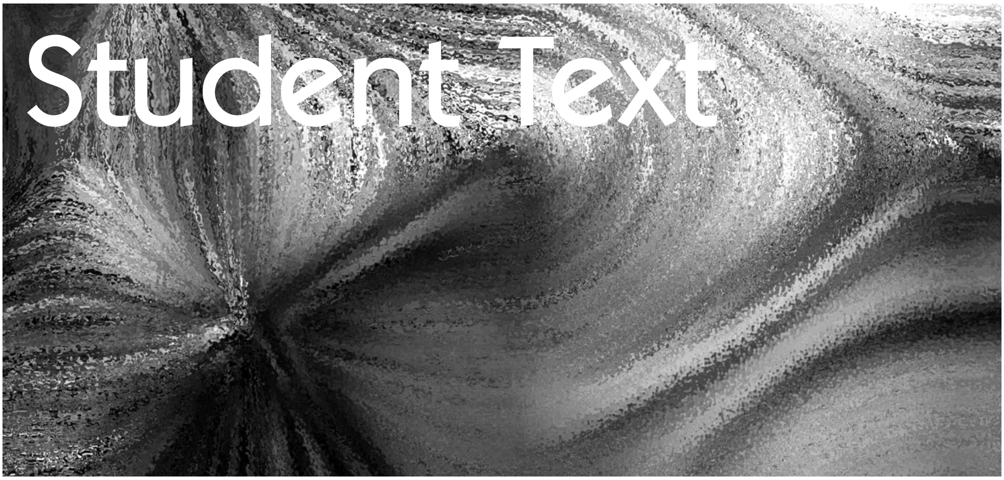
For **Edexcel** Specifications

Advanced Subsidiary

Biology



AS Unit 2B

Exchange Transport and Reproduction

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Edexcel Unit 2B
Exchange, Transport and Reproduction

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Edexcel Unit 2B
Exchange, Transport and Reproduction

2B.1
Exchanges with the Environment

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Exchanges with the environment

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- The features of exchange surfaces which aid passive and active transport.
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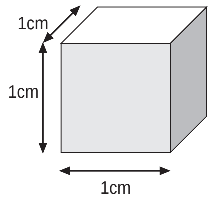
EXCHANGES WITH THE ENVIRONMENT

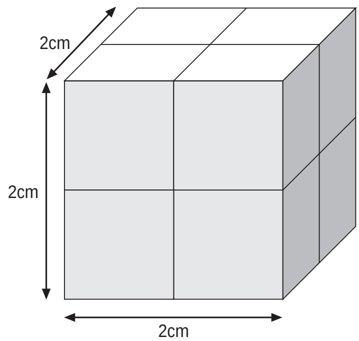
All living cells obtain oxygen and nutrients from, and excrete waste substances into, the fluid environment which surrounds them. In the case of single celled organisms, the fluid environment is the habitat in which they live, normally fresh or salt water. The individual cells of multicellular organisms are surrounded by a fluid medium called **tissue fluid** or extracellular fluid, with which they exchange materials. This is referred to as the '**internal environment**' and for exchange to occur between the internal and the external environment in larger organisms, specialised systems have evolved.

Exchange processes

Smaller organisms have larger surface area to volume ratios (surface area divided by volume) than larger ones.



Surface area = $6cm^2$
Volume = $1cm^3$
Surface area to volume = 6:1 = 6



Surface area = $24cm^2$
Volume = $8cm^3$
Surface area to volume = 24:8 = 3

This means that in smaller organisms all parts of their body are close enough to the surrounding medium not to require a specialised transport system. In unicellular and small multicellular organisms oxygen, carbon dioxide and waste materials may be transported by simple diffusion between the external and internal environments. Internal transport by diffusion is further aided by the particular shapes of some organisms and their parts. For example in the jellyfish and sea anemones there is a large body cavity which is filled with the external medium (water), effectively doubling their surface area in contact with the sea water; in the Platyhelminthes (the 'flat' worms eg the tape worms and liver flukes) there is a flattened body shape, and flowering plants have leaves with a flattened form with large internal air spaces.

In large multicellular organisms the external surface area is increased relative to the body volume by specialised exchange surfaces, e.g. lungs, with huge surface areas. These provide for rapid and efficient exchange of gases, nutrients and waste substances with the environment.

The exchange of substances is by **passive diffusion** and/or **active transport**.

In passive diffusion the rate is dependent upon the concentration gradient between the external environment and the exchange surface, and the distance travelled. In general it conforms to the following equation, known as Fick's law.

$$\text{Rate of diffusion} = \frac{\text{surface area X difference in concentration}}{\text{thickness of the exchange surface}}$$

In principle, the greater the surface area, the greater the concentration difference, and the thinner the separating layers, the more rapid the diffusion.

Surface areas for exchanges are increased dramatically by dividing them up into small components, e.g. gill lamellae or alveoli in the lungs, and the separating layer is made from flattened epithelial cells which minimise the distance between the environment and the blood.

Gas exchange surfaces have a large surface area, which is well supplied with capillaries of the blood vascular system, and thin to reduce the diffusion distance between the external medium (air or water) and the blood. If the external medium is air, there is an unavoidable loss of water over the surface so it is covered with a layer of water, and mucus is secreted to reduce losses by evaporation.

These delicate systems are protected in specialised internal organs, e.g. lungs, gills; and require mechanisms to move the external medium (air or water) over the surface. Such mechanisms are called ventilation mechanisms (note that flowering plants do not possess a ventilation mechanism and rely solely on diffusion gradients). In fish and mammals the ventilation mechanisms involve muscular contractions which serve to maintain a constant flow of water or air over the gas exchange surfaces. The process of air or water intake is called **inspiration** and the expulsion of air or water is called **expiration**.They are also supplied with blood by mass transport circulatory systems for the rapid and efficient transport of substances to and from the external medium, and between the different tissues and organs.

The uptake of digested nutrients from the gut into the blood also involves **active transport,** and the epithelial cells lining the gut are specialised for this purpose, being equipped with numerous mitochondria to supply energy demands and microvilli to increase their surface area.

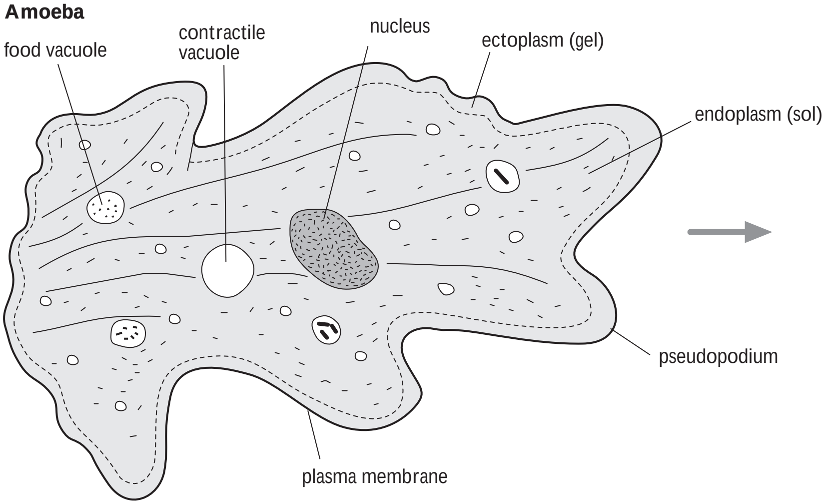
◆ CHECKPOINT SUMMARY

- ◆ Living organisms need to take up nutrients, exchange respiratory gases, which includes an element of excretion in the elimination of carbon dioxide, and eliminate other excretory products.
- ◆ Surface area increases with increasing size but the surface area to volume ratio decreases.
- ◆ Where SA/V sufficiently large, simple diffusion suffices for exchanges with environment and internal transport.
- ◆ SA/V increased by flattened body shapes and sub-divided structures e.g. exchange surfaces which aid passive and active transport.
- ◆ Exchange surfaces have other special features which aid passive and active transport in addition to their large surface area. They are thin, well supplied with blood vessels, and exposed to the external environment.
- ◆ Gas exchange surfaces must be ventilated to continually replace the external medium in order to maintain the diffusion gradients between it and the blood.
- ◆ Protozoa are single celled organisms with a large SA/V ratio, which is sufficient for gas exchange and internal transport to be by diffusion. Oxygen is absorbed and carbon dioxide eliminated.

Gas exchange in protozoa (protoctists)

Protoctists are single celled eukaryotic organisms (previously referred to as protozoa and algae) e.g. *Amoeba*. They are microscopic (the larger species just being visible to the naked eye) so have a large surface area to volume ratio, and do not possess special structures for gas exchange. Not only can oxygen and carbon dioxide be exchanged efficiently across the surface, they have the additional advantage of being able to excrete nitrogenous waste in the form of ammonia (NH_3). Ammonia is very toxic but very soluble and quickly diffuses out of single celled aquatic organisms. In most larger multicellular animals ammonia can not be tolerated in the tissue fluids and is converted to urea or uric acid for excretion by specialised organs, e.g. the kidneys in vertebrates.

Amoeba

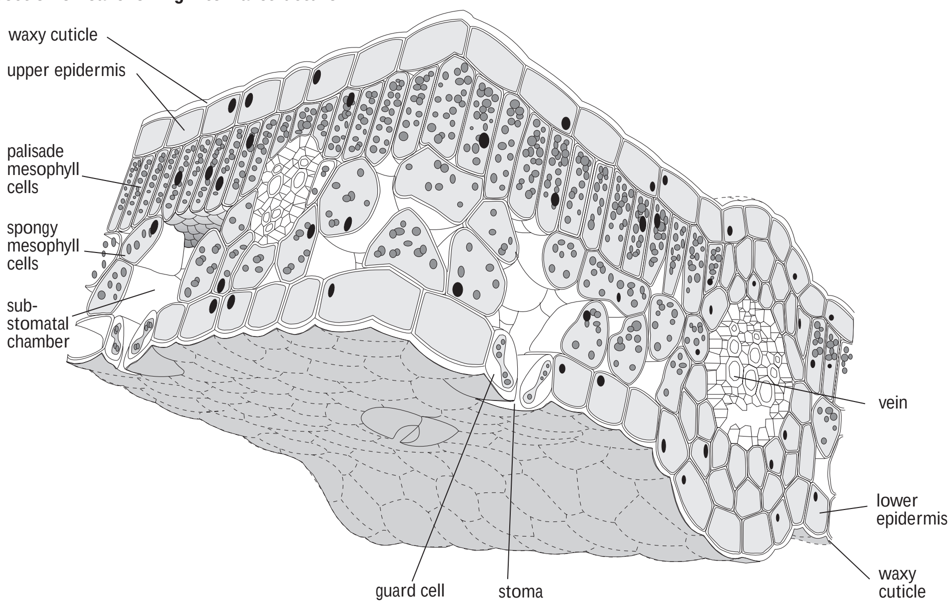


Gas exchange in flowering plants

Gas exchange occurs in flowering plants wherever living plant cells are exposed to the external medium. Most of the plant surface is protected by an almost impermeable waxy cuticle, so gas exchange in aerial parts occurs via special openings, the **stomata.** Woody plant stems are protected by layers of impermeable dead tissue (the bark) and the stomata are replaced by openings (lenticels) full of loosely packed dead cells which permit gaseous exchange. It should not be forgotten that the tips of roots are provided with a large exchange surface composed of **root hair cells**, across which gaseous exchange occurs between the root and the soil air and water film.

The main organ for gaseous exchange is the leaf.

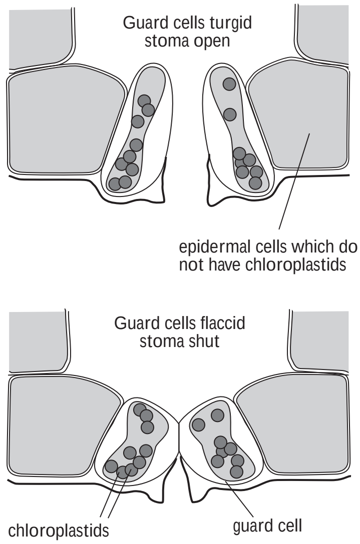
Section of leaf showing internal structure



A typical mesophyte leaf adapted to average water supplies, as opposed to xerophyte (dry adapted) and hydrophyte (wet adapted) leaves, shows many external and internal adaptations to gaseous exchange. As described above, the one cell thick epidermis is covered by an impermeable waxy cuticle which reduces water loss by evaporation. Stomata may be found on both surfaces, but more occur on the under surface of the leaf, where they are more protected from direct sunlight and air currents. Each stoma (singular) is surrounded by two guard cells which control its opening and closing. Each stoma connects to a sub-stomatal cavity inside the leaf, which in turn connects with an extensive system of inter cellular air spaces in the spongy mesophyll. The spongy mesophyll tissue is made up of relatively large irregular cells with a thin cell wall. The air spaces further connect with air spaces between the palisade mesophyll which is the main photosynthesising layer situated below the upper epidermis. In this way gases can be exchanged by diffusion between the external air and all the cells of the leaf, for respiration and photosynthesis.

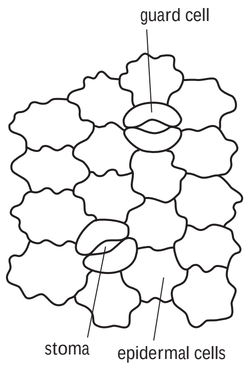
The rate and direction of exchange depends upon the diffusion gradients of oxygen and carbon dioxide. Remember that photosynthesis occurs during the light periods only but respiration occurs all the time. The air in the air spaces is refreshed by incoming supplies when the stomata are open. There are no 'breathing movements' so the rate of exchange is determined entirely by diffusion gradients. Carbon dioxide and oxygen in the air dissolve in the thin layer of water coating the surface of the spongy and palisade mesophyll cells, then diffuse through the cell wall and the cell membrane.

The stomata and their guard cells control the entry and exit of air. The stomata open in the light to permit carbon dioxide to enter by diffusion to supply the photosynthesising palisade mesophyll cells, and to allow oxygen to diffuse out. Whilst open there is a danger of excessive loss of water vapour, and the stomata must strike the correct balance between the needs for gaseous exchange and the control of loss of water vapour (transpiration). A reduction in size of stomata reduces water loss by more than it reduces carbon dioxide uptake. When the rate of respiration exceeds the rate of photosynthesis the diffusion gradients are reversed, and oxygen would diffuse in and carbon dioxide diffuse out, however this mainly occurs in low light intensities when the stomata are closed. In windy conditions the leaves are buffeted and there can be mass flow of air into and out of the leaf, in a form of ventilation.



The guard cells on either side of each stoma are banana shaped and have specially thickened walls. The mechanism by which stomata open and close is still not fully understood, but all theories depend on explanations of the changes in the shape of the guard cells due to changes in their water content or turgidity. When the guard cells are distended with water (turgid), they bend outwards due to the unequal thickening of their walls and the stomata open; when they are not so distended the stomata are closed.

Surface view of leaf epidermis and stomata

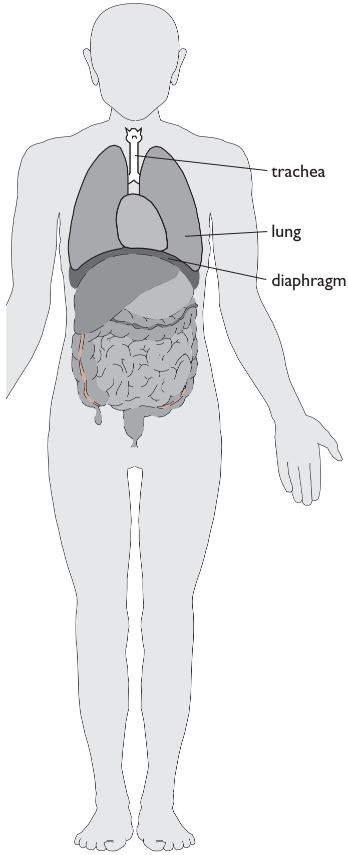


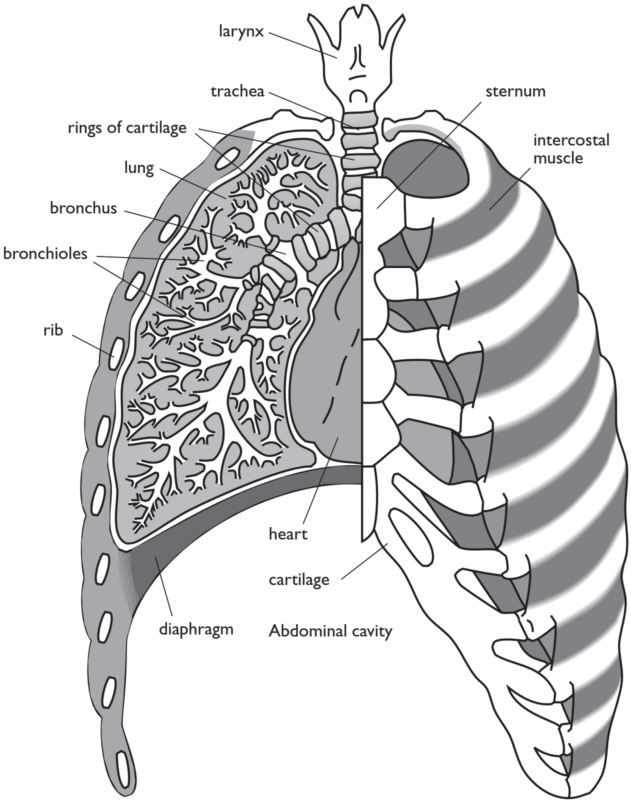
Guard cells are the only epidermal cells to possess chloroplasts and their presence could indicate that photosynthesis is involved in some way. The simple explanation is that the guard cells produce sugars in the light by photosynthesis, and that these sugars increase the concentration of the cell contents so that water is drawn in by osmosis. This increases their turgidity and results in the opening of the stomata. However, this cannot explain the opening and closing of all stomata since many stomata open at night, or at certain times of the day, and changes in the rate of sugar production by photosynthesis would be too slow to account for the rapid opening sometimes seen. It is thought that the mechanism is, at least to some degree, an active process which involves ion transport across the cell membranes of the guard cells. When potassium ions are pumped in the water potential is lowered and water enters by osmosis from the surrounding cells, the cells become turgid and the stomata open. When potassium ions are pumped out the water potential is raised and water leaves by osmosis into the surrounding cells, the guard cells become flaccid and the stomata close.

GAS EXCHANGE IN HUMANS

The structure of the thorax

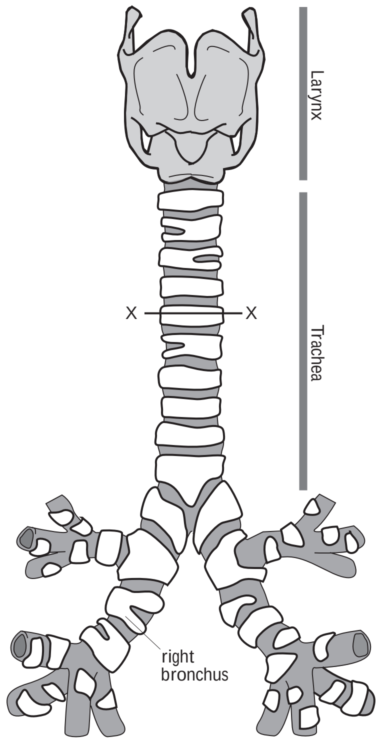
The organs of gas exchange in mammals are the lungs which, together with the heart, fill all the available space in the air tight **thorax** (chest cavity). The thorax is bounded by the ribs and the muscular and tendonous sheet known as the **diaphragm,** which separates it from the abdominal cavity.





Air travels through a series of tubes which make up the respiratory system, having first been warmed and moistened in the nasal cavity (if the mouth is shut). The **trachea, bronchi and bronchioles** form a system of branching air tubes referred to as the 'bronchial tree'. The wall of the trachea and bronchi are composed of four layers. These are the inner mucous membrane or **epithelial** layer, a layer consisting of connective tissue, elastic fibres and mucous glands, a layer of **smooth muscle** and **cartilage**, and a tough outer coat of **connective tissue**. Bronchioles differ in that they have less cartilage and do not have mucous glands.

Cartilage supports the trachea and bronchi and prevents their collapse when the internal pressure drops, or when the neck is twisted. In the trachea the cartilage forms C-shaped rings which are arranged so that the open ends of the C are at the back of the tube, facing towards the spine. Between the ends of the Cs at the posterior (back) of the trachea, smooth muscle completes the tube. The incomplete nature of these 'rings' of cartilage allow a degree of compression as a result of the expansion of the oesophagus when swallowing food. In the bronchi the cartilage does not form rings but instead forms plates within the smooth muscle layer to strengthen the tubes.



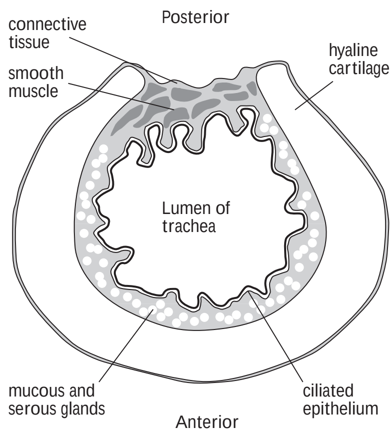
Involuntary (smooth) muscle found in the trachea, bronchi and bronchioles also helps maintain the shape of the tubes and prevent collapse of the airways. The smooth muscle receives nerve impulses from the autonomic nervous system, and hormones such as adrenaline, which can regulate the diameter of the tubes. This is significant in diseases like asthma and anaphylaxis (allergic shock) where constriction of the bronchioles occurs restricting air flow.

Epithelium lining the trachea, bronchi and bronchioles is known as the mucous membrane, and consists of **ciliated columnar epithelium**. This is composed of: ciliated cells and goblet cells. At the very end of the bronchioles, close to the alveoli no goblet cells are found, only ciliated cells.

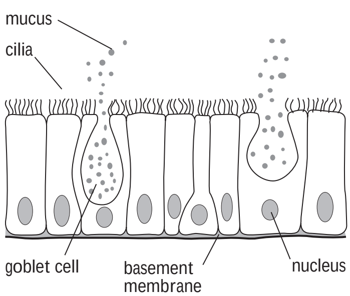
Ciliated epithelial cells have a protective function as they work in a co-ordinated fashion sweeping the mucous coat of the air passages)which contains small inhaled particles such as dust towards the back of the throat and mouth, where they can be swallowed or removed by the cough reflex. This prevents such particles from entering the alveoli and interfering with gaseous exchange. Goblet cells are found amongst the ciliated cells in the trachea and bronchi and secrete mucus within the respiratory tract. The layer of mucus which lines the airways traps dust and bacteria. It may also play a role in humidifying inhaled air.

The lungs are surrounded by double pleural membranes which enclose a fluid filled pleural cavity. These lubricate any movements of the lungs against the inside wall of the thorax, and prevent the lungs collapsing under their own elasticity. If air enters the pleural cavity, either as a result of an external penetration or by alveoli bursting outwards, the lungs do collapse.

Section X - X



Respiratory ciliated columnar epithelium

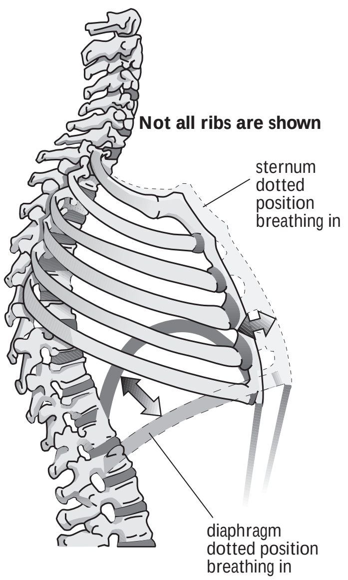


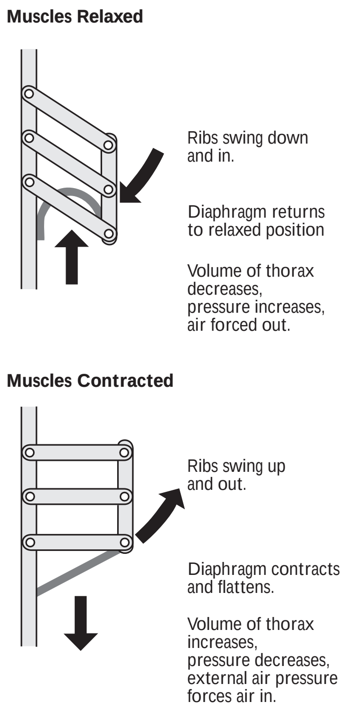
The mechanism of ventilation

Ventilation in mammals is achieved by the breathing movements of the **intercostal muscles** of the ribs and the muscular **diaphragm** which are controlled by the autonomic and voluntary nervous systems.

During **inspiration** (breathing in) the external intercostal muscles contract pulling the ribs upwards and outwards. At the same time the diaphragm contracts, moving downwards. Both movements increase the volume of the thorax, reducing the pressure in the thorax below atmospheric pressure causing air to enter, inflating the lungs. At rest **expiration** (breathing out) does not involve active muscle contractions, but depends upon the elasticity of the tissues of the lungs and thorax.. The intercostal muscles relax, allowing the rib cage to move downwards and inwards, and the diaphragm relaxes and regains its domed shape. The volume of the thorax is reduced, pressure increased and air forced out of the lungs. During forced breathing, for example as a result of exercise or in speech, expiration is active, with the internal intercostal muscles and abdominal muscles contracting to increase the pressure within the thorax.

Breathing movements thus result in certain volumes of air passing into and out of the lungs.



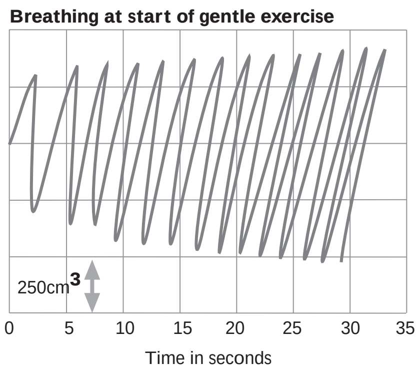


How breathing is controlled

Normally, respiratory movements are involuntary, being controlled by rhythmic discharges of nerve impulses from the respiratory control centres in the **medulla** region of the brain. These impulses travel down the **phrenic nerves** to the diaphragm, and down the **intercostal nerves** to the external intercostal muscles causing them to contract and bring about inspiration. When the alveoli are stretched at the end of inspiration, stretch receptors in the bronchioles send impulses to the **inspiratory control centre** in the medulla to inhibit it and the diaphragm and external intercostal muscles are caused to relax. This leads to expiration. Normally, expiration is passive but it may be assisted by nerve impulses originating in the **expiratory control centre** in the medulla which cause the internal intercostal muscles to contract pulling the ribs in and downwards.

The inspiratory control centre and expiratory control centres are antagonistic to each other, each inhibiting the activity of the other so that neither can operate at the same time. The two centres are responsible for maintaining the basic rhythm of breathing.

