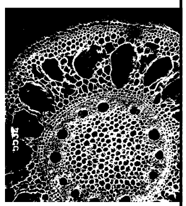
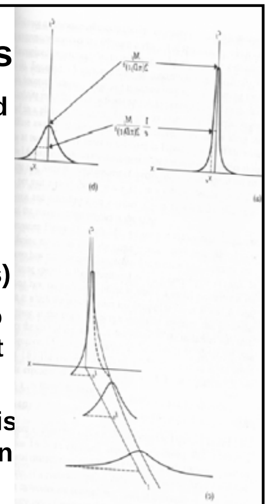
Plant Hydraulic Structure and Function

1. Central Role in Plant Function
2. Water Potential
3. ***Water in plant cells***
4. Transport of water
   - -Soil to root
   - -Root to leaf
5. Water Limitations and Plant Responses
6. Measurement techniques



Water relations of cells

- **The primary mode of water and solute movement within living cells is by diffusion**
- **Time for a species to diffuse increases as the square of distance (Fick's 1st and 2nd laws)**
- **It takes seconds for solutes to diffuse across a 50 um cell, but years to travel 1m.**
- **As a result, maximum cell size is limited by properties of diffusion**



Water relations of cells

A major distinction between cells with regard to water relations is whether they are:

1. Membrane bound ("symplastic"), or

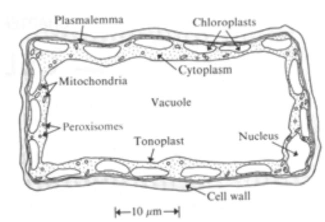
2. Non-membrane bound ("Apoplastic")

Live cells always have a membrane – dead cells lose membranes.

First, let's consider membrane bound cells

In membrane bound cells (leaf mesophyll cells, parenchyma, etc…), osmotic regulation of turgor dominates water exchange.

The plasmalemma (or cell membrane) pushes against the cell wall, which elastically expands and pushes back.



Cell membrane function be characterized by

1. **Hydraulic conductance, and**
2. **Degree of semi-permeability (leakage of solutes)**

These two factors are embodied in the transport equation:

$$J = L (\sigma\Delta\Psi_S - \Delta\Psi_P)$$

Where J is flux rate (ms^{-1}), L is hydraulic conductance ($m\ s^{-1}\ Pa^{-1}$), σ is a 'reflection coefficient' (0 = totally 'leaky' membrane to solute; 1 = totally impermeable to solute leakage),

And $\Delta\Psi_S$ and $\Delta\Psi_P$ are the pressure and osmotic potential differences across the membrane.

Membrane-bound cells (cont.)
How do cells increase solutes?

Cells can convert insoluble starches into soluble sugars as one way of controlling Ψ_s

Soluble photosynthate can also accumulate in water stressed cells (rather than be stored or translocated)

Inorganic ions can also be 'pumped' using ATP and membrane spanning proteins

Different cell types can react differently to the same osmotic load.

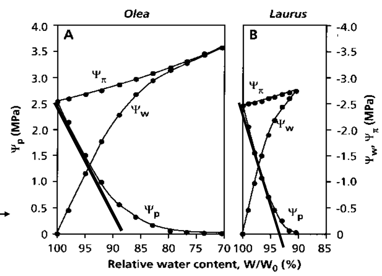
The degree of turgor generation is controlled not only be amount of osmotica, but also by the cell wall elasticity.

The modulus of elasticity (ε) is used to quantify this – a larger ε is less elastic.

Modulus of Elasticity is given By HÖfler diagrams

$\varepsilon = dP/dV / V$

The red lines are the moduli of elasticity – the initial slope of change in turgor pressure with change in cell relative volume (or water content)



Olive has a smaller modulus than Laurel – e.g. more elastic cell wall; can maintain + turgor over a greater range of dessication

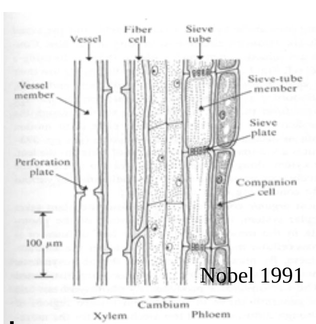
What's the tradeoff then?

Very elastic cells are also often very 'extensible' cells, allowing irreversible cell growth and expansion that translates ultimately to leaf expansion. In arid areas, more rigid cell walls with greater ε may be less prone to wilting, better regulators of cell/leaf size, and hence water loss.

