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HOW PLANTS WORK

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

As with animals, simply speaking, the larger the plant, the smaller is its surLearning Outcomesface 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.

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 ve 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.

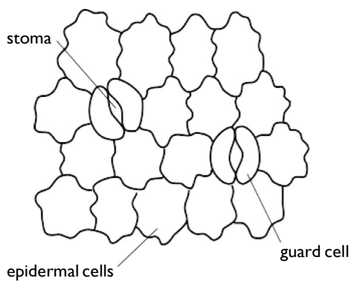
Factors affecting transpiration include anything that affects the supply of water to the leaves, and the evaporation of water from the leaves. The main factors are:

- 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 10°C doubles the steepness of the humidity gradients from leaf to air, thus increasing transpiration.
- Air movements increase the rate of water loss by transpiration as molecules of water 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.

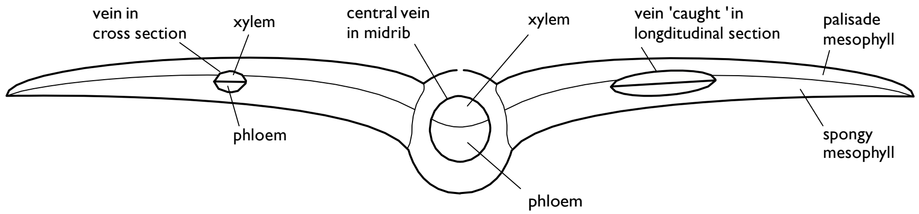
◆ CHECKPOINT SUMMARY

- 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

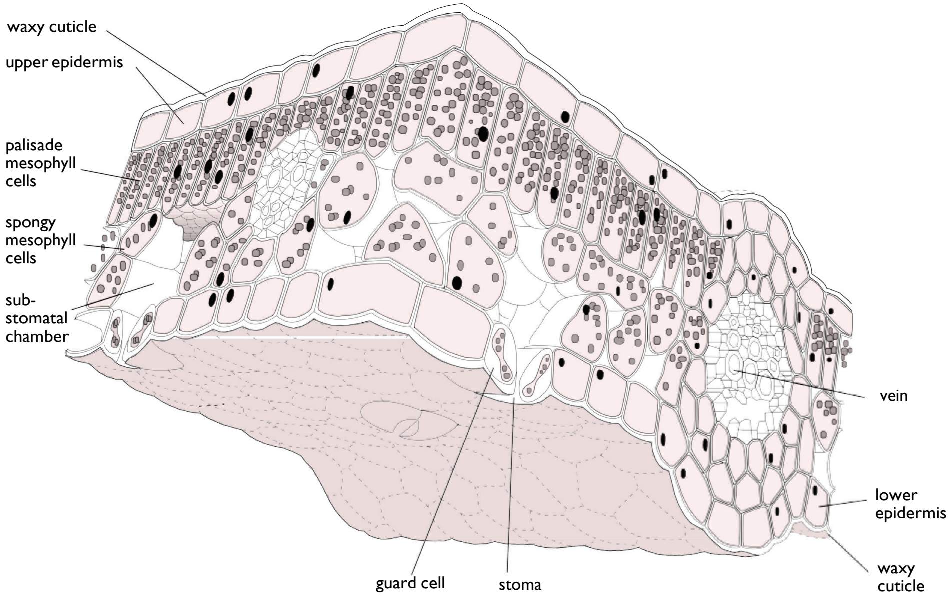
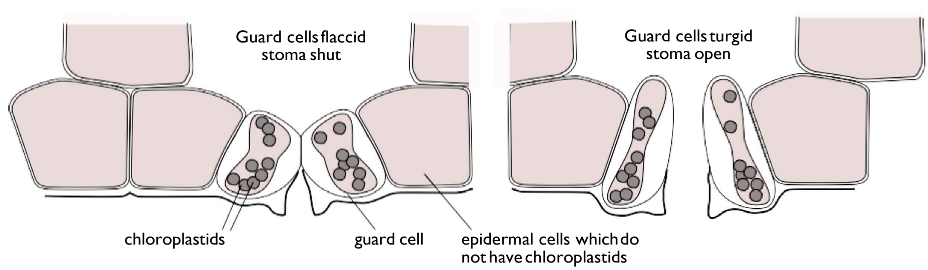
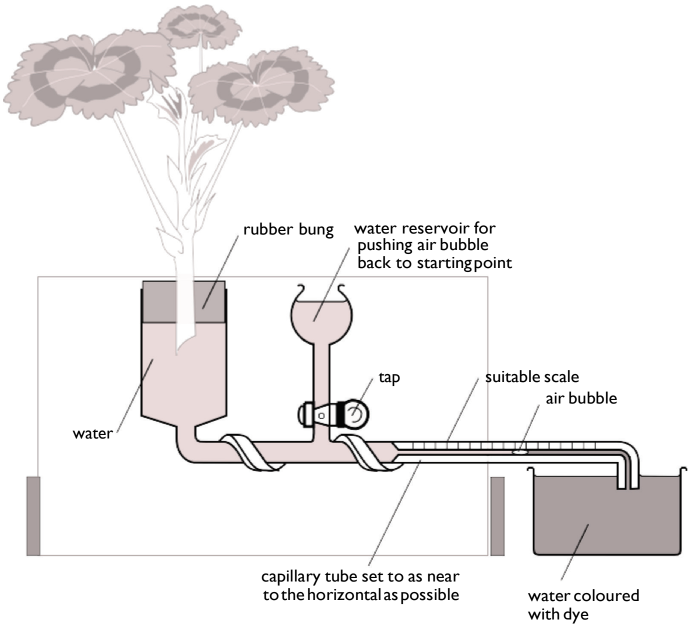


