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Plant–Water Relations

John B Passioura, *CSIRO Plant Industry, Canberra, Australia*

Plant–water relations concerns how plants control the hydration of their cells, including the collection of water from the soil, its transport within the plant, and its loss by evaporation from the leaves.

Introduction

Well-watered plants are turgid. Their cells, which are enclosed in a strong but slightly elastic wall, are distended by an internal pressure that may be as high as 1 MPa, five times the pressure in a car tyre and 10 times the pressure of the atmosphere. Plants perform best when they are turgid. Many of the structures of higher plants serve to maintain their cells sufficiently hydrated to function – to grow, to photosynthesize, to respire – even though most of these cells are in the shoots of the plants and so are not only remote from their supply of water in the soil, but are also exposed to a dry environment.

A well-hydrated leaf may transpire several times its own volume of water during a day. Water evaporates from wet cell walls into the internal gas spaces of the leaf. It then flows away as vapour, largely through stomata, which are variable pores in the surface of the leaf. The loss is an unavoidable consequence of the stomata being open, as they must be to allow carbon dioxide to enter the leaf. The relative humidity inside a leaf is typically greater than 99%, and thus there is usually a large difference of absolute humidity across the stomata that induces rapid diffusion of water vapour out of the leaf.

Although a leaf may lose much water by evaporation, its net loss of water is usually small. Evaporation from cell walls creates in them a large suction that replenishes water by drawing it from the soil, principally via the plant's vascular system, but also through flow across cells in roots and leaf.

Properties of Water

The physico-chemical properties of water have shaped many of the processes in plants and, indeed, in all organisms. Several of these properties, together with selected values, are listed in **Table 1**.

One of the most important features of water is that it forms strong hydrogen bonds. These greatly influence several biologically important bulk properties. Water has unusually large latent heats of evaporation and freezing, which help plants cope with frosts or heat loads. It has great cohesive strength, which enables it to withstand the very large tensions that develop in the xylem and thus to

maintain continuity of liquid water throughout the plant. It has a large surface tension at an air–water interface, which creates a strong skin that ensures that suitably small pores in soil or plant remain filled with water even if the water is under great tension, as is often the case.

On the molecular scale, hydrogen bonds ensure that macromolecules such as proteins and DNA are surrounded by a shell of water molecules that acts as a spatial buffer between the macromolecules, preventing them from adhering to each other and thereby precipitating. This shell also penetrates interstices in such molecules, thus helping to maintain the three-dimensional structures on which their reactions depend.

Water is polar: despite being electrically neutral, it has a slight excess of electrons on one side of each molecule and a slight deficit on the other. Its polar nature, coupled with its ability to form hydrogen bonds, makes it a very good solvent for ions and small organic molecules such as sugars. Molar concentrations of these are possible, and often occur, thereby enabling cells to generate osmotic pressures of several MPa, a requirement for plants to remain turgid in a saline or droughted environment. The polar nature is especially important in enabling fatty acids to organize themselves into the membranes that bind cells and organelles. Fatty acids have a nonpolar hydrocarbon tail attached to a polar carboxylic acid group. These nonpolar tails, eschewing an aqueous environment, line up to form two sheets that are appressed together to form a lipid bilayer, with the polar heads presenting a hydrophilic surface on each side.

Other biologically important properties of water include: its viscosity, which influences how fast water flows in response to a pressure gradient; and its ability to dissociate into hydrogen- and hydroxyl ions, which is central to the pH scale.

As with all materials above absolute zero temperature, water and solute molecules are in thermal motion. This motion ensures that gradients in solute concentration or temperature are eventually dissipated by diffusion.

