

6

Tree Water Relations

Water is Fundamental to Tree Development

Providing temperatures are suitable for growth, water is the factor that most constrains the development and growth of all plants, including trees. Consequently, the availability of water is critically important in determining their relative success in different environments. This is not surprising when you consider that water is not only a major constituent of plants, but it is involved with almost every physiological process.

Non-woody plant parts are made up of 70–95% water; even wood (when fresh) is made up of about 50% water. Water held with the cells maintains the stiffness of the cell (cell turgor) and provides the substrate for biological activity, including key processes such as photosynthesis. It provides the solvent in which gases, minerals and other compounds can be transported from cell to cell or over longer distances between different parts of the tree. Indeed, growth can only occur if the positive turgor pressure (the internal pressure of cells) achieved in well-hydrated cells provides a driving force for cellular enlargement.

In addition to the large amount of water held in a tree, water is required in huge quantities just for the tree to function. Plants are able to incorporate the vast majority of absorbed minerals, such as nitrogen, phosphorous and potassium, into new tissues, but only a tiny fraction (1–5%) of water that enters the tree is retained in biomass. Most of the water taken in by the tree will be lost back to the atmosphere by transpiration (the evaporation of water from plant surfaces). This apparent profligacy in water use is an unavoidable consequence of photosynthesis. Stomata in the leaf must be open to enable access to carbon dioxide from the atmosphere, but in so doing they provide a gateway for water to be lost from the leaf. However, this water should not simply be seen as a waste because the evaporation of water provides the pulling force that draws water and minerals up the tree from the soil. Regardless of how you look at it, trees need large volumes of water (see Chapter 4). Consequently, understanding how trees maintain their water supply and respond to variable water availability is of central importance to all those managing trees or seeking to understand how climate and environment affect tree performance.

Importance of Water Potential

A hugely valuable, unifying concept used to describe the status of water in the soil, plant and atmosphere is that of *water potential*.

Box 6.1 gives the technical definition of water potential but, more simply, water potential can be thought of as a pressure difference, with water moving from a place with a higher pressure to a place where it is lower. In plants, such movement is often in response to a suction (referred to as tension), and because suction is below atmospheric pressure, it has a negative value. In this case water will move towards the place with the greatest suction (i.e. the most negative pressure).

In most circumstances, water will move down this *water potential gradient*. Therefore, by assessing the differences in water potential between different parts of the soil–plant–atmosphere continuum (SPAC), it is possible to predict the direction water will move in. For example, water will be released from the soil to the root if the water potential of the root (e.g. -0.1 MPa) is lower than the soil water potential (e.g. -0.01 MPa): the water moves towards the more negative pressure of -0.1 MPa. The water will move from the root (-0.1 MPa) to the shoot (e.g. -1.5 MPa) as long as the shoot water potential is lower (more negative) than the root water potential (see Ascent of Sap from Roots to Shoots).

Potential is written as the Greek letter psi Ψ with a subscript letter to indicate what sort of potential it is. Whilst water potential (Ψ_w) inside any part of a tree is often presented as a single value, it is actually made up of a series of other potentials: *osmotic potential* (Ψ_π), *pressure potential* (Ψ_p) and *gravitational potential* (Ψ_g).

The osmotic potential is always negative, as it is a measure of the amount of substances dissolved in the water (technically called *solutes*) held in the solution that act to suck water towards them; the higher the solute concentration, the lower (more negative) the osmotic potential. The pressure potential is derived from the positive pressure inside cells caused by water pressing the cell membrane against the internal cell walls (turgor pressure), or from the tension (negative pressure) caused by evaporation of water. The gravitational potential is important in tall trees but, as it only varies by 0.1 MPa per 10 m in height, it is often ignored in plants that are not very tall.

Soils also have their own water potentials. In soils, the *matric potential* (Ψ_m) describes how tightly the water is held by the soil particles, and is the most critical component of soil water potential. The matric potential always has a negative value, as the forces at

Box 6.1 Technical Definition of Water Potential

Water potential is derived from a calculation of the chemical potential of water in a particular part of the system. Whilst this is measured in joules per mole of water compared with pure free water at atmospheric pressure and a temperature of 298 Kelvin ($\sim 25^\circ\text{C}$), this value is converted to pressure units, normally megapascals (MPa). The exact derivation of these units is quite complex; interested readers can consult Kramer and Boyer (1995) or Jones (2013) for a comprehensive explanation.

For ease of conversion, 0.1 MPa is equivalent to 1 bar, which is in turn roughly equivalent to 1 atmospheric pressure.

play tend to want to hold water on to the soil particles or colloids. The overall soil water potential (the matric potential plus the sum of the other potentials) may be slightly negative or even positive.

In saline soils, the osmotic potential of the soil solution acts to further reduce the soil water potential (it becomes more negative), making it harder for the roots to access water at a given soil water content. This is exacerbated as the soil dries and the salts become more concentrated (the osmotic potential becomes even more negative). Once the soil water potential becomes lower than the root water potential, then conditions exist whereby water may be drawn out of the root and into the soil (reverse osmosis). Although this is not a major problem in moist, humid environments that experience plenty of rainfall, spray (or run-off) from salt-treated roads can result in saline soils along roadsides. If these salts are not adequately flushed through the soil profile, the osmotic effect can seriously inhibit water uptake during the growth season, even in apparently well-watered conditions. Incorrect use of fertilisers can also create soils with low osmotic potentials that can limit water uptake.

Trees Experience Soil Water Potential, Not Soil Water Content

It is easy to think that the soil water availability simply depends on the quantity of water in the soil. Of course, this has to be partly true: moist soils provide easier access to water than dry soils. However, soils are very variable in texture, pore size, organic content and compaction (see Chapter 4) and, as a consequence, the total volume of water retained by the soil and the way in which water is released from the soil is very different from soil to soil.

The best way to visualise how soil will release water as it dries is to plot soil water potential (MPa) against the soil water content (typically presented as a volume, m^3 water per m^3 soil, or simply as a percentage of soil volume) in a *soil water release curve* (Figure 6.1a). In a drying soil, water will be available to the plant until some minimum soil water potential threshold is met, often referred to as the *permanent wilting point* (PWP). This relates to the water potential in the plant, where leaves reach their *turgor loss point* (Ψ_{p0}) (i.e. they irreversibly wilt) and are unable to recover. (Note that plants with wilted leaves may recover after watering because they have not reached the *permanent wilting point*.) In agricultural crops, this PWP is widely considered to be -1.5 MPa, but it can be much lower in temperate trees (-2.0 to less than -4.0 MPa) and even lower in some very drought-tolerant trees of the Mediterranean or other arid areas. Water will cease to become accessible by the plant when the soil water potential is lower than the turgor loss point of the species in question. Therefore, the quantity of water that is available to the plant corresponds to the water content between when the soil is full of water at field capacity,¹ and when the soil has little water and the plant reaches the turgor loss point.

