Cell and Plant Water Relations

Chapters 3 and 4

Availability of water is the factor that most strongly restricts plant production on a global scale.

![Graph of crop yield vs. crop water use]

![Graph of productivity vs. annual precipitation]
Plant cells build up large intracellular pressure (turgor pressure) as a result of their normal water balance. Turgor pressure is essential for cell enlargement, gas exchange in leaves, transport in the phloem, and transport processes in membranes.

Plants use a tremendous amount of water. ~97% of the water absorbed by roots is carried through the plant and evaporates from leaves (transpiration).

Only ~3% of water absorbed by roots is retained in the plant for growth biochemical reactions.

Inefficient use of water is an unavoidable result of photosynthesis. Open stomata, which allow CO₂ to enter the leaf, provide a pathway for water loss.
The Role of Water in Plant Physiology

• Water is the medium that transports metabolites into the cell.
• Water is the medium that transports carbohydrates, nutrients and hormones from one plant organ to another.
• Water provides hydraulic support to the plant.
• Water provides evaporative cooling.

Properties of Water
Water is an excellent solvent. Why?

Water has a high specific heat. What are the implications of this?
Water has a high latent heat of vaporization (44 kJ mol⁻¹ specific heat for water at 25°C), the highest of any liquid. This is the energy needed to separate molecules from the liquid phase and move them into the vapor phase. Most of this energy is used to break hydrogen bonds.

Why is it called latent heat?

What are the implications of high latent heat of vaporization for plants?

Water molecules are highly cohesive because of mutual attraction between molecules via hydrogen bonding.

Water molecules adhere (are adsorbed) to surfaces such as cell walls and soil particles due to formation of hydrogen bonds.

Cohesion, adhesion, and surface tension lead to capillarity.
Water has a high tensile strength. What are the implications of this for plants?

Fick’s Law and Diffusion

\[ J_s = -\frac{D_s}{\Delta x} \frac{\Delta c_s}{\Delta x} \]

where \( D_s \) is the diffusion coefficient that measures how easily substance \( s \) moves through the medium, \( \Delta c_s/\Delta x \) is the concentration gradient (difference in concentration between two points separated by distance \( \Delta x \)). \( D_s \) increases with temperature, and is greater for small molecules than large molecules.

What happens to \( J_s \) when the concentration difference increases?

What happens to \( J_s \) when the path length (\( \Delta x \)) increases?
What happens to $J_s$ when the size of the molecule increases (e.g. CO$_2$ vs H$_2$O)?

What happens to $J_s$ when temperature increases?

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**Water Potential**

The free energy in water that is available to do work is described by *water potential*. By definition, water potential is the chemical potential of water (J mol$^{-1}$) by the partial molal volume of water ($18 \times 10^{-5}$ m$^3$ mol$^{-1}$).

What are the units of water potential?

For water, 1 J m$^{-3}$ = 1 Pa.
Water potential is defined in relation to a reference state, which is pure water at ambient temperature and atmospheric pressure.

KEY POINT:
If the free energy of the water is lower than that of the reference state, $\Psi$ is negative. If the free energy of the water is higher than that of the reference state, $\Psi$ is positive.

Note: The more negative the $\Psi$, the lower is the water potential. -1 MPa < -0.8 MPa

KEY POINT:
Water in plants and soil moves in response to differences in water potential ($\Psi_w$).
The factors (forces) that influence water potential are solute concentration, pressure, and gravity, so that

$$\Psi_w = \Psi_s + \Psi_p + \Psi_g$$

**Osmotic (solute) potential** ($\Psi_s$) is the potential of the water component of a solution containing solutes.

Solute concentration reduces free energy by diluting the water. Mixing of solutes and water increases entropy.

For an ideal solution,

$$\Psi'_s = -RTc_s$$

where $R$ is the gas constant ($8.32$ J mol$^{-1}$ K$^{-1}$), $T$ is temperature (K), and $c_s$ is solute concentration (moles of dissolved solutes per L of water).

What happens to $\Psi_s$ when $T$ and $c_s$ increase?
Pressure potential ($\psi_p$) refers to the hydrostatic pressure of the solution, and it can be positive or negative. Positive pressure raises the water potential, negative pressures reduce it.

Water inside turgid cells is under a positive hydrostatic pressure (turgor) exerted by the cell walls.

Water in xylem of transpiring plants is under tension, and its $\psi_p$ is negative.