Now let's consider membrane-free cells

Across unbound cells, hydrostatic pressure (i.e. tension almost always) dominates Ψ and water exchange – i.e., no osmosis is possible without a membrane

The primary water conducting tissue in plants is called xylem, and is membrane free



Nobel 1991

Xylem cells come in 2 basic forms:

Tracheids (gymnosperms)

Vessels (angiosperms)

Tracheids

•Tracheids (gymnosperms) are evolutionarily older than vessels (angiosperms)

•An indication of this is that Angiosperms have vessels and (relatively few) tracheids, but gymnosperms only have tracheids.

•Typical dimension: 10-50 um diameter, 1-4 mm long

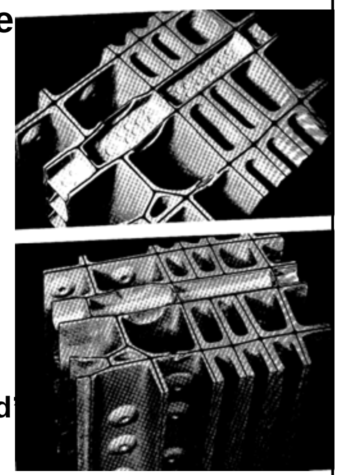
•"kayak" shaped

•Water must move laterally from tracheid to tracheid – a very tortuous path!

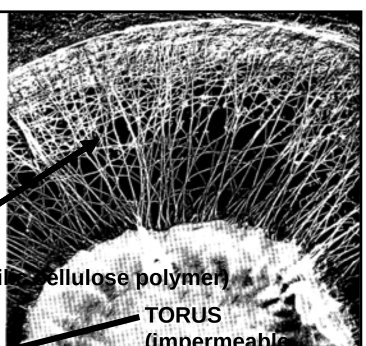
Here is an example of tracheid anatomy (pinus ponderosa)

Note the bordered pit area that connects adjacent tracheids

Also, note how 'latewood' cells are smaller than 'earlywood' cells



Bordered pits between tracheids control water flow and act as amazing 'safety' valves



Margo
(hydrophilic cellulose polymer)

TORUS
(impermeable

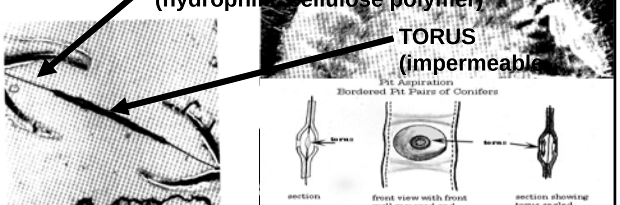


Figure 38 Electron micrograph of a bordered pit pair showing the torus x 7150. (Courtesy of Norman P. Kutscha)

Vessels

•Typical dimension: 50-300 um diameter, a few mm to 10's of m long! (not a lot known about controls on or shapes of length distributions)

•Individual vessels are composed of many shorter vessel members, which are longitudinally connected with open (non-membrane covered) ends.

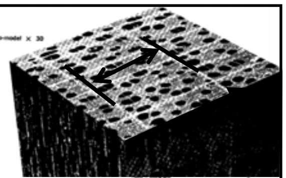
•Water also moves laterally from vessel to vessel, but with much less tortuosity than tracheids.

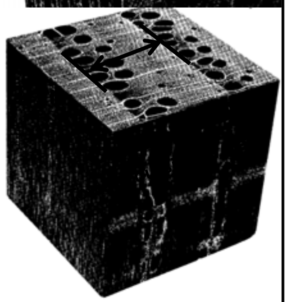
Vessels

Two main types:

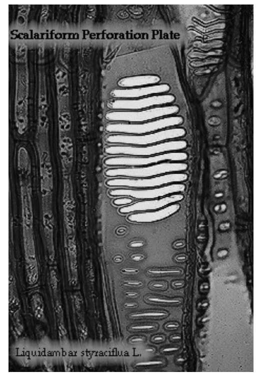
Diffuse porous (birch – example on right)

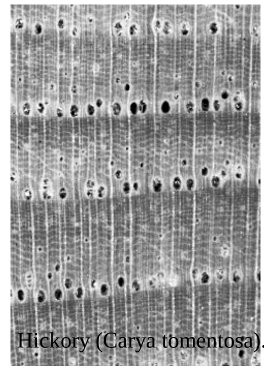
Ring-porous (ash – example on right)





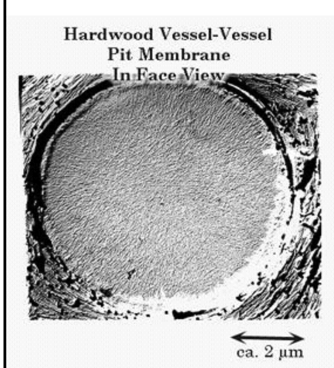
Here are typical pictures of vessel anatomy