¹ Field capacity is the water content after the soil becomes saturated, minus the water drained away under the influence of gravity. Typically, the water potential of soils at field capacity is between -0.01 and 0.03 MPa.

When you compare two contrasting soil types, it is easy to see that measurement of the soil water content gives you rather limited information on the availability of soil water. For example, in Figure 6.1(a), the field capacity of the sand is at approximately 10% soil water content whilst in the loam, the extra silt, clay and organic matter increases

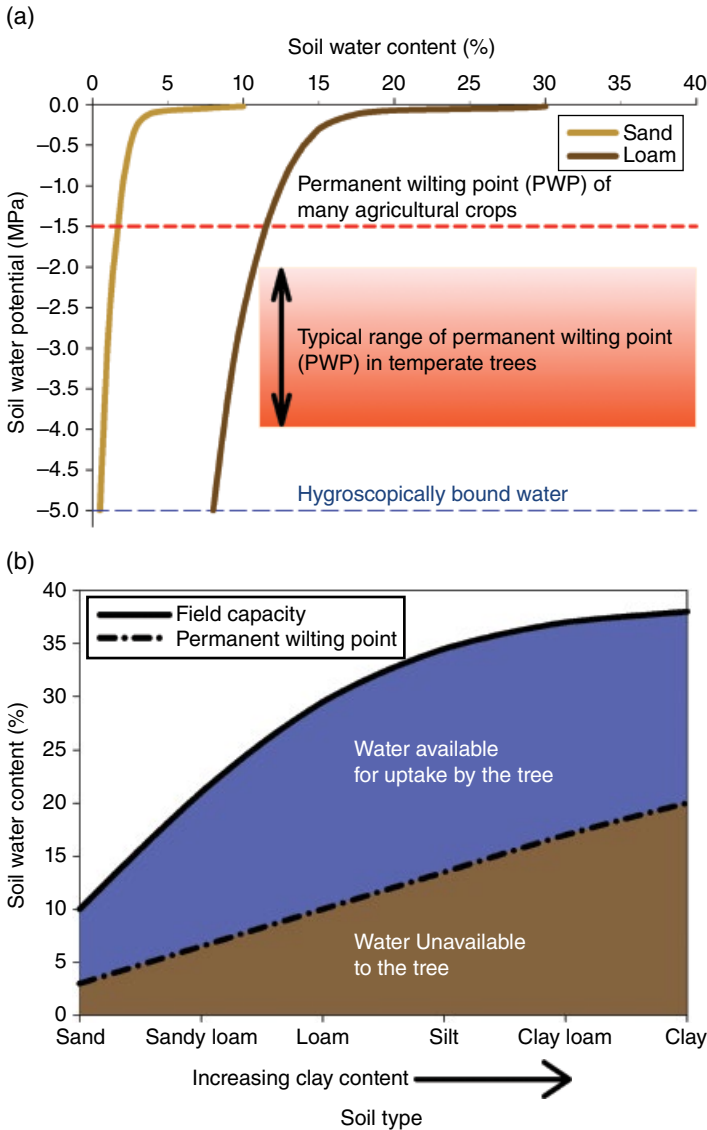


Figure 6.1 (a) Soil water release curves for a sand and a loam soil, showing the typical relationship between the soil water content and the soil water potential (the ease with which a plant can extract water from the soil). The turgor loss point (below which plants cannot grow) for many agricultural crops is taken as -1.5 MPa, and for many temperate trees it ranges between -2 and -4 MPa. At soil water potential below -5 MPa, water is hygroscopically bound to the soil so tightly that it is completely unavailable to plants. (b) A general relationship between soil water content and soil type.

the water retained in the soil to a little over 30%. The rate of decline in soil water potential also differs between the soils as they dry. At 10% soil water, all the water in the sandy soil is available to the plant, whilst the loam at 10% soil water has no water available to roots because its water potential is lower than the PWP: that is, the soil is holding the water too tightly for the plant to be able to remove any. Additionally, the sandy soil may only be able to hold 5% of its volume as available water, whilst the loam may be able to hold 15–20% of its volume as available water. These characteristics can make substantial differences to the volume of soil that trees require and the duration of time that trees can survive without rainfall or irrigation (see Chapter 4 for a discussion of this).

The way in which soil releases water differs widely with soil type, so the first challenge in managing soil water is to understand this relationship in the soil with which you are working. The construction of water release curves requires specialist equipment so it may be best to seek expert analysis from a professional laboratory. Once the soil water release curve is established, it is relatively easy to use a soil moisture probe to estimate the soil water content, and therefore predict the soil water potential. However, if a precise water release curve is unavailable, more general relationships between soil water content and soil type can help inform those trying to estimate the amount of water available to plants (Figure 6.1b).

Managing Soil Water Availability

Approaches to managing soil water availability will depend to a great extent on the context. For landscape trees, the first priority should be to ensure that opportunities are taken to minimise any major physical restrictions to root development. Large soil volumes are of very limited value if they are compacted and physically restrict root development (see Chapter 4). It may be that reducing soil compaction will substantially increase the rootable soil volume and therefore the availability of soil water. Equally, the prevention of soil compaction to protect rootable soil volumes can be just as important. Where it is possible to design rooting environments, soil volumes should be maximised within the constraints of other below-ground infrastructure (again, see Chapter 4).

In some situations, it may be possible to increase the water-holding capacity of the soil using amendments. For example, sandy soils are likely to benefit from the addition of organic matter and silt and clay particles. There is evidence that *biochar* from non-woody plants added to sandy soils does a similar job (Basso *et al.* 2012). Other factors important in determining how to manage soil water availability are the scale of the site, the number of trees, the potential value of the trees (or their crops) and, ultimately, the budget available for irrigation.

In recently planted landscape trees, before roots have had time to grow extensively, the small soil volume occupied by roots means that the available water is very rapidly depleted. Therefore, water deficits are a major challenge to tree establishment, even in humid areas with relatively high levels of rainfall. Impermeable surfaces will further compound the problems young landscape trees have in accessing water if rainfall does not adequately recharge the soil water. Supplementary irrigation will almost always be a good thing for young landscape trees, providing the soil does not become waterlogged.



Figure 6.2 (a) An irrigation tube being installed in a tree planting pit. (b) A watering bag placed around a recently planted tree in Copenhagen, Denmark. The bag has a porous base that slowly releases water to the root ball and surrounding soil over a number of hours. This helps reduce surface run-off and ensures deeper soil water recharge. Here, a Tregator® bag is being used, but a number of different brands and designs are available.

