General Principles of Plant Water Relations
R. A. Bueckert. Crop Physiology, Department of Plant Sciences
University of Saskatchewan, 51 Campus Drive, Saskatoon, S7N 5A8. E-mail: rosalind.bueckert@usask.ca

Introduction
The term “water relations” describes plant water status at a cell, individual organ (leaf, internode, flower) or whole plant level, furthering our understanding of basic plant growth and development, and plant response to the environment. At the field level, water use and water use efficiency are the common means of evaluating a crop and its yield performance to seasonal water availability. Water use and water use efficiency measure overall crop water use in a field over a season whereas water relations measures plant water status at a point in time. Water relations is a subject that spans plant physiology, crop science, agronomy and irrigation management through the common concept of water potential – thus allowing measurement and detailed description of plant response to water availability within part of the cropping season or field. The subject of plant water relations is large; this article will be restricted to major principles associated with plant water status and several key measures of stress physiology.

Water relations encompasses measurement techniques that describe general plant water status, the quantification of water in cell and tissue expansion, maintenance of turgor, and the overall stomatal gas exchange of plants according to moisture in the soil and aerial environment. Water enters plants through the roots, and travels both through and around cells. Water is moved up the plant mainly in the xylem vessels of the stem and in leaf veins, and water is transpired from the plant via stomata on the leaf surface (Figure 1). From the 1960s, the discipline of water relations expanded mainly through the concept of water potential, allowing multidisciplinary research spanning soil, plant and aerial environments, and culminated in the practical management of crop water requirements. In simple terms, water relations allow direct measurement of how much water is in the plant. This information directly indicates how well the plant is performing and how the plant copes with stress – in contrast to indirect measurements of soil moisture content or rainfall deficit.

1. Water potential

The most widely used description of the water status of plants has been the chemical potential concept introduced by Slatyer and Taylor\textsuperscript{11}. The water status in plants is measured by water potential, \( \Psi \), a measure of free energy available to do work, as in “move water”. The simplified form is:

\[
\Psi_{\text{leaf or plant}} = \psi_{\text{solute}} + \psi_{\text{pressure}} \quad [1]
\]

Here the leaf water potential (\( \Psi_l \)) or plant water potential (\( \Psi \)) is the sum of the solute potential (\( \psi_s \)) and the pressure potential (turgor, \( \psi_p \)), all in units of MPa (1 MPa=10 bar, and 1 bar=14.5 psi). The solute potential is also called osmotic potential by some researchers. Both \( \Psi_l \) and \( \psi_s \) are negative, being a tension. Solutes in the cytoplasm are dissolved in water and lower the free energy so \( \psi_s \) is always negative, and \( \psi_p \) is usually positive but can be negative or zero. A positive \( \psi_p \) is similar to vehicle tire pressure. The potential of free water at one atmosphere is given the value zero by convention. The chemical potential of water (J mol\textsuperscript{−1}), when expressed per unit partial molar volume, becomes units of pressure in Pascal (Pa). The Pa units arise from 1 J = Kg m\textsuperscript{2} s\textsuperscript{−1} and J mol\textsuperscript{−1} m\textsuperscript{3} = Kg m\textsuperscript{−1} s\textsuperscript{−1} or Newton m\textsuperscript{−1}=Pa. A more complex version of the water potential equation includes additional potential terms such as matric potential, \( \psi_m \), and the gravitational potential, \( \psi_g \), added to \( \psi_s + \psi_p \). The matric potential is influential when a dried matrix is present such as an exceedingly dehydrated cell wall, or dry seeds. The gravitational component is ignored in most crop systems but is used for tall trees, when \( \psi_g \) is –0.1 bar or –0.01 MPa for every 1 m in height.
Figure 1. General scheme of water movement in a higher plant.
Water relations is commonly used to assess the water status of already expanded organs such as leaves, $\psi_l$, and $\psi_t$ is used to infer the overall plant water status $\Psi$ (note the capital Greek letter). In a well-watered plant, direct measurements of tissue $\psi_t$ can be made using a pressure chamber or psychrometers. The pressure chamber (commonly known as a pressure-bomb) was first used by Scholander $^{6,12}$, and consists of a machined metal cylinder with a removable but gas-tight lid, which is capable of controlling incoming air pressure to pressures approaching 30 bar (3 MPa), a gas pressure gauge and a gas venting mechanism (Figure 2, left). An excised leaf or plant is placed in the chamber, with the leaf or plant inside and a small part the leaf petiole or plant stem protruding through a rubber stopper inserted through the lid. Pressure is slowly applied to the leaf in the chamber by a stream of compressed air or nitrogen gas until xylem sap appears as tiny water droplets exiting the xylem of veins in the stem. A leaf blade of grass can also be measured this way. When tiny water droplets appear at the xylem in the leaf veins or the cut stem, the pressure applied exactly balances the leaf water tension or potential.