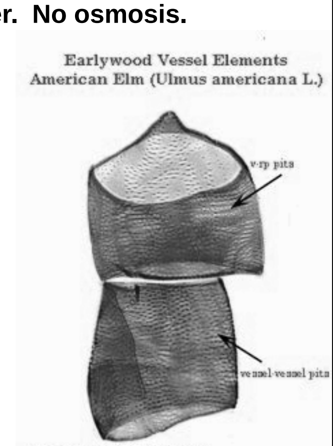




Wide diversity of perforation plate geometry – function may be to restrict bubble spread

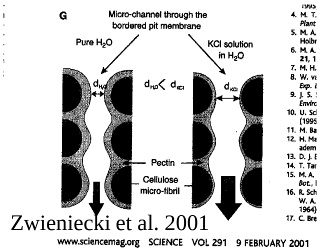
Vessels have more 'membrane-like' pits. Consistency of filter paper. No osmosis.





A slight digression…

Recent work has suggested that hydrogels in the vicinity of bordered pits may shrink (swell) with low (high) xylem sap ion concentration

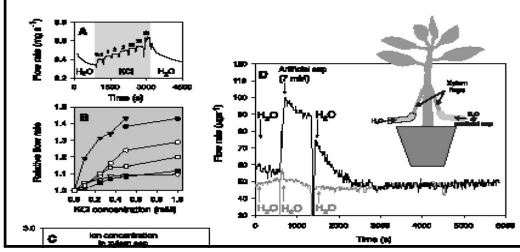


Zwieniecki et al. 2001

Can roots or phloem load solutes in xylem sap? If so, plants may have much more control on water flux than just stomata.

…

Feb, 2001



REPORTS

Hydrogel Control of Xylem Hydraulic Resistance in Plants

Maciej A. Zwieniecki,* Peter J. Melcher, N. Michele Holbrook

Increasing concentrations of ions flowing through the xylem of plants produce rapid, substantial, and reversible decreases in hydraulic resistance. Changes in hydraulic resistance in response to solution ion concentration, pH, and nonpolar solvents are consistent with this process being mediated by hydrogels. The effect is localized to intervessel bordered pits, suggesting that microchannels in the pit membranes are altered by the swelling and deswelling of pectins, which are known hydrogels. The existence of an ion-mediated response breaks the long-held paradigm of the xylem as a system of inert pipes and suggests a mechanism by which plants may regulate their internal flow regime.

Xylem vessels, composed of dead cells, are well known for their passive role in water transport (1–3), and the possibility that these tubes might be capable of rapid flow control has been overlooked. The prevailing view among plant biologists is that xylem conduits have two hydraulic states: They either transport water at a constant resistance or are blocked by embolism (2, 4). However, reports of short-term changes in xylem resistance (5, 6) question this view. Over two decades ago, it was first observed that the hydraulic resistance of perfused stem segments was significantly decreased when deionized water was replaced by tap water (7). This finding has been recently confirmed (8). Initially, the effect of ions on xylem hydraulic resistance was seen as a methodological problem of limited biological importance (9). However, this phenomenon might substantially contribute to the regulation of water flow through plants. For example, an ion-dependent mechanism for altering the hydraulic resistance of the xylem could allow plants to compensate for increases in resistance due to cavitation.

We examined the effect of ion concentration

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Fig. 1. Effect of KCl concentration on flow rate through xylem. (**A**) Time course of typical experiment showing a slow decline in flow rates with deionized water and increasing flow rates with KCl. Numbers above the curves indicate KCl concentration (mM). Sharp drops in flow rate between consecutive treatments reflect temporary pressure drops associated with switching between solutions. (**B** and **C**) Relative flow rate (flow rate with indicated solution/flow rate with deionized water) as a function of KCl concentration (0 to 1 mM and 0 to 50 mM, respectively). Symbols represent different stem segments. The average increase in flow rate in re-

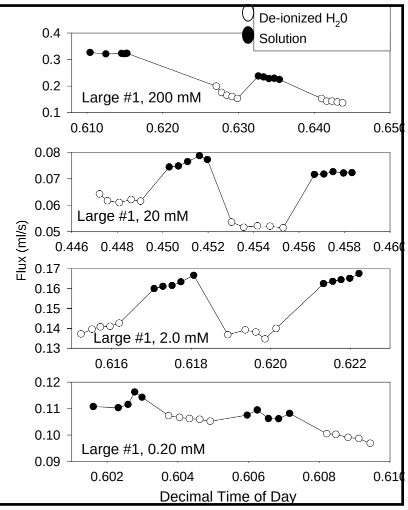
Decreased sapwood flow resistance in tall trees?

