PLANT BIOLOGY

(38p)

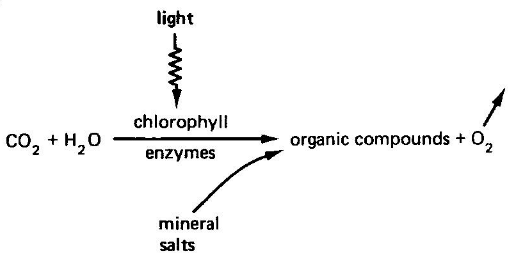
CONTENTS

PLANT NUTRITION

Most plants and many bacteria are capable of synthesizing all their organic nutritional requirements from inorganic materials, using energy from sunlight, by the process of photosynthesis. Some bacteria are chemosynthetic, using energy from chemical reactions for their synthetic reactions. Both photosynthetic and chemosynthetic types are also called **autotrophic**. The fungi and some bacteria are **heterotrophic**, which means that they cannot synthesize their own organic compounds and so require an external supply.

Photosynthesis

The key factor of photosynthesis is that light energy is trapped as chemical energy in a wide variety of stable chemical compounds that do not spontaneously break down, and which can therefore be stored. In outline the process can be represented by the following equation:



Photosynthesis occurs in two main stages:

(a) a light-dependent stage and
(b) a non-light-dependent stage or so-called 'dark stage'.

It is the main source of organic compounds in the world and the only source of atmospheric oxygen.

Conditions necessary for photosynthesis

WATER

Water is never a direct limiting factor in photosynthesis as water shortage would produce other disturbances to plant metabolism before it could directly affect photosynthesis. It supplies the hydrogen ions for the reduction of the fixed[129] carbon dioxide into organic compounds; oxygen is released as a by-product.

CARBON DIOXIDE

On warm, sunny days the atmospheric level of 0.03 per cent carbon dioxide is the factor that slows up the process more than any other. Under these conditions the carbon dioxide concentration is known as the **limiting factor.** Carbon dioxide supplies carbon and oxygen atoms for the organic compounds.

LIGHT

Only about 1 per cent of the light falling on a plant is used in photosynthesis, and it usually only acts as a limiting factor during early morning and dusk or in shaded positions (although shade plants have an optimum rate of photosynthesis at relatively low light intensities). It supplies the energy for the synthesis of carbon dioxide into organic compounds.

TEMPERATURE

Since photosynthesis is an enzyme-catalysed process, there is an optimum temperature of about 20–30 °C. However, only the non-light-dependent carbon assimilation process is affected by temperature. The light-dependent reaction is unaffected by temperature changes and thus at low light intensities temperature cannot be a limiting factor.

The effects of CO_2 concentration, light intensity and temperature, on the rate of photosynthesis show an interesting interdependence (see Figure 6.1).

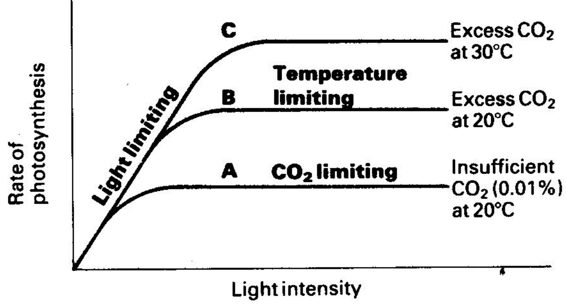


Figure 6.1 *Rate of photosynthesis under varying conditions of CO_2 concentration, light intensity, and temperature*

At low light intensities, the 'dark' stage is receiving only a limited amount of the products that it requires from the 'light', stage and is therefore being slowed or limited by it; light is the *limiting factor*. As the light intensity increases a point is reached when the dark stage is at is maximum and any further increase in light intensity has no effect. At this point factors that affect the dark stage become limiting such as CO_2 concentration (curve A) and temperature (curve B).

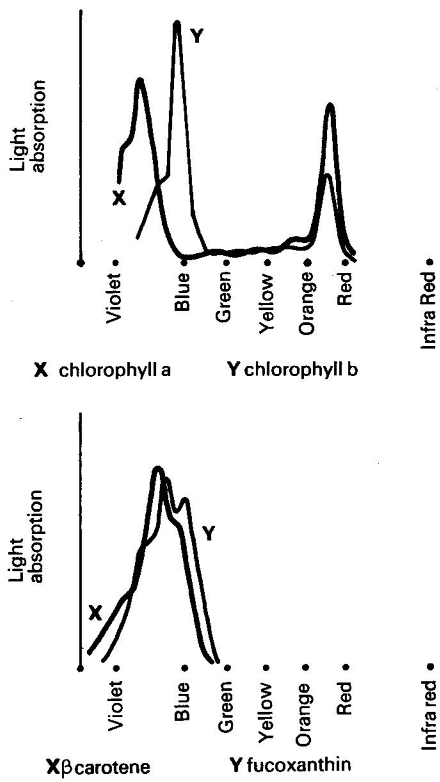


Figure 6.2 *Absorption spectra of photosynthetic pigments*

Chlorophyll

This is a complex organic molecule containing magnesium. There are two main types, **chlorophyll a**, which is present in all photosynthetic organisms which evolve oxygen, and **chlorophyll b**, which is present in the higher plants and green algae only.

The chlorophyll is localized within chloroplastids, and converts the electromagnetic energy[371] from the sun into chemical energy of chemical bonds. It is usually associated with accessory pigments such as carotenoids which protect the chlorophyll from photo-oxidation and absorb light energy which is transferred to chlorophyll a.

Chlorophyll is rarely a limiting factor, except in extreme cases of **chlorosis**, when the plant loses chlorophyll and becomes yellowy-green in colour. This may happen when the plant grows in the dark, or is lacking in certain essential chemical elements.[132]

Absorption and action spectra

An **absorption spectrum** is obtained by measuring the amount of light absorbed by the different photosynthetic pigments in a leaf, namely chlorophyll a, chlorophyll b, carotenoids and xanthophyll.

An **action spectrum** is obtained by measuring the amount of photosynthesis that takes place under lights of different wavelengths.

When the two spectra are compared for the same plant it can be seen that they correspond closely. This indicates that most of the wavelengths of light absorbed by the complex of pigments in the chloroplasts are used in photosynthesis.

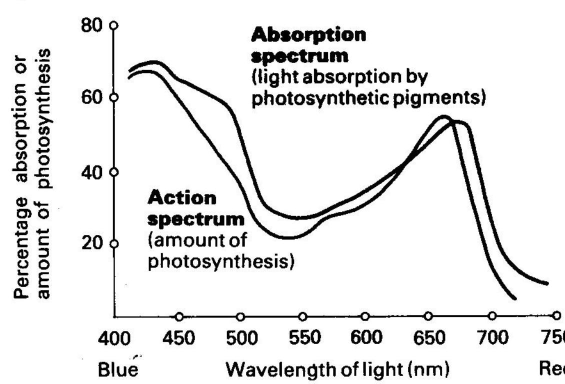


Figure 6.3 *Absorption and action spectra compared*

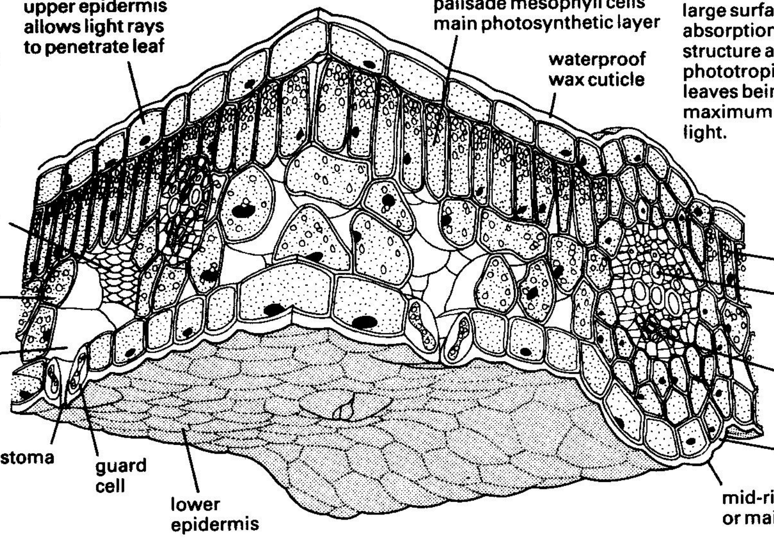


Figure 6.4 *T.S. dicotyledonous leaf (highly magnified)*
Palisade mesophyll cells are elongated with many chloroplastids at the edge for rapid CO_2 uptake from the extensive vertical intercellular spaces. Also light can penetrate without having to pass through many cross walls and air spaces.

The outline biochemistry of photosynthesis

A simple equation for photosynthesis is often given as:

$$6CO_2 + 6H_2O \xrightarrow[\text{chlorophyll}]{\text{light}} C_6H_{12}O_6 + 6O_2$$

However, this equation implies that at least some of the oxygen produced comes from the CO_2. In fact isotope labelling with ^{18}O demonstrate that all the oxygen liberated in photosynthesis comes from water. Therefore a more accurate form of this simple equation would be:

$$6CO_2 + 12H_2O \xrightarrow[\text{chlorophyll}]{\text{light}} C_6H_{12}O_6 + 6O_2 + 6H_2O$$

This equation, however, still gives no indication of the complex sequence of steps or the complex range of products of photosynthesis.

LIGHT-DEPENDENT STAGE

In this stage light is absorbed by the chlorophyll and accessory pigments (carotenoids) in the grana of the chloroplasts. Chlorophyll is involved in the light-assisted dissociation or photolysis of water which results in the dissociation of water into hydrogen ions (H^+) and hydroxyl ions (OH^-):

$$4H_2O \xrightarrow[\text{Chlorophyll}]{\text{light}} 4(OH^-) + 4(H^+)$$

At the same time electrons are raised to higher energy levels in the chlorophyll molecules. These electrons pass along a chain of electron-carriers and combine with the hydrogen ions (H^+) from the water to convert the co-enzyme NADP to $NADPH_2$. This is then used as a reducing agent in the non-light dependent stage in which organic compounds are synthesized from CO_2.

Electrons from the hydroxyl ions pass down an electron-carrier system to the chlorophyll molecule, replacing those that combined with the hydrogen ions in $NADPH_2$. As the electrons pass down the electron-carrier systems, 'energy-rich' ATP is generated from ADP and phosphate. This ATP is used as a source of energy in the synthetic reactions of the non-light dependent stage.
The hydroxyl ions reform into water, and oxygen is liberated in the process:

$$4(OH^-) \rightarrow 2H_2O + O_2$$

The products of the light stage are $NADPH_2$ (a reducing agent) and ATP (an energy-rich carrier) both of which are used in the non-light dependent stage; and water and oxygen as by-products.