Pressure chamber measurements are rapid, and provided that the leaf is first wrapped in plastic with sufficient leaf lamina (blade) within the chamber compared to the length of tissue outside the stopper, measurements are fairly accurate. With psychrometry, a portion of leaf is cut from the plant and placed in a small chamber where the leaf surrounds a small psychrometer junction. Chambers are incubated for eight or more hours in a water bath at 25°C, and when the leaf-chamber humidity has come to equilibrium, the psychrometer is read using a voltage signal. The sample voltage reading is converted to water potential using a calibration equation unique to each psychrometer chamber.

Solute potential is determined by rapid freezing and then thawing leaf tissue to disrupt cells, squeezing the sap onto filter paper disks, and measuring it on a vapor pressure osmometer (Figure 2, right). These instruments are used for juice testing in the food industry, and tissue fluid testing in medical laboratories. The thawed leaf tissue can also be measured after equilibration in a psychrometer. Turgor pressure can be indirectly calculated by subtraction using equation 1, or directly measured with a microscopic pressure probe $^6$. Under extreme stress a leaf or plant becomes severely wilted ($\psi_p=0$), eventually reaching the permanent wilting point. Should the plant then be rehydrated, leaves and branches will not recover, and frequently the stem and meristematic regions die too.

When all leaves of a plant are measured at various times of day, patterns of water potential emerge. Young meristematic tissue has less negative $\psi_l$, expanding leaves have more negative $\psi_l$, and expanded leaves have most
negative $\psi_l$. Leaves with the most transpiration and photosynthesis are likely to be the more negative, and such leaves are fully expanded and situated at the top of the canopy, usually two nodes down from the newest expanded leaf. Root and soil potential are much greater (less negative), being closer to zero. Soil water potential is measured in KPa, being orders of magnitude greater (less negative) than plant water potential (MPa).

When a plant becomes stressed, all $\psi_l$ values become increasingly negative. Values more negative than -20 bar or -2.0 MPa are considered to represent very stressed leaves. If all these measurements are taken at various times during the day, the predawn measurements have $\psi_l$ values which are less negative (from -6 to -2 bar or -0.6 to -0.2 MPa), and as the day progresses the water potential decreases (more negative) as the plant transpires. At mid-afternoon as photosynthesis and transpiration decline, $\psi_l$ increases (becomes less negative). As a plant ages, the upper canopy fully expanded leaves tend to become more negative but never in the ‘stressed’ range of -17 bar to -25 bar if water is plentiful. The major patterns are illustrated in Figure 3.

2. Plant growth

Plant growth is optimized under adequate moisture availability and nutrition, among other factors. Plant growth can be described as a series of additions of plant nodes or phytomers (leaf, petiole or leaf stem, stem internode and one node junction, and its axillary bud), and related to $\Psi_l$. Although $\Psi_l$ itself may not be directly controlling physiological processes, it is a reasonable indirect and quantifiable method of investigating plant response. New phytomers are added to the plant by an apical meristem – an area where cell division and cell organization processes occur. This very new young tissue expands from a small volume to the final expanded organ size through the concerted action of water and increasing complexity of metabolism and cell structure. Cell number potentially limits final organ size, but water allows maximal organ size via cell expansion. Plant growth depends on water, nutrient and sugar availability, whereas growth itself is controlled by plant hormones and is influenced by biotic and abiotic signals. Plant growth therefore directly depends on cell volume and thus on cell turgor pressure.
Figure 3. Comparison of water and solute potential (10 bar = 1.0 MPa) of an irrigated plant (upper panel) and a stressed plant (lower panel) during a two week cycle of drought stress on a cotton crop in southern USA. Measurements were taken on days 1, 4, 7 and 13 from an upper fully expanded leaf from one plant per field plot. Within each panel and measurement day, the difference between osmotic (solute) and water potential is the turgor pressure of the leaf, usually a positive value between 5 bar and 0 bar. The range of values are fairly typical for field crops grown in temperate and subtropical regions.
The traditional view of plant growth linked to turgor pressure describes the change in cell or tissue volume per unit time as a function of cell wall extensibility and turgor pressure. Practically, the Lockhart equation is re-arranged and the tissue growth rate, the change in volume per time (dV/dt), is expressed as the product of cell wall extensibility (m) and the effective turgor (ψp – Y) where ψp is the turgor pressure and Y is the wall yield threshold for irreversible cell extension:

