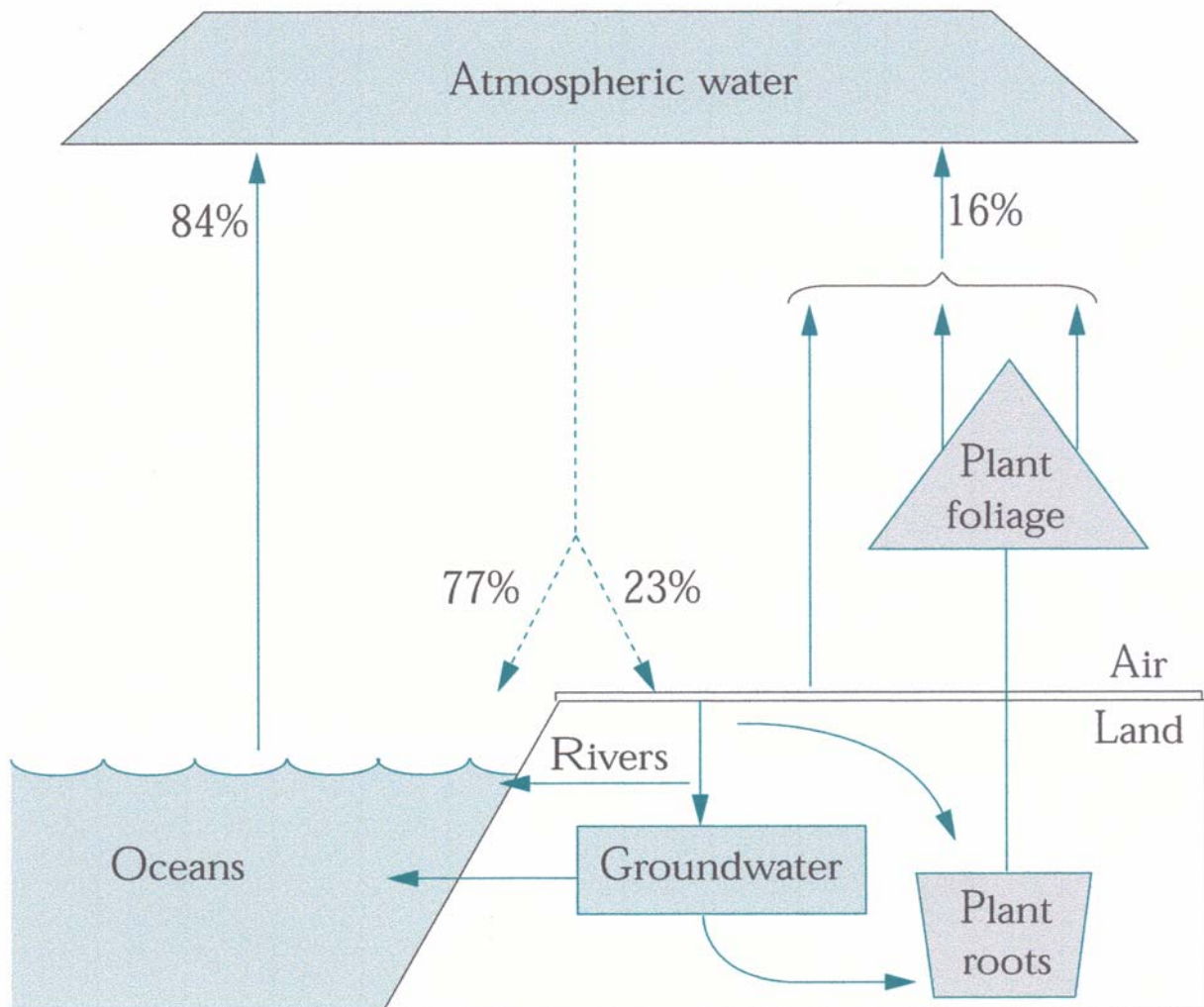


WATER

- water in the biosphere
- water in the landscape
- water in the soil
- water in the plant



(Atwell, Kriedemann & Turnbull 1999)

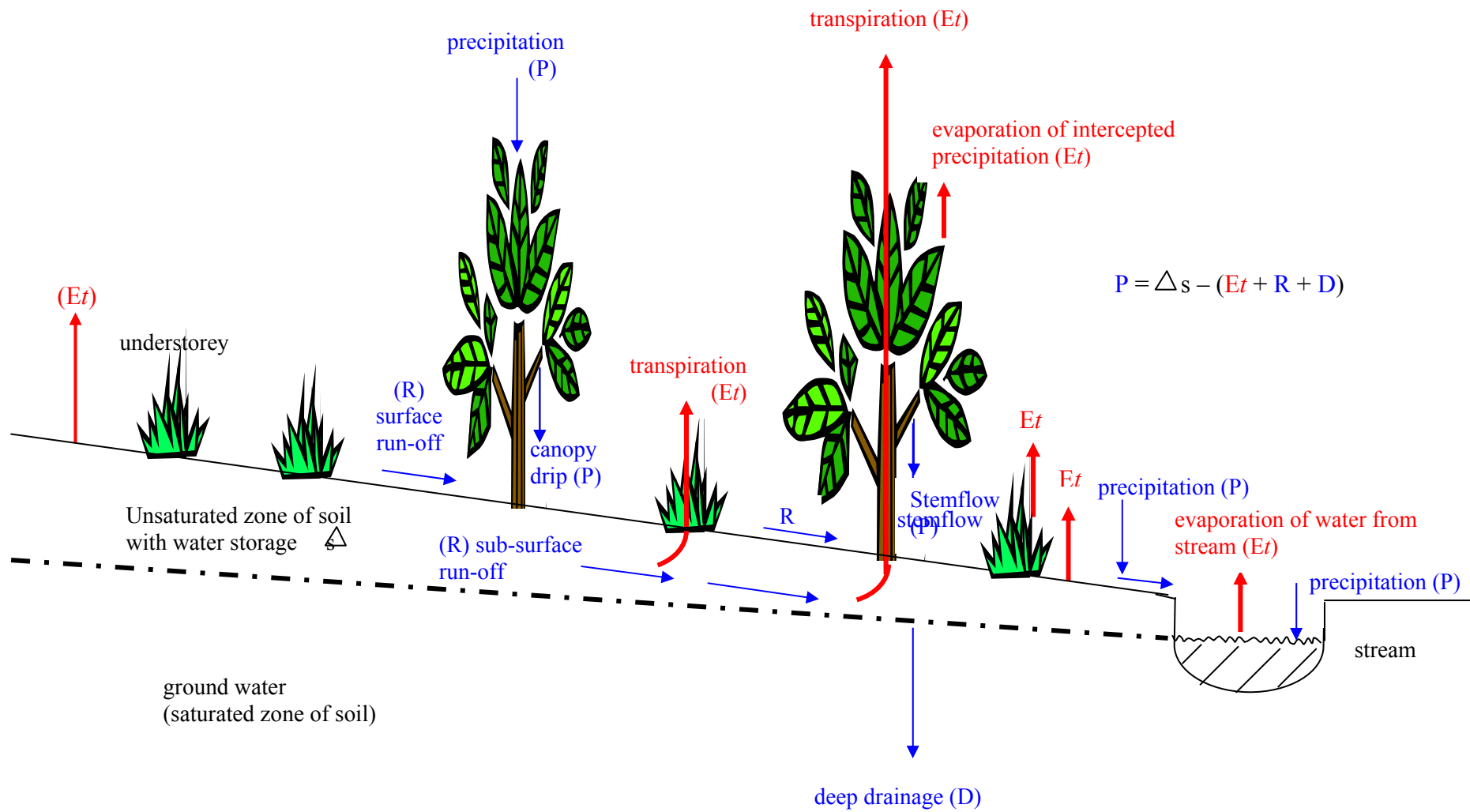


Figure 3.2

hydrologic cycle

$$\Delta S = P - (E_t + R + D)$$

where

ΔS = soil storage

P = precipitation

E_t = evapotranspiration

R = runoff (surface and subsurface)

D = deep drainage

water in the soil (ΔS)

coarse soils (sands) contain relatively less water and more air.

fine soils (eg clays) contain relatively more water and less air.

medium textured soils (eg loams) have sufficient water and air and are optimal for growth.

water in freely draining soils is held in tension in the soil pores.

the water potential of the soil represents the energy required to release the water from this tension.

