How trees defy gravity

some conceptual and historical remarks on the theory of the ascent of sap

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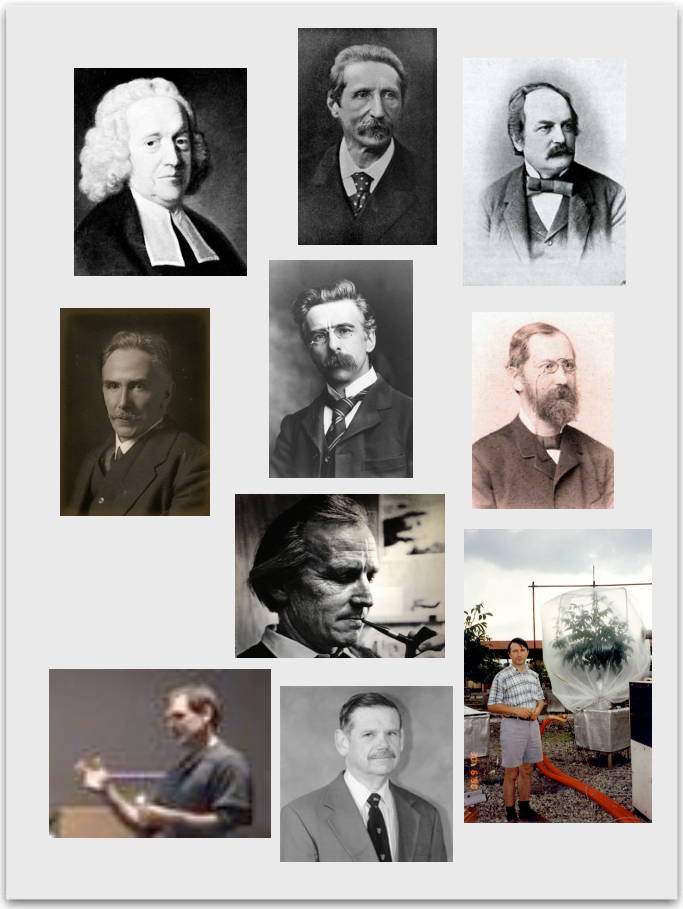


Based on:

H.R.B., "The theory of the rise of sap in trees: some historical and conceptual remarks", *Physics in Perspective* **15**, 320-358 (2013). Revised and updated version:
http://philsci-archive.pitt.edu/id/eprint/10608
http://arxiv.org/abs/1404.3066

Simon Schwendener (1886):

"I absolutely stand by the fact that the vital activity of cells is somehow intervening in sap motion. The lift of water up to heights of 150 to 200 feet and more, is simply impossible without this intervention. And all the endeavours to break through existing barriers by uncertain physical concepts, are not much more than seeking the philosopher's stone."

Francis Darwin (1896):

"The ... question [concerning the forces producing ascent] has a curious history, and one that is not particularly creditable to botanists generally. It has been characterized by loose reasoning, vagueness as to physical laws, and a general tendency to avoid the problem, and to scramble round it in a mist of vis à tergo [root pressure], capillarity, Jamin chains [a succession of bubbles of air separated by water], osmosis and barometric pressure. …

To believe that columns of water should hang in the tracheals like solid bodies, and should, like them, transmit downwards the pull exerted on them at their upper ends by the transpiring leaves, is to some of us equivalent to believing in ropes of sand."

Overview

- some motivational remarks
- key elements of the Cohesion-Tension Theory and its limitations
- history and its lessons
- different types of explanation