The rate of respiration is dependent mainly upon the carbon dioxide concentration of the blood. Any increase in carbon dioxide levels is detected by sensory receptors (chemoreceptors) located in the aorta and carotid arteries which inform the medulla of the need to increase the breathing rate. Carbon dioxide also has a direct effect on the respiratory centres of the medulla. These sensory messages are backed up by other receptors which inform the medulla of increases in temperature and decreases in oxygen levels.



Tidal volume

This is the volume of air breathed in and out in a single breathing cycle. During normal quiet breathing at rest, a healthy, active mature male of average height would have a tidal volume of about 500 cm^3. Of this 500 cm^3, about 350 cm^3 reaches the alveoli where it mixes with the **stationary air** which is not moved in tidal breathing at rest, and where gaseous exchange occurs. The remaining 150 cm^3 fills the pharynx, larynx, trachea, bronchi, and bronchioles, which compared to the alveoli are poorly supplied with blood capillaries, so that very little, if any, gaseous exchange occurs here. This space where no gaseous exchange occurs is known as the anatomical **dead space**, and the air that occupies it as the **dead air volume**.

By breathing in as deeply as possible an extra volume of air, in addition to the tidal volume and the stationary air, can be taken into the lungs. This is the **inspiratory reserve volume** and can be up to 2000 cm^3. By breathing out as forcibly as possible after returning to normal breathing, it is possible to expel some of the stationary air in addition to the tidal volume. This is known as the **expiratory reserve volume** and can be up to 1500 cm^3. However the lungs cannot be emptied entirely, otherwise they would collapse, and this remaining air is known as the **residual volume** which can be up to 1500 cm^3.

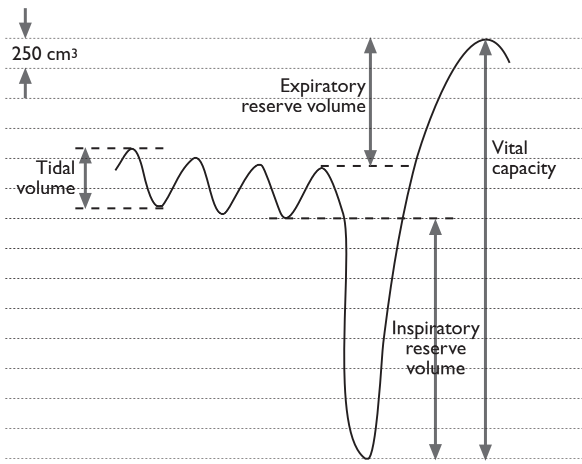
Vital capacity

This is the sum of the inspiratory reserve volume, the tidal volume, and the expiratory reserve volume. The vital capacity represents the maximum total amount of air that can be moved into and out of the lungs by one inhalation and one exhalation, and is about 3000cm^3 - 4000 cm^3 in the adult male.

These volumes and the lung capacities vary considerably between individuals. They are generally smaller in females than in males, due to smaller average body size in females, and correlate closely with body size, height and surface area up to age 25. Smoking and associated lung diseases can considerably reduce lung volumes and capacities.

◆ CHECKPOINT SUMMARY

- The thorax is defined by the rib cage and its associated intercostal muscles, and the diaphragm.
- A system of air tubes; the trachea, bronchi and bronchioles form the 'bronchial tree' supplying the air sacs (alveoli) of the lungs.
- Inspiration occurs when the intercostal muscles contract raising the rib cage, and the diaphragm contracts and flattens, increasing the volume and decreasing the pressure within the thorax below that of the external air pressure, resulting in the entry of air.
- The pleural fluid between the two pleural membranes lubricate the movement, and keep the lungs inflated against the wall of the thorax. Surfactants secreted inside the alveoli lower their surface tension and decrease their risk of collapse.
- Expiration at rest is passive, as the intercostal muscles and the diaphragm relax and the tissues of the thorax recoil as a result of their elasticity.
- The volume of air that is breathed during a complete breathing cycle of one breath in and one out is known as the tidal volume. Breathing becomes deeper as well as more rapid with exercise, and expiration becomes active.
- The vital capacity is the total amount of air that can be breathed with the deepest possible breath in and the deepest possible breath out.
- Breathing is controlled by the respiratory centre in the brain which receives stimuli from chemoreceptors in the blood vessels detecting the level of carbon dioxide, oxygen and pH in the blood, and stretch receptors in the lungs.



This trace does not show the total lung volume and residual volume, which are not easily measured. With increasing age the residual volume increases from about 20% of the total lung volume to more than 30%.

Alveoli

Alveoli or air sacs make up the mass of the lungs. The ends of the bronchioles terminate in alveolar ducts which lead to the alveoli where gas exchange occurs. Although each alveolus is very small, the large numbers of alveoli provide an enormous surface area for gas exchange.

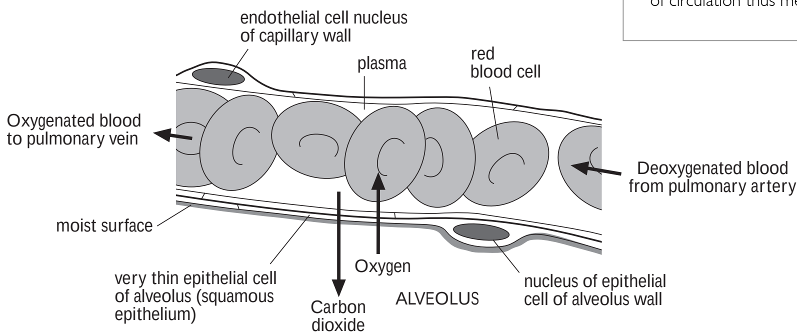
Each alveolus is surrounded by a net of capillaries which together form the **alveolar-capillary complex**. As this name suggests, the endothelium of the capillaries is attached to the thin squamous epithelium of the alveolus via a shared basal membrane. The air inside the alveolus and the blood in the capillaries is thus separated by a distance of just the thickness of two layers of cells. This is one feature that helps rapid diffusion of oxygen from alveolus to blood and carbon dioxide from blood to alveolus. Other features include the large surface area already mentioned, and the steep diffusion gradients which are maintained between the blood and the alveolus due to the constant movement of the blood and the constant ventilation of the lungs.

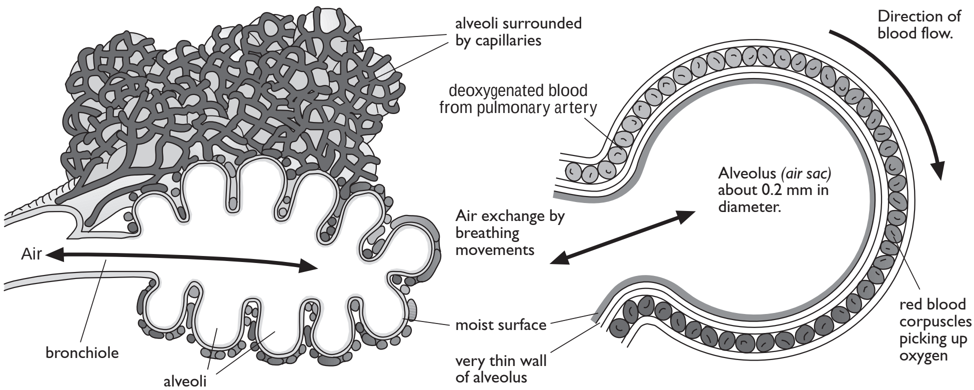
The presence of a phospholipid material called **pulmonary surfactant** acts like a detergent, reducing the surface tension of fluids at the alveolar surface ensures that the tiny air sacs do not collapse.

◆ CHECKPOINT SUMMARY

- ◆ Gas exchange occurs over large surface area of alveoli which is a product of their relatively small size and large number.
- ◆ Diffusion gradients of oxygen and carbon dioxide dependent upon partial pressures of gases on either side of diffusion surface.
- ◆ Diffusion surface composed of thin squamous epithelium ridged around the sandwiched capillaries, which further increases their surface area.
- ◆ Air in alveoli remains fairly constant in composition independent of breathing cycle.
- ◆ Surface water an inevitable consequence of a permeable surface exposed to air decreases diffusion of oxygen more than the diffusion of carbon dioxide.
- ◆ Diffusion gradients maintained by circulating blood and ventilation of lungs.
- ◆ As demand for oxygen increases so does steepness of diffusion gradients and speed of circulation thus meeting extra demand.

Gas exchange alveolus/capillary



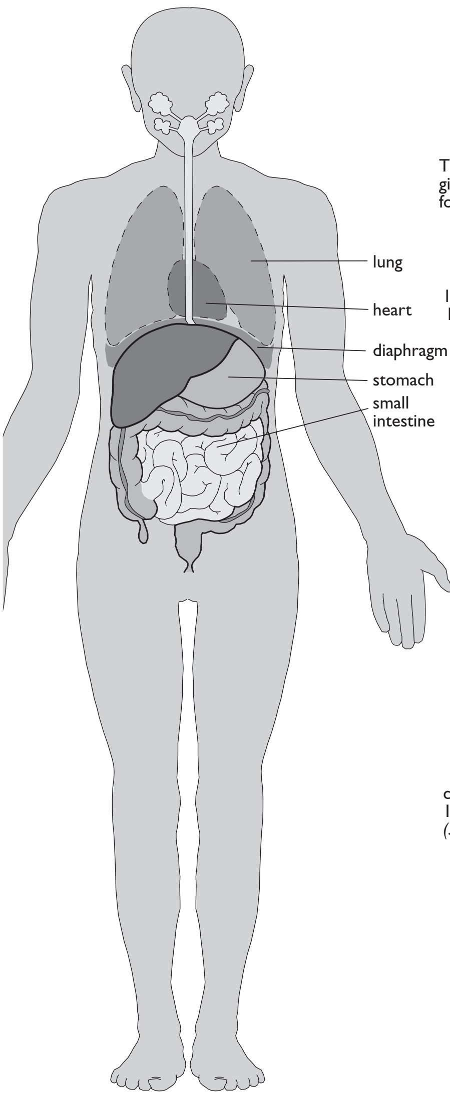


DIGESTION AND ABSORPTION

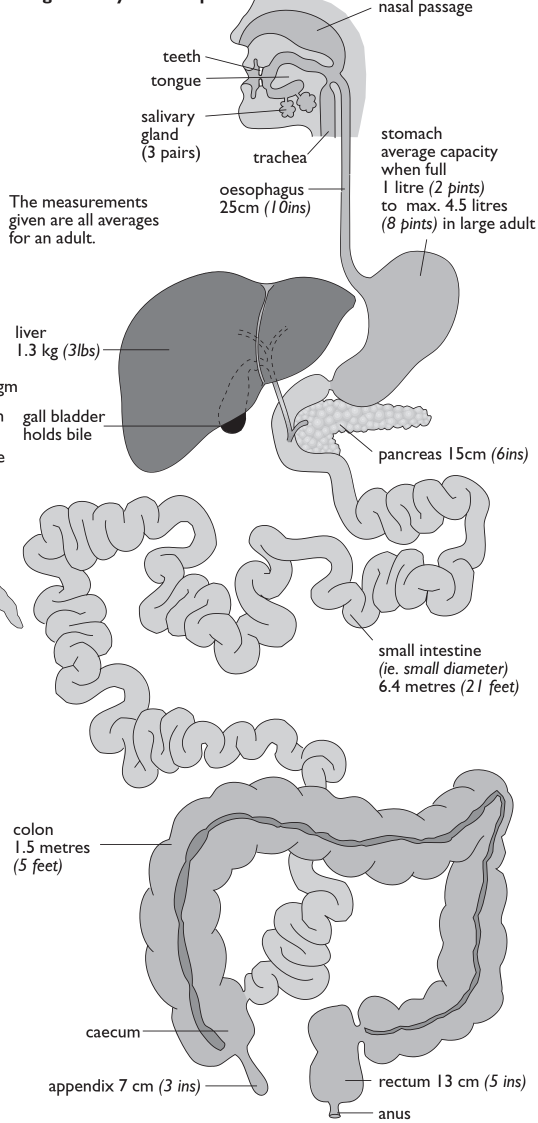
The structure of the alimentary canal

In humans, as in all other mammals, food is processed within a highly specialised alimentary canal or gut. Here the processes of digestion and absorption occur.

Digestive System in Place



Digestive System Displaced



Digestion is the process whereby large complex organic molecules are broken down into smaller, soluble molecules by enzyme catalysed hydrolysis.

Absorption is the process whereby the simple, soluble products of digestion, along with water and inorganic mineral ions and vitamins move through the wall of the gut and enter the blood and lymphatic systems for distribution around the body.

The alimentary canal forms a long, continuous tube from mouth to anus but is is divided into distinct regions with differences in structure and function. A striking feature of most regions are the modifications, at both gross and microscopic level, to create a very large surface area for digestion and absorption to occur.

Food is ingested via the mouth where both **physical** and **chemical digestion** (by enzymes) begins. Within the mouth the food is moved between a range of specialised teeth by the muscular tongue and the cheeks. Molar teeth are adapted to grind the food, incisors to cut the food and canines to piece and tear the food. As food is chewed it is mixed with saliva from the three pairs of salivary glands which contains the enzyme salivary amylase. This physical processing in the mouth has several important functions: it breaks the food into smaller pieces to make swallowing easier; it mixes the food with saliva to lubricate the food and again aid swallowing; it increases the surface area of the food for the action of enzymes and brings the food into contact with salivary amylase, the first of the carbohydrase enzymes. This begins the digestion of starch to maltose.

Movement of food along the gut.

Food is not moved through the gut by the forces of gravity: it is possible to swallow food and maintain normal movement of food through the gut whilst standing on your head! Instead the movement relies on smooth muscle in the muscularis externa (see below) of the gut wall. The muscles are controlled by the nerves of the autonomic nervous system (the branch of the nervous system which controls the basic processes of the body) which run through them. Along with hormonal signals these regulate the speed of movement of food through the gut and also allow the gut to move the food around as it goes.

The movement of food along the gut from the oesophagus towards the anus is known as **peristalsis**. Moving the food around within a region of the gut to allow it to be mixed with enzymes and other secretions hence aiding digestion and absorption is known as **segmentation**.

Peristalsis relies on two layers of muscle within the gut wall: the inner circular muscles and the outer longitudinal muscles contracting against the material in the gut lumen. Although the process is really continuous, an individual wave can be considered in two stages. Firstly contraction of the longitudinal muscle and relaxation of the circular muscle leads to a widening of the lumen and shortening of the section of gut. Secondly relaxation of the longitudinal muscles and contraction of the circular muscles behind a bolus of food leads to a an elongation of the gut section and a constriction of the gut lumen. Between them these moves have the effect of squeezing the gut contents together and then pushing them along the gut. (A similar effect is achieved in trying to move toothpaste up a tube. When food is present 10-12 such waves occur in the duodenum each minute with a smaller number (3-4) in the colon.

The histology of the ileum (small intestine) wall

The ileum, the longest part of the small intestine is where the majority of digestion and absorption of food (proteins, fats and carbohydrates) takes place. In view of this the wall layers of this region of the gut are highly specialised for these functions.

In the ileum, as in all parts of the alimentary canal, the wall of the gut is composed of four layers: the innermost mucosa, submucosa, muscularis externa and outermost serosa.

Mucosa. This innermost layer lines the gut lumen consists of epithelial cells overlying connective tissue and a thin layer of muscle. The epithelial cells have a range of secretory and absorptive functions in different gut regions. In all regions the mucosa contains numerous lymphocytes (white cells) to help protect from harmful foreign substances.

Submucosa. A layer of dense connective tissue containing blood vessels, lymphatic vessels and nerve fibresl. The role of the capillaries and the lymphatics is to absorb the products of digestion and soluble nutrients and transport them away from the gut.

Muscularis externa. Consists in most regions of an outer longitudinal muscle layer and an inner circular muscle layer. Together these aid movement of food within and through the gut by peristalsis. Nerves fibres run through the muscle layers to control the movements of the muscles.

Serosa. An outer layer of squamous epithelial cells forming a membrane which contributes to the support of the gut in the abdominal cavity.

The submucosa and mucosa layers of the ileum form folds which increase the surface area for the absorption of food and slow the movement of food through this region. The mucosa forms finger like villi (0.5-1mm in height) which greatly increase the surface area.

Each villus contains blood capillaries to absorb small molecules such as glucose, and a lymphatic capillary (the lacteal) to absorb fats. A thin muscle layer helps the villus to move and hence come into contact with digested food molecules.

The cells of the villus are also specialised. Most bear surface projections called microvilli further increasing the surface area for absorption. Some of these microvilli have digestive enzymes attached to the cell membrane. Goblet cells on the villi secrete mucus to aid lubrication of food.

Cells found in the crypts of Lieberkuhn between the villi secrete a fluid containing mucus, salts and antibacterial substances. Some enzymes are released by the breakdown of cells at the tips of the villi.

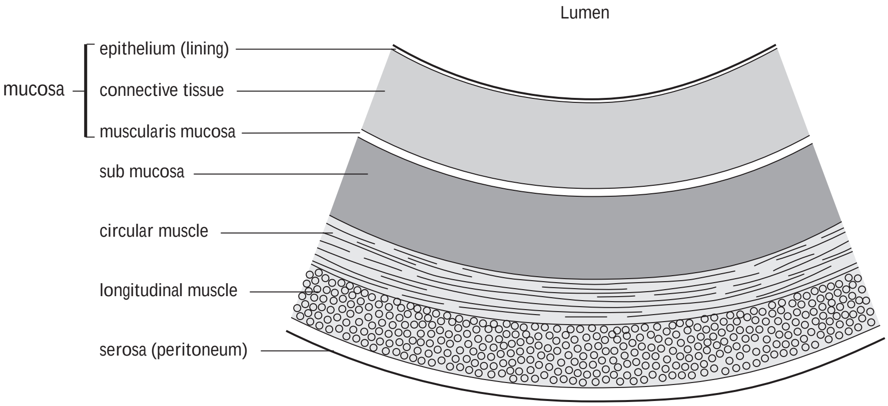
Mucus and an alkaline fluid to neutralise the acid chyme of the stomach are secreted in the duodenum by the Brunner's glands located in the sub mucosa.

The muscularis externa in this region is responsible for peristalsis and segmentation as in other gut regions.

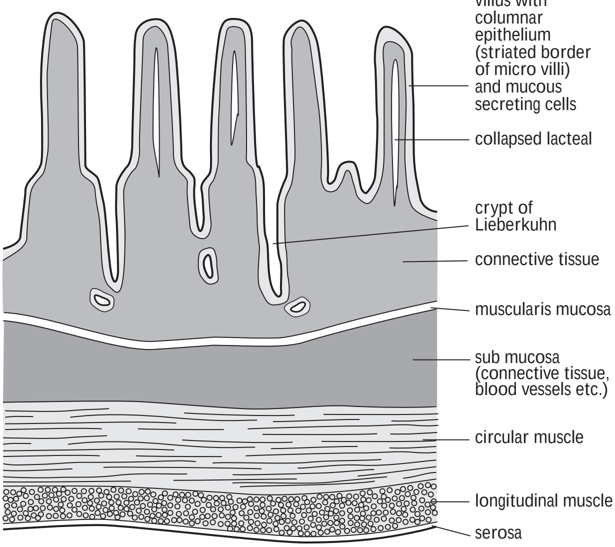
◆ CHECKPOINT SUMMARY

- Food is masticated by the teeth and the tongue to increase the surface area for digestion and to mix it with saliva for ease of swallowing.
- The smooth muscle moves the food through the gut by autonomic waves of contractions (peristalsis).
- The main regions of the gut are, the mouth (buccal cavity), oesophagus, stomach, duodenum, ileum, colon, and rectum.
- From the oesophagus to the rectum the wall of the gut is comprised of four layers: the innermost mucosa, submucosa, muscularis externa and outermost serosa. These layers are modified in each region in accordance with its function.
- The oesophagus is lined with stratified epithelium. This is several layers of cells thick and protects underlying structures from damage. Mucous glands secrete mucus to lubricate the food, and thick layer of smooth muscle pushes food down by peristalsis.
- The stomach wall is folded and contains gastric glands which open into gastric pits. There are three types of secretory cells in these glands: mucus secreting cells, oxyntic cells secreting hydrochloric acid and chief cells secreting pepsinogen (later converted to the pepsin). Smooth muscle mixes and moves food into the small intestine

General plan of tissues of alimentary canal



T.S ileum



◆ CHECKPOINT SUMMARY

◆ The small intestine submucosa and mucosa form folds and villi which increase the surface area for the absorption of food and slow the movement of food.

◆ Goblet cells secrete mucus whilst Paneth cells found in the crypts of Lieberkuhn between the villi secrete antibacterial lysosome.

◆ Each villus contains blood capillaries to absorb all nutrients, and a lymphatic capillary (the lacteal) to absorb fats. The cells of the villus bear surface projections called microvilli.

◆ Brunners glands are restricted to the duodenum and secrete mucus and an alkaline fluid to neutralise the acid chyme.

◆ The large intestine consists of the colon where most water is absorbed, the caecum and appendix which are much reduced (vestigial) in humans, and the rectum into which faeces move before defaecation.

The digestion and absorption of carbohydrates.

Up to 70% of the human diet consists of carbohydrates. A small proportion of these are taken as simple sugars (e.g. fructose in fruit) which do not require digestion, but the majority is in the form of starch, a large complex polysaccharide requiring digestion by enzymes. Non-starch polysaccharides, mainly cellulose, are also eaten but provide no nutrients for humans since they cannot be digested, but act as bulk (roughage) which provides resistance for the contraction of the muscular walls in peristalsis.

Carbohydrate digestion begins in the mouth where the enzyme salivary amylase begins to hydrolyse the 1-4 α-glycosidic bonds and digests starch to maltose (a disaccharide). When food reaches the stomach the action of this enzyme persists for a while but is soon inhibited by the acid conditions.

The bulk of carbohydrate digestion occurs in the small intestine. Pancreatic amylase, produced by the pancreas and secreted into the duodenum continues the digestion of starch to maltose. The alkaline salts in the pancreatic juice provide the optimum pH (8.5) for pancreatic amylase to function. The release of pancreatic juice and pancreatic enzymes is stimulated by the hormones cholecystokinin (CCK) and secretin which are released in response to the presence of food in the gut.

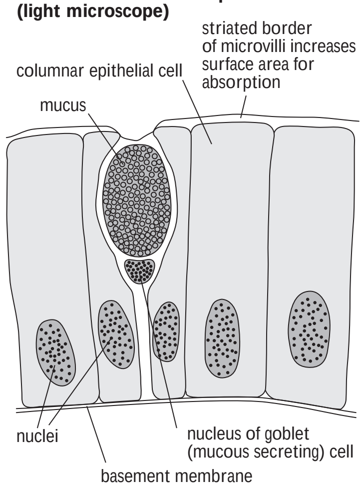
Maltose is digested to glucose by the enzyme maltase which is embedded in the membrane of the microvilli of the mucosa. The glucose is then taken into the epithelial cells of the mucosa by active transport and passed into the bloodstream by facilitated diffusion.

In addition to maltase other disaccharide digesting enzymes are found on the surface of the microvilli. Here sucrase breaks down sucrose to form glucose and fructose, and lactase breaks down lactose to form glucose and galactose. Of these monosaccharides glucose and galactose are taken up into the cells by active transport whilst fructose moves in by facilitated diffusion.

All monosaccharides pass through the single layer of epithelium and into the blood capillaries to be transported to the liver.

The table below shows the sites of production, sites of action and function of some of the main groups of enzymes involved in carbohydrate digestion.

Detail of the intestinal epithelium (light microscope)



Name of enzyme	Site of production	Site of action	Function
Salivary Amylase	Salivary glands of mouth	Mouth	Digest starch to maltose
Pancreatic amylase	Pancreas	Lumen of small intestine	Digest starch to maltose
Sucrase	Epithelial cells of ileum	Ileum	Digest sucrose to glucose and fructose
Lactase	Epithelial cells of ileum	Ileum	Digest lactose to glucose and galactose
Maltase	Epithelial cells of ileum	Ileum	Digest maltose to glucose

2B.2
Transport Systems

Content

Transport systems

- The need for transport systems in relation to size and surface area to volume ratio
- The concept of mass flow and the movement of molecules within organisms

Transport in flowering plants

- The structure of the vascular tissues; xylem tissue composed of vessels, tracheids, fibres and xylem parenchyma
- The role of vessels in relation to transport
- Phloem tissue composed of sieve tube elements, companion cells, phloem fibres and phloem parenchyma
- The role of sieve tube elements and companion cells in relation to transport

Movement of water

- The structure of a dicotyledonous root
- The uptake of water and its transport across the root to the xylem
- The way in which water is moved through the plant; the apoplast, symplast and vacuolar pathways; the role of the endodermis
- The structure of vessels in relation to the cohesive and adhesive forces of water and their contribution to the movement of water through the plant
- The functioning and roles of the transpiration stream; roles of stomata
- The effect of different environmental conditions on the transpiration stream

Movement of nutrients

- The roles of diffusion and active transport in the uptake of mineral ions by roots
- The transport of mineral ions through the plant
- The translocation of organic solutes
- The difference between the transport of water and organic solutes
- The structure and arrangement of sieve tube elements, companion cells and transfer cells in relation to the movement of organic solutes.

continued....

Transport in mammals

- The functions of the circulatory system in the transport of respiratory gases, metabolites, metabolic wastes and hormones.
- The double circulatory system.
- The structure of the mammalian heart and coronary circulation.
- The cardiac cycle; myogenic stimulation; coordination of the cardiac cycle.
- The structure and roles of arteries, veins and capillaries

Blood and body fluids

- The composition of blood as plasma and blood cells, including erythrocytes and leucocytes (neutrophils, eosinophils, monocytes and lymphocytes).
- The structure of erythrocytes and their role in transport.
- The roles of leucocytes in phagocytosis and secretion of antibodies.
- The transport of oxygen and carbon dioxide.
- The roles of respiratory pigments (haemoglobin, fetal haemoglobin and myoglobin).
- Dissociation curves of haemoglobin and the Bohr effect.
- The interchange of materials between capillaries and tissue fluid, including the formation and reabsorption of tissue fluid.

TRANSPORT SYSTEMS

Unicellular organisms and small multicellular organisms have a large surface area to volume ratio, which means that most cells are close enough to the external medium for diffusion to be sufficient for the exchange and internal transport of substances. For example the uptake of oxygen and nutrients, and the elimination of waste products. Therefore there is no need for specialised transport systems.

The larger a living organism is, the smaller its surface area to volume ratio is likely to be. All large multicellular organisms require a transport system to carry substances from the specialised organs located at the source of their nutrient and oxygen supply to the most remote of their tissues where the materials are being utilised (the sink). In many animals the mass flow of fluid (blood) is achieved by pumping hearts and blood vessels, and in plants with vascular tissue (xylem and phloem) it is achieved by water potential and pressure gradients.

