4.1.2 Transport of molecules across cell membranes

(a) Diffusion and selectivity

Transport proteins play a critical part in solute movement because membranes constitute a barrier to free diffusion of molecules. If membranes allowed rapid diffusion of both ions and water, gradients of ions would be slight and osmotic pressure could only be achieved with enormous energy consumption. Instead, some molecules, such as water and gases, move rapidly across membranes. Unrestricted movement of water relative to solutes is the basis of osmosis, and in plants the generation of P.

Similarly, if the movement of CO$_2$ and O$_2$ to and from the sites of photosynthesis and respiration were substantially impeded, steep concentration gradients would reduce the efficiency of these vital processes. The principles of diffusion and selectivity, which are used to describe differential rates of molecular movement, provide a physical rationale for osmosis.

In a homogeneous medium, net movement of molecules down their concentration gradient is described by Fick’s First Law of diffusion. The molecule and medium may be a solute in water, a gas in air or a molecule within the lipid bilayer; a version of this equation describing water movement in soil appeared in Section 3.2. Fick’s Law holds when the medium is homogeneous in all respects except for the concentration of the molecule. If there was an electric field or a pressure gradient then Fick’s Law may not be appropriate (Section 4.1.2(b)). Considering the case of a solute in water, say, sugar, Fick’s Law states that net movement of this solute, also called the net flux ($J_s$), is proportional to the concentration gradient of the solute $\frac{\Delta C_s}{\Delta x}$:

$$J_s = -D_s \frac{\Delta C_s}{\Delta x}$$

(4.1)

The diffusion coefficient ($D_s$) is a constant of proportionality between flux, $J_s$, and concentration gradient (mM m$^{-1}$), where solute concentration ($C_s$) varies over a distance ($\Delta x$). Flux is measured as moles of solute crossing a unit area per unit time (mol m$^{-2}$ s$^{-1}$), so $D_s$ has the units m$^2$ s$^{-1}$. $D_s$ has a unique value for a particular solute in water which would be quite different from $D_s$ for the same solute in another medium, for example the oily interior of a lipid membrane.

When we consider diffusion of a molecule across a membrane from one solution to another, Fick’s Law can be applied to each phase (solution 1–membrane–solution 2). However, flux across the membrane also depends on the ability of the molecule to cross boundaries (i.e. to partition) from solution into the hydrophobic membrane and then from the membrane back into solution. Another difficulty is that the thickness of membranes is relatively undefined and we need to know this for Fick’s
equation above (?x). The two solutions might differ in pressure and voltage and these can change steeply across a membrane; however, if for simplicity we consider a neutral solute at low concentration, these factors are not relevant (see below for charged molecules). A practical quantitative description of the flux of neutral molecules across membranes uses an expression intuitively related to Fick’s Law stating that flux across a membrane \( (J_s) \) of a neutral molecule is proportional to the difference in concentration \( (?C_s) \):

\[
J_s = P_s \times \Delta C_s
\]  

(4.2)

The constant of proportionality in this case is the permeability coefficient \( (P_s) \), expressed in m s\(^{-1}\). When \( P_s \) is large, solutes will diffuse rapidly across a membrane under a given concentration gradient. \( P_s \) embodies several factors: partitioning between solution and membrane, membrane thickness and diffusion coefficient of the solute in the membrane. It can be used to compare different membranes and to compare treatments that might alter the ability of a solute to move across the membrane. Note that Equation 4.2 assumes that the membrane limits the rate of solute flux and that concentration gradients leading to diffusion in solutions adjacent to the membrane will not be significant. If the two solutions

Figure 4.1 Concentration profiles across a plant cell wall and membrane when solutes diffuse from outside into the cytoplasm. Imposed concentration gradients will always be greater than gradients driving diffusion across the lipid membrane. Unstirred layers immediately adjacent to the cell wall, in the wall and in cytoplasm will result in measurements of permeability coefficients being underestimates of their true value for the membrane. Corrections can be made, for example by measuring solute diffusion across the wall without a membrane present and then subtracting wall effects (Based on Hope and Walker 1975; reproduced with permission of Oxford University Press)
are stirred rapidly then this will help to justify this assumption (Figure 4.1). How-ever, there is always an unstirred layer adjacent to the membrane through which diffusion occurs, and for molecules that can permeate the membrane very rapidly the unstirred layer can be a problem for the correct measurement of permeability.