Diagram of guard cell action



Potometer



EXPERIMENTAL INVESTIGATION of FACTORS AFFECTING TRANSPIRATION RATE

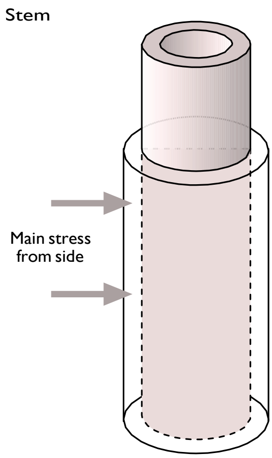
Investigations of the effect of many of these factors can be carried out using a simple piece of laboratory equipment, the **potometer**, in which a cut shoot is exposed to different conditions and its water uptake is measured. The rate of water uptake is assumed to be the same as the rate of transpiration, 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

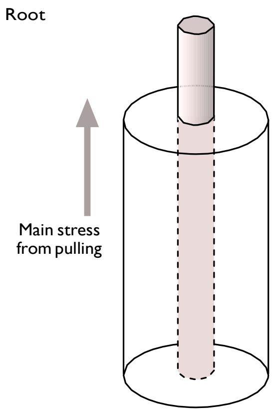
- Transpiration can be measured using a potometer. The principle of which, is that as the water evaporates from the leaves of the shoot an air bubble is drawn along the capillary tube at the same rate - thus giving a measure of the rate of transpiration.
- Actually it is the rate of water uptake that 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.

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



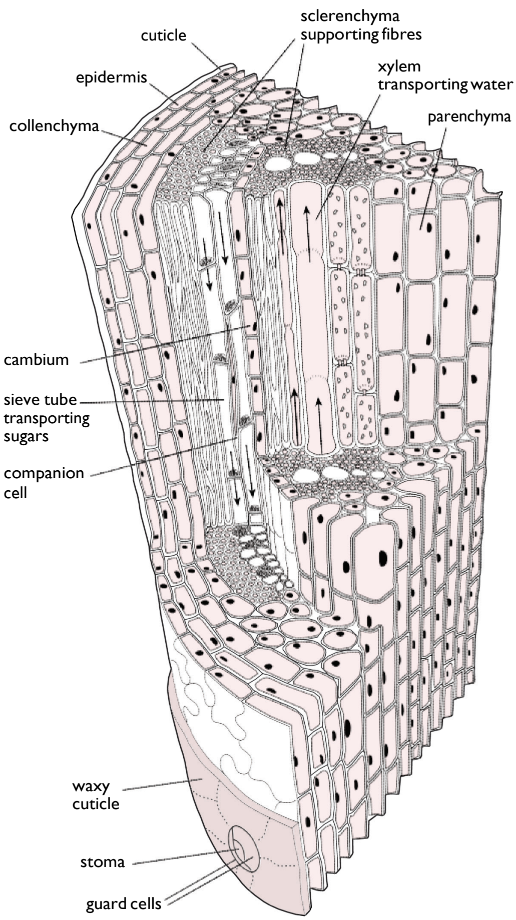
Vascular tissue forms a strengthened inner core which resists pulling action

