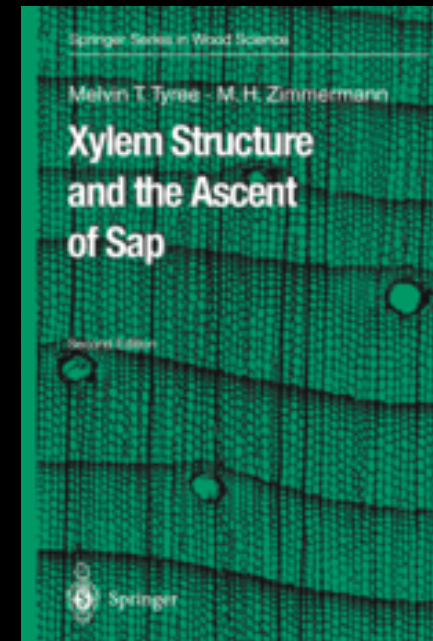
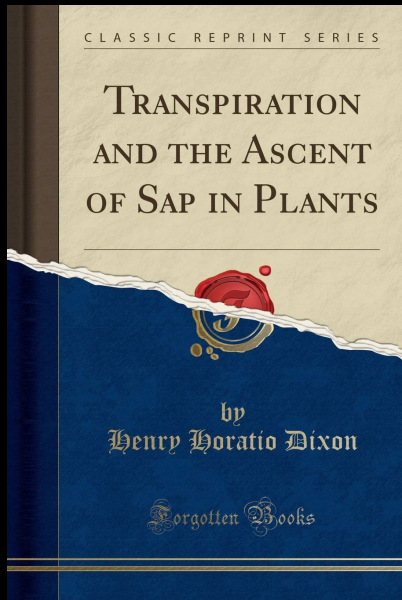


Plant water transport and photosynthesis in water-limited environments

Assaad Mrad

Collaborators: Gabriel Katul, Jean-Christophe Domec, Sanna Sevanto, Yanlan Liu, Mazen Nakad, Cheng-Wei Huang, Frederic Lens



AM, GGK and J-CD acknowledge support from the U.S. National Science Foundation (NSF-AGS-1644382, and NSF-IOS-1754893)



Medical doctors comparing fluid transport in animals and plants

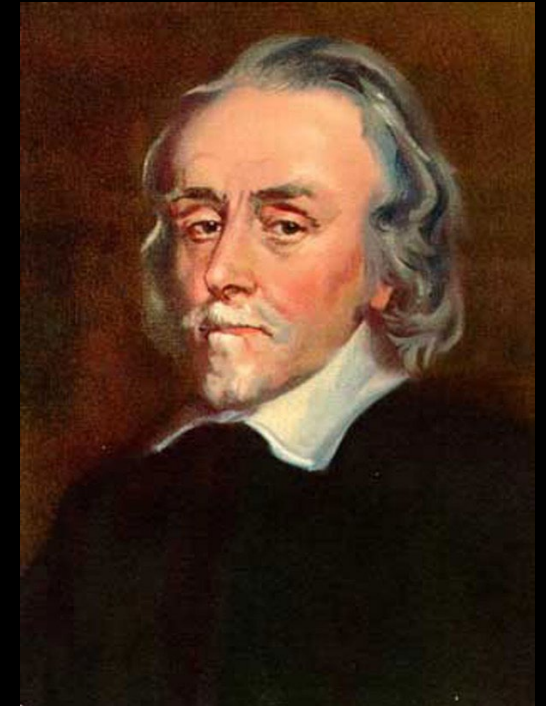
Marcello Malpighi



“From the roots the crude sap is conveyed in the woody vessels to the shoot. In the cells of the stem (parenchyma) it is mingled with the crude sap already present.”

From Marcello Malpighi's *Anatome Plantarum* (1675)

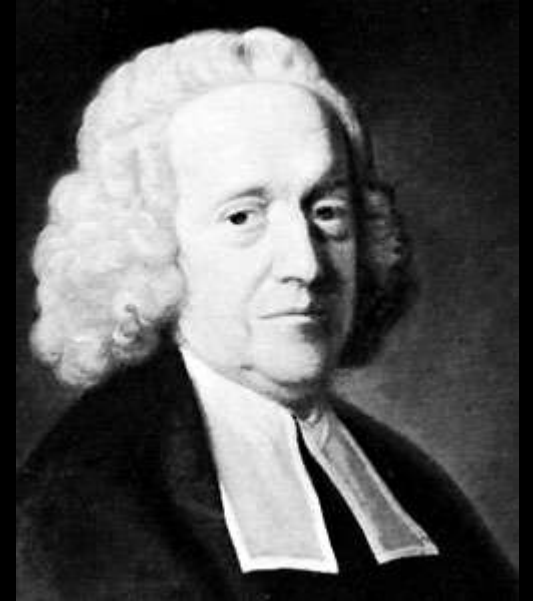
William Harvey



Stephen Hales as the pioneered the cohesion theory of plant water (18th century)

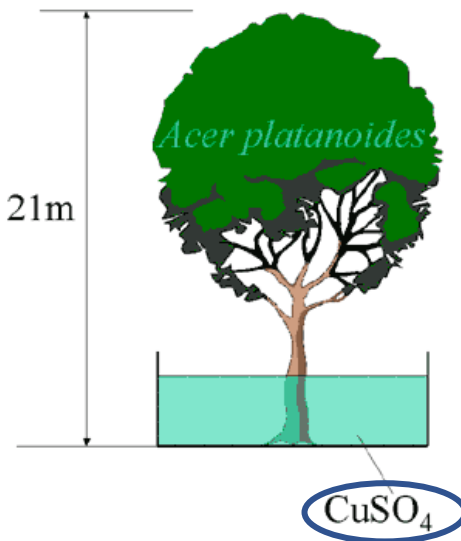
“plants imbibe moisture so vigorously up their fine capillary vessels; which moisture,..., by the action of warmth, thereby gives the sap-vessels liberty to ... attract of fresh supplies; ... sap-vessels are adapted by their exceeding fineness, to raise a sap to great heights”

Hales' Vegetable Statics (1727)



Heinrich Cotta identified sapwood as sap conductive pathway (19th century)

Eduard Strasburger: only dead cells are involved in plant water transport (1891)



The diagram shows a tree labeled *Acer platanoides* with a height of 21m. The tree is placed in a container of CuSO_4 solution. The tree's trunk is shown to be impregnated with the solution up to 20m. Below the diagram, it is noted that 30 liters of solution were used over 14 days.