\[
dV/dt = m ( \psi_p - Y )
\]  

[2]

This relationship means that cells require a certain amount of turgor pressure to irreversibly expand, and the greater the ψp, the more the cell expands. As tires or balloon are inflated, they become larger as the inside air pressure is increased. During stress the turgor or pressure potential of plant cells decreases (less positive, approaching zero), but there is only slight deflation in plant cell size – which is in contrast to a flat tire or flat balloon. In the case of plant cells, once expanded the cell walls do not contract to the original pre-inflated state when pressure is lost. Under stress a plant loses water and eventually turgor declines to a point where the expanded leaf becomes floppy and wilted, or flaccid. However, the leaf will retain its original area, not volume, like a deflated air mattress. The cell wall extensibility and the wall yield threshold of expanding tissue can vary depending on tissue type, tissue age, and cell wall characteristics (fiber, cellulose deposition). An additional equation relates the ratio of the change in turgor pressure and water potential to the bulk modulus of elasticity and initial solute potential. This additional equation is used when a plant, organ or cell loses water, and solutes concentrate due to water loss, but no additional solutes are actively produced in the cell cytoplasm (osmotic adjustment does not occur, see section 4 below). Rigid tissue has a bulk modulus of elasticity of more than 6 MPa and a modest ψs of -1.5 MPa, and very young elastic tissue has bulk modulus of elasticity of about 4 MPa and shrinks more at the same ψs.

**Figure 4.** Comparison of irrigated cotton plants in the rear, and shorter water-stressed plants with wilting leaves in the forefront (left). The crop was located in Fayetteville, Arkansas, USA. Note the smaller canopy coverage of the field due to stress compared to complete canopy closure of the irrigated crop behind at the same age. Modest stress and leaf rolling of cotton at early flowering (right).

### 3. Water potential and stress

Field-grown crop plants are often subjected to periods of stress and are rarely grown under optimal conditions (Figure 4). Stress is defined as the action of an external abiotic (light, temperature, water availability etc.) or biotic (bacteria, insect, grazing animal etc.) factor to a plant that reduces or adversely changes growth and development. Drought, or water-deficit stress, is the major type of abiotic stress that reduces crop yield (followed by adverse temperature), and measuring water relations is the direct approach of assessing the impact of stress on crop performance. Plants sense increasing water limitation as the soil dries and water uptake by roots diminishes. As metabolism in plant cells decrease, cells accumulate osmotically compatible solutes in the cytosol, mainly small sugars and amino acids, and some ions. The accumulation of these solutes lowers the solute potential (i.e. ψs becomes more negative) as leaf water potential Ψl.
becomes more negative - thus enabling the plant to maintain a positive turgor pressure ($\psi_p$):

$\Psi_l$ and $\psi_s$ become more negative with stress, but eventually $\psi_p$ decreases to zero.

Example. In well watered conditions, the osmotic potential is lower than water potential, pressure potential is positive, the leaf has turgor and the leaf can expand:

$$\Psi_l = \psi_s + \psi_p$$

$$-1.0 \text{ MPa} = -1.3 \text{ MPa} + 0.3 \text{ MPa}$$

In drought $\Psi_l$ and $\psi_s$ become lower or decrease (more negative), $\psi_p$ also decreases (approaches zero), and in the following example with only 0.05 MPa pressure potential the leaf is not very turgid, but wilting:

$$-1.6 \text{ MPa} = -1.65 \text{ MPa} + 0.05 \text{ MPa}$$

4. Osmotic adjustment

Many plants adapt to a steadily increasing drought conditions by increasing the solute concentration in the cell cytosol. Sugars, organic acids, sugar alcohols, and free amino acids are all solutes that come from suspended carbon and protein metabolism, and ion solutes ($K^+$, $Na^+$, $Cl^-$, $NO_3^-$) are pumped from the vacuole. The aim is to lower (make more negative) $\psi_s$ as $\psi_t$ declines while maintaining cell and cytosol (symplast) volume by maintained turgor $\psi_p$. In plain English, as stress proceeds a plant can maintain its turgidity and avoid wilting by increasing the solutes in the cell cytoplasm. Osmotic adjustment is an active process, meaning that the plant has to expend energy to pump ions or produce these solutes. The use of ions that can be readily pumped back into the vacuole is especially useful to avoid cells bursting in response to rapid rehydration. This mechanism is used in desert plants. Furthermore, the stomata of all leaves control their opening and closing via ion-pumping and turgor pressure. A familiar example of ‘suspended metabolism’ occurs in mature tomato plants that are water stressed for over a week which results in accumulation of solutes in developing fruits. If watered too quickly with too much water, these tomato fruits increase in volume by rehydration due to excessively low (negative) $\psi_s$ and this causes a split of the epidermis (skin). Crops using the mechanism of osmotic adjustment include wheat, cotton, sunflower, sorghum, maize, sugar beet, temperate forage grasses, tropical forage grasses, apple, citrus and grapes. Occasionally, cultivars of some of these crops (e.g. wheat) do not perform osmotic adjustment. Other crop plants, for example soybean, do not perform osmotic adjustment at all. Osmotic adjustment also occurs in reproductive structures and roots of some crops; its purpose in roots is to maintain root growth and water uptake longer in a drying soil.

5. Stomatal conductance

Stomatal conductance ($g_s$) is a measurement of how open the stomata are in a leaf or plant, and infers plant transpiration. Stomata are specialized pores (mouths) in the leaf epidermis or outer layer that open during the day for gas exchange and close during the night. In the older literature, stomatal resistance ($R_s$) was often used, being the reciprocal (1/x) of stomatal conductance, with units of s cm$^{-1}$. The original resistance/conductance terminology and equations were adapted for plant water flow studies from physics and electricity, specifically from electric current and resistors in series or in parallel. Mechanically, a high stomatal conductance value can come from many open stomata per unit leaf area, many small open stomata, or fewer, larger open stomata. The measurement can be made by a mass flow porometer. The mass flow porometer exerts a pressure on a unit area of leaf clamped in a small hand-held chamber and records the pressure loss per unit time (e.g. Delta-T porometer). A rapid decrease in pressure would indicate that many stomata are open, and no decrease in pressure would suggest that the stomata are closed. A more common instrument for measurement of stomatal conductance is a steady state or diffusion porometer, which measures the humidity of air in a flow of gas passed over a unit area of leaf clamped in a small hand-held chamber (e.g. Licor porometer in Figure 5, and newer photosynthetic infrared gas analyzers, such as Licor-6400XT). Here, a greater reading means the stomata are open more, i.e. transpiring more water per unit area of leaf per second. Approximate measurements of stomatal frequency on leaf surfaces can be made by leaf peals. Here the leaf is coated with clear nail polish or a similar polymer,
or even transparent adhesive tape, and the layer is then
stripped off and the number of stomata per unit area is
counted under a microscope at low magnification.
Stomata are quantified as number and degree of
aperture per unit area, but such information does not
quantify transpiration rates.

The number of stomatal pores vary depending on plant
or crop type, with grasses generally having equal
numbers on upper (adaxial) and lower (abaxial) leaf
surfaces, and dicots having more stomata on lower
surfaces than upper surfaces.  Dicot leaves tend to be
positioned horizontally to a soil surface in a canopy, so
having more stomata on the lower surface away from
sunlight is an advantage for controlling transpiration.
In grasses, leaves are positioned at more upright angles
(vertically) so either side of the leaf can be in the
sunlight.  Plants that have evolved in arid, hot or
extremely dry environments have physiological and
anatomical features that place stomata within cripts or
surround them with leaf hairs to minimize
transpirational loss via a small boundary microclimate,
or they modify the timing of stomatal opening to
minimize transpirational loss during the hotter (light)
hours of the day.  When cereal crops, grasses and some
dicots roll their leaves in response to drought stress
(Figure 4), they mitigate the effect of severe water loss
by use of a microclimate within the leaf roll to
minimize further lowering of \( \psi_l \) and to reflect more
heat back to the atmosphere.