coastal redwood, California
115m; ~2000 yr old

"Oldest"
bristlecone pine
California
~ 4800 yr

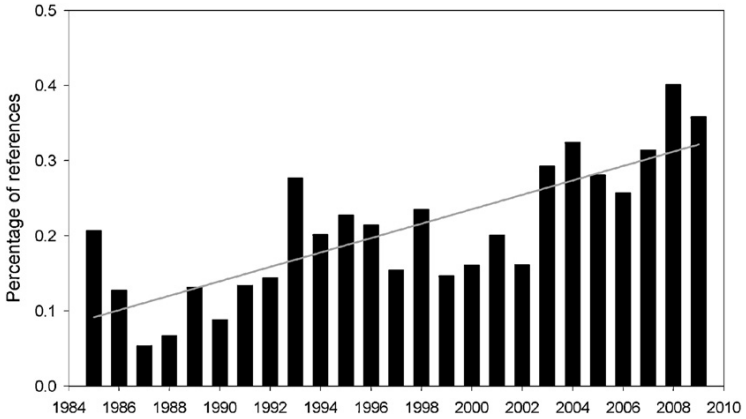
Threats: storms, floods, frost, fire, drought, bacterial and viral infections, infestations of fungi and insects, and grazing by animals

Plants add 32 trillion tons of water vapor to the atmosphere per year

water barometer (vacuum pump): ~ 10.4m
xylem capillarity: ~ 3m
osmotic root pressure ~ 10m

Trees and climate change

(i) trees provide evidence of global warming: drought-induced mortality

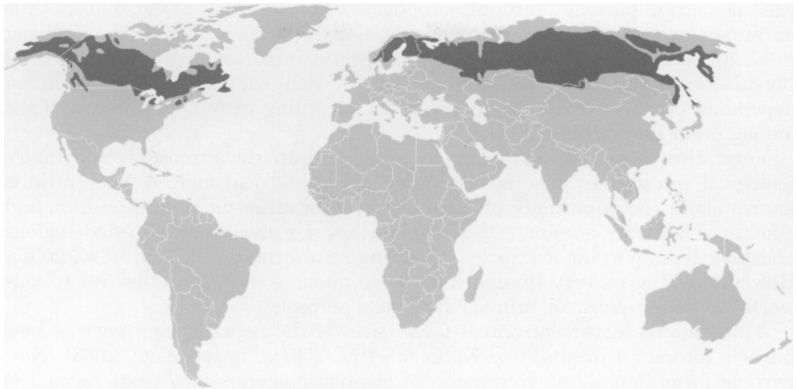


Recent satellite observations suggests that the recent occurrence of droughts in Amazon forest at 5–10 year frequency may lead to persistent alteration of the forest canopy.

Large scale death within high altitude pine forests in North America owing to increasing beetle and fungal infestation.

(ii) trees provide evidence of past climate:
dendrology and the use of stomata number and leaf size as CO_2 proxy