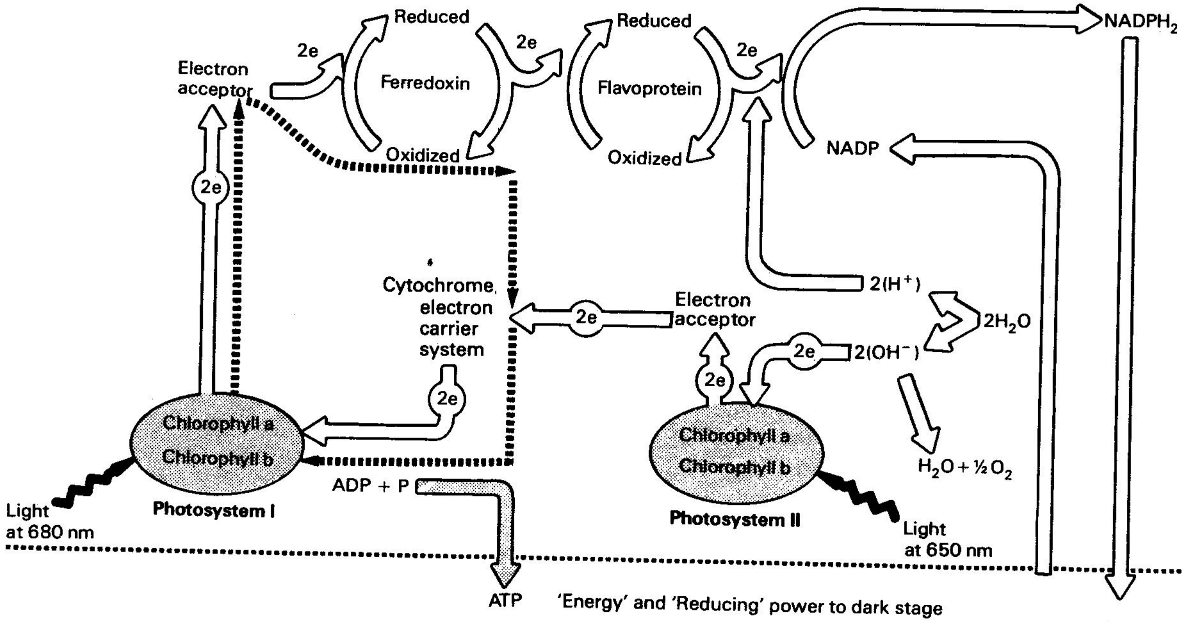


Figure 6.5 *Outline of the light-dependent stage of photosynthesis*
Chlorophyll is activated by the absorption of light. The photo-excited chlorophyll of photosystem I yields electrons which pass along a series of carriers to join up with protons (H^+) from the water and reduce the co-factor NADP to $NADPH_2$. This provides the so-called reducing power for the dark reaction. The electrons that are lost from photosystem I are replaced by electrons from the dissociation of water via photosystem II. As the electrons pass along the electron-carrier system, energy is 'trapped' in ATP. This process of ATP formation is known as **non-cyclic photophosphorylation** as the electrons that return to photosystem I are not from the same source as those that left. Another process of ATP formation known as **cyclic photophosphorylation** exists in which the electrons generated in photosystem I return to it (this pathway is shown by the red dotted line).

LIGHT INDEPENDENT ('DARK') STAGE

The dark stage does not have to occur in the dark, it is simply not dependent upon light so it can, and does, proceed in the light.

The carbon dioxide in the air must first of all be trapped, or fixed, by an acceptor molecule into a form which can then be reduced and synthesized into organic compounds. There are two main pathways by which carbon dioxide is 'fixed' or trapped.

C_3*-type plants*

Here the carbon dioxide combines with a five carbon (5C) acceptor substance to form a six-carbon compound which then breaks down into a three-carbon compound (3C). The 5C acceptor substance is **ribulose bis phosphate,** and the 3C compound is **phosphoglyceric acid.**

The ATP and $NADPH_2$ from the light reaction are used to convert the phosphoglyceric acid into carbohydrates and other organic compounds; and to regenerate the ribulose bisphosphate.

C_4*-type plants*

Here the carbon dioxide combines with a three-carbon acceptor substance to form a four-carbon compound.

Examples of C_4 plants are maize and sugar cane.

At high light intensities four-carbon plants have a photosynthesis rate two to three times greater than three-carbon plants. The leaves have a large internal surface area, short carbon dioxide diffusion pathways, and steep diffusion gradients,[368] all of which increase the rate of carbon dioxide uptake. The mesophyll cells feed their photosynthetic products into specialized **bundle sheath cells** which contain chloroplastids which are larger than normal and lack grana. These bundle sheath cells lie close to the phloem of the vascular bundles in the leaf and their products can be rapidly translocated away.

Transport in Multicellular Plants

Content

- The need for, and functioning of, a transport system in multicellular plants.

Learning Outcomes

Candidates should be able to:

a) explain the need for transport systems in multicellular plants in terms of size and surface area to volume ratios.

b) define the term transpiration and explain that it is an inevitable consequence of gaseous exchange in plants.

c) describe how to investigate experimentally the factors which affect transpiration rate.

d) describe the distribution of xylem and phloem tissue in roots, stems and leaves of dicotyledonous plants.

e) describe the structure of xylem vessels, sieve tube elements and companion cells.

f) relate the structure of xylem vessels, sieve tube elements and companion cells to their functions.

g) explain the movement of water between plant cells and between them and their environment, in terms of water potential. (No calculations involving water potential will be set.)

h) describe the pathway and explain the mechanism by which water is transported from roots to leaves.

i) explain translocation as an energy-requiring process transporting assimilates, especially sucrose, between the leaves (sources) and other parts of the plant (sinks).

j) describe one possible mechanism of transport in phloem, and the evidence for and against the mechanism.

k) describe how the leaves of xerophytes are adapted to reduce water loss by transpiration.

Learning Outcome (a)

The need for TRANSPORT SYSTEMS in MULTICELLULAR PLANTS in terms of SIZE and SURFACE AREA to VOLUME RATIOS

As with animals, simply speaking, the larger the plant, the smaller is its surface area to volume ratio. This relationship is used to explain the development of transport systems to supply internal cells far removed from the exchange surfaces with the environment, and to transport materials between different regions of the plant.

Algae e.g. seaweeds, do not have specialised transport systems. Typically Algae are aquatic or semi-aquatic, and absorb water and nutrients over the whole surface. They also tend to be relatively small with large surface area to volume ratios which ensures that all parts of the plant are close to the surface and can be supplied by diffusion. Some seaweeds have fronds several metres in length which could not be considered as 'small'. However, the fronds are thin and flattened and have a huge surface area to volume ratio.

Terrestrial plants, namely ferns, conifers and flowering plants, have special problems associated with being rooted in the soil with their aerial parts being exposed to the drying atmosphere. They have true roots, stems and leaves, and can reach a very large size. They have transport systems (vascular tissues) running throughout the plant, the xylem and the phloem. Many of these plants can be relatively small, and become secondarily aquatic (e.g. the water lily, Canadian pondweed etc) but still retain their transport systems albeit in a reduced form. Thus it is important to remember that discussions of the development of transport systems also involves the level of complexity of the organism involved.

Xylem transports water and inorganic ions from the roots up the stems to the leaves for photosynthesis.

Phloem transports sugars (sucrose) mainly from the leaves to the root and shoot tips for their respiration, or to food storage structures in various parts of the plants.

Learning Outcome (b)

TRANSPIRATION

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 transpiration occurs through the stomata of the leaves when they 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 a transport stream (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.

◆ CHECKPOINT SUMMARY

- Principles of relationship between size, shape and surface area to volume ratio hold for plants as previously discussed with animals.
- In terrestrial plants, transport systems are necessary (independent of SA/V) as they are rooted in the soil and have leaves for photosynthesis in the air.
- Large plants (trees) have large surface area to volume ratios as a result of their leaves, but still have transport systems as diffusion is insufficient to account for the rate of transport throughout the plant.
- Xylem transports water from roots to leaves.
- Phloem transports organic compounds (assimilates) e.g. sucrose from sources (leaves or storage organs) to sinks (regions where respiration predominates e.g growing tips of roots and shoots).
- Transport in xylem unidirectional.
- Transport in phloem in both directions.

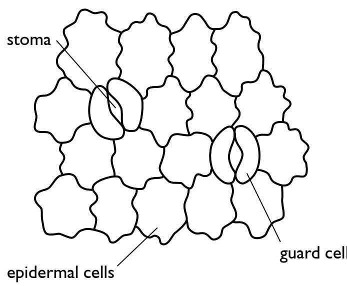
Factors affecting transpiration include anything that affects the supply of water to the leaves, and the evaporation of water from the leaves. The main factors are:

- 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; it decreases as temperature increases. A rise of 10ºC 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 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.

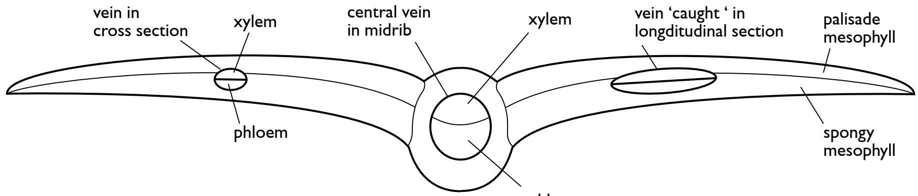
◆ CHECKPOINT SUMMARY

- Transpiration is the loss of water vapour from the leaves.
- An unavoidable consequence of having stomata opening for the uptake of carbon dioxide (and release of oxygen) in the light.
- Evaporation provides upward movement of water column in xylem - the transpiration stream.
- Transpiration stream provides for upward transport of water and dissolved inorganic ions (and some organic compounds) from roots to leaves.
- Evaporation from leaves provides some cooling effect, but not when most needed as stomata shut, and leaves wilt in conditions of extreme heat.
- Transpiration rate affected by any factor that affects evaporation of water: relative humidity, temperature. air speed, availability of water, light intensity, stomatal number, distribution, and degree of opening.

