

I1 PLANTS AND WATER

Key Notes

Properties of water	Water is polar and a good solvent for charged or polar solutes. Hydrogen bonding means water is a liquid at temperatures common for plant growth and has high cohesive (tensile) strength.
Water movement	Water moves from high water potential to low water potential. Water movement occurs by diffusion and by mass flow, where flow rate depends on the cross-sectional area of the tube, the pressure gradient and the viscosity of the liquid. Embolism may block flow. Water potential is the sum of the pressure potential and the osmotic potential. A cell generating a positive hydrostatic pressure is turgid; one in which it is negative is flaccid.
Transpiration	Evaporation of water from the leaves through stomata generates a low water potential and results in the movement of water from the soil through the root system and into the xylem.
Xylem water flow	The cohesion-tension theory suggests that water is drawn upwards through the xylem by tension created by transpiration at the leaves. Root pressure and capillary action contribute.
Water transport in roots	Water predominantly enters roots largely via root hairs. Water transport may be apoplastic or symplastic (transcellular via plasmodesmata, or transmembrane via membrane transporters). At the endodermis, water movement must be cytoplasmic. Water enters the xylem as a result of the low water potential generated by the transpiration stream.
Related topics	Roots (C2) Water retention and stomata (I2) Movement of nutrient ions across membranes (I3) Uptake of mineral nutrients by plants (I4)

Properties of water	Water is essential for plant growth. All cells contain water as the solvent in which biochemical reactions take place and in which cell structures are maintained. Water shows hydrogen bonding (between electronegative oxygen and electropositive hydrogen) which means it is a liquid at temperatures common for plant growth. As it is polar, it is a good solvent for polar molecules like ions and charged organic molecules. The strong forces between water molecules (cohesion) give it several other key properties: it has a very high surface tension and adheres strongly to surfaces. It also has a high tensile strength, and is able to form columns under high tensions without breaking, for example in xylem.
Water movement	Water molecules are in constant random motion. Diffusion occurs when molecules migrate as a result of this motion. Molecules will move progressively from

regions of high free energy (high concentration) to regions of low free energy (low concentration) down a concentration gradient. Diffusion may be considered important over short distances, for instance within a plant cell, but not over long distances, such as from soil to leaf.

Mass or bulk flow

Movement of water through xylem is largely by **bulk flow** that occurs as a response to a pressure gradient. Fluid flow through a pipe depends on the pressure gradient between the ends of the pipe, the radius of the pipe and the viscosity of the fluid. As the radius doubles, the flow rate increases by a factor of 2^4 (16); therefore, flow in larger pipes can be much faster than in small ones. Larger pipes are much more susceptible to **embolism** and **cavitation**, the formation of air bubbles and the break-up of the water column. This occurs as the pressure gradient is provided by a tension, a force drawing from above, rather than a pressure below.

Water potential

The **chemical potential** of water is the amount of free energy associated with it. **Water potential** is defined as the chemical potential of water divided by the volume of a mole of water. It is measured in J m^{-3} or Pascals (Pa). The symbol used for water potential is ψ_w ; it has two major components, **solute or osmotic potential**, ψ_s , and **pressure potential**, ψ_p , such that $\psi_w = \psi_s + \psi_p$. The solute or osmotic potential, ψ_s , is dependent on the solute concentration and the temperature. The pressure potential, ψ_p , is the hydrostatic pressure in excess of atmospheric pressure developed by the cell or tissue. Water moves from areas of high water potential to areas of low water potential (i.e. to areas where the solute concentration is higher and therefore the 'water concentration' is lower).

Water entering a cell will result in an increase in volume. If the cell wall stops that volume increase, the **hydrostatic pressure** will increase. Eventually, the positive hydrostatic pressure equals the negative osmotic potential and the water potential of the cell reduces to zero (i.e. $\psi_w = 0$ on both sides of the membrane). At this point there is no net movement of water into or out of the cell.

Turgidity and plasmolysis

A cell in a **hypotonic** solution, i.e. one with a lower solute concentration and therefore a more positive osmotic potential than the cell cytoplasm will take up water, generating a **hydrostatic pressure (turgor pressure)** in the cell. In such a cell, the cell contents exert a pressure on the cell wall and the cell is turgid. A cell in a **hypertonic** solution (i.e. one with a higher solute concentration, and therefore a more negative osmotic potential than the cell cytoplasm) will tend to lose water, until the hydrostatic potential becomes negative. At this point, the plasma membrane will pull away from the cell wall and the cell will be **plasmolysed (flaccid)**. The **point of incipient plasmolysis** occurs when the plasma membrane is in contact with the cell wall, but no hydrostatic (turgor) pressure is generated; at this point, $\psi_w = \psi_s$ as $\psi_p = 0$ (Fig. 1).

Water channels (aquaporins)

The movement of water across cell membranes is limited by its low solubility in the lipid bilayer. Aquaporins are proteins which permit water to cross a membrane. Their regulation is likely to be important in regulating water potential.

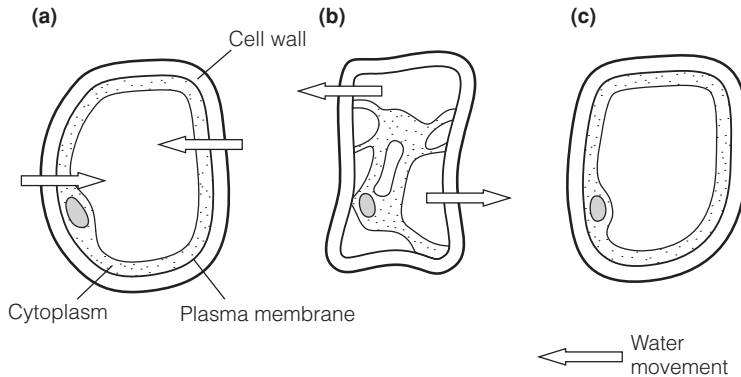


Fig. 1. (a) A cell in a hypotonic medium is fully turgid, ψ_w and ψ_p are positive. (b) Cells in a hypertonic solution will lose water by osmosis and both ψ_w and ψ_p are negative. (c) At the point of incipient plasmolysis $\psi_p = 0$ and $\psi_p = \psi_s$.

Transpiration

Transpiration is the process by which water is drawn from the soil through the plant as a result of evaporation from the leaves. Surfaces exposed to the air are generally covered with a layer which resists water loss (Topic C5). **Stomata** in the leaf surface permit water loss by evaporation from the leaf (Topic C5). Most transpiration (90–95%) occurs through these pores. The rate of transpiration increases with temperature and with wind speed. Changing the stomatal aperture (Topic I2) varies the rate of water loss in changing environmental conditions.

Xylem water flow

The water-conducting tissue of the plant is the **xylem**. It is made up of **elongated cells** with walls thickened and strengthened by secondary wall deposits. Its structure is given in detail in Topic C1. Three possible driving forces exist for water flow in the xylem: **root pressure**, **capillary action** and **cohesion-tension** (in which a column of water is drawn up from the soil by forces generated by evaporation at the leaf surface).