Table 1 Some physico-chemical properties of water and aqueous solutions

Property	Value and units
Cohesive strength	> 25 MPa
Surface tension	0.073 N m ⁻¹ at 20°C
Viscosity	0.0018 Pa s at 0°C 0.0010 Pa s at 20°C
Diffusion coefficient of small solutes in water	~ 1 × 10 ⁻⁹ m ² s ⁻¹
Molar volume (pure water at 20°C)	1.81 × 10 ⁻⁵ m ³ mol ⁻¹
Latent heat of evaporation at 20°C	2.5 MJ kg ⁻¹
Latent heat of melting	0.34 MJ kg ⁻¹
Saturated vapour pressure of pure water	0.61 kPa at 0°C 1.23 kPa at 10°C 2.34 kPa at 20°C 4.24 kPa at 30°C 7.38 kPa at 40°C

Water at Equilibrium: Water Potential and Its Components

Although plants are never at true equilibrium, owing to their incessant biochemical activity, they are often close enough, so far as water is concerned, for it to be useful to describe the status of their water in terms of classical equilibrium thermodynamics. The chemical potential of water, which is uniform in a system at equilibrium, is the difference in Gibbs free energy per mole (the energy available to do work) between the water of interest and pure water at standard temperature and pressure. It has units of J mol⁻¹. Because of the importance of pressure in the functioning of plants, plant physiologists have chosen to express chemical potential in terms of pressure, which has the dimensions of force/area or energy/volume, and whose SI unit is the Pascal (Pa). They have therefore introduced the term 'water potential', denoted by ψ , which is the chemical potential divided by the volume of one mole of water.

The notion of water potential can be applied to any sample of water, whether inside a cell, in the cell wall, in xylem vessels, or in the soil. Water potential thus defined is always negative in plants, for by convention it is zero in pure water at atmospheric pressure, and the addition of any solutes or the imposition of suction (negative hydrostatic pressure) for drawing water into a plant necessarily lowers the water potential. It can be divided into two components, hydrostatic pressure (P) and osmotic pressure (Π), according to eqn [1].

$$\psi = P - \Pi \quad [1]$$

Osmotic pressure

Osmotic pressure is a measure of the attraction of solutes for water. It is defined as the hydrostatic pressure that must be applied to a solution to prevent water flowing into it when it is separated from pure water by a membrane that allows the passage of water, but not of solute. It is a colligative property, that is, its value depends simply on the number of solute molecules present. To a good approximation, at least for dilute solutions, the relation between osmotic pressure and solute concentration is described by van't Hoff's law (eqn [2]).

$$\Pi = cRT \quad [2]$$

In this equation c is the sum of molar concentrations of all solute species (mol L⁻¹), R is the universal gas constant (0.0083 L MPa mol⁻¹ K⁻¹, or 8.3 J mol⁻¹ K⁻¹) and T is the absolute temperature (K). For example, a tenth molar solution of sucrose has an osmotic pressure of 0.25 MPa at 25°C.

The influence of gravity

The concept of water potential excludes effects of gravity on the energy status of water, but in some circumstances, in tall trees, or when dealing with the flow of water in soil, gravity must be included. Where the effect is important it is appropriate to define total water potential, Φ (Pa), which is the sum of the water potential, ψ , and a gravitational term, as in eqn [3].

$$\Phi = \psi + \rho gh = P - \Pi + \rho gh \quad [3]$$

Here ρ (kg m⁻³) is the density of water, g (9.8 m s⁻²) is the acceleration due to gravity, and h (m) is the height (relative to a given reference) in the gravitational field. Φ is constant in a system at equilibrium with respect to water even when height varies. The gravitational term, ρgh , increases by 9.8 kPa for each metre increase in height. Hence, in a system at equilibrium, the hydrostatic pressure, P , falls by approximately 10 kPa for each metre increase in height.