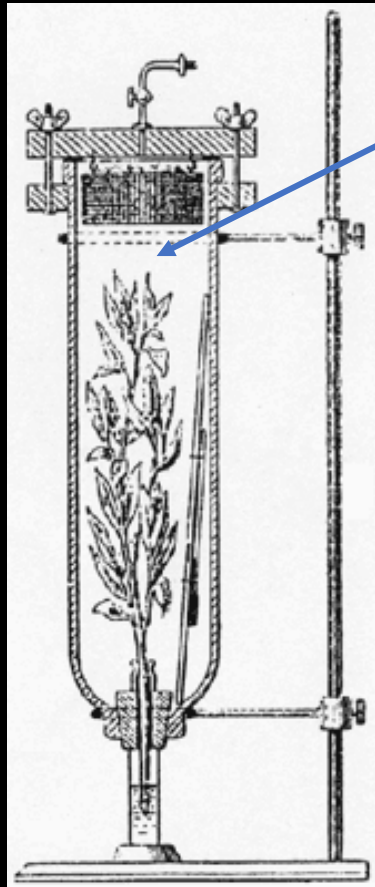
Experiments
Stems of living trees killed by heat or poison taken up in solution

Conclusions

- Involvement of living cells excluded
- Physical forces of an unknown nature are active (but not barometric pressure or root pressure)

Credit: L. Taiz, E. Zeiger, Ian M. Møller, and A. Murphy

J. Joly and H. H. Dixon recognize cohesion-tension as the driver of sap flow in plants (1894)



3 MPa



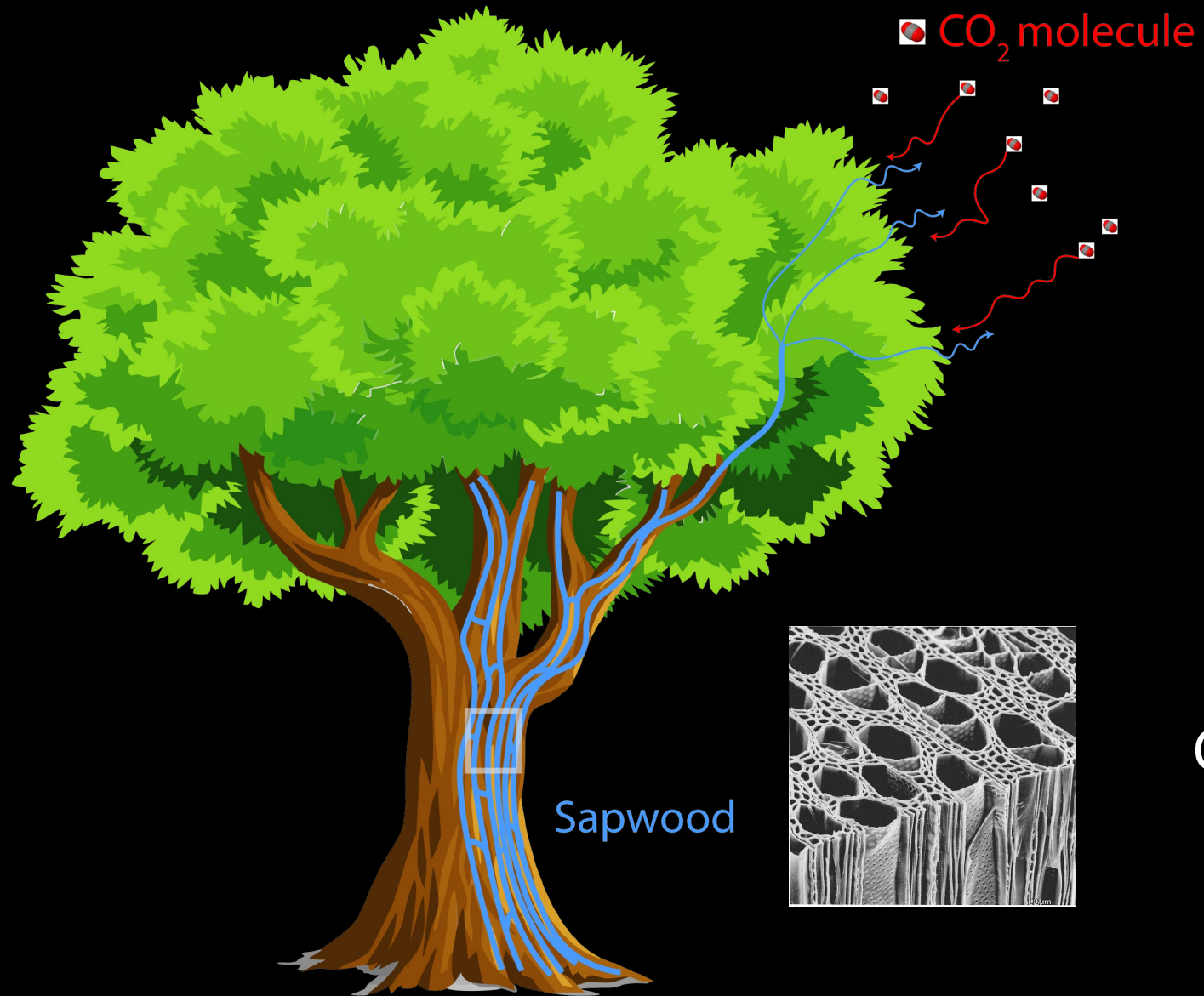
Gottlieb Haberlandt recognized sapwood as unsaturated, with both water and air

“Vessels and tracheids normally contain both air and water, the relative amounts of the two substances varying according to the season and the time of day.”

Physiological Plant Anatomy (1914)