Root pressure

When the stem of a plant is cut, xylem fluid often exudes from the cut. This exudation is driven by root pressure. It occurs where accumulated solutes in the xylem cause the influx of water into the xylem by osmosis. The suberized endodermal layer prevents back-flow of water and a hydrostatic pressure is generated, causing water movement. Root pressure is insufficient to explain water movement to the upper leaves of a tall tree and is not observed in all plants. It is therefore unlikely to be the major cause of xylem water flow.

Capillary action

Capillary action is generated by the adhesive forces between the surface tension in the meniscus of water and the wall of a tube. While capillary effects occur, the total elevation of water achieved by capillaries of a diameter typical of xylem elements are less than a meter, insufficient to explain water transport to the top of a tall tree.

Cohesion-tension

Cohesion-tension explains water flow through large plants. The driving force is provided at the leaf, where evaporation generates **tension** (negative pressure, or 'suction'). This is particularly strong where the water surface bridges microscopic

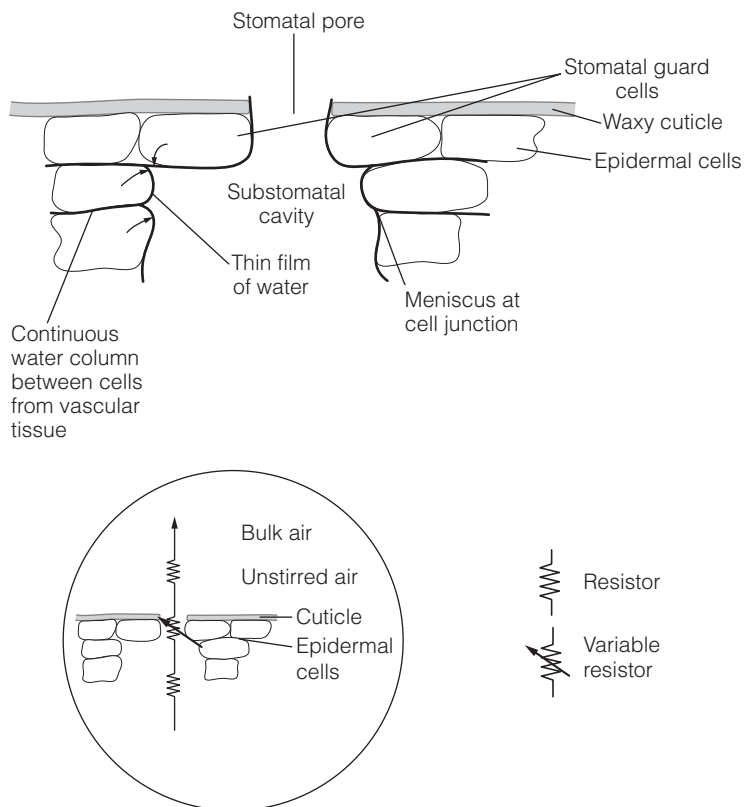


Fig. 2. Water is drawn by evaporation from cells bordering the sub-stomatal cavity. As water retreats to the small spaces between the cells, a meniscus with a high surface tension develops and a negative pressure results.

gaps, for instance at the junction of two mesophyll cells (Fig. 2). Evaporation from the surface of the leaf causes the water to retreat to microscopic pores in these cell wall junctions, where it adheres to hydrophilic wall components. Cohesion of the water molecules (surface tension) results in the formation of a concave **meniscus**. This is pulled by adhesion and cohesion, of water molecules to the walls and of water molecules to each other, generating a negative pressure. A meniscus drawn into a pore of radius $0.01 \mu\text{m}$ has a tension of -15 mPa , more than sufficient to explain water movement from the soil. The leaf water is in a continuous column running through the xylem to the root. The whole water column is therefore under tension and water is drawn upwards from the soil. This places the column under considerable tension; in a 100 m tree, a force of up to -3.0 MPa is present. A gas-free water column can withstand a tension about 10 times this; however, the presence of dissolved gas greatly reduces this as **embolisms** (gas bubbles) form. Damage due to embolisms is minimized as the xylem is divided into many small pipes, with interconnections via pits (see above). Figure 3 illustrates the action of pits and perforation plates in containing an embolism.

Water transport in roots

In most plants, water uptake occurs predominantly through **root hairs**, fine, extensions of single epidermal cells that enter the water film on soil particles (Fig. 4). They provide a very large surface area for absorption. Mycorrhizal fungi may also fulfill this function (Topic M1). The internal anatomy of the root is also

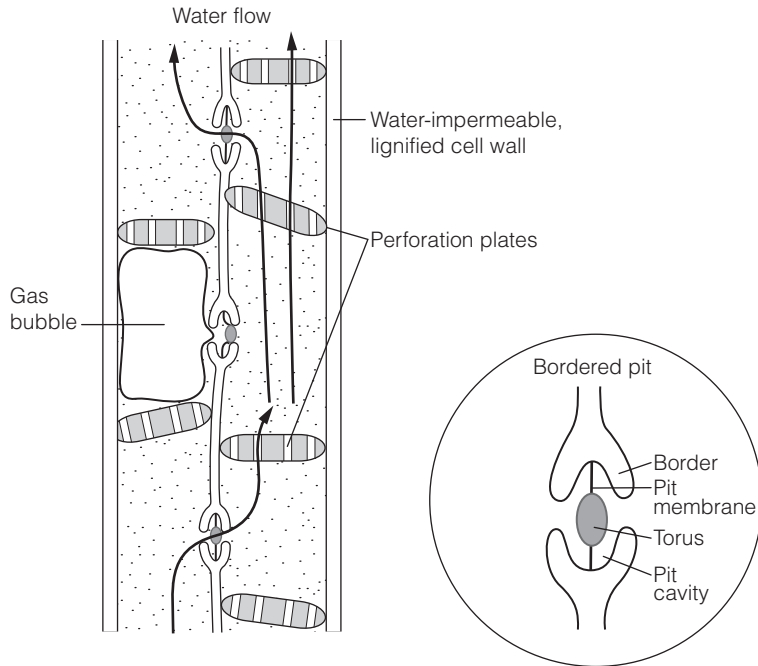


Fig. 3. The action of bordered pits and perforation plates to contain a gas bubble (embolism) formed in either a vessel element or tracheid. Note that the central torus acts as a valve to seal the pit in the region of the bubble.

important. The xylem and endodermis (a water-impermeable cell layer with suberized cell walls, through which water movement must be symplastic; Topic C2) develops some distance behind the root tip. Water flows either through the cell wall spaces (the **apoplast**) or through the cell contents (the **symplast**). Water may be taken up from, or lost to, the apoplast by any cell in the pathway. Movement of a water molecule across the root involving both pathways is termed **transcellular transport**.