Surface view of leaf epidermis



Low power plan leaf (section)



Section of leaf showing internal structure

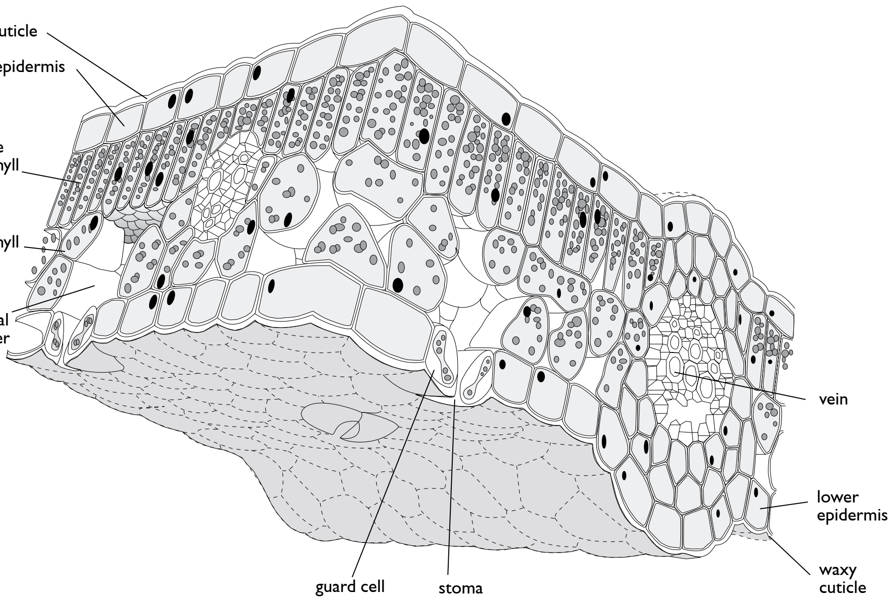
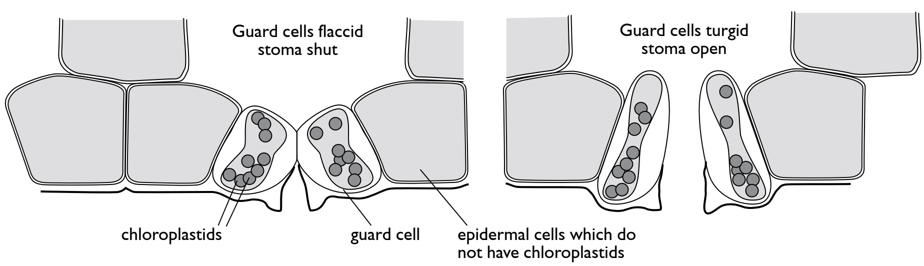
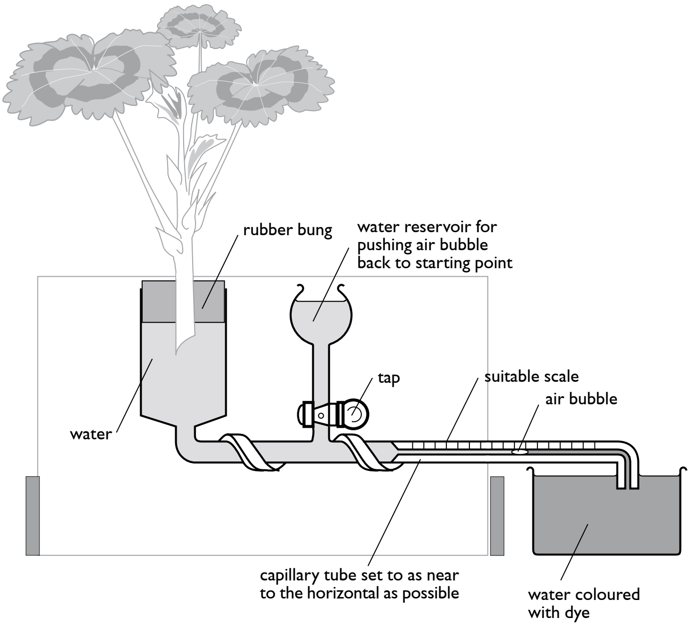


Diagram of guard cell action



Potometer



Learning Outcome (c)

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.

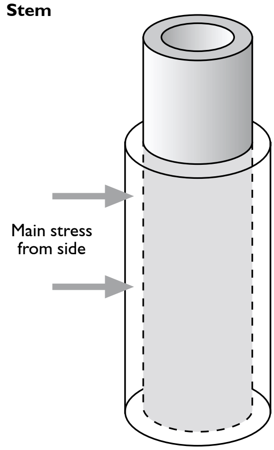
◆ CHECKPOINT SUMMARY

- Transpiration can be measured using a potometer. The principle of which, is that as the water evaporates from the leaves of the shoot an air bubble is drawn along the capillary tube at the same rate - thus giving a measure of the rate of transpiration.
- Actually it is the rate of water uptake that is being measured
- In this experiment the cross sectional area of the cut shoot is not as large as the equivalent area of root hairs that would normally supply the leaves, therefore the rate of uptake is less than the rate of transpiration.

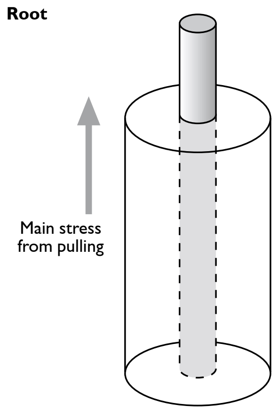
Learning Outcome (d)

The DISTRIBUTION OF XYLEM and PHLOEM in ROOTS, STEMS and LEAVES of DICOTYLEDONOUS PLANTS

Flowering plants may be classified into two main groups on the basis of the number of their seed leaves (cotyledons), namely the **monocotyledons** with one and the **dicotyledons** with two. There are a wide variety of other features that members of each group have in common including the distribution of xylem and phloem tissues in the vascular bundles in the roots, stem and leaves. As xylem has an important structural and supporting role, the distribution of vascular tissues in the root, stems and leaves reflects the mechanical stresses endured by the particular region. In dicotyledonous plant stems, vascular tissue 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 plants 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 for photosynthesis.



Vascular tissue forms a strengthened cylinder which resists bending



Vascular tissue forms a strengthened inner core which resists pulling action

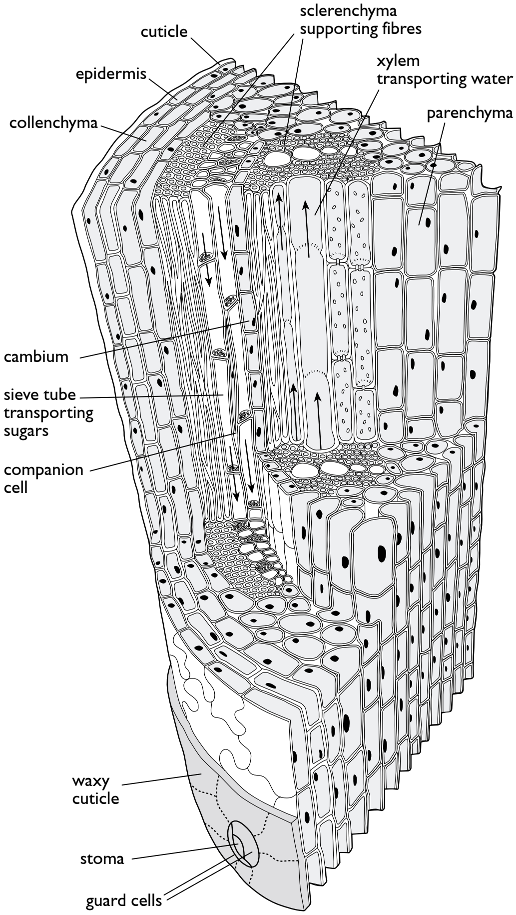
Learning Outcome (e) & (f)

STRUCTURE and FUNCTION of XYLEM VESSELS, SIEVE TUBE ELEMENTS and COMPANION CELLS

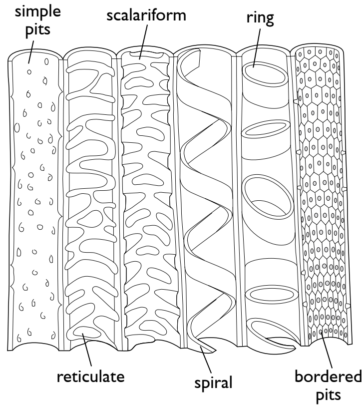
Xylem tissue of flowering plants consists of elongated tracheids and vessels, which have no living contents, and form tubes in which water travels from the roots to the leaves. Tracheids and vessels have strong lignified walls. Lignin is a tough, hard, waterproof substance, and lignified tissue makes up what is commonly known as 'woody tissues' or 'wood'. These lignified tissues are important in supporting the plant. 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. Each tracheid (about 5 mm long) has end walls, but 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, allowing much quicker 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.

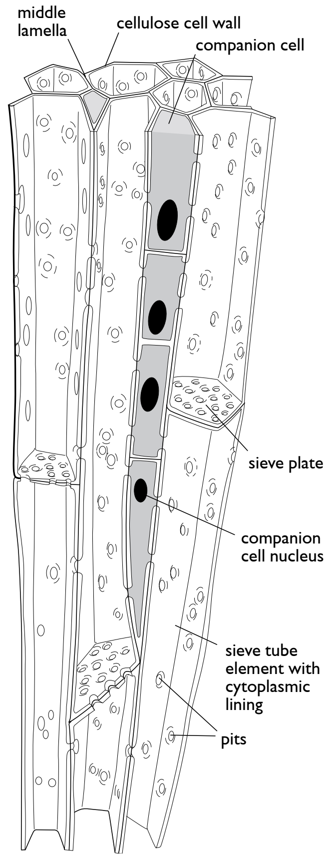
Diagram of plant stem structure



Xylem vesssels showing different types of lignified thickening



Phloem Cells



Learning Outcome (g)

MOVEMENT of WATER between PLANT CELLS and between them and their ENVIRONMENT in terms of WATER POTENTIAL

In plant cells a non-living cellulose cell wall surrounds the cell surface membrane. The cell wall is freely permeable to water and dissolved substances (solutes.) By contrast, the cell surface membrane is partially permeable, restricting the movement of solutes but allowing water to diffuse in and out more freely. Where a solution is separated by a partially permeable membrane from pure water or a solution of different concentration, the movement of solutes by diffusion is restricted and water will diffuse into the more concentrated solution until equilibrium is reached. The special case of the diffusion of water across a partially permeable membrane is known as **osmosis**.

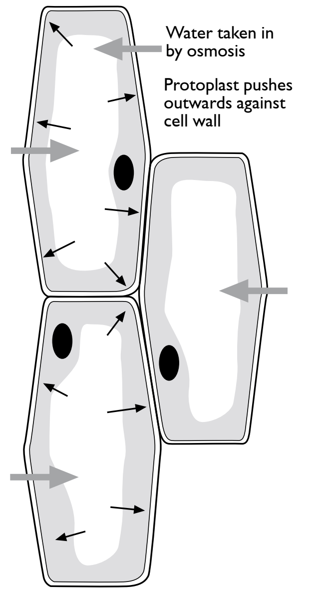
Water moves into and out of the cell protoplast according to the relative numbers of water and solute molecules on either side of it. The water potential of a fluid is measured in relation to pure water. If the fluid is pure water, there is no movement, so the **water potential of pure water is zero**. The water potential of any solution is less than pure water and is therefore negative. The more negative the water potential the greater the tendency of water to move into that system.

Water will always tend to move from regions of high water potential to regions of lower water potential. Where a plant cell is surrounded by a solution with a higher water potential than that of the cell contents (protoplast), water will move into the cell. As it does so, the cell contents expand until this tendency is counterbalanced by the force exerted by the stretched cell wall. At this equilibrium point the cells are described as fully **turgid**. In a well watered plant, the turgid cells exert pressure on each other making the whole structure rigid (especially the spongy mesophyll in leaves.) Loss of water causes a loss in turgor, the cells become **flaccid**, and the leaves wilt.