The more water a plant transpires through stomata, the
greater is the water demand by the roots in the soil.
The decreasing (more negative) water potential pattern
as the sun approaches its highest point for the day
means a plant increases transpiration as it maximizes
photosynthesis for growth.  During a cycle of drought,
at noon a plant has a high transpiration rate but as the
drought proceeds, at some point during the day the
stomata have to control gas exchange if root water
uptake is insufficient to compensate for transpiration
losses.  As soon as a plant is unable to return \( \psi_l \) during
the night to a predawn point each day, leaf stomatal
conductance will begin to be reduced for several hours
around solar noon.  That said, noon stomatal
conductance readings with hand-held porometers are
relatively fast and easy to take in the field providing
that plants are not extremely water stressed.  Stomatal
conductance is used in screening plants in plant
breeding, and by physiologists interested in drought or
other stress responses.  For crops that maintain
stomatal opening to some extent into a cycle of stress,
cultivars with the greatest yield have been shown to
exhibit greater values of stomatal conductance (e.g.
wheat, pima cotton)\(^2\).  Some crops, such as soybean,
close stomata rapidly in response to stressful
conditions, and cultivars with the highest yields do not
exhibit the same associations between stomatal
conductance and yield.

6. Relative water content
Perhaps the simplest measure of water status, relative
water content (RWC) assesses the amount of water
gravimetrically in a plant or leaf by first cutting the
plant material, weighing it to obtain fresh weight (FW),
rehydrating the material overnight in water for turgid
weight (TW), and then drying the material in an oven for dry weight (DW). RWC is the ratio (in percent) of the plant water present in a leaf (organ) relative to the total water in the rehydrated leaf:

\[
\text{RWC} = 100 \times \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \quad [3]
\]

While RWC gives an overall estimate of water in an organ or plant at the time of sampling, it is also used to correct measurements for osmotic adjustment after a cycle of stress (see Hall² for equations). Relative water content is specific to the plant and experimental conditions, but the range is usually small (between 70 and 85%) during a typical drought cycle. Because RWC is a ratio of water mass in a plant or tissue, this measurement is inferior to water potential because \( \Psi \) is applicable in more relationships, specifically in principles of water flow.

7. Symplastic versus apoplastic water

The plant cytosol is the source of osmotic potential. Plant cell walls and spaces between cells in tissue, as well as vascular tissues outside the phloem, provide another way of water storage and water transport, termed the apoplasm or apoplast (Figure 1). In roots, the apoplast is separated from the symplast to control water and ion uptake by a waterproofing layer containing suberin, termed the casparian strip. With respect to water measurements, the water associated with cell walls is very difficult to displace. However, in freeze-thaw techniques to access cell sap from tissues, cytoplasmic water and apoplastic water are mixed, usually increasing \( \psi_s \) (less negative) by about 15%. Mature tissue that is well irrigated has a greater dilution error, and stressed tissue will have a smaller error¹. Techniques to correct for apoplastic dilution use RWC, or by extrapolation from a pressure-volume curve of leaf water potential.

When grown at low (cold) temperatures, leaf and stem tissues will avoid freezing first by decreasing \( \psi_s \). As cold stress is intensified, plant tissue will first form ice in the apoplast, which is reversible and does not damage tissue on thawing. When symplastic freezing occurs in plant tissue at even lower temperatures, ice crystals form in the cytoplasm and rupture cells and membranes, thus causing irreversible damage. Maple syrup is an example of apoplastic water carrying what used to be symplastic solutes. In the maple tree, sucrose formed in fall is stored in ray cells within the heartwood (xylem tissue), and later actively released into the apoplast and xylem sap in early spring, before leaves are formed. This sugary sap solution is collected in early spring during freeze-thaw cycles, when the tree begins to transport sap across and up the stem prior to growth. Sap can be collected when the ground is still frozen or at temperatures close to 0 °C and roots cannot uptake much soil water - demonstrating the tremendous power of solutes shifted to the apoplasm. A similar observation can be made when a branch is removed from a tree in late winter; in spring the buds break and leaves may even begin to expand due to apoplastic activity, but the partially expanded leaves are not yet photosynthetically active and the branch has no new water supply.