A number of mechanisms can be used to deliver water to the root-ball. In some tree pit designs, an irrigation pipe may be pre-installed into the planting pit (Figure 6.2a). In these cases it is simply a matter of connecting a water source to this pipe and delivering a prescribed volume of water to the root environment. In other cases, watering bags can be used (Figure 6.2b). These bags typically hold around 75 L which is slowly released over a number of hours to help ensure that the water sinks in, rather than running off across the surface. This will reduce the frequency that trees need to be irrigated. For high value trees, hydrogels (usually super-absorbent polyacrylate) can also be mixed into the soil backfilled around planted trees. There is some evidence that, at least in the short term, they can improve survival and growth (Orikiriza *et al.* 2013), but the extra expense must be factored in. In some more managed landscapes, sprinkler systems may be in place and, of course, a hose-pipe can be used to water a tree. However, it is also important to remember that saturated soils can be just as bad for the tree as dry soils. If managed incorrectly, there are risks associated with all of these methods:

- Irrigation pipes must be expertly installed to ensure that water is delivered to the actual root-ball and not just the surrounding soil.
- Watering bags must not be left around the stem for long periods of time as they cause high levels of moisture around the lower stem (extended use of watering bags may also discourage root development out into a wider soil volume).
- Manual watering can lead to excessive surface run-off, or superficial surface wetting.
- Irrigation systems using timers are not responsive to actual tree water demand.



Figure 6.3 A permeable geotextile barrier reduces soil evaporation and, importantly, weed competition in a field trial based at the Swedish University of Agriculture (SLU), Alnarp, Sweden.

To encourage root development beyond the root-ball, it is better to irrigate with larger volumes of water less often than with smaller volumes more often. Small, frequent irrigation often encourages roots to develop higher in the soil profile, making them more vulnerable to soil drying once irrigation is removed. Larger irrigation volumes recharge the soil water to a greater depth and so encourage root development in a larger volume of soil. In turn, this can slow the impact of tree water deficits during dry periods because the tree roots occupy a greater volume of soil, and deeper soil water is less prone to evaporation or uptake from shallow-rooted herbaceous competitors, such as grass. The use of mulch or a geotextile barrier to limit soil evaporation and competing herbaceous plants is always helpful when trying to establish young trees, particularly with regards to managing available soil water (Figure 6.3).

Commercial operations may need to irrigate trees to produce high-quality plants or profitable crop yields. With increasing pressures on regional water resources, water abstraction rights may only be granted if the grower can demonstrate sustainable water-management practices. Even then, in some dry regions, the water available for irrigation may not be adequate to provide irrigation throughout the year. Precise scheduling of irrigation and periods of *deficit irrigation* (delivering less water than the tree is losing by evapotranspiration²) may be necessary to preserve this precious resource.

² Evapotranspiration (ET) is a measure of total plant water use, including *evaporation* from the soil surface over the roots and *transpiration* from within the leaves. Potential evapotranspiration (ET_p) is predicted from environmental variables, such as temperature and humidity, and what is known about the resistance to water loss offered by the plant.

Box 6.2 Types of Soil Moisture Sensors

The two main types of soil moisture sensor are those that measure soil water content by volume and those that measure the availability of soil water to the plant (soil water potential) (see Trees Experience Soil Water Potential, Not Soil Water Content for the distinction). Sensors based on time domain reflectometry (TDR), neutron-attenuation and measurements of soil conductance of a current (based on dielectric properties) will estimate soil volumetric content. If calibrated correctly, these work well over a wide range of soil moisture contents, are reliable and relatively maintenance free. Tensiometers directly measure soil water potential, but have the limitations of being quite labour intensive to maintain and they only work in a narrow range of soil moisture (0 to -0.1 MPa). Porous matrix sensors estimate soil water potential from dielectric properties and can operate across the plant available range, albeit with a small loss in accuracy compared to tensiometers. Regardless of the sensor used, irrigation scheduling decisions should always be made with reference to the soil water potential because this most closely represents the availability of water to the root (see main text).

Although many irrigation decisions still rely on the tree manager's intuition, there are now a number of ways to schedule irrigation more precisely to ensure sustainable practice. These are typically based on feedback from soil moisture sensors, the measurement of plant water status, or on an estimation of evapotranspiration (ET) or potential evapotranspiration (ET_p).

A range of soil moisture sensors are available commercially (Box 6.2). The major limitation of using these to help in irrigation decisions is that the volume of soil measured tends to be very small compared with the soil volume from which roots extract water. Differences in the soil texture, drainage properties and root absorption rate can lead to variable soil moisture over small distances, so sampling in just a few places may mean making an irrigation decision based on atypical soil conditions. More sensors can be used to overcome this, but this is invariably limited by time and cost. In tree nurseries growing many species, the selection of a suitable reference tree under which to monitor soil moisture is particularly challenging because the demands of one type of tree may not be the same for other species or sizes of tree. Nevertheless, when installed and calibrated correctly, soil moisture sensors assist in assessing when to irrigate and how much water to apply. Figure 6.4 shows the various components needed in an irrigation system that uses soil moisture sensors. This system is used for scheduling irrigation for containerised trees but there is no reason why a similar approach could not be used for high value landscape trees.

It is possible to judge the need for watering by looking carefully at a tree. This might be as simple as watching for wilting or could involve measuring water potential, stomatal conductance, sap flow or crown temperature. The main drawback is that not all species behave in the same way. Consequently, it is important that the response of a species to water shortage is known so that a suitable *bioindicator* can be used to help schedule irrigation events. A general disadvantage to using plant-based approaches is that they do not give any information on how much water needs to be added to the soil (Jones 2004).

In some scenarios, it may be possible to use other plants as *biological sensors* to help guide irrigation decisions. For example, the wilting point of a sunflower has been

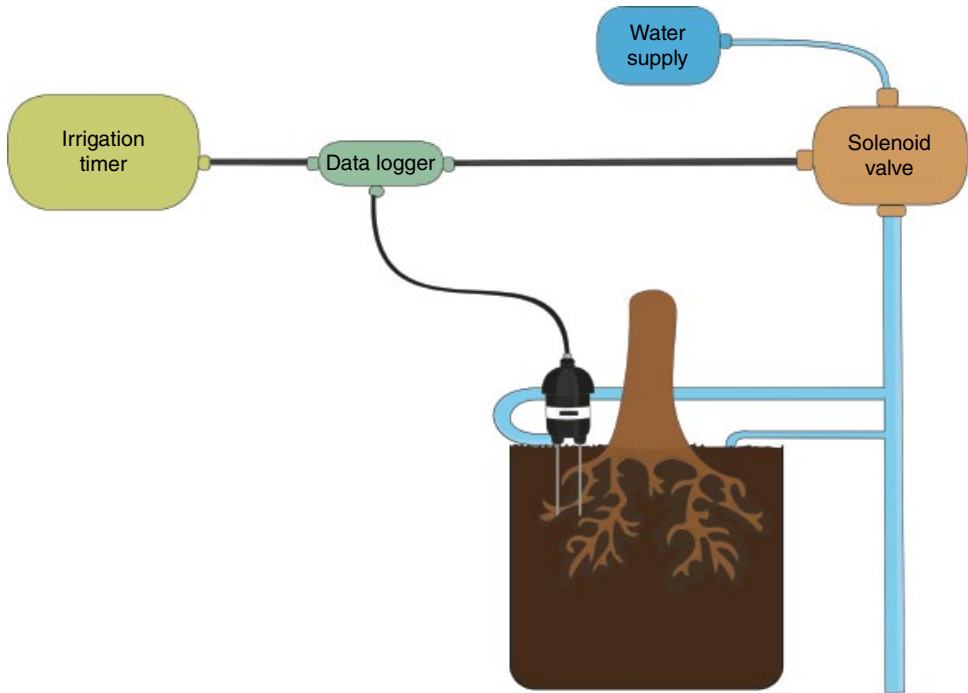


Figure 6.4 Soil moisture sensors pass information on the moisture status of the soil to a data-logger. When this is integrated with an irrigation timer and a solenoid valve, irrigation scheduling is very responsive to the demands of the tree. However, it only delivers feedback from one root system, so it may not fairly represent the needs of other plants on the same irrigation line.