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

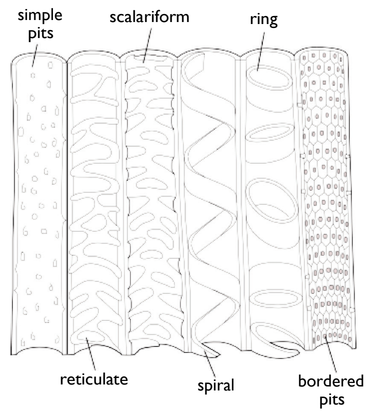
Xylem tissue of flowering plants consists of elongated tracheids and vessels, which have no living contents, and form tubes in which water travels from the roots to the leaves. Tracheids and vessels have strong lignified walls. Lignin is a tough, hard, waterproof substance, and lignified tissue makes 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.

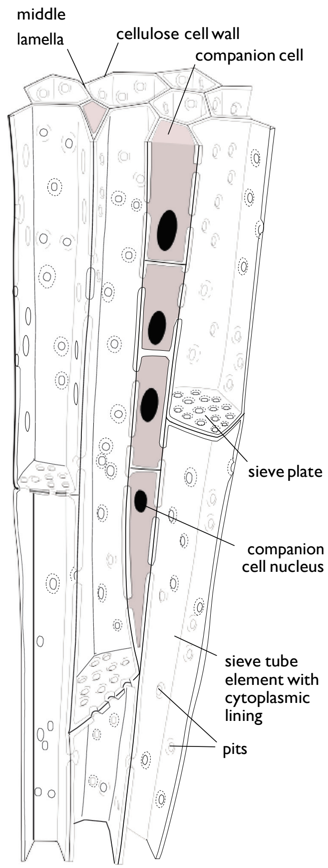
Diagram of plant stem structure



Xylem vesssels showing different types of lignified thickening



Phloem Cells



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**.

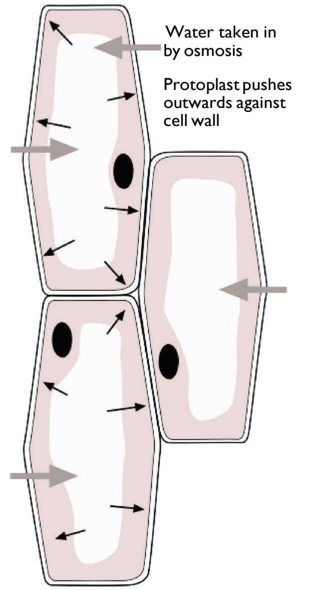
Water moves into and out of the cell protoplast according to the relative numbers of water and solute molecules on either side of it. The water potential of a fluid is measured in relation to pure water. If the fluid is pure water, there is no movement, so the **water potential of pure water is zero**. 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.

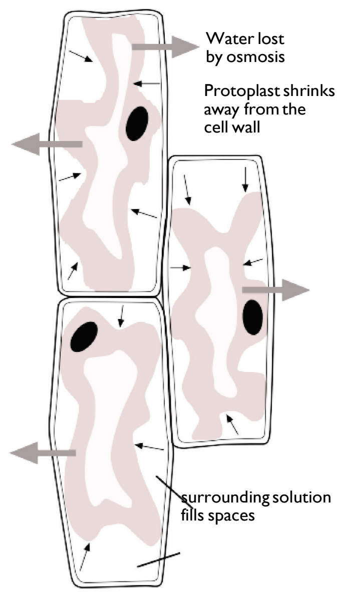
In the very unusual case of the surrounding water having a lower water potential than the plant cells (for example, where the soil is flooded with salty water) water will move out of the cell by osmosis so that, in extreme cases the membrane shrinks away from the cell wall. Cells in this state are said 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