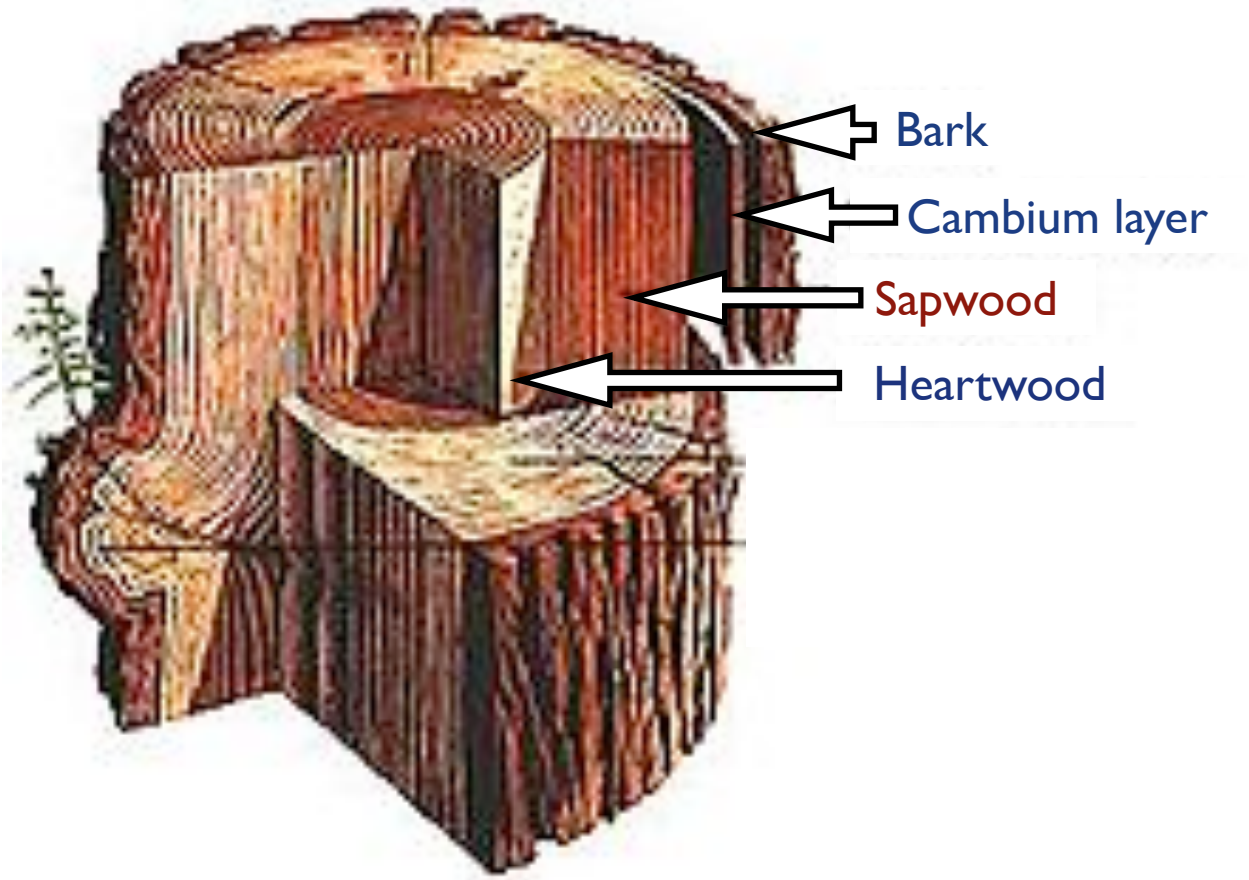
(iii) forests mitigate
and enhance global warming



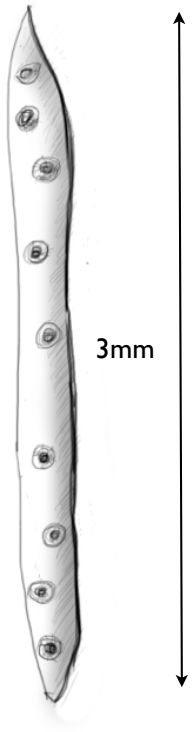
The Man Who Plants Trees
Jim Robbins
Profile Books 2013