Positive and negative hydrostatic pressures

Hydrostatic pressure, P , is usually expressed as 'gauge' pressure, the difference from the normal atmospheric pressure of approximately 100 kPa absolute pressure—that is, a gauge pressure of zero equals an absolute pressure of 100 kPa. Large positive values of hydrostatic pressure, induced by osmosis, are typical in plants cells, where they are often called turgor pressure. Large negative values are also common, both in plants and the soil they are growing in. These large negative values arise because of capillary effects – the attraction between water and hydrophilic surfaces, such as cell walls and soil, coupled with the surface tension at an air/water interface. For a cylindrical pore of radius a (m), the impact of this interaction on the

pressure in the adjacent water is given by the Laplace–Young equation.

$$\Delta P = \frac{2\gamma}{a} \quad [4]$$

Here ΔP is the drop in pressure across the meniscus, and γ is the surface tension of water, which is about 0.75 N m^{-1} at room temperature, so that ΔP is approximately $0.15/a$ (Pa). Thus a fully developed (hemispherical) meniscus in a cylindrical pore of radius, say, $15 \mu\text{m}$ would have a pressure drop across it of 10 kPa. The pressure, P , in the water would therefore be -10 kPa if the surrounding gas were at atmospheric pressure. Water would rise to a height of about 1 m (from eqn [3]) in a capillary tube of this size (Figure 1), or, more generally, to a height of $15 \times 10^{-6}/a \text{ m}$.

It is such capillary action that generates the suctions in the water-filled pores in soil or cell walls. The pores in cell walls are especially small (of the order of 5 nm), and are therefore able to develop very large suctions without emptying, as in severely water-stressed plants.

The connection between water potential and the vapour pressure of water

Water and air in a closed container at constant temperature will develop a steady saturated vapour pressure in the gas phase. The vapour pressure above a salt solution is lower than that above pure water, because the water molecules are attracted to the solutes, and are therefore less likely to escape from the surface of the liquid to enter the gas phase.

The saturated vapour pressure is related to water potential as shown in eqn [5].

$$\psi = \frac{RT}{V} \ln \left(\frac{p_s}{p_0} \right) \quad [5]$$

Here R is the gas constant ($8.3 \text{ J mol}^{-1} \text{ K}^{-1}$), T is the absolute temperature (K), V is the volume of one mole of water, p_s is the saturated vapour pressure above the test sample, and p_0 is that above pure water. The equation shows that ψ is very sensitive to small changes in p_s . For example, when $p_s/p_0 = 0.99$, $\psi = -1.35 \text{ MPa}$ at 20°C , which is close to the limit in the soil at which roots can extract water. Thus the vapour pressure of water is close to saturation in moist soil and in all but the most severely water-stressed plants.

Water in Motion: Drivers of Flow

Water flows in three different ways: by osmosis across semipermeable membranes, that is, membranes that allow the passage of water but not of solutes; by diffusion in liquid or gas; and in bulk.

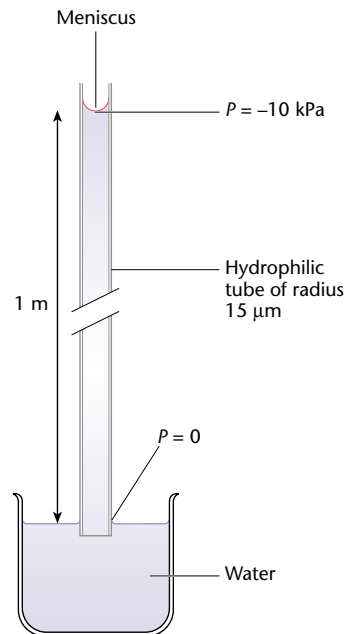


Figure 1 Capillary action. Surface tension generates an upward pull on the water in the capillary tube. The water rises to a height of 1 m in a tube of radius $15 \mu\text{m}$, or more generally to a height of $15 \times 10^{-6}/a$ (eqns [3] and [4]) for a tube of radius a (m).

Osmotic flow across semipermeable membranes is driven by differences in water potential. While the molecular mechanisms for this flow are still not fully understood, the process is well characterized phenomenologically, and is essential to the creation of turgor pressure. A commonly used general transport equation for the flow of water, J_v (m s^{-1}), across a membrane is given by eqn [6].

$$J_v = L_p(\Delta P - \sigma\Delta\Pi) \quad [6]$$

In this equation L_p ($\text{m s}^{-1} \text{ Pa}^{-1}$) is the hydraulic conductance of the membrane, and ΔP and $\Delta\Pi$ are the differences across the membrane of hydrostatic pressure and osmotic pressure, respectively. σ is the reflection coefficient, which is a measure of how impermeable the membrane is to the solute; it is dimensionless, and ranges from zero to one, with zero signifying that the membrane is completely permeable to the solute, and one signifying that the membrane is completely impermeable. The value of L_p depends on the activity of aquaporins.