![Figure 4.2 The range of permeability coefficients for various ions, solutes and water in both membranes (bars) and artificial phospholipids (arrows). Note that the permeability of ions as they cross membranes is higher than that through a lipid bilayer, especially for potassium, indicating the presence of specialised permeation mechanisms in plant membranes. Water permeabilities are high in both membranes but can range over an order of magnitude in plant membranes. This variability may be partially accounted for by the activity of aquaporins.](image1)

![Figure 4.3 Relative permeability plot.](image2)
$P_s$ differs markedly for different molecules passing through lipid-based membranes. Permeabilities can differ by eight orders of magnitude (Figure 4.2), reflecting the selectivity of native lipid bilayers. Differences in membrane permeabilities between molecules are much larger than differences in diffusion coefficients in free solution, the latter depending on the size of molecules rather than membrane properties. Collander (1954) showed that partitioning between water and oil phases (expressed as partition coefficient) was a determining factor for membrane permeability (Figure 4.3). Charged molecules and large polar molecules do not easily partition into the oily membrane while some polar molecules such as water, methanol and urea permeate faster than predicted from their partition coefficients. This indicates that there are special pathways for the movement of these small molecules other than through the lipid phase. A comparison of artificial lipid membranes with biological membranes supports this notion because it shows that many molecules and ions permeate biological membranes much faster than would be predicted on the basis of oil solubility and size (Figure 4.2). For these solutes there are transport proteins in biological membranes that increase solute permeability.

Section 4.3 describes how $P$ (the difference in pressure across the membrane and wall) in a plant cell is equivalent to the osmotic pressure difference ($P_i - P_o$) across the membrane when there is no water flow:

$$\Delta P = \Pi_i - \Pi_o \quad (4.3)$$

where $i = \text{inside}$ and $o = \text{outside}$. This is the case only if a membrane is ideally semipermeable, that is, water permeability is much larger than solute permeability. The degree of semi-permeability that a membrane shows for a particular solute is measured as the reflection coefficient ($\sigma$).

$$\sigma = 1 - \frac{\text{Solute permeability}}{\text{Water permeability}} \quad (4.4)$$
The reflection coefficient usually ranges between zero and one. Some substances such as mercuric chloride decrease water permeability of plant membranes so much (Section 4.1.3(a)) that $s$ becomes negative. Close consideration of $P$ in the presence of different solutes (Figure 4.4) reinforces the importance of $s$ for osmosis. Using a pressure probe (Figure 4.5a) to measure $P$, the membrane is found to be ideally semipermeable for sucrose ($s = 1$); that is, the membrane almost totally ‘reflects’ sucrose.

Figure 4.4 Turgor pressure ($P$) in a *Tradescantia virginiana* epidermal cell as a function of time after the external osmotic pressure was changed with different test solutes. Measurements were made with a pressure probe (see Figure 4.5a). The initial decrease in $P$ is due to water flow out of the cell and is larger for solutes with a reflection coefficient near one (sucrose and urea). Propanol induces no drop in $P$, indicating that its reflection coefficient is zero. Subsequent increase in $P$ is due to penetration of particular solutes such as alcohol across the cell membrane. Water flows osmotically with the solute thereby increasing $P$ to its original value. Removing solutes reverses osmotic effects. That is, a decrease in $P$ follows the initial inflow of water as solutes (e.g. alcohols) diffuse out of cells (Tyerman and Steudle 1982; reproduced with permission of CSIRO)

Figure 4.5 Techniques employing fine glass capillaries to probe plant cells. Glass capillaries are heated and pulled to a fine point with an opening as small as 1 µm. (a) A miniaturised pressure probe. An oil-filled capillary is inserted into a cell whose turgor pressure ($P$) is transmitted through the oil to a miniature pressure transducer. The voltage output of the transducer, which is proportional to $P$, can be read off on a computer or chart recorder. A metal plunger acting as a piston can be used via remote control to vary cell $P$. (b) A probe for measuring membrane voltage. The capillary is filled with 1 mol L$^{-1}$ KCl and connected to a silver/silver chloride electrode that acts as an interface between solution voltage and input to the amplifier. A voltage is always measured with respect to a reference (in this case, a bath electrode). The headstage amplifier is close to the electrodes to minimise noise.
Over long periods, sucrose is taken up slowly but permeability relative to water is negligible. In this case, the change in $P$ would be equivalent to the change in $P$ (Figure 4.4, sucrose). If $s$ is near zero, then water and the solute (say, propanol) are equivalent in terms of permeability. No change in $P$ can be generated across a cell wall if $s$ is zero (Figure 4.4). If $s$ is negative, this leads to the intriguing situation where $P$ changes in the opposite way to that which we normally expect.