The Cohesion-Tension Theory

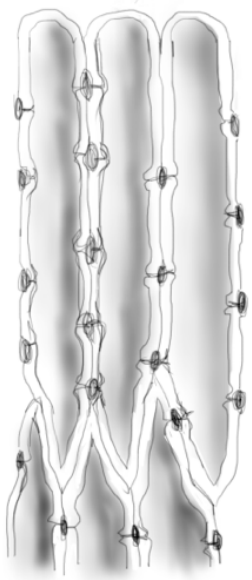
The redwood tree



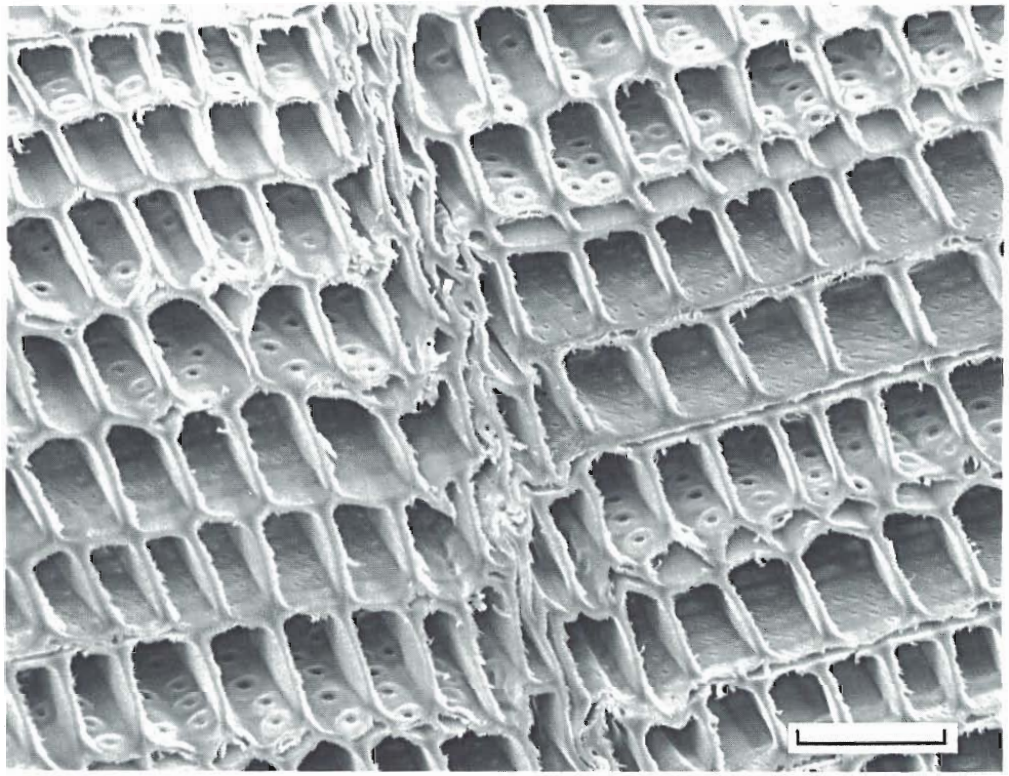
Xylem structure in conifers: tracheids



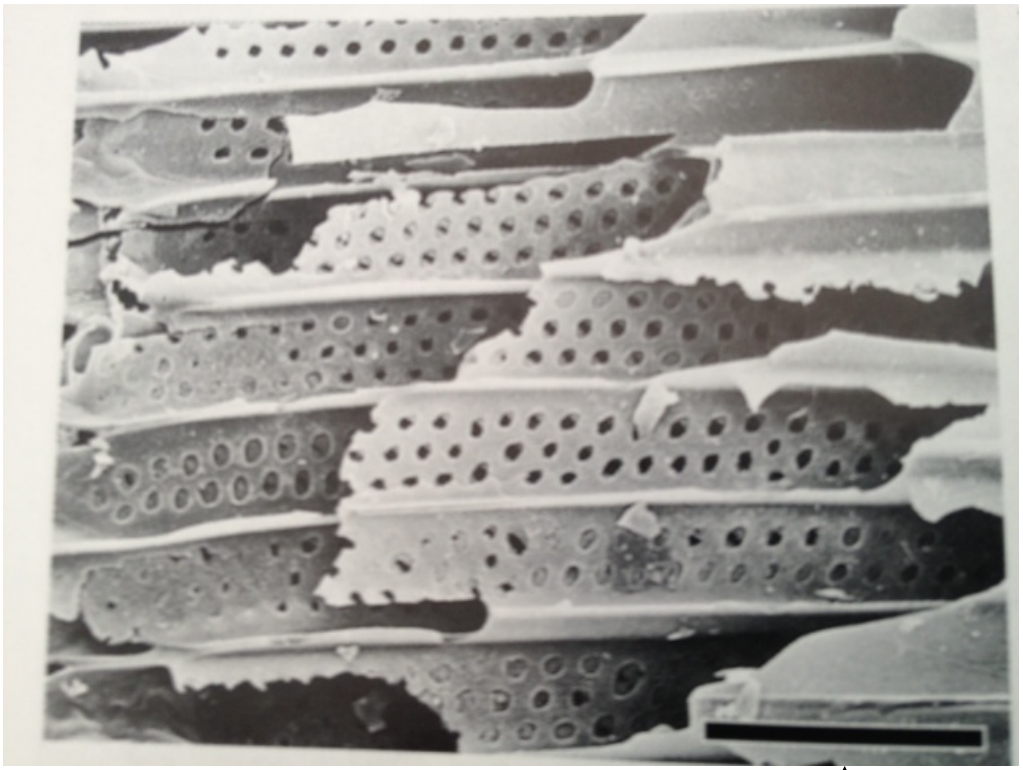