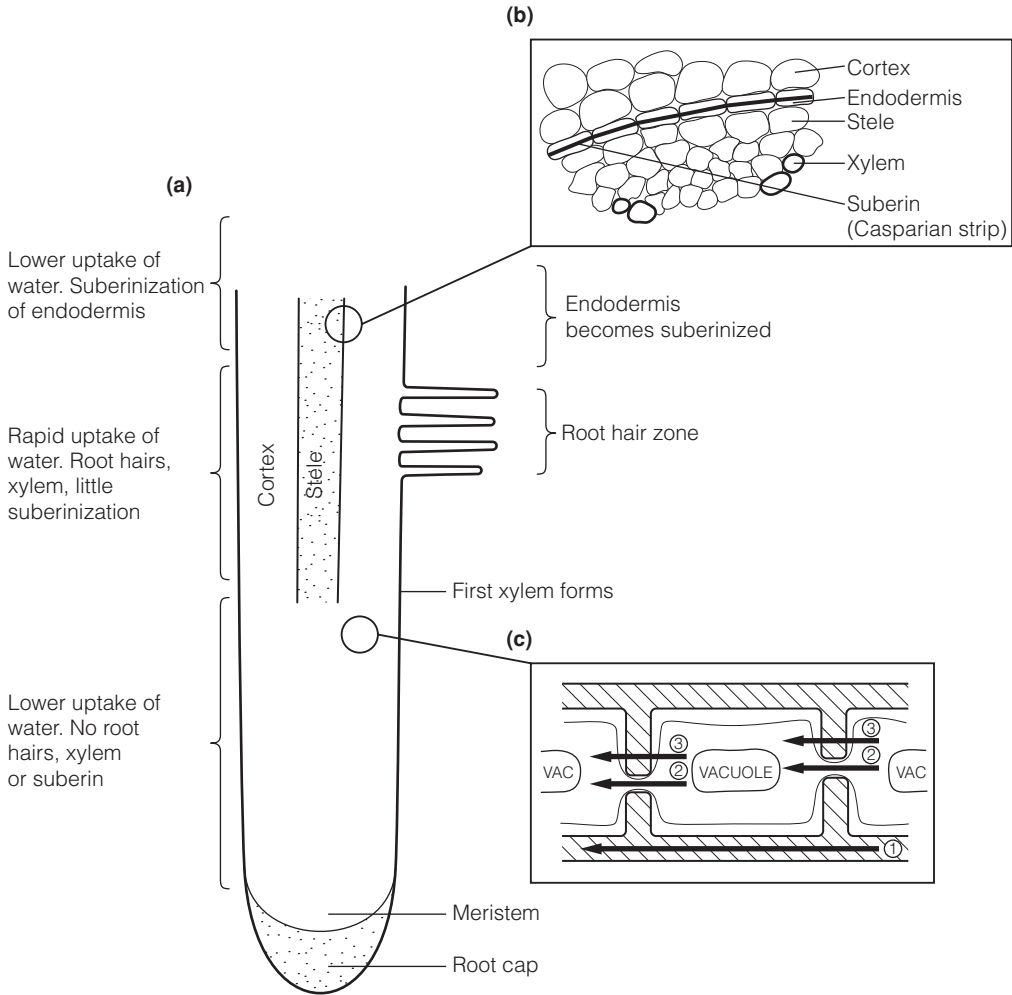


Fig. 4. Key features of water transport in a primary root. (a) Root hairs increase root surface area in contact with films of water around soil particles. The suberinized endodermis of older tissue restricts water uptake. (b) Illustrates the position of the endodermis between the cortex and vascular tissue. (c) Shows the possible pathways of transport through root cells: (1) apoplastic; (2) symplastic through plasmodesmata; and (3) symplastic (transmembrane).

I2 WATER RETENTION AND STOMATA

Key Notes

Plant types

Plants are categorized as mesophytes adapted to an environment in which water is available, xerophytes adapted for areas of low water availability and hydrophytes adapted to the presence of large amounts of water or to growth entirely in water.

Plant structure and surfaces

Leaf structure is adapted to regulate and minimize water loss in unfavorable conditions. The close-packed, flattened epidermal cells of leaf surfaces are covered in hydrophobic cuticles made of cutin and wax, which minimize evaporation. Stomata are most abundant on the lower side of the leaf and may be sunken into the leaf surface.

Stomata: structure

Diffusion of gas is essential for photosynthesis. Stomata (singular, stoma) permit gas diffusion into the leaf while minimizing and regulating water loss. The stomatal pore penetrates the epidermis into the substomatal cavity in the mesophyll. The pore is bounded by two guard cells, which are associated with subsidiary cells in the epidermis. Stomata are open when the guard cells are turgid and closed when they lose turgor.

Stomata: action and regulation

Stomatal opening responds to a number of environmental factors, in addition to drought, including: CO₂ concentration, light and temperature. Stomata are held open by turgor from high solute concentrations in guard cells. Absciscic acid causes release of solutes via regulated anion channels in the plasma membrane. This reduces the osmotic potential of the guard cell and water flows from the cells. Opening results when the anion channels close and solutes re-enter the cell.

Stomatal adaptations of xerophytes

Xerophytes are adapted to low water availability. Typical characteristics include: thick fleshy leaves or no leaves (succulence), protected stomata and thick cuticles. Plants showing crassulacean acid metabolism (CAM) open their stomata at night to fix CO₂ as malate which is stored in the vacuole, while they remain closed in daytime when evaporative losses are greatest.

Related topics

Roots (C2)

Stress avoidance and adaptation (G5)

Plants and water (I1)

C3 and C4 plants and CAM (J3)

Plant types

Mesophytes are adapted to an environment in which water is generally available in the soil and can be extracted by transpiration to supply the needs of the plant. Mesophytes can restrict water loss by the closure of stomata, but desiccation to below 30% total water content normally results in death. Mesophytes

may show adaptations to either drought or waterlogging to different degrees depending on species. Some, like corn, form **aerenchyma** in response to waterlogging, while in others (e.g. rice) it is always present (Topic C1). Presence of thicker **cuticles**, fleshier leaves, sunken stomata and photosynthetic modification indicate increasing adaptation to drought conditions. Other adaptations to drought include **drought avoidance**, for instance over-wintering as seeds and loss of leaves or other aerial parts.

Xerophytes are adapted to environments in which water is generally very scarce. They display a range of adaptations, including: **sunken stomata** (that entrap a layer of unstirred air); stomata open at night; modified photosynthetic mechanisms (Topic J3); thick cuticles and **succulence** (thick, fleshy leaves or the absence of leaves and presence of fleshy, modified stems). **Cacti** and some **euphorbias** are examples of xerophytes.

Hydrophytes are adapted to live submerged or partially submerged in water. They display modified leaves and stems, and frequently contain air-spaces (**aerenchyma**) to supply oxygen to underwater organs.

Plant structure and surfaces

Land plants face a dilemma; how to acquire sufficient carbon dioxide and light for photosynthesis without losing large quantities of water by exposing large evaporative surfaces to the atmosphere. In xerophytes, the area exposed is reduced and lower growth rates occur. Mesophytes with a large leaf area also show adaptations to minimize water loss. Surfaces are coated with a **cuticle** of lipids, cutin, suberin and waxes which both reduces water loss and the access of pathogens to the cells of the leaf.

