and the glyoxylate cycle were discovered by Hans Krebs (1900–1981) and Hans Kornberg (1928–2019). But metabolic pathways are very elaborate. Many pathways are interrelated and together make up a complex metabolic network in a cell. These pathways are vital to homeostasis and cell function. Some pathways are connected by intermediate products, and products of one pathway may be substrates for another.

#### To consider:

1 Most biochemical studies are made using carefully controlled experiments that look at one part of a pathway. To what extent can looking at component parts of a complex system give us knowledge of the whole?

#### Links

- How do plants and algae convert light energy into organic compounds, or chemical energy, to use in their metabolism? (Chapter 3.3)
- How does metabolism help to maintain constant internal conditions? (Chapter 8)
- Why is compartmentalisation in cells important for the control of metabolism? (Chapter 5)

## 3.2 Respiration

#### LEARNING OBJECTIVES

In this section you will:

- understand that cell respiration is the controlled release of energy from organic substances to produce ATP (adenosine triphosphate)
- learn that cell respiration is a series of complex enzyme-catalysed reactions that involve hydrolytic breakdown of glucose and other molecules
- understand that much of the energy is released to the environment as heat
- discover that ATP from respiration is an immediately available source of energy in the cell
- understand that anaerobic respiration (called fermentation in microorganisms) gives a small yield of ATP from glucose and occurs in the cell cytoplasm
- recall that yeast cells respire anaerobically and are used in baking and brewing
- recognise that humans can respire anaerobically for a short time in the absence of oxygen, which produces lactate
- understand that lactate produced by some bacteria is useful in yoghurt production
- learn that aerobic respiration requires oxygen and gives a much larger yield of ATP from glucose
- learn that aerobic respiration starts in the cytoplasm and requires mitochondria
- learn that during cell respiration electron carriers are oxidised and reduced
- understand that phosphorylation of molecules increases their energy level making them less stable, and decarboxylation generates carbon dioxide
- understand that glycolysis does not use oxygen. It takes place in the cytoplasm and each glucose molecule in converted into two pyruvate molecules with a small net gain of ATP
- | learn that during anaerobic respiration reduced NAD from glycolysis is oxidised and reduces pyruvate to avoid it building up in the cytoplasm
- understand how in aerobic respiration pyruvate is decarboxylated and oxidised. In the link reaction it is converted to an acetyl compound and then attached to co-enzyme A to form acetyl co-enzyme A
- understand that in the Krebs carboxylic acid cycle the oxidation of acetyl groups is coupled with the reduction of hydrogen carriers and carbon dioxide is released
- learn that energy released during oxidation reactions is carried by reduced NAD and FAD to the cristae of mitochondria
- learn that the transfer of electrons between carrier molecules in the electron transport chain (ETC) in the membrane of the cristae is coupled to proton pumps
- understand how during chemiosmosis, protons diffuse through ATP synthase to generate ATP
- $\rightarrow$  discover how oxygen binds with free protons to form water, thus maintaining the H $^+$ (proton) gradient.

#### **GUIDING QUESTIONS**

- What is the role of adenosine triphosphate (ATP) in the transfer of energy in cells?
- How do living organisms release the energy on which their cells depend?
- Why does aerobic respiration generate a much larger yield of ATP per molecule of glucose than anaerobic respiration?

## 3.2.1 Cell respiration and ATP

All living cells need energy to stay alive. The energy is used to power all the activities of life including digestion, protein synthesis and active transport. A cell's energy sources are the sugars and other substances derived from nutrients, which can be metabolised in a series of chemical reactions to release the energy that holds their molecules together. Much of the energy is eventually transferred to the environment as heat.

Cell respiration is the gradual breakdown of nutrient molecules such as glucose and fatty acids in a series of enzyme-controlled metabolic pathways that ultimately release energy in the form of ATP (or adenosine triphosphate).

#### **KEY POINT**

ATP (adenosine triphosphate) is the immediately available energy currency of a cell. It is needed for every activity that requires energy. Cells make their own ATP in mitochondria. When energy is used, ATP is broken down to ADP (adenosine diphosphate) and inorganic phosphate. This conversion releases energy for use and a cyclic process reforms the ATP during respiration.

Glucose is the most commonly used source of energy. Enzymes hydrolyse each glucose molecule in a number of stages, which release energy in small amounts as each covalent bond is broken. If there is insufficient glucose available, fatty acids or amino acids can be used instead.

The energy in glucose or other nutrient molecules can be released in a single reaction. This is what happens when glucose burns in the reaction known as combustion. In this case, the energy in the glucose is released as heat. In the series of reactions that occur during respiration, glucose is broken down gradually, with each step catalysed by a different enzyme. This releases energy in small amounts so that it can be used by cells. Nevertheless as energy is used much of it is lost to the surroundings as heat. We can experience this for ourselves when we use energy during exercise and our bodies become hot.

#### Glycolysis

The first stage in cell respiration is **glycolysis**. Glucose that is present in the cytoplasm of a cell is broken down by a series of enzymes, to produce two molecules of a simpler compound called pyruvate. As this occurs, there is a net production of two molecules of ATP (Figure 3.2.1).

glucose 
$$\rightarrow$$
 2 pyruvate + 2 ATP six-carbon sugar 2 × three-carbon sugar

Glycolysis actually uses two molecules of ATP to get the process under way but produces four molecules of ATP in total, per molecule of glucose. Thus we say there is a net production of two ATPs.

$$ADP + Pi \leftrightarrow ATP + H_2O$$

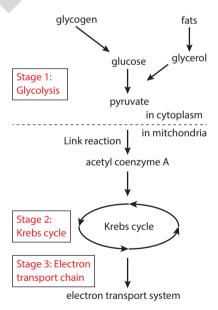
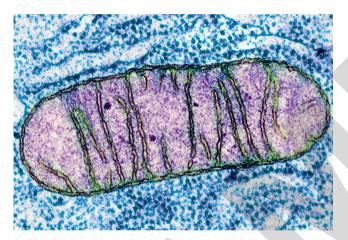


Figure 3.2.1: A summary of the stages in aerobic respiration.

## 3.2.2 Aerobic and anaerobic respiration

The next stage of cell respiration depends on whether or not oxygen is available. In the presence of oxygen, aerobic respiration can take place; without it, respiration must be anaerobic.

Aerobic respiration is the most efficient way of producing ATP. Aerobic respiration is carried out by cells that have mitochondria and it produces a great deal of ATP. A labelled micrograph of a mitochondrion is shown in Figure 3.2.2. Pyruvate molecules produced by glycolysis enter the mitochondria and are broken down, or oxidised, in a series of reactions that release carbon dioxide and water and produce ATP.



**Figure 3.2.2:** Coloured electron micrograph of a mitochondrion (× 72 000).

In the first step, two pyruvate molecules are transported into the mitochondria in the **link reaction**, as shown in Figure 3.2.1. Each pyruvate loses a carbon atom which forms carbon dioxide and a hydrogen atom, so that they become two molecules of acetyl CoA. Acetyl CoA then enters a stage called the **Krebs carboxylic acid cycle** (also known as the citric acid cycle) and is modified still further, releasing more carbon dioxide. The Krebs cycle takes place in the matrix of the mitochondria. Finally, on the inner membranes of the mitochondria, products of the cycle react directly with oxygen and the result is the release of large amounts of ATP. The original glucose molecule is completely broken down to carbon

dioxide and water so the equation for aerobic respiration is often summarised as:

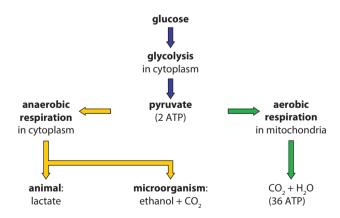
glucose + oxygen  $\rightarrow$  carbon dioxide + water + 36 ATP  $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 36$  ATP

#### **EXAM TIP**

You should be familiar with the general structure of a mitochondrion (Figure 3.2.2), you don't need to remember all the details but thinking about where the reactions of respiration take place can help you understand the different stages. You will learn more about mitochondria in Section 5.2.