Diffusive flow results from gradients in concentration and the random thermal motion of molecules. It is rapid over small distances but is very slow over large. The characteristic time (s) taken for a concentration gradient to disappear is approximately L^2/D , where L (m) is the distance over which the variation is initially present and D ($\text{m}^2 \text{ s}^{-1}$) is the diffusion coefficient of the solutes. Small solutes, such as potassium ions or amino acids, have diffusion coefficients of about $1 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$. Thus, the

characteristic time for diffusion within a cell of diameter $10\ \mu\text{m}$ is only about $0.1\ \text{s}$, whereas that for diffusion in a compartment of diameter $100\ \text{mm}$ (say, through the soil in a plant pot) is about $10^7\ \text{s}$, which is many weeks.

Bulk flow is driven by gradients in hydrostatic pressure. It is much faster than diffusive flow over large distances because the molecules are all travelling in the same direction and hence their movement is cooperative. This is the flow that occurs in xylem vessels, in the interstices of cell walls, and in water-filled pores in soil. The resistance to such flow depends very strongly on the size of the channels. The wider the channel, the greater is the scope for cooperative flow. Bulk flow in a cylindrical tube of radius a is proportional to a^4 , of which a^2 accounts for the area available for flow and the other factor a^2 accounts for the fact that such flow is intrinsically easier in wide tubes. Wide vessels, therefore, have much more carrying capacity than narrow ones. The dependence of flow rate on radius is described by Poiseuille's law (eqn [7]).

$$Q = \frac{\pi a^4}{8\eta} \times \frac{\Delta P}{L} \quad [7]$$

In this equation Q ($\text{m}^3\ \text{s}^{-1}$) is the flow rate through a tube of radius a (m) and length L (m), ΔP (Pa) is the difference in pressure across the length of the tube, and η (Pa s) is the viscosity of water.

As water in the transpiration stream moves from the soil to the roots, through the plant, and out through the stomata, all three types of flow are involved at various stages. A good example of the relative impacts of the diffusive and bulk mechanisms is given by the flow of water in the phloem from the leaves to the roots, which runs counter to the transpiration stream. This flow is against the overall gradient in water potential and is, in energetic terms, uphill. It is powered by the loading of solutes, principally sucrose, into the phloem in the leaves, which there generate a large local hydrostatic pressure. This in turn induces bulk flow of the sucrose solution towards the roots, where the sucrose is unloaded. The gradient in osmotic pressure of the sucrose exceeds the opposing gradient in turgor pressure, but because bulk flow is so much faster than diffusive flow for a given gradient over distances greater than about $1\ \text{mm}$, the solution as a whole moves against the gradient in water potential.

Water in the Soil

Soil is porous, and holds water in its pores by capillarity (eqn [4]). The distribution of pore sizes in the soil, together with its depth, determine how much water the soil can hold for use by plants. In practice, pores larger than about $15\ \mu\text{m}$ radius drain so fast – within about a day after rain may have filled them – that they do not contribute much to the

reservoir. They drain because gravity generates a suction that the capillary effects cannot withstand: for example, all pores greater than $15\ \mu\text{m}$ in radius would be empty in a parcel of soil that is in equilibrium with a water table $1\ \text{m}$ below it (eqns [3] and [4] and accompanying discussion). They drain quickly because flow is so much faster in large pores than in small (eqn [7]).

At the other end of the suction scale, plants cannot extract much water from pores smaller than about $200\ \text{nm}$ in diameter. The pressure in such pores is about $-1.5\ \text{MPa}$, and from that has to be subtracted large differences in suction in the soil, between bulk soil and root surface, if water is to move to the roots at reasonable rates through such small pores. Leaves typically experience water potentials lower than about $-2.5\ \text{MPa}$ in such circumstances, low enough for most plants to be wilting.