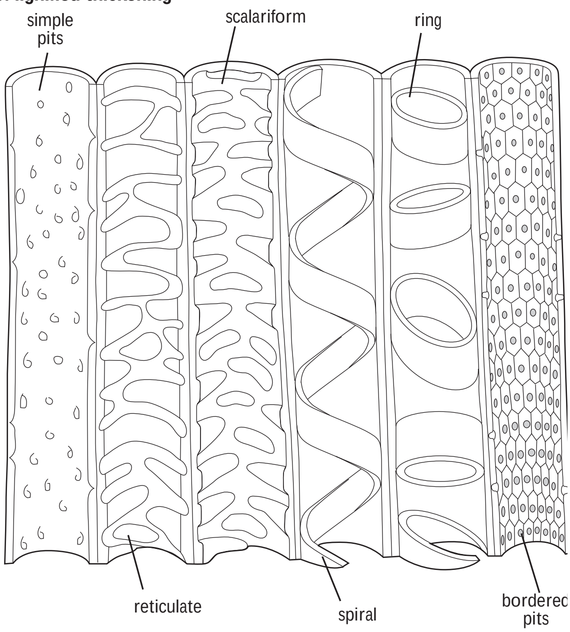
At the interfaces between the mass flow transport fluid and the external environment, and the fluid and the tissues movement of molecules is by diffusion and/or active transport occurs across cell surface membranes.

TRANSPORT IN FLOWERING PLANTS

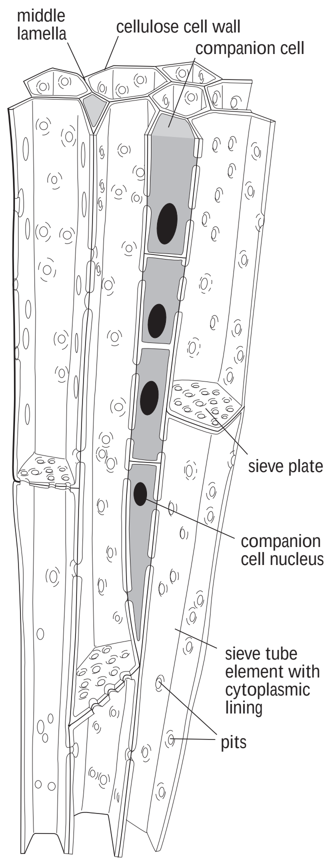
The structure of the vascular tissues

The vascular (transport) tissues in flowering plants are made up of xylem elements (vessels and tracheids) which transport water and inorganic nutrients, and phloem elements (sieve tube elements and companion cells) which transport sugars and other organic substances. Both xylem and phloem tissue also contain fibres (supporting cells) and parenchyma (packing cells).

Xylem vessels showing different types of lignified thickening



Phloem Cells



Xylem vessels have thickened lignified walls and no living contents, and form tubes in which water travels from the roots to the leaves. Lignin is a tough, hard, waterproof substance, and lignified tissue makes up what is commonly known as 'woody tissues' or 'wood'. Lignin is waterproof, and this ensures that the water is restricted to the large clear lumen which is produced as a result of the death of the living contents. The strong lignified walls can also withstand the negative pressures which exist inside the the xylem elements as a result of the upward pull of the transpiration stream. The walls are pitted to allow for passage of water through the lignified walls between neighbouring elements of the xylem. In vessels most of the cross walls that were originally present between vessel elements break down, leaving long clear, uninterrupted tubes (up to a metre or more long) with diameters ranging from 20 -600 μm, presenting much less resistance to water movement.

Phloem is made up of living sieve tube elements and their companion cells. Sieve tube elements are elongated cells 150 - 1000 μm long with a diameter of 10 - 50 μm which lose their nucleus in the process of maturation, and whose end walls develop into sieve plates with numerous pores. This allows for the passage of materials up and down the long columns of sieve tube elements which run between the roots and the leaves in the vascular tissue. Each sieve tube element is associated with up to six companion cells along its length. These companion cells do have nuclei in their dense cytoplasm, and are thought to exert some regulating action on the sieve tube elements.

◆ CHECKPOINT SUMMARY

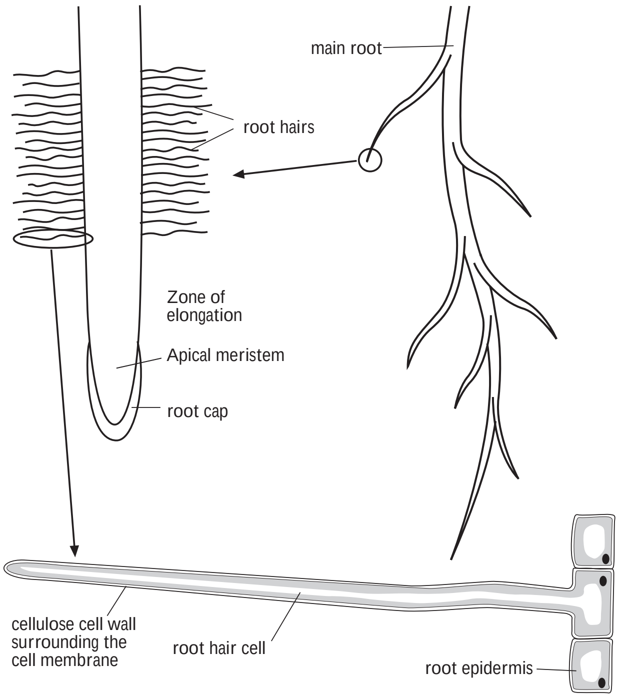
- ◆ Surface area increases with increasing size but the surface area to volume ratio decreases.
- ◆ SA/V increased by flattened body shapes and structures.
- ◆ Where SA/V sufficiently large, simple diffusion suffices for exchanges with environment and internal transport.
- ◆ Discussions of development of transport systems also involve level of complexity of organism.
- ◆ Development of transport systems involve the mass flow of fluids.
- ◆ Development of transport systems involve development of specialised exchange surfaces with large surface areas.
- ◆ Diffusion still important in all exchanges, but not in transport throughout volume of organism.
- ◆ Xylem tissue is composed of vessels, tracheids, fibres and xylem parenchyma.
- ◆ Vessels have lignified walls with pits, empty lumen, reduction of cross walls, diameters range from 20 - 600 mm, and they can be up to a metre long.
- ◆ These elongated empty elements are well adapted to the rapid transport of water, offering little resistance to flow of water in transpiration stream.
- ◆ Xylem tracheids are very similar to vessels except they have pitted cross walls at regular intervals, and they are smaller in cross section. They are also used in the transport of water.
- ◆ Fibres are elongated narrow lignified elements for support.
- ◆ Xylem parenchyma are living cells which occur in the medullary rays and act as food storage regions.
- ◆ Phloem tissue is composed of sieve tube elements, companion cells, phloem fibres and phloem parenchyma.
- ◆ Sieve tube element have cellulose cell walls, sieve tube plates at regular intervals, and living contents but no nuclei. They are involved in the transport of organic compounds, mainly sucrose.
- ◆ The companion cells do have nuclei and play some role in the functioning of the sieve tube elements.
- ◆ Phloem fibres and phloem parenchyma are found associated with the sieve tubes and companion cells in the vascular bundle.

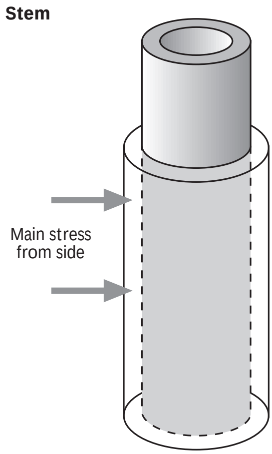
MOVEMENT OF WATER

Root structure

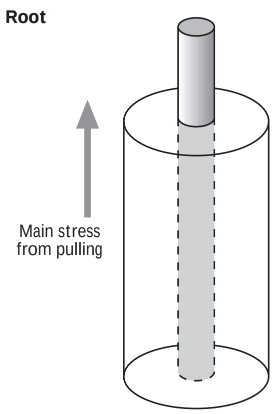
The source of water and inorganic nutrients for plants is the soil. Plant roots are specialised to provide a large surface area for the absorption of water and inorganic ions whilst securing the plant in the ground and protecting it from the pulling forces exerted as a result of the action of the wind on the stem and leaves.

The uptake of water and ions occurs only at the root hairs, situated just behind the root tips of newly formed root branches. The hairs are extensions of single, thin walled, epidermal cells. Individually they have a large surface area to volume ratio, and collectively they create a huge surface area for exchanges with the soil.





Vascular tissue forms a strengthened cylinder which resists bending



Vascular tissue forms a strengthened inner core which resists pulling action

The internal anatomy of roots differs from that of stems in a number of respects, notably the arrangement and position of the vascular tissues (xylem and phloem). As xylem has an important structural and supporting role, its distribution in the root, stems and leaves reflects the mechanical stresses endured by the particular region. In dicotyledonous plant stems, it is arranged in a cylindrical fashion, giving resistance to bending forces created by the wind. In the roots it is concentrated in the centre, resisting pulling forces. (It is interesting to note that aquatic flowering plant species adapted to growing in flowing currents have the stem vascular tissue in the centre, as this best resists the pulling strain of the currents.) In the leaf veins, it ensures that the leaf is supported in a position favourable to photosynthesis.

Another difference between the anatomy of roots and stems is that the root has a cylinder of specialised cells, the **endodermis**, enclosing the central vascular tissues. This had an important role in transport, as you will see later, and crucial to that role is the ring of waterproof thickening (Casparian strip) which seals its cell walls and ensure that all materials transported from the soil solution to the xylem pass through the cytoplasm of the endodermal cells.

The uptake of water and its transport across the root to the xylem

Water entering the root may travel along three pathways.

The **apoplastic** pathway involves water moving through the porous cellulose walls of the cells of the root cortex. It is pulled in by the transpiration stream (see below). However, the waterproof Casparian strip gives the endodermis control over this process, effectively blocking the apoplastic route and ensuring that all water passes through the cytoplasm of the living passage cells of the endodermis.

The **symplastic** pathway involves water moving through the cell membranes and cytoplasm of the cells of the cortex of the root down a water potential gradient by osmosis.

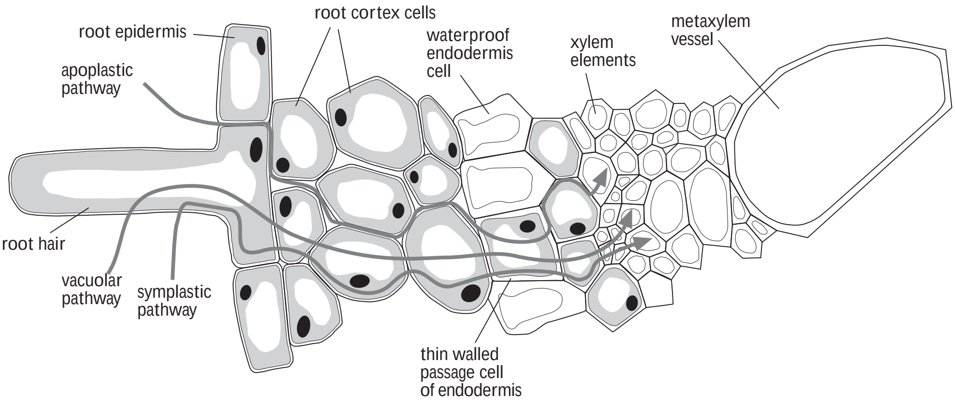
The **vacuolar** pathway involves water moving through the cell membranes and cytoplasm of the cells of the cortex of the root, and through the vacuolar membranes and vacuoles, down a water potential gradient by osmosis

The apoplastic pathway offers the least resistance to the movement of water, as the water does not have to pass through any living membranes or cytoplasm (except at the endodermis), and most water passes across the root this way. The symplastic and vacuolar pathways are routes of high resistance as the water must pass through the many membranes and the cytoplasm, and are mainly involved in the supply of water to individual root cortex cells from the main flow of water streaming across into the xylem.

◆ CHECKPOINT SUMMARY

- ◆ Roots provide anchorage, and take up water and inorganic ions from the soil solution.
- ◆ As roots have to resist predominately pulling strains, the vascular (transport) tissue containing the phloem and woody xylem is found in the centre.
- ◆ Uptake of water and ions from the soil solution is via the root hairs which present a large total surface area for uptake.
- ◆ The endodermis is a cylinder surrounding the central vascular tissue, it is composed of cells the walls of which become impregnated with impermeable waterproof suberin and eventually die, except for living passage cells.
- ◆ Water can enter and travel through the root along three pathways; the apoplast, symplast and vacuolar pathways.
- ◆ The endodermis acts as a barrier to prevent the loss of accumulated ions in the root, and to force the water and ions being taken up to pass through the contents of living cells at least once in its passage across the root.
- ◆ The apoplast pathway is in the porous cellulose cell walls, and the water is pulled directly through by the transpiration stream, and it only passes through a living membrane in the passage cells of the endodermis.
- ◆ The symplast pathway involves water entering into the cytopasm of a root hair cell and passing in the cytoplasm from cell to cell via the plasmodesmata.
- ◆ The vacuolar pathway involves water passing down a water potential gradient from vacuole to vacuole, the pathway of greatest resistance.

Passage of water through the root



Pathway and mechanism of water transport from roots to leaves

Transpiration is the loss of water from the leaves by evaporation. Although a tiny amount of water may be lost directly through the 'waterproof' cuticle of the upper and lower epidermis of the leaves, virtually all of it occurs through the stomata of the leaves when they are open. Transpiration is an unavoidable consequence of gaseous exchange. As stomata open in the light to take in carbon dioxide for photosynthesis, so water vapour escapes. However, transpiration does have some beneficial effects, it provides the force for the mass flow (transpiration stream) bringing water and mineral ions to the leaves from the roots. It also exerts a cooling effect. Under very hot conditions, however, when the cooling effect is most required, the stomata tend to close, thus stopping transpiration.

Transpiration provides the main force for water transport from root to leaf. The greater bulk of water is pulled in directly by the transpiration stream, acting through a continuous system of water between the soil solution and the xylem in the porous cellulose cell walls of the cells, the apoplastic pathway.

Water and dissolved solutes move up the stem in the xylem tissue. The generally accepted explanation of the mechanism for the upward transport of water is that known as the **cohesion-tension mechanism**. It is based on purely physical forces and does not involve the activities of living cells. Evaporation through the leaf pores or stomata causes a gradient of water potential across the mesophyll cells of the leaf, and a direct force on the water in the porous cellulose cell walls which causes water to be withdrawn from the xylem. Cohesive forces between water molecules result in a column of water being drawn up the plant in the xylem as the water evaporates from the leaves. This transpiration 'pull' generates a tension which results in the sap being under a negative pressure. It can produce a measurable decrease in stem diameter (and even trunk diameter) when transpiration is high. The strong lignified walls of the xylem vessels withstand this negative pressure which tends to collapse the tubes. The water column is supported and prevented from falling back down under gravity in the xylem elements by adhesion of the water to the smooth lignified walls of the xylem vessels. A continuous water column is necessary for this mechanism, and any breakages caused by storm damage or freezing (which forces air out of solution) can be by-passed via the system of lateral pits in the lignified walls. In woody plants only the most recently formed 'sap wood' functions in water transport, and the remaining 'heartwood' is used as a depository for waste products (but is still important in support).

This mass flow of water carries along dissolved inorganic ions in solutions by 'solvent drag' and contributes to the uptake of inorganic ions from the soil solution by the plant.

Factors affecting transpiration include anything that affects the supply of water to the leaves, and the evaporation of water from the leaves. The main factors are:

Availability of soil water determines the supply of water to the plant. Any factor that decreases the availability of soil water will decrease transpiration, which eventually can lead to the stomata closing and in extreme cases to wilting of the plant.

Relative humidity is a measure of the water vapour content of the air. The diffusion of water vapour out through the stomata of a leaf only occurs when the relative humidity of the surrounding air is lower than that of the internal leaf spaces. The rate of transpiration increases with decreasing relative air humidity. Relative humidity is dependent mainly on temperature, decreasing as temperature increases. A rise of 10°C doubles the steepness of the humidity gradients from leaf to air, thus increasing transpiration.

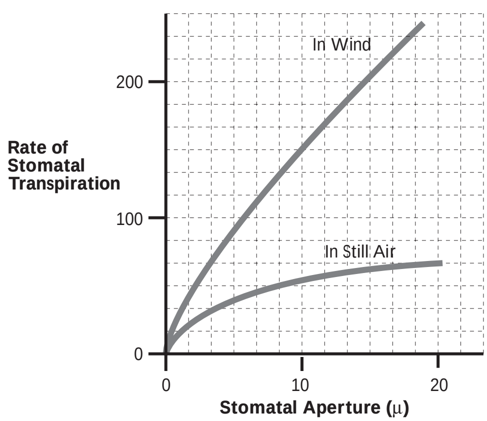
Air movements increase the rate of water loss by transpiration as molecules of water vapour are carried away from the leaf surface reducing the relative humidity of the air that is immediately surrounding it.

Temperature increase provides energy for an increase in evaporation of water from the leaf.

Light intensity exerts its main effect directly on the guard cells surrounding the stomata. These are the only cells on the surface of the leaf which possess chlorophyll, and an increase in light intensity typically results in their daytime opening and a consequent increased transpiration rate. Indirectly it will also raise the temperature of the leaf as its radiant energy is absorbed.

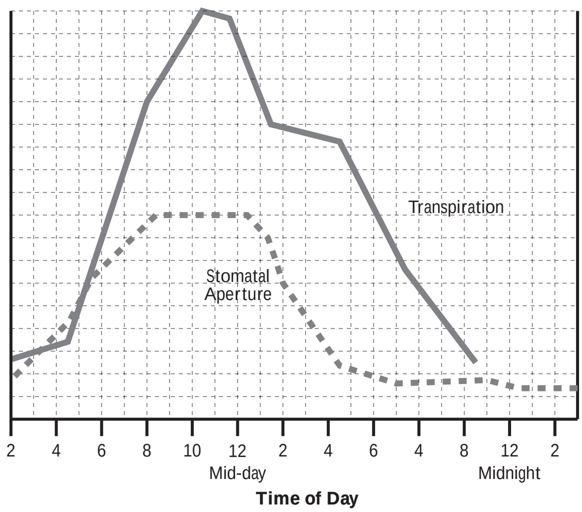
Stomatal number and size vary widely between species, typically being directly correlated with the availability of water. There are usually more stomata on the lower side of leaves. Some plants (e.g. laurel) have stomata only on the lower side. Grasses having vertical leaves have roughly equal numbers on both surfaces. On average there are about 300 per mm^2 of leaf surface.

Stomata allow the uptake of carbon dioxide for photosynthesis but at the same time they control the rate of water loss. Changes in stomatal size affect water loss more critically than carbon dioxide gain, for example if the pore size is reduced, the transpiration rate is reduced more than the rate of carbon dioxide uptake.

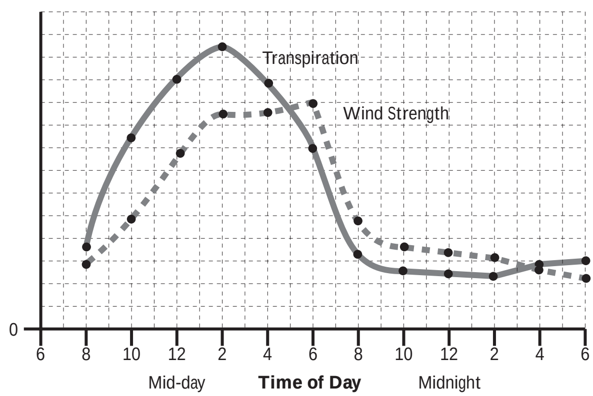


Factors affecting rate of transpiration over a 24 hour period

1 Stomatal aperture

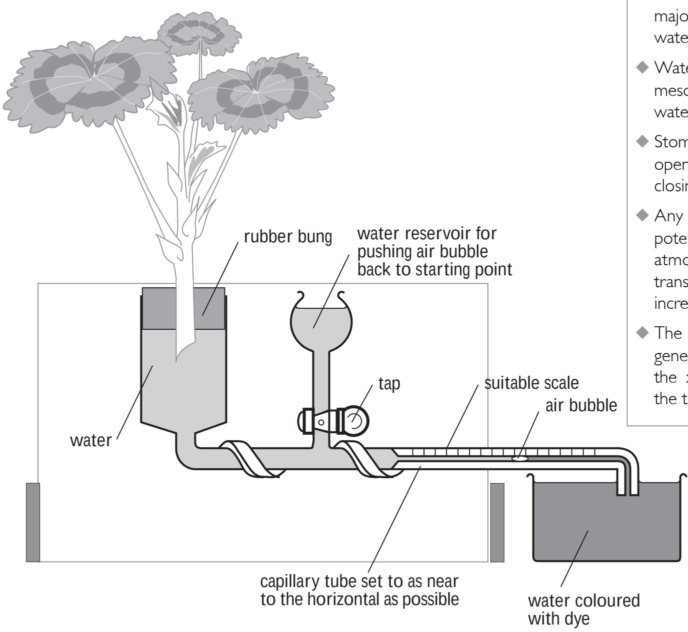


2 Wind strength



Experimental investigation of factors affecting transpiration rate

Investigations of the effect of many of these factors can be carried out using a simple piece of laboratory equipment, the potometer, in which a cut shoot is exposed to different conditions and its water uptake is measured. The rate of water uptake is assumed to be the same as the rate of transpiration, but with a cut shoot the cross sectional area of the cut stem is not as great as the surface area of roots that would normally supply water to that shoot. The transpiration rate from the shoot would therefore be greater if still attached to the rooted plant.

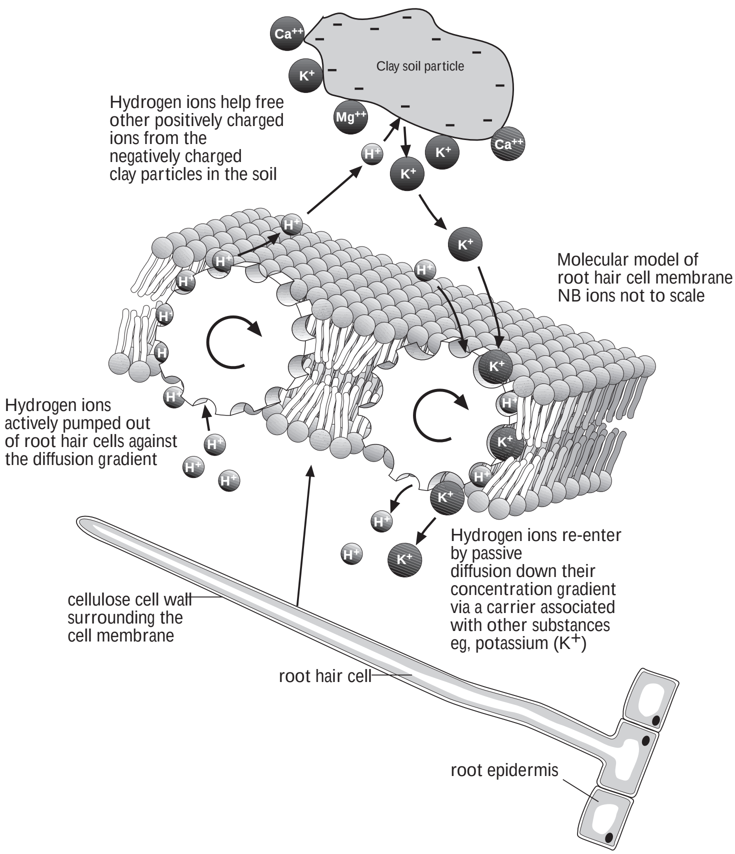


◆ CHECKPOINT SUMMARY

- ◆ The xylem vessels are adapted to the mass transport of water.
- ◆ The lignified walls are waterproof, avoiding absorption and keeping water in the lumen.
- ◆ They are strong to withstand huge negative pressures 'suction' generated by the transpiration stream as the water column is pulled up by cohesion (there is a measurable decrease in diameter of tree trunks under conditions of high transpiration).
- ◆ The smooth lignified walls also offer good adhesion for the water, thus supporting the water column as it moves up the plant.
- ◆ Pits in the walls allow for a continuous system of water to by-pass any air bubbles and breaks in the columns of water, as a result of columns of water breaking under tension or wind movements, or freezing forcing air out of solution in the xylem.
- ◆ Root hairs actively take up inorganic ions and water follows passively down a water potential gradient generating a root pressure.
- ◆ Root pressure can only account for a rise of a few metres but could be important before leaves are fully open in the spring in temperate climates.
- ◆ Once in xylem capillarity aids rise but main force is generated by transpiration at the leaves.
- ◆ Transpiration from the leaves generates the major force for the upward movement of water in the transpiration stream.
- ◆ Water evaporates from the surfaces of the mesophyll tissue in the leaves, and the water vapour diffuses out of open stomata.
- ◆ Stomata have to strike a balance between opening for carbon dioxide uptake and closing to control loss of water vapour.
- ◆ Any factor that increases the water potential gradient between the leaf and the atmosphere will increase the rate of transpiration, e.g. dry air, moving air, and increase in temperature.
- ◆ The evaporation of water in the leaves generates an upward pull on the water in the xylem vessels and tracheids, creating the transpiration stream.

Movement of nutrients

Root hair cells take up inorganic ions from the soil across their membrane by **diffusion** and **active transport**. Root hair respiration produces ATP which is used to supply energy for the active uptake of inorganic ions from the soil solution. Respiration also releases hydrogen ions (protons), which are actively pumped out of the root hair cells, setting up a transmembrane potential and creating both the directional stimulus and energy for the inward flow of nutrient ions. The exported hydrogen ions also release other positively charged ions (Na^+, K^+, Ca^{++}) from the negatively charged clay particles of the soil and make them more available for active uptake by the roots. By this means ions may be taken up by the plant against their concentration gradient.



As the root hair cells accumulate inorganic ions so a diffusion gradient is created and the absorbed ions tend to move inwards via the cytoplasmic connections (plasmodesmata) between the cells of the epidermis and cortex towards the central vascular region. The endodermal cells assist the passage of ions inwards to the xylem by a further active transport mechanism amplifying the concentration difference between the soil solution and the xylem elements in the centre of the root.

If roots are starved of oxygen, as may happen if the soil is flooded, then mineral uptake will stop, as the production of ATP in respiration for active uptake requires oxygen. This has a consequence for water transport because it is the active uptake of mineral ions which provides the gradient along which some water passively enters the root.

At night, the transpiration stream slows down or stops altogether but root hair cells continue the active uptake of ions. The xylem contents therefore become relatively more concentrated at night and, as their water potential is lowered, so water moves by osmosis out of the surrounding cells of the root cortex. This creates a positive pressure of fluid within the root xylem called **root pressure,** the effects of which can be observed by cutting the stem of a plant just above ground and measuring the force with which fluid flows out of the cut from the roots.Root pressure is not a mechanism of water transport; rather a by-product of the active uptake of ions by roots. It is very much less evident during the day when the plant is transpiring because the accumulating ions in the root xylem are quickly carried out of the plant by the transpiration stream.