reliably established to be -1.5 MPa. This is very likely to be higher (less negative) than the wilting point of tree species so the wilting of a sunflower planted close to a tree could be used as an early warning that irrigation for the tree may be necessary. This low-tech surrogate sensor for soil drying also has the advantages of being cheap and responsive to local climatic conditions. In gardens with a wide range of species, well-established plants that are known to be sensitive to drying soils can be used to inform irrigation decisions for the rest of the garden. In this way, paying close attention to the indicator species can be an efficient way of guiding decisions for a much larger group of plants. Clearly, some precision is lost using this technique, but no system is perfect and this type of approach is both cheap and useful.

Irrigation may also be scheduled by calculating ET using the standard Penman–Monteith equation (for details see Allen *et al.* 1999). Used appropriately, this approach can give very good information on how much irrigation is required to replace that lost via ET. However, it does rely somewhat on the uniformity of plant material, as large diversity in plant size and species can reduce accuracy. As a result, this technique is most useful for scheduling irrigation in orchards.

Variation across soils, species, tree size and climate make precise recommendations for the irrigation of trees difficult without knowledge of all these factors. However, Table 6.1 gives some important general principles for managing soil water availability.

Table 6.1 Important principles when managing soil water availability for trees.

Principle	Considerations
Maximise the volume of soil that roots have access to	<ul style="list-style-type: none"> ● Ensure that potential rooting volume is not compacted ● Provide root paths through other below-ground infrastructure to 'breakout zones' or new volumes of soil ● Prevent future soil compaction
Improve the soil water holding capacity where possible	<ul style="list-style-type: none"> ● In very sandy soils, consider adding silt, clay, organic matter or biochar to increase water retention ● Ensure any ameliorants actually increase available soil water and do not lock up soil water
Understand the water release characteristics of the soil	<ul style="list-style-type: none"> ● Remember that it is soil water potential that the tree experiences, not soil water content ● A small investment in a laboratory analysis to get a soil water release curve can substantively increase the confidence in irrigation scheduling decisions ● Accuracy in the 0 to -5 MPa range is most important
Reduce soil evaporation and competition from other vegetation	<ul style="list-style-type: none"> ● Ensure that water applied to the tree is taken up by the tree, and not lost via evaporation. Therefore, consider the time of day water is applied: avoid irrigating in the middle of the day when evaporative demand is highest ● Organic mulches have numerous benefits, including reducing soil evaporation ● Geotextile membranes can be useful in reducing evaporation from the soil, but they offer no nutritional value and do not readily biodegrade ● Keep a circle around the tree (ideally to the dripline) clear of competing vegetation
Ensure water that is being applied gets to the roots	<ul style="list-style-type: none"> ● Pre-installed irrigation infrastructure may hydrate soil beyond the absorbing roots, especially on recently planted trees ● Minimise surface run-off by slowly wetting the soil, rather than delivering high volumes of water very rapidly
Decide on timing of irrigation based on the tree's requirement for water	<ul style="list-style-type: none"> ● If the timing of irrigation events is not underpinned by tree physiology, then inefficient water use should be expected ● Irrigation should be responsive to the requirements of the tree, not an arbitrary maintenance schedule
Avoid over-application of water	<ul style="list-style-type: none"> ● Saturated soils are very low oxygen soils and can be very damaging to trees without specialist adaptations ● Excessive irrigation can cause the leaching of nutrients and reduce the fertility of the soil ● Water is a precious commodity; use it sustainably
Ensure that the osmotic potential of the soil solution does not hinder root absorption	<ul style="list-style-type: none"> ● Excessive salt or fertiliser use can make it much harder for roots to absorb water ● Flushing (leaching) soils is the best way to reduce the affect of saline soils (assuming water is available to do this)

Fine Roots are Critical for Water Absorption

It is the intricately branched fine roots and their root hairs that are responsible for the vast majority of water absorption from the soil. Whilst the larger, woody roots are capable of taking up some water, the resistance to water absorption caused by lignin and suberin impregnated cells is marked. Indeed, part of the role of secondary growth and suberised cell walls is to prevent water being lost from the roots system to a dry soil. It stands to reason therefore that the structures within older roots that inhibit water being leaked back to the soil are incompatible with efficient water absorption. For this reason, the removal or loss of fine roots can have catastrophic consequences for the delivery of water to a transpiring crown. So the preservation, protection and promotion of fine roots should be at the core of any tree health-care programme. Even in soils with plenty of available water, trees must still have sufficient root surface area to absorb enough water to supply it to the crown.

Uptake of water from the soil to the roots occurs along gradients of decreasing water potential. During the day, evaporation from the leaves creates a tension (negative pressure or 'suction') in the column of water extending from the leaf to the root. In turn, this acts to reduce the water potential of the root and water is drawn into the root, providing the soil water potential remains higher (less negative) than that of the root. This mechanism for water uptake is most important in transpiring trees. However, at night and during other periods of very low transpiration, water can still be drawn into the root by osmosis. To maintain this form of uptake, roots produce various osmotically active substances to keep a water potential gradient between the root and the soil. This active process uses energy so is only efficient in well-aerated soils when suitable temperatures exist around the roots. Therefore, warm, well-drained soils provide better conditions for this active uptake of water than cold, waterlogged soils.

The active production of ions and compounds, such as sugars, by the xylem parenchyma also appears to be the source of root pressure that can push water several metres up the tree. For the tree, this positive root pressure, sometimes in combination with stem pressure, is likely to be very useful in making sure that the vessels and/or tracheids start the growth season full of sap and not gas bubbles. It may also be a way of speeding the supply of sugars from the roots to the growing points on the trunk. In some species, particularly within the genera *Acer*, *Betula*, *Juglans* and *Ostrya*, this positive pressure within the xylem causes stems to 'bleed' when cut. For this reason, it is best to avoid pruning these trees in spring.