8. Hydraulic conductance

Cell growth is not only related to turgor and tissue extensibility, but also to the supply of water to growing cells⁵,⁶:

\[
\frac{dV}{dt} = L (\psi_x - \psi_l) \quad [4]
\]

where \( L \) is the hydraulic conductivity coefficient (units of \( m^2 \ s^{-1} \ Pa^{-1} \)) of the tissue, \( \psi_x \) is the water potential of the xylem and \( \psi_l \) is the water potential of the expanding region. Equation 2 can also be re-expressed as a water transport equation where \( J_v \) is the volume of water that crosses a cell membrane per unit area (\( m^3 \ m^{-2} \ s^{-1} \) or \( m \ s^{-1} \)), assuming a semi-permeable membrane, so \( J_v \) also equals the term \( L_p (\psi_x - \psi_l) \), where \( L_p \) is the hydraulic conductance (\( m \ s^{-1} \ Pa^{-1} \)). The hydraulic conductivity coefficient \( L \) corresponds to a diffusion coefficient from Fick’s Law. For hydraulic flow through pipes, Poiseuille’s law is used to relate an average flow rate \( J_p \) of sap to the radius of the pipe or conduit. Poiseuille’s equation is:

\[
J_p = (r^2/8 \eta l) \Delta P \quad [5]
\]

where \( r \) is the radius of the pipe or the xylem vessel, \( \eta \) is the dynamic velocity of the fluid or sap (\( 1 \times 10^{-3} \) for water at 20°C, units of \( kg \ m^{-1} \ s^{-1} \) or \( Pa \ s \)), \( l \) is the path length, and \( \Delta P \) is the pressure (or potential) gradient from equation 4. The hydraulic conductance for a capillary, \( L_p \), is therefore \( r^2/8 \eta l \). This simple
term allows calculation and measurement of xylem flows. Calculations of flow velocities in xylem range from 5 to 125 mm s\(^{-1}\) (5 to 125 x 10\(^{-3}\) m s\(^{-1}\)), but in reality measurements of maximum sap flow in trees range from 0.2 to 12 mm s\(^{-1}\), and up to 28 mm s\(^{-1}\) in herbaceous plants (10 mm s\(^{-1}\) is 1 x 10\(^{6}\) m s\(^{-1}\), which is the same as 36 m per hour or about 0.04 km per hour). From pressure probe measurements, \(L_p\) in plant cells ranges from about 1 x 10\(^{-7}\) m s\(^{-1}\) MPa\(^{-1}\) (pea epicotyl, barley root cortex, wheat and maize root cortex, wheat root hairs) to about 1 x 10\(^{6}\) (soybean hypocotyl epidermis), plus or minus an order of magnitude.

Three practical applications of hydraulic conductance are movement of herbicides in the plant xylem stream, measurement of the ascent of sap in long xylem vessel elements and very large stems – tree trunks in orchards and forests, and rationing water in certain crop cultivars by specific root diameters (xylem diameter) to control the pattern of seasonal water use. Xylem consists of vessel elements and tracheids. Xylem vessel elements are found in flowering plants; they vary from several cm to several m in length and are 20 to 500 \(\mu\)m in diameter. Xylem tracheids are single cells found in all vascular plants, they are several mm in length and 15 to 80 \(\mu\)m in diameter. Both types of xylem cells are found in files or stacks of cells in a continuous length. Xylem vessel elements are bigger, lack cell ends, and can be likened to a drinking straw. Presently, the ascent of sap up a plant is explained by the cohesion-tension theory\(^6\). The upward pull of water is generated by leaf transpiration, but water movement in stems is via mostly non-living cells of the xylem (Figure 1). Living cells are used to control transpiration at the stomata level, leaf veins and, indirectly, at various points within the xylem system. Most of the xylem tissue is dead, being heavily reinforced with secondary thickening and lignin, an alcohol polymer. Xylem elements contain pores and pits which have effects on sap flow, and many tiny bubbles on the internal vessel walls have additional impact. Blockage of xylem pores and pits by fungal disease or insects impedes “normal” flow. Water forms a continuous stream from soil (contact with the root hair surface), continuing through the root and stem apoplast, xylem vessels and leaf apoplast, and eventually evaporating from open leaf stomata. Water has high cohesive force and withstands many MPa of tension in the xylem. When water evaporates from a leaf, \(\psi_l\) is lowered (is more negative) which draws water up the plant through the xylem.