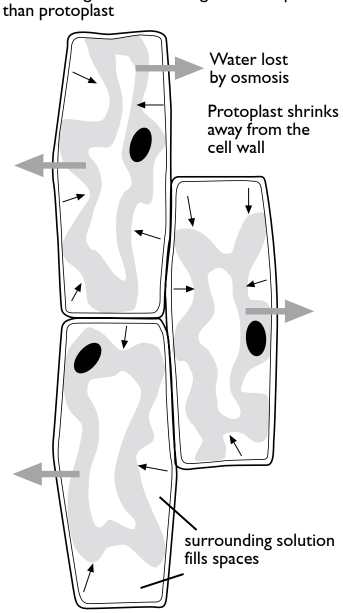
In the very unusual case of the surrounding water having a lower water potential than the plant cells (for example, where the soil is flooded with salty water) water will move out of the cell by osmosis so that, in extreme cases the membrane shrinks away from the cell wall. Cells in this state are said to be **plasmolysed**. (Note that all plasmolysed cells are flaccid, but not all flaccid cells are plasmolysed.)

All these considerations affect the movement of water between plant cells and between them and their environment. For example root hair cells gain or lose water in relation to the relative water potentials of their contents and the soil solution, and leaves lose water to the atmosphere according to the same principles.

Turgid Cells
Surrounding solution has lower water potential than protoplast



Plasmolysed Cells
Surrounding solution has higher water potential than protoplast



Learning Outcome (h)

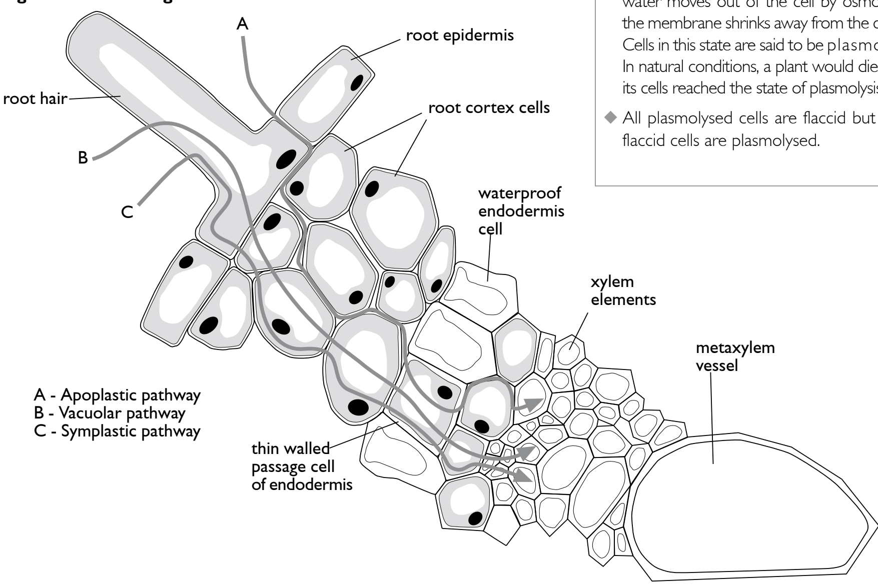
PATHWAY and MECHANISM of WATER TRANSPORT from ROOTS to LEAVES

Transpiration provides the main force for water transport from root to leaf. At the other end of the plant, water is taken up by the root hair cells which occupy a small region just behind the growing tips of new roots. Root hairs take up mineral ions by active transport, an energy-requiring process, against the diffusion gradient. This leads to accumulation of ions in greater concentrations inside the plant than in the soil solution. 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.

There are three main pathways of water movement across the root to the xylem in the centre. Two involve movement of water from cell to cell down a water potential gradient as the contents of adjacent cells become successively diluted by the incoming water. One of these, the **vacuolar pathway** involves the movement of water through the cytoplasm and the vacuoles and their membranes. The other involves the movement of water through the cytoplasm avoiding the vacuoles and their membranes, the **cytoplasmic pathway**. Both these are high resistance pathways as they involve water moving through the cytoplasm and membranes.

The vast majority of water, however, is pulled in directly by the transpiration stream acting through a continuous system of water between the soil solution and the xylem travelling in the porous cellulose cell walls of the cells, the **apoplastic pathway**. This is a pathway of low resistance as the water does not enter the cells as such.

Passage of water through the root



◆ CHECKPOINT SUMMARY

- The cell membrane is partially permeable allowing water molecules to pass through it but not most solute molecules.
- The cell wall is freely permeable to everything.
- As partially permeable membrane prevents free diffusion of solute molecules, water moves by osmosis down a water potential gradient.
- Water potential is a measure of the tendency to gain or lose water in relation to pure water. If the fluid is pure water there is no movement and the water potential is zero.
- The presence of solutes slow the movement of water molecules giving any solution a negative water potential at normal pressures.
- Water will move from regions of high to low water potential (from less negative to more negative values).
- Plant cells in solutions (or water) more dilute than their contents gain water by osmosis and the cell contents expand until this force is counterbalanced by the force exerted by the stretched cell wall. At this equilibrium point the cells are described as turgid. In a well watered plant, the turgid cells exert pressure on each other making the whole structure rigid.
- Loss in water causes a loss in turgor, becoming flaccid, resulting in wilting of leaves.
- If the water potential of the cell contents is greater than that of the surrounding solution water moves out of the cell by osmosis and the membrane shrinks away from the cell wall. Cells in this state are said to be plasmolysed. In natural conditions, a plant would die before its cells reached the state of plasmolysis.
- All plasmolysed cells are flaccid but not all flaccid cells are plasmolysed.

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 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 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 water column is supported and prevented from falling back down under gravity in the xylem elements by adhesion to the lignified walls of the xylem elements. 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 it is still important in support).

◆ CHECKPOINT SUMMARY

- Transpiration in the leaves generates the major force for the upward movement of water in the transpiration stream.
- 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.
- Three main pathways of water movement across the root, are the vacuolar pathway, the cytoplasmic pathway, and the apoplastic pathway.
- Once in the xylem, capillarity aids rise of water, but main force is generated by transpiration at the leaves.
- Cohesion prevents breakage of continuous water column as it is pulled up under negative pressure (tension).
- Adhesion to the walls of the xylem support the water column.
- Breakages (air bubbles) caused by frost and/or wind damage can be by-passed via pits in lateral walls of xylem tracheids and vessels.
- Endodermis passage cells are the only point where water must pass through cell surface membranes on its passage through the plant.

Learning Outcome (i)

TRANSLOCATION of ASSIMILATES especially SUCROSE

Translocation is the name given to the energy-requiring process in which organic materials synthesised by the plants, particularly sucrose are transport 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.

Translocation from sources to sinks

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 are 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 shoot tips, 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.

◆ CHECKPOINT SUMMARY

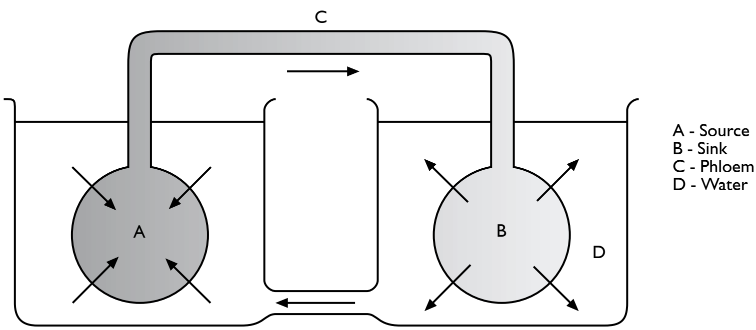
- Translocation of assimilates (organic substances synthesised in the plant) e.g. sugars, amino acids, hormones, nucleic acids etc. occurs in the phloem tissue.
- Organic materials move from an area of manufacture (source) to an area where they are used (sink). Sucrose thus moves from the leaves (sources) to actively growing and respiring regions such as the roots, flowers, and new buds (sinks).

Learning outcome (j)

MECHANISM of TRANSPORT in PHLOEM

Diffusion is not sufficient to account for the observed rates of flow in the phloem which are many times faster than could be explained by diffusion alone. 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 results in 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 pressure gradient, for example from leaves to roots. The flow is 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).

Mass flow diagram



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' exude out of the broken ends for periods as long as 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 of 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 largest distances required in the tallest trees.

Evidence against this mechanism

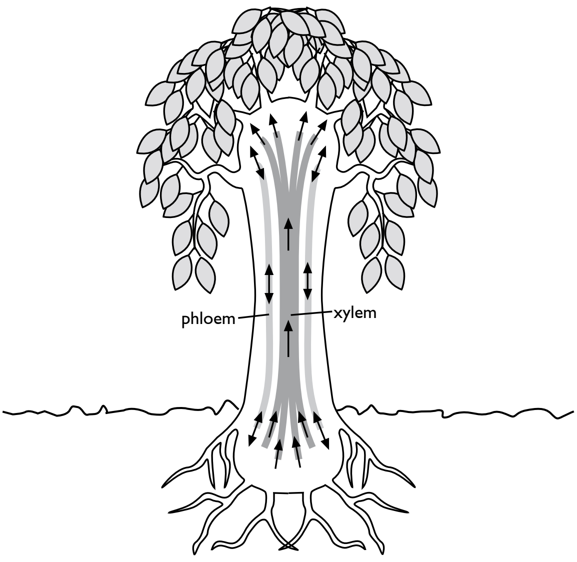
Evidence against this mechanism is provided by radioactive tracer studies which indicate that substances move in different directions at the same time (although this could be occurring in different sieve tube elements, which would still be explicable in terms of the mass flow theory).

Also the movement is not simply from source to sink. Mature leaves kept in the dark, unable to photosynthesis and supply their own sugars for respiration, fail to 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. root tips, food storage organs and apical meristems 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.

Mass flow in xylem and phloem



NB. Movement in the phloem can occur in both directions

◆ CHECKPOINT SUMMARY

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

Learning outcome (k)

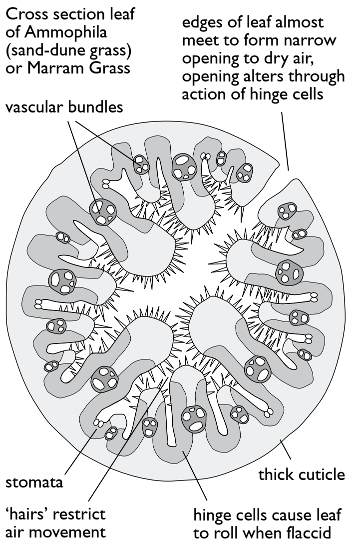
XEROPHYTIC ADAPTATIONS to REDUCE WATER LOSS by TRANSPIRATION

Plants adapted to growing in conditions of water shortage are known as xerophytic plants or xerophytes. This group includes plants from desert regions, as well as those in temperate regions on rapidly draining sandy soils.

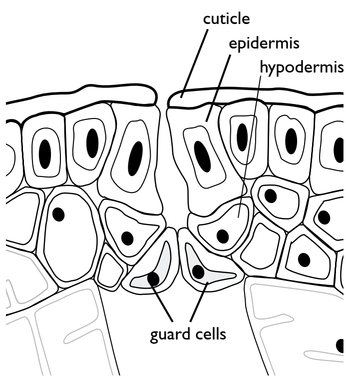
The main way in which terrestrial plants lose water is by evaporation from their leaves, a process known as transpiration. Some water is lost in this way over the whole leaf surface through the cuticle (cuticular transpiration), but most is lost through the stomata, which typically open in the light for the absorption of carbon dioxide for photosynthesis. Xerophytes show many structural adaptations of the leaves which decrease the rate of transpiration, and individual species can show any combination of these adaptations.