To enter a root, water must move through the outer cortex of the root and through the endodermis (Figure 6.5), before reaching the xylem of the root (more detail on root structure can be found at the beginning of Chapter 4). There are three different pathways that water can move along: water may pass *between* the cells of the cortex (the *apoplast* pathway) before they reach the endodermis; make its way *through* the cells (the *symplast* pathway); or pass through the *transmembrane* pathway (all are explained further in Figure 6.5). Inevitably, the relative importance of these alternative pathways varies somewhat between species, the nature of the driving force for uptake, root maturity and the surrounding soil environment. However, it is clear that roots are able to exert a high degree of control through the active adjustment of cell osmotic potentials, and the use of specialised water channels known as aquaporins. Research is still unravelling the

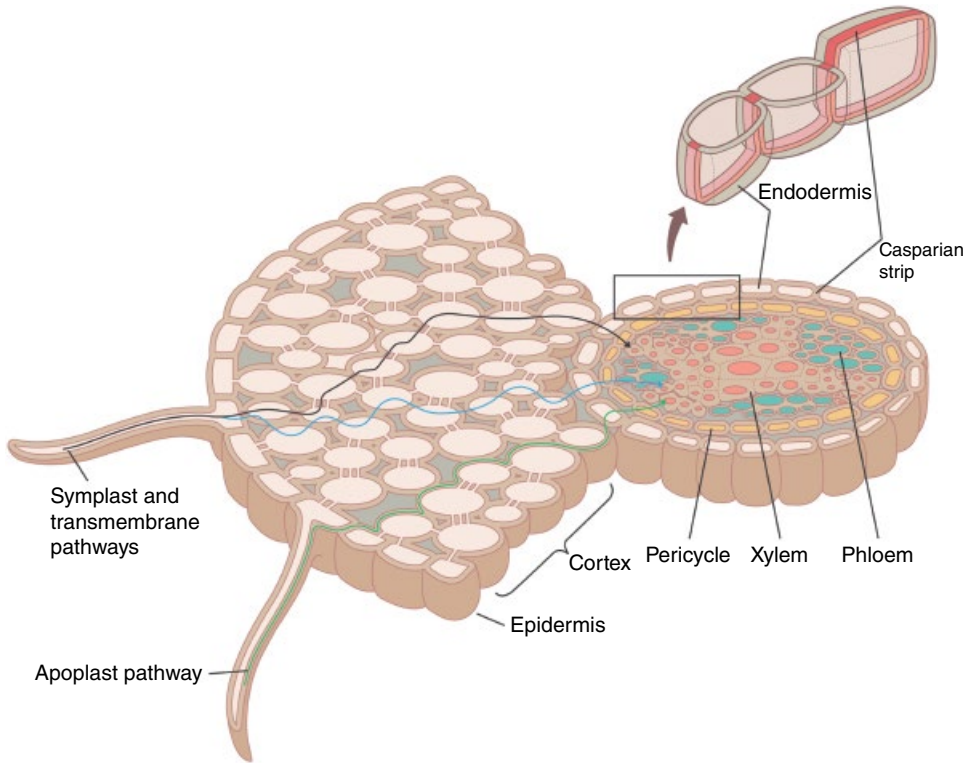


Figure 6.5 Alternative pathways for water and nutrient uptake by the root. In the *symplastic* pathway, water and nutrients cross the plasma membrane into a cell, and so move *through* the cells along the interconnected symplast (the inner surfaces of the cell or plasma membrane) via channels between cells known as plasmodesmata. In the *apoplastic* pathway, water and nutrients move *between* cells by following the gaps between cells and along the outside of cell walls until they reach the endodermis, at which point they must cross a plasma membrane into a cell before it can be taken into the xylem. A further route is known as the *transmembrane* or *transcellular* pathway, where water has to cross two cell membranes as well as the cell wall between two adjacent cells. Specialised water channels, known as *aquaporins*, mediate this transcellular pathway. Regardless of how the water crosses the root cortex, water must pass through the endodermis before entering the xylem. The Casparian strip in the endodermis is a corky, suberised layer that ensures that nothing enters the centre of the root without going through a cell. In this way the root has control over everything that enters. *Source:* Taiz and Zeiger (2010). Reproduced with permission of Oxford University Press.

relative importance of these alternative pathways for water uptake and the resistances that they confer to water movement through the plant. However, whilst these finer questions regarding root water uptake deserve scientific attention, for those trying to manage trees it is the preservation of fine roots and the provision of a high quality root environment that will make the greatest difference to the uptake of water.

For water to be efficiently absorbed into the root system, fine roots must be in contact with moist soil. Well-drained, uncompacted soils help ensure sufficient oxygen around the roots, and also tend to be warmer. Adding mulch can also help buffer temperature extremes, which is of particular importance in spring when night-time temperatures still regularly fall below 5 °C and limit root growth (see Chapter 4).

Hydraulic Redistribution

The tree's coarse roots are important, not just for linking the fine roots to the trunk, but also for the movement of water within the soil and even into the soil. Careful measurement of soil moisture and sap flow has yielded some fascinating insights into the way trees respond to variable water availability. At night, when transpirational demand is negligible and stomata close, the ascent of sap from the roots to the crown is halted. At this point, small remaining water potential gradients between different parts of the root system and between the crown and the roots can induce sap flow. This *hydraulic redistribution* (HR) (Burgess *et al.* 1998) can take place in a number of different forms (Figure 6.6), but it is a vital process for many trees. Importantly, HR not only moves water around the tree, it can also release water back into the soil so that other vegetation and soil organisms can benefit.

Where shallow soil layers are drier than deeper soil layers, water can flow from the deeper roots up to shallow roots via a process termed *hydraulic lift* (HL). *Lateral redistribution* (LR) can also occur where water is moved horizontally through roots found at the same depth but experiencing differing water potentials (water flowing from wetter to drier areas). This may occur naturally in trees at the edge of a group that have part of the root system sheltered under a canopy and other roots in an open environment or it may be brought about by localised irrigation. After rain (or irrigation), when deeper soil is drier than shallow soil layers, *downward hydraulic redistribution* (DHR) can occur to aid the water recharge of deeper soil compartments. In very humid conditions, such as those caused in fog or drizzle where the soil does not really experience rewetting, *foliar uptake* (FU), the absorption of water through the leaves, can move

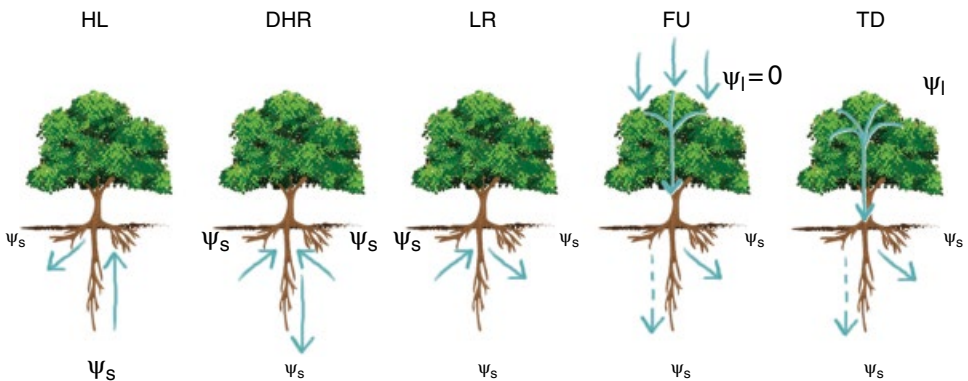


Figure 6.6 Alternative types of hydraulic redistribution in trees. Hydraulic lift (HL) brings water from deeper roots to the shallower roots. Downward hydraulic redistribution (DHR) moves water from shallower roots to deeper roots. Lateral redistribution (LR) moves water horizontally through roots of similar depth. Foliar uptake (FU) occurs when water moves from a very moist atmosphere through the crown and stems to the root system. In very dry circumstances, tissue dehydration (TD) can also occur. Soil and plant water potentials are shown by the symbol Ψ : different sizes of symbol indicate different sizes of water potential, with the bigger symbol representing the higher water potential (i.e. greater moisture). Arrows indicate the direction of water movement and dashed arrows indicate alternative pathways for water movement. *Source:* Adapted from Prieto *et al.* (2012). Reproduced with permission of John Wiley and Sons.