In trees, Zimmerman’s group and others have looked at xylem flow, and researchers found that lateral (horizontal) transfer of water can occur in stems, but this transport is complex and shares various vascular bundles to spread risk of blockage but cavitation by air bubbles does occur\(^12\). Measurement of the exact forces within tissues is difficult. Sap movement in large trees starts in the upper parts of a tree in the morning, and the rest of the plant lags behind by several hours\(^6\). Sap velocity tends to be greatest in the most active stem areas – not the heartwood and not the vessels directly adjacent to the phloem. Sap flow rates can be converted to distance per hour, and are between 1 and 15 m per hour in mature trees. Rates can approach 40 m per hour in large and actively growing trees, they are greatest at midday, and slow during rainy cloudy days and at night. The greatest velocities are seen in woody vines. There, water movement is mostly upward, although reverse flux can and does occur, particularly in developing fruit during the night. Stems can also store water temporarily via a storage (capacitance) effect, because transpiration can exceed root uptake by day, and root uptake by night can exceed transpiration (at night stomata shut). Water storage in tissues is important for large plants like trees or for plants adapted to arid environments, but is less important in small plants like crops.

In crops, selection for xylem diameter is a means of improving drought tolerance by changing the rate of flow of water through the plant. For example, germinating wheat seed has seminal (seed) roots with large diameter xylem vessels. For Western Australia, a dry environment with end-of-season drought, xylem vessel diameter was reduced to force the wheat plant to ration water throughout its life cycle so sufficient water would be available for grain filling. A reduction from 65 \(\mu\)m to 55 \(\mu\)m diameter xylem resulted in new ‘narrow’ xylem cultivars that exhibited about a 10% yield increase in drought environments compared to the unimproved wider diameter cultivars\(^9\).

9. A cycle of stress
When rainfall is infrequent crops can experience drought stress. Different plant physiological processes are not equally sensitive to drought stress as was demonstrated by Hsiao\(^3\) in the original units of bar. One of the first signs of a drought-stressed crop is reduced shoot growth and reduced leaf area expansion. As \(\psi_l\) is further decreased from a well irrigated \(\psi_l\)
value (e.g. -12 bar or -1.2 MPa), a range of physiological processes are affected depending on stress intensity (Table 1).

Growth stages are also not equally sensitive to stress. The most sensitive stages to drought stress are germination, development of ovules and pollen, flowering (pollination) and very early fruit growth.

When a crop is exposed to a cycle of drought stress, the impact depends on growth stage and size, plant population density (which determines the overall rate of soil moisture consumption), rooting depth, and soil composition. Sandy soils hold less water than silt loams and clay soils, and greater organic matter in soils increases the water holding capacity. Generally, plant water potential follows a diurnal pattern of decreasing (more negative) potential around solar noon to 3 pm when radiation and temperature are greater, with recovery to the predawn state at night. Each day of successive drought stress leads to a small but steady decrease in potential and recovery to the original predawn state is not achieved. Eventually values of $\psi_l$ decrease to < -16 bar (-1.6 MPa) and the crop closes its stomata to reduce transpiration loss between 11 am and 3 pm. If the drought persists for longer, $\psi_l$ decreases further, stomata remain closed and photosynthesis drops to zero, $\psi_p$ decreases to zero, leaves wilt, and the crop approaches permanent wilting point. Permanent wilting point can be reached within less than a week if a large plant in a small pot is not watered, and within four weeks for a vegetative grain crop in a silt loam or clay soil in field conditions – assuming weather is not excessively hot and windy – which would cause the crop to wilt sooner.

**Table 1.** Relative sensitivity of plant physiological processes to drought stress (after Hsiao). The stress severity was measured as a further lowering of leaf water potential from its well irrigated reference value.