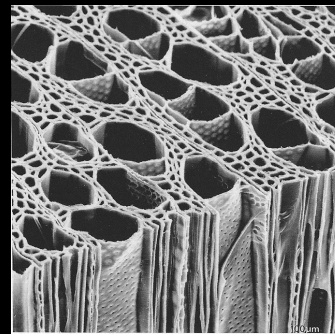


Outline



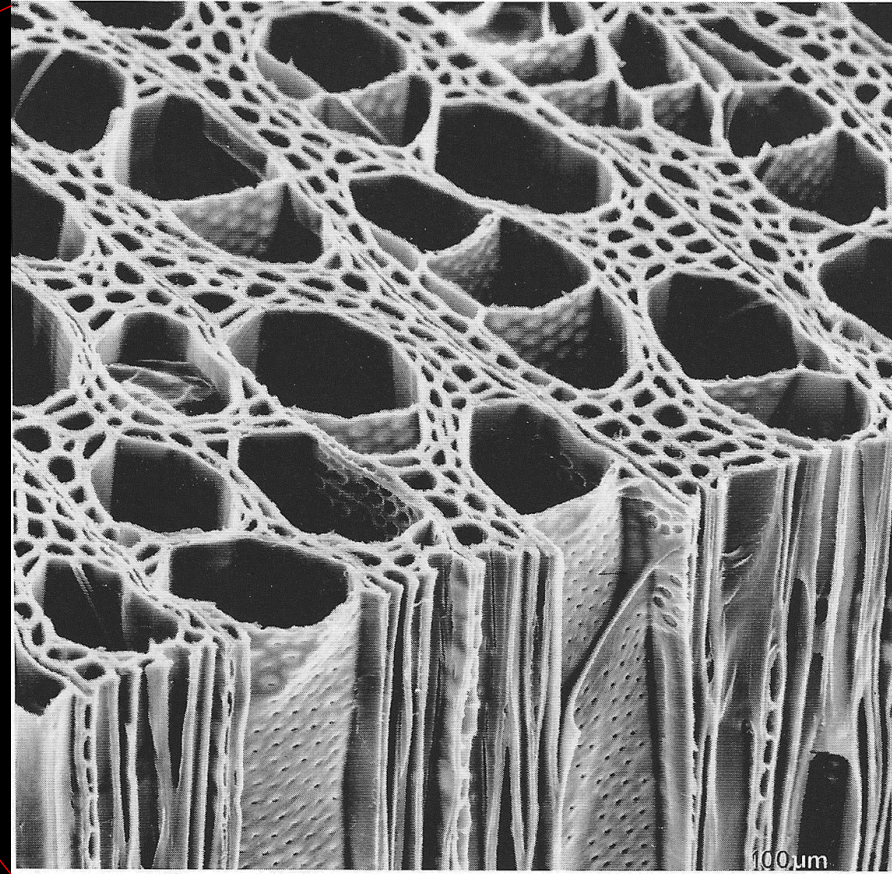
Chapter 3

Sapwood

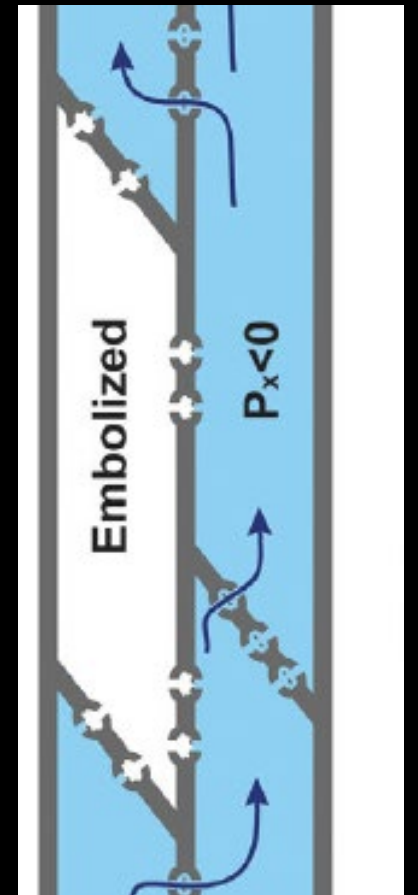


Chapters 1 & 2

Sapwood is made of conduits containing water and air embolisms

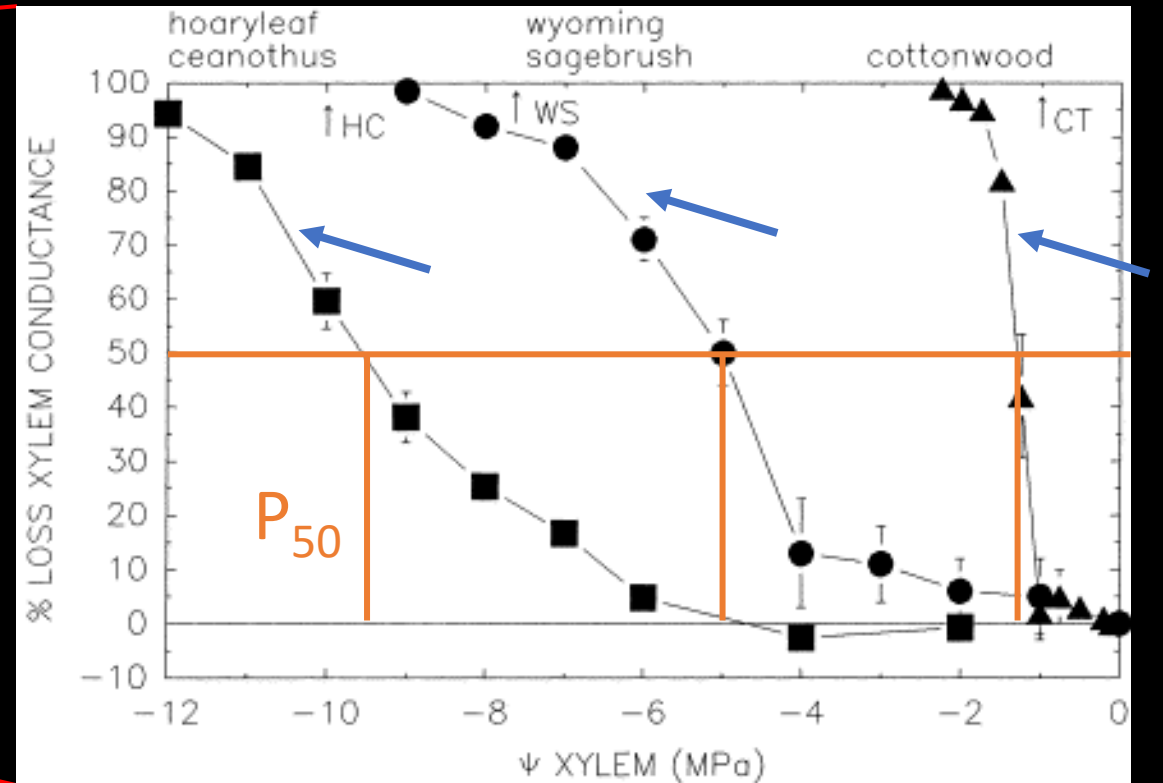


Tyree, M. T. & M. H. Zimmerman
(2002)