For plant and animal cells, most major osmotic solutes have a $s$ of about one so Equation 4.3 can be presented without $s$ as a variable. However, $s$ could be important when highly permeable solutes like ethanol, urea and ammonia reach significant levels, for example when membranes of waterlogged plants are exposed to ethanol and ammonia.

(b) Chemical potential

Diffusion of neutral molecules at low concentrations is driven by differences in concentrations across membranes (Section 4.1.2(a)). There are other forces that may influence solute diffusion, including the voltage gradient when considering movement of charged molecules (ions) and the hydrostatic pressure when considering movement of highly concentrated molecules (such as water in solutions). These forces can be added to give the total potential energy of a particular molecule relative to a reference value:

Total potential = Reference potential + Concentration + Electrical + Pressure

Gravitational potential energy could also be added to this equation if we were to examine the total potential over a substantial height difference, but for movement of molecules across membranes this is not relevant. The formal relationship for the chemical potential of a molecule $j$ ($\mu_j$), measured as energy content per mole (joules mol$^{-1}$) and using the same order of terms as the expression above, is:

$$\mu_j = \mu_j^* + RT \ln C_j + z_j F E + \tilde{V}_j P$$  \hspace{1cm} (4.5)

The concentration term is a measure of the effect on chemical potential of the concentration (actually the activity which is usually somewhat less than total concentration). The gas constant, $R$ (8.3143 joules mol$^{-1}$ K$^{-1}$), and absolute temperature, $T$ (equals 273.15 plus temperature in degrees Celsius, expressed in degrees Kelvin), account for the effects of temperature on chemical potential. Incidentally, from this term and the pressure term, the well-known van ‘t Hoff relation can be derived for osmotic pressure: $P = RTC$.

The electrical term is a measure of the effect of voltage ($E$) on chemical potential. The charge on a solute ($z$) is obviously relevant since if it was zero this term would not contribute to the total potential. The sign also determines whether an ion is repelled or attracted by a particular voltage. Electrical charge and concentration are related by the Faraday constant ($F$) which is 96 490 coulombs mol$^{-1}$. The electrical and concentration terms form the basis of the Nernst equation (see below).

The pressure term measures the effect of hydrostatic pressure on chemical potential, where $P$ = pressure and $\tilde{V}_j$ is the partial molar volume of the solute.
Molecules diffuse across a membrane down a chemical potential gradient, that is, from higher to lower chemical potential. Diffusion continues until the difference in chemical potential equals zero, when equilibrium is reached. The direction of a chemical potential gradient across a membrane is important because it indicates whether energy is or is not added to make transport proceed (Figure 4.6). Osmotic ‘engines’ must actively pump solutes against a chemical potential gradient across membranes to generate $P$ in a cell. Sometimes ions move against a concentration gradient even when the flux is entirely passive (no energy input) because the voltage term dominates the concentration term in Equation 4.5. In this case, ions flow according to gradients in electrical and total chemical potential. For this reason, the chemical potential of ions is best referred to as the electrochemical potential.

**Ions, charge and membrane voltages**

Ions such as potassium and chloride ($K^+$ and $Cl^-$) are often major osmotic solutes in plant cells. In fact, deficiency of either of these two inorganic nutrients can increase a plant’s susceptibility to wilting. In addition, most other inorganic nutrients are acquired as ions and some major organic metabolites involved in photosynthesis and nitrogen fixation bear a charge at physiological pH. For example, malic acid is a four-carbon organic acid that dissociates to the divalent malate anion at neutral pH. Besides the role in generation of $P$, ionic fluxes and the associated electrical effects of these fluxes are components of signalling in plants. Calcium ($Ca^{2+}$) fluxes across cell membranes are involved in cell signalling and although not osmotically significant they play a crucial role in the way cells communicate and self-regulate. Finally, some ions are used to store energy but need not occur at osmotically significant concentrations. Cell membranes from all kingdoms use hydrogen ($H^+$) ions (protons) in one way or another to store energy that can be used to move other ions or to manufacture ATP (Section 1.2). The highest concentration of $H^+$ that occurs is only a few millimoles per litre yet $H^+$ plays a central role in energy metabolism. Other ions such as sodium ($Na^+$) can also be used to store energy in plant cells (see the discussion of secondary active transport below).