Flow of water through the soil

Horizontal flow of water through soil is induced by gradients in hydrostatic pressure, P . The rate of flow, F ($\text{m}\ \text{s}^{-1}$), depends on the gradient in P according to Darcy's law (eqn [8]).

$$F = K \frac{dP}{dx} \quad [8]$$

Here x (m) is distance and K ($\text{m}^2\ \text{s}^{-1}\ \text{Pa}^{-1}$) is hydraulic conductivity. K varies enormously, by about a million-fold, over the range of water content available to plants. The range is so large because water flows much more easily in large pores than in small (eqn [7]) and as the soil dries the largest water-filled pores drain first.

Vertical flow of water (drainage or capillary rise), which involves doing work against gravity, is driven by gradients in 'hydraulic head', the sum of P and ρgh (cf. eqn [3]).

Measurement of Water Status in Soil and Plant

Techniques for measuring water status in soil or plant depend in the main on one of two principles: measuring the vapour pressure of the sample of soil or plant; or measuring the pressure of water in pores. The former measures water potential, with the help of eqn [5]; the latter, hydrostatic pressure.

The vapour pressure technique (psychrometry) relies on two principles. One is that the saturated vapour pressure depends markedly on temperature (Table 1). The other is that the temperature of a thermocouple junction can be controlled by passing an electric current through it (the Peltier effect). In practice, one places a sample of soil or plant (for example, a leaf disc) in a small closed compartment at a very precisely controlled temperature,

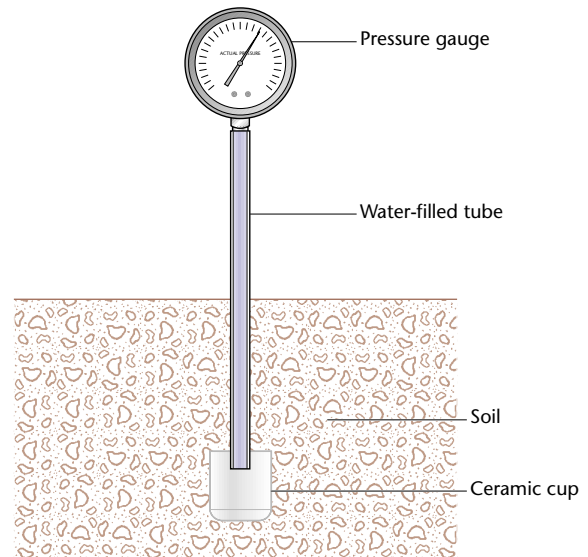
and allows it to equilibrate. The compartment contains two thermocouples. One of these is used to measure the temperature. A current is passed through the other to cool it to the point at which water vapour just condenses on it, and then its temperature is recorded. The saturated vapour pressure (p_s , see eqn [5]) above the sample is then found, using a detailed version of the data shown in **Table 1**, from the temperature of the cool junction. The saturated vapour pressure of pure water at the given temperature (p_0) is found in the same way. Water potential is then calculated from eqn [5]. Precise control of temperature is essential with this technique, because water potential is very sensitive to small changes in p_s/p_0 (eqn [5]), and p_0 varies markedly with temperature (**Table 1**). In practice, an error of 0.001°C in measuring the difference in temperature between the two thermocouples gives an error of 80 kPa in water potential.

The pressure of pore water in soil can be measured directly by using a 'tensiometer', or 'pressure plate apparatus' (**Figure 2**). A tensiometer is a closed water-filled compartment with a porous ceramic cup attached, which is placed in contact with the soil. The pores in the cup are fine enough to remain filled with water despite a substantial difference in pressure across their menisci (eqn [4]). Water passes through the ceramic until the pressure within the tensiometer (which can be readily measured) equals that in the soil pores. This instrument is suitable for use in the field, but its range is limited to gauge pressures higher than -100 kPa , that is to absolute pressures above zero. In contrast to the xylem, where water can remain in a metastable state at negative absolute pressures, it has proven technically impossible to achieve the same robustness in a tensiometer.