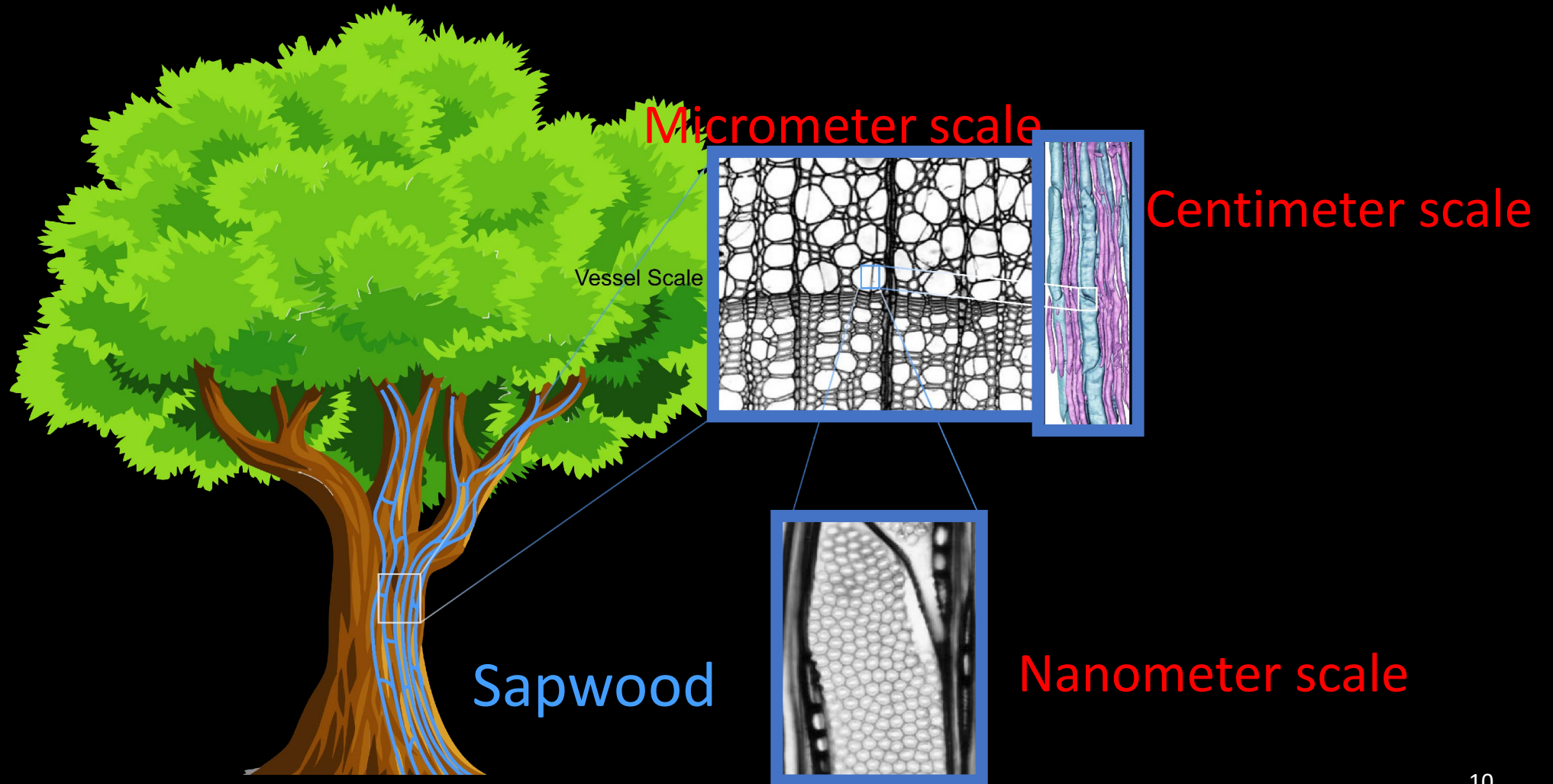


Venturas, M. D.
et al. (2017)⁸

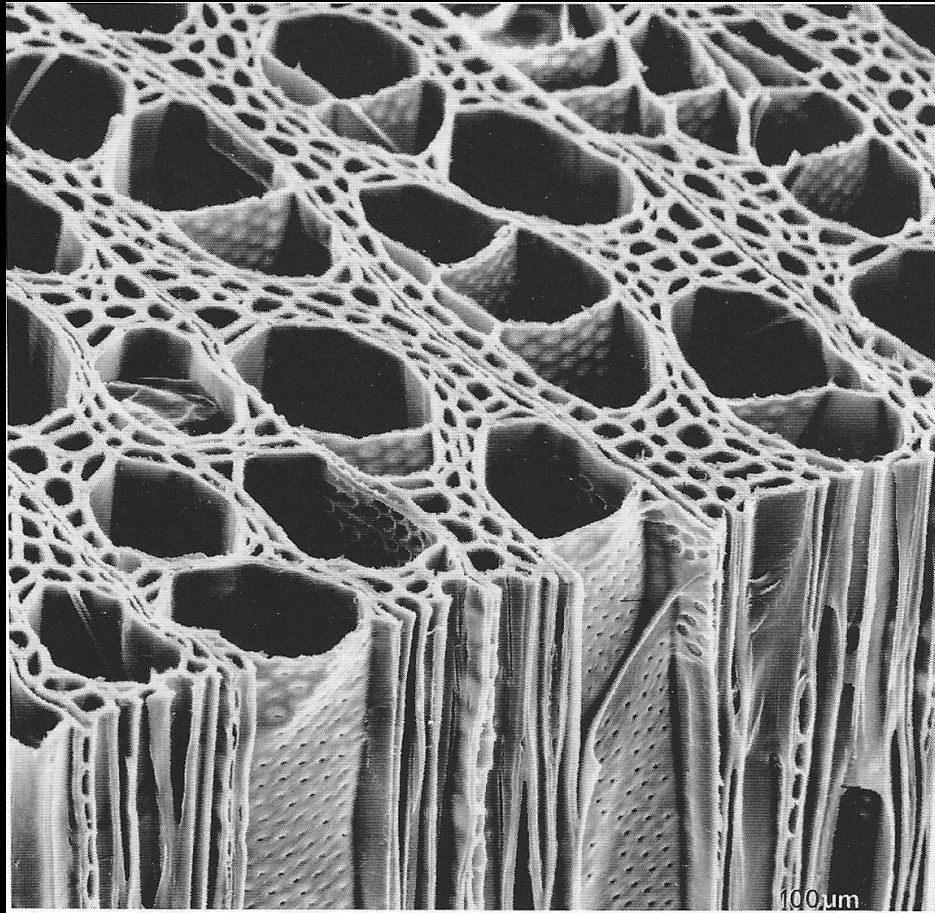
Vulnerability Curve (VC): loss of branch conductivity with decreasing water potential