Cutin is a polymer of **long-chain fatty acids** forming a rigid mesh through ester linkages. **Suberin** contains long-chain fatty acids joined through ester linkages with dicarboxylic acids and phenolics. It is the predominant coating of underground parts of the plant and is also found in the Casparian strip of the endodermis (Topic C2). Associated with cutin and suberin are waxes, long-chain acyl lipids which are solid at ambient temperatures. The cuticle is deposited in layers (*Fig. 1*); first a cuticular layer of cutin, wax and carbohydrates at the epidermal cell wall, then a layer of cutin and wax and finally a waxy surface layer exposed to the atmosphere.

Stomata: structure

Stomata are pores through which gas exchange to the leaf takes place. The pore is formed by two specialized cells, the **guard cells**, that open and close the pore, frequently associated with **subsidiary cells** (*Fig. 2*). The pore structure leads to the **sub-stomatal cavity** surrounded by cells of the **spongy mesophyll**. The stomata may themselves be sunken in order to minimize evaporative air movement.

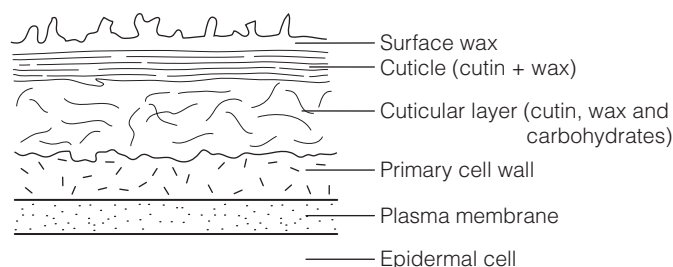


Fig. 1. The structure of the cuticle of a higher plant leaf.

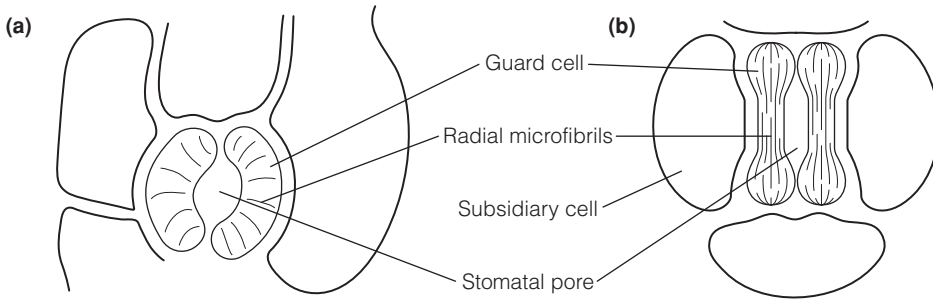


Fig. 2. Stomata of (a) a dicot and (b) a grass.

Stomata of dicots are typically kidney-shaped, while those of grasses are dumb-bell shaped. In both types, **microfibrils** of the cell wall (Topic B2) are arranged radially, causing enlargement of the pore when the guard cells swell (Fig. 2).

Stomata: action and regulation

Stomatal aperture is tightly regulated by the plant, in a system, which integrates **carbon dioxide** requirement with **light** and **water stress**. Stomatal aperture often varies according to a **circadian** (day/night) **rhythm**. Low CO_2 concentrations in the guard cells result in opening, while high CO_2 concentrations result in closure. Stomata in most species open at dawn and remain open in daylight, given adequate water availability; this may in part be due to changing CO_2 concentrations as a result of photosynthesis and respiration.

Stomatal guard cells are also very sensitive to **water stress**. Localized **turgor** loss results in wilting of the guard cells (**hydro-passive closure**) and stomatal closure. Water stress elsewhere in the plant results in the production of **abscisic acid** (ABA, Topic F2) which results in stomatal closure. The mechanism of ABA sensing probably involves **ABA receptor proteins** (Topic F3) and may involve the action of calcium as an intracellular messenger that alters membrane ion channel activity, giving altered turgor and stomatal closure.

Guard cells take up K^+ and increase in **turgor** in favorable conditions, resulting in swelling of the cells and opening of the pore. Potassium is rapidly lost from the guard cells during stomatal closure. The driving force for potassium uptake is provided by the **plasma membrane proton pump** (Topic I3). This is stimulated during stomatal opening and the resulting **membrane hyperpolarization** is believed to open K^+ channels in the plasma membrane which permit a passive K^+ influx. This, together with influx of Cl^- and organic anions such as malate provides the increase in turgor. When stomata close, other plasma membrane ion channels open resulting in a rapid efflux of anions and a drop in turgor.

Stomatal adaptations of xerophytes

Xerophytes show a number of adaptations to water stress, including sunken stomata, thickened cuticles and succulence. A key adaptation is the presence of crassulacean acid metabolism (CAM; Topic H3). CAM plants show a specialized rhythm of stomatal action that minimizes water loss. Coupled with their unique metabolism their stomata only open at night, when they fix CO_2 as malate in the vacuole. The stomata then remain closed during the day, when evaporative losses would be greatest.

13 MOVEMENT OF NUTRIENT IONS ACROSS MEMBRANES

Key Notes

Transport of nutrients into cells

Mineral nutrients are transported as ions. They are soluble in water but cannot cross membranes without the presence of transport proteins. This transport is coupled to the transport of protons (H^+), which are pumped actively across the membrane by the activity of primary pumps using adenosine triphosphate (ATP) as energy source.

Studying membrane transport

Advances in understanding membrane transport have been made by use of membrane vesicles and radioactive isotopes, by electrophysiology and by molecular techniques. The identity of many nutrient transport proteins is now known.

Primary pumps

There are two major primary ion pumps in plant cells: the plasma membrane proton pump, which uses ATP as energy source and pumps H^+ out of the cell; and the vacuolar (or tonoplast) proton pump which pumps H^+ into the vacuole. Both pumps are electrogenic (generate a membrane potential). The apoplast and vacuole are therefore more acidic than the cytoplasm. Other primary pumps exist for calcium and the vacuole contains a second proton pump using pyrophosphate as energy source.

Secondary coupled transporters

Primary pumps generate a proton electrochemical gradient across the plasma membrane and tonoplast. Secondary coupled transporters couple the energy in this gradient to move other ions against their own electrochemical gradients. Antiporters transport an ion in the opposite direction to the transported ion; symporters transport two ions in the same direction.

Ion channels

Ion channels permit nutrient ions to move across membranes driven by the electrochemical gradient. Channels are gated (they open and close) in response to changes in membrane potential (voltage gated channel), binding signal or other molecules (ligand gated channel) or tension at the membrane (stretch activated channels).