tracheid cell



longitudinal section of bundle

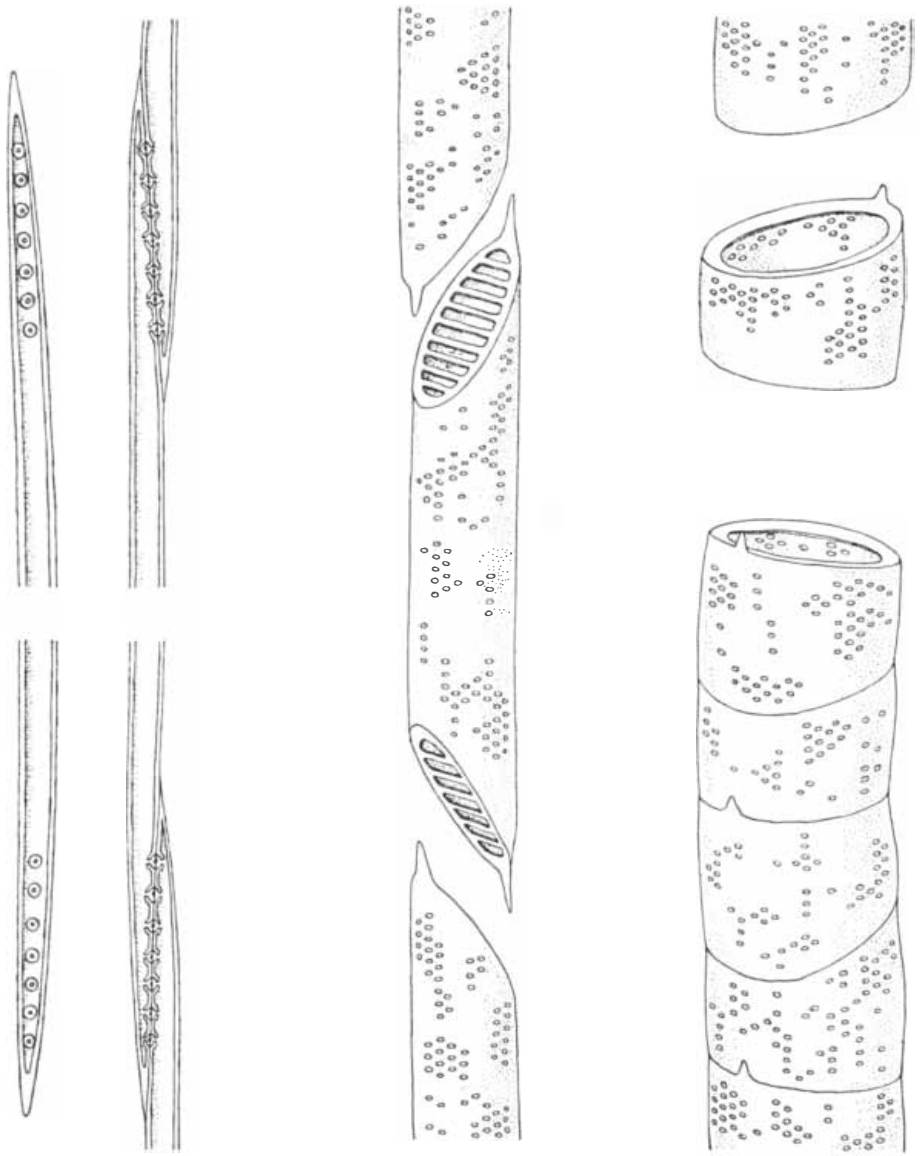


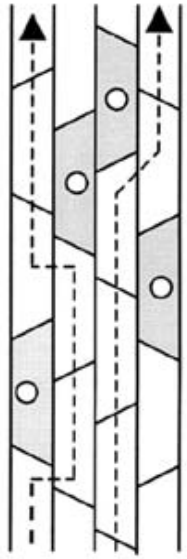
transverse section in air-dried spruce
scale bar = 10^{-4}m