- 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 in 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 protects 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, indeed 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 photosynthesisis 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.

Marram Grass T.S.



Pine Needle Stomata



SEXUAL REPRODUCTION

(7 PAGES)

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

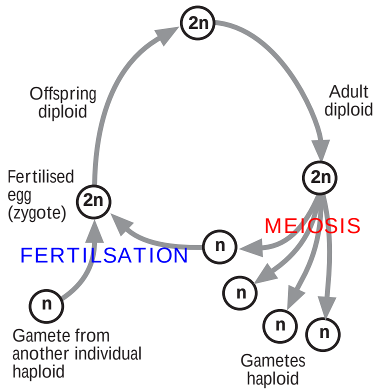
- The structure and functions of the principal parts of an insect-pollinated dicotyledonous flower and a grass.
- Pollination and the events leading to fertilisation.
- The adaptations related to insect and wind pollination.
- The significance of the mechanisms for ensuring cross-pollination; protandry,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

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 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.

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 so that 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.

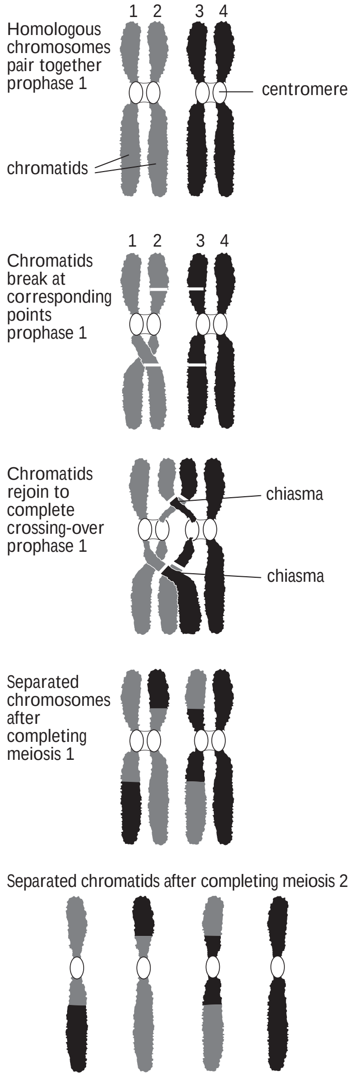
Crossing over, and the random alignment and separation of maternal and paternal chromosomes, ensures any gametes being formed are unique and therefore introduces genetic variation into the gametes.

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 in 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.



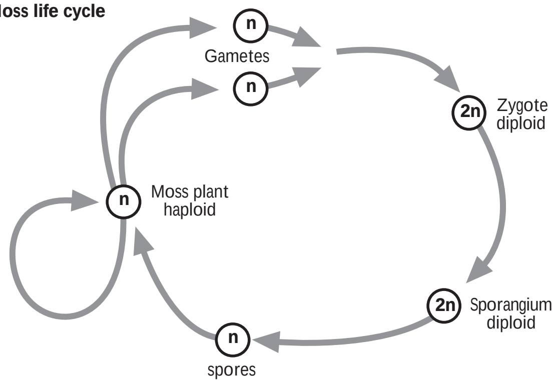
Usually 2 or 3 cross-overs affect each chromosome pair. Note cross-overs can occur between 1&3; 1&4; 2&3; 2&4, but not 1&2 or 3&4

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.

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.

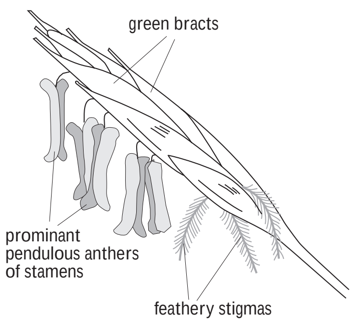
Insect pollinated flowers typically have various combinations of the following features.

- 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.

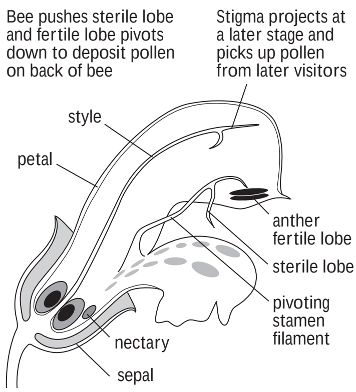
Wind pollinated flowers typically have various combinations of the following features.

- 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.

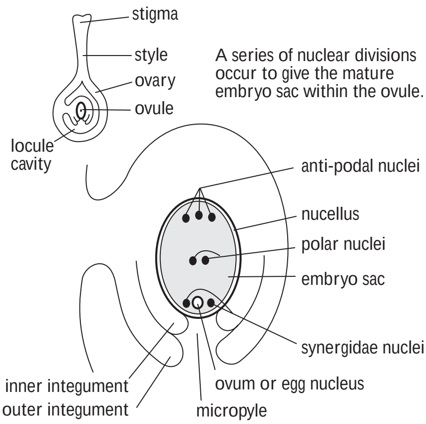
Fertilisation

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.

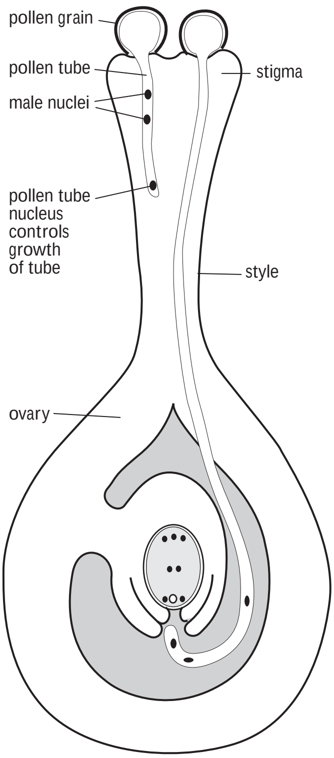
When a pollen grain lands on a receptive stigma, it germinates forming a pollen tube which grows through the tissues of the style and ovary until it reaches the ovule, absorbing energy-rich nutrients along the way. Growth of the pollen tube is under the control of the pollen tube nucleus, whilst the 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



APPLIED PLANT SCIENCE (13 pages)

Cultivated plants and the manipulation of the environment to increase productivity

Contents

Adaptations of cereals

- Structural and physiological adaptations to different parts of the world
  - Rice as a swamp plant with hollow aerenchyma and a tolerance to ethanol produced by anaerobic respiration.
  - Sorghum as a plant which grows in hot, dry conditions; its xerophytic modifications include the presence of an extensive root system, a thick cuticle and a reduced number of sunken stomata; both the adult plants and the embryos can tolerate high temperatures.
  - Maize as a tropical plant with a specialised method of photosynthesis; the advantages of this method of photosynthesis in increased efficiency at high temperature and low carbon dioxide concentrations.

Controlling the abiotic environment

- Human control of the abiotic environment of crop plants
- The effect of light intensity, temperature and carbon dioxide concentration on rate of photosynthesis and productivity. Enhancement of these factors in commercial glasshouses.

Fertilisers

- The use of fertilisers to replace nutrients lost by harvesting crops.
- The advantages and disadvantages of organic and inorganic fertilisers. The relationship between yield and quantity of fertiliser added. The environmental issues arising from the use of fertilisers. Leaching and eutrophication.

Pesticides

- Interspecific competition between weeds and crop plants. Reduction of crop yield by insects either directly or indirectly by reducing the photosynthetic tissues of the plant.
- The principles of using chemical pesticides, biological agents and integrated systems in controlling pests of agricultural crops.
- The environmental issues associated with pest control. Toxicity and bioaccumulation.
- Evaluation of the issues involved in using different methods to control pests

ADAPTATIONS OF CEREALS

Cereals are seed crops derived from the family of plants known as the Graminae, or grasses. They have formed the main energy providing component (staple food) of most human diets since our early ancestors turned from a hunter-gatherer existence to the collection and cultivation of selected wild grass seeds. The civilisations of the ancient world were founded on settled agricultural communities and their cereal crops; rice in the Far East, wheat and barley in the Middle East, *Sorghum* in Africa, and maize in Central and South America. All of these crops could be eaten as whole grains, ground into flour and baked into bread of some kind, or simply mixed into a porridge-like paste.

Rice

The ancestral grass plants from which rice has been developed were adapted to live partially submerged in marshy regions. It is possible to grow rice on dry land like wheat, even in semi -temperate areas but the yield increases up to three times when it is grown in paddy fields in tropical or sub-tropical temperatures. Over half the world production is in irrigated soil, notably in the great deltas of Asian rivers such as the Ganges, Irrawaddy and Mekong. Modern varieties are fast growing, taking as little as 120 days from seed to harvest, and it is common for three crops to be produced each year. For most of the growing period the rice plants are partially submerged but the land is drained just before harvest so that the dry seed can be collected efficiently.

Most plants can not survive flooding. This is because plant roots require a good supply of oxygen for aerobic respiration. 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. Rice roots have an unusually high tolerance to ethanol and their seeds can germinate in oxygen starved soils. In common with other water adapted plants they also develop 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.

Rice seeds are stripped of their outer coat and embryo (the parts containing proteins and minerals) by a process called ‘polishing’ to produce the product which you find in the supermarkets. It is virtually pure starch and provides virtually all of the daily energy intake for over 50% of the world’s population.

Maize

The ancestry of maize is uncertain. There are no modern grasses which are obviously related to it, but it is certain that the plant originated in Central America, probably in Mexico. It thrives in hot climates with well watered soils, and is adapted to photosynthesise successfully at light intensities and temperatures higher than most plants can tolerate, and with a reduced supply of carbon dioxide.

When all other conditions for photosynthesis are at their optimum level, the rate of carbohydrate production will increase with increasing light intensity until it reaches a maximum value called the **light saturation point**. At high levels of illumination the enzyme Rubisco, which normally catalyses the fixation of carbon dioxide into sugars, starts to react with oxygen in a process called **photorespiration**. Photorespiration uses up oxygen and releases carbon dioxide. It yields no useful energy and is therefore an essentially wasteful process consuming up to 25% of the carbohydrate manufactured by photosynthesis. In order to recapture the lost carbon dioxide, plants are required to open their stomata at the hottest and brightest times of day, thereby suffering a further loss of water by transpiration. This is particularly significant in tropical climates where light intensities commonly exceed the light saturation point. Maize and some other tropical plants, notably sugar cane and *Sorghum*, have evolved a mechanism referred to as **C4 photosynthesis** which overcomes the problem of photorespiration by increasing the concentration of stored carbon dioxide in their leaves. This gives them a higher light saturation point, and therefore a higher productivity.

Maize is most commonly encountered in the form of sweet corn, pop corn or tortilla chips in Western Europe. In Central and South America, maize flour is the basic material for the manufacture of tortillas, tamales and a variety of drinks. It is the single most important crop in the United States although 90% of the production is for animal feed.