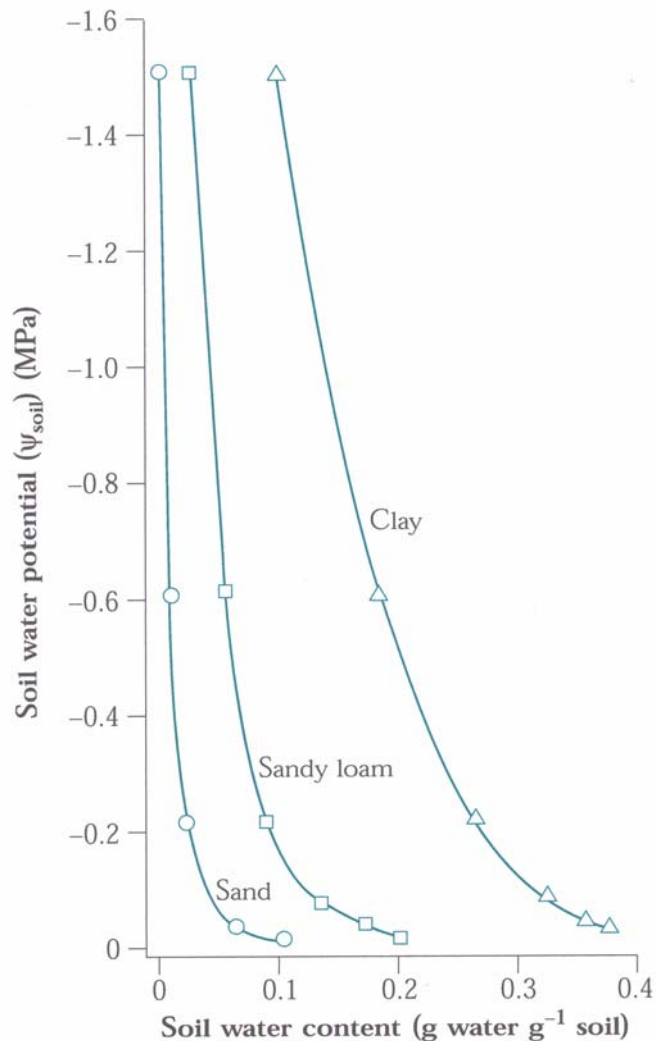
the water content when the soil is full of water after drainage is *field capacity*.

the water content when the water is held too tightly for plants to extract it is called the *wilting point*.

Table 15.1 Variation in soil water holding capacity according to texture. Field capacity represents water held against gravity after the excess has drained, and wilting point represents the stage where a transpiring plant cannot generate a sufficiently low water potential to extract further moisture (commonly regarded as equivalent to a soil water potential of about -1.5 MPa)

Soil texture	Water held (mm per metre depth of soil)		
	Field capacity	Wilting point	Plant-available moisture
Sand	90	20	70
Sandy loam	230	90	140
Loam	340	120	220
Clay loam	300	160	140
Clay (well structured)	500	300	200

(Derived from various sources including Handreck 1979)



(Atwell, Kriedemann & Turnbull 1999)

water in plants

- **properties of water**
- **importance of water**
- **water contents**
- **water movement**
- **water stress**

properties of water

- **high specific gravity**
- **high specific heat**
- **high heat of vaporisation**
- **high heat of fusion**
- **large cohesive forces between molecules**
- **H-bonding capacity**

importance of water

- **reactant in photosynthesis (and other reactions)**
- **medium in which most metabolic reactions occur**
- **provides the hydrostatic pressure for cell enlargement**
- **major constituent of protoplasm and required for structural integrity**

water contents

- **> 500% in leaves and herbaceous tissue**
- **50-200% in sapwood**
- **30 –0 100% in heartwood**
- **<5% in seeds**
- **water potential is more important than water content when considering water movement in plants**

water potential

- **represents the amount of work done on or by the water to bring it to the condition of pure water at atmospheric pressure and at the same temperature (measured in units of energy or pressure)**

$$\Psi = \psi_p + \psi_\pi + \psi_m + \psi_z$$

where

Ψ = total water potential

ψ_p = pressure potential

ψ_π = osmotic potential

ψ_m = matric potential

ψ_z = gravitational potential

- **value for all components are negative or zero except for ψ_p and ψ_z which may sometimes be positive**

total water potential (ψ)

- **decreases as soil water potential decreases**
- **varies diurnally and seasonally**
- **gradient from less negative in the roots to more negative in the leaves**

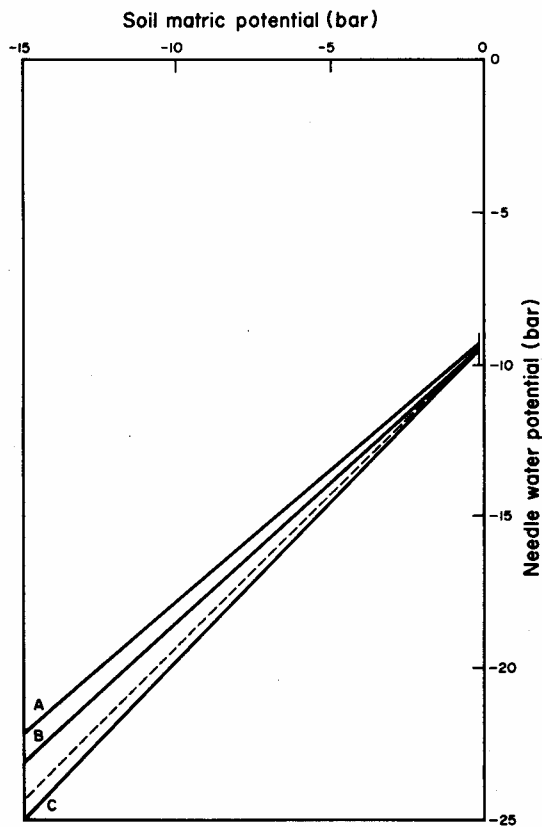
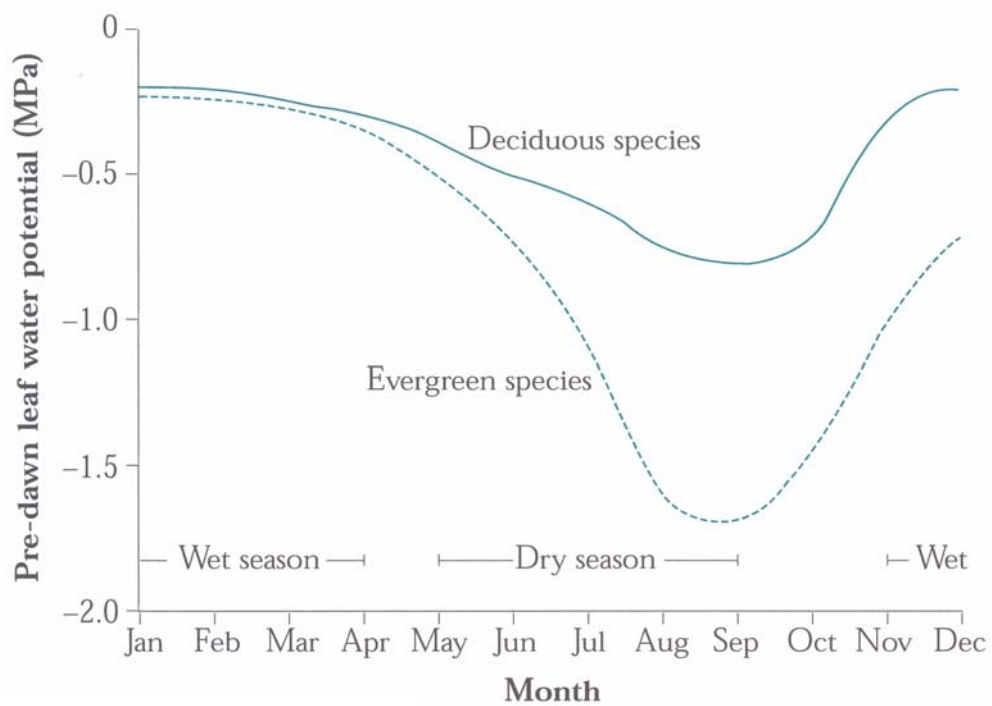