Studies with radioactive tracers indicate that inorganic ions do not arrive at the leaves in the same relative proportions that they leave the root and could indicate that there is some control over their movement in the xylem. It should be noted that new xylem which is involved in the transpiration stream (sap wood) is produced by the living cambium tissue, which forms a cylinder of living tissue next to the functional xylem. It is suggested that the cambium tissue is removing and adding inorganic ions to the transpiration stream as it passes by. In addition some inorganic ions which accumulate in actively growing regions, can be mobilised to travel to newer actively growing regions in the phloem.

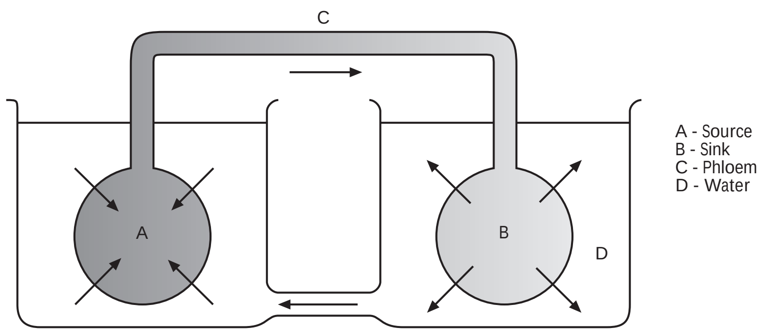
Translocation

Translocation is the name given to the energy-requiring process in which organic materials synthesised by the plants, particularly sucrose are transported in the phloem sieve tube elements. Organic substances synthesised by plants are also known as **assimilates**, as they have been synthesised (assimilated) from simple inorganic substances.

The transport of sucrose and other organic compounds occurs from the point of origin or '**source**' of the organic material to the point of destination or '**sink**'. Typically the main 'source' of sucrose is the photosynthesising leaves. **Transfer cells** found next to sieve tubes, especially in small leaf veins, have a characteristic dense cytoplasm and many organelles, and appear to be involved in transferring substances to and from the sieve tubes of the phloem. The main 'sink' is the respiring roots. However, other 'sinks' are fruits and seeds, and food storage organs e.g. tubers and bulbs, in the autumn. Tubers and bulbs can in turn act as 'sources' and the growing shoots and leaves as 'sinks' in the spring. Thus, transport of sucrose and other organic compounds in the phloem can be in two directions, unlike the xylem where transport of water is only in one direction from the roots towards the leaves. If the 'source' is in the roots and the 'sink' is in the aerial parts, then some organic material can move in the transpiration stream up the xylem.

Mechanism of transport in phloem

Diffusion is not sufficient to account for the observed rates of flow in the phloem. The pressure flow (**mass flow**) mechanism suggests that the 'source' regions have a lower water potential than the 'sinks', due to the presence of greater concentrations of solutes, such as sucrose. This causes water uptake and an increased turgor within the cells at the source. As a result of this and the fact that the two regions are in direct cytoplasmic contact, it is suggested that the organic materials are forced along the resultant hydrostatic (water) pressure gradient, for example from leaves to roots. The flow being maintained by active pumping of sugars into the sieve tube elements in the leaves by companion-transfer cells, and their removal at the 'sink' as a result of their use (e.g. in respiration or conversion to insoluble starch).



Evidence for this mechanism

Aphids (greenfly) feed specifically on living phloem by means of their long tubular mouthparts which they can insert directly into the phloem sieve tube elements. If they are knocked off whilst feeding, their mouthparts are left protruding from the phloem, and the sugary contents, referred to as 'honey dew', may exude out of the broken ends for several days, in volumes up to 100 000 times the volume of the one penetrated sieve tube element. This demonstrates that the contents of the sieve tube elements are indeed under positive pressure as the mechanism would require (in contrast to the negative pressure of the contents in the xylem elements) and that the flow is significant. On a larger and less precise scale, cut phloem in large woody plants can exude sucrose rich sap in volumes up to many litres (dm^3) per day.

Direct measurements of the pressure within the sieve tube elements indicate that the pressure gradients between sources and sinks are in the right direction and great enough to account for the mass flow of sugars over the longest distances required in the tallest trees.

Evidence against this mechanism

Evidence against this mechanism is provided by the fact that the movement is not simply from source to sink. Mature leaves kept in the dark, unable to photosynthesise and supply their own sugars for respiration, do not import sugars and eventually die. This observation supports the suggestion that the growth substance auxin is in some way involved. Mature leaves have low auxin levels, whereas virtually all 'sinks' are actively growing tissues e.g. roots, food storage organs and apical meristems (dividing cells of shoot tips) and have high auxin levels. Furthermore, when auxins are applied artificially to a region of a plant the flow of sucrose in the phloem is redirected towards it.

Observations that translocation relies on the activities of living cells, argue against the simple mass flow mechanism, which could operate more easily through dead empty elements like the xylem, as long as the loading and unloading regions were living. These observations include the following:

- translocation only occurs in young phloem sieve tube elements with actively streaming cytoplasm;
- metabolic poisons (e.g. those inhibiting respiration) inhibit translocation;
- when the phloem tissue is killed with heat or poisonous substances translocation stops;
- companion cells are metabolically active along the length of the sieve tube elements, suggesting some role in translocation.

The use of radioactive tracers and ringing experiments to determine the movement of ions and organic substances through plants

Certain substances (elements) have radioactive forms (radioactive isotopes). Radioactive isotopes have the same chemical properties as the non-radioactive form of the element, but are unstable and emit radiations known as 'radioactivity'. These emissions can be detected by a Geiger counter, and by photographic film to produce an autoradiograph, so that the presence of the radioactive isotope of an element can be located. As radioactive isotopes have the same chemical properties as the normal form, they can be used as **radioactive tracers** to trace the path of an element such as carbon (and compounds containing that element such as sucrose) through the plant.

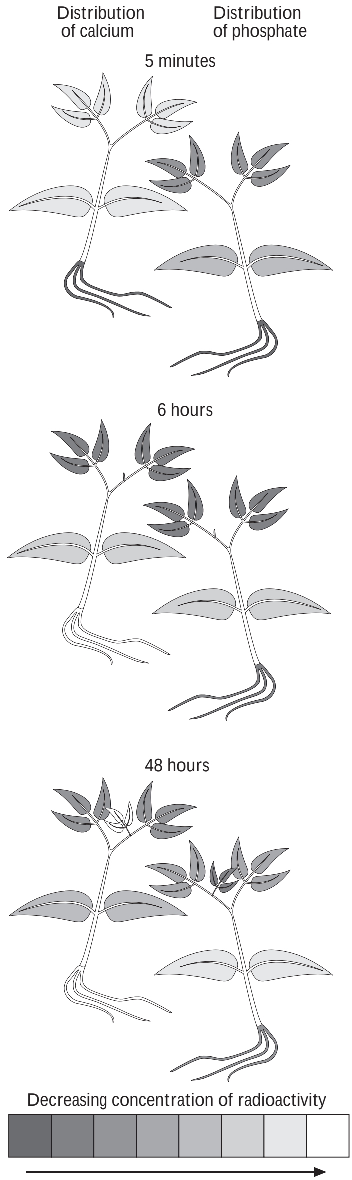
The roots and leaves of plants can be exposed to radioactive isotopes and their subsequent movement through the plant can be traced to determine the movement of ions and organic substances through plants in the xylem and phloem. As the phloem is situated outside of the xylem in woody stems, it can be removed easily by '**ringing**' leaving the central xylem intact, allowing insights into the roles of the xylem and phloem.

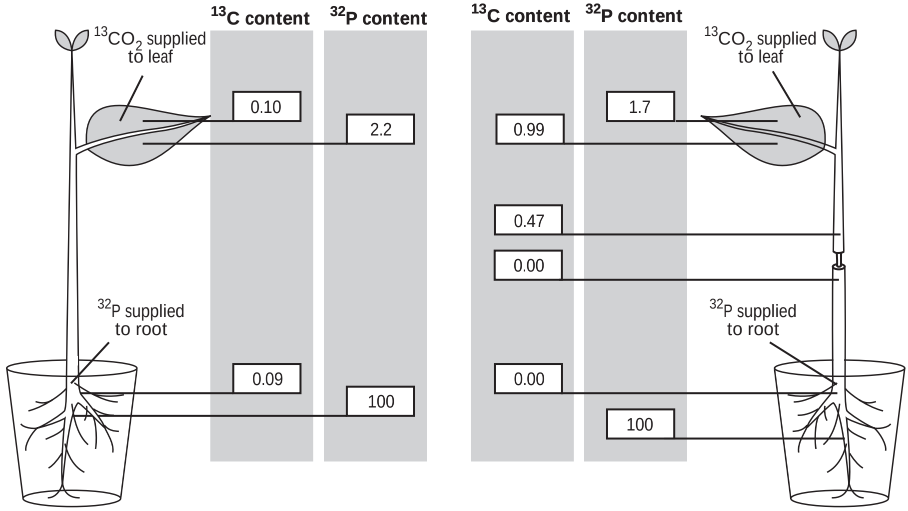
If the roots are exposed to radioactive calcium and phosphorus ions in calcium phosphate solution for an hour, and then removed to a non-radioactive solution, and pressed onto photographic film after 5 minutes, 6 hours, and 48 hours, the uptake of the ions and subsequent movement in the plant can be studied. It can be seen that the phosphate ions quickly reach the young leaves, and transfer to each batch of new young leaves as they emerge, whereas the calcium arrives more slowly in the young leaves and remains there. Ringing the stem has no effect on these movements, indicating that the movement up the plant is in the xylem. However, for the phosphate ions to move from one set of leaves to another, they must also be moved in the phloem. The different rates of arrival in the leaves indicate that the uptake and movement of the two ions in the xylem differs, not what would be expected from them being taken up by solvent drag and being swept along passively in the transpiration stream.

When leaves are exposed to radioactive carbon in carbon dioxide, the radioactivity eventually reaches the roots, but ringing the stem (removing the phloem) stops this downward movement, indicating that it is in the phloem.

Sections of the stem can be taken and autoradiographs produced, but lateral transfer occurs between xylem and phloem so the results can be inconclusive, for example when radioactive ions are taken up by the roots they appear in both the xylem and the phloem. Waxed paper barriers placed between the xylem and the phloem prevent this and the radioactive ions appear mainly in the xylem.

Radioactive tracer studies also indicate that substances move in different directions at the same time in the phloem, which would argue against the mass flow mechanism, although this could be occurring in different sieve tube elements, which would still be explicable in terms of the mass flow theory.





◆ CHECKPOINT SUMMARY

◆ Mineral ions are taken up by the root hairs, which have a large total surface area, by diffusion and active transport. Only actively growing roots absorb substances from the soil.

◆ Mineral ions are transported by solvent drag in the transpiration stream from the roots to the leaves.

◆ However, they arrive in different proportions and at different rates, indicating that the process is not simply one of being swept up by solvent drag.

◆ The cylinder of active living cambium lies next to the water transporting xylem of the sap wood, and may have a role in importing and exporting ions to and from the transpiration stream.

◆ Translocation of assimilates (organic substances synthesised in the plant by photosynthesis) e.g. sugars, amino acids, hormones, nucleic acids etc. occurs in the phloem tissue.

◆ Organic materials move from an area of manufacture (source) to an area where they are used (sink). Sucrose thus moves from the leaves (sources) to actively growing and respiring regions such as the roots, flowers, and new buds (sinks).

◆ Phloem tissue (unlike most of the Xylem) is composed of living cells and elements.

◆ Mechanism of movement still not fully understood.

◆ Mass flow mechanism postulates high hydrostatic pressure in sources and low in sinks, which results in the mass flow of sucrose in solution from sources to sinks. Transfer cells in the leaves being responsible for moving sugars into the sieve tube elements.

◆ Contents are under positive pressure but there is no clear evidence of the necessary pressure gradients.

◆ Movement occurs in both directions, although this could be accounted for by considering the mass flow mechanism in respect to single columns of sieve tube elements within the phloem tissue as a whole.

◆ Movement of assimilates is stopped if the phloem is poisoned with a respiratory inhibitor, exposed to high or low temperatures i.e. translocation is an active process, only occurring in those sieve tube elements showing cytoplasmic streaming.

◆ Ringing removes all tissues (including the phloem) outside of the xylem, and radioactive tracers e.g. ^{32}P and ^{14}C allow the movement of materials in the xylem and phloem to be detected.

◆ ^{32}P supplied to the roots will pass through the ringed region, whereas ^{14}C taken up the leaves and assimilated into sucrose will accumulate above the ring.

Transport in mammals

The living cells of the body obtain oxygen and nutrients from the fluid environment which surrounds them and they excrete waste substances into this environment. They are surrounded by a fluid medium called **tissue fluid** or extracellular fluid, with which they exchange materials. This is referred to as the '**internal environment**' and for exchange to occur between the internal and the external environment in larger organisms, specialised systems have evolved. Also essential to this process is an efficient circulatory system composed of closed blood vessels. In the mammalian circulatory system, the blood flows entirely within a virtually closed system of vessels from the heart in the arteries, arterioles, capillaries, venules and veins back to the heart (although there are invariably some small blood spaces where the blood leaves the vessels e.g. in the liver).

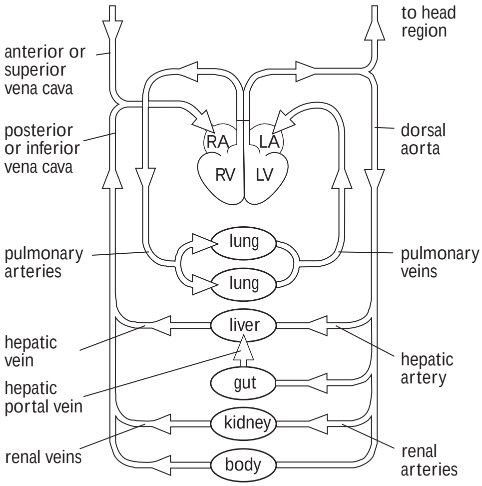
The blood transports respiratory gases, metabolites (nutrients and materials synthesised within the body), metabolic wastes (e.g. urea). It also acts as a chemical messenger service, carrying hormones from the glands where they are produced to the target organs upon which they act.

The double mammalian circulation

Closed circulations can be either single or double. In single circulation systems the blood only passes through the heart once during each complete circulation of the body. Therefore the blood passes through two sets of capillaries (e.g. in fish, the gills and the body tissues) before returning to the heart. This results in a high resistance to flow, a slow flow, and ultimately a low pressure in the tissues.

The mammalian heart has four chambers, and is divided into right and left 'halves'. Blood passes through the heart twice during each complete circulation of the body. This is referred to as a double circulatory systems. Double circulatory systems are more efficient than single systems. The blood travels from the heart to the lungs and back to the heart in the **pulmonary circulation**, and then from the heart around the rest of the body and back to the heart in the **systemic circulation**.

This arrangement means that the blood can be pumped through the capillaries of the delicate alveoli of the lungs at a lower pressure, than that of the systemic circulation in which a higher pressure is required for the circulation around the body. The lower pressure is a result of the less muscular wall of the right ventricle, and the lower resistance presented by the relative thinness of the elastic walls of the pulmonary arteries, and their arterioles. If the blood pressure was any higher in the pulmonary circulation (as it sometimes is in people suffering from hypertension or 'high' blood pressure) the lungs would be at risk of filling with tissue fluid, which would have serious consequences for gas exchange. Passage through the pulmonary capillaries further lowers the blood pressure and the return of the blood to the left side of the heart allows the left ventricle to pump the blood powerfully round the body under a raised pressure.



◆ CHECKPOINT SUMMARY

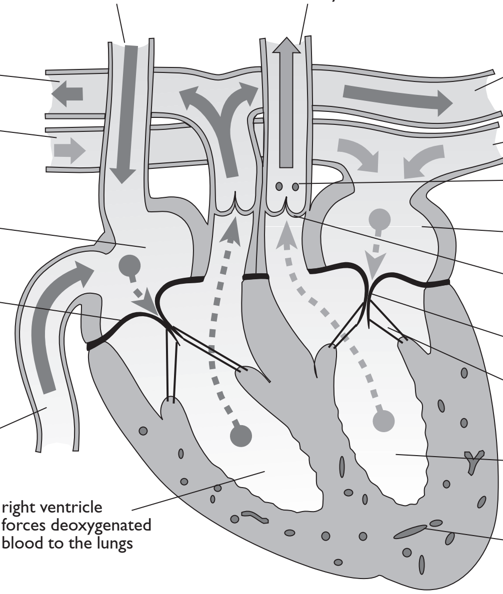
- The functions of the circulatory system include the transport of oxygen and carbon dioxide between the lungs and the tissues of the body, metabolites to and from the gut, liver and kidneys, metabolic wastes from the liver to the kidneys, and hormones from and between the endocrine glands.
- In single circulations blood only passes through the heart once on each complete circulation of the body.
- Means that blood passes through two sets of capillaries on each circulation, respiratory surface and body tissues.
- Represents large resistance to overcome before blood returns to heart, resulting in slow flow and low pressure in veins which are typically large blood sinuses to lower resistance to flow.
- Closed systems blood almost entirely restricted to vessels: arteries, arterioles, capillaries, venules, veins.
- Tissue fluid exuded to bathe tissues directly.
- Double circulation blood passes through heart twice on each circulation.
- Pressure relatively low to lungs.
- Pressure raised for systemic circulation to body giving high pressure and fast flow.

The structure of the mammalian heart and coronary circulation

The heart is situated slightly to the left of the midline of the chest, protected by the ribs and by a tough membrane (pericardial membrane) which surrounds it in a fluid filled pericardial cavity.

It is composed of four muscular chambers, two upper thinner walled atria, and two lower thicker walled ventricles. The right and left sides are divided from each other by a muscular septum. The right atrium receives blood in the venae cavae from the body, and the left atrium receives blood in the pulmonary veins from the lungs. (Note that diagrams of internal organs are always viewed from the front of the body, so that the right atrium and right ventricle appear on the left side of the diagram.)

The atria are separated from the main pumping chambers, the right and left ventricles, by flaps of fibrous tissue which act as one way valves. These atrio-ventricular valves differ from each other. The **tricuspid** valve on the right has three flaps, and the **bicuspid** valve on the left has two. These are attached to tendons and muscles which prevent them opening upwards under pressure.



Inside the entrance of the main arteries which leave the heart, the aorta and pulmonary artery, are two more sets of valves called semi-lunar or pocket valves which when filled with blood block the arteries. Immediately above the semi-lunar valve in the aorta is the entrance to the **coronary artery** which supplies the heart muscle with nutrients and oxygen. The artery spreads its branches all over the surface of the heart. Deoxygenated blood is collected into the coronary vein which empties directly into the right atrium. The heart requires its own blood supply despite being filled with blood, as the blood that it is pumping is passing through too quickly, and the heart walls are too thick for diffusion to supply the needs of the heart muscle fibres.

The walls of the atria are less muscular than those of the ventricles, and the wall of the left ventricle is more muscular than that of the right ventricle. These differences reflect the different pressures that need to be generated in the chambers. The atria only have to pump blood into the ventricles. The right ventricle pumps blood to the lungs at a relatively low pressure. The lungs are close to the heart, and too high a pressure could damage the delicate alveoli and result in the filling of the lungs with fluid. The left ventricle must generate a high pressure to pump blood right around the body.

However, it is important to remember that the volumes of the lumens (cavities) of the chambers on the right side of the heart are the same as those on the left side of the heart, otherwise the right side would not be able to supply the left side with sufficient blood.

◆ CHECKPOINT SUMMARY

- ◆ External appearance of heart shows small ‘flap-like’ atria, coronary blood vessels, fat deposits, and major vessels entering and leaving (venae cavae, pulmonary arch, and aortic arch.
- ◆ Coronary arteries arise just above the pocket valves at base of pulmonary and aortic arches, and supply cardiac muscle of theart wall with its own blood supply. Coronary veins return blood to right atrium.
- ◆ Internal structure of two atria and two ventricles separated by bicuspid and tricuspid valves.
- ◆ Chordae tendinae and muscles prevent back-opening of bicuspid and tricuspid valves when ventricles contract.
- ◆ Atria walls thinner than ventricle walls.
- ◆ Pocket valves at base of pulmonary artery and main aorta prevent backflow of blood into ventricles when they relax.
- ◆ Left ventricle wall thicker than right ventricle wall to pump blood around body.
- ◆ Right ventricle wall thinner than left ventricle wall as only has to pump blood via pulmonary circulation around lungs, reduced pressure also prevents formation of tissue fluid in alveoli.
- ◆ Volumes of both left and right ventricles the same as right ventricle supplies the left ventricle with blood via the lungs and left atrium.

The cardiac cycle

The sequence of events that occurs during the filling and emptying of the heart is known as the cardiac cycle. At a rate of 70 beats per minute (bpm) the complete cycle takes about 0.86 seconds. It is a continuous sequence of events that occurs simultaneously on the left and right sides, but for the purposes of explanation it is convenient to consider it as occurring in a series of stages.

There is a point in the cardiac cycle when all the heart valves are shut, which can be taken as the starting point of the cardiac cycle.

Blood returning under low pressure in the main veins (superior and inferior venae cavae) from the upper and lower body enters the right atrium, and at the same time blood returning from the lungs in the pulmonary veins enters the left atrium.

The atria fill with blood, and the rising pressure of the blood in the atria pushes open the tricuspid and bicuspid valves, and both ventricles begin to fill.

As the heart fills with blood both atria contract (**atrial systole**) forcing even more blood into the ventricles. These are now stretched, and they both contract (**ventricular systole**) forcing the blood upwards.

This upsurge of blood forces the tricuspid and bicuspid valves shut. These valves are prevented from back-opening into the atria by tough tendons, which are held taut by contraction of the papillary muscles to which they are attached. The closing of these valves makes the first heart sound (described as 'lub').

The blood is thus forced along the pulmonary artery to the lungs, and along the main aorta to the rest of the body, pushing open both sets of pocket or semi-lunar valves on the way.

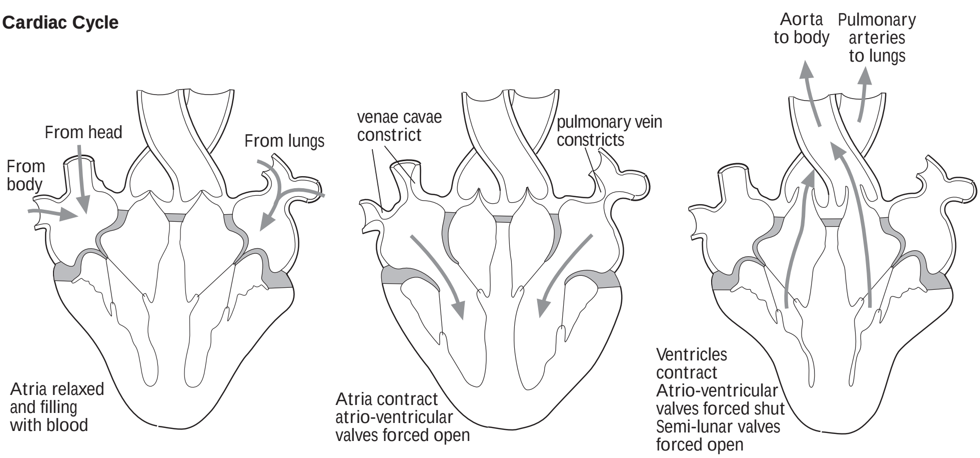
When the ventricles relax (**ventricular diastole**) the blood tends to fall back down the pulmonary artery and main aorta under gravity, thus filling and shutting the pocket valves. The closing of these valves makes the second heart sound (described as 'dup'). All valves are now shut and the cycle is repeated.

The heart sounds can be heard with the use of a stethoscope.

◆ CHECKPOINT SUMMARY

- ◆ The cardiac cycle refers to the events of a complete filling and emptying of the heart.
- ◆ It is a continuous cycle, the start point of which can be taken when heart is empty and all valves shut.
- ◆ Atria fill and internal pressure rises forcing bicuspid and tricuspid valves open.
- ◆ Ventricles fill so that whole heart full.
- ◆ Atria contract (atrial systole) so that ventricles overfilled and stretched.
- ◆ Ventricles contract with a force proportional to their degree of stretch (ventricular systole).
- ◆ Blood forced up shutting bicuspid and tricuspid valves (first heart sound) and opening pocket valves as blood forced up pulmonary artery and aorta.
- ◆ Ventricles relax (ventricular diastole) blood falls back in pulmonary artery and aorta shutting pocket valves (second heart sound).

Cardiac Cycle



Myogenic stimulation and the coordination of the cardiac cycle

Cardiac muscle is myogenic, that is the stimulus for contraction arises internally, rather than externally from branches of the nervous system, as seen with skeletal muscle.

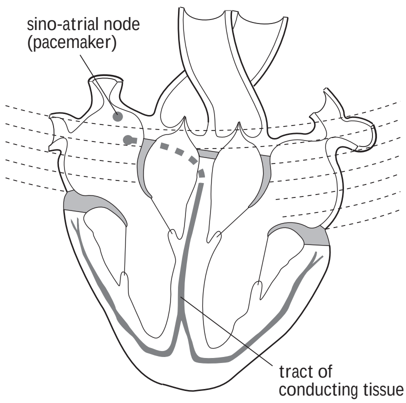
The **sino-atrial node** (SA node) or 'pacemaker' is a mass of specialised tissue in the right atrium from which coordinating waves of electrical activity originate and radiate through the muscle of the heart wall. The sino-atrial node thus coordinates the basic rhythm of the heart contractions.

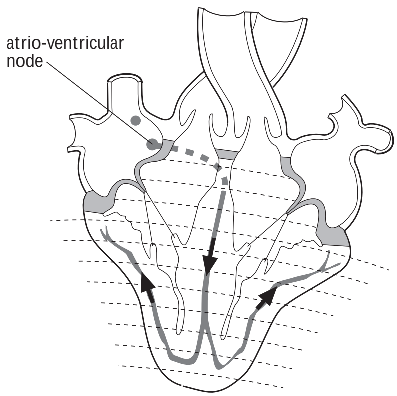
The wave of excitation spreads rapidly through the interconnected cardiac muscle fibres of the atria allowing both to contract simultaneously. A band of fibrous connective tissue between the atria and ventricles prevents the wave of excitation spreading down into the ventricles.

Another mass of specialised tissue, the **atrio-ventricular node** is located at the bottom of the atria. It is stimulated by the waves of electrical impulses radiating from the SA node, and transmits the impulses through the insulating band of connective tissue between the atria and ventricles. The impulse travels to the base of the ventricles in a tract of conducting tissue, composed of modified cardiac muscle fibres and neurones known as Purkyne tissue, from where the impulses radiate upwards through the cardiac muscle of the ventricles.