Decreased sapwood flow resistance in taller trees

Methods

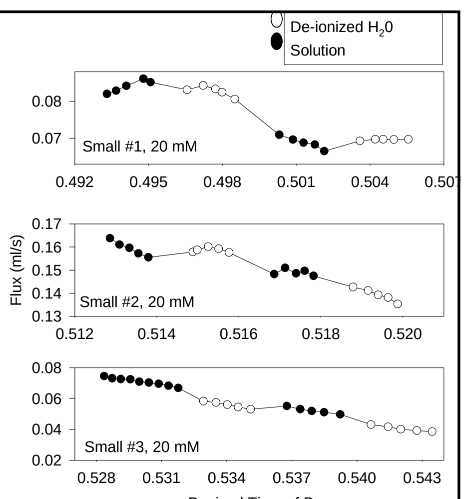
Results

- Large effects of KCl in 30 m trees.
- Repeatable both within and among trees



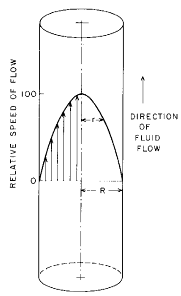
Results

- Weak or no effect in 3 small (5 m) trees.



Flow through tracheids or vessels is governed by the Hagen-Poiseuille Law

(at least ideally)



Flow (kg s^{-1}) = L_p x dP/dl

Where L_p is tube conductance and dP/dl is hydrostatic pressure gradient

But $L_p = \pi R^4/(8\mu)$, where R is tube radius and μ is fluid viscosity.

Therefore, for a given dP/dl, Flow is $\propto R^4$!

	Velocity, Meters per Hour	Vessel Diameter in Microns
RING POROUS		
White Oak	43.6	200-300*
Ash	25.7	120-350*
Hickory	19.2	180-300*
* earlywood vessel diameter		
DIFFUSE POROUS		
Willow	3.00	80-120
Tulip Poplar	2.62	50-120
Birch	1.60	30-130
CONIFERS		**Tracheid diameter**
Eastern White Pine	1.7	up to 45
Spruce	1.2	up to 45

Thus, a doubling of conduit radius increases flow by 16X!

Consider the following:

A 100 um vessel conducts the same as 10,000 vessels of diameter 10um!

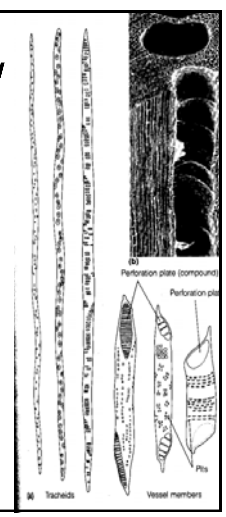
Angiosperms, with typically much greater diameter conduits than gymnosperms, are generally more efficient at conducting water.

Why don't all trees make huge vessels?? – We're getting there….

Water flow in conduits doesn't conform to ideal Poiseuille flow for the following reasons:

- **Rough inside walls**
- **Non cylindrical tubes**
- **Ends of tubes are not open**
- **Lateral flow through pits may be a significant source of hydraulic resistance**

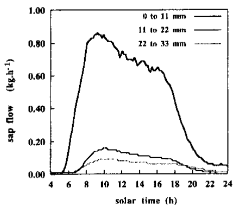
Still, Poiseuille flow is a decent first order approximation to flow differences among species.



Strategies of water use can be deduced from wood anatomy

Ring-porous species appear to have a dual strategy of high efficiency (but low safety margin against failure of vessels…) for water transport when water is available, and a 'safe' but inefficient backup system of much smaller diameter vessels.

Granier et al. 1994 Tree Physiology showed this elegantly for Quercus petraea



Bulk flow through wood (as opposed to microscopic Poiseuille flow) uses a bulk hydraulic conductance:

The form is exactly like that of previous transport equations (i.e. Fick's, membrane flux, Poiseuille)

$J = K \, \Delta\Psi$

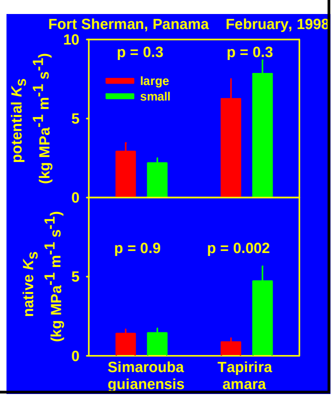
Where J is flux through a cross section of conductive xylem (kg/sec), K is the xylem conductance, and $\Delta\Psi$ is the water potential gradient across a length of xylem

Ideally, bulk K should equal Σ ($\pi R^4/(8\mu)$) (since conductances in parallel add)

Phillips et al. 1999

But not in reality:

Vessel roughness,
Constrictions,
Cavitation.