Maize crop

Male flower

Female flower

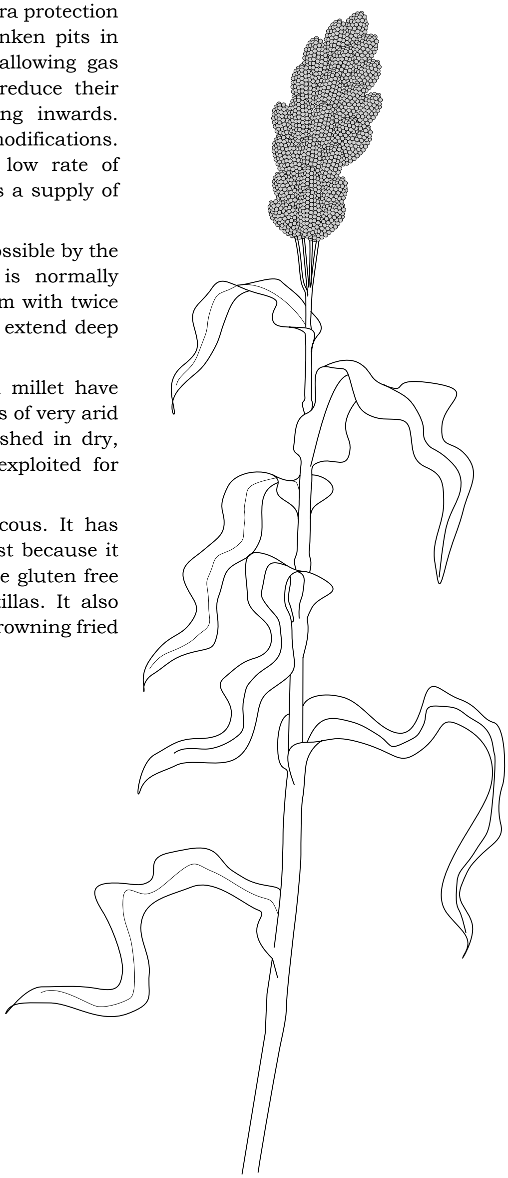
Sorghum

Like maize, sorghum is a C4 plant, specialised to maximise photosynthetic yield in high light intensities and hot climates. Compared to maize, however, *Sorghum* is able to tolerate dry conditions, requiring 20% less water to produce equivalent yields of dry matter, and is able to grow in more hostile climates than any other cereal crop. Plants which are specially adapted to tolerate dry conditions are called **xerophytes**. The adaptations (xerophytic features) centre on ways of reducing water loss whilst retaining photosynthetic activity. Sorghum is similar to maize in its general structure but its leaves are more specialised for water conservation. They are coated with a white waxy layer, giving them extra protection from desiccation, and the stomata are situated in sunken pits in order to reduce unnecessary water loss, whilst still allowing gas exchange. In conditions of water stress, the leaves reduce their exposed surface area by becoming erect and curling inwards. Photosynthetic production is not hampered by these modifications. Sorghum retains high photosynthetic yields with a low rate of transpiration. As in maize, the C4 mechanism provides a supply of carbon dioxide even when the stomata are closed.

Survival of grasses over extended dry periods is made possible by the possession of a much larger rooting system than is normally necessary. Sorghum has a very extensive rooting system with twice as many side branches as that of maize. Its roots also extend deep enough to extract water in drought conditions.

Sorghum and the even more drought resistant cereal millet have become the staple foods of people living on desert fringes of very arid land. These crops have also been successfully established in dry, nutrient depleted and wind eroded soils previously exploited for cotton production.

Sorghum is used to make bread, porridge and couscous. It has enjoyed a period of renewed market interest in the west because it yields a gluten-free flour which may be used to produce gluten free pizza bases, breakfast cereals and Mexican style tortillas. It also caramelises very easily and is suitable as a coating for browning fried foods.



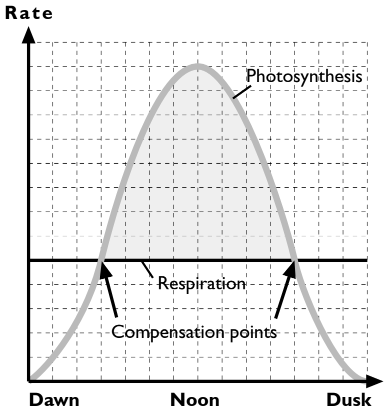
CONTROLING THE ABIOTIC ENVIRONMENT

Human control of the abiotic environmental factors affecting productivity

A permanent increase in plant dry mass only occurs when the amount of carbohydrate produced by photosynthesis exceeds the amount oxidised in respiration and photorespiration. Remember that respiration is continuous over the whole 24 hours, whilst photosynthesis and photorespiration can only occur in the light, and it is the difference between these processes which determines plant productivity. The zero position at which the rate of photosynthesis and respiration are the same is referred to as the **compensation point**.

Productivity is measured as the gain in plant dry mass per square metre of land surface, but it is important to take into account the ratio between the leaf area of a crop and the land space it occupies. This ratio is called the **Leaf Area Index** or **LAI,** and it is calculated as the total leaf area per square metre of land. In the early stages of crop growth when new leaves are developing the LAI is small, but as more leaves are formed, it rapidly increases. Some leaves will shade each other, and in mature plants, older leaves die back as new ones are produced. For this reason it is rarely possible for a crop to use more than 95% of the available light.

Compensation points



Light intensity

The efficiency of light energy conversion into carbohydrate in crops depends not only on the amount of light received, but must also take into account losses through respiration and photorespiration (see above). The upper leaves of a plant tend to be illuminated at a level above the light saturation point for most plants. For a typical temperate crop, crop yields expressed as dry matter production relative to total incident light energy represent a less than 1% conversion of the solar energy input into chemical energy.

Productivity can be increased significantly by using crops bred to achieve high short term growth rates by maximising their percentage light utilisation. Crop research has also focussed on reducing losses by photorespiration, or increasing the availability of carbon dioxide which, under natural conditions, is normally the limiting factor.

Temperature

The ecological distribution of plants, their seasonal vegetative and reproductive cycles, and day to day carbohydrate assimilation, are all influenced, to a greater or lesser degree, by the ambient temperature. Temperature, like carbon dioxide and light, can be a limiting factor in photosynthesis, but it is more accurately regarded as an indirect influence, because above 15-20°C, it affects the rate of respiration more strongly than the rate of photosynthesis.

The most important factor affecting productivity is the average night temperature. 'Dark respiration' uses up twice as much assimilated carbohydrate at 25°C than at 15°C, for example, so cool nights may promote better growth.

Temperature has other indirect effects on the rate of photosynthesis, notably on stomatal opening but this is only in the extreme range. At temperatures above 30°C stomata generally close, probably as a result of higher carbon dioxide levels created by increased respiration.

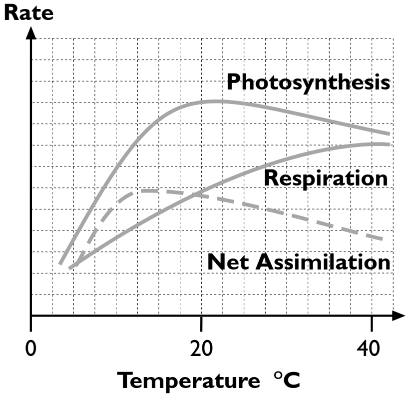
Most temperate crops give their best production between 10 -15°C, but the optimum for other regions varies from 5 °C in some arctic species to 30°C for a tropical crop like maize.

Carbon dioxide

Carbon dioxide forms a very small proportion of the atmosphere, just 0.04% by volume, but it is estimated that crop plants fix an average 160 000 kg.km^{-2}.year^{-1}. Although the quantity of carbon dioxide in the atmosphere remains relatively constant, local concentrations around a crop can range from 0.015-0.1%. Photosynthesis depletes the available carbon dioxide, particularly in a closed environment like a greenhouse. The most important source for replenishment comes from the respiration of soil organisms carrying out decomposition of dead organic matter (soil respiration). In a fertile soil with adequate dead organic matter and soil organisms, the carbon dioxide produced by soil respiration and released to the air will exceed photosynthetic requirements.

The amount of carbon dioxide available to crops is limited by the frequency and degree of opening of its leaf stomata and also by the **microclimate** which surrounds the individual leaves. Around each leaf a **boundary layer** of still air tends to reduce the concentration gradient for diffusion. Air turbulence is important to replace the layer of air which surrounds the leaf canopy. Windy conditions help to overcome the problem of carbon dioxide depletion in a field of photosynthesising maize in high light intensity.

Productivity (net assimilation)



Glasshouse production and Hydroponic Systems

An understanding of the various environmental factors controlling plant growth has led to the development of soil-free or **hydroponic** plant culture systems. Hydroponic systems provide a 'state of the art' illustration of how a detailed knowledge of the effects of abiotic factors can be applied to plant production. By maintaining all the limiting environmental and nutritional factors at their optimum level in controlled glasshouses it is possible to achieve a high yield in a small space and a short time period.

Hydroponic systems can be set up anywhere regardless of soil conditions and climate, even, as the Japanese have shown, within urban hypermarkets to provide fresh clean vegetables with zero transport and minimum packaging costs. Pest and disease problems are minimal, and weeds do not have a chance to enter the system. With no large scale mechanical cultivation and no release of agrochemicals and fertilisers into the environment, hydroponic crops are environmentally friendly, particularly in systems where the water and nutrients are recycled.

Balancing these obvious benefits are the large set-up and skilled labour costs. It must also be considered that although disease is largely eliminated, if a crop does become infected, the process can be rapid and devastating.

The most common hydroponic system for growing tomatoes, cucumbers and lettuces is the **Nutrient Film Technique,** where plants are grown within gullies made from plastic film. Typically, the gully is constructed from a sheet of plastic, 65-80cm wide, coated black on the inside and white on the outside. It is stapled together between the plants and gently inclined so that the nutrient solution drains into catchment pipes which re-circulate it via a catchment tank and associated pumping system.

If plant roots require extra aeration, the nutrient solution may be supplied intermittently (in bursts).

Problems may arise when vigorous root growth prevents circulation of fluids.

◆ CHECKPOINT SUMMARY

- ◆ Productivity is measured as the gain in plant dry mass per square metre of land surface. This reflects the relative rates of photosynthesis and respiration
- ◆ The abiotic environment includes light intensity, temperature, and carbon dioxide concentration
- ◆ Increasing light intensity increases the rate of photosynthesis up to a certain point, the light saturation point, past which there are no further gains as the result of light stimulated photorespiration
- ◆ Temperature, like carbon dioxide and light, can be a limiting factor in photosynthesis, but it is more accurately regarded as an indirect influence, because above 15-20°C, it affects the rate of respiration more strongly than the rate of photosynthesis
- ◆ The most important factor affecting productivity is the average night temperature. 'Dark respiration' uses up twice as much assimilated carbohydrate at 25°C than at 15°C, for example, so cool nights may promote better growth
- ◆ Most temperate crops give their best production between 10 -15°C, but the optimum for other regions varies from 5 °C in some arctic species to 30°C for a tropical crop like maize.