This pattern of the spread of excitatory waves through the heart, ensures that the atria contract first to force the blood **down** into the ventricles, and that the ventricles subsequently contract to force the blood **up** into the pulmonary arteries and main aorta. The spread of the wave of excitation throughout the heart can be detected by electrodes attached to the skin of the chest and displayed as an electrocardiograph (**ECG** trace).

ECG trace of electrical activity of heart





Although the sino-atrial node initiates contractions of the heart it cannot vary the rate of stimulation on its own. The basic rate of the sino-atrial node, can, however, be altered by a variety of influences, over a range from about 30 beats per minute (bpm) to as many as 220 bpm.

It is influenced by the activity of the sympathetic and parasympathetic nerves of the autonomic nervous system, which originate from a control centre in the brain.

The sympathetic nerve endings secrete noradrenaline, which stimulates an increase in the heart rate directly.

The parasympathetic nerves, release acetylcholine which causes a decrease in the heart rate. During exercise, the progressive increase in the heart rate is due at first to a decrease in parasympathetic activity, and then to the increasing activity of the sympathetic nervous system.

Also, in response to a general activation of the sympathetic nervous system, adrenaline is released from the adrenal glands, which also increases the heart rate, acting via the blood circulation.

Stimuli for these changes include the levels of blood carbon dioxide, pH, and temperature. Increases in these levels, associated with increased activity, result in an increase in the rate of contraction of the heart (beats per minute).

◆ CHECKPOINT SUMMARY

- ◆ Cardiac muscle is myogenic.
- ◆ Rate modified by sino-atrial node (pacemaker) in wall of right atrium.
- ◆ Waves of electrical activity spread rapidly down through cardiac muscle of atria.
- ◆ Prevented from passing directly into ventricles by barrier of connective tissue, stimulus picked up by atrio-ventricular node.
- ◆ Bundle of His composed of Purkyne tissue transmits stimulus to base of ventricles from where it radiates up through the walls back to the connective tissue barrier.
- ◆ Detected by electrodes on the skin as an ECG.
- ◆ Pacemaker influenced by sympathetic (faster) and parasympathetic (slower) nervous systems, and the hormone adrenaline.
- ◆ Pressure receptors in the main veins and arteries close to the heart detect pressure changes and regulate the cardiac output by reflexes via the medulla of the brain.
- ◆ All influences on heart rate coordinate heart rate and therefore blood supply to body (cardiac output) with demands of body.

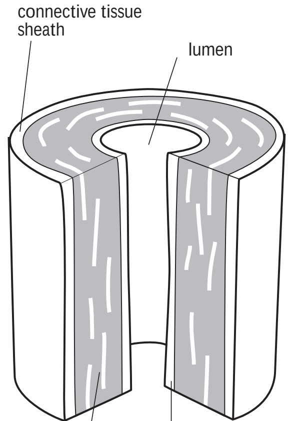
The structure and roles of arteries, veins and capillaries

In mammals the blood circulates around the body in a continuous system of blood vessels. From the heart, blood travels in the arteries and arterioles, into the capillaries supplying the tissues, and then returns to the heart in the venules and veins. All blood vessels are lined with smooth endothelium (epithelium found lining tubes) which reduces friction. Arteries and veins have varying amounts of muscle in their walls, which is always involuntary (smooth / unstriated) muscle under the control of the autonomic nervous system and hormones.

Arteries

Arteries close to the heart have a large cross sectional area, and thick elastic walls. Arteries are stretched by the cardiac output when the heart contracts, and they recoil when the arterial blood pressure drops as a result of the heart relaxing between beats. The recoil of the elastic artery walls in this way assists the circulation of the blood around the body. It helps smooth the flow between contractions of the heart, and helps to maintain the blood pressure. This stretching and recoiling of the arteries is felt as the pulse in places where arteries come close to the surface of the body (the inside of the wrist, the side of the neck, and in the temple).

Artery in section



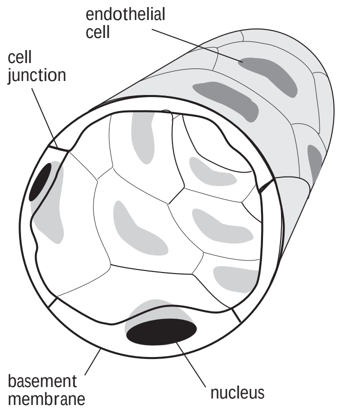
The main artery leaving the left ventricle of the heart, the aorta, branches into arteries supplying all the main regions of the body. Further from the heart, there is a gradual transition from the elastic arteries to muscular arteries that have circular layers of involuntary muscle in their walls. These arteries branch into smaller **arterioles** the walls of which, although thinner, also have circular layers of involuntary muscle. The state of contraction or 'tone' of these muscle layers alters the diameter of these vessels, which changes the resistance to the flow of the blood, which in turn effects the blood pressure and distribution of the blood to different parts of the body. The arterioles penetrate all tissues of the body and connect to beds of finely branching capillaries.

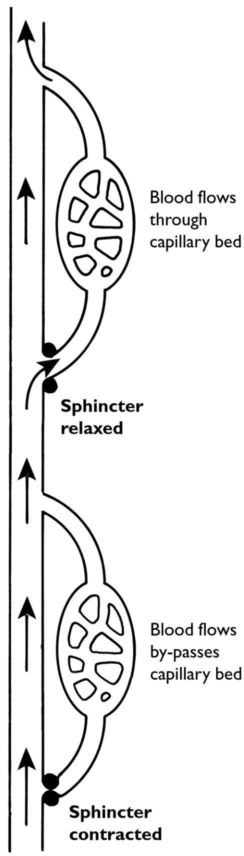
Capillaries

Capillaries form a fine network which penetrate all tissues. They have the smallest diameter of all blood vessels, about 6-8 μm (0.007 mm), which is the same as that of the red blood cells. For this reason the red cells are forced to move slowly through the capillaries in single file, ensuring a short diffusion distance between the corpuscles and the tissues. Capillary walls are just one cell thick, which further aids exchanges by diffusion between the blood and the tissues. The huge number of capillaries provide a very large total surface area across which these exchanges occur. As more capillaries open up in working muscles, the surface area between the blood and tissues is increased, and the diffusion distance between the two is decreased, resulting in more rapid and efficient exchanges between them. The blood pressure and rate of flow both drop in the capillaries. The slow flow also increases the time available for exchange of materials between the blood and the tissues.

There are so many capillaries in the body that they cannot all be supplied with blood at the same time. Consequently, there is competition for blood between different regions of the body, especially during exercise, when blood must be shunted to the working muscles, and consequently withdrawn from other regions. For example, when the body is at rest, about 45% of the cardiac output passes through the capillaries of the gut wall and associated glands, and the kidneys. During maximum exercise this can be reduced to about 3% of the cardiac output, as blood is redirected to the working muscles. The reduced flow rate is compensated for by a greater extraction of oxygen from the blood, by these tissues. The shunting of blood between competing tissues is achieved by constriction and dilation of the arterioles, and of the arterio-venous vessels, which are direct connections between the arterioles and venules. The entrances to the capillary beds are controlled by circular precapillary sphincter muscles which, when contracted, shut off the capillaries and when relaxed, open them.

Section of typical capillary





Estimated blood flow in cm^3 per minute, to different organs/systems in a trained male at rest and during maximum effort.

Organ system	At rest	%	Max. effort	%
Skeletal muscle	1000	20	26 000	88.00
Coronary vessels	250	5	1200	4.00
Skin	500	10	750	2.50
Kidneys	1000	20	300	1.00
Liver & gut	1250	25	375	1.25
Brain	750	15	750	2.50
Whole body	5000	100	30 000	100.00

Veins

Capillaries join up to form **venules**, which in turn join to form veins which return the blood to the heart. The individual veins have a larger cross sectional area than the comparable arteries, and as there are more veins than arteries, the veins therefore also have a greater total cross sectional area. The walls of the veins are thinner and less elastic than those of the arteries, and in the veins of the legs and arms there are semi-lunar or pocket valves at intervals along their length. These valves oppose any back flow of blood under gravity, and ensure one-way flow of blood to the heart when the veins are 'massaged' by movement of surrounding tissues (especially contracting skeletal muscles). The thin walled veins with their large cross section present little resistance to the flow of the blood, so that although the blood pressure in the veins is low after passage of the blood through the capillary beds, the remaining pressure still helps move the blood in the veins back to the heart.

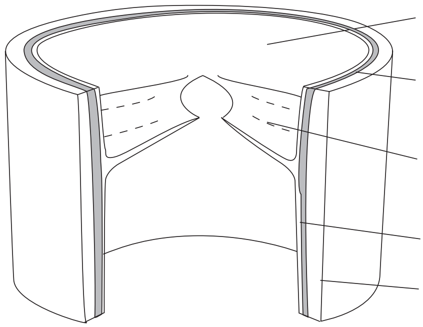
Because the blood in the veins is under low pressure, and their walls are thin, the veins are easily compressed by the smallest movements of the surrounding structures, particularly the skeletal muscles. As the muscles contract and relax during exercise they exert a massaging effect on the deep veins, especially for example in the legs, when running, swimming, or cycling. This massage effect of the 'muscle pump' is random and in no particular direction, but the pocket valves in these veins ensure that the flow is one-way, back to the heart.

In addition, breathing movements assist the return of blood in the veins to the heart. On breathing in, the diaphragm contracts and moves downwards. This decreases the pressure within the thorax, and increases the pressure within the abdomen. These changes in pressure compress the large veins in the abdomen, and assist the flow of blood into the veins of the thorax which return blood to the heart.

At rest the veins act as a large reservoir of blood for use when circulatory demands increase, for example during exercise. During exercise when the output of blood from the heart (cardiac output) increases, the muscle fibres in the walls of the veins are stimulated to contract (venous tone) and the veins constrict. As a result a larger proportion of the venous blood is shunted back to the heart, especially from the veins in the legs and the abdomen. This is especially important in preventing blood from 'pooling' in the legs under the force of gravity during upright exercise, and immediately afterwards.

In these ways the venous return of blood balances the rising cardiac output during exercise. This is essential as the heart would be unable to maintain a high cardiac output unless it was receiving an equal volume of blood back from the veins.

Section of vein showing pocket valve



◆ CHECKPOINT SUMMARY

- ◆ Elasticity of arteries is important in smoothing flow of cardiac output.
- ◆ Finer branches and arterioles are main sites of generation of resistance to blood flow.
- ◆ Capillary beds supply all tissues providing large surface areas for exchanges by diffusion and short diffusion distances.
- ◆ Capillaries have large total cross sectional surface areas. Therefore resistance to flow, blood pressure and rate of flow all drop in capillaries.
- ◆ Diameter of capillary same as red blood corpuscles thus forcing them to pass through capillaries in single file, bringing all close to tissues.
- ◆ Plasma minus proteins exuded through thin walls to bathe tissues directly.
- ◆ Thin walls and large lumen of veins offer little resistance to flow of blood back to heart, and allow ease of massage by surrounding muscles.
- ◆ Pocket valves ensure one way flow back to heart.
- ◆ Venous blood under low pressure but flow fast enough to ensure return of blood to heart at same rate as blood flow in the arteries.

BLOOD AND BODY FLUIDS

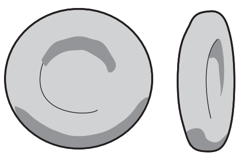
Composition of the Blood

Blood consists of the fluid plasma, which carries red blood cells, white cells, and fragments of cells from the red bone marrow known as platelets.

Plasma consists of 90% water, and 10% materials in suspension and solution. Plasma proteins, formed mainly in the liver, include albumin (to which the plasma calcium is bound), globulins (some of which are antibodies and others are important in the carriage of hormones and vitamins), and fibrinogen (which is important in blood clotting). These proteins also have an important function in buffering the blood (preventing sudden changes in acidity and alkalinity). Plasma proteins are also involved in regulating the movement of water between blood and tissues, they lower the water potential of the plasma which helps to control the volume of tissue fluid being formed and reabsorbed. Plasma also contains many dissolved organic and inorganic substances which are being transported, e.g. amino acids, hormones, glucose, fats, urea, creatine, bicarbonate, some oxygen and carbon dioxide. The characteristic yellow straw colour comes from a pigment called bilirubin which is formed from haemoglobin when old red blood cells are broken down in the liver.

Red blood cells (**erythrocytes**) lose their nucleus and most of their cytoplasmic organelles in their process of maturation in the red bone marrow. They become 'corpuscles' with a flexible membrane, filled with the oxygen carrying pigment haemoglobin. The loss of the nucleus accounts for their biconcave shape which increases their surface area to volume ratio.The total surface area of the red blood cells in man is about 3500 m^2 and this facilitates the exchange of gases between the red cells and the tissues. The biconcave shape also gives them some resilience in absorbing water without bursting should the plasma become temporarily diluted for any reason. The flexible membrane enables them to 'squeeze' through capillaries.

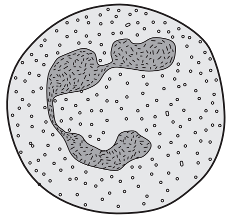
Red blood cells comprise about 30-40% of the blood volume. This can be determined by centrifuging a blood sample which results in the red blood cells being forced down to the bottom of the sample to give a 'packed red cell volume' or haematocrit. The haematocrit (and the red blood cell count) are proportional to the haemoglobin content of the blood which is quoted in grams per litre (decimetre cubed (dm^3), with normal values being within 140-180 for men, and 115-160 for women. (Clinically the figures are quoted in grams per decilitre (one tenth of a litre) and are given as 13 - 17g for adult males and 11.5 - 16.0g for adult females.) Levels below the lower limits being known as anaemia.



Red cell approx. 7µm in diameter

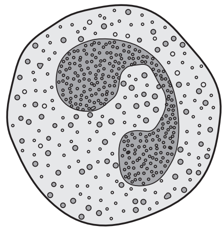
White cells (leucocytes) form the basis of the immune system. They comprise just 1% of the total blood volume. There are four main types of leucocyte which differ in both structure and function. They are all found in the blood, although most actually function outside of the capillaries in the tissues.

Neutrophils are the most common type and make up approximately 70% of leucocytes. They are small phagocytic cells which engulf foreign particles e.g. disease causing invading micro-organisms (pathogens). They have a characteristic multi-lobed nucleus, surrounded by granular (grainy) cytoplasm.



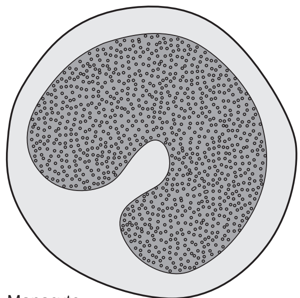
Neutrophil

Eosinophils possess a bi-lobed nucleus and granular cytoplasm, these leucocytes usually only comprise 1.5% of the total leucocyte population. However, in the blood of individuals suffering from allergic conditions, the proportion of eosinophils is increased as they play a role in allergic responses. They are also involved in the destruction of large parasites such as flatworms.



Eosinophil

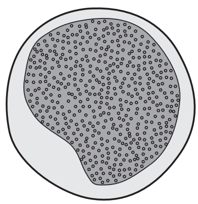
Monocytes can be identified by their large 'bean-shaped' nucleus and non-granular cytoplasm. They originate in the bone marrow, spend a short time in the blood, and then settle in tissues where they become known as **macrophages**. Monocytes secrete chemical known as cytokines which are essential for the functioning of the immune system. Macrophages are involved in the phagocytosis of micro-organisms and other large particles. Macrophages are also found in the alveoli of the lungs where they attack pathogens entering via the air.



Monocyte

Lymphocytes are involved in specific immune responses to pathogens or other foreign cells. They are round in shape with a large, densely staining nucleus. The small amount of cytoplasm is non-granular. There are two main types:

B-lymphocytes which produce antibodies and **T-lymphocytes** which are involved in the direct killing of infected cells.



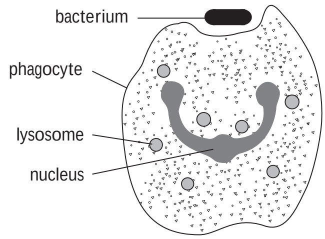
Lymphocyte

Role of leucocytes in phagocytosis

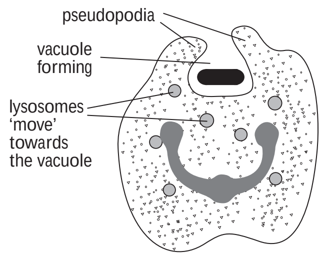
Phagocytosis is the process by which pathogens, other foreign material and dead or infected cells are engulfed and digested by neutrophils or monocytes/macrophages (collectively known as **phagocytes**). These phagocytes are non-specific in their actions so will deal with any type of foreign material which they come across. Phagocytes are found in the blood and the lymphatic system, especially in the lymph nodes as well as in the intercellular spaces of tissues.

- Neutrophils appear in blood, lymph and tissue sites, and macrophages are found primarily in tissues. This is important as it allows them to act in any tissue which becomes infected with pathogens.
- The process of phagocytosis in both neutrophils and macrophages involves several stages.
- The phagocytes comes into direct contact with the foreign particle or microorganism.
- The cell membrane and cytoplasm of the phagocyte moves out forming 'pseudopodia' around the particle or micro-organism.
- The particle or micro-organism is enclosed in a vacuole (called a phagosome) formed from the cell membrane of the phagocyte.
- Lysosomes in the cytoplasm, containing enzymes and other chemicals, fuse with the phagosome and discharge their contents.
- The micro-organism or other cell material is killed and digested, and the products of digestion are absorbed by the phagocyte or released from the cell.

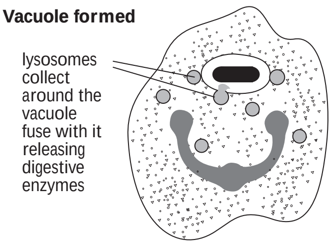
Phagocyte 'moves' towards bacterium

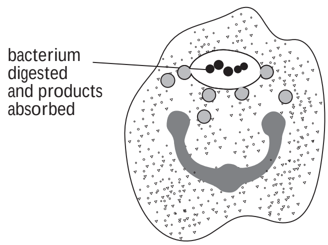


Vacuole forming



Vacuole formed





◆ CHECKPOINT SUMMARY

- Blood consists of fluid plasma with erythrocytes (red blood cells), and leucocytes (white blood cells) and blood platelets.
- Plasma composed of 10% materials in suspension and solution.
- Plasma proteins wide variety of functions and act to buffer changes in pH.
- Materials carried in solution not strictly part of the plasma.
- Red blood cells lose nucleus in development and become biconcave corpuscles of haemoglobin.
- Red blood cell volume 30-40% of total blood volume.
- Large surface area to volume ratio individually due to biconcave shape, and huge total surface area due to small size (6-8 mm) and huge numbers.
- Males higher blood count/haemoglobin than females.
- There are several types of leucocytes (neutrophils, eosinophils, monocytes and lymphocytes) and they form basis of immune system.
- Leucocytes engulf foreign particles e.g. bacteria and viruses by phagocytosis, and secrete antibodies against foreign antigens, including bacteria and viruses.
- Platelets are fragments of white cells.

Role of leucocytes in the secretion of antibodies

B-lymphocytes are involved in the specific immune response to pathogens (or other foreign antigens) via the production of antibodies.

On the cell surface membrane of B-lymphocytes are a number of specific antigen receptors or membrane bound antibodies. These are sites to which antigens on the surface of pathogens or other foreign material may become attached, leading to a sequence of events in which free antibodies are produced to destroy the foreign material.

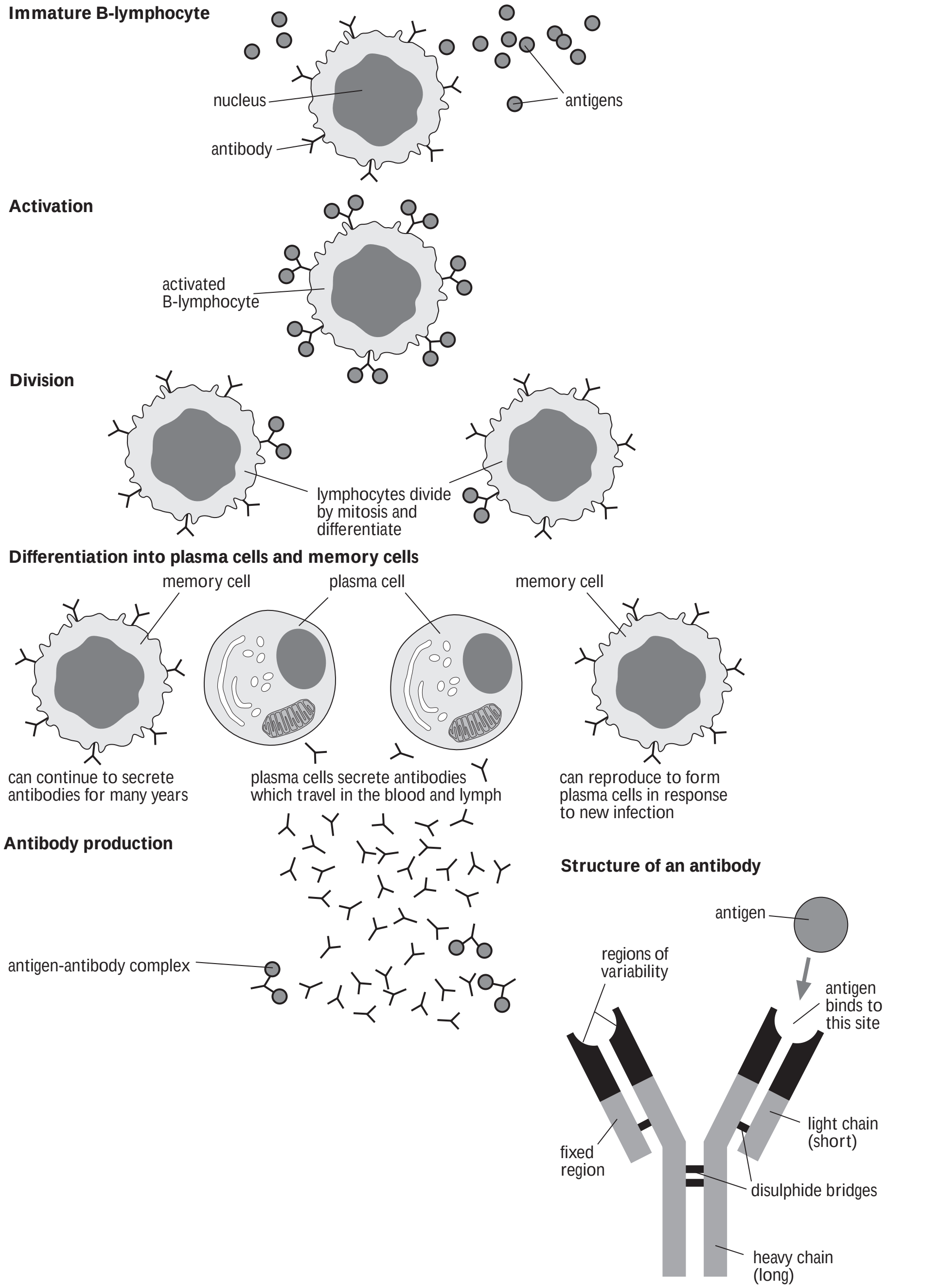
Antibodies are a type of protein molecule known as immunoglobulins which are secreted by activated B-lymphocytes when a specific antigen is encountered. Antibodies do not directly destroy foreign material but target it for destruction by other branches of the immune system, including phagocytes.

Sequence of events in the production of antibodies

- Antigens on surface of foreign material come into contact with their specific antigen receptor on a B-lymphocyte. (Note there are thousands of types of B-lymphocyte each with different receptors and the ability to make just one type of antibody.)
- Binding of antigen to antigen receptor activates the B-lymphocyte and causes it to divide by mitosis producing a clone of identical B-lymphocytes.
- Most of the B-lymphocytes turn into **plasma cells** and the rest turn into **memory cells**.
- The plasma cells begin to secrete specific antibodies against the foreign material concerned. Antibody molecules are secreted at a very high rate (up to 30 000 molecules per second).
- The antibodies attach to the antigens on the foreign material and lead to the destruction of it in one of three ways.
- By coating foreign cells or objects and causing them to stick together in such a way that they can then be engulfed by phagocytes (another type of white blood cell).
- By binding to the foreign cells or objects at sites which interfere with their activities. For example, by covering the protein coat of a virus and preventing it from attaching to host cells.
- By stimulating the release of other blood components to break up and destroy foreign cells.

Once the foreign material has been destroyed, the plasma cells eventually die and antibodies stop being secreted. But the memory cells remain in the lymph nodes and the circulation. If a subsequent infection with the same pathogen occurs then some of these will turn into plasma cells and start producing antibodies. This is the basis of **natural active immunity** to diseases and underlies the practice of immunisation or vaccination.

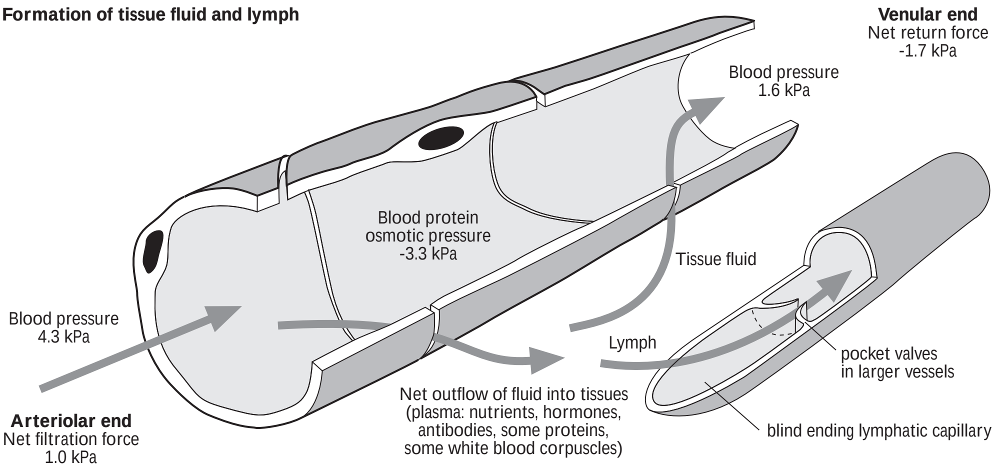
Platelets are white cell fragments, which have an important function in the clotting process.


Immature B-lymphocyte
nucleus
antibody
antigens
Activation
activated B-lymphocyte
Division
lymphocytes divide by mitosis and differentiate
Differentiation into plasma cells and memory cells
memory cell
plasma cell
memory cell
can continue to secrete antibodies for many years
plasma cells secrete antibodies which travel in the blood and lymph
can reproduce to form plasma cells in response to new infection
Antibody production
antigen-antibody complex
Structure of an antibody
antigen
regions of variability
antigen binds to this site
light chain (short)
fixed region
disulphide bridges
heavy chain (long)

Tissue fluid

Tissue fluid is formed when plasma, minus its proteins, is pushed out under pressure through the capillary walls to bathe the tissues. Depending on the degree of activity and health and fitness, most of the tissue fluid is reabsorbed back into the blood capillaries. Tissue fluid forms the internal environment of multicellular animals. It bathes each cell and is the medium for the exchange of materials between the individual cells and the blood system.