Related topics

Membranes (B4)
Plants and water (I1)

Uptake of mineral nutrients by plants (I4)

Transport of nutrients into cells

Membranes are impermeable to charged molecules and large molecules that are polar (have a charge imbalance). As mineral nutrient ions are charged, they cannot cross cell membranes without the action of specific membrane proteins. These proteins fall into three categories: primary pumps, which use the energy of adenosine triphosphate (ATP) to transport ions actively; secondarily-coupled

transporters, which couple the movement of one ion to that of another; and channels that permit the passive movement of ions. Transport of most ions is coupled to the transport of protons (H^+), which are pumped actively across the membrane by the activity of primary pumps using ATP as energy source. The action of the transport proteins is tightly regulated and they are specific for given nutrients. They provide selectivity and specificity of uptake and, together with the properties of membranes, result in the concentration of nutrients within a cell or tissue being different from that outside it.

Movement of nutrient ions into and out of a cell, or subcellular compartment, is driven by a combination of concentration and electrical effects at any membrane (the electrochemical gradient). The force driving an ion across a membrane is made up of two parts, an electrical driving force, and a chemical driving force. The two forces are balanced (equal and opposite) at equilibrium, when no net movement of the ion occurs across the membrane. Plant cells generally maintain a membrane potential of -120 to -200 mV at the plasma membrane as a result of the action of primary proton pumps. This electrical driving force is used to maintain the required concentration of anions and cations on each side of the membrane. Figure 1 illustrates the key transporters for ions in a typical plant cell.

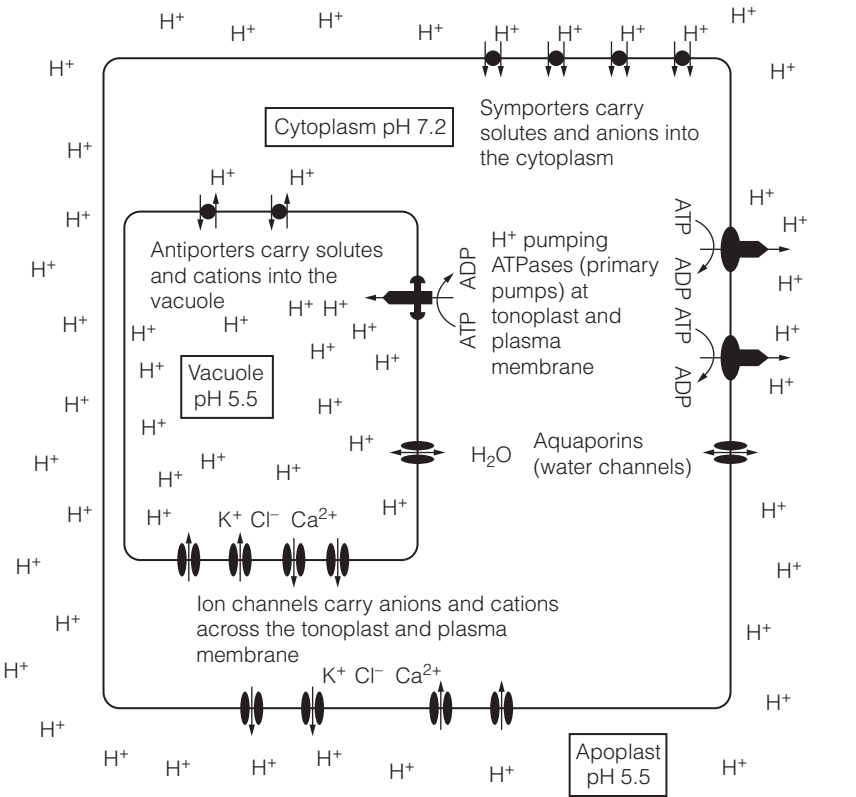


Fig. 1. Transporters for nutrient ions at the plasma membrane and tonoplast of a plant cell. The primary driving force for ion movement is created by electrogenic H^+ pumps at the plasma membrane and tonoplast which create a trans-membrane electrical potential ($\Delta\psi = -120$ mV at the plasma membrane and -90 mV at the tonoplast) as well as steep trans-membrane proton gradients (pH 5.5 in apoplast and vacuole; pH 7.2 in the cytoplasm).

Studying membrane transport

The transport of an ion across plant membranes was first investigated using **radioactive isotopes** and **membrane vesicles**, sealed spheres of membrane which are formed when membranes are purified. The properties of many transporters have been determined by these methods.

The technique of **patch clamping** (Fig. 2) permits the transport properties of single proteins in the membrane to be assayed. A small piece of membrane (patch) is attached to the tip of a fine pipette and sealed to it by gentle suction. By measuring currents flowing through the membrane, the activity and properties of ion channels can be described.

Advances in describing nutrient transporters have resulted from cloning transport proteins. The overall structures of membrane proteins have been established and the role of regions of the protein investigated by altering key amino acids and expressing them in foreign host cells, like yeast cells, or giant egg cells of the African frog *Xenopus laevis*. Use of mutants has also been important; for instance, the nitrate transporter CHL1 was identified using an arabidopsis mutant *chl1* that is insensitive to chlorate, an inhibitor of the transport of nitrate. Finally, new membrane transport proteins have been detected by studies based on their homology with known ion transporters from other organisms.

Primary pumps

The primary pumps of plant cell membranes are proton (H^+) pumps, located at the plasma membrane and vacuolar membrane (tonoplast). The plasma membrane proton pump uses ATP as substrate and expels H^+ from the cell. The process generates an electrical gradient of about -120 mV across the membrane. The tonoplast has two primary pumps: an adenosine triphosphatase (ATPase) and a pyrophosphatase (which uses pyrophosphate rather than ATP as substrate) which pump H^+ into the vacuole. These pumps generate a membrane potential across the tonoplast of about -90 mV. The transport of all other nutrient ions except Ca^{2+} depends on these electrochemical gradients. Ca^{2+} concentrations are regulated by active Ca^{2+} pumps.

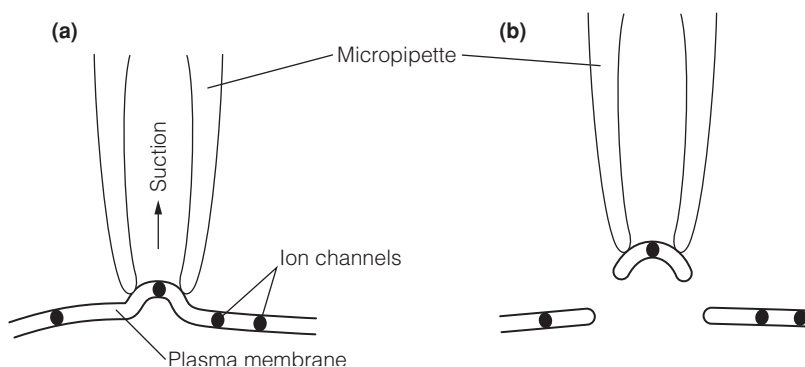


Fig. 2. The patch clamp technique. A fine glass micropipette is pushed against the plasma membrane. Gentle suction is applied (a) and the pipette withdrawn (b) with a small patch of membrane adhering to the tip. The patch is sufficiently small to contain only a few membrane proteins. Their transport properties can then be measured by measuring the electrical current carried by ions as they cross the membrane.