**Anaerobic respiration** occurs in the cytoplasm of cells. In animal cells, the pyruvate produced from glucose by glycolysis is converted to lactate (Figure 3.2.3), which is a waste product and is taken out of the cells. In humans, anaerobic respiration occurs if a person is doing vigorous exercise and their cardiovascular system is unable to supply sufficient oxygen for aerobic respiration to provide ATP at the necessary rate. Although anaerobic respiration releases far less energy per molecule of glucose than aerobic respiration, the extra ATP enables the person to continue exercising for a short period, at a time of great exertion, to maximise power output. One consequence of the build-up of lactate in the muscles that occurs during anaerobic respiration is the sensation of cramp, so this type of respiration cannot be sustained for very long. The word equation for anaerobic respiration in animals is:

Glucose  $\rightarrow$  pyruvate  $\rightarrow$  lactate



**Figure 3.2.3:** Simple diagram to show the products of aerobic and anaerobic respiration.

#### **EXTENSION**

You'll often see both the terms lactate and lactic acid used when you read about anaerobic respiration, so what is the difference? Like other acids, lactic acid is a substance that is able to donate hydrogen (H+) ions. When it loses an electron it is called a base and known as lactate:

Lactic acid → lactate + H<sup>+</sup>

When lactic acid is produced in muscles it will dissociate into lactate and hydrogen ions so the terms are used interchangeably.

Humans can only respire anaerobically for a short period of time. A sprinter running a 100 metre race can run an entire race anaerobically, but a long-distance runner will use only aerobic respiration for maximum efficiency.

Lactate is carried in the blood from muscles to the liver where it is converted back to pyruvate. Pyruvate may either be converted back to glucose, a process which requires energy, or used as a fuel, producing carbon dioxide and water.

In microorganisms, such as yeast, anaerobic respiration is also known as fermentation, and produces a different outcome. The pyruvate molecules from glycolysis are converted to ethanol (alcohol) and carbon dioxide (Figure 3.2.3).

Glucose  $\rightarrow$  pyruvate  $\rightarrow$  ethanol + carbon dioxide

No further ATP is produced by the anaerobic respiration of pyruvate, so this type of respiration gives only a small yield of ATP from glucose.

## 3.2.3 Anaerobic respiration in food production

People have benefitted from the anaerobic respiration of yeast in baking and brewing for thousands of years. Today, many different types of yeast are used in the production of bread, wine and beer.

The strains of yeast used for baking and brewing are different and each has been selected for its specific characteristics. Baking yeasts feed on sugar and flour in bread dough and grow more quickly than brewing yeasts, which are slow-growing but able to tolerate higher alcohol concentrations. In bread making, the yeast initially respires aerobically, releasing carbon dioxide gas and water into the dough in a very short period of time. Carbon dioxide in the dough causes it to rise as the gas becomes trapped in pockets between gluten fibres in the flour. When oxygen in the dough has been depleted, the yeast continues to respire anaerobically, producing ethanol which evaporates during baking. The yeast cells are also killed by the high temperature of the oven.

Yoghurt production also relies on anaerobic respiration. Two bacteria that are often used to make yoghurt are Streptococcus thermophilus and Lactobacillus bulgaricus. Milk, either raw or pasteurised, is first heated to denature the whey proteins so that the final yoghurt that is made will form a stable gel and not separate if it is stored. Next, it is cooled to about 40 °C. This is the optimum temperature (Section 3.1) for the bacterial enzymes involved in fermentation. Live bacterial cells are put into the milk and they feed on lactose sugars, converting the sugars into lactic acid as they respire. After about 12 hours, lactic acid causes the milk to thicken and produces the characteristic acidic taste and texture of yoghurt.

#### INTERNATIONAL MINDEDNESS

Cow's milk is used to produce yoghurt and kefir in many parts of the world, but milk from yaks, buffalo, goats, sheep and camels is also used where it is available. In Central Asia mare's or donkey's milk is used to produce koumiss, a fermented drink similar to thin yoghurt. The flavour and texture of each product depends on the types of milk and bacteria that are used.

#### NATURE OF SCIENCE

## Assessing ethics in science: using invertebrates in a respirometer

A simple respirometer, such as the one shown in Figure 3.2.4, can be used to monitor respiration in small organisms such as woodlice or in germinating seeds. The apparatus can demonstrate that oxygen is used and carbon dioxide is produced during respiration. Test organisms are placed in two large boiling tubes as shown, so that one contains living organisms (tube A) and the other, which acts as a control, contains either dead organisms or is left empty (tube B). Soda lime or another alkali such as potassium hydroxide absorbs carbon dioxide. As oxygen is used by the living things in tube A, the level of liquid rises in the arm of the manometer attached to tube A. If required, measurements of

time can be made so that the rate of respiration can be estimated. The temperature in the apparatus is kept constant by immersing the tubes in a water bath. This minimises any change in volume due to temperature change.

#### To consider:

- How can we ensure that the invertebrates used in experiments like this are treated ethically?
- What measures would you use to minimise the distress and disturbance to the organisms and also to the habitat from which they are taken?
- 3 How can we know whether the organisms are experiencing distress?

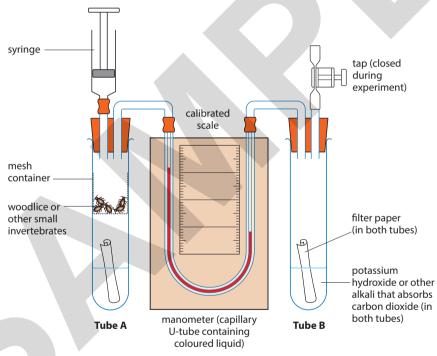


Figure 3.2.4: A simple respirometer.

#### **TEST YOUR UNDERSTANDING**

- **10** Which stage of respiration takes place in both aerobic and anaerobic respiration?
- 11 Where does aerobic respiration take place in eukaryotic cells?
- **12** Outline the role of anaerobic respiration in baking.

## 3.2.4 Biochemistry of cell respiration

#### Oxidation and reduction

#### **KEY POINT**

redox reaction a reaction in which reduction and oxidation occur simultaneously.

Cell respiration involves several oxidation and reduction reactions. Such reactions are common in biochemical pathways. When two molecules react, one of them starts in the oxidised state and becomes reduced, and the other starts in the reduced state and becomes oxidised, as shown in Figure 3.2.5.

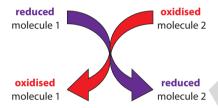


Figure 3.2.5: Oxidation and reduction are linked processes - as one molecule is reduced another is oxidised in a redox reaction.

There are three different ways in which a molecule can be oxidised or reduced, as outlined in Table 3.2.1. In biological oxidation reactions, addition of oxygen atoms is an alternative to removal of hydrogen atoms. Since a hydrogen atom consists of an electron and a proton, losing hydrogen atoms (oxidation) involves losing one or more electrons.

Oxidation	Reduction	
loss of electrons	gain of electrons	
loss of hydrogen	gain of hydrogen	
gain of oxygen	loss of oxygen	

Table 3.2.1: Changes involved in oxidation and reduction.

Oxidation and reduction occur together in biochemical reactions. As one compound loses electrons, another one gains electrons. In the simple equation for respiration, glucose is oxidised as hydrogen atoms, and therefore electrons, are gradually removed from it and added to

hydrogen acceptors (the oxygen atoms on the left side of the equation), which become reduced.

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

Chemical reactions like this are referred to as redox reactions. In redox reactions, the reduced molecule always has more potential energy than the oxidised form of the molecule. Electrons passing from one molecule to another carry energy with them.

The electron carriers used during cell respiration are NAD<sup>+</sup> and FAD<sup>+</sup>.

#### **KEY POINT**

NAD+ is a hydrogen carrier that accepts hydrogen atoms removed during the reactions of respiration. During glycolysis, two hydrogen atoms are removed and NAD+ accepts the protons from one of them and the electrons from both of them.

$$NAD^+ + 2H \rightarrow NADH + H^+$$

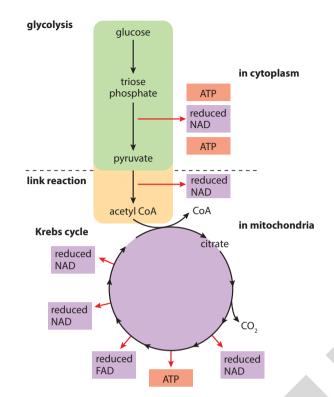
Cell respiration is the controlled breakdown of food molecules such as glucose or fat to release energy, which can be stored for later use. The energy is most commonly stored in the molecule adenosine triphosphate, or ATP. The respiration pathway can be divided into four parts:

- 1 glycolysis
- 2 link reaction
- Krebs cycle
- electron transfer chain and chemiosmosis.