Formation of tissue fluid and lymph



◆ CHECKPOINT SUMMARY

- ◆ The hydrostatic pressure of the blood in the capillaries causes plasma minus its proteins to be forced through the thin walls of the capillaries.
- ◆ This fluid bathes all the tissues and is known as tissue fluid.
- ◆ It carries substances in solution from the blood to supply the tissues, e.g. oxygen, nutrients, hormones, antibodies etc; and drains waste products e.g. carbon dioxide away.
- ◆ Most of the tissue fluid is reabsorbed back into the capillaries as the hydrostatic pressure drops as the blood passes through the capillaries.
- ◆ Excess tissue fluid is drained away into blind ending lymphatic capillaries.
- ◆ Lymph is tissue fluid that has been drained into lymphatic capillaries, with lymphocytes added by lymph nodes which occur at intervals.
- ◆ Special lymph capillaries in the villi of the lining of the small intestine, known as lacteals, preferentially absorb and transport fats, so that lymph contains more fats than plasma.
- ◆ Eventually the lymph is returned to the general circulation in the major veins near to the heart.
- ◆ Movement of the lymph in the lymphatic system is maintained by the massaging effects of the muscles and breathing movements, and the one-way pocket valves; all features common to the veins of the circulatory system.

The transport of oxygen and carbon dioxide

Gas exchange occurs by diffusion between the air in the alveoli of the lungs and the blood in the capillaries. The relative amounts of oxygen and carbon dioxide in the air breathed in and out are measured as '**partial pressures**' in units of kiloPascals (kPa). (The continuous random movement of particles of a gas means that the particles will occasionally collide with each other and with the walls of any structure enclosing them within a space, thus exerting a pressure. The number of such collisions, and therefore the pressure, is proportional to the amount of substance present. In mixtures of gases, e.g. air, each substance exerts a partial pressure in that mixture proportional to the amount of that substance in the mixture. The partial pressure of a gas is a better measure of the amount of gas present than its percentage composition. Although the percentage of oxygen remains the same (21%) in air under different conditions, the amount of oxygen varies. At atmospheric pressures less than at sea level, e.g. at altitude, there is still 21% oxygen in air, but as the air is less dense there is a smaller amount of oxygen.)

As a result of its journey around the body, blood entering the capillaries of the alveoli has a lower oxygen and a higher carbon dioxide content (partial pressure) than the air in the alveoli. Therefore carbon dioxide diffuses out of the blood into the alveoli, and oxygen diffuses into the blood from the alveoli, each down their partial pressure gradients.

Roles of respiratory pigments (haemoglobin, fetal haemoglobin and myoglobin)

Oxygen absorbed into the blood in the alveolar capillaries combines with **haemoglobin** in the red blood cells to form **oxyhaemoglobin**. Each molecule of mammalian haemoglobin consists of four sub-units, each consisting of an iron-containing haem group combined with a protein globin part. Each sub-unit combines reversibly with one molecule of oxygen. Thus one molecule of haemoglobin can carry four molecules of oxygen. The formation of oxyhaemoglobin from deoxyhaemoglobin involves a physical holding of the oxygen by the haemoglobin sub-units as a result of their special 3-dimensional structure. In man each red blood cell contains about 300 000 000 molecules of haemoglobin. At rest and even during maximum exercise, at sea level, the haemoglobin in the blood leaving the lungs in healthy subjects is virtually saturated with oxygen. Therefore the capacity and functioning of the lungs is not normally the limiting factor in exercise. (The oxygen is easily displaced by carbon monoxide, which combines irreversibly with haemoglobin to form carboxyhaemoglobin. Major sources of carbon monoxide being smoking and car exhausts.)

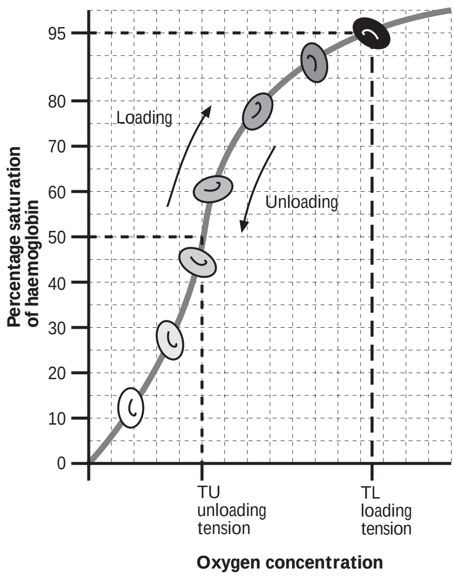
Gas exchange at the tissues is opposite to that at the lungs with oxygen being released and carbon dioxide taken up. Tissues vary widely in their demands for oxygen and in their production of carbon dioxide, particularly during exercise when the muscles become more active. The low oxygen partial pressure in the muscles during exercise increases the diffusion gradient between them and the red blood corpuscles, thus encouraging the dissociation of the oxyhaemoglobin and the release of oxygen in solution to diffuse to the tissues.

Fetal haemoglobin, found in the blood of the fetus developing in the uterus of the pregnant female, has a greater affinity (attraction) for oxygen than the adult haemoglobin of the mother, and thus can 'rob' it of oxygen, ensuring a good supply of oxygen to the developing fetus.

Myoglobin, found in skeletal muscle fibres, has a greater affinity (attraction) for oxygen than haemoglobin in the red blood corpuscles of the blood, and thus can 'rob' it of oxygen, ensuring a good supply of oxygen to the active muscles.

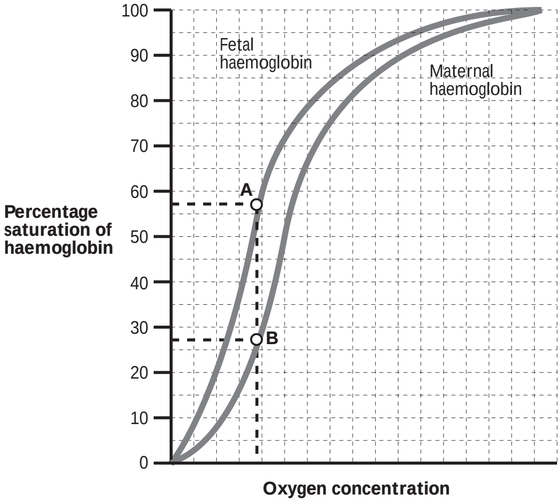
Some carbon dioxide is carried in the red blood cells in combination with haemoglobin as carbaminohaemoglobin. Some carbon dioxide is carried in the plasma in simple solution, but most is carried as hydrogen carbonate ions in the plasma. Carbon dioxide released as a waste product of cellular respiration enters the red blood cells where the enzyme carbonic anhydrase catalyses the formation of carbonic acid, which dissociates into hydrogen ions and hydrogen carbonate ions. The hydrogen carbonate ions enter the plasma to be carried to the lungs. The release of hydrogen carbonate ions into the plasma from the red blood corpuscles is balanced by the uptake by the red blood corpuscles of chloride ions from the plasma (the chloride shift). When the blood reaches the alveolar capillaries these events are reversed, hydrogen carbonate ions enter the red blood corpuscles, carbon dioxide is released to be breathed out, and chloride ions return to the plasma.

Haemoglobin association/dissociation curve

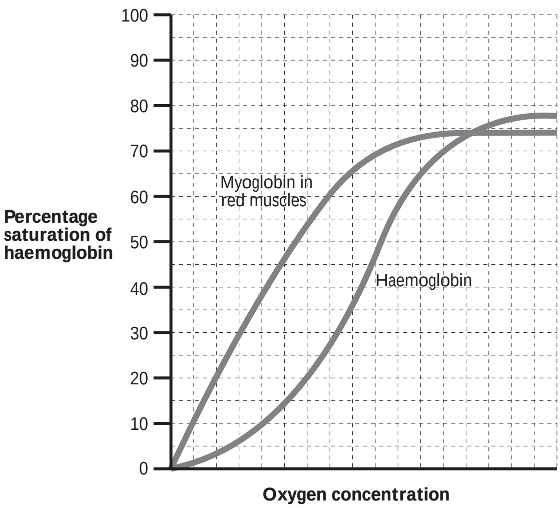


This basic type of curve is altered with differing conditions

Fetal and maternal haemoglobin

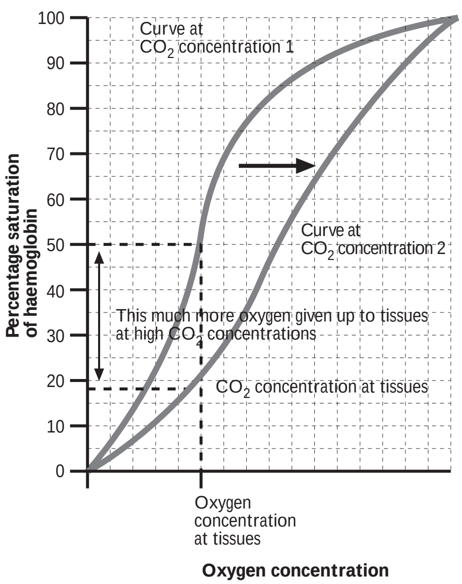


Myoglobin and haemoglobin



The effect of carbon dioxide on oxygen transport by haemoglobin (the Bohr Effect)

As has been described the red blood cells are involved in both oxygen and carbon dioxide exchanges and transport, each of which influence each other. At the tissues, the carbon dioxide, produced as a waste product of aerobic respiration in the mitochondria, diffuses in solution down its concentration gradient, from the high pCO_2 in the mitochondria to the lower pCO_2 in the blood. The greater the difference in pCO_2 the greater the amount of diffusion. The formation of carbonic acid (and lactic acid in anaerobic respiration) lowers the pH of the blood. Any increase in acidity (decrease in pH) and/or increase in temperature encourages oxyhaemoglobin to release its oxygen to the tissues. The way in which oxygen is held and released by haemoglobin at different partial pressures.can be represented by an oxygen association/dissociation curve, and an increased tendency by oxyhaemoglobin to release its oxygen is shown by the oxygen association/dissociation curve shifting to the right. This effect is called the **Bohr shift** and its significance is that the more active the tissue (e.g muscle) the more carbon dioxide, lactic acid, and heat are produced and the more oxygen is released to that tissue.



◆ CHECKPOINT SUMMARY

- Reversible combination of haemoglobin and oxygen in the capillaries of the pulmonary circulation is a physical association.
- During all exertions at sea level the haemoglobin in blood leaving the lungs is virtually always saturated, so that efficiency of lungs not normally a limiting (rate regulating) factor.
- Gas exchange at tissues is in effect the reverse of that at the lungs similarly explained in terms of diffusion gradients (partial pressure gradients).
- Bohr effect applies to conditions in tissues illustrates how conditions of increasing temperature and decreasing pH reduce the affinity of haemoglobin for oxygen ie oxygen is released to tissues.
- Fetal haemoglobin has a greater affinity for oxygen than adult haemoglobin therefore ‘robs’ it of oxygen. Note that the placental artery is some distance from the lungs of the mother and therefore not particularly well oxygenated.
- Myoglobin is a pigment found in red (endurance type) muscle fibres and has a greater affinity for oxygen than does haemoglobin, so that it is capable of loading up high with oxygen from relatively lower saturated haemoglobin. It acts as an intermediary between oxygen in the blood and the muscle fibres.
- Haemoglobin also has a role in transport of carbon dioxide as carbaminohaemoglobin.

2B.3 Adaptations to the Environment

Content

- Species are adapted to survive in particular environmental conditions.
- Structural adaptation; the relationship of the external features of organisms to the physical characteristics of a specific habitat; xeromorphic adaptations in flowering plants; hydrophytes.
- The structural and physiological adaptations shown by invertebrates to the varying oxygen concentrations found in freshwater; including external gills, direct access to air, presence of respiratory pigment.

External features are related to the physical characteristics of a specific habitat

The external features of an organism always give clues to its habitat. For example, dark green waxy leaves indicate that a plant is adapted to survive periods of drought, thick fur on a mammal would suggest a cold environment, and gills, an aquatic existence. Other features reveal more about an organism's feeding or reproductive behaviour and suggest a particular life style, e.g. forward directed eyes are characteristic of carnivores, whilst the peacock's colourful feathers are connected with sexual display. The following examples show clearly how structural adaptations can give a survival advantage to organisms in particular habitats.

Adaptations of flowering plants to the availability of water

Xeromorphic adaptations

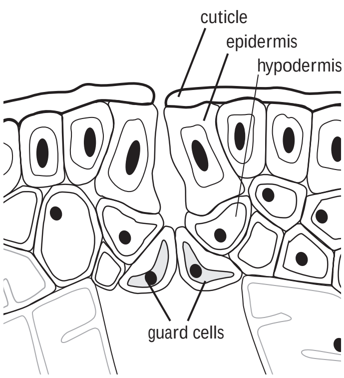
Plants growing in extreme conditions of water shortage show certain structural modifications which decrease the rate of water loss (transpiration) and allow them to survive periods of prolonged drought. Plants with these modifications of structure are known as **xeromorphic** and the plants themselves as **xerophytic plants**, or **xerophytes**. They can also show functional (physiological) adaptations e.g. the cytoplasm can survive almost complete desiccation, and the stomata may only open at night to prevent water loss in the heat of the day, as in the cacti.

Xerophytes are typically found in dry regions and conditions of potentially high water loss. However, some plants with xeromorphic features are found in areas where there seems to be plenty of water, e.g. salt marshes, and wet heathlands and moors. These plants are living in conditions of physiological drought' where the water is unavailable to them for some reason. For example 'salty' conditions are more concentrated than the contents of the root cells, therefore the water potential gradient is from the root cells to the external solution i.e. out of the plant, instead of into the plant. (plants growing in 'salty' conditions are also known as halophytes).

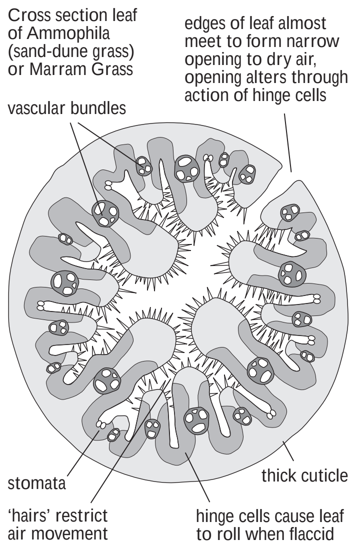
There are many xeromorphic adaptations which conserve water and xerophytes can show any combination of these.

- Thickened waterproof cuticle reduces water loss through the surface of the leaf, especially on the upper surface of the leaf which is most exposed to air currents and heat absorption from sunlight, both of which increase the rate of evaporation of water from the leaf during transpiration; e.g. laurel leaves.
- The surface of the leaf may be 'hairy' (not true hairs) which protect the stomata from air currents which would otherwise increase transpiration e.g.'Viper's Bugloss' (*Echium vulgare*).
- Stomata can be sunken in pits and grooves, which protect them from air currents, e.g. on pine 'needles'.
- Stomata can be reduced in number, especially on the upper surface of the leaves, where the exposure to the heat of the sun and air currents is the greatest, some e.g. laurel, have no stomata on the upper surface.
- Leaves can have a reduced surface area, which also reduces the number of stomata, e.g. pine 'needles'; and gorse and cacti where the leaves are reduced to spines and photosynthesis is carried out by the green stems.
- Leaf folding or rolling reduces water loss through the stomata by protecting them from air currents, and enclosing them in a zone of high humidity, e.g. sand dune grass (*Ammophila*), where the long ridged leaf rolls up along its length at times of excessive transpiration.
- Leaves can be succulent, with tissues where water can be stored for periods of drought, e.g. cacti.
- Cells of the leaves have mucilage and can withstand dehydration for longer periods than those of non-xerophytes (mesophytes).
- Leaf fall stops transpiration. Deciduous plants lose their leaves with the onset of winter in temperate regions, when the low temperatures inhibit water uptake by the roots, (you may have noticed that some of the xerophytes mentioned above (pine and laurel) are 'evergreens', i.e. they do not have to lose all their leaves in winter as they have a low transpiration rate). Some plants lose their leaves in dry periods for the same reason, and photosynthesis is carried out by their green stems e.g. broom.

Pine Needle Stomata



Marram Grass T.S.

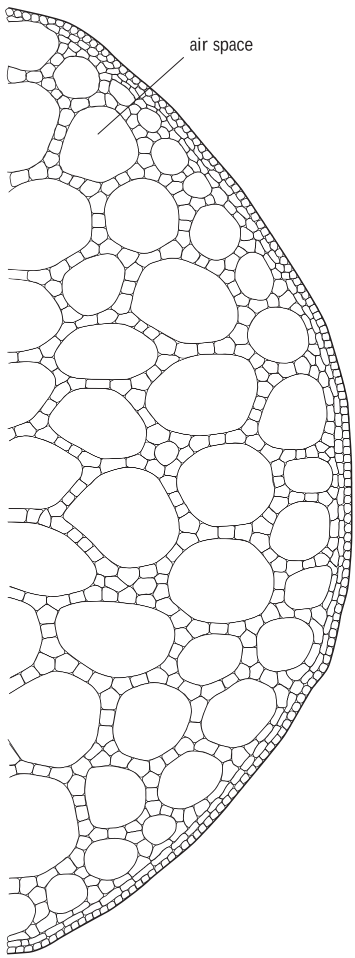


Plants which live in fresh water or inhabit the margins of rivers and lakes are abundantly supplied with water but face other problems, the most serious of which is the lack of oxygen for their roots.

Remember that the uptake of minerals is an active process requiring high energy levels. In the absence of oxygen the roots will respire anaerobically but this can not be tolerated for long because they are soon poisoned by the ethanol released as a bi-product. Plants adapted to live in flooded or aquatic habitats show **hydrophytic** features and the plants are called **hydrophytes**. Rice is a hydrophyte. Its roots have an unusually high tolerance to ethanol and its seeds can germinate in oxygen starved soils. In common with other water adapted plants it also develops an interconnecting system of large air spaces linking the roots with the leaves and other parts above water. This specialised tissue is called **aerenchyma** and it allows the flooded roots to breathe.

The water lily (*Nymphaea*) floats freely on the surface of fresh water and shows more extreme hydrophytic features. Its stem is perforated by large air channels which supply oxygen to the roots. Stomata are present only on the upper surface of its huge leaves, and the spongy mesophyll layer has very large air spaces acting as bouyancy chambers.

T.S. water lily stem *Aerenchyma*



Structural and physiological adaptations shown by invertebrates to varying oxygen concentrations found in fresh water

The amount of oxygen available to living organisms depends on its relative proportion in the surrounding medium. Air is a much more favourable environment than water in this respect because it contains 21% oxygen whilst the amount dissolved in water is much smaller. Furthermore, the amount of oxygen dissolved in water varies greatly according to the temperature, the warmer the water, the less oxygen it can contain.

Table of relation between temperature and oxygen content of water

Temperature °C	Volume of oxygen cm^3/dm^3
0	10.29
10	8.02
15	7.72
20	6.57
30	5.57

This poses a problem for aquatic invertebrates. Small size is an advantage because, as you have seen, the smaller the body, the larger the surface area to volume ratio. The surface area to volume ratio may be increased by some modification of the body shape, for example, in the flattened body of the flatworms which allows sufficient diffusion of oxygen to occur all over the animal's surface. The most successful aquatic species, however, have become adapted in more specific ways to make best use of the available oxygen. This is particularly true of the arthropods (animals with jointed limbs and an exoskeleton), some examples of which are considered below.

External gills

External gills are outgrowths from the body which increase the surface area for diffusion of gases between the water and the internal tissue fluids. These occur on different parts of the body in different organisms. Mayfly larvae have a row of paired gills on each side of the abdomen and, in poor oxygen conditions, e.g. shallow warm water, can be seen to undertake small 'press up' movements increasing the flow of water over the gills. Crustacea such as the fresh water shrimp have leaf like outgrowths on their limbs which are well supplied with 'blood' and are moved constantly to refresh the oxygen supply.

Direct access to air

A number of insect larvae, notably mosquito larvae have snorkel-like breathing tubes which enable them to breathe atmospheric air. This adaptation overcomes the problem of fluctuating oxygen supplies and allows them to survive in relatively warm and stagnant water. The diving beetle has a different strategy for air breathing. It has masses of fine hairs on the underside of its abdomen which trap air so that the animal has its own 'diving bell' supply of air when under water. Like terrestrial insects, these animals have a system of tracheal tubes which supply oxygen directly to all the body tissues and which connect to the external air supply by means of holes in the exoskeleton called spiracles. the spiracles may be closed to prevent the entry of water so that air is able to enter only at the site of the available oxygen supply.

Respiratory pigments

Respiratory pigments such as **haemoglobin** greatly increase the amount of oxygen available to body tissues. They take up oxygen form the external medium, releasing it readily to respiring tissues. It is a very significant advantage for aquatic invertebrates to possess respiratory pigments, particularly in the low oxygen conditions provided by warm water. Those which do not have respiratory pigments, for example the mayfly larvae are restricted to habitats which provide a good oxygen supply, e.g. fast flowing cold water. Tubifex worms and midge larvae possess haemoglobin pigments very similar to those of mammals and are abundant even in the most stagnant water. A number of crustacea, for example, crayfish and shrimps possess a blue pigment called **haemocyanin** with copper rather than iron forming the oxygen associating part of the pigment molecule.

◆ CHECKPOINT SUMMARY

- ◆ Hydrophytes are plants adapted to life in water.
- ◆ Flowering plants are secondarily aquatic, that is they have structural adaptations to a terrestrial life, which have become modified for life in water.
- ◆ Plants which live in fresh water or inhabit the margins of rivers and lakes lack oxygen for root respiration.
- ◆ The uptake of minerals is an active process requiring energy from aerobic respiration.
- ◆ Rice is a hydrophyte. Its roots have an unusually high tolerance to ethanol produced by anaerobic respiration and its seeds can germinate in oxygen starved soils.
- ◆ In common with other water adapted plants it also develops an interconnecting system of large air spaces (aerenchyma) linking the roots with the leaves above water.
- ◆ Invertebrates show structural and physiological adaptations to the varying oxygen concentrations found in fresh water, these include external gills, direct access to air, and the presence of respiratory pigments.
- ◆ External gills are outgrowths from the body which increase the surface area for diffusion of gases between the water and the internal tissue fluids. These occur on different parts of the body in different organisms.
- ◆ Direct access to air is found in a number of insect larvae, e.g. mosquito larvae have snorkel like breathing tubes which enable them to breathe atmospheric air. This adaptation allows them to survive in relatively warm and stagnant water.
- ◆ The diving beetle has masses of fine hairs on the underside of its abdomen which trap air so that the animal has its own 'diving bell'.
- ◆ Respiratory pigments such as haemoglobin greatly increase the amount of oxygen available to body tissues, releasing it readily to respiring tissues.
- ◆ A number of crustacea, for example, crayfish and shrimps possess a blue pigment called haemocyanin with copper rather than iron forming the oxygen associating part of the protein molecule.

2B.4
Sexual Reproduction

Content

Sexual reproduction

- Fusion of gametes, forming a zygote leading to genetic variation in offspring.
- Meiosis and its significance as the division of a diploid nucleus to give haploid nuclei; the behaviour of chromosomes during the first and second divisions of meiosis, including chiasmata formation.
- Haploid and diploid phases in the life cycles of organisms.

Reproduction in flowering plants

- The structure and functions of the principal parts of an insect-pollinated dicotyledonous flower and a grass.
- Pollination and the events leading to fertilisation.
- The adaptations related to insect and wind pollination.
- The significance of the mechanisms for ensuring cross-pollination; protandry, protogyny and dioecious plants.

Reproduction in humans

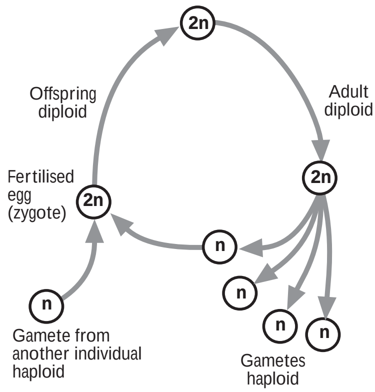
- The structure and functions of the male and female reproductive systems.
- The production of gametes in oogenesis and spermatogenesis.
- The events in the menstrual cycle; the roles of luteinising hormone, follicle-stimulating hormone, oestrogen, progesterone.
- The transfer of male gametes leading to fertilisation.
- Implantation; the functions of the placenta in relation to the development of the embryo.
- Birth and lactation, and the roles of oxytocin and prolactin.

SEXUAL REPRODUCTION

The fusion of gametes results in a diploid zygote

Sexual reproduction involves the fusion of the nuclei of the sex cells, or **gametes**, from the male and female sex organs, to form a **zygote** in a process of **fertilisation**. Individual organisms can be either single sexed (**dioecious**), or **hermaphrodite** (**monoecious**) bearing both male and female organs. Hermaphrodite organisms may be self-fertilising, or they may have outbreeding mechanisms which favour or compel cross fertilisation with another hermaphrodite individual.

During gamete production (**gametogenesis**) in animals, and in spore formation which precedes gamete production in plants, the number of chromosomes in the nucleus is halved in a process known as **meiosis**, so that normal gametes have half the normal number of chromosomes, that is they are **haploid**. A **diploid** zygote, which has twice the haploid number of chromosomes, is formed by fertilisation. Certain genetic 'mixing' events, which occur during meiosis, and the random fusion of the gametes result in genetic variation in the offspring which may be of adaptive advantage.



Meiosis

Meiosis is a special type of cell division called a **reduction division** in which the number of chromosomes is halved from the diploid to the haploid number. The mechanisms of cell division are very similar to that already described for mitosis.

Meiosis involves two divisions referred to as the first and second divisions (Meiosis I and Meiosis II). Remember that the nucleus of each cell contains two sets of chromosomes; one maternal, from the female gamete and one paternal, from the male gamete. As a result, each chromosome has a partner in the other set which carries genes for the same characteristics. Two such chromosomes are said to form a **homologous pair**.