Fig. 1. Linear regressions of Ψ_n on Ψ_s for radiata pine seedlings from families A, B and C. Each family line represents the mean of slopes and intercepts for twelve replicate trees per family. Differences in slope and intercept between families are not significant. The dotted line represents a constant potential gradient $\Psi_n - \Psi_s$ of -9 bar as Ψ_s decreases.

From: Sands, Kriedemann & Cotterill, (1984)



(Atwell, Kriedemann & Turnbull 1999)

pressure potential ψ_p

- is negative in the cell walls (apoplast) but positive inside the plasmalemma membrane where it is called turgor pressure
- is the hydrostatic pressure within cells exerted on cell walls that is associated with cell enlargement
- in turgid plants ψ_p is about 0.5 to 1.5 MPa; in wilting leaves it is 0 to 0.2 MPa

osmotic potential ψ_π

- is important in plants because the plasmalemma membrane is a semipermeable membrane
- when ψ is reduced, plants can reduce ψ_p (osmotic adjustment) by generating solutes inside the plasmalemma membrane
- the effect of osmoregulation is to reduce the decrease in ψ_p that occurs when ψ is decreased

ψ_π depends on the concentration of solutes

$$\psi_\pi = -miRT$$

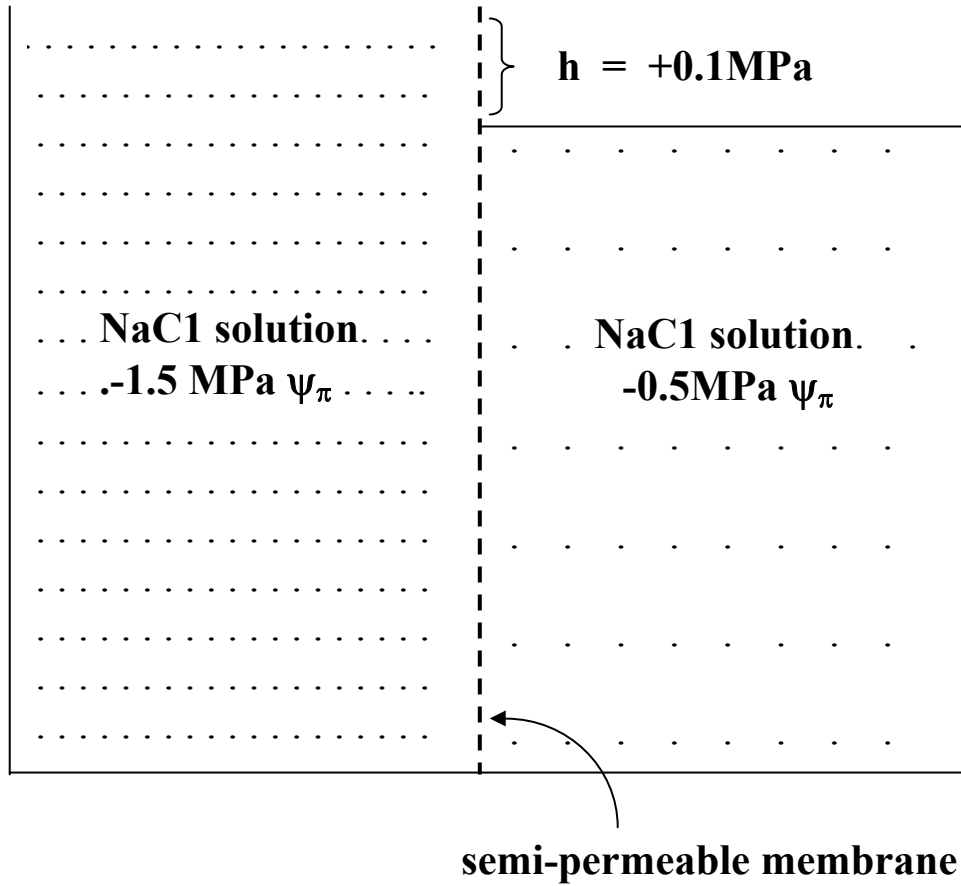
where

m = molality

i = ionisation constant

R = gas constant

T = absolute temperature



plasmalemma

**cell wall
(apoplast)**

$$\psi_{\pi} = -1.0 \text{ MPa}$$

$$\psi_{\pi} = 0$$

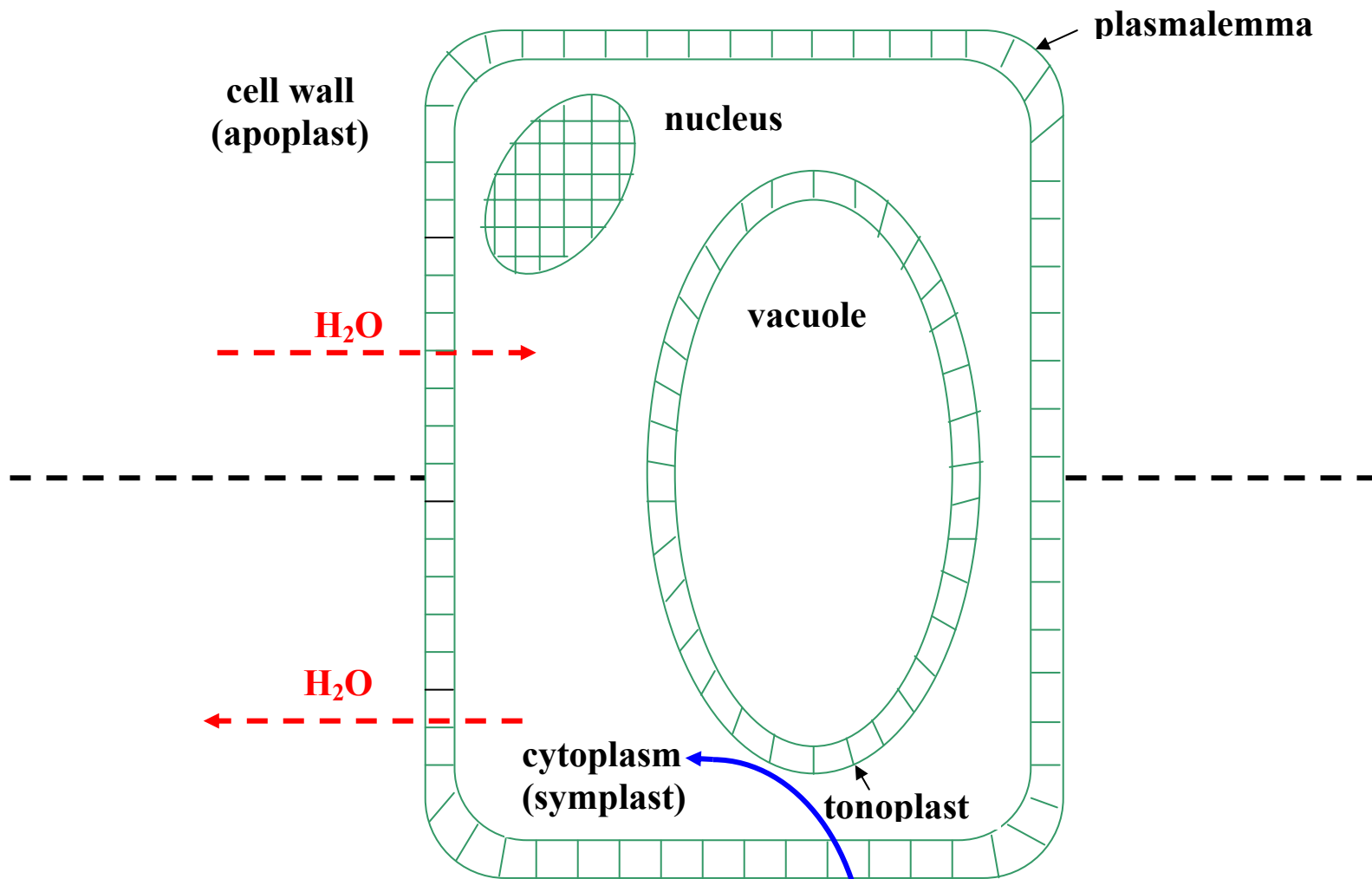
$$\psi_{\pi} = -1.0 \text{ MPa}$$

**protoplasm
(symplast)**

$$\psi_{\pi} = -1.0 \text{ MPa}$$

$$\psi_{\pi} = -2.0 \text{ MPa}$$

$$\psi_{\pi} = +1.0 \text{ MPa}$$

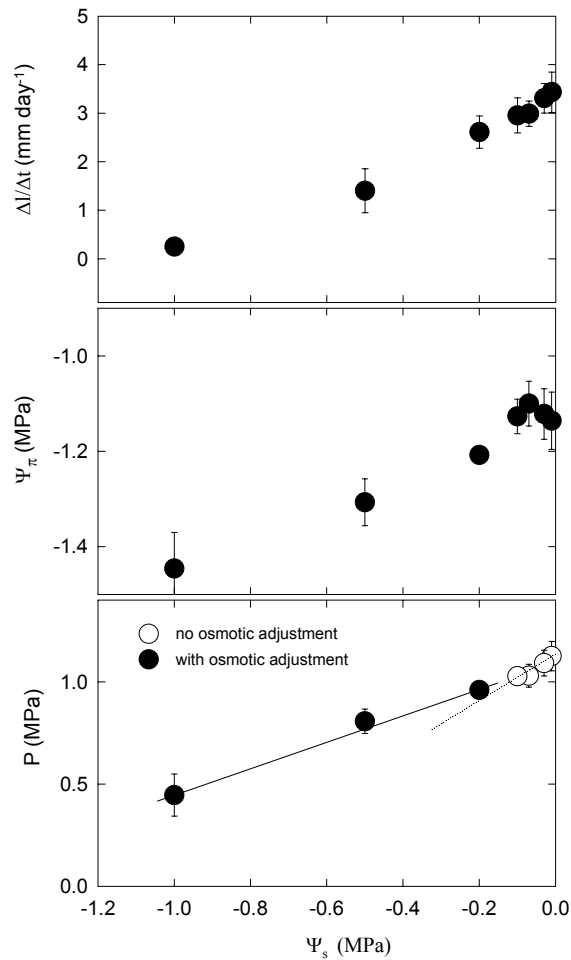


$$\Psi = -1.0 \text{ MPa}$$

$$\left[\begin{array}{l} \Psi_{\pi} = -2.0 \text{ MPa} \\ \Psi_p = +1.0 \text{ MPa} \end{array} \right]$$

midday leaf water potentials in MPa

	<i>wet soil</i>	<i>dry soil</i>
- osmoregulation		
Ψ	-0.5	-1.0
Ψ_p	+1.0	+0.5
Ψ_π	-1.5	-1.5
+ osmoregulation		
Ψ	-0.5	-1.0
Ψ_p	+1.0	+ 0.8
Ψ_π	-1.5	-1.8



From: Sands & Sun, (2000)

MOVEMENT OF WATER IN TREES

water moves along gradients in water potential ($\Delta\Psi$) from less negative (wetter) to more negative (drier).