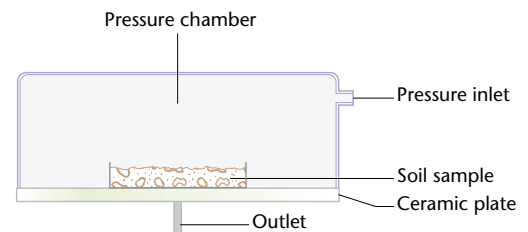
Negative absolute pressures can however be measured with pressure plate apparatus (**Figure 2**), which relies on the same principles as the tensiometer, but involves balancing the negative pressure in the soil water by applying just enough pneumatic pressure for water from the soil to be on the verge of flowing through the ceramic plate. Note that both the tensiometer and the pressure plate apparatus measure hydrostatic pressure and not water potential; the presence of any solutes has no effect on the measurements.

Osmotic pressure of a solution can be measured by psychrometry, or by measuring the depression of freezing point, which is uniquely related to osmotic pressure. Detailed tables relating the two are available.

The most common instrument for measuring water potential in plants, especially of leaves, is the 'Scholander' pressure chamber (**Figure 3**), which is similar in operation to the pressure plate apparatus. A leaf is cut from a plant and quickly put into the chamber with the cut xylem of petiole or leaf blade just protruding from a pressure-tight gland. Enough pneumatic pressure is then applied in the chamber to bring xylem sap to the point of bleeding from the protruding end of the leaf.



(a)



(b)

Figure 2 Instruments used to measure hydrostatic pressure of soil water. (a) Tensiometer. The porous ceramic cup allows water to move between the soil and the inside of the instrument. Eventually the pressures equalize; the pressure gauge of the instrument then gives the pressure in the soil water. (b) Pressure plate. Enough gas pressure is applied to the chamber to bring the water in the soil to atmospheric pressure, when it is on the verge of exuding from the outlet. The gas pressure is then equal and opposite to the original pressure in the soil water.

Movement of Water through Soil and Plant to the Atmosphere

Plants are almost continuously losing water through their leaves to the atmosphere. The loss is made good, in whole or in part, by water flowing from the soil into the roots and thence within the plant to the leaves. The flow from soil to leaf is essentially driven by the difference in hydrostatic pressure between the pores in the cell walls of the leaf from which water evaporates and the water-filled pores in soil.

Flow from soil through root, to the vascular system

Roots are branched and have tortuous paths through the soil. Despite their complex geometry, any given segment of

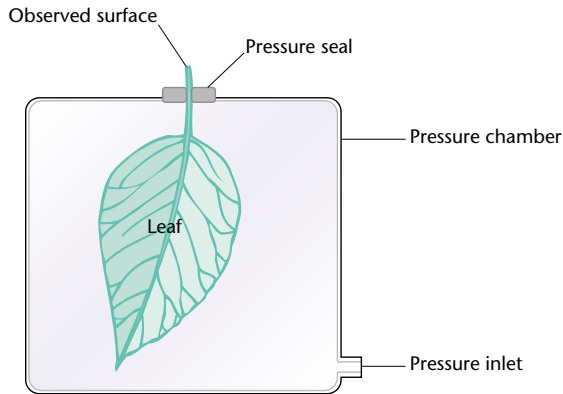


Figure 3 Pressure chamber for measuring the water potential of a leaf. The leaf is cut from a plant and quickly placed in the chamber, with a small piece of it protruding through the pressure seal. As with the pressure plate (Figure 2), enough gas pressure is applied to the chamber to bring the xylem sap to the point of bleeding from the cut surface. Because transpiration has stopped, the xylem sap is close to equilibrium with the cells of the leaf, and the applied balancing pressure is equal and opposite to that of the original pressure in the equilibrated xylem sap.

root can be treated as a cylinder to which water flows down a gradient of pressure in the soil water, according to eqn [8] suitably developed to account for flow with cylindrical geometry. General conclusions are that the potential uptake rate exceeds the plant's demand for water if the length of active root per unit volume of soil exceeds about 10^{-3} m m^{-3} , and if the soil water suction is less than about 300 kPa (when K , the hydraulic conductivity in the soil, is adequately large). With fewer roots and drier soil, a limit is soon reached in the soil's ability to supply water to the root surface. The stomata must then close, so that transpiration does not exceed the supply, otherwise the plant will desiccate.