Secondary coupled transporters

Transport of many other ions is coupled to the electrochemical gradient developed across the plasma membrane and tonoplast by the primary proton pumps. **Antiporters** are membrane proteins which couple the flow of H^+ down its electrochemical gradient to the movement of another ion against its electrochemical gradient. The tonoplast **calcium proton antiporter**, for instance, accumulates calcium in the vacuole by coupling its transport to the outflow of H^+ from the vacuole. **Symporters** similarly couple transport of an ion to the proton electrochemical gradient, but with the movement of the ion occurring in the same direction as the proton movement.

Ion channels

Some transport proteins permit the passive movement of nutrients across membranes driven by the electrochemical gradient for that nutrient. These passive transporters are also membrane proteins and are known as **uniporters**. **Ion channels** are a specialized type of uniporter; they generally show a high degree of **selectivity** for individual ions and are **gated** (can either open to permit ions to cross the membrane or close to prevent them from crossing). Channels may be gated by the membrane potential (**voltage gated**), by signal molecules within the cell (**ligand gated**) and by tension in the membrane (**stretch activated**). The combination of these properties permits very close regulation of ionic concentration within the cytoplasm or vacuole.

14 UPTAKE OF MINERAL NUTRIENTS BY PLANTS

Key Notes

Key properties of nutrients

The majority of plant nutrients are taken up by the plant in ionized form from films of water surrounding soil particles. Nutrients move in aqueous solution. They cannot cross lipid membranes unless transport proteins are present.

The soil–root interface

The root surface (the rhizodermis) makes limited contact with the nutrient film surrounding soil particles. Root hairs and, in many species, mycorrhizal fungi greatly increase the surface area in contact.

Symplastic, apoplastic or cellular?

Transport within the root may be across cell membranes (transmembrane) then through the cell cytoplasm (cellular transport) or between cells (apoplastic). Plasmodesmata provide continuous contact between the cytoplasm of adjacent cells giving direct cell-to-cell (symplastic) transport without contact with the apoplast.

The endodermis

Cells of the endodermis have suberinized cell walls which form a water-impermeable barrier surrounding the vascular tissue of the root. It prevents apoplastic movement of nutrients which must therefore either travel symplastically through the endodermis or enter the vascular system from below the endodermis.

Transport into the xylem

Water and nutrients leaving the endodermis enter xylem parenchyma cells that surround xylem vessels. These cells actively accumulate nutrients to a high concentration before they are loaded into the xylem for transport to the rest of the plant.

Distribution in the plant

Xylem extends throughout the plant and water flows to wherever transpiration is taking place. The apoplast of all tissues is in close contact with xylem fluid and nutrients are taken up from this space by cells. Rapidly growing tissues (e.g. fruits, tubers) may have low transpiration and in these tissues redistribution of ions in the phloem may be important.

Related topics

- Membranes (B4)
- Roots (C2)
- Plants and water (I1)
- Movement of nutrient ion across membranes (I3)
- Mycorrhiza (M1)

Key properties of nutrients

Nutrients are taken up as ions dissolved in water. Bulk movement occurs in the **transpiration stream** (via the xylem) to shoots and leaves. Movement depends on the unique size, charge and solubility of each nutrient ion. As ions cannot cross membranes without a specific transport protein being present, their

The soil-root interface

Symplastic, apoplastic or cellular?

uptake into cells and into the root can be regulated. This means that roots accumulate some ions against a concentration gradient, while others are excluded and some ions move through cells while others move in intercellular spaces.

Roots elongate into the soil by growth near the tip, pushing the root cap between soil particles (Topic C2). They deplete their immediate soil environment of nutrients creating a depletion zone. Good root-to-soil contact is provided by the secretions of the root cap (Topic C2) and by root hairs. **Fibrous root systems**, made up of fine roots with many root hairs, maximize the area available for uptake. In addition, many species have **mycorrhizal fungi** in symbiotic association with the root which greatly enlarge the available soil area from which nutrients are extracted (Topic M1). Nutrients become available at the root surface as a result of three processes: **interception**, growth of roots into new nutrient-rich area; **mass flow**, movement of ions in the water flow driven by transpiration; and **diffusion**, passive movement of ions to regions depleted in nutrients (Fig. 1).

Nutrient ions entering the root at the root hairs may travel directly through the cell cytoplasm until they reach the vascular tissue (Fig. 2). Cells of the rhizodermis (root epidermis) are linked by plasmodesmata to adjacent cells and solutes can move from cell to cell directly. Transport through the cell via plasmodesmata is termed **symplastic transport**. The second form of transport, **apoplastic transport** is through the walls of root cells. Water and nutrients can travel through this region (the apoplast) until the endodermis, where water and nutrients must cross a plasma membrane and enter a cell symplasm (**cellular transport**). Water and nutrients may also enter cells via the plasma membrane (**transmembrane transport**), then leave the cell to enter the apoplast before being taken up across the plasma membrane of an adjacent cell.

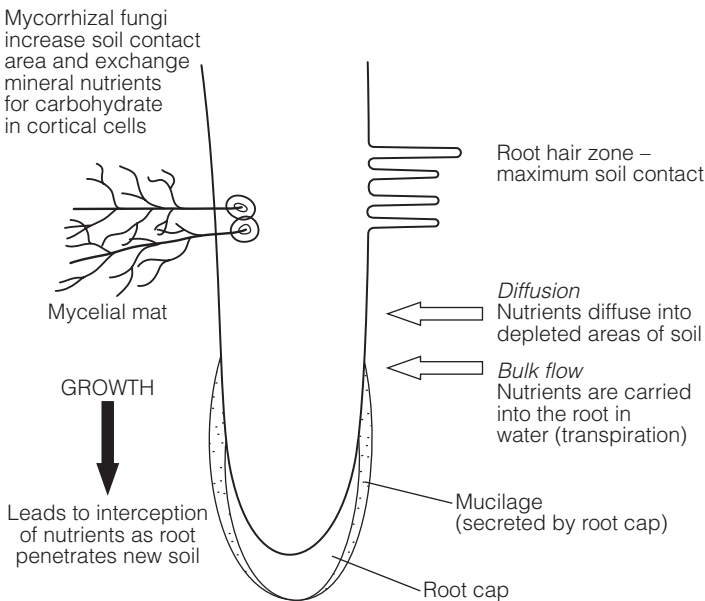


Fig. 1. Key features of nutrient uptake by roots.