To understand ion movement across membranes, two crucial points must be understood: (1) ionic fluxes alter and at the same time are determined by voltage across the membrane; (2) in all solutions bounded by cell membranes, the number of negative charges is balanced by the number of positive charges. Membrane potential is attributable to a minute amount of charge imbalance that occurs on membrane surfaces. So at constant membrane potential the flux of positive ions across a membrane must balance the flux of negative ions. Most biological membranes have a capacitance of about 1 microFarad cm$^{-2}$ which means that to alter membrane voltage by 0.1 V, the membrane need only acquire or lose about 1 pmol of univalent ion cm$^{-2}$ of membrane. A univalent ion is one with a single positive (e.g. $K^+$) or negative (e.g. $Cl^-$) atomic charge. In a plant cell of about 650 pL, this represents a change in charge averaged over the entire cell volume of 12 nmol L$^{-1}$!

The membrane voltage or membrane potential difference, as it is sometimes called, can be measured by inserting a fine capillary electrode into a plant cell (Figure 4.5b). Membrane voltage is measured with respect to solution bathing the cell and in most plant cells the voltage is negative across the plasma membrane. That is, the cytoplasm has a charge of $-0.1$ to $-0.3$ V ($-100$ to $-300$ mV) at steady state with occasional transients that may give the membrane a positive voltage. The tonoplast membrane that
surrounds the central vacuole is generally 20 to 40 mV more positive than the cytoplasm (still negative with respect to the outside medium).

Cell membrane voltages can be affected by ion pumps, diffusion potential and fixed charges on either side of the membrane.

Special mention needs to be made of one such fixed charge which arises from galacturonic acid residues in cell walls. Although cations move to neutralise this fixed negative charge, there is still a net negative potential associated with cell walls (Donnan potential). In spite of being external to the plasma membrane, the Donnan potential is in series with it and probably adds to what we measure as the membrane potential with electrodes.

Most charge on macromolecules in the cytoplasm is also negative (e.g. nucleic acids, proteins) and because of their size it can be regarded as a fixed negative charge. This has osmotic consequences. Macromolecules and their balancing cations result in a relatively high osmotic pressure (up to 200 mmol L\(^{-1}\) of total solutes) that results in inflow of water by osmosis and generation of \(P\) in most freshwater environments. In animal cells, where a cell wall is not present, body fluids must be regulated so that cell membranes do not rupture. For wall-less eukaryotes living in fresh water, a considerable amount of energy is expended in excreting water, for example by contractile vacuoles (see Case study 4.1). Walled eukaryotes have the luxury of letting water enter the protoplasm by osmosis where \(P\) is developed rather than the cell expanding until it ruptures.

**Figure 4.7 How a diffusion potential develops through differential movement of an ion across a membrane.** This is achieved here by separating a concentrated KCl solution from a dilute KCl solution by using a membrane which is permeable to K\(^+\) but not Cl\(^-\). Letter sizes indicate concentrations. Initially (a), a minute amount of K\(^+\) crosses the membrane along its concentration gradient. This K\(^+\) movement creates a positive charge in the right-hand compartment as K\(^+\) concentration there rises above Cl\(^-\) concentration. At equilibrium (b), a diffusion potential is established, reflecting movement of...
Different ions have different permeabilities in membranes. Potassium, for example, is usually the most permeable ion, entering under most conditions about 10 to 100 times faster than Cl\(^{-}\) (Figure 4.2). Since ions diffuse at different rates across membranes, a slight charge imbalance occurs and gives rise to a membrane voltage (Figure 4.7). This voltage in turn slows down movement of the rapidly moving ion so that the counter-ion catches up. The result is that when net charge balance is achieved, a diffusion potential has developed that is a function of the permeabilities (\(P_{\text{ion}}\)) of all diffusible ions present and concentrations of each ion in each compartment. The Goldman equation describes this phenomenon and gives the membrane voltage (\(\Delta E\)) that would develop due to diffusion of ions. The Goldman equation for the ions that mostly determine this diffusion potential (K\(^{+}\), Na\(^{+}\) and Cl\(^{-}\)) is given by:

\[
\Delta E = \frac{RT}{F} \ln \frac{P_K C_K^i + P_{Na} C_{Na}^o + P_{Cl} C_{Cl}^i}{P_K C_K^o + P_{Na} C_{Na}^i + P_{Cl} C_{Cl}^o} \tag{4.6}
\]

The superscripts refer to the inside (i) or outside (o) of the membrane and \(R\), \(T\), \(F\) and \(C\) are defined elsewhere (Equation 4.5). Note that the concentration terms for Cl\(^{-}\) are reversed in the numerator and denominator compared to the cations. This is because Cl\(^{-}\) is the only anion represented. Many texts do not include H\(^{+}\) in the Goldman equation because, in spite of high permeability of H\(^{+}\), diffusion of H\(^{+}\) is unlikely to have a strong effect on \(\Delta E\) at such low (micromolar) concentrations. However, membrane potential is occasionally dominated by the diffusion of H\(^{+}\), indicating that H\(^{+}\) permeability must be exceedingly high. For example, local variations in pH cause alkaline bands to form on Chara corallina cells and in the leaves of aquatic plants at high pH.