- (a) *transpiration*
(evaporation of water from leaves into the atmosphere)

- (b) *ascent of sap*
(movement of water from roots to leaves)

- (c) *water uptake by roots*

transpiration

occurs due to gradients from leaf to air in

- water potential
- relative humidity
- vapour pressure

leaf

$$\Psi = -2.8 \text{ MPa}$$

$$\text{RH} = 98\%$$

atmosphere

$$\Psi = -95 \text{ MPa}$$

$$\text{RH} = 50\%$$

gradient

$$\Delta\Psi = -92 \text{ MPa}$$

$$\text{RH} = 48\%$$

gradients are steep and the area available for evaporation is enormous

$$A_s > A_l > A_g$$

where

A_s = surface area of stomata

A_l = surface area of leaf

A_g = surface area of ground

stomata

stomata provide a variable conductance (1/resistance) in the pathway which can modify transpiration

evaporation of water from the walls of the stomatal cavities (transpiration) reduces the water potential of the leaves

water moves to the leaves from below in response to this gradient

this lowering of water potential is transmitted through the plant to provide a continuous gradient in water potential ($\Delta\Psi$) for water movement

freely transpiring plants may transpire more than their volume in a day

99% of absorbed water may be transpired and 1% kept in the plant

transpired water is about 1000 times carbon dioxide uptake

large amounts of water are required to produce biomass

stomata are required to let in carbon dioxide for photosynthesis

transpiration is an inevitable consequence of this

is transpiration useless, an unavoidable consequence of the need for a pathway for carbon dioxide into the leaf?

uses of transpiration

- mineral transport
- leaf cooling
- providing the gradients for the ascent of sap

$$Tr = C_p \rho_a D g / \gamma \lambda$$

where

Tr	=	transpiration
C _p	=	specific heat of dry air at density ρ _a
D	=	vapour pressure deficit
g	=	canopy conductance
γ	=	latent heat of vaporisation of water
λ	=	psychrometric constant

transpiration

depends on

- radiation
- temperature
- relative humidity
- factors affecting conductance
 - radiation
 - temperature
 - relative humidity
 - soil water status
 - wind
 - canopy configuration
 - leaf shape