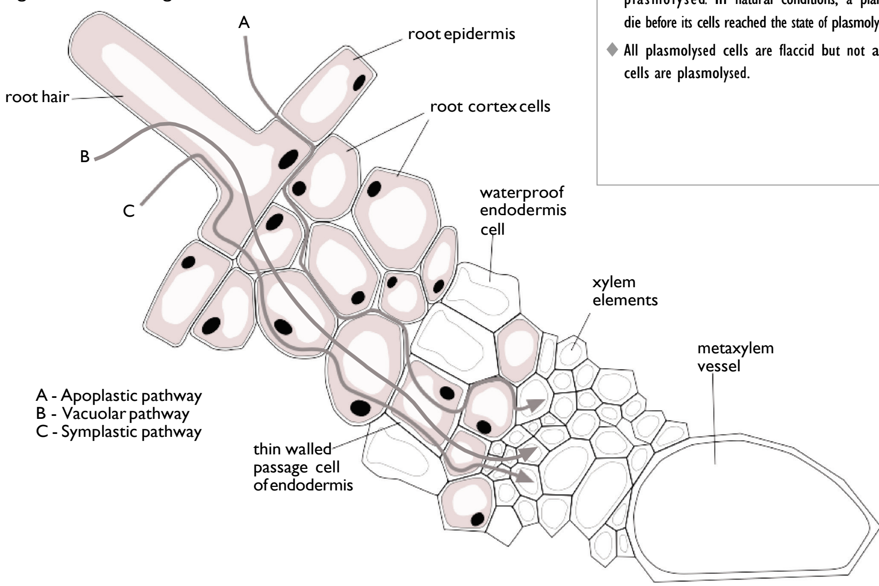
PATHWAY and MECHANISM of WATER TRANSPORT from ROOTS to LEAVES

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.

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.

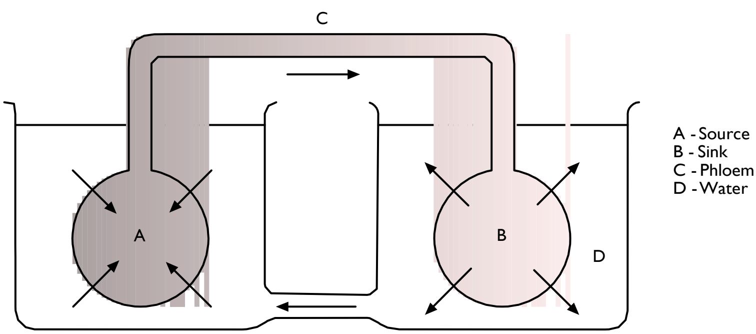
◆ CHECKPOINT SUMMARY

- 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).

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

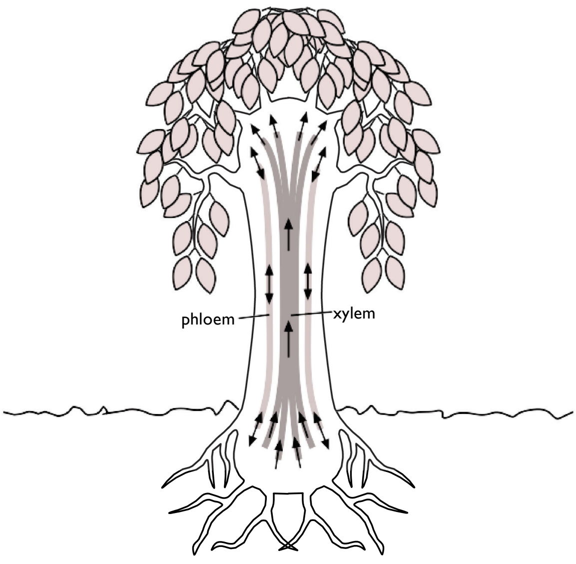
Evidence against this mechanism is provided by radioactive tracer studies which indicate that substances move in different directions at the same time (although this could be occurring in different sieve tube elements, which would still be explicable in terms of the mass flow theory).

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.

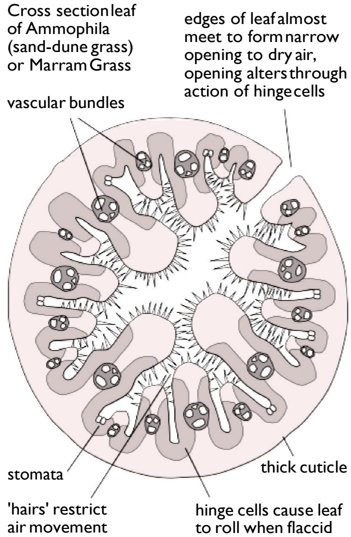
XEROPHYTIC ADAPTATIONS to REDUCE WATER LOSS by TRANSPIRATION

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