Radial flow through a root to the xylem is partly through the cell walls. Impervious walls block the way at the endodermis and possibly hypodermis, thus ensuring that the water must enter the symplasm in the root cortex and leave it in the xylem parenchyma cells next to the vessels. The resistance to water flow across the membranes involved is large, and often is responsible for most of the fall in water potential between the soil and the evaporating surfaces of the leaves, at least in well-watered plants.

Longitudinal flow in the xylem

Xylem sap of a transpiring plant is usually under tension, with pressure typically in the range of -0.5 to -1.5 MPa in well-watered plants. Providing that the sap remains in this metastable state, the xylem usually offers little hydraulic resistance. The cohesive strength of water is so large (Table 1) that tensile failure seems never to occur. However, the (porous) walls surrounding the vessels are not perfect at preventing the ingress of air, and in some circumstances gas bubbles (embolisms) will form and

block the flow of water. In desert plants especially, propensity to embolize may have evolved to enable the plants to sacrifice, progressively, small branches, so that the transpiring leaf area is reduced to levels that the roots can service.

From the xylem to the substomatal cavities in the leaf

For many years the prevailing view was that the transpiration stream travelled through the apoplasm (cell walls and other compartments outside the cell membranes) to the substomatal cavities, where water evaporated and diffused out of the leaf through the stomata. There is now compelling evidence that most of the water enters the symplasm (the interconnected cell contents) very soon after it leaves the vessels, and that solutes in the xylem sap may be substantially excluded as the water enters the symplasm. As with radial flow in the roots, the passage of water across cell membranes results in a substantial fall in water potential.

Stomatal control of transpiration

The rate of flow out of the leaf, E ($\text{mol m}^{-2} \text{ s}^{-1}$), the transpiration rate, is driven by diffusion as vapour through the stomata. It is controlled by the conductance of the stomata to water vapour, g ($\text{mol m}^{-2} \text{ s}^{-1}$), according to eqn [9].

$$E = g \frac{p_i - p_e}{p_a} \quad [9]$$

Here p_i and p_e (Pa) are the vapour pressures inside and outside the leaf, respectively, and p_a (Pa) is the atmospheric pressure. For a given value of g , the water potential of the leaf has almost no influence on E , because within the usual range of water potential (zero to -3 MPa) the inside of the leaf is so close to being saturated with water vapour (eqn [5]) that p_i is essentially independent of water potential.

Hence, insofar as water potential influences transpiration rate, it does so by affecting the stomata, which close when water potential is low. Stomatal conductance is also influenced by many other factors, including light level, concentration of carbon dioxide and hormonal levels, which are affected by adverse conditions in the soil such as salinity, dryness and compaction.

While stomatal conductance is the plant's main means of controlling transpiration rate on an hourly or daily basis, at time scales of a week or more the development or shedding of leaf area is an equally powerful means of controlling overall water use, and that, too, is strongly influenced by water relations.

Further Reading

- Atwell BJ, Kriedemann PE and Turnbull CG (eds) (1999) *Plants in Action*. Melbourne, Australia: Macmillan.
- Boyer JS (1995) *Measuring the Water Status of Plants and Soils*. San Diego, CA: Academic Press.
- Canny MJ (1990) What becomes of the transpiration stream? *New Phytologist* **114**: 341–368.
- Nobel PS (1983) *Biophysical Plant Physiology and Ecology*. New York: WH Freeman.
- Passioura JB (1988) Water transport in and to roots. *Annual Review of Plant Physiology Plant Molecular Biology* **39**: 245–265.
- Tyree MT and Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology Plant Molecular Biology* **40**: 19–38.