Glycolysis, the link reaction and the Krebs cycle are summarised in Figure 3.2.6, and the electron transfer chain and chemiosmosis are discussed later in this chapter in the section on 'the electron transport chain, oxidative phosphorylation and chemiosmosis'.

### **Glycolysis**

Glycolysis is the first stage in the series of reactions that make up respiration. It literally means 'breaking apart glucose'. The glycolysis pathway occurs in the cytoplasm of the cell. It is anaerobic (that is, it can proceed in the absence of oxygen) and produces pyruvate and a small amount of ATP. One molecule of the hexose sugar glucose is converted to two molecules of the threecarbon molecule called pyruvate with the net gain of two molecules of ATP and two molecules of NADH + H<sup>+</sup>. The process is shown in detail in Figure 3.2.7.



**Figure 3.2.6:** Summary of glycolysis, the link reaction and the Krebs cycle.

- 1 The first steps are to add two phosphate groups from ATP, in a process called phosphorylation, which destabilises the glucose molecule. A hexose bisphosphate molecule is produced. (This appears contrary to the purpose of respiration, which is to *make* ATP, but the two lost ATPs are recovered later.)
- 2 The hexose bisphosphate is now split into two triose phosphates in a reaction called lysis.
- 3 Now, another phosphorylation takes place but this time an inorganic phosphate ion, P<sub>i</sub>, is used and not ATP. Two triose bisphosphates are formed. The energy to add the P<sub>i</sub> comes from an oxidation reaction. The triose bisphosphate is oxidised and at the same time NAD<sup>+</sup> is reduced to NADH + H<sup>+</sup>.
- 4 There now follows a series of reactions in which the two phosphate groups from each triose bisphosphate are transferred onto two molecules of ADP, to form two molecules of ATP: this is ATP formation. A pyruvate molecule is also produced for each triose bisphosphate molecule.

#### **FXAM TIP**

NADH + H<sup>+</sup> must not be simplified to NADH<sub>3</sub>.

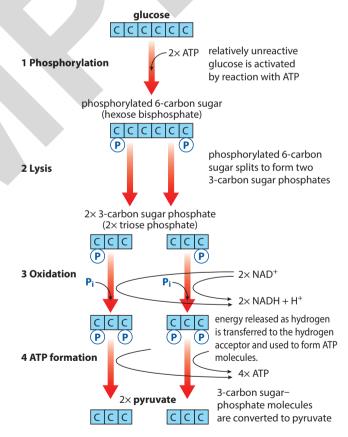
Four molecules of ATP are formed by converting one molecule of glucose to two molecules of pyruvate. However, two molecules of ATP were required to start the pathway and so there is a net gain of two molecules of ATP per glucose. In addition, two NADH + H<sup>+</sup> are formed.

To summarise, the net products of glycolysis per glucose molecule are:

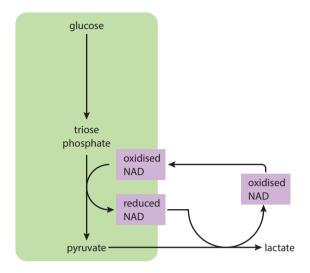
- 2 ATP
- 2 NADH + H<sup>+</sup> (reduced NAD)
- 2 molecules of pyruvate.

#### **EXAM TIP**

Try to think of your own acronym, such as People Love Outdoor Activities, to help you recall the steps in glycolysis.



**Figure 3.2.7:** The stages of glycolysis. Note that for each molecule of glucose, two molecules of ATP are used and four are formed, so there is a net gain of two ATPs.



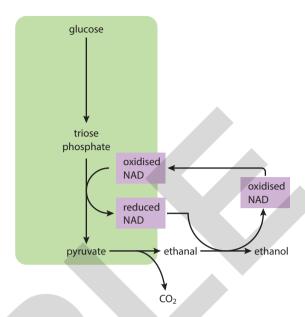


Figure 3.2.8: During anaerobic respiration reduced NAD is used to remove pyruvate from glycolysis so that it does not build up. Left: anaerobic respiration in animal cells; right: anaerobic respiration in yeast cells.

In anaerobic respiration the reduced NAD (NADH + H<sup>+</sup>) is oxidised (dehydrogenated) and used to reduce pyruvate. This prevents a build-up of harmful concentrations of pyruvate in the cell cytoplasm. In microorganisms this leads to the production of ethanol and carbon dioxide, while in animals the product is lactate. No further ATP is produced by the anaerobic respiration of pyruvate, so this type of respiration gives only a small yield of ATP from glucose (Figure 3.2.8).

#### **KEY POINT**

Phosphorylation of glucose is the first stage in its breakdown and involves the addition of phosphate groups from ATP. This turns glucose into a more unstable phosphorylated compound which can be split to form two three-carbon sugars.

Energy coupling involves a sequence of reactions in which energy from an energy-releasing process is used to drive an energy-requiring process. Phosphorylation is an example of energy coupling: the transport of a phosphate group from ATP to a reactant molecule in the coupled reaction supplies energy for that reaction. The reactant molecule becomes a phosphorylated intermediate, an unstable molecule compared to the unphosphorylated state.

#### TEST YOUR UNDERSTANDING

- 13 List three ways in which a substance can be reduced.
- 14 Name the molecule used to phosphorylate glucose at the start of glycolysis.
- **15** Outline the importance of phosphorylation in glycolysis.

## 3.2.5 Aerobic respiration

### The link reaction and Krebs cycle

If oxygen is present, pyruvate formed during glycolysis moves into the mitochondrial matrix by facilitated diffusion. The structure of a mitochondrion is shown in Figure 3.2.9.

The link reaction and the Krebs cycle pathways occur in the mitochondrial matrix (Figure 3.2.10).

The link reaction converts pyruvate to acetyl CoA using co-enzyme A, and a carbon atom is removed as carbon dioxide. This is called a decarboxylation reaction. At the same time as the carbon dioxide is removed, pyruvate is oxidised by the removal of hydrogen. The hydrogen atoms are removed by  $NAD^+$  to form  $NADH + H^+$ .

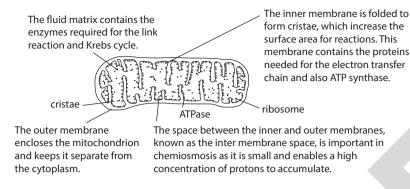


Figure 3.2.9: Diagram of a mitochondrion in longitudinal section.

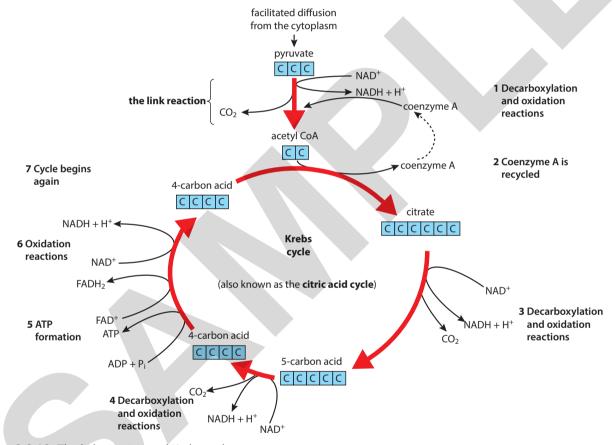


Figure 3.2.10: The link reaction and Krebs cycle.