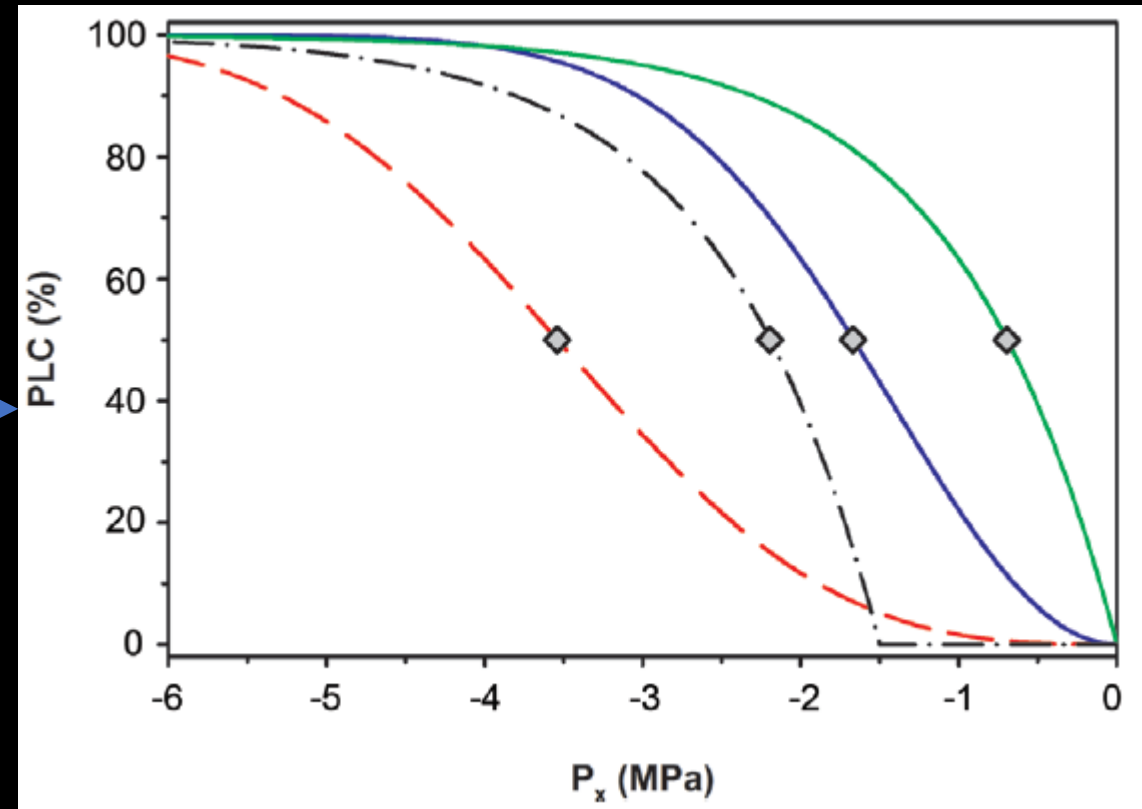
The sapwood consists of anatomical elements ranging many spatial scales



How do we link these anatomical elements to branch hydraulics?

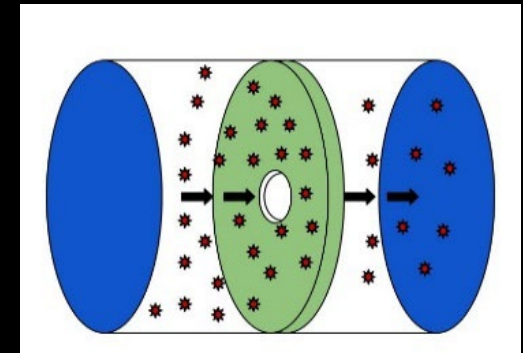
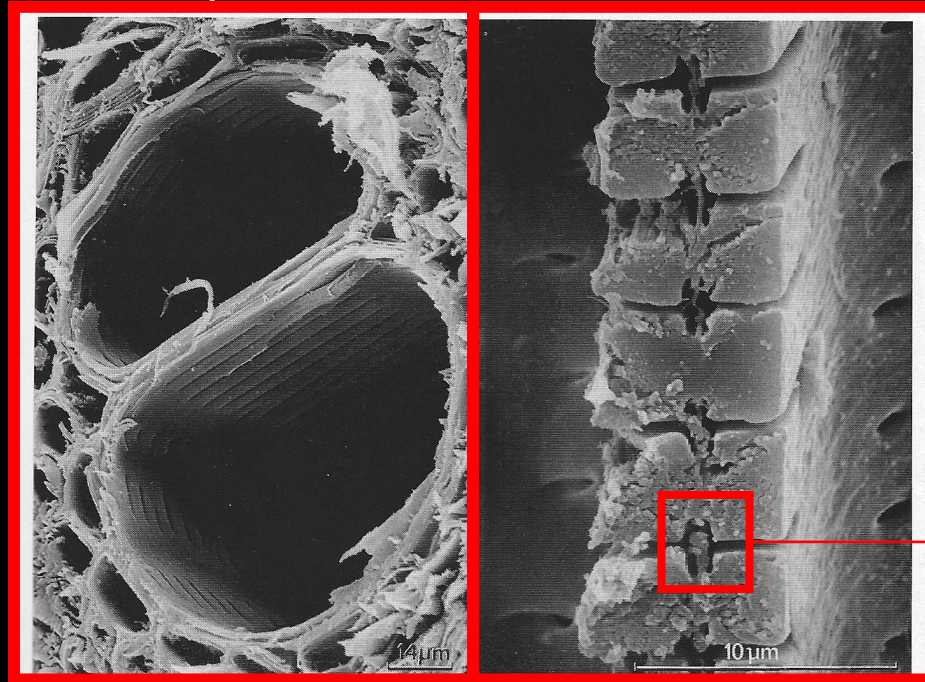
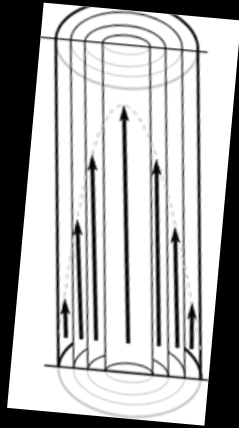


?