radiation

stomata close at night and transpiration becomes very small

radiation also determines ambient and leaf temperatures

temperature and relative humidity

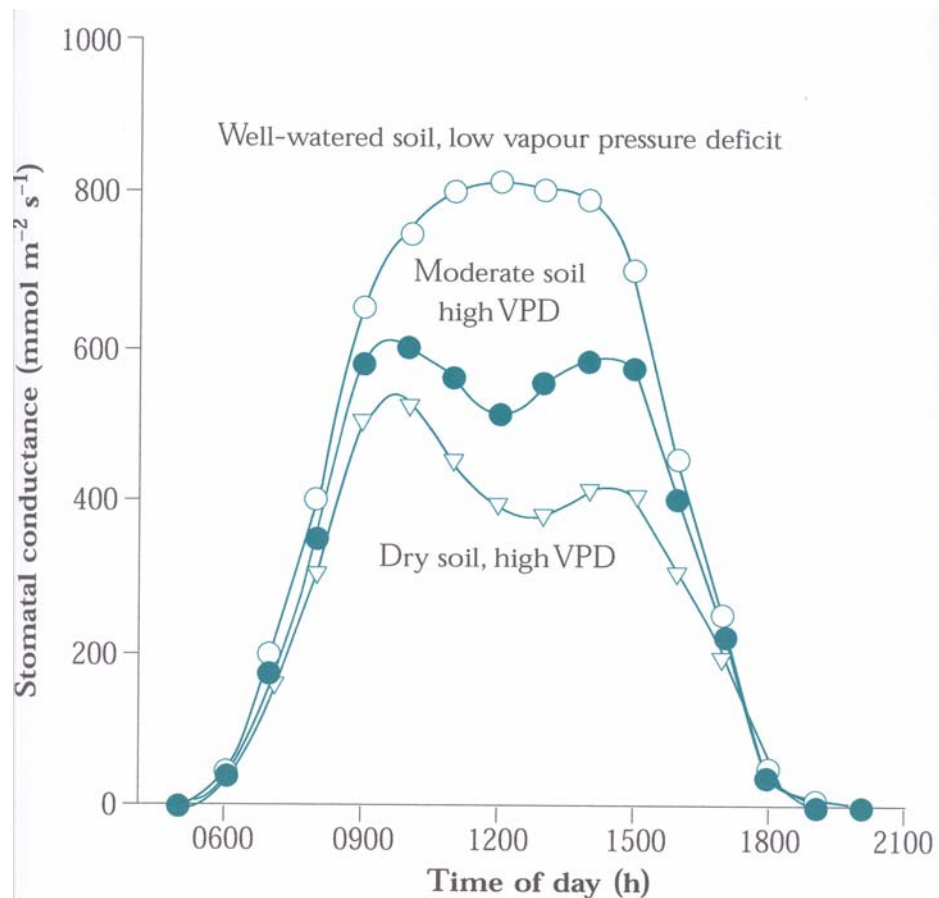
together determine VPD

at high temperatures and/or low RH, Tr is increased

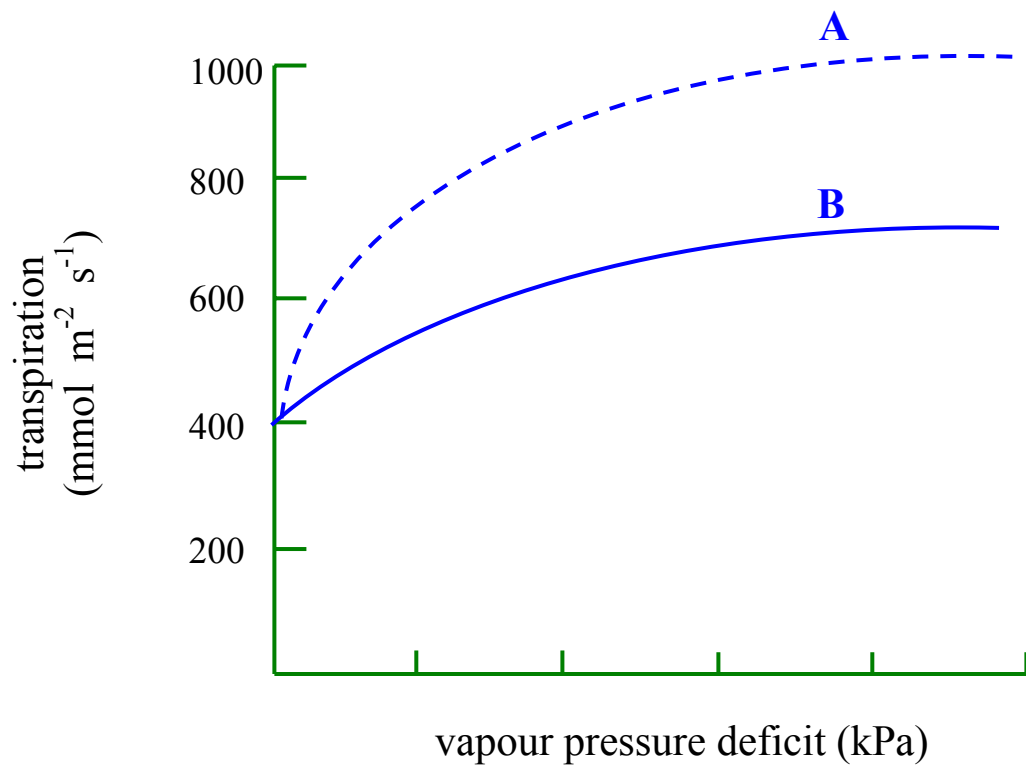
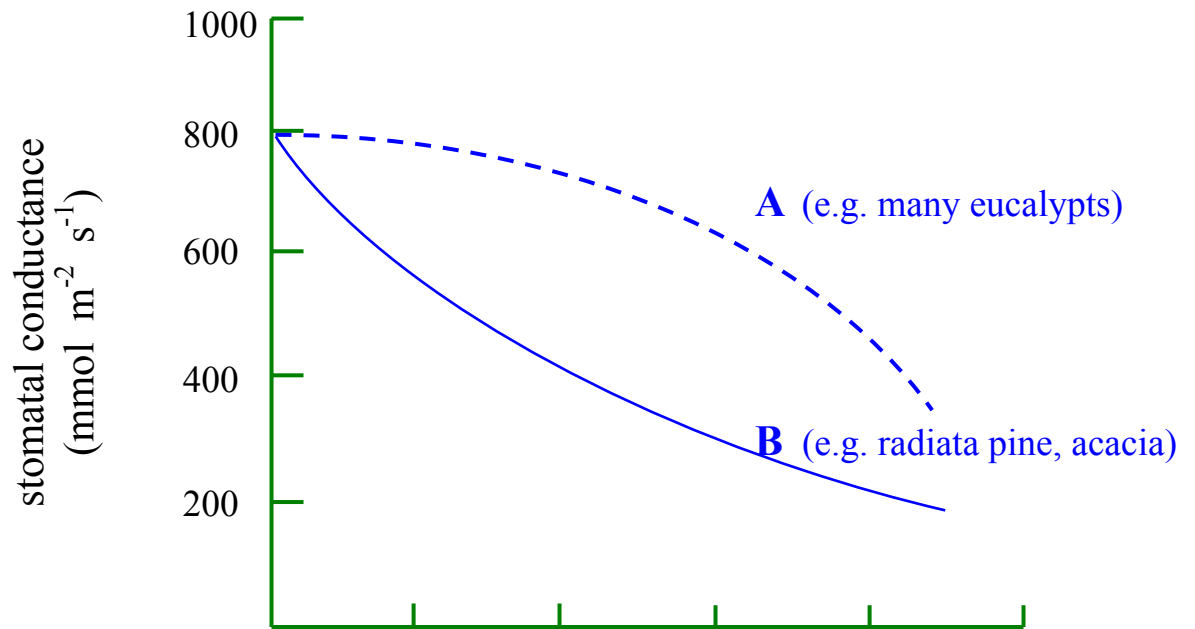
but also

g is reduced and transpiration is decreased

the end result will be a compromise between the two



(Atwell, Kriedemann & Turnbull 1999)



soil water

shortage of soil water will reduce g (close stomata) which will reduce Tr

wind

increased wind will increase g by increasing boundary layer conductance and therefore Tr

canopy configuration

canopy configuration determines the amount of radiation and temperature at leaf surfaces

leaf shape and surface characteristics

small and deeply dissected leaves have greater boundary layer conductances and therefore greater g and greater Tr

ascent of sap

in forest trees water may move a vertical distance of over 100 metres

the pressure or suction to do this (allowing for resistance) is about 2MPa

is it pressure or suction or a combination of both ?

suction (tension)

water is under tension in plants and there are gradients of Ψ (> 2 MPa) sufficient to lift water to the top of the tallest tree

this is the cohesion theory of Dixon (1914)

for the cohesion theory to be credible it must be shown that:

- **water can exist as a liquid when under tension (it can)**
- **water has sufficient tensile strength to withstand the large tensions involved (it does)**
- **mechanisms exist to avoid catastrophic cavitation (they do)**

pressure

- **atmospheric pressure can support a water column of 0.1MPa only**
- **root pressures are about 0.1 to 0.2 MPa**
- **some evidence that companion cells associated with tracheids and vessels can also contribute to pressure**

there is still considerable controversy about the relative merits of suction (cohesion theory) versus pressure (compensating pressure theory).

probably both suction and pressure contribute with suction accounting for most of the water transpired and pressure contributing relatively less but still necessary to rehydrate tissues at night.