- 2 Acetyl CoA now enters the Krebs cycle to continue the processes of aerobic respiration. Immediately, the co-enzyme A is removed to be recycled. The acetyl component of the acetyl CoA combines with a four-carbon compound to form the six-carbon compound, citrate.
- **3, 4** The acetyl (two-carbon) groups are dehydrogenated to release four pairs of hydrogen atoms and decarboxylated to form two molecules of carbon
- dioxide so that the two carbons that enter with acetyl CoA leave as carbon dioxide.
- **5** One molecule of ATP is formed.
- 6 Hydrogen is removed during oxidation reactions to the two hydrogen carriers NAD<sup>+</sup> and FAD<sup>+</sup>.
- 7 Since the Krebs cycle is a cyclic process, what enters must eventually leave so that the cycle begins and ends with the same substances.

#### EXAM TIP

Reduced FAD is written as FADH<sub>2</sub>.

Because each molecule of glucose forms two molecules of pyruvate during glycolysis, each glucose molecule requires two link reactions and two rotations of the Krebs cycle. Thus, when working out the products of the cycle we must consider two sets of products. To summarise, the products of the link reaction and Krebs cycle, per glucose molecule, are:

- 8 molecules of NADH + H<sup>+</sup>
- 2 molecules of FADH,
- 2 molecules of ATP
- 6 molecules of CO<sub>2</sub>.

## The electron transport chain, oxidative phosphorylation and chemiosmosis

Most of the ATP produced from glucose breakdown occurs in the last phase of respiration at the end of the electron transport chain (ETC). Reactions take place on

the inner mitochondrial membrane of the cristae and in the intermembrane space between the inner and outer membranes (Figures 3.2.2 and 3.2.9). The inner membrane holds molecules called **electron carriers**, which pick up electrons and pass them from one to another in a series of oxidations and reductions. The pathway is called the electron transport chain because electrons from hydrogen are moved along it. Just as the inner lining of the small intestine is folded to increase its surface area to absorb food, so the inner mitochondrial membrane is highly folded into cristae to increase its surface area. The cristae provide a large area for the protein molecules used in the electron transport chain. Several protein molecules are electron carriers and the three key ones are shown in Figure 3.2.11.

Electrons from NADH + H<sup>+</sup> are transferred onto the first electron carrier. As they pass through the carrier, they lose energy and this is used to pump a proton (H<sup>+</sup>) from the matrix to the intermembrane space, lowering the pH of the space. The electrons are then transferred to two further carriers and the process is repeated. As the electrons from one NADH + H<sup>+</sup> pass along the chain, a total of nine protons are pumped into the intermembrane space. At the end of the chain, the electrons are combined with protons and

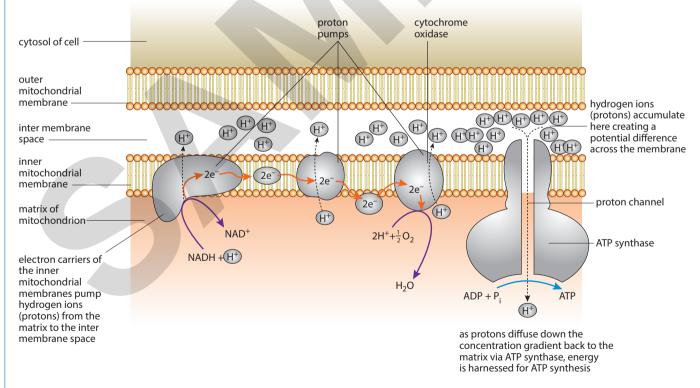


Figure 3.2.11: The electron transport chain showing oxidative phosphorylation and chemiosmosis.

oxygen atoms to make water, in the oxidative part of **oxidative phosphorylation**. This completes the release of energy from the oxidation of glucose to produce ATP. The formation of water ensures that the H<sup>+</sup> gradient is maintained.

The space between the membranes is very narrow and allows for a rapid increase in the concentration of the protons that are pumped into it during the electron transfer reactions. The protons in the intermembrane space create a concentration gradient between the space and the matrix. These protons can now flow passively down this concentration gradient back into the matrix, through a very large integral protein. This is called **chemiosmosis**. The large protein contains the enzyme ATP synthase, which joins ADP and P. to form ATP. Three protons flowing through this enzyme result in one ATP being formed. Since the electrons from one NADH + H<sup>+</sup> pump nine protons into the intermembrane space, each NADH + H<sup>+</sup> results in the formation of three ATP. This is the phosphorylation part of oxidative phosphorylation.

FADH<sub>2</sub> also supplies electrons to the electron transport chain but further down the chain than NADH + H<sup>+</sup>, missing the first protein pump. FADH<sub>2</sub> allows the production of just two ATPs.

## Overall ATP production during aerobic respiration

Stage		ATP use	ATP yield
glycolysis	2 ATP used at the start	−2 ATP	
	2 NADH + H+		+4 ATP
	ATP formation		+4 ATP
link reaction	2 NADH + H <sup>+</sup>		+6 ATP
Krebs cycle	ATP formation		+2 ATP
and electron	6 NADH + H+		+18 ATP
transport chain	2 FADH <sub>2</sub>		+4 ATP
net energy yield			+36 ATP

**Table 3.2.2:** Together, glycolysis, the link reaction and the Krebs cycle and the electron transport chain can yield 36 ATP molecules for each molecule of glucose broken down by aerobic respiration.

#### **NATURE OF SCIENCE**

#### Changing views with new discoveries

As Table 3.2.2 shows, the net production of ATP from one molecule of glucose is, in theory, 36. Biochemists have discovered that the actual production is closer to 30 ATPs and propose that this discrepancy occurs because some protons are used to transfer ATP from the matrix to the cytoplasm. There are also losses such as the cost of moving pyruvate, phosphate and ADP (for ATP synthesis) into the mitochondria.

#### **EXTENSION**

The reactions of respiration have the potential to release about 36 molecules of ATP from one molecule of glucose. The process of glycolysis produces 2 ATP and all the rest are produced during the electron transport chain.

But the exact number of ATP molecules generated from glucose is not as precise as the theory suggests. For example, the number of hydrogen ions pumped through the electron transport chain varies between species and ATP yield can also be reduced because the intermediate compounds in the respiration reactions are used for other reactions. The ribose sugars that build nucleic acids and some amino acids are made from intermediates of glycolysis which means fewer molecules proceed to the next stages of respiration. The percentage of potential ATP molecules that are actually produced from the catabolism of glucose can be as low as 40%.

#### **NATURE OF SCIENCE**

## Paradigm shift: the chemiosmosis theory required a significant change of view

A paradigm shift occurs when a new theory radically changes our understanding of key concepts. It can change our view of how the natural world works.

The chemiosmosis hypothesis was proposed in 1961 by Peter Mitchell (1920–1992) to explain how the mitochondria convert ADP to ATP. At the start of the 1960s, scientists did not understand the exact mechanisms by which electron transfer is coupled to ATP synthesis. Various hypotheses at the time proposed a direct chemical relationship between oxidising and phosphorylating enzymes and suggested that a high-energy intermediate compound was formed. Mitchell's theory was completely new and proposed an indirect interaction between these enzymes with no intermediate compound. He suggested that ATP synthesis is driven by a reverse flow of protons down a concentration gradient, the so-called 'chemiosmotic theory'. This theory was first received with scepticism as his

work was considered to be radical and outside the popularly held view. Mitchell struggled to persuade his contemporaries to reject the more accepted theories because his theory used a completely different approach. After several years of research, he published detailed evidence to support his theory, both in a pamphlet in 1966 and also in further publications in 1968, which were known as 'the little grey books' because of their bland covers. Eventually in the early 1970s, Mitchell's chemiosmosis theory gained scientific acceptance, and scientists conceded that no high-energy intermediate compounds were likely to be found. Mitchell was awarded the Nobel Prize for Chemistry in 1978.

#### To consider:

- 1 Despite Peter Mitchell's strong evidence for chemiosmosis, which falsified earlier theories, he struggled to have his work accepted.
- Why is it often difficult for a paradigm shift to gain acceptance?

#### **TEST YOUR UNDERSTANDING**

- **16** State the sites of the link reaction and the reactions of the Krebs carboxylic acid cycle.
- 17 Name the molecule that enters the Krebs cycle.
- 18 Where is ATP synthase located?