There are many variations on the previous expression for hydraulic conductance:

$K = J/\Delta\Psi$	**Hydraulic conductance** (where $\Delta\Psi$ could be across any portion of a tree, or even soil-leaf) (kg s^{-1} MPa^{-1})
$k = J/(\Delta\Psi/dl)$	**Hydraulic conductivity** (kg m s^{-1} MPa^{-1})
$k_s = k/A_s$	**Sapwood specific conductivity (can be thought of as wood porosity)** (kg m^{-1} s^{-1} MPa^{-1})
$k_l = k/A_l$	**Leaf specific hyd. Conductivity** (kg m^{-1} s^{-1} MPa^{-1})

The integrated measure of the capacity for a plant's vascular system to supply water to leaves ("hydraulic sufficiency") is the leaf specific conductance:

$$K_l = k_s A_s/(A_l h)$$

This shows a couple of possible degrees of freedom available to trees to vary K_l if water availability changes, or they grow in height.

For example, trees can drop leaves, which increases A_s:A_l, as a compensation for increased h. (What is the tradeoff here?). Or they can increase k_s (also possible tradeoffs)

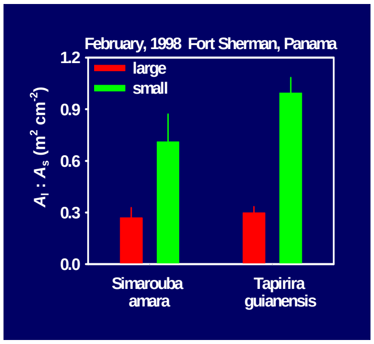
Trees in moist environments do have greater Al:As!

TABLE 7. Typical ratios of foliage area (A_f) to sapwood area (A_s) of conifers.

Species	Common name	$A_f:A_s$ ($m^2 m^{-2}$)
Mesic environments		
Abies balsamea	Balsam fir	6700–7100
A. amabilis	Pacific silver fir	6300
A. grandis	Grand fir	5100
A. lasiocarpa	Subalpine fir	7500
Larix occidentalis	Western larch	5000
Picea abies	Norway spruce	4600
P. engelmanni	Engelmann spruce	2900–3400
P. sitchensis	Sitka spruce	4500
Pseudotsuga menziesii	Douglas fir	3800–7000
Tsuga heterophylla	Western hemlock	4600
T. mertensiana	Mountain hemlock	1600
Average		5000 ± 500
Xeric environments		
Juniperus monosperma	One-seeded juniper	800
J. occidentalis	Western juniper	1800
Pinus contorta	Lodgepole pine	1100–3000
P. edulis	Pinyon pine	2500
P. nigra	Austrian pine	1500
P. ponderosa	Ponderosa pine	1900
P. sylvestris	Scotch pine	1400
P. taeda	Loblolly pine	1300–3000
Average		1800 ± 200

Source: Margolis et al. 1995.

Larger trees also generally show greater Al:As (but with some puzzling exceptions – norway spruce, oregon white oak, eucalyptus grandis)



By the way, As:Al is also known as the Huber value

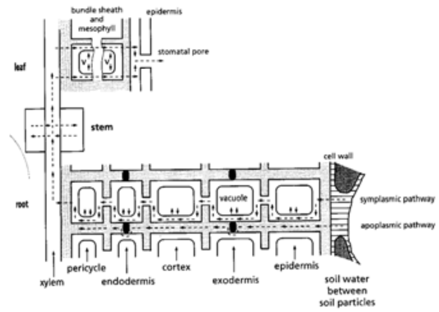
(although sometimes it is expressed as stem cross section / distal leaf area instead of sapwood area/ leaf area)

So far we've treated hydraulic conductance for an *arbitrary* section of conducting xylem.

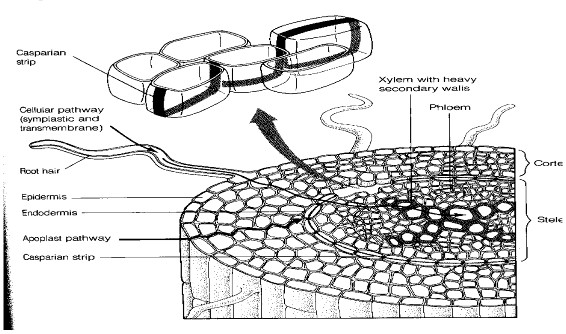
Now let's consider the water transport pathway through the whole plant.