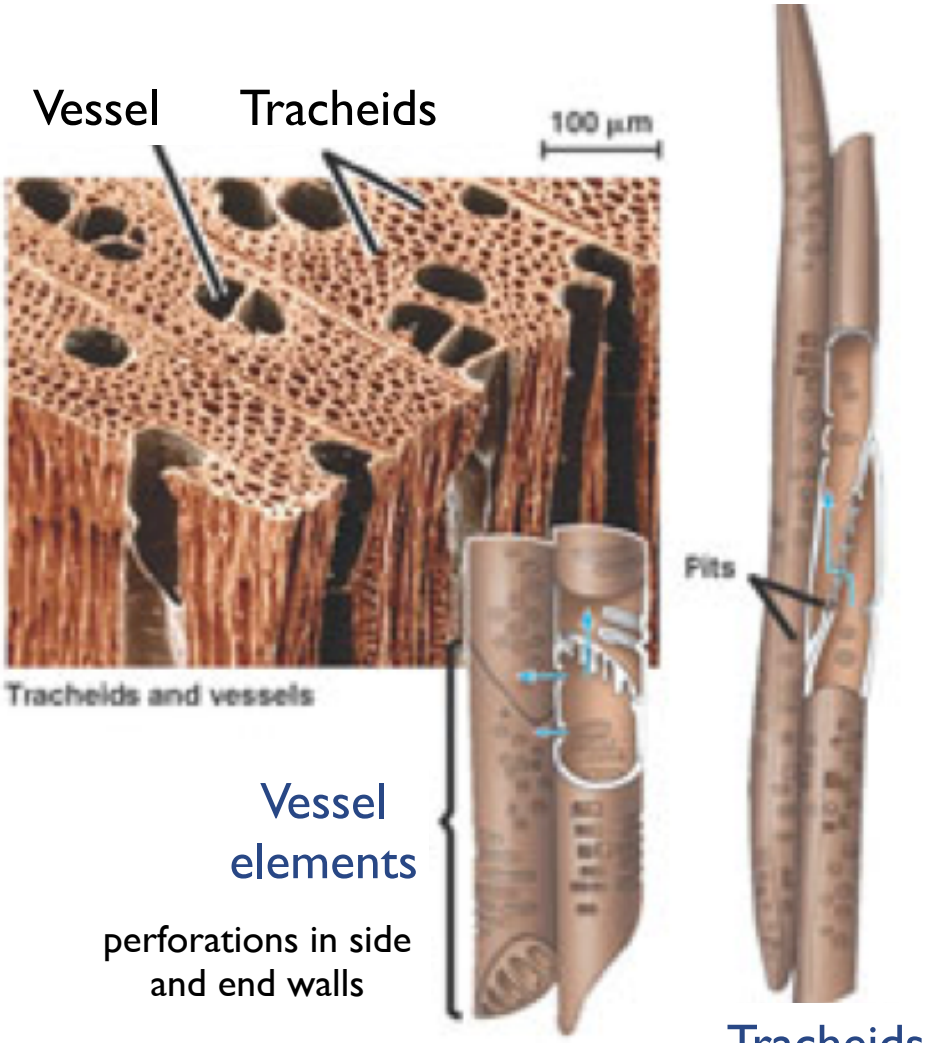


scale bar 100 microns

Fossil charcoal
from wildfire in Nova Scotia
300 million years


pine
birch
oak
evolution





transverse cuts experiments

“The main driving force of water uptake and transport into a plant is transpiration of water from leaves.”