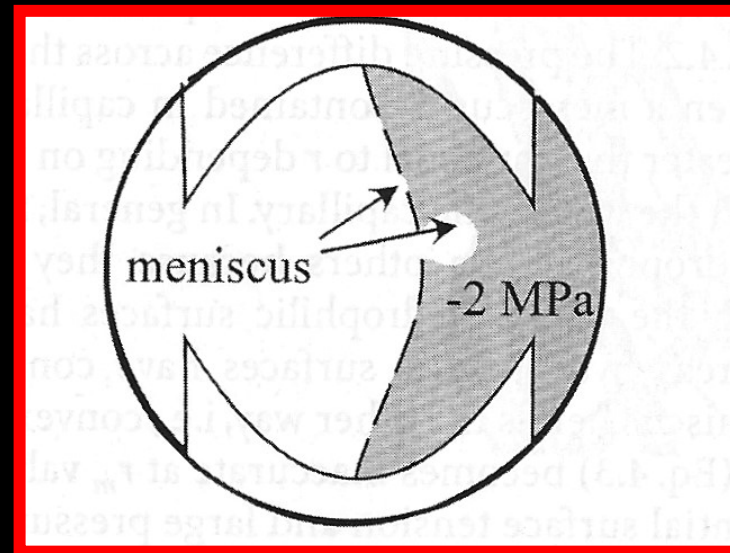
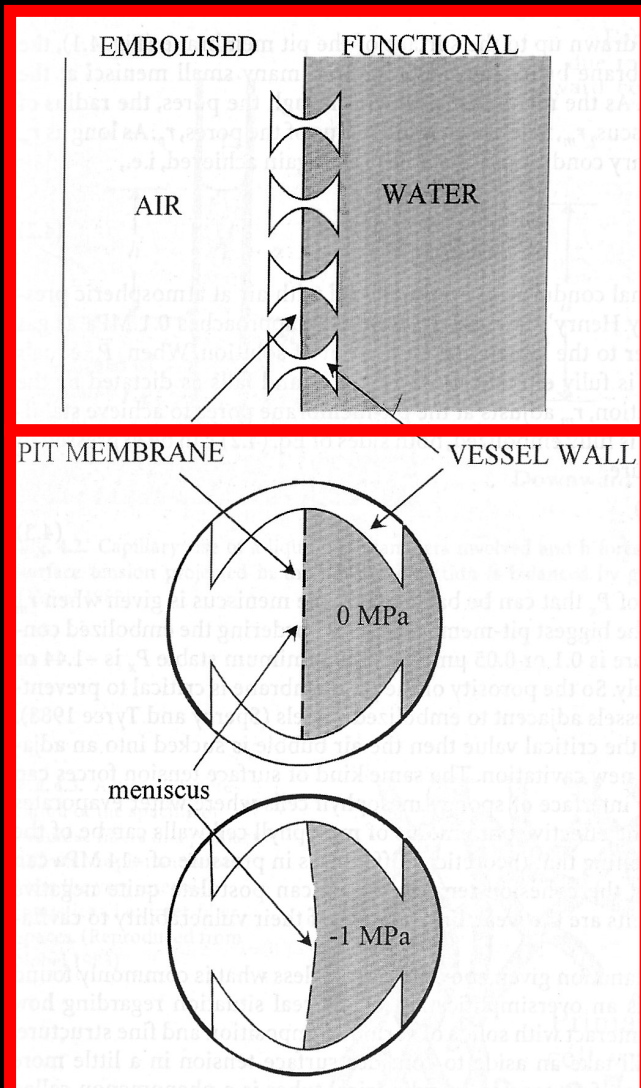
Water flow through vessels is Poiseuille and through pit membrane pores is Sampson.

Hagen-Poiseuille flow: $Q = \frac{\pi R^4}{8\mu L} \Delta P$



Sampson flow: $Q_p = \frac{R_p^3}{3\mu} \Delta P$

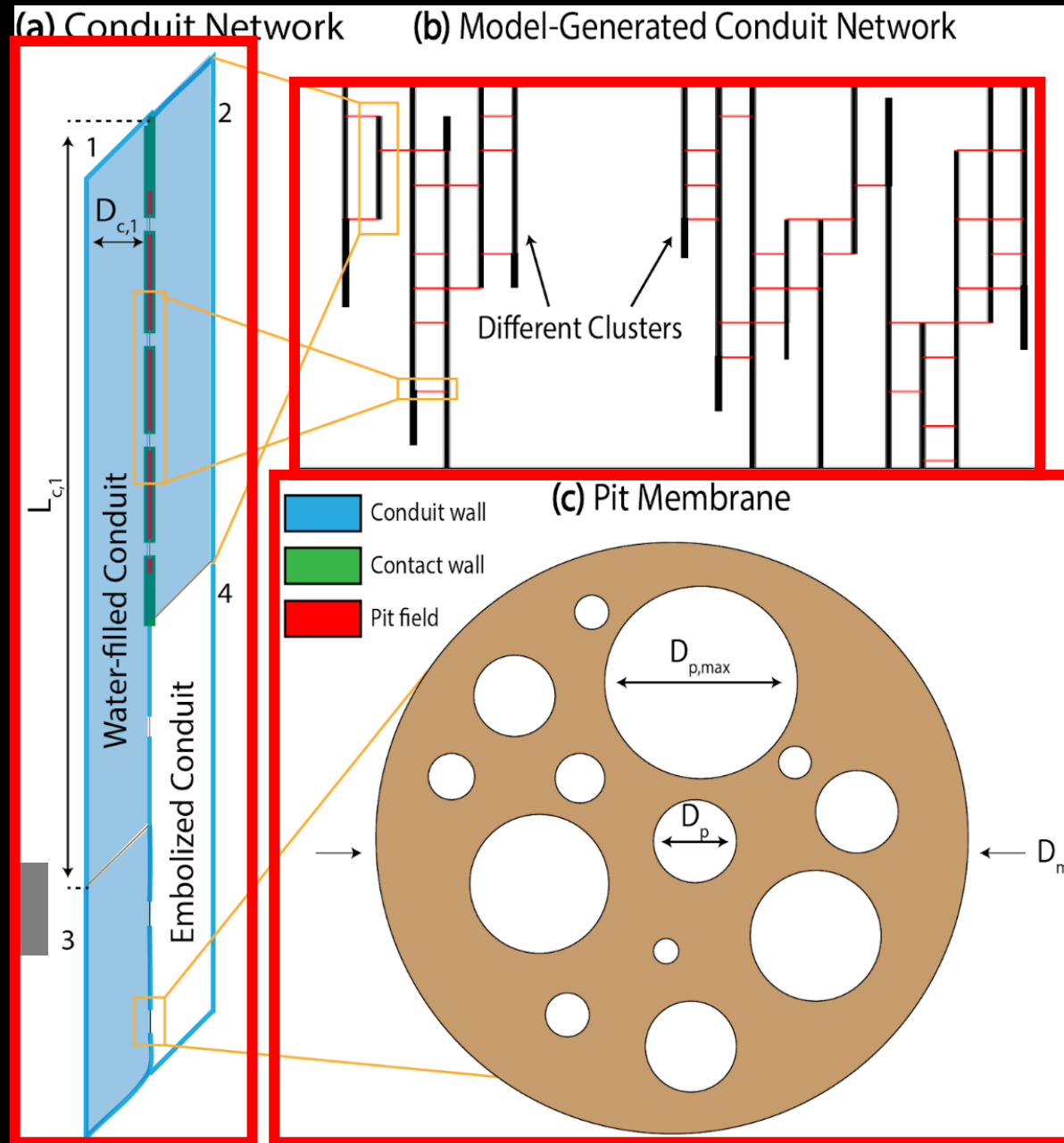
Air-seeding: pit membranes stop bubble spread in flowering plants