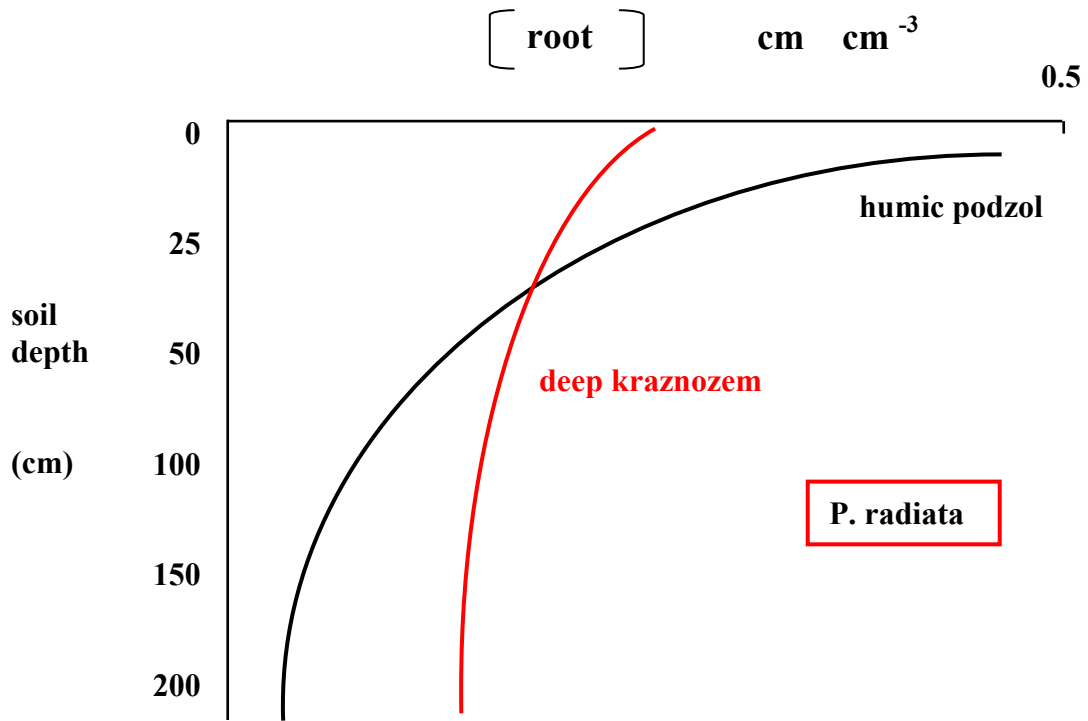
(see American Scientist 86: 214 (1998) for a discussion of the conflict)

water uptake by roots

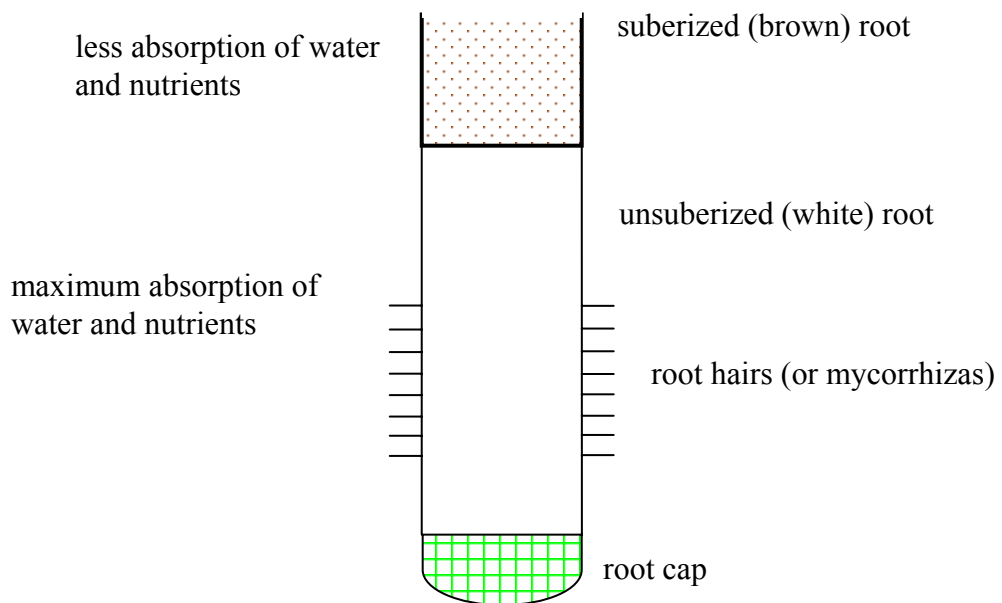
root systems may be large and deep and use up to 70% of assimilate

most roots are concentrated near the surface and most uptake of water (and nutrients) occurs in the white (non-suberised) zone near the root tip

this white root contains an endodermis which is important in controlling the uptake of water and nutrients



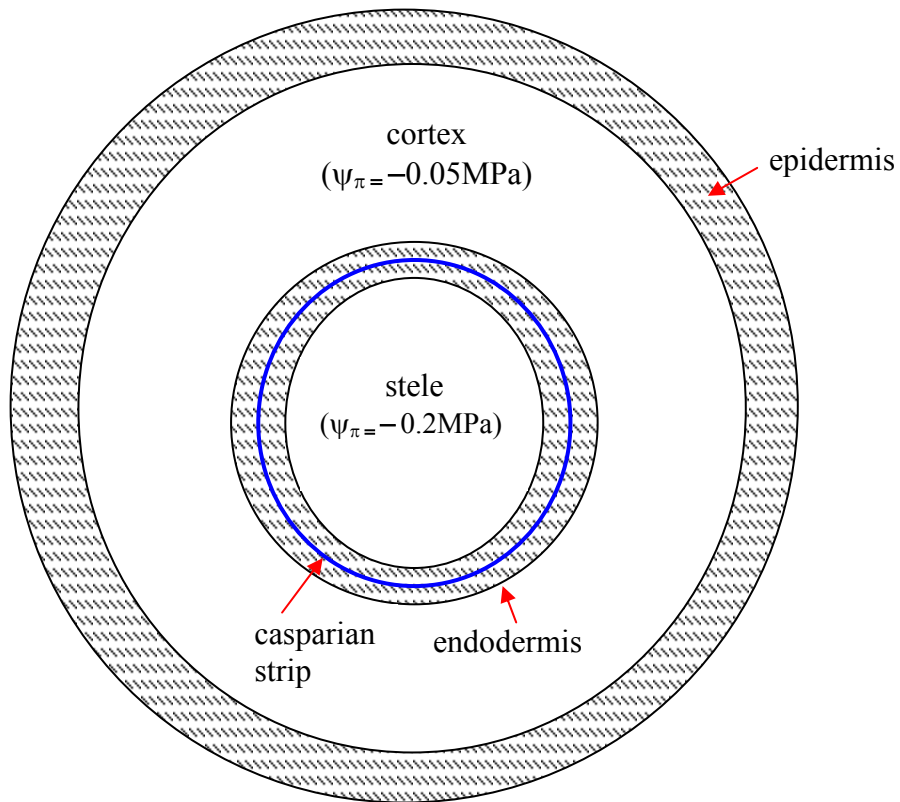
(Davis, Neilson & McDavitt, 1983)