D J Merhaut

key elements of the Cohesion-Tension Theory

- transpiration is the trigger of the driving force behind the ascent of sap: surface tension and adhesion to cell walls (capillarity) in leaves
- tension propagated through unbroken threads of water from leaves to roots
- increase in tension in the roots leads to greater passive absorption of water from the soil, so that water lost in transpiration in the foliage is replaced (trees are thirsty)
- the energy for the whole process ultimately comes from the sun
- the threads of sap are in a metastable state with respect to the formation of large air bubbles, but nonetheless (mostly) survive intact during rise

Glaring omission(s)

mechanisms for priming

growth: cell division and elongation takes place in aqueous medium. *Osmosis*

"Water moves to the tops of plants as they grow and transpiration merely increases the quantity and speed of movement." Kramer and Boyer (1995)

tree-specific methods of recovery from cavitation (due to dehydration and freezing):

annual growth of new xylem conduits *Osmosis*

root pressure (especially vines) *Osmosis*

post 1990s: active daily filling of embolized conduits

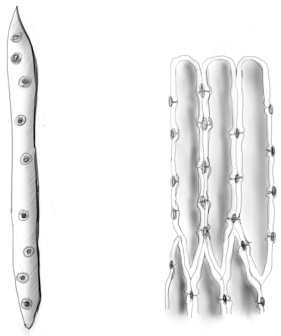
(*mysterious and recently called into question*)

freeze-thaw cycle (sugar maple trees)

capillary storage

tapered ends of wood fibres and tracheids

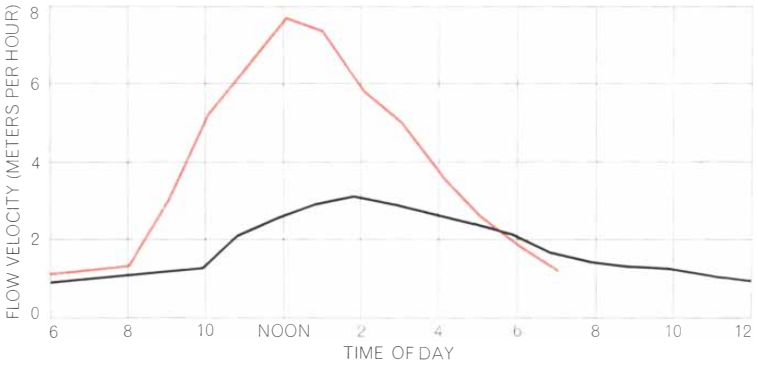
release controlled by stomata



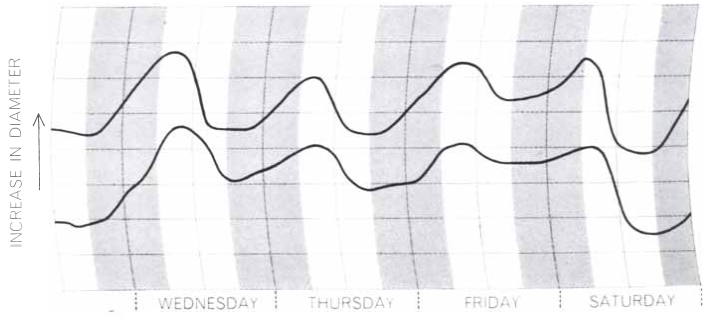
None of these processes is driven by transpiration

evidence

- xylem (negative) pressure measurements using most techniques, and the (1935) Huber experiment



- acoustic evidence of cavitation, and diurnal fluctuations in stem diameters



Josef Friedrich 1897

- coherence and lack of something better.