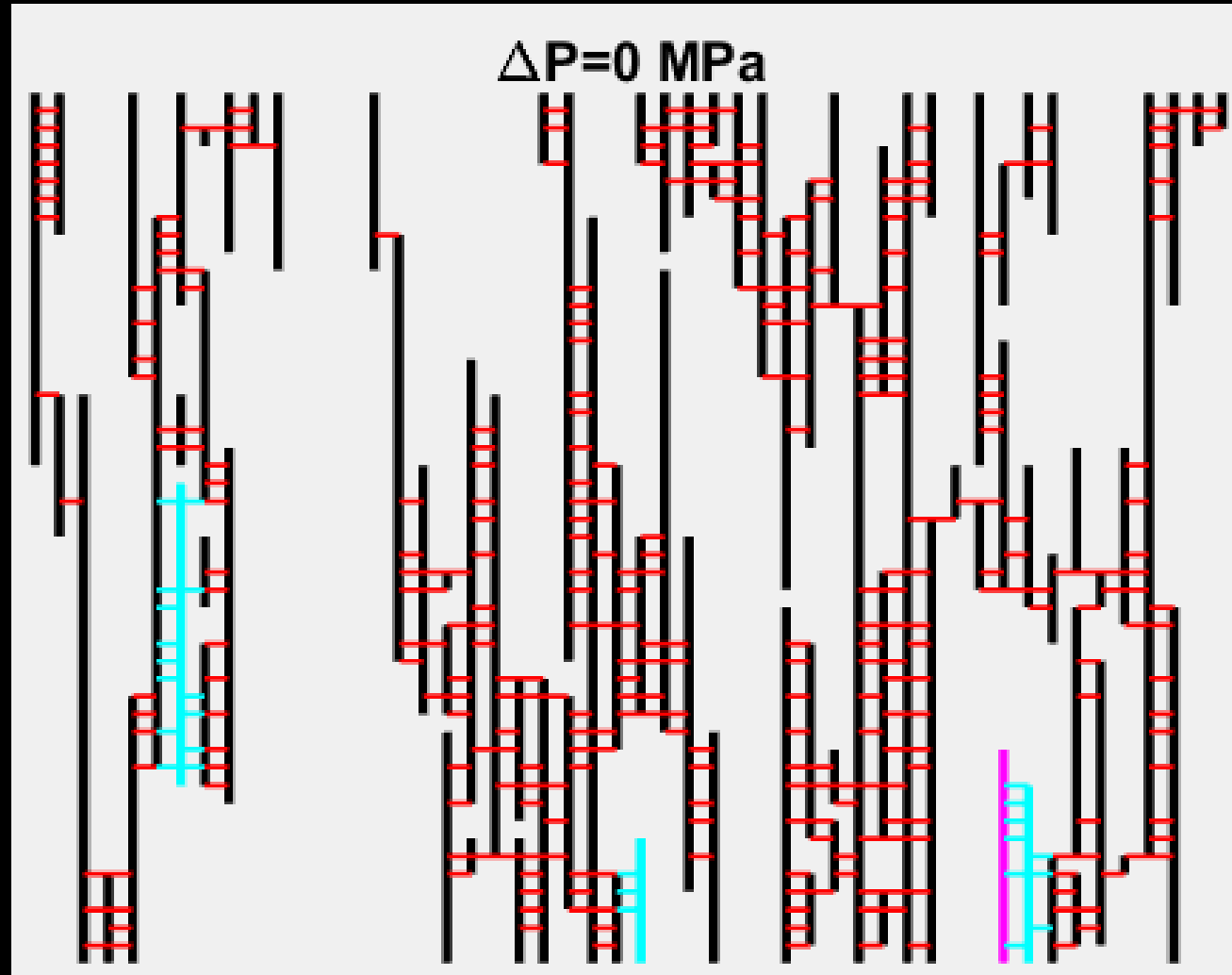
Xylem model: represents anatomy and physics of water flow

Model freely available online!

Mrad, A. et al. PC&E (2018)



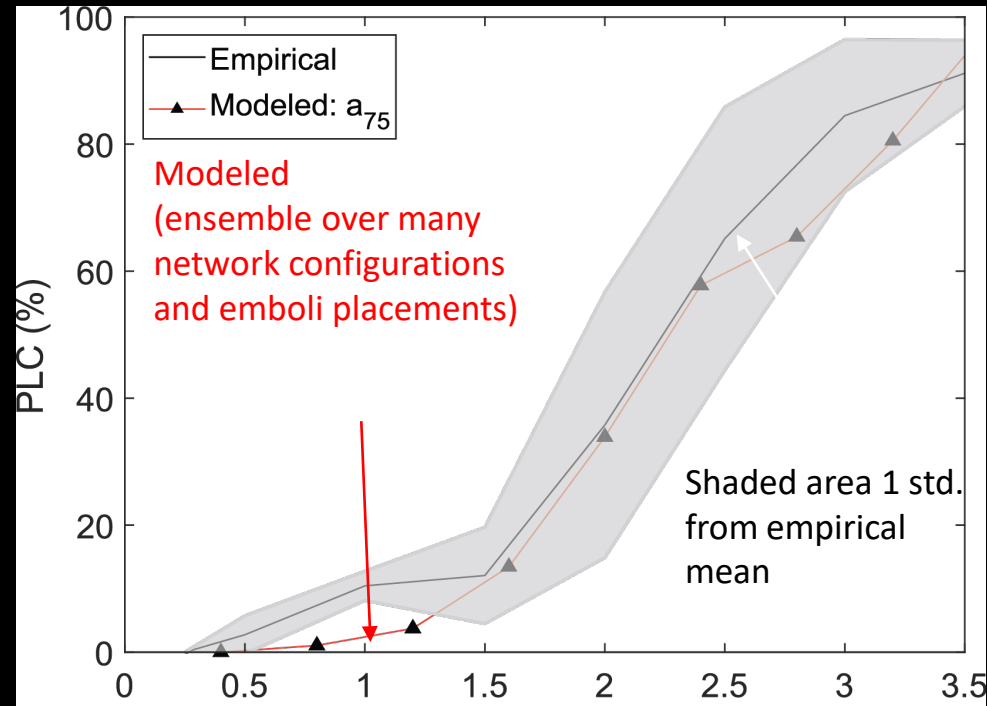
Embolism spread is modeled as an air-seeding process at the vessel level