water from the crown, down the stem and into the roots. At the end of prolonged periods of water deficit, when all soil compartments are dry, the root system acts as a competing sink for the remaining water within the tree, and *tissue dehydration* (TD) of the crown can occur (Nadezhdina *et al.* 2010).

Intuitively, if a tree is rooted into deep soil compartments that remain moist through dry periods, the transpirational demand can simply be supplied from deeper roots. What then are the benefits of this redistribution of water around the root system? First, shallow lateral roots do have a number of advantages over deep roots. They offer lower resistance for water uptake into the crown so the leaves find it easier to draw water up from these shallow roots than they might from deeper roots. Secondly, shallow lateral roots are also much better placed to intercept rainfall than deep roots. Therefore, there is an advantage in keeping the lateral roots alive during dry periods, particularly keeping the fine roots healthy (Bauerle *et al.* 2008). If these shallow roots become dysfunctional through embolism, lose contact with the soil or die, they cannot take up rainfall. As seen in Figure 6.6, HL can also result in the release of water into the surrounding soil environment. This increase in soil water can improve nutrient availability either directly, by nutrients dissolving into the soil solution, or by increasing the activity of soil microorganisms, such as mycorrhizae. Needless to say, increases in water and nutrient availability can lead to a cascade of effects that can improve the performance of individual trees, as well as having larger-scale effects across whole ecological communities (Prieto *et al.* 2012).

During periods of plentiful rainfall, the preservation of lateral roots also means that the tree can recharge deep soil compartments through downward hydraulic redistribution. This effectively locks water away where it is less vulnerable to surface evaporation and competition from other vegetation. Then, during dry periods, the recharged deeper soil compartments release water back to the roots, so that the effects of water deficit are less pronounced and the growing season can be extended. Indeed, in a velvet mesquite *Prosopis velutina* savannah in Arizona, USA, this deep-water recharge during a wet period was able to provide 16–49% of the tree's water requirements throughout the dry season (Scott *et al.* 2008).

Lateral redistribution is unlikely to be able to extend the growing season in the same way that DHR can, but it can help areas of the crown survive in trees with a highly sectorized vascular system (see Chapter 2). Here, LR will help maintain the water supply to a larger proportion of the crown when soil moisture availability would otherwise be low in some parts of the rooting zone.

Foliar uptake only occurs when the soil is dry and the atmosphere is saturated by fog or drizzle. The significance of fog is seen in coastal redwood *Sequoia sempervirens* in its natural Californian environment. During the frequent heavy fogs coming off the Pacific Ocean, foliar uptake (where sap flows in the direction of the roots) accounts for 5–7% of the water demanded by the crown. However, it is likely that some of the water taken up via the leaves is used to rehydrate plant tissues near the height limit for water transport up the xylem, thereby providing an important source of water to the crown but not a substantial source of water to the roots and soil (Burgess and Dawson 2004). Extra water can be acquired, however, without it entering the leaves. Intercepted fog will drip off the leaves and stem to reach the soil. In coastal redwood forests, this accounts for around one-third of the annual water input into the forest (Dawson 1998). In other coastal environments, such as the laurel forests of Tenerife in the Canary Islands, fog collection supplies up to 20 times that received from rainfall (Thomas 2014).

Whilst it is clear that HR is an important process, particularly in regions that experience extended periods of drought, it is difficult to manipulate through land management. Planting species known for HR certainly has long-term merit but, as with so many ecosystem services provided by trees, their greatest contribution is only seen when they reach maturity. Indeed, the fact that HR occurs most effectively in mature root systems underscores the importance of protecting mature trees in the landscape, especially in water limited environments where HR is likely to be an important component of the local hydrological cycle.

Understandably, the significance of HR to trees growing in urban environments has not been investigated to the same extent as to those growing in natural environments but, given that soil water is likely to be very variable under urban trees as hard landscapes and soil compaction alter infiltration and drainage, urban tree roots will certainly experience variation in soil moisture and water potential gradients across their root-zone. HR is likely to be a feature of urban trees and may well be critical to the survival of some individuals: it is easy to see how this strategy could be used to take advantage of a water leak from a damaged pipe (providing there is no waterlogging). Thus, it is preferable to design root paths (trenches) from areas with impermeable surfaces to areas of open ground (break-out zones), to provide future opportunities for HR. Roots growing in these break-out zones can then move water and nutrients to portions of the root system in less favourable conditions, and the whole tree is likely to fare better.

Ascent of Sap from Roots to Shoots

The ascent of sap within trees has intrigued scientists for centuries: just how do trees manage to move water up over 100 m in height? If plants had only managed to reach a few metres in height, then it might be possible to explain water movement as capillary rise in the very narrow xylem conduits, or the positive force caused by root pressure. However, these forces cannot explain water movement through trees that are tens of metres high.

The origins of what is now referred to as the *cohesion–tension* (CT) theory can be traced back hundreds of years to the insight provided by an English clergyman, Stephen Hales (1677–1761), who suggested in his book *Vegetable Staticks* (Hales 1727) that ‘sap...is probably carried up to great heights in those vessels by the vigorous undulations of the sun’s warmth’. Although our understanding is much more developed now, Hales was essentially right that evaporation of water from the leaves provides the driving force for the ascent of sap. It is, perhaps, too generous to give Hales the credit for what we now understand as the CT theory, this is usually reserved for Dixon and Joly (1895), but a number of scientists have been involved in its refinement since (see Brown 2013). Perhaps the most complete review can be found in Tyree and Zimmermann (2002).