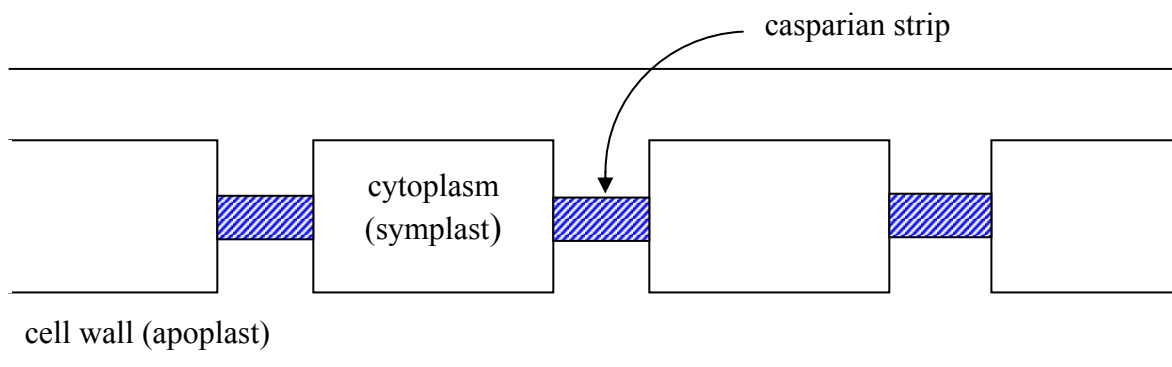
the casparian strip in the endodermis is a barrier to the passage of water (and nutrients)

therefore water must pass through the plasmalemma membrane aqt or before the endodermis

transverse section of white



transverse section of endodermis



the greatest resistance to the uptake of water is:

in the soil in coarse dry soils especially when rooting density in soil is low

at the root/soil interface when plants are transplanted

radially across the root (especially in the endodermis) for all other situations

except axially in the xylem conduits when water is being extracted along long roots and depths and the surface soil is dry

usually radially at the endodermis

water uptake mechanisms

active uptake

passive uptake

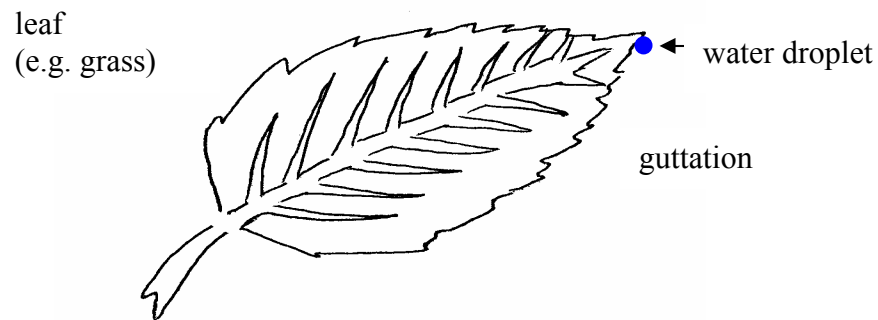
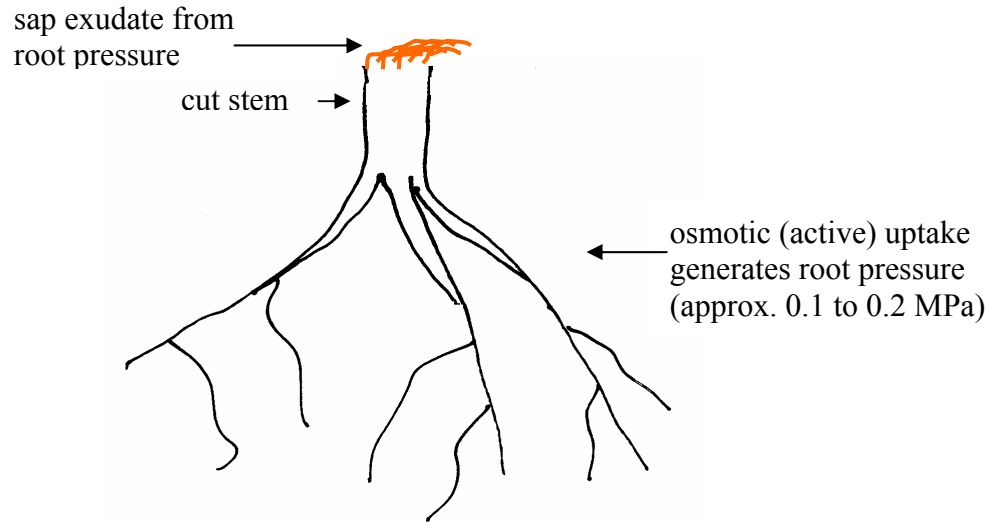
active uptake

active uptake is caused by an osmotic gradient

solute are accumulated in the stele against a concentration gradient with the use of metabolic energy

active uptake requires

- **requires energy**
- **generates root pressure**
- **can cause guttation**
- **cyclic**



passive uptake

occurs along gradients in water potential

passive uptake >> active uptake when transpiration is high (eg in the day)

but passive uptake is less and approaches active uptake when transpiration is low (eg at night)

active uptake, although small, is important for rehydrating tissues at night

water stress

occurs when there are less than optimal water contents in plant tissues

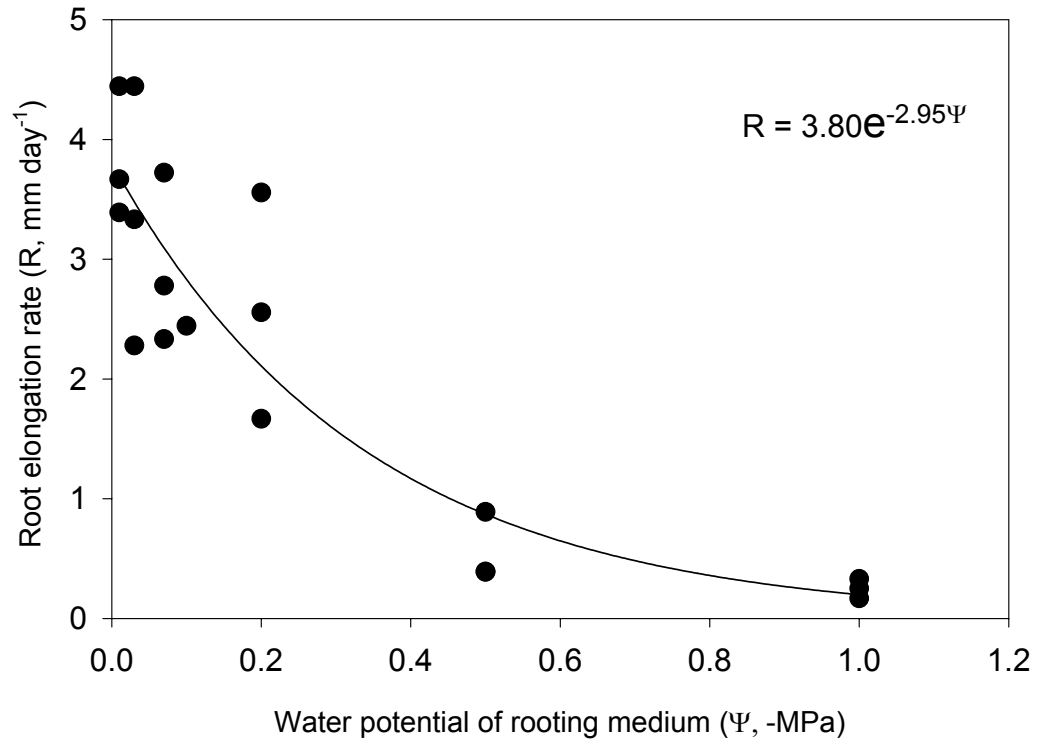
ie when there are plant water deficits

effect of plant water deficits

- **reduces plant water potentials**
- **reduces turgor pressure**
- **reduces osmotic potential**
- **reduces stomatal conductance**
- **reduces photosynthesis**
- **reduces respiration**
- **interferes with metabolism**
- **cell enlargement ceases**
- **growth is reduced**
- **plant eventually dies**

causes of water stress

- **low soil water**
- **high VPD (accelerates soil water loss)**
- **insufficient roots**
- **poor plumbing**
- **poor root to soil contact**
- **cool soil + warm air**
- **water logging**