"There is a great deal of evidence which is supportive of cohesion-tension, some which finds no easy explanation within it, and none which decisively contradicts it. In this attribute the cohesion-tension theory is unique. It is therefore the accepted theory." Pickard (1981)

See Denny (2012)

a little history

evidence of liquids under tension

natural world: rare other than in trees
spore ejection from sporangia
octopus suckers in sea water

artificial world (laboratory)
Huygens 1661
Boyle 1663
Young and Laplace: early 19th century theories of capillarity
Donny 1846
Berthelot 1850
Reynolds 1882
19th century development of propellors

But for some plant scientists, the notion of transpiration pulling water up trees was like believing in "ropes of sand". (Darwin 1896)

Stephen Hales

Vegetable Staticks 1727

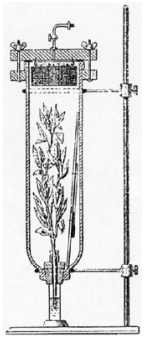
the "Newton of plant physiology"
Rom Harré (1970)

- transpiration is driving force behind flow, not root pressure
- sap does not circulate in trees like blood
- nourishment partly provided by air
- rise of sap has mechanical, not vitalistic causes, despite lack of pump
- recognised the distinction between priming (through capillarity) and summer flow

father of CT theory? Floto (1999)

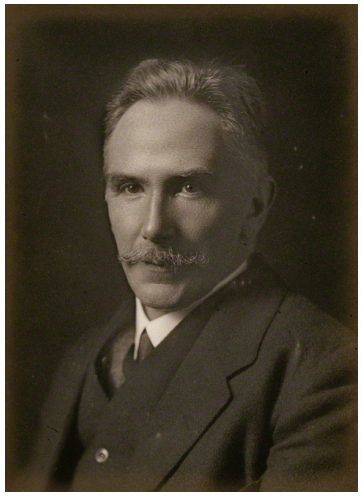
M. Massimi, *Stud Hist Phil Sci* (2011)

The big breakthrough 1894-6:



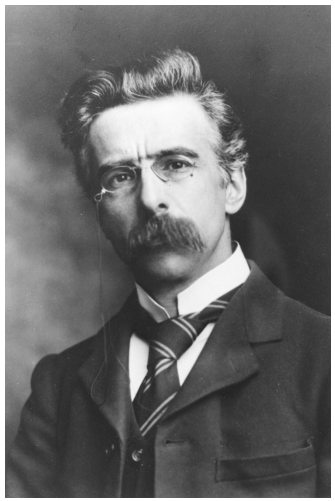
supplying the missing details in Böhm's 1893 cohesion theory:
the role of leaves, cavitation and providing quantitative analysis

Henry H Dixon
1869-1953



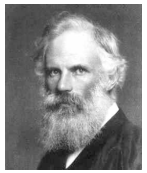
&

John Joly
1857-1933



Trinity College Dublin

Like Hales, Dixon and Joly made clear distinction between (summer) flow and priming: the role of root pressure



G F FitzGerald

Eugen Askenasy
1845-1903

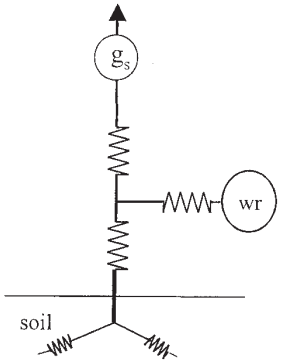
University of Heidelberg

Shades of Wallace and Darwin!

types of explanation in CTT

19th century: capillarity and cohesion. The full microscopic details (hydrogen bonds between water molecules etc.) provided in 20th century

mid 20th century phenomenological turn. Van den Honert (1949): holistic soil-plant-atmosphere system: analogy with Ohm's law for electrical circuits



language of resistances, capacitances and water potentials; much phenomenological research relating conductance to climate and soil conditions

late 60s: emergence of "hydraulic architecture" paradigm

combination of original CTT and Ohmic analogy; detailed study of *tree-specific* vulnerability to dehydration and cavitation, and recovery processes

summary

- the CT theory addresses (summer) flow but not not "priming"
- cell growth is key to priming, but not the whole story
- The current version of CTT ("hydraulic architecture") is a mixture of microscopic and phenomenological principles ("constructive" and "principle" theory)
- a systematic historical study is lacking

Thank you