#### Links

- What is the importance of ATP for the movement of substances across cell membranes? (Chapter 6)
- How does the structure and function of a mitochondrion compare with that of a chloroplast? (Chapter 6)
- What is the significance of the inefficiency of respiration and heat losses to the environment? (Chapter 12)

## 3.3 Photosynthesis

#### **LEARNING OBJECTIVES**

In this section you will:

- learn that photosynthesis is a series of metabolic pathways carried out by plants, algae and some prokaryotes, uses light energy to make carbon compounds in cells
- recognise that the inputs for photosynthesis are water, carbon dioxide and light and the outputs are oxygen and glucose
- learn that light from the Sun is made up of a range of wavelengths, visible light has wavelengths between 400 nm (violet) and 700 nm (red)

#### CONTINUED

- understand that chlorophylls are the main photosynthetic pigments and they absorb most red and blue light but reflect green more than the other colours. This phenomenon is shown by absorption spectra
- discover that action spectra demonstrate the wavelengths that are most effective for photosynthesis
- learn that photosynthesis consists of a light-dependent and a light-independent stage
- learn that the light-dependent stages take place in the thylakoids of chloroplasts.
- learn that enzymes in the stroma of chloroplasts produce glucose using energy from the lightdependent stages
- understand how temperature, light intensity and carbon dioxide concentration affect the rate of photosynthesis and can be limiting factors
- understand why the net uptake or production of carbon dioxide and oxygen depend on both the rate of photosynthesis and cell respiration
- learn that the light-dependent reactions occur in the intermembrane space of the thylakoids and the intergranal lamellae and involve photosystems
- \rightarrow understand how the light-dependent reactions lead to the production of reduced NADP
- discover how absorption of light excites electrons which are transferred between electron carriers
- learn that two photosystems are involved; excited electrons from photosystem I are used to reduce NADP and electrons from both photosystems are used to generate a proton gradient
- understand that the photolysis of water generates electrons to replace excited electrons and produce oxygen as a waste product
- learn that light-independent reactions occur in the stroma and are controlled by enzymes
- learn that a carboxylase catalyses the carboxylation of RuBP in the light-independent reactions of the Calvin cycle
- understand that reduced NADP<sup>+</sup> and ATP are used to reduce glycerate 3-phosphate to triose phosphate understand how ATP synthase in thylakoids generates ATP using the proton gradient
- > learn that triose phosphate is used to produce carbohydrates and regenerate RuBP and ATP is also needed
- > recognise that a wide range of organic molecules are derived from the glucose produced by photosynthesis.

#### **GUIDING QUESTIONS**

- How do plants and algae convert light energy into chemical energy that is stored in organic compounds?
- Why does photosynthesis depend on the presence of pigment molecules?
- Where in cells do the reactions of photosynthesis take place?

## 3.3.1 Photosynthesis and light

The Sun is the source of energy for almost all life on Earth. Plants, algae and some prokaryotes are able to convert light energy into chemical energy in organic compounds by the process of photosynthesis. Photosynthesis is a complex series of metabolic pathways which use carbon dioxide and water to produce glucose, other organic compounds and oxygen. Oxygen is released as a waste product. The series of reactions that occurs during photosynthesis is summarised as:

#### **KEY POINT**

photosynthesis 'making things with light'. Glucose is the molecule most commonly made.

carbon dioxide + water 
$$\rightarrow$$
 glucose + oxygen  
6CO<sub>2</sub> + 6H<sub>2</sub>O  $\rightarrow$  C<sub>6</sub>H<sub>12</sub>O<sub>6</sub> + 6O<sub>2</sub>

The energy stored in molecules such as glucose provides a source of food for organisms that cannot use light energy directly and, within the photosynthesising organisms, it can be converted into other organic compounds that are required for life.

Visible light is composed of a spectrum of colours, which can be separated using a prism (Figure 3.3.1). A prism bends rays of light and separates the colours because each one has a slightly different wavelength and is refracted (bent) to a slightly different degree. Visible light has a range of wavelengths that are between 400 and 700 nm. Violet light has the shortest wavelength and red the longest, but the most important regions of the spectrum for photosynthesis are red and blue.



Figure 3.3.1: 'White light', such as sunlight, is composed of a range of wavelengths, which become separated as they pass through a glass prism.

The colour of any object is determined by the wavelength of the light that it reflects back into our eyes. A blue shirt appears blue because it reflects blue light, which our eyes can perceive, but the shirt absorbs other wavelengths that fall on it and we do not see those colours. A black object absorbs all wavelengths of light, while something white reflects them all.

Most plants have green leaves and many other photosynthesising organisms also appear green. This tells us that they do not absorb the green part of the spectrum well; green light is reflected and makes

a leaf appear green. Looking closely at the structure of plant cells such as those shown in Figure 5.2.5 we can see that the green colour is due to the chloroplasts, which contain green pigments called chlorophylls. Chlorophylls are unable to absorb green light, which is reflected, but do absorb other wavelengths well. Red and blue light are absorbed particularly well and provide the energy needed for photosynthesis. The top graph in Figure 3.3.2 shows that the red and blue ends of the visible spectrum are the wavelengths that the photosynthetic pigments in plants absorb most efficiently. The bottom graph, known as an action spectrum, shows that the rate of photosynthesis is highest when plants absorb these wavelengths.

#### **KEY POINT**

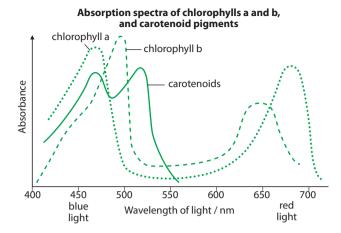
chlorophyll the name for the most important group of photosynthetic pigments of green plants, found in the grana of chloroplasts and responsible for trapping light energy (some bacteria have a chemically different form called bacteriochlorophyll).

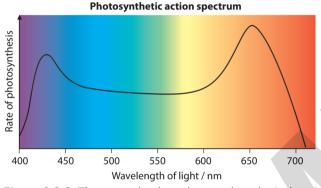
#### Photosynthetic pigments

Chloroplasts contain a number of different pigments that are associated with light absorption. Figure 3.3.2 shows absorption spectra and action spectra for two types of chlorophyll pigment and carotenoid pigments found in green plants. There is a strong correlation between the absorption spectra (the range of wavelengths of light that a pigment is able to absorb) of the pigments and the action spectrum (showing the rate of photosynthesis at each wavelength). In the figure, both have two peaks, one in the blue region and a smaller one in the red region, and both are lower in the green and yellow areas of the spectrum.

Chromatography is a simple technique used to separate different substances in a mixture and it can be used to separate the pigments in extracts from plant leaves.

Two techniques are commonly used: paper chromatography, which uses a special high-grade paper with carefully controlled spaces between the cellulose fibres, and thin-layer chromatography (TLC), which is carried out on a thin plate of glass or plastic coated with a layer of adsorbent material such as silica gel or cellulose (known as the stationary phase).





**Figure 3.3.2:** These graphs show the wavelengths (colours) of light absorbed by plants and the rate of photosynthesis that occurs at each wavelength.

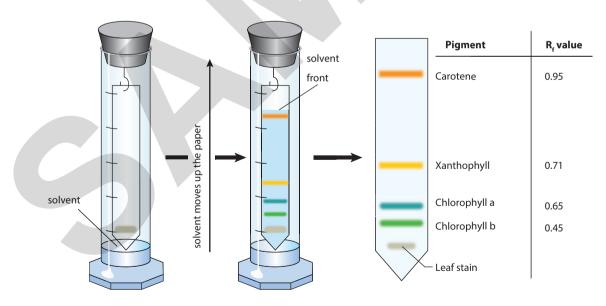
During chromatography a solvent moves up the paper or plate by capillary action and carries pigments with it by mass flow. Smaller molecules are able to move more easily and so can travel further than larger molecules. After a period of time, photosynthetic pigments from chloroplast extracts become separated (Figure 3.3.3) and can be compared and measured.

#### **EXTENSION**

The  $R_{\rm f}$  value is a ratio that is used to identify components in a mixture from a chromatogram. It is calculated by dividing of the distance travelled by a component of the mixture by the distance travelled by the solvent front from the origin. The  $R_{\rm f}$  value can be used to identify each pigment by comparing its  $R_{\rm f}$  value to that of a known standard at the same temperature using the same type of chromatogram.