Controlling the glasshouse environment

Seasonal and climatic changes in light intensity, wavelength and duration may be compensated for in a variety of ways. Where day length influences flowering, e.g. chrysanthemums, it is controlled by the use of artificial light and/or partial shading.

The optimum temperature for tomatoes and lettuces is 18-22°C. It is important to lower the night temperature by 6-12°C in order to minimise dark respiration. Control is achieved through thermostatic monitoring and the use of heaters, vents, shades and, where necessary, coolers. The temperature directly affects humidity so fine mist sprays are linked to the same control system.

Glasshouse plants, being confined to an enclosed space, quickly use up the available carbon dioxide and so it is very important to supply this by some external means. Where heating is the norm, a hydrocarbon burner may be used to supply carbon dioxide. Alternatively, dry ice or gas cylinders may be used.

Insect pests are potentially disastrous in the glasshouse environment. They are sometimes controlled by pesticides introduced via the fine mist spray system, although biological control agents are increasingly common. In the absence of chemical insecticides, bee hives may be kept in glass houses providing natural pollinators for fruits such as tomatoes, cucumbers, and strawberries. Otherwise pollination must be achieved manually.

FERTILISERS

Crop productivity is affected by the availability of inorganic nutrients in the soil. Plants take up inorganic elements from the soil solution in the form of anions (negatively charged ions) and cations (positively charged ions). Some elements, like nitrogen, phosphorus, and potassium are required in relatively large quantities (up to 150 kg per hectare). These are called **macronutrients**. Others such as zinc and copper are needed in trace amounts only and these are termed **micronutrients**. Some make up structural components of plant cells; nitrogen, for example, is essential for amino acid synthesis, phosphorus occurs in DNA and ATP, and magnesium forms part of the chlorophyll molecule. Other elements such as potassium are involved in enzyme systems. Iron is a component of the cytochromes which make up the respiratory electron transport chain; calcium controls membrane permeability, preventing leakage of other ions from plant cells.

The mineral nutrients most frequently applied to soils as fertiliser are nitrogen, phosphorus and potassium. They are often combined in what is known as an **NPK mixture**. The relative amounts of each component and the timing of the application can influence both the development and yield of a crop. In a maize crop, for example, nitrogen is important at the end of the growing season when the protein content is being laid down in the seed.

Nitrogen is the most important limiting nutrient because without it, plants cannot make proteins. Nitrogen exists in the soil as nitrate (NO_3^-), nitrite (NO_2^-) and ammonium (NH_4^+) ions. All of these can be directly utilised by plants but by far the most commonly available form is the nitrate ion (NO_3^-). Nitrate is released as a result of the activity of nitrifying bacteria such as ***Nitrosomonas*** and ***Nitrobacter*** which oxidise ammonium compounds utilising the energy derived from these reactions to manufacture organic food compounds.

◆ CHECKPOINT SUMMARY

- The quantity of carbon dioxide in the atmosphere remains relatively constant at 0.04%, but local concentrations around a crop can range from 0.015 - 0.1%, and under natural conditions in daylight carbon dioxide is the rate regulating (rate limiting) factor for photosynthesis
- By maintaining all the limiting environmental and nutritional factors at their optimum level in controlled glasshouses it is possible to achieve a high yield in a small space and a short time period
- An understanding of the various environmental factors controlling plant growth has led to the development of soil-free or hydroponic plant culture systems.
- Where day length influences flowering as in the case of chrysanthemums it is controlled by the use of artificial light and/or partial shading
- The optimum temperature for tomatoes and lettuces is 18-22°C. It is important to vary the day and night temperature by 6-12°C in order to minimise dark respiration. The temperature directly affects humidity so fine mist sprays are linked to the same control system
- Glasshouse plants, being confined to an enclosed space, quickly use up the available carbon dioxide. Where heating is the norm, a hydrocarbon burner may be used to supply carbon dioxide. Alternatively, dry ice or gas cylinders may be used.

Nitrate ions (being negatively charged) are not held by the negatively charged clay particles in the soil. and are very susceptible to being washed out of the soil (leaching). This causes variations in the soil concentration even on a daily basis. By contrast, ammonium ions (NH_4^+) are held by the negative charges on soil particles and are directly usable by plants.

Phosphorus is an essential component in three major biomolecules, ATP, nucleic acids and phospholipids. It is taken up by plants in the form of $H_2PO_4^-$ or HPO_4^{2-} ions. These ions do not tend to move freely in the soil and become fixed in compounds not available to plants. Up to 80% of phosphate fertiliser, normally applied in the form of 'super phosphate' (P_2O_5), can be wasted in this way, so it is sometimes introduced with the seed as it is sown, a practice called **banding**, ensuring that the nutrient is available where the roots actually grow.

Potassium is absorbed in large quantities by plant roots, reaching concentration levels up to ten thousand times that of the soil solution in some *Brassica* (cabbage and rape) species. Potassium ions have a role as activators in enzyme systems, notably in protein synthesis, and they play a key role in the opening and closing mechanisms of stomata.

Organic and inorganic fertilisers

Organic fertilisers should be seen as complementary to, rather than an alternative to, the inorganic (chemical) fertilisers described above. The main source of organic nutrients is animal waste, either in solid form mixed with bedding materials (farmyard manure, FYM) or as liquid or semi-liquid (slurry). The quality of animal manure depends on the type of animal, what it is fed on, and how much bedding is used. It is ploughed into the soil, yielding a slow release of nutrients. More importantly, it improves soil structure by binding small particles together and retaining water.

Modern intensive animal farming methods tend to use less bedding, and mechanical devices shift the dung to storage tanks in liquid or semi-liquid form. Liquid manures are potentially very hazardous to the environment. They have a high biological oxygen demand (BOD) causing eutrophication, and far from improving soil structure, they tend to create anaerobic conditions by flooding the soil air spaces. For these reasons strict regulations apply to their use where flooding may occur near rivers.

Other sources of organic nutrients include sewage sludge, seaweed, waste material from the cotton and wool industries and dried blood and bone meal. Sewage sludge whilst cheap and easily available, may contain pathogens and heavy metals and is best avoided altogether. The use of other sources depends upon the relative local costs and benefits.

Green manure

Green manure is the term used to describe the practice of growing and ploughing into the soil a green (non-seed) crop such as white mustard or clover. Green crops may be used as 'cover crops' which cover the soil during the winter months, preventing the erosion and leaching of valuable inorganic nutrients.

◆ CHECKPOINT SUMMARY

- Harvesting removes nutrients from the soil by preventing the nutrients in the crop from returning to the soil as a result of decomposition
- Crop productivity is affected by the availability of inorganic nutrients in the soil, which are supplemented by the addition of fertilisers
- The mineral nutrients most frequently applied to soils as fertiliser are nitrogen, phosphorus and potassium. They are often combined in what is known as an NPK mixture
- Nitrogen is the most important limiting nutrient
- Up to 80% of phosphate fertiliser, normally applied in the form of 'super phosphate' (P_2O_5), can be wasted by becoming fixed in compounds not available to plants
- Organic fertilisers should be seen as complementary to, rather than an alternative to, the inorganic (chemical) fertilisers described above. The main source of organic nutrients is animal waste
- Organic fertilisers improve soil by binding small particles together and retaining water
- In modern intensive animal farming methods the dung is stored in tanks in liquid or semi-liquid form. Liquid manures are potentially very hazardous to the environment. They have a high biological oxygen demand (BOD) causing eutrophication and tend to create anaerobic conditions by flooding the soil air spaces
- Green manure is the term used to describe the practice of growing and ploughing into the soil a green (non-seed) crop such as white mustard
- The main nutrient which leaches out of the soil to pollute rivers and lakes is nitrate, which acts as a fertiliser in the aquatic ecosystem causing 'super feeding' or eutrophication
- Eutrophication causes unnaturally rapid growth of plants, occasionally forming algal blooms on the surface of the water
- The increase in plant material, over a period of time leads to increased amounts of dead organic matter which become food for aerobic bacteria. Bacteria have a high biological oxygen demand (BOD) and consequently starve the other oxygen uses of essential supplies. The highest oxygen users, notably fish and certain insect larvae suffer population decline and extinction
- In extreme cases conditions become anaerobic and the ecosystem collapses.

Leaching and Eutrophication

The main nutrient which leaches out of the soil in any quantity to pollute rivers and lakes is nitrate. The effect of nitrate in aquatic ecosystems is to fertilise the water causing 'super feeding' or **eutrophication**. This causes unnaturally rapid growth of plants, occasionally forming **algal blooms** on the surface of the water. The increase in plant material, over a period of time leads to increased amounts of dead organic matter which become food for aerobic bacteria. Bacteria have a high biological oxygen demand (BOD) and consequently starve the other oxygen users of essential supplies. The highest oxygen users, notably fish and certain insect larvae suffer population decline and extinction. In extreme cases, especially in lakes and ponds, conditions become anaerobic and the aquatic ecosystem collapses. In running water there is an 'oxygen sag' immediately downstream of the source of pollution, which slowly recovers further downstream. The quantity of nitrate applied as fertiliser to the soil should be calculated on the basis of **optimum use** by the crop and not simply on maximum crop yield.

The CONTROL of BIOTIC FACTORS (PESTS and COMPETITORS)

Weeds

Weeds compete aggressively with crops for water, light and mineral nutrients and generally show better tolerance to limited supplies. They are characterised by high rates of photosynthesis, and a rapid development of roots and leaves, so they gain access to their needs more quickly than their neighbours. Weeds tend to be the first colonisers of waste and disturbed ground, more resistant than other plants to environmental extremes, and more tolerant of changing conditions. Some, like couch grass, secrete toxic or growth retardant substances called **allelochemicals** to fight off the competition.

It is very difficult to isolate the specific effects of individual weeds in a crop because several weed species compete with the crop, and with each other simultaneously for light, water, and minerals, and the resources being competed for, are often in short supply (limiting), and interrelated. One principle, however, is universal. The closer the requirements of crop and weed, the more damaging the competition, and the more difficult it will prove to control the weed. This is most obvious when the weed and crop belong to the same plant family, for example, wild oat *(Arvena fatua)* in cereal crops, fat hen (*Chenopodium album*) in sugar beet and charlock (*Sinapsis arvensis*) in oilseed rape. If the relationship is very close there is a further danger of hybridisation between weed and crop to produce an even stronger competitor.

The degree of competition between weed and crop depends largely upon the relative timing of their vegetative and reproductive cycles. Harvest yields will be affected most seriously if the growth and reproductive stages of the weed coincide with those of the crop.

Insects

The success of insects as competitors for human food may be explained by two main biological features. One is the hard exoskeletal material, **chitin**, which can be fashioned into so many different feeding accessories that no plant part is immune from attack. Consider the mandibles and maxillae of the locust and aphid. In the locust, the mandibles form pincer like cutting tools whilst the maxillae are designed to guide a leaf blade into position for biting. In the aphids, both the mandibles and maxillae are sharpened and lengthened into a piercing hypodermic structure which penetrates the tissues of plants gaining direct access to the sugary sap in the phloem.The other biological feature of insects which accounts for their phenomenal success is their ability to survive and multiply rapidly in the harshest of conditions.