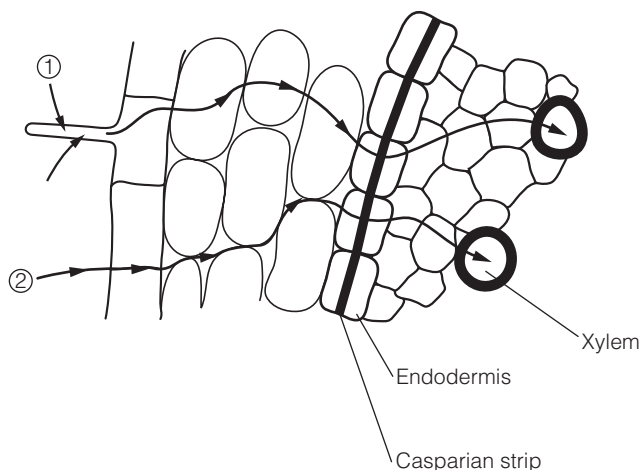


Fig. 2. Pathways of nutrient transport in roots. (1) Symplastic throughout; (2) apoplastic until endodermis, then symplastic.

The endodermis

The **endodermis** develops near the point of development of the root vascular tissue (Topic C2). Cells of the endodermis have suberinized cell walls which form a water-impermeable barrier surrounding the vascular tissue of the root. This prevents water and nutrients moving into the vascular tissue through the apoplast and the only transport possible at this point is **symplastic**. Most nutrient ions entering the vascular tissue will therefore have passed through living root cells at some point. This permits **selectivity** and filtration of the transported ions. Older endodermal cells become entirely enclosed in a suberin layer. These cells provide a barrier to the back-flow of water from the xylem.

Transport into the xylem

After crossing the endodermis, ions enter the xylem from the cells surrounding it, the **xylem parenchyma**. These cells actively accumulate nutrients to a high concentration before they are loaded into the xylem for transport to the rest of the plant. Influx into the xylem occurs via specific membrane proteins down the concentration gradient. Nutrient flow in the xylem to leaves and shoots occurs in the transpiration stream.

Distribution in the plant

Mineral nutrient ions and water move in the xylem and reach all parts of the plant. Xylem tubules branch out from the main **vascular bundles** of the stem to reach leaves and buds and branch again to form finer tubules in the **leaf veins**. Water and nutrients leave these tubules as water evaporates from the leaf surface; the cells of the leaf are surrounded by water and dissolved nutrients which permeate the leaf wall spaces (leaf apoplast). Cells extract water and nutrients from this. Some nutrient ions may be redistributed through the plant in the **phloem**, while others only move in the xylem. Some areas of the plant undergoing rapid growth, e.g. fruits and tubers, do not have high transpiration rates and the xylem flow is low. This may lead to nutrient deficiency if nutrient transport in the phloem does not occur. Blossom end rot of tomato occurs in these circumstances, due to lack of calcium. Ions may be moved from xylem to phloem by **transfer cells** that lie between the two pathways or ions may leave source tissue as it loads organic nutrients into the phloem. Not all ions are **phloem mobile** and there are marked differences between species.

15 FUNCTIONS OF MINERAL NUTRIENTS

Key Notes

Essential macro- and micronutrients

Plants depend on a range of essential mineral nutrients, which are extracted from the soil by the roots. These are categorized as macro- and micronutrients depending on the quantity required. Examples of macronutrients are sulfur, phosphorus, nitrogen, magnesium, potassium and calcium.

Essential, beneficial and toxic elements

Minerals may be categorized according to their effects on the plant. Essential elements are those without which a plant cannot reproduce; beneficial elements have beneficial effects on plant growth, but the plant can complete its life cycle without them. Toxic elements are deleterious to growth. Some elements are essential at low concentrations, but toxic at higher concentrations.

Key macronutrients

Nitrogen is a constituent of amino acids and proteins and is taken up as either nitrate or ammonium from soils or by nitrogen-fixing organisms. Nitrogen is transported as reduced nitrogen compounds. Sulfur is required in sulfur-containing amino acids to maintain protein structure. Phosphorus is required for membranes, nucleic acids and ATP. It is transported either as inorganic phosphate or as sugar phosphates. Its uptake is enhanced by mycorrhizal fungi. K^+ , Mg^{2+} and Ca^{2+} are all water-soluble cations. K^+ is required for enzyme activity and osmo-regulation, Ca^{2+} for membrane stability and as an intracellular regulator and Mg^{2+} for chlorophyll and enzyme activity.

Nutrient deficiency and toxicity

Plants growing without enough of a nutrient show deficiency symptoms related to the function of the nutrient in the plant. Toxic ions such as aluminum may result in deficiency symptoms as they act by restricting the availability or uptake of nutrients. Good agricultural practice seeks to maximize the availability of nutrients and minimize toxic ions.

Related topics

Plants and water (I1)	Uptake of mineral nutrients by plants (I4)
Movement of nutrient ions across membranes (I2)	

Essential macro- and micronutrients

A nutrient is **essential** if: (i) it is required for the plant to complete a normal life cycle; (ii) it can be shown to be a component of the plant, either as part of structure or metabolism; and (iii) its function cannot be substituted for another element. Nutrients are either **macronutrients** (required in large amounts) or **micronutrients (trace elements)** required in much smaller amounts. *Table 1* lists a range of both macro- and micronutrients. The **available form** (i.e. the form in which the nutrient is transported into the plant) is usually either an **anion**

Table 1. Nutrient elements and their functions

Element	Available form	Typical concentration (mmol kg ⁻¹ dry weight of plant)	Typical use
Macronutrients			
Hydrogen	H ₂ O	60 000	Turgor; photosynthesis; carbohydrates
Carbon	CO ₂	40 000	Carbohydrate; protein; metabolism
Oxygen	O ₂ , CO ₂ , H ₂ O	30 000	Carbohydrate; metabolism
Nitrogen	NO ₃ ⁻ (nitrate)	1000	Amino acids; proteins; nucleic acids
	NH ₄ ⁺ (ammonium)		
Potassium	K ⁺	250	Remains a free ion for turgor regulation; cofactor for many enzymes
Calcium	Ca ²⁺	125	Cell signaling; cell wall linkages
Magnesium	Mg ²⁺	80	Chlorophyll (photosynthesis)
Phosphorus	HPO ₄ ⁻ (phosphate)	60	Phospholipids; nucleic acids; ATP-metabolism
	HPO ₄ ²⁻		
Sulfur	SO ₄ ²⁻ (sulfate)	30	Amino acids and proteins
Micronutrients			
Chlorine	Cl ⁻ (chloride)	3	Turgor regulation; photosynthesis
Iron	Fe ²⁺ (ferric)	2	Photosynthesis, respiration and nitrogen fixation in cytochromes and nonheme proteins
	Fe ³⁺ (ferrous)		
Boron	BO ₃ ³⁻	2	Complexed in cell walls
Manganese	Mn ²⁺	1	Cofactor for various enzymes
Zinc	Zn ²⁺	0.3	Cofactor for various enzymes
Copper	Cu ²⁺	0.1	Cofactor for enzymes and electron carrier proteins
Nickel	Ni ²⁺	0.05	Constituent of urease
Molybdenum	MoO ₄ ²⁻ (molybdate)	0.001	Constituent of enzymes in nitrogen metabolism

(negative) or a **cation** (positive). The distinction between macro- and micro-nutrients is to some extent arbitrary as some species contain more and others less of a particular nutrient; macronutrients are conveniently defined as those present at >10 mmol kg⁻¹ dry matter.