Pressure potential includes the force with which water is adsorbed onto surfaces such as cell walls and soil particles. Adsorption lowers the water potential below that of pure water. This force becomes stronger as the adsorbed water film becomes thinner.

In some texts, this component of pressure potential is treated separately as matric potential.
**Gravitational potential** ($\Psi_g$) depends on the height ($h$) of the water above the reference-state water, the density of water ($\rho_w$) and acceleration due to gravity ($g$), so that

$$\Psi_g = \rho_wgh.$$  

A vertical distance of 10 m produces a 0.1 MPa change in water potential.

**Cell Water Relations**

**KEY POINTS:**

Water moves into and out of cells, through the plasma membrane, in response to water potential gradients.

The plasma membrane is semi-permeable, allowing free movement of water through it, but restricting movement of solutes (e.g. water moves through membrane, but solutes are retained inside the membrane).
KEY POINTS:

Water flow is a passive process. There are no pumps that drive water across membranes against free energy gradients.
What happens to $\Psi_s$, $\Psi_p$, and $\Psi_w$ when water is lost from the cell?

What happens to $\Psi_s$, $\Psi_p$, and $\Psi_w$ when water enters the cell?

Solute concentration (metabolites, inorganic salts and macromolecules) in the symplast is high so that $\Psi_s$ is low, typically ranging from -1 to -2 MPa.

The cell wall exerts a positive hydrostatic pressure (turgor) on water in the symplast, so that $\Psi_p$ is positive.
Solute concentration in the apoplast is low so that $\Psi_s$ is high (-0.1 MPa).

$\Psi_p$ in the apoplast is low because water in the xylem is under tension, and can reach values as low as -5 MPa in severely stressed desert plants.

To summarize, $\Psi_w$ in the symplast consists of a low (more negative) $\Psi_s$ and a high, positive $\Psi_p$.

$\Psi_w$ in the apoplast consists of a high (less negative) $\Psi_s$ and a low (more negative) $\Psi_p$.

At equilibrium, the total water potential of the symplast ($\Psi_{w,s}$) equals that of the apoplast ($\Psi_{w,a}$). Thus,

$$\Psi_{w,s} = \Psi_{w,a}$$

or

$$\Psi_{p,s} + \Psi_{s,s} = \Psi_{p,a} + \Psi_{s,a}.$$
If the total water potential in the symplast is -0.7 MPa, and the osmotic potential is -1.4 MPa, what is the turgor pressure?

KEY POINT:

If total water potential of the apoplast is less than that of the symplast, water will flow through the plasma membrane into the cell wall and xylem. This is what happens in actively transpiring plants.
**KEY POINT:**

Plants can accumulate solutes to lower $\Psi_s$ and $\Psi_w$ by taking up ions from the soil, or transporting ions from other plant organs to the root. This **osmotic adjustment** maintains water potential gradients between plant and soil, so that plants can continue to take up water as the soil dries.

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**Ions accumulate in vacuoles.**

**Diagram:**

- (A) External $\Psi_w = -0.6$ MPa
- (B) External $\Psi_w = -3.8$ MPa

Compatible solutes accumulate in the cytosol to maintain water potential equilibrium.

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**Physiological changes due to dehydration:**

- Abiotic acid accumulation
- Solute accumulation
- Photosynthesis
- Stomatal conductance
- Protein synthesis
- Wall synthesis
- Cell expansion

**Diagram:**

- Pure water
- Well-watered plants
- Plants under mild water stress
- Plants in arid, desert climates

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Water Balance of Plants

Transpiration
KEY POINT:

The driving force for transpiration (diffusion of water vapor from leaf interior to the atmosphere) is the difference in water vapor concentration between the leaf interior ($c_{wv(leaf)}$) and the external bulk air ($c_{wv(air)}$).

\[
E \ (\text{mol m}^{-2} \text{ s}^{-1}) = \frac{c_{wv(leaf)} - c_{wv(air)}}{r_s + r_b}
\]

where $r_s$ and $r_b$ are stomatal and boundary layer resistances (s m$^{-1}$) and water vapor concentrations are expressed as mol m$^{-3}$.
E (mol m\(^{-2}\) s\(^{-1}\)) = \frac{c_{\text{wv\(\text{(leaf)})}} - c_{\text{wv\(\text{(air)})}}}{r_s + r_b}

What happens to E when leaf temperature increases?

What happens to E when water vapor concentration of the air increases?

What happens to E when either stomatal or boundary layer resistance increases?