**The Nernst equation**

When one ion has a very high permeability compared to all other ions in the system the membrane will behave as an ion-sensitive electrode for that ion (e.g. Figure 4.7). A pH electrode which is sensitive to H\(^{+}\) flux across a glass membrane serves as an analogy. In the case of a single ion, the Goldman equation can be reduced to the simpler Nernst equation that yields the equilibrium membrane potential which would develop for a particular concentration gradient across a membrane.

\[
\Delta E = \frac{RT}{zF} \ln \frac{C_o}{C_i} \tag{4.7}
\]

where \(R\) and \(T\) are the gas constant and temperature (degrees Kelvin) and \(F\) is the Faraday constant. Typical charges on ions (\(z\)) would be –1 (Cl\(^{-}\)), +1 (K\(^{+}\)) and –2 (divalent anions) and so on. This term in the Nernst equation gives the correct sign for the calculated membrane potential.

---

**Table 4.1 Examples of comparison between Nernst potentials (\(E_K\)) and recorded membrane voltages. In most cases an electrogenic pump is inferred from a recorded membrane voltage that is more negative than the most negative Nernst potential, in these cases for potassium. For Arabidopsis (bottom) the fact that the Nernst potential for potassium is mostly more negative than the resting membrane potential indicates that potassium must be pumped in, probably by a proton symporter.**

<table>
<thead>
<tr>
<th>Cells</th>
<th>(E_K) (mV)</th>
<th>Membrane voltage (mV)</th>
<th>Medium (mM)</th>
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The Nernst equation is routinely used by electro-physiologists to calculate the equilibrium potential for each ion. Theoretical equilibrium potentials can then be compared with the actual membrane potential in order to decide whether the membrane is highly permeable to one particular ion. For example, in many plant cells there are $K^+$ channels that open under particular circumstances. When this occurs, the membrane becomes highly permeable to $K^+$ and the measured membrane potential very nearly equals the Nernst potential for $K^+$. The Nernst equation can also be used as a guide in deciding whether there is active transport through a membrane. For example, when the measured membrane potential is more negative than the most negative Nernst potential there must be active movement of charge across that membrane (Table 4.1).

Equation 4.7 can be rewritten with constants solved and $\log_{10}$ substituted for the natural logarithm. This yields a useful form as follows:

$$\Delta E = \frac{58}{z} \log_{10} \frac{C_o}{C_i}$$

showing that 10-fold differences in concentration across a membrane are maintained by a 58 mV charge separation for monovalent ions. For example, $-58$ mV inside a cell will keep $K^+$ concentrations 10 times higher inside a cell than in the external medium and $Cl^-$ concentrations 10 times lower.

(d) Active and passive transport

Plant cells acquire solutes and water across their membranes (plasma membrane and tonoplast) through the combined action of passive and active transport. During passive transport, a solute moves down its electrochemical potential gradient with no expenditure of energy. In active transport a solute moves against its electrochemical potential and hence energy input is required. The extra energy may be derived from the chemical energy released from hydrolysis of ATP or pyrophosphate (PP$_i$, a high-energy polymer of phosphate) or it may be derived from the movement of a cotransported solute or coupled solute down its electrochemical gradient. Coupling of downhill movement of one solute to uphill movement of another is a common feature of membrane transport.