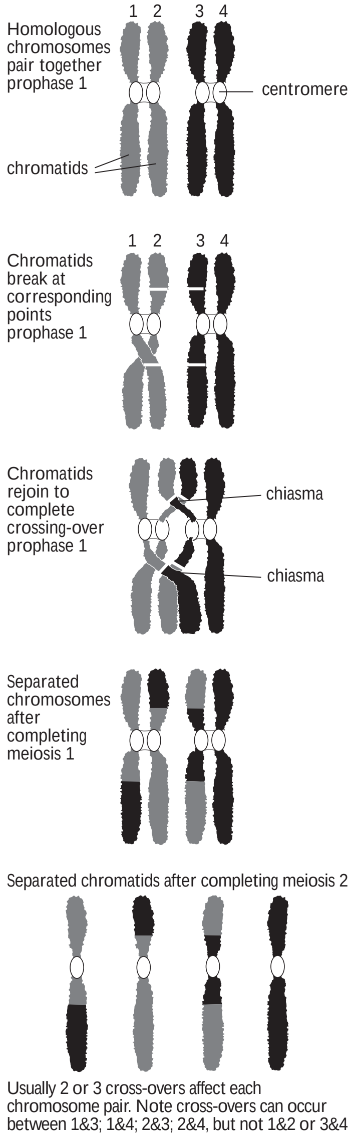
During interphase, before nuclear division by meiosis starts, the DNA replicates

During prophase I the chromosomes are formed as double structures of a pair of **sister chromatids**. They then pair up with their homologous partners to form structures called **bivalents**. They twist around each other, and breaks occur in the chromatids. A break in one chromatid is matched by another in the corresponding non-sister chromatid. The broken ends rejoin with the ends of the non-sister chromatid resulting in a **crossing over** between non-sister chromatids. The homologous chromosomes begin to repel each other, and the points where crossing over has occurred serve to slow the repulsion and appear as a cross shape (**chiasma pleural chiasmata**). These crossing over points occur in a random fashion serving to reshuffle the genetic pack, mixing the DNA of the maternal and paternal chromosomes. Crossing over during meiosis is an important source of genetic variation in organisms which reproduce sexually.

Prophase I may take several days to complete. In metaphase I the chromosomes are pulled to the equator of the cell, held only by the junction points of the chiasmata. They line up on the equator at random, with maternal and paternal chromosomes on either side. During anaphase I the homologous chromosomes pull apart from each other, separating towards the opposite poles of the cell, the completion of which is known as telophase 1.

Crossing over, and the random alignment and separation of maternal and paternal chromosomes, prevents any gametes being formed from being replicas of gametes that formed the original cell undergoing meiosis, and therefore introduces genetic variation into the gametes.

Two new spindles are formed at right angles to the first, one at each pole, and the chromosomes (each composed of two sister chromatids) move to the equator for a second metaphase (metaphase II). From here on, the events are similar to those of mitosis as the sister chromatids now move to opposite poles, i.e. anaphase II, and telophase II. Cytokinesis results in the formation of four new haploid daughter cells. Note that the result of meiosis is four cells (gametes) each containing half the original number of chromosomes with mixed up sections of maternal and paternal DNA sequences, as well as mixed up sets of maternal and paternal chromosomes.

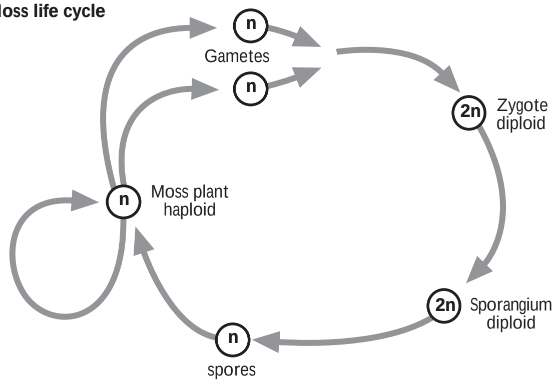


The life cycle of plants involves haploid and diploid phases.

In all sexually reproducing plants there is an alternation of haploid and diploid phases in the life history. The cells of the haploid phase contain one set of chromosomes and the cells of the diploid phase contain two sets of chromosomes. This alternation is most clearly seen in the mosses in which a haploid, sexually-reproducing gamete producing plant (gametophyte) alternates with a diploid asexually-reproducing spore producing plant (sporophyte). Fertilisation is dependent upon the presence of a surface film of water. The gametophyte moss plant produces male gametes which swim in a surface film of water to the female organs. By contrast the process of spore dispersal depends on dry wind currents so it is important that the sporophyte lifts the spore cases so that they are exposed to air currents.

Although the life cycle of Flowering plants is so different from that of mosses, their reproductive structures and the sequence of events leading up to fertilisation reflects this alternation between haploid and diploid stages. In Flowering plants the main plant is the diploid sporophyte generation, and the haploid gametophyte generation is reduced to a few cells and nuclei within the pollen grains and ovum.

Moss life cycle



◆ CHECKPOINT SUMMARY

- Offspring result from the fusion of gametes, forming a zygote.
- This fusion of gametes involves various genetic mixing events and therefore leads to genetic variation in offspring.
- These genetic mixing events include events in the nuclear division (meiosis) involved in the production of gametes, and in the random fusion of gametic nuclei from different sexes.
- Meiosis is a reduction division in which the diploid number of chromosomes (two sets) is reduced to the haploid (one set).
- In the first phase of meiosis (Meiosis I) the two sets of chromosomes pair up, so that chromosomes occur in homologous pairs. Each chromosome is duplicated into two chromatids, so one pair of chromosomes is made up of four chromatids.
- The homologous chromosomes of a pair entwine, one chromatid of each pair breaks and rejoins with the broken chromatid of the other pair, in a process known as genetic recombination or crossing over.
- The chiasmata align on the equator of the nuclear spindle apparatus (NSA), before the homologous chromosomes repel each other to opposite poles.
- Cross overs are visible under the light microscope and are known as chiasmata (Greek for crosses), they result in the exchange of genes (alleles) between homologous chromosomes.
- Either chromosome of each pair can go to a particular pole, resulting in mixing of the original sets (independent assortment).
- Two daughter nuclei are thus formed, each with one (haploid) set of chromosomes, with each chromosome composed of two chromatids.
- The second phase of meiosis (Meiosis II) involves the centromeres of the chromosomes aligning on the equator of a each of two new NSA formed at right angles to the first.
- The chromatids then repel each other to form four new haploid nuclei.
- Animals and plants are typically diploid and have haploid gametes, but mosses have haploid plant bodies, produce gametes without meiosis which fuse to form a diploid sporophyte which produces haploid spores by meiosis to produce new haploid moss plants.

Reproduction in flowering plants

Flowers are the reproductive organs of plants in which gametes are produced and fertilisation occurs. Most flowers are bisexual (hermaphrodite) bearing both male and female organs, the stamens and carpels. Where separate male and female flowers occur on the same plant it is said to be monoecious. In a few cases, the stamens and carpels are found on separate male and female plants (dioecious). Dioecious plants have the obvious advantage of enforced out breeding, but rely entirely on external agents for the transfer of gametes. The structure of flowers is closely related to their method of pollination, with the two main agents of pollination being insects and the wind.

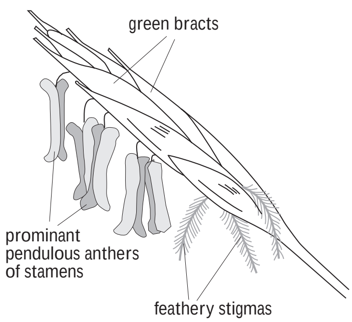
Insect pollinated flowers typically have various combinations of the following features.

- Coloured petals and other flower parts, white flowers often have UV light reflecting strips visible to insects.
- Nectaries containing sweet nectar.
- Scent glands.
- Various structural modifications to guide insects to the correct positions to deliver and/or pick up pollen.
- Compared to wind pollinated plants, relatively small amounts of large sticky pollen grains.
- Compared to wind pollinated plants, relatively small stigmas.

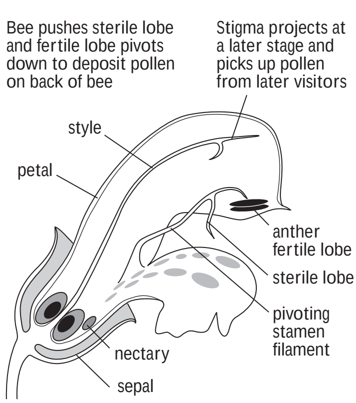
Wind pollinated flowers typically have various combinations of the following features.

- Reduced petals and other flower parts.
- No nectaries.
- No scent glands.
- Compared to insect pollinated plants, relatively large amounts of small light smooth pollen grains produced by dangling stamens exposed to air currents.
- Compared to insect pollinated plants, relatively large feathery stigmas exposed to wind currents.
- Flowers often produced before leaves emerge.

Wind pollinated flower



Insect pollinated flower



Pollination

Pollination is the process by which pollen is transferred from the anther lobes of the stamen to the stigma of the carpel. Flowers may be self-pollinating or cross-pollinating.

Self-pollination occurs when the stigma receives pollen from the stamens of the same flower. This is only possible in hermaphrodite flowers when the stamens and carpels mature at the same time. The stamens are often arranged so that the pollen can fall on to the stigma(s). Many self-pollinating flowers, e.g. the garden pea, self-pollinate in the bud stage before the flower opens. Indeed, in some the flower never opens and is eventually destroyed by the development of the fruit.

In **cross-pollination** the stigma receives pollen from the stamens of a different flower, which may either be on the same or on a different plant. It must be noted however that if a flower is cross pollinated by pollen from a flower on the same plant then, like self-pollination, this is still a case of **in-breeding**. It is only cross-pollination between flowers on different plants that results in true genetic **out-breeding**. There are a variety of devices which favour cross-pollination, but only some of these ensure out-breeding, that is cross-pollination between flowers on different plants.

Devices preventing self-pollination and favouring cross-pollination in hermaphrodite flowers

Hermaphrodite flowers can have their stamens and stigmas maturing at different times. In some plants, the anthers mature first (**protandry**) for example, Geranium spp., whilst in others (less commonly) the carpels mature first (**protogyny**), for example Luzula (woodrush). In many cases, however, there is an 'overlap' period when both anthers and stigmas are mature during which self-pollination could occur if the flowers have not been cross-pollinated for some reason.

Hermaphrodite flowers frequently have special arrangements of their parts to prevent self-pollination. For example, the iris has a flap on its style which prevents pollen on the back of a withdrawing insect from coming into contact with the stigma; similarly the viola has an arrangement by which the stigma is exposed to pollen on the incoming insect but is covered as the insect leaves.

Devices preventing in-breeding and favouring out-breeding

If a species has separate male plants and female plants, that is if it is dioecious, then clearly out-breeding must always occur. Some species, despite having hermaphrodite flowers, encourage out-breeding by means of genetically determined **incompatibility** by which pollen will not grow normally on the stigmas and styles of flowers on the same plant. In some cases the incompatibility is complete and pollen on the stigma of the same flower or on a different flower on the same plant never develops correctly, so that in-breeding never occurs. In others it is only partial. In these cases the pollen tube grows down the style of flowers on the same plant more slowly than pollen from another plant, but can eventually lead to fertilisation of the ovule. Partial incompatibility allows for in-breeding should out-breeding not occur.

◆ CHECKPOINT SUMMARY

- The structure of flowers is adapted to the mode of pollination, the two main ones being insect and wind pollination.
- Pollination is the transfer of pollen from the pollen sacs of the male stamens to the stigma of the female carpel.
- Insect pollinated flowers typically have bright coloured floral parts (espcially petals), nectar, and scent to attract insects.
- Petals may be modified as landing platforms for insects, stamens are designed to deposit pollen on visiting insects, and stigmas are arranged to have pollen grains deposited on them from visiting insects.
- Wind pollinated flowers have reduced floral parts, no nectar, prominent hanging stamens exposing, and large 'hairy' stigmas collecting, pollen carried on air currents.
- Wind pollinated plants typically flower before the emergence of the leaves in the spring of temperate climates.
- Various arrangements exist to reduce the possibility of pollen reaching the stigma of the same plant.
- Protandry (development of the stamens before the stigma of the carpel).
- Protogyny (development of the stigma before the stamens).
- Dioecious species with separate male and female plants.
- Pollen germinates on a compatible stigma, and the pollen tube grows down through the style, to reach the egg cell (ovum) nucleus in the ovule.
- The pollen tube nucleus degenerates, and the generative nucleus divides into two male gametic nuclei.
- One of the male gametic nuclei fuses with the ovum nucleus to form the diploid zygote nucleus, and the other fuses with the two polar nuclei to form the triploid endosperm nucleus.
- This double fertilisation is unique to flowering plants.

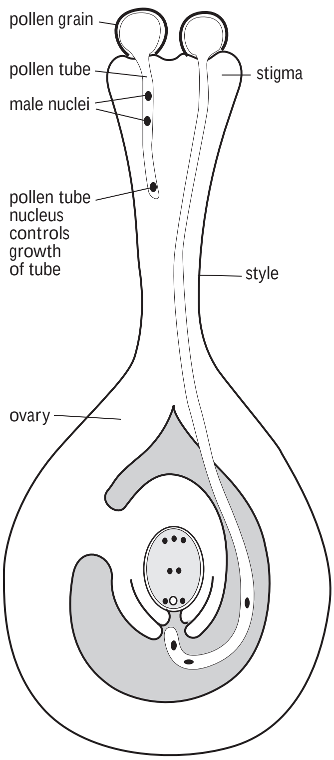
Fertilisation

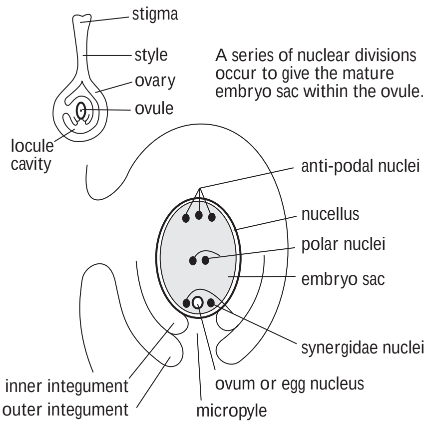
At an early stage in the development of the ovule, whilst the flower is still in bud, nuclear divisions, in which the chromosome number is halved by meiosis, occur to produce a haploid cell which divides and grows into a small structure called the **embryo sac**. This contains eight nuclei, only three of which are directly involved in the reproductive process, namely, the **egg nucleus** and the two **polar nuclei**. The embryo sac is surrounded by a nutrient-rich tissue called the **nucellus,** located within the ovule, the whole structure being surrounded by a double wall (inner and outer **integuments**). A small gap in the wall **(micropyle)** allows the entry of the pollen tube.

When a pollen grain lands on a receptive stigma, it germinates forming a pollen tube which grows through the tissues of the style and ovary until it reaches the ovule, absorbing energy-rich nutrients along the way. Growth of the pollen tube is under the control of the pollen tube nucleus, whilst the generative nucleus is carried along at the advancing tip. Before it reaches its destination, the generative nucleus divides to form two male gamete nuclei.

Fertilisation in flowering plants is a double event involving both of the male nuclei. One of these fuses with the egg nucleus to form a diploid zygote which will divide and grow into the plant embryo. The other fuses with both polar nuclei to form a triploid (triple fusion) nucleus.

After fertilisation, the ovule undergoes a number of changes to become a seed. The zygote develops into the embryo of the new plan; the triple fusion nucleus develops into the endosperm (food store) in endospermous seeds (mainly members of the grass family e.g. wheat and rice) and in others it degenerates; the integuments develop into the seed coat (testa). The wall of the ovary develops into the fruit.



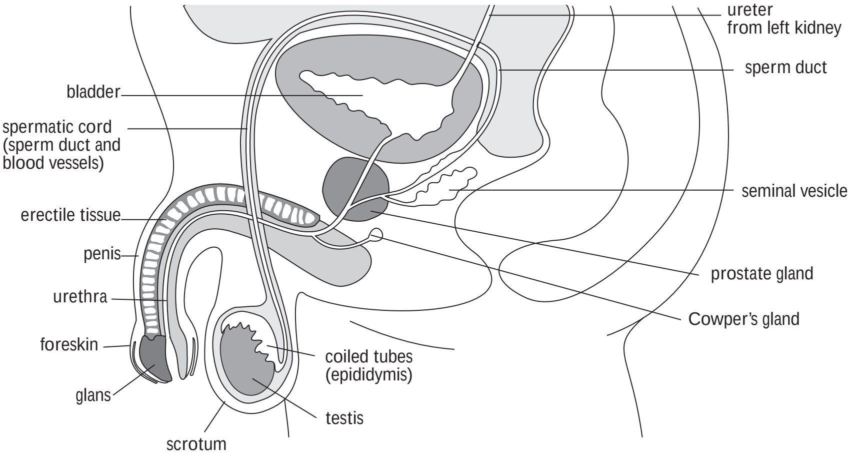


All nuclei shown are haploid
Tissues not shaded are diploid

REPRODUCTION IN HUMANS

Structure and function of the male reproductive system

The male reproductive system



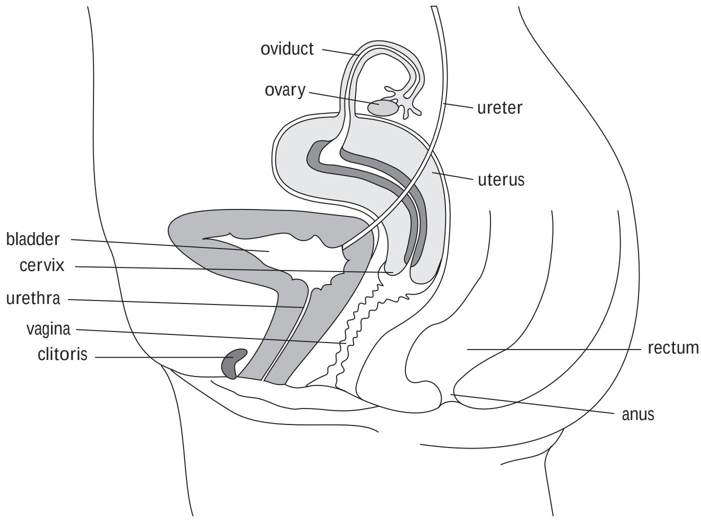
The male gamete producing organs (**testes**) have two functions. Firstly, the production of haploid male gametes (sperm) capable of fertilising an ovum and so passing on the male's genes into a new generation. Secondly, the production of male hormones, particularly testosterone. This allows the development of the secondary sexual characteristics of the male and is also needed for sperm production and sexual activity. Both functions are performed in the **semeniferous tubules** which are packed into lobules inside each testis. **Spermatogenesis** (the production of sperm discussed later) occurs in the walls of the tubules whilst testosterone is secreted by cells in between the tubules (interstitial cells). The testes lie outside the body in the **scrotum**. The function of this is to keep the testes slightly cooler than body temperature (about 35ºC) for optimal sperm production.

The remaining components of the reproductive system are all concerned with moving sperm from the testes to the **urethra** and into the female reproductive tract during sexual intercourse. The sperm are moved from the seminiferous tubules and transported to the **epididymis**, a long coiled tube where fluid is reabsorbed from the sperm and chemicals secreted which allow sperm to complete their maturation and develop the ability to swim. From here sperm are moved to the sperm ducts (vas deferens), which lead into the urethra just below the exit from the bladder.

In order to perform their functions, sperm are mixed with a variety of secretions to form **semen** before they leave the body during ejaculation (see below). The paired **seminal vesicles** secrete a watery alkaline fluid containing sugars (e.g. fructose) for nourishing the sperm. Mucus is also secreted. The **prostate gland** and **Cowper's glands** also secrete alkaline fluid and mucus. The alkaline fluid helps to neutralise any traces of urine present in the urethra and to neutralise the acid environment of the vagina, so providing more suitable conditions for the sperm to function.

The **penis** is used to convey sperm into the reproductive tract of the female during sexual intercourse. It contains **erectile tissue** and a central tube, the urethra through which semen from the sperm ducts pass. At other times this tube carries urine from the bladder. A system of **sphincter muscles** closes the exit from the **bladder** during sexual activity.

The female reproductive system



The female gamete producing organs (ovaries) lie inside the abdomen. As in the male these have two functions: the production of haploid female gametes (ova) containing genetic information from the female; and the production of female hormones, particularly oestrogen and progesterone.

These hormones control the development of secondary sexual characteristics and, along with hormones from the pituitary gland, control the events of the menstrual cycle.

Close to the border of each ovary is the **oviduct**. The oviducts are narrow tubes whose function is to transport ova released from the ovary to the uterus. The oviducts aid the movement of ova to uterus in two main ways. Firstly they have a fringed funnel which help to 'catch' the ova and guide them into the oviduct. Secondly they are lined with ciliated epithelial cells which beat and so move the ovum along towards the uterus. Fertilisation usually takes place in the oviduct.

The **uterus** is a muscular organ about 7 x 5 cm in size in a non-pregnant woman whose function is to house a developing embryo. Its wall consists of three layers: an outer covering; a thick middle layer of smooth muscle (the **myometrium**); and the inner **endometrium** containing a dense network of blood vessels and glands. The characteristics of the endometrium vary during the menstrual cycle as discussed below. During pregnancy the uterus can expand to up to 10 times its normal size.

The **cervix** or neck of the uterus is a ring of smooth muscle containing mucus secreting cells which help to provide optimum conditions for sperm survival at around the time of ovulation. The cervix is normally tightly closed but during birth will dilate to allow the baby's to emerge head first.

The **vagina** is a short muscular tube which receives the penis during sexual intercourse. It is lined with epithelial cells secreting vaginal fluids. Like the cervix it must stretch to several times its normal size during birth.

The external female genitalia or **vulva** consists of the **labia majora** and **labia minora** which surround the vaginal opening, opening of the **urethra** and the **clitoris**, a small erectile structure. The clitoris is similar in structure to the penis. Stimulation of the clitoris may result in orgasm.

Glands within the vulva secrete mucus to lubricate the penis during sexual intercourse.

Spermatogenesis and oogenesis

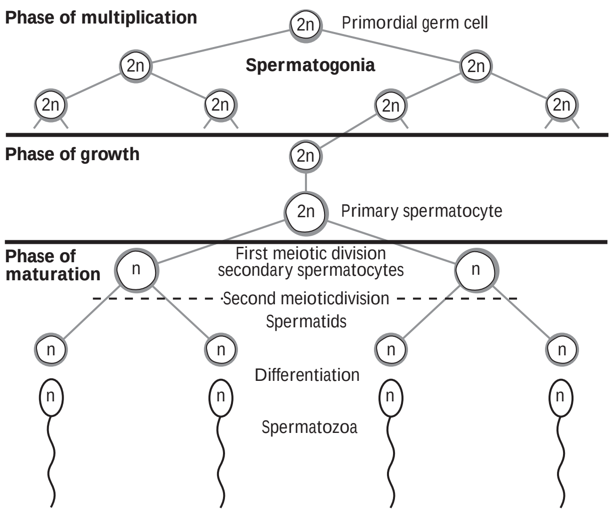
Spermatogenesis is the term used to describe the production of male gametes (sperm). Oogenesis is the production of female gametes (ova). These two processes share many essential similarities, such as the central role of meiosis in creating haploid gametes. There are however several differences in the timing and organisation of the processes. These can help to explain why adult males produce several million small sperm per day whilst women produce just one large, mature 'egg cell' per month.

Spermatogenesis

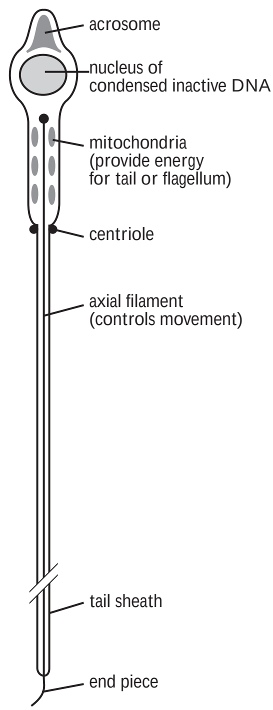
Sperm are produced in the seminiferous tubules within the testes of the adult male. The process of spermatogenesis is initiated by the hormone testosterone at the time of puberty. Epithelial germ cells in the outer layer of the seminiferous tubule divide by mitosis to form a population of diploid **spermatogonia**. These divide by mitosis and grow into **primary spermatocytes**. Each primary spermatocyte undergoes meiosis, forming two haploid **secondary spermatocytes** in Meiosis I and four **spermatids** in Meiosis II. In the final stage each spermatid develops from a round cell into a fully functional sperm cell (**spermatozoa**). This complete process of spermatogenesis takes about 70 days.

As spermatogenesis progresses, the developing sperm cells move towards the lumen of the seminiferous tubule into which they will eventually be released.The cells are attached to large **Sertoli cells** (nurse cells) until maturity. These cells provide oxygen and nutrients and remove waste products. They also play an essential role in remodelling the spermatid to form a sperm cell.

A mature sperm is approximately 20 µm in length and 2.5 µm in diameter, the smallest cell in the human body. It consists of a **head**, containing a haploid nucleus and a membrane bound sac of enzymes at the tip, (the **acrosome**), a **middle piece** containing many mitochondria to provide energy for swimming, and a **tail** containing microtubules.



Spermatozoon



Oogenesis

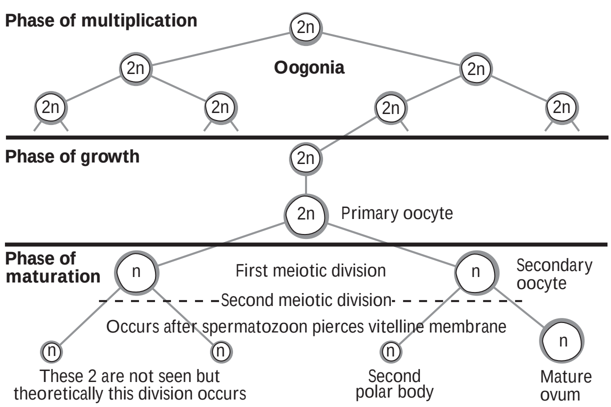
Unlike spermatogenesis, oogenesis does not begin at puberty, but in fetal life. Oogenesis begins in the germinal epithelium of the ovary where germ cells divide by mitosis to form **oogonia**. Further mitosis and growth of these cells produces **primary oocytes**. These cells begin Meiosis I but are halted during prophase. A layer of granular cells develops around each primary oocyte forming a **primary follicle**. Several million of these follicles are present at birth of which only a fraction will complete their development into gametes during the reproductive life span of the woman. From puberty onwards one follicle per month will complete its development into an **ovarian follicle** (Graafian follicle) containing a female gamete (secondary oocyte). The stages in the development of one follicle and the primary oocyte within it can be summarised as follows:

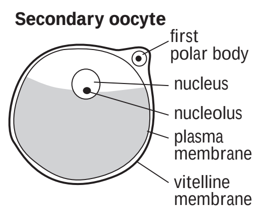
The primary oocyte inside the follicle enlarges whilst its surrounding granular cells increase in number, and are surrounded by an outer layer of cells (the **theca**) derived from the tissue of the ovary. Under the influence of **follicle stimulating hormone** (FSH) and **luteinising hormone** (LH) the follicle continues to grow into a secondary follicle, developing a central space filled with fluid secreted by the granular cells. Further enlargement, under the influence of oestrogen secreted by the granular cells, produces a mature Graafian follicle up to 1cm in diameter.