Soil-root
Root-stem
Stem-branch
Branch-leaf

Water gets into roots via some combination of apoplastic and symplastic pathways.
Both pathways have high resistance compared to xylem, and soil-root transfer
is one of the dominant resistances in the entire pathway



At the endodermis, all water must go through a symplastic 'checkpoint' – thus, we have a solute regulator at the entry way to the plant

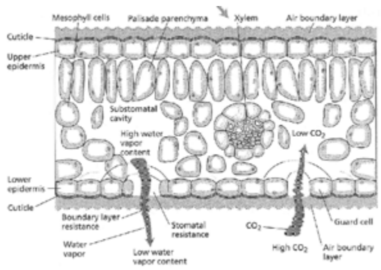


Branch junctions are generally areas of higher resistance within the soil-leaf liquid Pathway, but can vary greatly across species.

The cause is generally smaller diameter conducting cells at the junction.

One possible adaptive purpose of this is that branches get sacrificed before (relatively) irreplaceable stems if drought gets severe.

In the leaf, also a dual symplastic/apoplastic pathway into the vapor phase – questions remain about their relative magnitudes!



Xylem is always close to phloem in leaves – occur together in vascular bundles. Possibility for ion loading/hydrogel regulation? 252 7. Transpiration

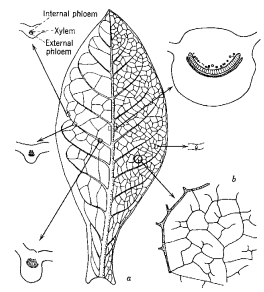


Figure 7.22 (a) Diagrams of venation of a mature tobacco leaf, showing midrib anc lateral veins, also cross sections of midvein and lateral veins of various sizes. (b) Enlarg small section of a leaf blade to show the network of small veins. There were 543 mm o square centimeter on this leaf. From Kramer (1983), after Avery (1933).

Finally, with regard to whole plant water transport, we can link liquid to vapor phase flux, using the equation:

$$(G_c * \Delta D) = K_l * \Delta\Psi$$

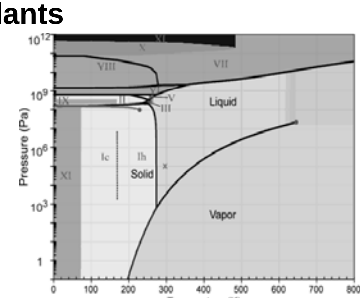
or, breaking it down further,

$$(G_c * \Delta D) = \Delta\Psi\ k_s\ A_s/(A_l\ h)$$

This predicts that, with other factors constant, G_c should decrease as h increases
A hydraulic limitation to tree height?

Water Limitations and Plant Responses – Cavitation Vulnerability

1. Water is almost always in a precarious state in plants



Liquid water in trees 'shouldn't' exist!!

Water Limitations and Plant Responses – Cavitation Vulnerability

- **The cohesion-tension theory of sap ascent: States that the cohesive properties of water, and its adhesion to cell walls, are sufficient to maintain liquid water in the conducting xylem of trees.**
- **Support (?): degassed water has a tensile strength of -30 MPa – much more negative than we ever see in live plants. But water is never degassed in plants and bubbles form easily.**
- **A little lab experiment convinced me of this.**

So how do trees avoid this??

The exception seems to prove the rule:

Cavitation happens!

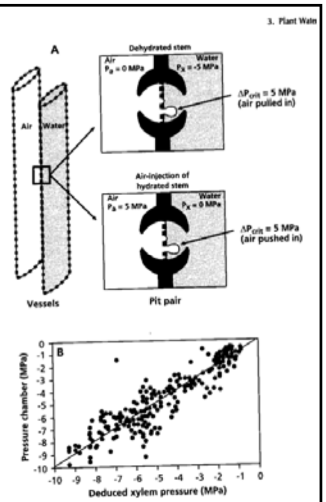
(we can hear it (ultra-sonic acoustics), see it (NMR imaging), and measure it (dry out stems and see how many tubes are lost to cavitation)

The air seeding hypothesis explains how cavitation happens.

If we + pressurize a stem to a given level, this seems to cause the same reduction in flow that the (-) water potential caused.