In simple terms, water evaporates from inside the leaf (transpiration), creating a *tension* (negative pressure) in the mesophyll cells inside the leaf. Put another way, a water potential gradient is generated between the moist cells inside the leaf and the comparatively dry air outside, causing water loss. Strong *cohesive* forces hold the water molecules together, helped by adhesive forces between the water molecules and the cell walls, so the tension acts to pull water towards the drier cells from adjacent wetter cells. This tension is transmitted through the mesophyll, into the xylem, and all the way down

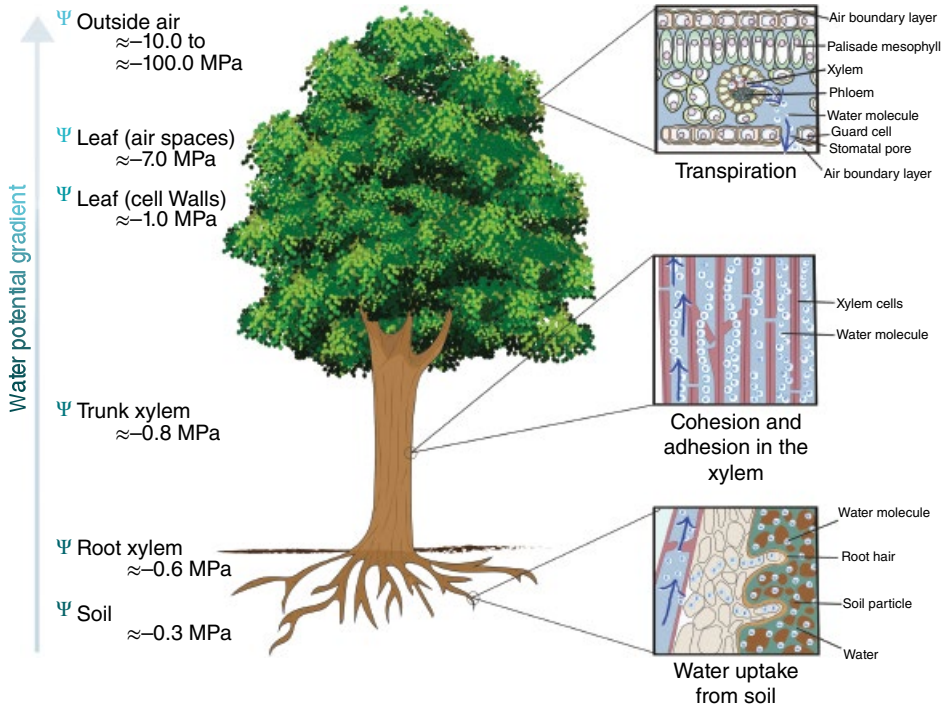


Figure 6.7 Sap moves up through a tree down a water potential gradient (Ψ): the more negative the value, the greater the suction or tension. Water is lost from the leaves to the relatively dry air which generates tension within a continuous column of sap that extends from the leaves to the roots, which then acts to pull water up through the xylem. The reduction in the amount of water in the roots (the reduced root water potential) passively draws water into the root and causes soil water to move towards the root down a water potential gradient. Water potential values shown on the left are indicative only.

a continuous column of sap held within the tracheids and/or vessels. Cohesive forces within the sap act to pull sap up from the roots to replace that lost from the leaves. In turn, this action reduces the amount of water inside the roots, reducing the water potential and thus drawing soil water into the root. Subsequently, water moves towards the root down a gradient of decreasing water potential within the soil (Figure 6.7). The continuous system of water from the evaporating surfaces in the leaves to the absorbing surfaces of the roots is known as the soil-plant-air-continuum (SPAC).

One of the most remarkable things about the ascent of sap is that the whole process simply relies on physics: it does not require any energy from the tree to lift sap from the deepest roots to its uppermost leaves; if it did, the energy demands of getting water to any height would have prevented trees from ever evolving. Sap is pulled up the tree by the evaporation of water from the leaf (causing tension), the incredible tensile strength of water (from cohesion) and the extraordinary ability of wood (xylem) to withstand these forces. However, this is not without its limits. Where the supply of water is not able to keep pace with transpiration demands, tension within the sap becomes ever greater. Eventually, under high tension, water columns will break and gases will be drawn into the tracheid or vessel via a pit in the cell wall; embolism will occur (see

Chapter 2). Embolism can disrupt the water supply to the leaves and so may lead to hydraulic failure, so numerous mechanisms and adaptations have evolved to help prevent this from occurring (again, see Chapter 2).

Transpiration

More than 95% of the water ascending the tree is lost via transpiration (McElrone *et al.* 2013). This is the process by which water evaporates from the plant and moves to the atmosphere. While this may seem very wasteful, the tree has little choice. In order to allow carbon dioxide and oxygen to diffuse in and out, the tree has to be 'leaky,' a key side effect of which is loss of water. On the positive side, this transpiration stream helps cool heated leaves and is one of the main ways of delivering minerals that are dissolved in the water to the growing points of the tree. However, trees have ways of regulating this loss.

Although water can evaporate from any internal surfaces that come into contact with the air, and also the entire outer surface of the plant (hence, trees still lose some water when they have no leaves; look back to Figure 4.28), most of the water lost from the plant is lost via the leaves. Water evaporates from the moist internal surfaces of the leaf, and so the air spaces in the leaf mesophyll contain a higher concentration of water vapour relative to the dry air surrounding the plant. Thus, a *vapour concentration gradient* between the interior of the leaf and the outside air causes water vapour to move, via diffusion, from the inside of the leaf to a *boundary layer* of unstirred air surrounding the leaf, and then into the atmosphere. The air inside the leaf is typically saturated with water vapour, and the air outside the leaf contains less vapour, so the magnitude of this gradient in vapour concentration is described by its *vapour pressure deficit* (VPD).

However, it is more practical to think of the difference in vapour concentration as a difference in water potential. This can then be readily compared with other measures of water potential in the tree (e.g. shoot or leaf water potential). The conversion is quite complex (see Nobel 2009) as it depends upon relative humidity and temperature, but a range of air water potentials are given in Table 6.2. What should be clear is that in all but the most humid atmospheres (i.e. close to 100% relative humidity), the water potential of the air is extremely low and drives water loss from the leaves.

Resistance to Water Loss

Transpiration is essentially a process of evaporation, but there is substantial resistance to evaporation provided by the leaves. Leaf cuticles with their embedded waxes provide the greatest resistance to water loss. This resistance is not apparently related to the thickness of the cuticle, as commonly assumed (Kerstiens 1996): thicker cuticles do not lead to reduced water loss. It is therefore likely that the chemical composition of the waxes have a dominant role in regulating cuticular water loss. The boundary layer of very still air surrounding the leaf also provides some resistance to water loss because the water vapour has to diffuse further to escape, but this varies quite substantially with leaf size and wind speed. In fact, unless the leaf has dense leaf hairs (or similar) that increase

Table 6.2 The water potential of the air (Ψ_{air}) at different levels of relative humidity (%) and temperature ($^{\circ}\text{C}$). Relative humidity describes the degree of saturation in the air as a percentage of the maximum possible saturation at a given temperature. The more negative the water potential, the greater the forces leading to evaporation of water from inside the leaves.