Meanwhile, inside the follicle the primary oocyte completes its first meiotic division, forming a haploid **secondary oocyte** and a small functionless **polar body** (containing the other half of the chromosomes). The second meiotic division begins but is halted in metaphase. At this point, mid way through the menstrual cycle, the Graafian follicle bursts to release the secondary oocyte. Meiosis II is not completed until the moment of fertilisation when a second polar body is formed. Strictly speaking the term **ovum** should not be used until that point.

The secondary oocyte which is released at ovulation is a large cell, about 140 μm in diameter. It contains a haploid nucleus and a large quantity of grainy cytoplasm. It is surrounded by a jelly like layer, the **zona pellucida**. The ovarian (Graafian) follicle after releasing the secondary oocyte becomes the **corpus luteum** which has an important role in the secretion of progesterone and oestrogen.

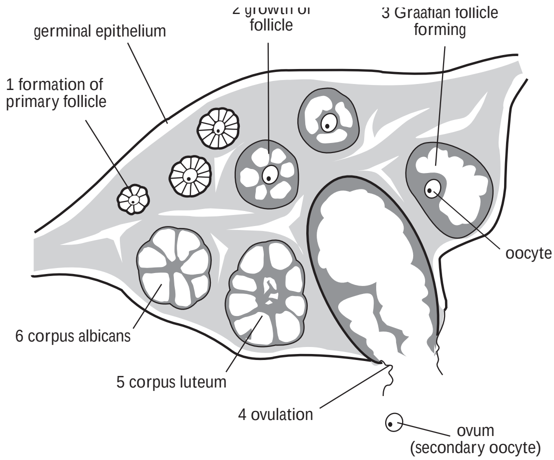
All of the changes described above occur during a single menstrual cycle. Further details of the menstrual cycle are given below.





Polar bodies take no part in reproduction and disappear, therefore only one functional cell is produced from the primary oocyte.

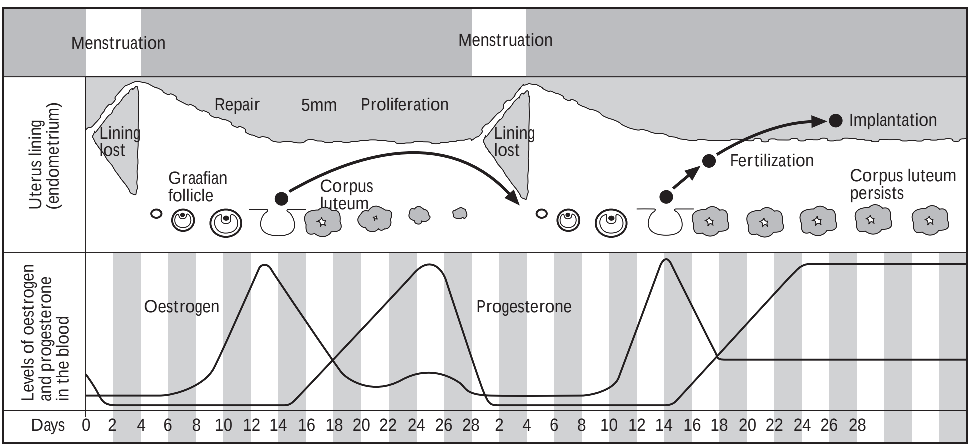
Mammalian ovary section



The menstrual cycle

Between puberty (average age 12) and the menopause (average age 45) human females experience regular sexual cycles, known as menstrual cycles. Each cycle is approximately 28 days long and involves a series of changes within the ovary and uterus. These can be considered as two separate but closely linked cycles: the **ovarian cycle** which is concerned with the development and release of an 'egg cell' around the mid point of the cycle, offering the chance of fertilisation if mating occurs; and the **uterine cycle** which is concerned with the development of the endometrium (uterus lining) to ensure the highest chance of implantation of a fertilised ovum or zygote.

Unless pregnancy occurs, one menstrual cycle will follow directly on from the next. (Therefore when interpreting graphs of the cycle note that day 28 is followed by day 1.)



The events of the menstrual cycle

The menstrual cycle relies on interactions between four main hormones: the ovarian hormones oestrogen and progesterone and the pituitary hormones Follicle Stimulating Hormone (FSH), and Luteinising hormone (LH). A further hormone, from the hypothalamus, Gonadotrophin Releasing Hormone (GnRH) is also involved. The events of the menstrual cycle are summarised below:

- Release of GnRH from the hypothalamus causes FSH to be released from the anterior pituitary. FSH travels in the bloodstream to the ovaries where it stimulates the development of several follicles (primary oocytes). One or more of these will eventually mature into an ovarian (Graafian) follicle containing the secondary oocyte.
- FSH stimulates the production of oestrogen from the follicles within the ovaries. This oestrogen in turn stimulates the growth of the endometrium, replacing cells lost during the previous menstrual period. At this point oestrogen has a negative feedback effect on FSH, reducing its production.
- Oestrogen levels increase until the mid point of the cycle when they bring about a peak of LH production from the anterior pituitary causing ovulation (the release of the secondary oocyte from the Graafian Follicle). A small peak of FSH production also occurs at the time of ovulation.
- LH causes the Graafian Follicle to develop into a corpus luteum which begins to secrete progesterone and oestrogen.
- Progesterone stimulates further development of the endometrium, in particular an increase in the density of spiral arteries and an increase in the secretion of mucus and fluid from glands in the endometrium. This is sometimes known as the secretory phase and its function is to prepare the uterus in case the newly released secondary oocyte ('egg' cell) is fertilised.
- The other function of progesterone is to inhibit the production of both FSH and LH and hence the development of further follicles. This is an example of negative feedback.
- If fertilisation does not occur, the corpus luteum degenerates and secretion of progesterone and oestrogen falls. This fall causes the uterine blood vessels to rupture and the uterus lining to degenerate and pass out of the body via the vagina. This is known as menstruation or the menstrual period and lasts for 4-5 days. Decline in progesterone levels causes the inhibition of FSH and LH to be removed and a new cycle can begin. Note that a new cycle begins whilst menstruation is still occurring.
- If fertilisation does occur then the corpus luteum does not degenerate but continues to secrete progesterone and oestrogen, maintaining the uterus lining and preventing further follicles from developing. After about 12 weeks of pregnancy in humans and corresponding times in other mammals the developing placenta takes over this hormonal (endocrine) role.

CHECKPOINT SUMMARY

- The male reproductive system consists of the testes which produce spermatozoa by meiosis.
- A system of tubes and erectile tissue transfer them to the female reproductive tract.
- Accessory glands are important in secreting substances essential for successful fertilisation of the female.
- The female system consists of ovaries which release egg cells (ova) into the abdominal cavity, from where they are swept down the oviducts by ciliated epithelium, into the uterus where they may or not be implanted.
- The uterus connects to the exterior by the vagina.
- The ova are produced (oogenesis) by meiosis in the germinal epithelium of the ovaries. Of the products of meiotic nuclear division, one accumulates all the cytoplasm to form the relatively large ovum, and the others are reduced to polar bodies.
- Spermatozoa are produced (spermatogenesis) by meiosis in the germinal epithelium of the testes. The four products of meiosis all develop into spermatozoa.
- The menstrual cycle is a monthly version of the ovarian cycle found in all mammals.
- A sequence of hormonal secretions from the brain, pituitary gland, and the ovaries themselves, coordinated by negative feedback loops control the events of the cycle.
- Luteinising hormone stimulates the release of the an ovum from an ovarian follicle, and the development of the corpus luteum. In the male it stimulates the secretion of testosterone by the testes.
- Follicle stimulating hormone initiates the development and growth of the ovarian follicles, and stimulates the ovary to secrete oestrogen. In males it stimulates spermatogenesis by the testes.
- Oestrogen stimulates the development of the primary and secondary sexual characteristics, the development of the uterus lining in the first half of the menstrual cycle.
- Progesterone stimulates the secretory phase of the uterus in the second half of the cycle, and maintains pregnancy whilst suppressing further ovulation

The transfer of male gametes and fertilisation

If fertilisation is to occur then male gametes must come into contact with the female gametes. Under natural circumstances male gametes are transferred into the reproductive tract of the female via the penis during sexual intercourse.

For sexual intercourse to occur, the male's penis must first become erect. This occurs following sexual stimulation and involves an increase of blood flow into the spongy erectile tissue of the penis. Movement of the erect penis inside the vagina during intercourse stimulates the sensory cells at the tip of the penis. A series of stages, co-ordinated by the sympathetic nervous system then follow, eventually leading to ejaculation: the release of semen containing sperm into the vagina. These stages include:

- contraction of the involuntary muscle lining the sperm duct and epididymis so forcing the sperm towards the urethra;
- contraction of the seminal vesicles, Cowper's and prostate glands which add their secretions to the sperm;
- closure of the bladder sphincter muscle; and reflex contractions of the muscles surrounding the urethra, forcing the semen out of the penis and high into the vagina of the female. Ejaculation is accompanied by the intense sensation of orgasm.

A single ejaculation can contain several hundred million sperm. Once in the vagina these sperm acquire the ability to swim and begin their journey through the cervix (first aligning themselves with long chains of mucus), across the uterus and up into the oviducts. The speed with which they may reach the oviducts suggests that muscular movements of the uterus and oviduct may in fact be more important than swimming at this stage. It has been suggested that chemicals called prostaglandins contained in seminal fluid could bring about this effect. If ovulation has occurred within 24 hours prior to this, a secondary oocyte should be present in one of the oviducts and it is here that fertilisation may take place.

Fertilisation

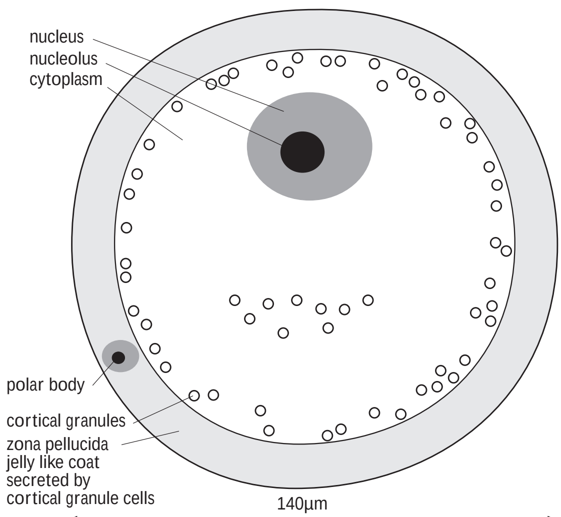
Fertilisation is the process by which the haploid nucleus of a single sperm cell fuses with the haploid nucleus of a single ovum creating a diploid zygote.

Before a sperm can fertilise the secondary oocyte it must undergo a process known as **capacitation** where it is 'primed' for the process by the acid environment of the uterus. The main feature of this involves changes in the cell membrane of the sperm in the region around the acrosome vesicle. Firstly the membrane is weakened and becomes more permeable, and the acrosome membrane fuses with the cell membrane.

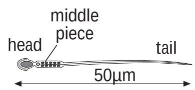
When a sperm comes into contact with the zona pellucida of a secondary oocyte the acrosome reaction occurs. This involves the acrosome splitting open and releasing the lytic enzymes contained within it. These begin to digest the zona pellucida, allowing the sperm to move through it to reach the cell membrane of the secondary oocyte. When it reaches the membrane it fuses with it and its head enters the cytoplasm. The tail is left behind. Entry of the sperm stimulates the nucleus of the secondary oocyte to complete its second meiotic division so that it can fuse with the nucleus of the sperm.

One of the surprising things about fertilisation is the mechanism which allows just one single sperm to penetrate the secondary oocyte when several hundred or thousand sperms are surrounding this cell. As the sperm enters the secondary oocyte a number of changes occur which result in the layer surrounding the egg cell (zona pelucida) becoming impermeable to other sperm.

Human female gamete (secondary oocyte) just before fertilisation



Human male gamete just before fertilisation



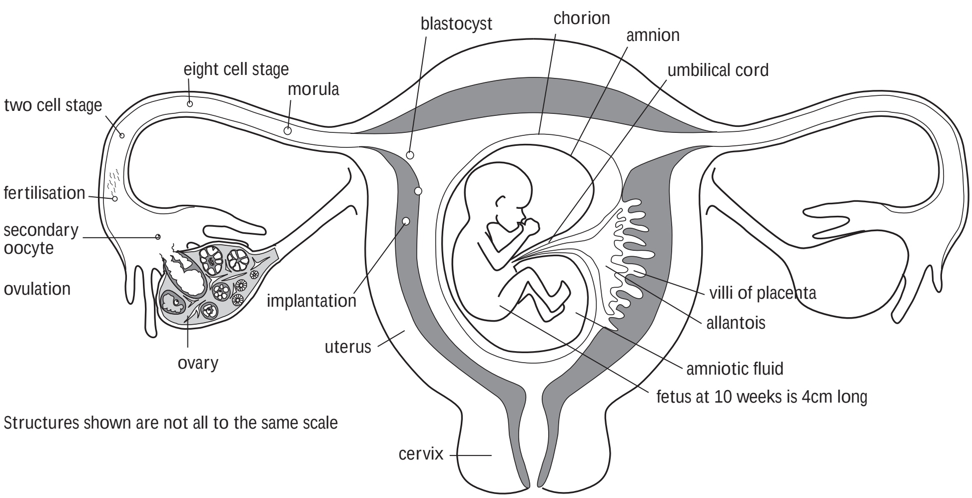
140µm is smaller than the smallest dot you can make with a fine ball point pen

Implantation

Following fertilisation the zygote undergoes cell division by mitosis forming a small ball of identical cells within a few days. Gradually the cells start to differentiate (become specialised for different tasks) and the ball of cells becomes a hollow sphere filled with fluid (blastocyst). The outer wall of the blastocyst is made of cells called **trophoblasts** which will form the villi which grow into the wall of the uterus at implantation. A small mass of cells inside this layer will form the embryo. As these changes occur, the zygote moves slowly down the oviduct and towards the uterus where it must implant in the uterine wall if further development is to take place. The cells secrete a hormone called **human chorionic gonadotrophin (hCG)** which maintains the corpus luteum, ensuring that it continues to secrete oestrogen and progesterone. (The presence of hCG in the urine is detected in a 'pregnancy test'.)

When the blastocyst arrives in the uterus it is still contained within the zona pellucida. As this breaks down the trophoblastic cells of the blastocyst come into contact with the endometrium of the uterus. They begin to invade the endometrium, secreting digestive enzymes and growing into the maternal tissues. This process, which results in the blastocyst becoming embedded in the endometrium, is known as implantation. It occurs as early as seven days after fertilisation.

Implantation is the first stage in the crucial association between maternal and fetal tissues and circulation which form the basis of mammalian development. As the trophoblastic cells become embedded in the endometrium of the uterus they differentiate to form finger like projections which penetrate deep into the endometrium. These are the **chorionic villi**. Enzymes secreted by the cells of the villi digest the walls of the spiral arteries and veins within the endometrium and create blood filled spaces around each villus. From here the maternal blood nutrients and oxygen diffuse into the villi and are delivered to the cells of the blastocyst. Carbon dioxide and other waste materials diffuse out of the blastocyst and into the maternal blood down their concentration gradients. The efficiency of these exchanges is improved by the large surface area of chorionic villi.



Structures shown are not all to the same scale

Over the following weeks rapid growth and development of both the chorionic region and the embryo occur. Within three to four weeks of fertilisation blood is circulating through embryo and villi. This improves the efficiency of exchange.

The structure and function of the placenta

The placenta is fully formed 12 weeks after fertilisation. On the maternal side it consists of projections of the endometrium between which lie a series of blood filled spaces. Blood from the maternal arteries enters the spaces where exchange is performed and then returns to the circulation in the maternal veins. On the fetal side, chorionic villi project into the blood filled spaces. Each villus contains branches of the umbilical artery and vein which form a dense network of capillaries. These join up to form the **umbilical artery** and **veins** which run through the umbilical cord to the embryo (at this stage called the fetus). It should be noted that the blood of mother and fetus are kept entirely separate. This helps to regulate exchanges between mother and fetus, protects the fetus from the effects of high maternal blood pressure which would damage its small blood vessels, prevents possible immune reactions which might occur if the fetus was of different blood group to the mother, and prevents the entry of mature female hormones which would be dangerous even for a female fetus.

The placenta has two main roles in relation to the development of the human embryo and fetus. Firstly it is the organ of exchange between mother and fetus, supplying the fetus with nutrients and oxygen and removing carbon dioxide and urea. Antibodies are also supplied to the fetus which protect it from infections in the first months of life. Secondly it is an endocrine organ producing several hormones throughout the gestation period (development time before birth).

In order to perform its exchange roles efficiently the placenta must provides a large surface area for exchange of nutrients and gases; a thin yet selectively permeable barrier between maternal and fetal blood; and a steep concentration gradient for each substance in the appropriate direction.

A large surface area is provided by the numerous villi and the highly branched capillaries within the villi between the fetal blood contained in vessels and the maternal blood in the large blood filled spaces of the placenta. Maternal and fetal blood are separated by just a few layers of cells creating a short diffusion distance. Small molecules (eg. oxygen, carbon dioxide, urea, water) move across by simple diffusion whilst amino acids and glucose cross by facilitated diffusion. Some vitamins and minerals move by active transport.

Oxygen, glucose, amino acids and other substances required by the fetus need to be at a much higher concentration in the maternal blood than they are in the fetal blood for efficient diffusion to occur. Similarly, carbon dioxide and urea must be at a low concentration in the maternal blood if they are to diffuse out of the fetal blood and be removed. Favourable gradients are maintained by the fact that the fetus has a small volume of blood but a high rate of blood flow whilst the mother has a slower rate of blood flow but a larger volume of blood in the spaces of the placenta, and by an overall counter-current system of blood flow in which the maternal and fetal blood flow in opposite directions maintaining steeper diffusion gradients. Just before birth about 10% of the mothers blood flows through the placenta on each circuit of the body, aiding rapid exchanges.

Hormones secreted by the placenta

The placenta secretes three main hormones:

- Human chorionic gonadotrophin (hCG)
- Progesterone
- Oestrogen.

Each has specific roles relating to fetal development and/or maternal changes associated with pregnancy, birth and lactation (milk production).

hCG is secreted in only small amounts by the placenta but is thought to have roles in suppressing FSH and LH from the pituitary and in stimulating development of some fetal systems.

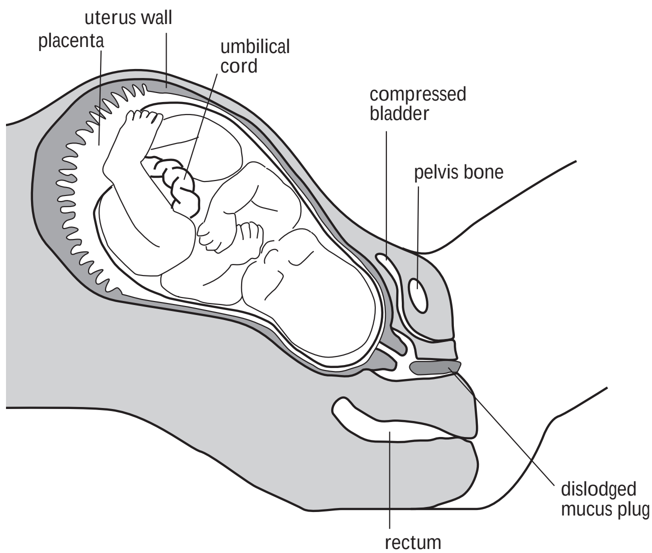
Progesterone is secreted in relatively large quantities (250-350mg/day). High levels prevent shedding of the endometrium, inhibit ovulation and may aid breast development.

Oestrogen is necessary for the maintenance of pregnancy (perhaps through inhibiting FSH) and is thought to be involved in preparing the body for birth and in breast development.

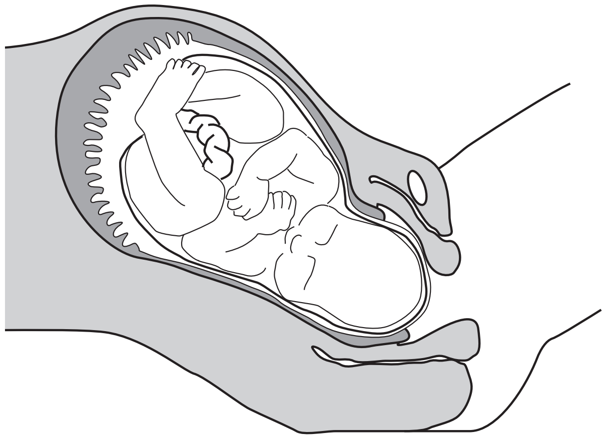
Birth

Approximately 38 weeks after fertilisation the fetus is ready to be born. At around this time the level of the hormone progesterone decreases rapidly and the level of oestrogen increases. The effect of this is to make the uterus wall more susceptible to the effects of **oxytocin**, a hormone produced by the posterior pituitary gland, which causes contraction of the muscle layer of the uterus (the myometrium). The exact signals which trigger these changes in hormone levels and hence initiate the birth process are not clear but are thought to involve a mixture of physical and hormonal signals from both mother and fetus.

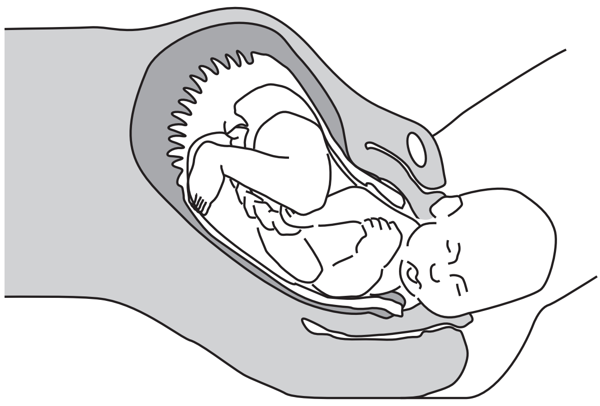
The birth process can be divided into several stages.

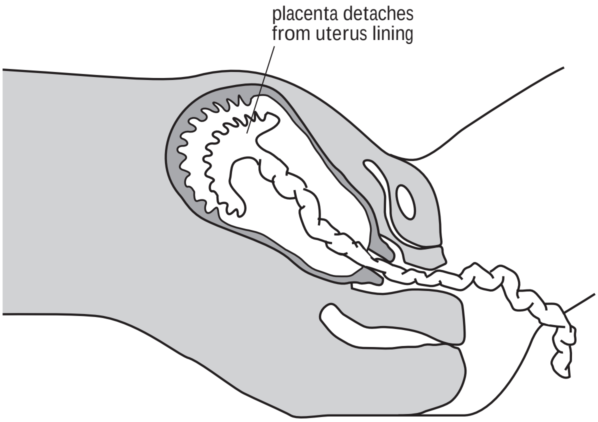


In the **first stage**, which may last 12 hours or more, the uterus begins to contract and the cervix begins to dilate. During, or sometimes before the main contractions begin the amniotic sac bursts and the fluid is released via the vagina. A plug of mucus which blocks the cervix during pregnancy also detaches and passes out of the vagina. Over time the force and frequency of the contractions increases under the control of oxytocin and they spread out through the muscle fibres of the uterus from top to bottom, gradually pushing the fetus downwards toward the cervix. By the end of this stage the cervix has dilated to about 10cm in diameter, wide enough to allow the fetal head to 'engage' and then pass through.



The **second stage** involves the actual birth of the baby which is pushed out of the uterus, through the cervix and down the vagina. The majority of babies are born head first, having moved into this position in the uterus in the weeks leading up to birth. The head and shoulders of the baby are the widest part so once these have passed through the cervix the rest of the body, still attached to the placenta via the umbilical cord, follows more easily. Once it emerges the baby begins to breathe. Since it no longer requires an oxygen supply via the placenta the umbilical cord is cut and tied/clipped.





The third stage involves the loss of the placenta from the body. Final contractions allow this structure to detach itself from the uterus wall and pass out of the vagina. Although a large loss of blood may be expected, muscle fibres around the blood vessels contract to limit this.

Lactation

In its first nine months of life before birth the fetus obtains all its nutritional requirements via the placenta. After birth it must ingest milk produced by the mammary glands of the mother and delivered via the nipple. Suckling begins soon after birth and a new born baby may spend several hours per day engaged in feeding. For the first four months of life babies are rarely given any other food or drink, and in many cultures breast feeding may continue to supplement other foods for several years. The production of milk is known as lactation.

Milk, is a watery fluid containing the sugar lactose along with fat, and proteins, some vitamins and minerals. It is produced in the milk glands of the breast and its secretion is stimulated by suckling. The substances contained in milk are easily digested in and absorbed from the baby's gut.

Milk production is controlled by the interaction of several hormones. During pregnancy, the hormones oestrogen and progesterone stimulate the development of breast tissue containing milk glands and milk ducts. However, milk is not produced and released at this stage as progesterone and oestrogen inhibit another hormone, **prolactin** which is also required. The fall in levels of progesterone and oestrogen after birth removes this inhibition and allows prolactin from the anterior pituitary gland to act on the breast tissue. It stimulates the milk glands of the breast which are lined with milk producing epithelial cells to secrete milk.

Milk is not released until the milk ejection reflex is initiated by the sucking action of a baby. The following steps are involved:

- nerve impulses from sensory receptors in the nipple are sent to the hypothalamus; this stimulates the posterior pituitary gland to produce **oxytocin**;

- oxytocin acts on the involuntary muscle around the milk glands which contract, forcing milk through the ducts and out of the nipple.
- At the same time, suckling also causes the release of prolactin from the anterior pituitary, hence maintaining milk production.

By these feedback mechanisms it can be seen that continued milk production and release will only continue if a baby is suckling.

◆ CHECKPOINT SUMMARY

- Spermatozoa are ejaculated by the erect penis in the region of the cervix at the entry to the uterus.
- Peristaltic movements of the female tract and the motility of the spermatozoa themselves result in movement up the oviducts.
- If these events coincide with the release of one or more ova, fertilisation can occur high up in the oviduct.
- The fertilised egg immediately enters into mitotic cell division, and is a hollow ball of cells (blastocyst) by the time the uterus is reached.
- The blastocyst becomes implanted in the pre-prepared lining of the uterus, and secretes gonadotrophic hormone.
- The lining of the uterus is maintained and the menstrual cycle is suspended.
- The placenta develops and secretes progesterone which helps to maintain the pregnancy and suppress further ovulation.
- The placenta attaches the fetus to the uterine wall and has a large surface area for the exchange of materials with the maternal circulation, e.g the absorption of oxygen and nutrients, and the elimination of waste products, e.g. urea and carbon dioxide.
- The efficiency of exchanges is increased by extensive breakdown of tissue in the placenta and the uterus wall, reducing the diffusion distance between the two circulations.
- At full term the fluid filled amnion which surrounds the fetus bursts, the fluid lubricates the system and birth is initiated.
- The hormone oxytocin secreted by the posterior pituitary lobe produces powerful contractions of the uterus, induces lactation, and stimulates the ejection of milk during suckling.
- The hormone prolactin secreted by the anterior pituitary lobe stimulates lactation.