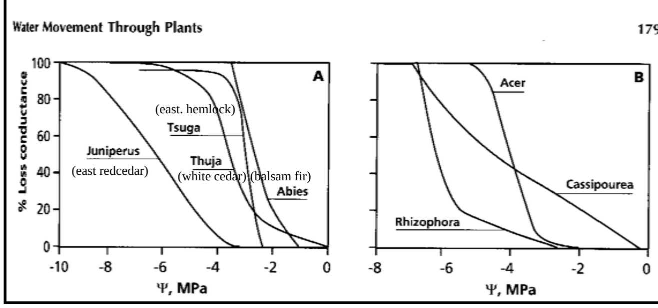
So blowing a bubble into a conduit is equal in effect to a bubble being sucked into a conduit.

Larger pores in pit membranes allow bubbles to be sucked in at lesser pressures (or tensions).

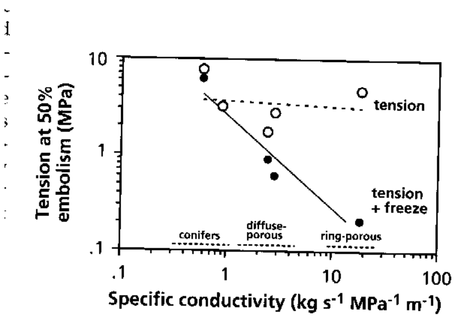


Cavitation vulnerability curves let us know at what level, and how fast, conducting systems in plants fail.

Some species are 'safer' than others: why?



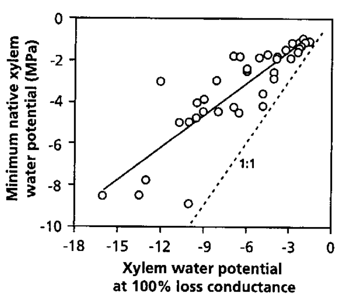
Freezing appears to have a much bigger impact on cavitation vulnerability than drought stress alone – with larger conduits more vulnerable to freezing induced cavitation



The process of freezing water that has dissolved gases inside leads to degassing – i.e. bubble formation. Gases are insoluble in ice.

If the bubbles are large enough, then small tensions developed after thawing will be enough to cavitate the conduit. Larger conduits allow for larger bubbles to expand.

Plants appear to regulate stomata to keep xylem tension above a level that would cause massive cavitation: the "safety margin"



This graph also shows more mesic species Operate closer to the cavitation threshold

Tradeoff related to cavitation vulnerability

Smaller conduits are both less vulnerable to cavitation and less efficient at conducting water. Plants growing in mesic versus xeric environments negotiate this tradeoff to balance efficiency with safety.

Also, smaller conduits generally confer greater mechanical stability – e.g. lianas don't need small vessels!

Other plant responses to water limitation:

•Stored Water (capacitance)

$C = \Delta\theta / \Delta\Psi$

Capacitance = change in water content per change in water potential

Use of stored water causes a time lag between transpiration and soil uptake

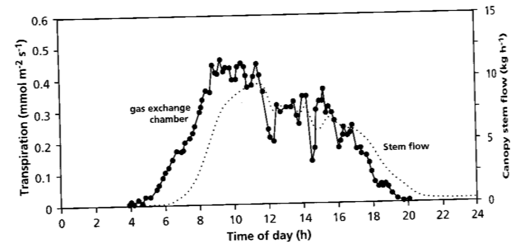
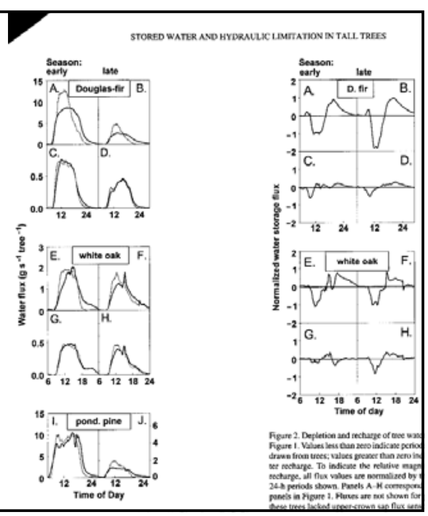


FIGURE 23. Diurnal pattern of water flow in the stem and water loss from transpiring leaves of a *Larix* (larch) tree. The difference between the two lines represents stem storage (Schulze et al. 1985).

These time traces can reveal both short term (24 hr) and long term use of storage

Trees utilize more stored water during drought, and larger trees appear to rely on more stored water than smaller trees.

(Phillips et al. 2003)



Stored water is important to the carbon economy of plants

In Douglas-fir, 60 m trees were estimated to have 18% greater photosynthesis as a result of stored water use than if they could not use stored water. In comparison, 15 m trees had 10% greater photosynthesis than if they could not use stored water.