Both the tonoplast and plasma membrane of plants and fungi contain pumps that move $H^+$ across membranes. These pumps use chemical energy from the hydrolysis of ATP or PP$_i$. By moving positive charge out of the cytoplasm they establish a large membrane voltage (inside negative) and a steep pH gradient. The electrochemical gradient for $H^+$ can be very large, the equivalent of about 400 mV. Bioenergetic analyses suggest that the energised proton pump in plasma membranes moves one $H^+$ per ATP hydrolysed.
The $\text{H}^+$ gradient established by the primary active $\text{H}^+$ pumps is then used to drive coupled active movement of other solutes across membranes. These coupled transport systems can be referred to as secondary active transport to indicate that they rely on a previously established gradient of another ion. There are many examples of $\text{H}^+$-coupled transport in plants (Figure 4.8). One example is the uptake of a $\text{Cl}^-$ ion, which is coupled to the influx of two $\text{H}^+$ ions. Chloride must be actively transported across the plasma membrane because the membrane potential is usually so much more negative than the equilibrium potential for $\text{Cl}^-$. Coupling each $\text{Cl}^-$ entering the cell to the inflow of two $\text{H}^+$ ions means that there is a net charge transfer of +1 into the cell as each $\text{Cl}^-$ enters. This is more energetically favourable than zero net charge and definitely more favourable than a net negative charge. Another example is $\text{H}^+$/sucrose cotransport which is important in the process of phloem loading (Chapter 5).

Secondary active transport in plants is not exclusively driven by $\text{H}^+$. $\text{Na}^+$ ion gradients sometimes drive secondary transport. This was first discovered in Chara but also occurs in some higher plants. A gene has been cloned from wheat roots for an $\text{Na}^+$-powered $\text{K}^+$ transporter and when expressed in frog oocytes (see Section 4.1.3(a)) the transporter uses an inwardly directed Na$^+$ gradient to drive uptake of $\text{K}^+$. $\text{Na}^+$-driven transport may have evolved in plants because under alkaline conditions (high external pH), the $\text{H}^+$ gradient may not be sufficient to drive transport. Such conditions exist in seawater which is well buffered at a pH of about 8.3 but contains abundant Na$^+$. The discovery of Na$^+$-driven transport is especially interesting because as yet no one has identified a primary Na$^+$ pump in plants. In animal cells, where Na$^+$ gradients are generally used in secondary active transport, there is a primary Na$^+$ pump that pumps three Na$^{out}$out and two K$^{in}$in for every ATP molecule hydrolysed. This pump does not seem to exist in plant cells but an Na$^+$–H$^+$ antiporter has been shown to occur on the plasma membrane and tonoplast of some plants.

Solute movement across membranes by either active or passive processes can be regarded as analogous to an enzymatic reaction. Transport proteins within membranes act as enzymes, catalysing solute transport by lowering the activation energy for transport. As with ordinary enzymes, the reaction may be coupled to the hydrolysis of ATP or some other high-energy molecule or it may proceed (energetically) downhill. The analogy with enzymes is especially useful to calculate affinity of the transport protein for its substrate. If we plot the rate of transport versus concentration of substrate being transported, a hyperbolic curve is often obtained. Analysis of this Michaelis–Menten curve (see Case Study 4.1) reveals an affinity constant ($K_m$) and the maximum transport rate at saturating concentrations (equivalent to $V_{\text{max}}$).

The affinities of both passive and active transport vary widely between different transport systems in...
plants. Values of $K_m$ can be in the range of micromoles per litre, or less, in which case we refer to the transport system as having a high affinity for its substrate (Figure 4.9a). Alternatively, $K_m$ may be tens of millimoles per litre in which case it would be referred to as a low-affinity transporter (Figure 4.9b). There is no strict discrimination between active and passive transport systems on the basis of their affinity for substrates. Passive transporters can have high affinities and active transporters low affinities. Some transport systems do not saturate even if hundreds of millimoles of substrate per litre are present. This has often been attributed to transport through a pore in the membrane or a channel but there are many examples of channel-mediated transport that saturate at a few millimoles per litre and there is a Ca$^{2+}$ channel from plant plasma membrane that has a $K_m$ in the micromolar range. Finally plants often have multiple transporters for the same solute, providing a range of affinities. This allows transport to proceed efficiently over a wide range of external concentrations, as would be encountered by a root in soil.

![Figure 4.9](http://plantsinaction.science.uq.edu.au/edition1/?q=figure_view/168)

**Figure 4.9** Transport systems with high and low affinities for transported ions. (a) Sulphate uptake into membrane vesicles by a sulphate/proton cotransporter was measured as a function of external sulphate concentration. This transport system has a $K_m$ of 65 µM. (b) Ammonium (NH$_4^+$) transport through two classes of channel permeable to NH$_4^+$ was measured as a function of external NH$_4^+$ concentration. One channel did not show saturation (straight line) while the other did ($K_m = 20$ mM) ((a) From Hawkesford et al. 1993; (b) from Tyerman et al. 1995; reproduced with permission of Nature)


**Links:**