<table>
<thead>
<tr>
<th>Decrease in $\psi_l$ (bar)</th>
<th>Physiological process</th>
<th>Role in the plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.1 to -5</td>
<td>Cell extension growth</td>
<td>Reduced size of new leaves</td>
</tr>
<tr>
<td></td>
<td>Cell wall synthesis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protein synthesis</td>
<td></td>
</tr>
<tr>
<td>-2 to -10</td>
<td>Chlorophyll synthesis and seed germination</td>
<td>Chlorophyll decreased (new leaves more yellow), failure in germination</td>
</tr>
<tr>
<td></td>
<td>Abscisic acid (ABA) biosynthesis</td>
<td>ABA, a plant growth hormone, is induced to regulate stomata pore closure and inhibit certain metabolism</td>
</tr>
<tr>
<td>-4 to -10</td>
<td>Stomatal closure and reduced photosynthesis</td>
<td>Mesophytes (plants requiring frequent water) have reduced transpiration and photosynthesis</td>
</tr>
<tr>
<td>-9 to -23</td>
<td>Stomatal closure and reduced photosynthesis</td>
<td>Xerophytes (arid adapted plants) have reduced transpiration and photosynthesis</td>
</tr>
<tr>
<td>-5 to -16</td>
<td>Respiration associated with growth</td>
<td>Reduced growth</td>
</tr>
<tr>
<td>-6 to -18</td>
<td>Xylem conductance</td>
<td>Reduced flow of water in the xylem</td>
</tr>
<tr>
<td>-8 to -17</td>
<td>Proline accumulation</td>
<td>This amino acid accumulates during stress</td>
</tr>
<tr>
<td>-10 to -18</td>
<td>Sugar accumulation</td>
<td>Reduction in carbohydrate metabolism, accumulation of small sugars and amino acids and ions used in osmotic regulation</td>
</tr>
</tbody>
</table>

**10. Water potential and irrigation scheduling**

Irrigation scheduling is the calculation of how much water to apply to a crop and when to apply it to reduce yield loss from rain deficit. Methods can be divided into soil measurements, plant measurements, and meteorological measurements. Among plant measurements, leaf water potential can be used to...
quantify plant water status and then to irrigate the field back to a pre-stress water potential value to avoid a yield penalty. Even simpler, for vegetative and indeterminate crops, the leaf extension (monocots) or expansion (dicots) growth rate of newly expanding leaves can also be used. All you have to do is measure the leaf expansion rate (or water potential) of a stressed plot compared to the rate or potential in a well-watered plot, or have a well-watered reference value in mind. Current methods in wide use require automation because labor costs are too high to manually monitor plants. Automated plant methods include hydraulic conductance by heat pulse. But measurement of soil water potential remains the most common procedure for irrigation scheduling. Soil tensiometers are inserted into the soil profile to a specified rooting depth and the moisture potential of the soil recorded for a crop under well-watered conditions. As drought proceeds the soil dries, becoming progressively drier at depth. When the tensiometer records a pre-set low potential (more negative), the soil is dry and irrigation is applied until the reading increases (less negative) to the pre-set well-watered condition. The method can be refined by positioning two sets of tensiometers, with one set closer to the soil surface and the other at a deeper rooting depth. However, a soil tensiometer reading is only as reliable as its positioning and contact with the soil, whereas measuring $\psi_l$ of a leaf/plant can indicate actual plant water status.

11. Summary
Water is vital for plant growth and development. The water status of plants is quantified using the concept of water potential, a negative number with units of pressure (bar or MPa). Quantification of water potential allows assessment of water within the soil-plant-atmosphere continuum, because water is pulled through a plant by evaporative demand and water within a plant is held under tension. When solutes (ions, salts, sugars, amino acids) are added to free water or cell cytoplasm, the potential decreases or becomes more negative. The turgor pressure of a plant is usually a positive number, and the solute potential is smaller or more negative than water potential. As a plant becomes more stressed both its solute and water potential become more negative. Plants can use solutes and stomatal opening/closure to control turgor of leaves. As a plant loses water at a greater rate than replenishment or rehydration by root water uptake at night, leaves lose turgor until the plant wilts. Water potential can be used to monitor plant growth and development in response to a drought stress, and to schedule irrigation. Other aspects of water movement in a plant can be described by physical relationships related to water potential, such as drought adaption by osmotic adjustment, apoplastic versus symplastic movement, the ascent of sap up a plant or tree in xylem tissue, and loss of transpired water from leaves through stomata.

References
6. Kramer, P.J., and Boyer, J.S. 1995. Water relations of plants and soils. Academic Press, San Diego, CA. 495 pages. [This is the most prominent text on water relations written at the undergraduate level and targeted to a wide scientific audience]