What happens to E when wind speed increases?
KEY POINT:

Evaporation at cell wall – air interfaces generates negative pressures (tension) in the xylem. This creates the water potential gradient that causes water to flow from soil to leaf.
KEY POINT:

Evaporation, and thus transpiration, does not require input of metabolic energy.

What provides the energy for evaporation?

What controls the amount of energy that is available to evaporate water?

Ascent of Sap
KEY POINT:

Tension (negative $\Psi_p$) "pulls" liquid water (sap) through the xylem.

Why isn’t osmotic potential a factor in this process?

Poiseuille’s Law

$$ J \left( m^3 s^{-1} \right) = \left( \frac{r^4}{8\eta} \right) \frac{\Delta \Psi_p}{\Delta x} $$

where $r$ is the radius of the tube, $\eta$ is viscosity, and $\Delta \Psi_p/\Delta x$ is the pressure gradient.

What happens to volume rate of flow when the radius of the xylem is doubled?

What happens to volume rate of flow when the water potential gradient increases.
where $L_p$ (m$^3$ s$^{-1}$ MPa$^{-1}$) is the hydraulic conductivity of the plant.

If tension in the xylem gets too high ($\Psi_p$ gets too low), formation and expansion of gas bubbles (cavitation) can occur.

Is cavitation more likely to occur in large-diameter xylem, or small-diameter xylem?

What are the implications of this for water uptake from dry soil?
Parallel pathways allow cavitated xylem to be bypassed.

**Water Uptake**

**KEY POINT:**

Water enters the root when $\Psi_{w,root} < \Psi_{w,soil}$.

Water can flow from root to soil if $\Psi_{w,root} > \Psi_{w,soil}$.
KEY POINTS:
The Casparian strip blocks the apoplastic pathway, forcing water and solutes through plasma membranes to cross the endodermis.

Root permeability depends strongly on the presence of aquaporins.

KEY POINTS:
When transpiration is low and soil water potential is high, absorption of ions from the soil and transport to the xylem can produce a positive $\Psi_p$ (root pressure) in the xylem.

How does an increase in ion concentration produce a positive hydrostatic pressure?
Example of guttation

Water Flow in Soil

\[ J \, (m^3 \, s^{-1}) = -K \frac{\Delta \Psi_{\text{soil}}}{\Delta x} \]

where \( \Psi_w = \Psi_p + \Psi_g \), and \( K \) is hydraulic conductivity of the soil.
KEY POINT:

Water is held in the soil by capillary and adsorptive forces. As soil dries, water is removed first from the largest spaces between soil particles, and then from successively smaller spaces.
KEY POINT:

As roots absorb water from the soil, they deplete water near the root surface. This creates a gradient in water potential that causes water to flow toward the root.

Stomatal Regulation
The stomatal pore becomes wider when guard cells take up solutes and water, and swell. This requires massive transport of solutes across the plasma membrane of guard cells.

Guard cells have turgor superiority over adjacent (subsidiary) cells.
The major ion that is transported into the cells is K+. Ion-selective channels play a role in the transport of K+. These channels are open only when the membrane potential is very negative. This results from activation of an H+-pumping ATPase in the plasma-lemma of guard cells.

When these channels are open, K+ is transported from adjacent cells into guard cells. This reduces $\Psi_s$, and water flows into the guard cells, increasing turgor pressure.
Stomata close in response to water deficit. This protects the plant against immediate dessication.

When soil water deficits develop, roots send a signal to the guard cells in the form of ABA.

Three things happen when water deficits develop. When the mesophyll becomes mildly dehydrated, some of the abscisic acid (ABA) stored in chloroplasts is released to the apoplast. This redistribution of ABA results in transport of some of the ABA to guard cells via the transpiration stream.

ABA is also synthesized at a higher rate when water deficits develop. This enhances or prolongs the initial closure caused by stored ABA.

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Perception of ABA by a receptor (R) at the guard cells results in an increase in cytosolic free Ca\(^{2+}\) by influx through Ca\(^{2+}\) channels and release from internal stores.

Increased free Ca\(^{2+}\) promotes opening of anion and K\(^{+}\)\textsubscript{out} channels and inhibits opening of K\(^{+}\)\textsubscript{in} channels. Anions and K\(^{+}\) move from guard cells to subsidiary cells, resulting in an increase in Ψ\(s\) and loss of water and turgor in guard cells. Guard cells become flaccid and cover the stomatal opening.

Stomata also respond to CO\(_2\). Stomatal aperture decreases as CO\(_2\) concentration increases.