(Phillips et al. 2003)

Stored water comes from several sources (in order of increasing tensions-cite tyree/yang):

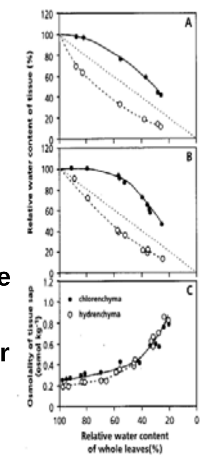
- **Elastic shrinkage (leaf cells, or parenchyma cells in xylem)**
- **Intercellular spaces (air/water pockets)**
- **Cavitation: I.e. cavitation may not always be a bad thing! (especially if refilling occurs)**

What plant organs contribute to storage?

In large woody plants, most stored water comes from stems and branches (Waring, Doug fir)

In smaller woody plants, herbaceous and succulents, much water comes from elastic shrinkage of cells.

Hydrenchema are specialized water storage cells (as opposed to chlorenchyma – which are specialized for photosynthesis)



Capacitance can be modeled using a electric circuit analogy. The response time for a simple capacitive circuit = R x C

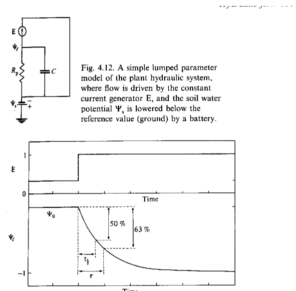


Fig. 4.12. A simple lumped parameter model of the plant hydraulic system, where flow is driven by the constant current generator E, and the soil water potential Ψ_s is lowered below the reference value (ground) by a battery.

The dynamics of water flow in trees reveals Their hydraulic characteristics (R and C)

Modeling plant capacitance

Drought: lots of definitions

•Meteorological (length of rainless period)
•Soil water deficit
•Physiological drought

For our purposes, drought can generally be considered to be some combination of all of the above.

Other Drought responses (short term)

•Stomata closure in response to ABA production
•Decreased cell turgor reduces cell expansion and leaf area growth
•Leaf abscission (ethylene)
•Cell Osmotic adjustment

Drought adaptations (long term)

•Drought tolerators:

- Two subclasses:

Dessication toleration

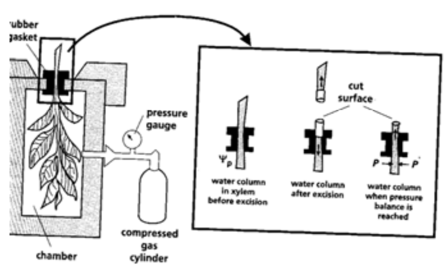
Dessication postponement

•Drought escapers (or, “avoiders”):

-Plants that complete life cycle before drought

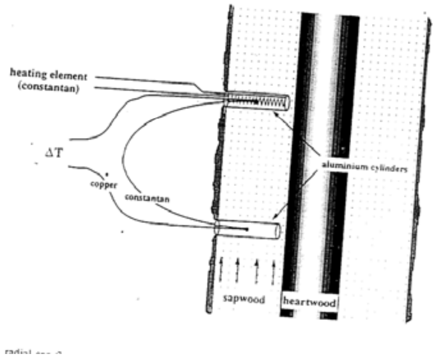
6. Measurement techniques

The pressure bomb, aka pressure chamber, Scholander chamber

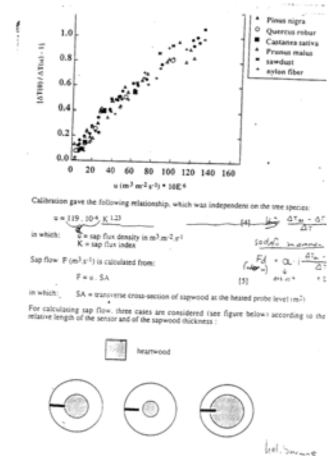


13. Schematic representation of the Scholander chamber that allows measurement of negative tic pressures in the xylem. A cut shoot or twig is ound the stem and placed upside down in the and the chamber is hermetically sealed. Positive is exerted on the shoot or twig, using a gas cylinder. When the exerted positive hydrostatic pressure equals the negative water potential (negative osmotic potential and negative pressure) in the xylem, the xylem fluid will appear at the cut surface. After determination of the osmotic potential of the xylem fluid, the negative hydrostatic pressure is calculated.

6. Measurement techniques
Granier sap flow measurement (one of many variants that use heat as a tracer)



This method is totally empirical (statistical) – other sap flow techniques establish an energy balance and compute sap flow based on the energy conservation principle



The small size of the granier probe is both a benefit and a drawback – we can probe variation in sap flow rates within trees, but its challenging to spatially integrate