From: Zou, Penfold, Sands, Misra & Hudson, (2000)

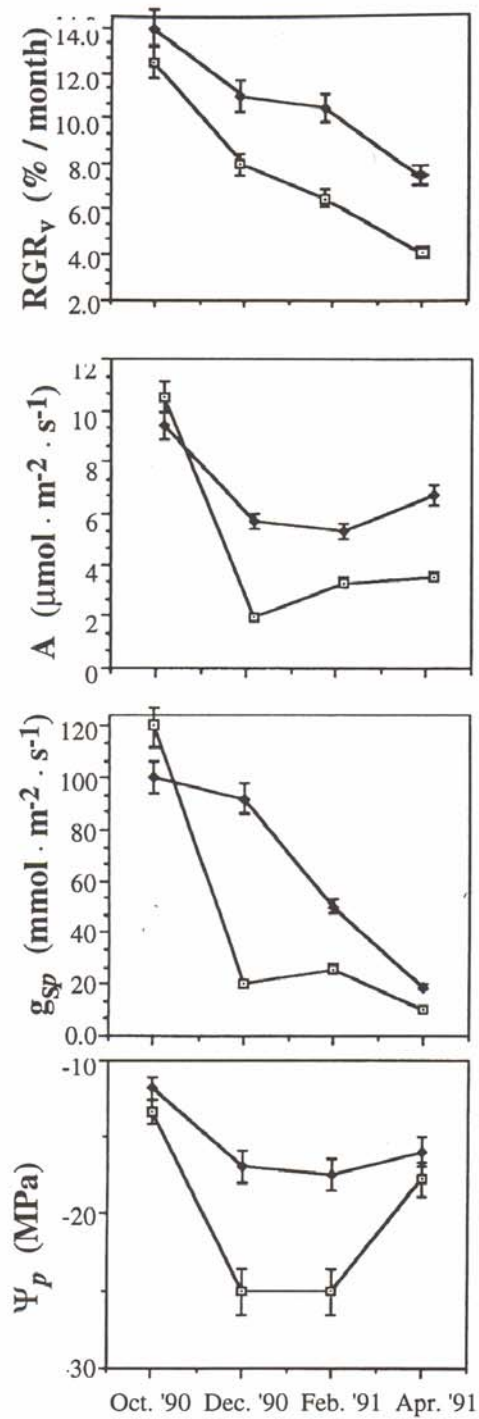
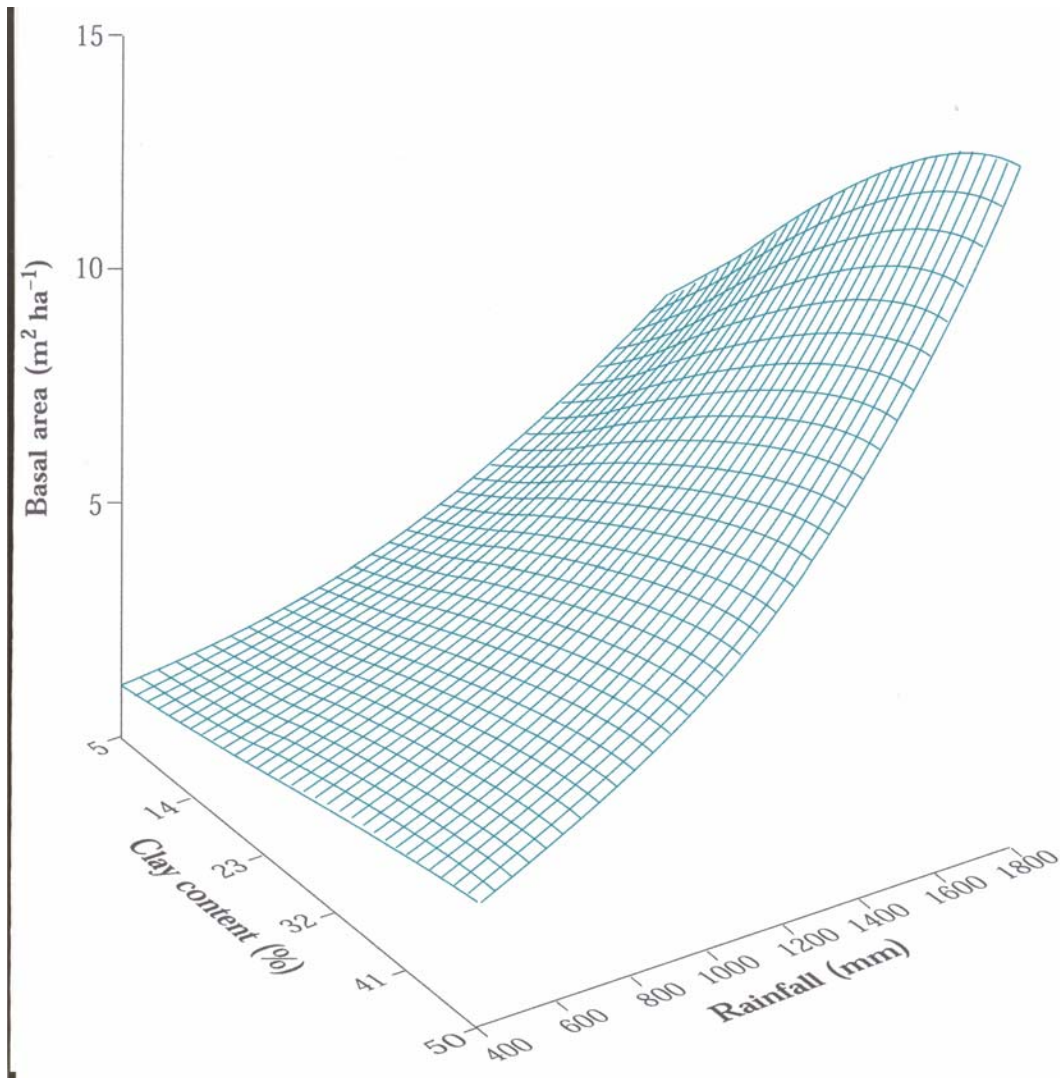


Figure 12.1 Relative growth rate in stem volume (RGR_v), net photosynthesis (A_p), stomatal conductance (g_{Sp}), and midday needle water potential (Ψ_p) of radiata pine in the Ballarat experiments with (open symbols) and without (closed symbols) weed control. $n=5$ and standard errors of the mean are shown. (This Figure was shown as previously unpublished data of Hadriyanto and Sands in Sands and Nambiar (1993) and is reproduced with permission).



(Atwell, Kriedemann & Turnbull 1999)

adaptations to water stress

- **Avoidance**
 - slow growth
 - escape
 - increase in root/shoot ratio
 - rooting depth and density
 - greater water extracting power of the roots
 - reduced incident radiation on the leaves
 - increased imperviousness of the cuticle
 - stomatal control
- **Tolerance**
 - more elastic cell walls
 - smaller cells
 - osmoregulation

- **Slow growth**
 - this is the main and universal adaptation to water stress

- **Escape**
 - some species can germinate, grow, flower and set seed in a short period of favourable conditions in an otherwise dry environment
 - eg desert ephemerals

- **Increase root/shoot ratio**
 - relatively greater investment of assimilate in root and less in canopy
 - increase rate of root turnover
 - discard leaves and branches
 - deciduous in the dry season

- **Reduce incident radiation on leaves**
 - vertical leaves
 - moving leaves
 - waxy leaves
 - hairy leaves
 - small leaves with small surface/volume

- **Increase imperviousness of the cuticle**
 - waxy leaves
 - thick leathery leaves

- **Stomatal control**
 - stomatal control will reduce water loss
 - it will also reduce photosynthesis and growth
 - not necessarily a good adaptation for competition
 - xerophytes need additional adaptations

silvicultural implications

- species and site selection
- competition control
- mulching
- spacing and thinning
- irrigation
- water harvesting
- transplanting
- wood quality