Relative humidity (%)	Ψ_{air} (MPa) at different temperatures ($^{\circ}\text{C}$)				
	10	15	20	25	30
100	0	0	0	0	0
99.5	-0.65	-0.67	-0.68	-0.69	-0.70
99	-1.31	-1.33	-1.36	-1.38	-1.40
98	-2.64	-2.68	-2.73	-2.77	-2.81
95	-6.69	-6.81	-6.92	-7.04	-7.14
90	-13.75	-13.99	-14.22	-14.45	-14.66
80	-29.13	-29.63	-30.11	-30.61	-31.06
70	-46.56	-47.36	-48.14	-48.94	-49.65
50	-90.50	-92.04	-93.55	-95.11	-96.50
30	-157.2	-159.9	-162.5	-165.2	-167.6
10	-300.6	-305.8	-310.8	-316.0	-320.6

Source: Lambers *et al.* (2008). Reproduced with permission of Springer.

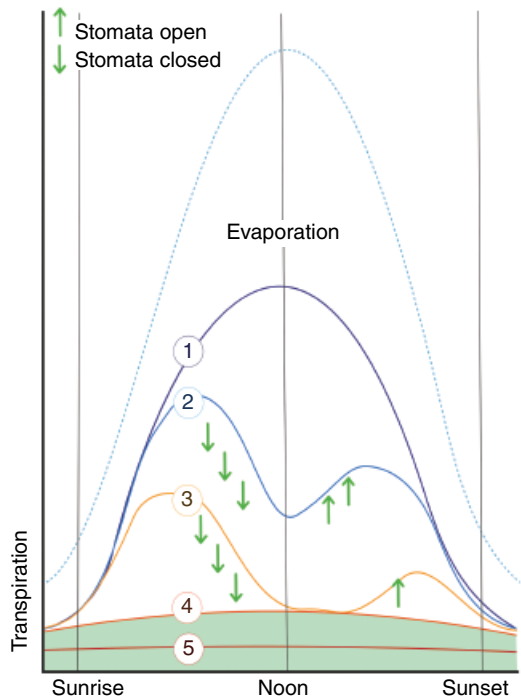
the boundary layer effect, as the wind speed rises above 2 m s^{-1} (7.2 km per hour/4.5 mph) the boundary layer resistance becomes negligible. For this reason, open-grown trees, those growing in exposed locations and those growing in wind tunnels caused by urban canyons are likely to have lower resistance to water loss than those growing in more sheltered environments. Neither the cuticle nor the boundary layer resistances provide the tree with any short-term control over water loss: this role is left to the stomata.

Stomata, tiny pores in the leaf surface, provide the gateway between the internal leaf environment (including those moist evaporating surfaces) and the atmosphere. Stomata have two guard cells that act as doors controlling the size of the pore. When they are closed, stomata are quite resistant to water loss; when they are open they conduct water. This can be measured as *stomatal conductance*.³ However, as noted above, the main role of stomata is to allow carbon dioxide into the leaf. Consequently, it is almost as if stomata have two masters: one telling them to make sure they do not lose too much water; the other telling them to make sure that they do not run short of that all important raw ingredient for photosynthesis. They have to walk the metaphorical tightrope, so it should come as no surprise that the regulation of their opening is complex.

When water is abundant, the advantage of maintaining a good supply of carbon dioxide for photosynthesis is greater than the disadvantage of losing water from the leaves. The cooling effect of transpiration can be vital in preventing leaf temperatures from reaching damaging levels. Therefore, during the day when light is available for

³ Stomatal conductance is a measure of water loss through the stomata, typically measured in millimoles of water lost per square metre of leaf area, per second ($\text{mmol m}^{-2} \text{ s}^{-1}$).

Figure 6.8 Daily changes in transpiration with decreasing soil moisture (curves 1–5). The dotted line indicates potential evaporation, arrows indicate stomatal movements and the green area shows where transpiration is only through the cuticle. (1) Unrestricted transpiration; (2) limitation to transpiration in the middle of the day; (3) full closure of stomata at midday; (4) complete cessation of stomatal transpiration by persistent closure of stomata (only cuticular transpiration continues); (5) even further reduced cuticular transpiration as the result of membrane shrinkage. *Source:* Adapted from Stocker (1956). Reproduced with permission of Springer.



photosynthesis, the stomata tend to open. If minor water deficits develop they often partially close around midday to prevent excessive water loss, then open again to allow photosynthesis in the afternoon. At night, when there is no photosynthesis, the stomata tend to close to prevent unnecessary water loss (Figure 6.8). However, some night-time water loss may still occur, particularly on warm, dry nights. For example, night-time flow of water through the trunk of coastal redwood *Sequoia sempervirens* can be 10–40% that of the daytime flow (Dawson *et al.* 2007). This might actually be really useful to provide water and nutrients to parts of the tree that did not receive much sap flow during the day. If night-time transpiration does not occur, the water potential of the shoot (or leaf) pre-dawn (Ψ_{pd}) provides a good surrogate measurement for the soil water potential experienced by the tree as, in the absence of transpiration, these water potentials equilibrate. A decline in Ψ_{pd} is therefore good evidence of soil drying across a substantial portion of the root system.

The real challenge for stomata comes when these two ‘masters’ start competing in those situations where water supply cannot keep up with water demand. Here, prodigious water loss must be controlled if leaf dehydration and lasting damage to the tree is to be avoided.

To control against dehydration, stomata close in response to a wide range of variables so that they are able to provide a compromise between carbon gain (photosynthesis) and water loss. Roots provide hydraulic signals as their ability to supply water is diminished and the root water potential declines (Kramer and Boyer 1995). They can also provide chemical signals, such as the hormone abscisic acid (ABA), which is produced when the root experiences drying soil and transported via the sap to the leaves where it

promotes stomatal closure (Davies and Zhang 1991). A range of variables, therefore, have the potential to impact stomatal aperture, but it seems that the hydraulic factors are usually dominant in forest trees (Augé *et al.* 2000).

Coordination between all the controlling variables helps to maintain the *water balance* of the tree. Only if the rates of water uptake, conduction and loss are adjusted to each other can a satisfactory water balance be maintained. Indeed, the difference between absorption and transpiration, measured over a given interval of time, gives a good idea of how well the water balance is maintained. The balance becomes negative as soon as the absorption of water is unable to meet the requirements of transpiration. If the stomata partially close and the rate of absorption remains unchanged, the balance can be restored.

During the day, the water balance almost always becomes negative as the supply of water struggles to match the demand from transpiration. The balance is restored in the evening or overnight, providing there is sufficient water in the soil. If soil water is not replenished by rainfall or irrigation, the water balance of the tree may not entirely recover overnight, so that the deficit accumulates from day to day. Inevitably, if the supply of water continues to fall behind the transpirational demand, then serious water deficits can develop. Ultimately, leaves may wilt, embolism may become widespread in the xylem and hydraulic failure can lead to the tree dying.

Species, tree size, rooting environment and climate can all have a profound effect on the volume of water a tree uses. Although this makes estimating the water use of trees complex, understanding the volume of water trees use can help answer important questions relating to forest hydrology, as well as the soil volumes required to support landscape trees. Chapter 4 discusses this in more detail.

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