Insecticides - the Chemical Approach to Control

A general distinction can be made between chemicals which act by penetrating the outer cuticle of insects, termed **contact insecticides**, and those which are ingested, the so-called **stomach poisons**.

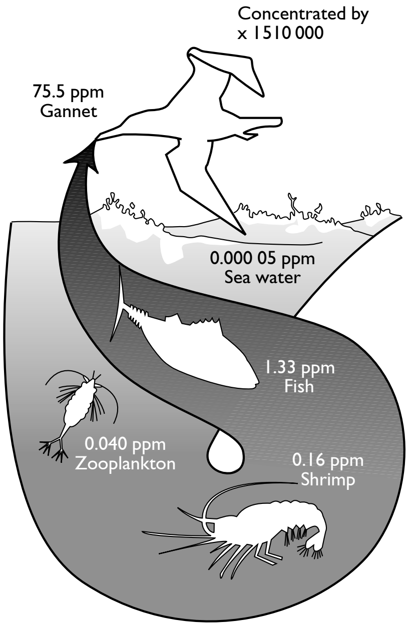
Of the older pesticides, Pyrethrum is a natural product extracted from several species of chrysanthemum (although synthetic versions have been developed) and is a contact insecticide which penetrates the cuticle of the insect as it rests against a sprayed surface.

Paris green (calcium acetoarsenite), was the first chemical insecticide used successfully on a large scale, is a stomach poison which is ingested as the insect feeds on sprayed vegetation.

Organochlorines were first developed as pesticides in the 1930s. They combine two important properties. They are **persistent**, remaining in a stable and active form for periods exceeding a year, and **residual**, accumulating in the fatty tissues without being excreted or broken down. Organochlorines destabilise the nerve membranes and tend to inhibit the respiratory enzyme cytochrome oxidase.

DDT was the first to be highlighted as having adverse effects on higher organisms quite unrelated to the target pest. The persistent and residual properties which made it so effective in eradicating the malarial mosquito and combating the insect pests of fruit trees, caused it to accumulate in natural food chains, particularly aquatic ones. Birds, such as pelicans and eagles, at the top of long food chains, diminished in number as the multiplied doses of DDT affected the shell forming mechanism in their reproductive tracts.

Organophosphates were first developed in the 1940s as poison gases for use in the Second World War. They include **parathion** and **malathion** which are still among the most widely used of all insecticides. They are easily formulated into sprays which coat the surface of leaves, and may penetrate into the epidermal tissues giving a **semi-systemic** action. When ingested by an insect pest, organophosphates act by combining with, and inactivating, the enzyme cholinesterase at nerve synapses. Cholinesterase is responsible for the removal from the synapse of the transmitter substance acetylcholine after each nerve impulse, so the result of organophosphate ingestion is the accumulation of acetylcholine in the synapses, leading to paralysis.



What are the alternatives? There are three other important approaches, namely biological control, cultural control, and the development of resistant crops, none of which alone forms a viable strategy for maintaining food levels. They should not be considered as alternatives to each other but as complementary strategies in a balanced and integrated approach to pest management.

◆ SUMMARY OF CHEMICAL CONTROL

The chemical control of insect pests poses four well publicised hazards:

- Insecticides may be directly poisonous (toxic) to man
- Insecticides may accumulate in food chains and have serious, even fatal, effects on top carnivores (including man)
- Insecticides may reduce populations of beneficial insect species.
- The use of insecticides encourages the increase of resistance in pest species.

Biological Control

Biological control involves the use of other organisms, usually predators or parasites, to reduce the numbers of a pest population. A good example is provided by the tiny parasitic wasp, *Encarsia formosa*, which has been used to control whitefly in commercial glasshouses since 1926.

Whitefly *(Trialeuroides vaporariorum)* is a sap sucking insect closely related to aphids, which owes its name to an opaque layer of wax coating its body and wings, giving it a white appearance. It is not a native British species, having been accidentally introduced from tropical America, but it thrives in glasshouses, and is very destructive of tomato, cucumber and chrysanthemum crops, not least because of its ability to transmit viral infections.

The tiny wasp, also tropical in origin, lays its eggs in young immature whiteflies referred to as ‘scales’ killing them before the young wasps eventually hatch out. The wasp was bred extensively for sale to glasshouse growers throughout the 30s and 40s but was made largely redundant by the advent of DDT. Biological control of whitefly using *Encarsia* enjoyed a revival in the 1970s as problems of pest resistance to chemical insecticides were recognised.

The development of a new biological control agent starts with a research programme to identify, collect and breed natural pest enemies in their natural habitat. Once sufficient numbers have been bred (and here it is important to get as much genetic variety as possible) the agent undergoes a quarantine phase in which it is assessed in laboratory conditions for its reproductive rate, climatic resistance, appetite for its pest prey, and potential threat to other organisms. After this it must undergo five years of field trials. The total cost of development is less expensive than the development of a new insecticide. Biological agents also have the advantage of reaching their target organisms in all conditions and in places inaccessible to sprays. They are keep reproducing once established in the field, and there is little chance of the pest developing resistance.

However, there are a number of problems associated with the use of biological control methods. In order to maintain a healthy breeding population of *Encarsia* it is necessary to keep the temperature of the glasshouse within very strictly controlled limits. If it is too cool, then the wasps will not breed effectively. Conversely, in warm conditions the wasps become overactive and wipe out all the young whitefly, thereby denying the next generation of its sole food supply.

You can see from this example how biological control programmes depend on carefully managed population dynamics. Despite the checks referred to earlier, there are also environmental risks resulting from a possible switch by the predator or parasite to alternative and beneficial insect prey species. New diseases are constantly imported with non-native plant introductions, many of them notifiable under strict government regulations. The penalties for delay in treatment are high, so growers are encouraged to seek rapid chemical remedies.

Cultural Control

In uncultivated land, plants, insects, and fungi co-exist within a balanced ecological system. Population numbers fluctuate, but no individual organism acquires the status of a pest. It is important to recognise that pests are created by agriculture, and the problem becomes more acute the more intensive the methods employed.

The practice of growing crops in single stands or **monocultures** accelerates the growth of particular insect populations. In uncultivated land, insects are scattered as widely as their host plants. Their populations tend to reach equilibrium at much lower densities because they encounter a greater diversity of natural enemies, and compete with each other more acutely. Intensive farming both eliminates many natural enemies, and ensures a plentiful food supply. Under such conditions, the pest population soars rapidly, reaching artificially high densities.

Cultural control is the term used to describe the application of different techniques of cultivation with the aim of reducing yield loss through pests and competitors.

Where crops are widely spaced, it is advantageous both for weed control and for moisture retention to provide ground cover between the plants. In small banana plantations this is done by **mulching** which involves covering the exposed soil surface after tillage with rotting banana leaves. A more high-tech (and costly!) version of mulching can be seen in 'pick-your-own' strawberry farms, where plastic sheeting is used to cover the ground between the rows of strawberries. A better option altogether is to fill the spaces by planting a secondary crop, for example cowpeas in maize, or groundnuts in coffee. This practice, called **intercropping** is both economically and environmentally sound.

Crop rotation is an obvious method of cultural control of insect pests. It is calculated that the maize, wheat, red clover rotation harbours up to 50 insect pest species, but no more than 3 are common to all three crops. This may be combined with the planting of mini-hedgerows, a practice referred to as **strip farming,** providing wild vegetation which will encourage the growth of natural predator populations. An ingenious method of cultural control has been used in Canada to protect wheat crops against a stem-boring sawfly. A small strip of brome grass is planted around the crop and this attracts the egg-laying female flies to deposit their cargo before reaching the wheat. When the young larvae hatch out, they tend to eat each other and little damage results to the crop. The brome grass acts as a decoy or **trap crop**.

Hygiene

Regardless of cultural practices or chemical control methods, a high degree of preventative hygiene is essential in order to avoid contamination of a crop with weed seed or fungal spores brought in on machinery or irrigation water. This is particularly important in the battle against fungal diseases. Machinery and storage facilities are disinfected after each harvest, and crop debris should be cleared, either by ploughing in or, ideally, by burning.

Integrated Crop Management

Attitudes to pest control have changed considerably over the last thirty years, not simply because of a wider consciousness and concern for environmental protection. The main change is a philosophical one, focussed by the rather late realisation that it is not possible to eliminate pest species. Instead of searching for the ultimate weapon, therefore, a more rational approach would concentrate on ways of managing pest populations.

Pest management depends upon systematic and long term evaluation of the biology of weeds, insects, and fungi, and that of their natural enemies. Computerised predictive models of infestation and crop yield assessment may be devised, and linked to weather information giving farmers early warning of potential economic damage. In this way, all the methods outlined above may be brought into play in a more coordinated manner, ensuring that war is only waged in cases where the cost of control is less than the cost of the loss in yield.

However, a new age and an additional defensive strategy has opened up with the development of transgenic resistant plants. It is now increasingly possible to manipulate all aspects of the crop, including crop protection.

Integrated crop management embraces chemical, biological, and cultural control, as well as the manipulation of plant genetics. The environmental and public health impact of any particular strategy must be assessed, both in isolation and in combination with other factors. Education of food consumers is also very important. Informed customers no longer accept indiscriminate spraying of fruit and vegetables with chemical pesticides, and they already tend to reject products from countries where such practice is common, regardless of attractive qualities such as the colour, size, price, and shelf life of the product.

◆ CHECKPOINT SUMMARY

- Weeds compete with crops for water, light and mineral nutrients and show better tolerance to limited supplies. They have high rates of photosynthesis, and development, so they out compete crop plants
- Weeds tend to be the first colonisers of cultivated ground, more resistant than other plants to environmental extremes, and more tolerant of changing conditions
- The closer the requirements of crop and weed, the greater the competition, and the more difficult to control the weed
- If related there is a further danger of hybridisation between weed and crop to produce an even stronger competitor
- Harvest yields are affected most if the growth and reproductive stages of the weed coincide with those of the crop
- The success of insects as competitors for human food may be explained by the wide variety of feeding methods, and their ability to survive and multiply rapidly in the harshest of conditions
- Contact insecticides penetrate the exoskeleton of insects, and stomach poisons are swallowed by the insect
- Organochlorines are persistent, remaining in a stable and active form for periods exceeding a year, and residual, accumulating in the fatty tissues without being excreted or broken down
- Organochlorines destabilise the nerve membranes and tend to inhibit the respiratory enzyme cytochrome oxidase
- The chemical control of insect pests poses four well publicised hazards. Insecticides may be directly poisonous (toxic) to man. Insecticides may accumulate in food chains and have serious, even fatal, effects on top carnivores (including man). Insecticides may reduce populations of beneficial insect species. The use of insecticides encourages the increase of resistance in pest species
- Biological control involves the use of other organisms to attack the pest, cultural control involves cultivation techniques which reduce conditions favourable to the pest, and the development of resistant crops involves the breeding-in of resistance to the pest
- None of these alone forms a viable strategy for maintaining food levels
- They should not be considered as alternatives to each other but as complementary strategies in a balanced and integrated approach to pest management.