#### **EXAM TIP**

You should be able use experiments like the one shown in Figure 3.3.3 to work out  $R_{\rm f}$  values and identify different pigments.



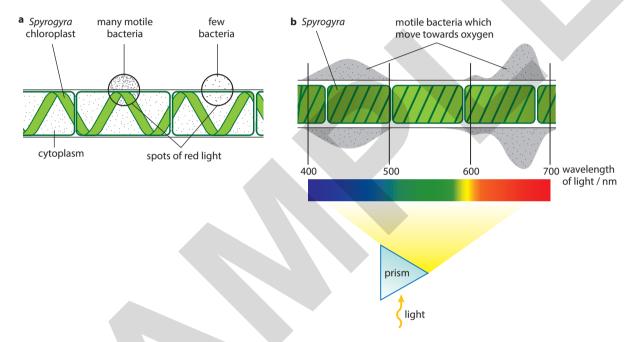
**Figure 3.3.3:** A chromatogram can be used to identify different photosynthetic pigments. Different pigments are found in different plants and the pigments may vary with the seasons.

#### **NATURE OF SCIENCE**

#### Careful observation: Engelmann's experiment

Theodor Wilhelm Engelmann (1843–1909) was a German botanist who used the filamentous alga *Spirogyra* to demonstrate not only that oxygen is evolved during photosynthesis but also that different wavelengths of light affect the rate of photosynthesis. *Spirogyra* is an alga that has cylindrical cells containing spiral-shaped

chloroplasts. Engelmann mounted a sample of *Spirogyra* under a microscope and, after a period of darkness, illuminated it with different colours of light. He carefully watched the movement of motile bacteria (*Pseudomonas*) that he had added to the water and noticed that, after a period of oxygen deprivation, they moved towards areas where there was a higher concentration of oxygen around the alga's chloroplasts (Figure 3.3.4).



**Figure 3.3.4:** Engelmann used bacteria in two experiments a and b to measure rates of photosynthesis and determine which wavelengths are most effective for photosynthesis.

#### **TEST YOUR UNDERSTANDING**

- 19 Use these questions to analyse the results of Engelmann's experiments.
  - Look at Figure 3.3.4a and explain why the bacteria moved towards certain areas of the Spirogyra and not towards others when a spot of red light was used.
  - **b** Explain why there are no bacteria between the areas of *Spirogyra* illuminated with light of 500–600 nm (Figure 3.3.4b).

## 3.3.2 The chemistry of photosynthesis

Photosynthesis is a complex series of reactions catalysed by a number of different enzymes. The processes take place in chloroplasts (Figure 3.3.5; see also Section 5.2). To help us understand the reactions, we can consider photosynthesis in two stages: the light-dependent reactions and the light-independent reactions.

### Light-dependent reactions

The first stage of photosynthesis is known as the 'light-dependent reactions' because light is essential for

them to occur. These take place in the thylakoids of the chloroplast.

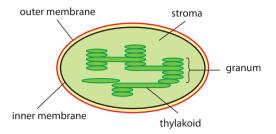


Figure 3.3.5: Structure of a chloroplast.

Chlorophyll in the **thylakoids** absorbs light energy and this energy is used to produce ATP. The energy is also used to split water molecules into hydrogen and oxygen in a process called **photolysis**. Hydrogen ions and electrons (from the hydrogen part of water) and oxygen are released. Oxygen is a waste product of photosynthesis but is vital to sustain the lives of aerobic organisms once it has been released into the atmosphere. The ATP, hydrogen ions and electrons are used in the light-independent reactions.

#### Light-independent reactions

ATP, hydrogen ions and electrons are used in the second stage of photosynthesis, the 'light-independent reactions', which take place in the stroma.

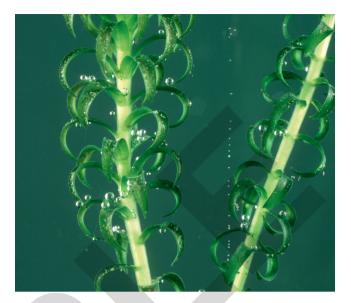
During the 'light-independent reactions', enzymes in the stroma use carbon dioxide, taken in from the environment, and combine it with hydrogen using energy from ATP. The reactions form mainly glucose, but also a range of other organic molecules for the plant. The conversion of inorganic carbon dioxide to organic molecules such as glucose is known as **carbon** fixation. ATP provides the energy for the process.

The series of reactions that occurs during photosynthesis is summarised as:

carbon dioxide + water 
$$\rightarrow$$
 glucose + oxygen  
6CO<sub>2</sub> + 6H<sub>2</sub>O  $\rightarrow$  C<sub>6</sub>H<sub>12</sub>O<sub>6</sub> + 6O<sub>2</sub>

## Measuring the rate of photosynthesis

The equation for carbon dioxide and water shows that when photosynthesis occurs, carbon dioxide is used and oxygen is released. The mass of the plant (its biomass) will also increase as glucose is used to produce other plant materials. Any of these three factors can be used to measure how quickly the reactions of photosynthesis are occurring.



**Figure 3.3.6:** The rate of oxygen production can be used as a direct measure of the rate of photosynthesis.

Aquatic plants release bubbles of oxygen as they photosynthesise and if the volume of these bubbles is measured for a period of time, the rate of photosynthesis can be determined directly (Figure 3.3.6).

Aquatic plants also remove carbon dioxide from their environment, causing the pH of the water to rise. Carbon dioxide dissolves in water to form a weak acid, so as it is removed the pH will go up. Therefore, another way of determining the rate of photosynthesis experimentally is to monitor the change in pH of the water surrounding an aquatic plant over a period of time.

Terrestrial plants also remove carbon dioxide from their surroundings but this is difficult to measure. It can be done experimentally by supplying a confined plant with radioactive carbon dioxide, which can be measured as it is taken up and released from the plant.

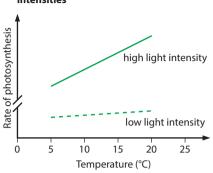
A third method of measuring the rate of photosynthesis in plants is to determine their biomass at different times. This is an indirect method. Samples of the plants can be collected and measured at different times and the rate of increase in their biomass calculated to determine their rate of photosynthesis.

## 3.3.3 Limits to photosynthesis

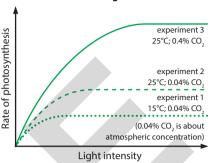
The rate at which a plant can photosynthesise depends on factors in the environment that surrounds it. On a warm, sunny afternoon, photosynthesis will be more rapid than on a cool, shady morning.

- a The rate of photosynthesis at different light intensities and constant temperature
- Rate of photosynthesis

  Light intensity
- b The rate of photosynthesis at different temperatures and constant light intensities



c The rate of photosynthesis at different temperatures, carbon dioxide concentrations and light intensities



**Figure 3.3.7:** These graphs show the effects on photosynthesis of varying light intensity, temperature and carbon dioxide concentration.

More oxygen will be produced and more carbon dioxide used. Temperature, light intensity and carbon dioxide concentration are all possible limiting factors on the rate of photosynthesis. But photosynthesis cannot increase beyond certain limits. The effect of light, temperature and carbon dioxide in the environment can be measured experimentally, varying one factor while keeping the others the same, and graphs such as those in Figure 3.3.7 can be drawn.

An increase in light intensity, when all other variables are unchanging, will produce an increase in the rate of photosynthesis that is directly proportional to the increase in light intensity. However, at a certain light intensity, enzymes will be working at their maximum rate, limited by temperature and the availability of carbon dioxide. At very high light intensities, light absorption (and therefore the rate of photosynthesis) reaches its maximum and cannot increase further. At this point, the graph reaches a plateau (Figure 3.3.7a).

Increasing temperature also increases the rate of photosynthesis as the frequency and energy of molecular collision increases (Figure 3.3.7b). Photosynthesis has an optimum temperature above which the rate will decrease sharply as enzymes are denatured, or the plant wilts and is unable to take in carbon dioxide.

An increase in the concentration of carbon dioxide causes the rate of photosynthesis to increase, as carbon dioxide is a vital raw material for the process. At very high concentrations, the rate will plateau as other factors such as light and temperature limit the rate of reaction (Figure 3.3.7c).