Essential, beneficial and toxic elements

Some minerals are important in plant nutrition, but not essential. Elements which result in improved growth or reduced disease susceptibility, but without which the plant can still complete its life cycle are known as beneficial. An example of such an element is silicon (Si), which causes increased structural strength of cell walls, increased tolerance of toxic elements in soils and improved resistance to fungal pathogens. Some other elements are usually toxic, or may be toxic at high concentrations. Aluminum is almost always toxic when available (at acidic soil pH) as it complexes phosphate. Sodium, zinc, copper, manganese, boron, molybdenum and iron can all be toxic if present at high concentrations in the soil. Species differ in their ability to tolerate toxic ions and in some instances ions, which are normally toxic, are known to be beneficial. The growth of the tea plant, for instance, is enhanced by the presence of available soil aluminum, which it takes up as an organic acid complex, and the growth of many halophytes by sodium.

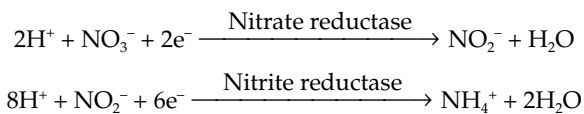
Key macronutrients

Nitrogen

Nitrogen gas is abundant in the aerial and soil environment, but unlike oxygen cannot be used directly. Nitrogen is **fixed** from the atmosphere by a number of microorganisms, which may be free-living, or in symbiotic association with some species of plants, mainly legumes (Topic M2). Other sources of available soil nitrogen may be decaying organic material, animal excreta and chemical fertilizers, frequently added to agricultural land.

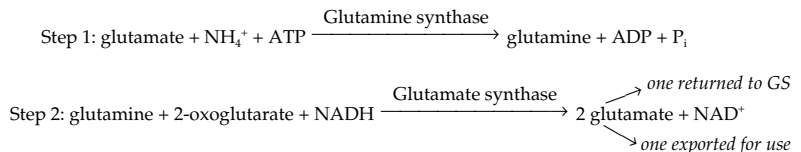
Nitrogen assimilation

Plants take up either nitrate (NO_3^-) or ammonium (NH_4^+) from the soil, depending on availability and species. Nitrate will be more abundant in well-oxygenated, non acidic soils, whilst ammonium will predominate in acidic or waterlogged soils. After uptake, nitrate is reduced to ammonium in two stages by **nitrate reductase** (NR) and **nitrite reductase** before assimilation into amino acids.



NR is a dimer of two identical subunits. Expression of the gene for NR requires light and nitrate. The gene is expressed in both shoots and roots, but in low nitrate conditions, almost all **nitrate assimilation** will occur in the roots. Crops grown at high temperatures but only moderate light intensity may accumulate nitrate in the vacuole as a result of low induction of the NR gene.

Ammonium is toxic to plants, and is therefore rapidly incorporated into amino acids via the **glutamine synthase-glutamate synthase (GS-GOGAT)** pathway:



The process runs as a cycle, one of the glutamates produced being used as substrate by GS while the other is exported to the plant. Inputs to the cycle are ammonium and **2-oxoglutarate** (from photosynthate imported via the phloem).

In plants with nitrogen-fixing nodules, nitrogen is exported to the plant from the nodule in the xylem flow as high-nitrogen containing compounds such as **amino acids** or **ureides**.

Sulfur

Sulfur is taken up in the form of **sulfate** (SO_4^{2-}) by high-affinity transport proteins at the plasma membrane. The expression of these proteins varies with sulfate availability, the genes being repressed by high sulfate and activated by low sulfate. Once in the plant, sulfate is reduced to the sulfur-containing amino acid **cysteine**. The entire process involves the donation of 10 electrons and a variety of **electron donors** is required. It is more active in photosynthesizing leaves as the chloroplast provides a supply of electron donors. Sulfur is predominantly transported around the plant in the **phloem**, as **glutathione**. Glutathione (GSH) is a tripeptide formed of three amino acids (γ -glutamyl-cysteinyl-glycine) and acts as a storage form of sulfur in the plant.

Phosphate

Phosphate is not reduced in the plant. Root cells contain **phosphate transporters** at the plasma membrane and after uptake it either travels in xylem as inorganic phosphate (P_i) or is **esterified** through a hydroxyl group on a sugar or other carbon compound. Phosphate taken up by the root is rapidly incorporated into **sugar phosphates**, but is released as P_i into the xylem. Roots of plants are frequently in symbiotic association with **mycorrhizal fungi** that extract phosphate efficiently from the soil (Topic M1). Phosphate is an essential constituent of nucleic acids and of many of the compounds of energy metabolism and it is utilized throughout the plant.

Nutrient cations

The **nutrient cations** (e.g. **potassium**, **magnesium** and **calcium**) are water soluble and transported as cations in the xylem. Potassium is very soluble and highly mobile, calcium being the least mobile of the three. Potassium is required for enzyme activity and osmotic-regulation, calcium maintains cell membrane stability, is an intracellular regulator and forms **calcium pectate** links in cell walls at middle lamellae (Topic B2). Magnesium is required as a central component of chlorophyll (Topic J1) and for the activity of some enzymes.

Nutrient deficiency and toxicity

Plants grown in the absence of sufficient quantities of a particular nutrient show visible **deficiency symptoms** that relate to the function of that nutrient in the plant. Key terms are **chlorosis**, a lack of chlorophyll and yellowing of the leaves, and **necrosis**, the death of cells, often the growing tip or in lesions in the leaf surface. The extent and nature of the symptoms observed depend on where the nutrient is required and whether it can be redistributed in the plant. Potassium deficiency, for instance, causes necrosis of leaf margins and tips, whereas deficiency of manganese (a micronutrient) causes necrosis of tissue between the leaf veins (intervinal necrosis).

Development of symptoms such as those for deficiency can result from the presence of **toxic elements**, which interfere with the availability or transport of nutrients. **Aluminum** is more available in acidic soils and complexes with phosphate, creating phosphate deficiency. Plants show adaptations for the nutritional characteristics of the soils in which they grow. **Calcicoles** are adapted for growth in an alkaline, high calcium environment, where other nutrients are of low availability, while **calcifuges** are adapted to acidic soils, with high levels of aluminum and low levels of phosphate. Sodium competes with potassium for uptake resulting in potassium deficiency and failure to osmoregulate. **Halophytes** show a range of adaptations for growth in saline conditions, including salt extruding glands, high levels of discrimination between sodium and potassium for transport and **xerophytic characteristics** to minimize transpiration and salt uptake.

Many agricultural crops make severe demands on the nutrients in the soils in which they are grown; growth of cereals, for instance, results in the removal of large quantities of soil nitrogen and sulfur in seed protein. Good agricultural practice aims to maintain soil nutrient levels and minimize the availability of toxic compounds. For instance **liming**, the application of calcium or magnesium oxides, hydroxides or carbonates, is used to neutralize acidic soils and reduce aluminum toxicity, thereby increasing phosphate availability.