#### **SCIENCE IN CONTEXT**

The effects of temperature, light and carbon dioxide concentration are well known to horticulturalists who grow crops in glasshouses. Commercial producers of cucumbers and tomatoes keep their glasshouses warm and well lit. They may also seal the greenhouse and introduce carbon dioxide to boost photosynthesis to its maximum rate, thereby increasing crop production and profits.

### Compensation point

The net production of oxygen (or uptake of carbon dioxide) will depend on both the rate of cellular respiration and the rate of photosynthesis. When the two are in equilibrium, the amount of oxygen being produced by photosynthesis will be equal to that which the plant is using in respiration. This is known as the compensation point (Figure 3.3.9).

#### **KEY POINT**

compensation point the light intensity at which the amount of carbon dioxide released in respiration equals the amount used in photosynthesis, and at which the amount of oxygen used in respiration equals the amount released in photosynthesis.

#### **NATURE OF SCIENCE**

#### Experimental design: controlling variables

Any investigations involving living organisms must be designed so that all the possible variables are controlled. Consider this diagram of apparatus (Figure 3.3.8) that has been set up in a laboratory to estimate the rate of photosynthesis of a pond plant.

#### To consider:

- 1 Which variable is being controlled by the presence of the beaker of water?
- 2 Why must this variable be controlled?
- 3 Photosynthesis is a metabolic reaction controlled by enzymes. List the factors that affect enzyme action (Section 3.1).
- 4 How could each one of these be controlled in this experiment?

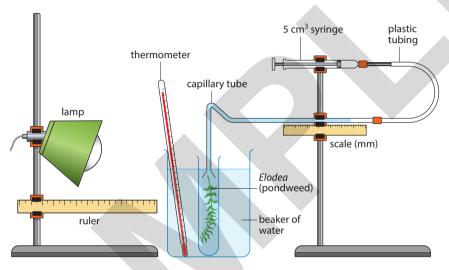
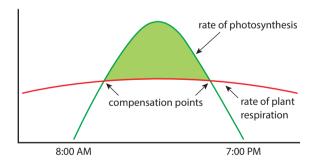


Figure 3.3.8: Diagram of experiment to determine the rate of photosynthesis.

#### **FXAM TIP**

Remember that photosynthesising organisms respire throughout the day and night but can only photosynthesise when light is available.



**Figure 3.3.9:** Graph showing the rate of photosynthesis and respiration for a plant over a period of 24 hours.

#### **TEST YOUR UNDERSTANDING**

- 20 If you want to make plants grow as efficiently as possible, what colour of light should you shine on them?
- 21 Suggest what would happen to a plant's growth if it was illuminated by green light.
- 22 Where in the chloroplast does the lightdependent reactions take place?
- 23 Outline two ways in which the rate of photosynthesis can be measured.

## 3.3.4 Advanced photosynthesis

Photosynthesis is the process by which light energy is harvested and stored as chemical energy, primarily in sugars but also in other organic molecules such as lipids. It occurs in green plants, algae and some bacteria. All these organisms are known as autotrophs, which means they can make their own food.

Photosynthesis can be divided into two parts:

- the light-dependent reactions
- the light-independent reactions.

The light-dependent reactions produce compounds that are used in the light-independent reactions.

Both the light-dependent and the light-independent reactions take place in the chloroplasts of plant cells (Figures 3.3.5, 3.3.10 and 3.3.11). The stroma contains the enzymes required for the light-independent reactions and the stacks of thylakoid membranes increase the surface area for the light-dependent reactions.

Both these sets of reactions are part of photosynthesis and can only occur when there is sufficient light. Lightdependent reactions can only take place in light and although light-independent reactions do not require light directly – and can take place when it is dark – they do require the products of the light-dependent reactions.

#### **KEY POINTS**

light-dependent reactions occur on the thylakoids and produce ATP and NADPH

light-independent reactions series of stages in photosynthesis that take place in the stroma and use the products of the light-dependent reactions to produce carbohydrate.



Figure 3.3.10: Coloured electron micrograph of a chloroplast (× 20 000).

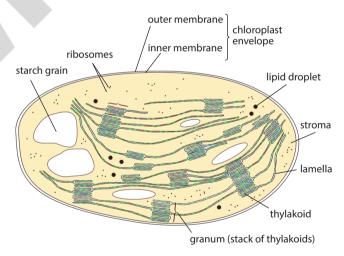


Figure 3.3.11: Diagram of a chloroplast.

### The light-dependent reactions

The light-dependent reactions are a series of stages in photosynthesis that occur on the grana of the chloroplasts. Light is used to split water, and ATP and NADPH + H<sup>+</sup> are produced.

The reactions take place on the thylakoid membranes that make up the grana of the chloroplast and are powered by light energy from the Sun. Each thylakoid is a flattened sac so the space in the middle is narrow. The thylakoid membranes form the stacks called **grana**, which may be joined together by intergranal lamellae (membranes). Light is absorbed by photosynthetic pigments, including the chlorophylls, which are found on the granal membranes. There are several pigments found in plants and each one absorbs light of a slightly different wavelength.

The photosynthetic pigments are combined into two complex groups called **photosystems** I and II (PSI and PSII), which absorb the light energy and use this to boost electrons to a higher energy level so that they become 'excited'. The pigments are associated with proteins that are involved in electron transport, proton pumping and chemiosmosis.

Both PSI and PSII have a chlorophyll a molecule at their centre together with accessory pigments, such as chlorophyll b and carotenoids, around them.

At the centre of each chlorophyll a molecule is a magnesium (Mg<sup>2+</sup>) ion which is essential to its structure and functioning (Section 1.1). Fluctuations in magnesium levels in the chloroplast regulate the activity of key photosynthetic enzymes.

In the light-dependent reactions, electrons are removed from water and passed through PSII and PSI before ending up in NADPH. This process needs light to be absorbed by both photosystems and it also produces ATP. The process is called **photophosphorylation** because it uses light energy to produce ATP from ADP.

The key stages of the light-dependent reactions are as follows:

#### 1 Photoactivation of PSII

Light is absorbed by pigments in PSII and passed to the reaction centre. Here energy boosts an electron in chlorophyll a to a higher energy level. The electron is passed to an acceptor molecule at the start of the electron transport chain.

Lost electrons must be replaced and this is done by taking them from water. Water is split into electrons, protons (hydrogen ions) and an oxygen atom. Since the splitting is brought about by light energy, it is called photolysis. The oxygen is released as a waste product and is the oxygen we breathe.

#### 2 ATP synthesis

Excited, high-energy electrons travel down the electron transport chain into PS I. As they do this, they lose energy which is used to pump protons into the thylakoid interior (in a similar way as occurs in the electron transport chain in the mitochondrion). The thylakoid interior is small and so a proton concentration gradient builds up quickly. The protons then flow out through a large channel protein, almost identical to the one in mitochondria, which contains the enzyme ATP synthase. Ions flow down their gradient and into the stroma, driving ATP production in a process known as chemiosmosis. This time though, the formation of ATP is called photophosphorylation and it occurs between PS II and I (Figure 3.3.12).

#### 3 Light absorption in PSI

Absorption of light energy causes photoactivation in PS I, boosting more electrons to an even higher energy level. The electrons that arrive from PS II replace those that are displaced.

#### 4 NADPH formation

The electrons at the higher energy level continue down the electron transport chain and are combined with protons in the hydrogen carrier NADP+ to form NADPH + H+.

The two products of the light-dependent reaction, ATP and NADPH + H<sup>+</sup>, are used to drive the light-independent reaction.

The net effect of these steps is to convert light energy into chemical energy in the form of ATP and NADPH. The ATP and NADPH from the light-dependent reactions are used to make sugars in the next stage of photosynthesis, the Calvin cycle.

## The light-independent reactions

The light-independent reactions occur in the stroma of the chloroplast. These reactions are catalysed by enzymes and therefore are temperature dependent.

#### **KEY POINT**

Calvin cycle cycle of light-independent reactions in the stroma of the chloroplast in which carbon dioxide reacts with ribulose bisphosphate (RuBP), producing glycerate 3-phosphate, triose phosphate and regenerating RuBP.

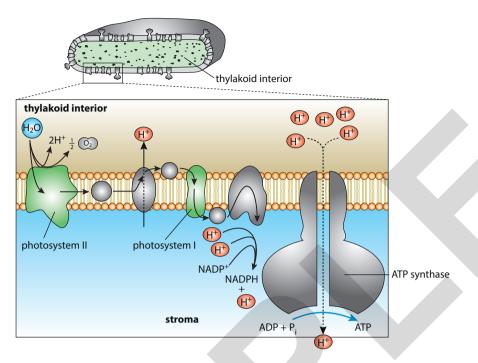


Figure 3.3.12: Chemiosmosis in photosynthesis.

The reactions follow a cyclic pathway called the Calvin cycle (shown in Figure 3.3.13). ATP and NADPH + H<sup>+</sup> formed during the light-dependent stage supply energy and reducing power for the Calvin cycle. The final product of the cycle is carbohydrate.

During each turn of the Calvin cycle, one molecule of carbon dioxide is used, so Figure 3.3.13 shows three cycles combined together. As this is a cycle, what goes in must leave, so three carbons enter in three molecules of carbon dioxide and three carbons leave in one molecule of triose phosphate, which can be used to form glucose or other organic compounds. There are three stages in the cycle, as follows.

#### 1 Carbon fixation

At the start of the cycle, the acceptor molecule ribulose bisphosphate (RuBP) combines with incoming carbon dioxide from the air to form glycerate 3-phosphate (GP). This reaction is called carbon fixation because it 'locks' the carbon into the cycle. It is catalysed by RuBP carboxylase (this enzyme is sometimes called Rubisco).

#### 2 Reduction of glycerate 3-phosphate

The ATP and NADPH + H<sup>+</sup> from the light-dependent reaction convert the glycerate 3-phosphate into triose phosphate (TP). Glycerate 3-phosphate is reduced to triose phosphate.

No more phosphate is added so the only input from ATP is energy.

Six molecules of triose phosphate are produced but only five are needed to reform the ribulose bisphosphate to keep the cycle going. The extra triose phosphate leaves the cycle and is used to synthesise organic molecules such as glucose or amino acids.

#### 3 RuBP regeneration

The triose phosphate that leaves the cycle takes a phosphate with it, so this is replaced in the cycle with a phosphate from ATP, as the five remaining triose phosphates are converted back to three ribulose bisphosphate molecules, and the cycle begins again. This is an example of a cyclic metabolic pathway.

Six 'turns' of the Calvin cycle produce two triose phosphate molecules, which can be combined to form

#### **KEY POINT**

RuBP carboxylase (Rubisco) the enzyme that catalyses carbon fixation in the Calvin cycle in the light-independent reactions of photosynthesis; in carbon fixation, the five-carbon acceptor molecule ribulose bisphosphate (RuBP) combines with carbon dioxide to form glycerate 3-phosphate.

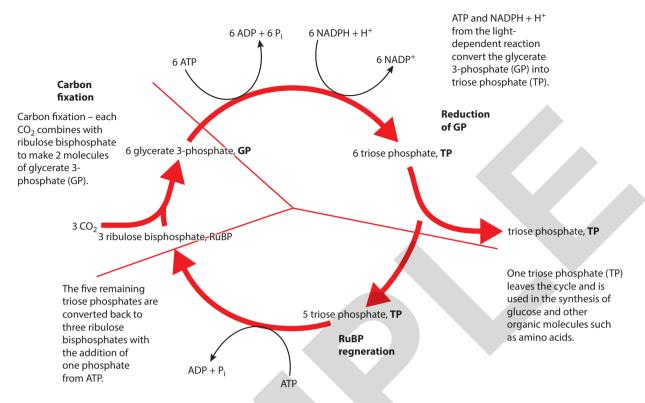


Figure 3.3.13: The light-independent pathway of photosynthesis – the Calvin cycle.

the final product, glucose. Many triose phosphate molecules will be converted immediately to starch. Other triose phosphate molecules are exported to the cytoplasm to be converted to sucrose and transported around the plant. The products of the Calvin cycle are used to make all the other different organic molecules the plant needs, such as cellulose, amino acids, fatty acids and vitamins.

#### **TEST YOUR UNDERSTANDING**

- **24** Where do the light-dependent reactions take place?
- 25 State the colour of light that is not absorbed by green plants and algae.
- 26 Where in a chloroplast do you find magnesium ions?
- 27 State the names of the two products of the light-dependent reactions that are needed for the light-independent reactions.
- **28** State the name of the acceptor molecule that reacts with carbon dioxide in the Calvin cycle.

#### Links

- How does the structure of chlorophyll compare with that of hemoglobin? (Chapter 1)
- How does the structure of a chloroplast compare with that of a mitochondrion? (Chapter 3)
- What is the origin of chloroplasts in eukaryotic cells? (Chapter 5)
- How is photosynthesis important to ecosystems?
   (Chapter 12)
- What are the similarities and differences between chemiosmosis in respiration and photosynthesis? (Chapter 3)

#### **SELF-ASSESSMENT CHECKLIST**

Think about the topics covered in this section. Which parts are you most confident with? Which topics require some extra practice?

I can	Subsection	Needs more work	Nearly there	Confident to move on
define metabolism and state that reactions may take place inside or outside cells	3.1.1			
recall that metabolic pathways may be linear or cyclical	3.1.1			
recall that metabolic processes may be anabolic or catabolic	3.1.1			
explain the importance of enzymes and their properties in metabolism	3.1.2			
outline the induced-fit hypothesis of enzyme action	3.1.2			
summarise the importance of temperature, pH and substrate concentration on enzyme action and interpret graphs which show these	3.1.2			
outline how enzymes lower activation energy	3.1.3			
summarise how enzymes can be affected by other molecules that bind to them at their active or allosteric sites	3.1.4			
describe the effects of competitive and non- competitive inhibitors on rates of reaction	3.1.4			
outline end-product inhibition	3.1.5			
define co-enzymes and co-factors and give an example of each	3.1.6			
explain the inputs and products of cellular respiration	3.2.1			
recall that respiration occurs as a series of metabolic pathways catalysed by enzymes	3.2.1			
outline the uses of energy-requiring actions and recall that energy is lost as heat	3.2.1			
outline the stages of anaerobic respiration and explain its lower energy yield	3.2.2, 3.2.3			
recall that aerobic respiration has a higher yield of energy, takes place in mitochondria and requires oxygen to produce carbon dioxide and water	3.2.2			
outline the importance of redox reactions involving NAD and FAD	3.2.4			
define phosphorylation, decarboxylation and explain their importance in cell respiration	3.2.4, 3.2.5			

#### CONTINUED

I can	Subsection	Needs more work	Nearly there	Confident to move on
list the four steps involved in aerobic respiration	3.2.4			
compare the products and energy output of aerobic and anaerobic respiration	3.2.5			<b>)</b>
draw a mitochondrion and indicate where reactions of respiration take place	3.2.5			
summarise the reactions that occur in the ETC	3.2.5			
define chemiosmosis and explain its importance in generating ATP	3.2.5			
explain the inputs and products of photosynthesis and write an equation that summarises the reactions	3.3.1			
recall the colours of light that are used for photosynthesis	3.3.1			
explain the difference between an absorption spectrum and an action spectrum	3.3.1			
name the two stages of photosynthesis and state where they take place	3.3.2			
name three limiting factors on the rate of photosynthesis and sketch graphs to show their effects	3.3.3			
explain how photosynthesis and respiration are related in algae and plants	3.3.3			
outline the location and structure of the two photosystems	3.3.4			
state the precise locations of the light-dependent and light-independent reactions in the chloroplast	3.3.4			
summarise the differences between the light-dependent and light-independent reactions	3.3.4			
name the products of the light-dependent reactions that enter the light-independent reactions	3.3.4			
summarise the three stages of the Calvin cycle	3.3.4			
outline the importance of carboxylase, RuBP and glycerate 3-phosphate in the Calvin cycle	3.3.4			

#### **REFLECTION**

How well is your understanding of respiration developing? Could you explain the various stages to a fellow student?

#### **EXAM-STYLE QUESTIONS**

You can find questions in the style of IB exams in the digital coursebook.