Modeled Maple VC matches measurement using only anatomy



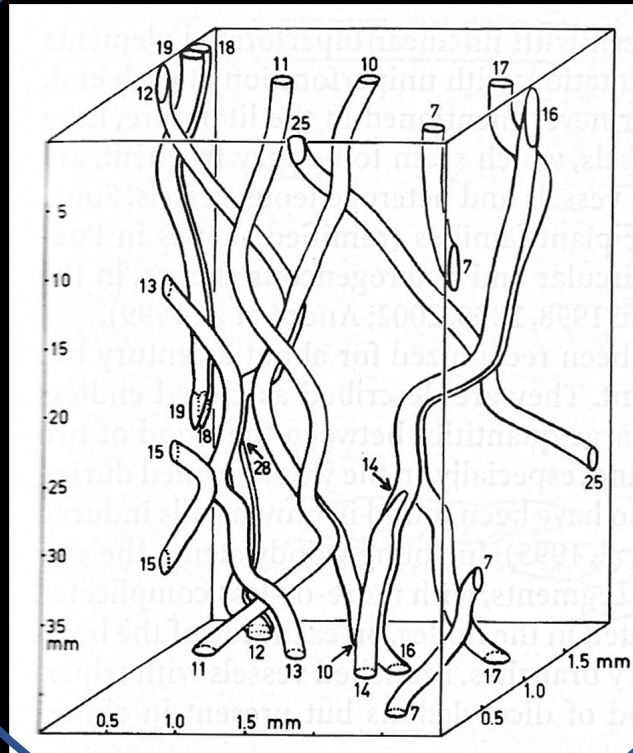
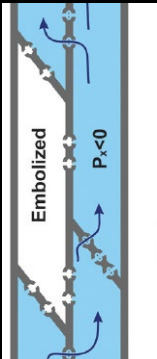
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Empirical curve: Lens et al. (2011) New Phytologist

The xylem network scale stands between the anatomy and total sapwood



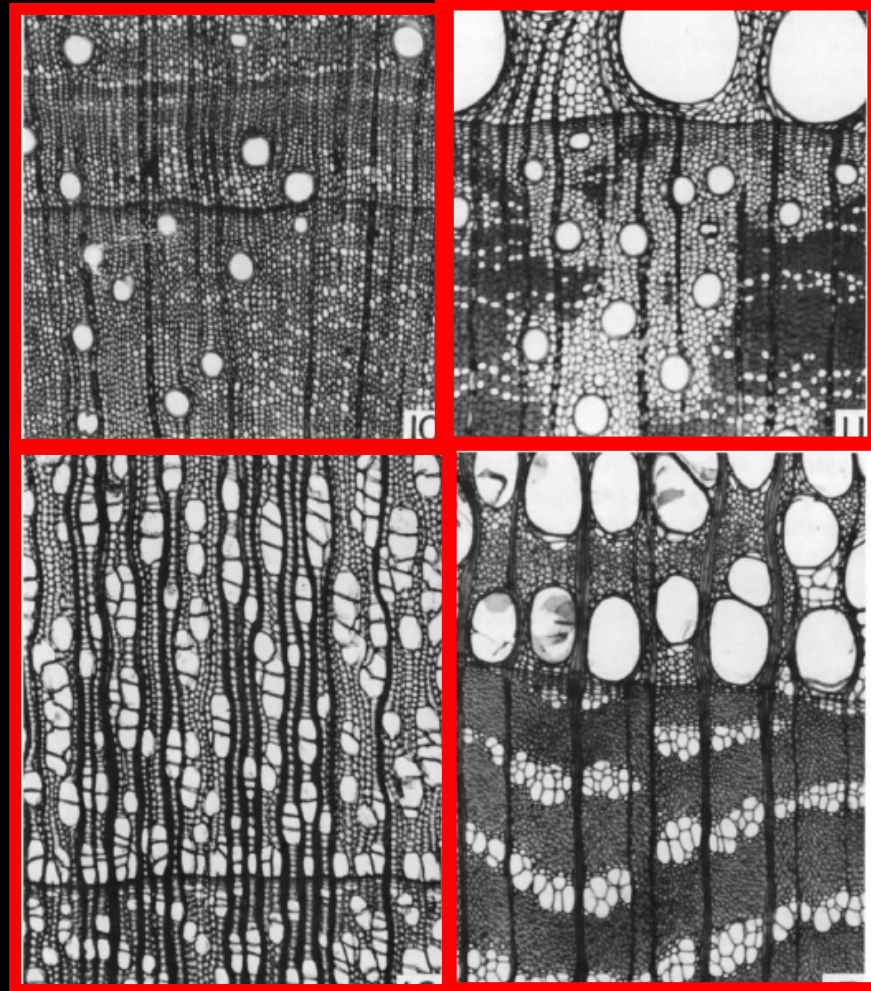
Venturas, M. D.
et al. (2017)

Tyree, M. T. and Zimmerman, M.H. (2002)



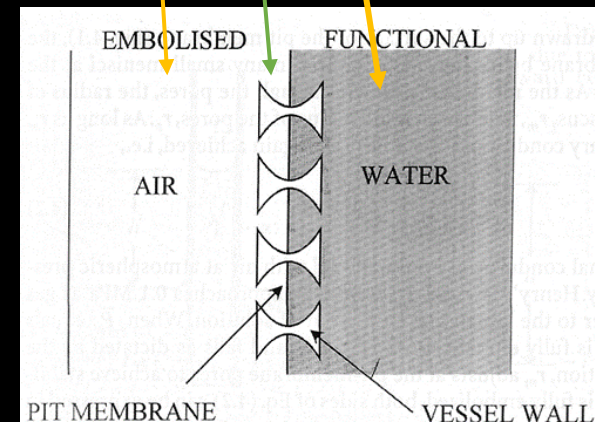
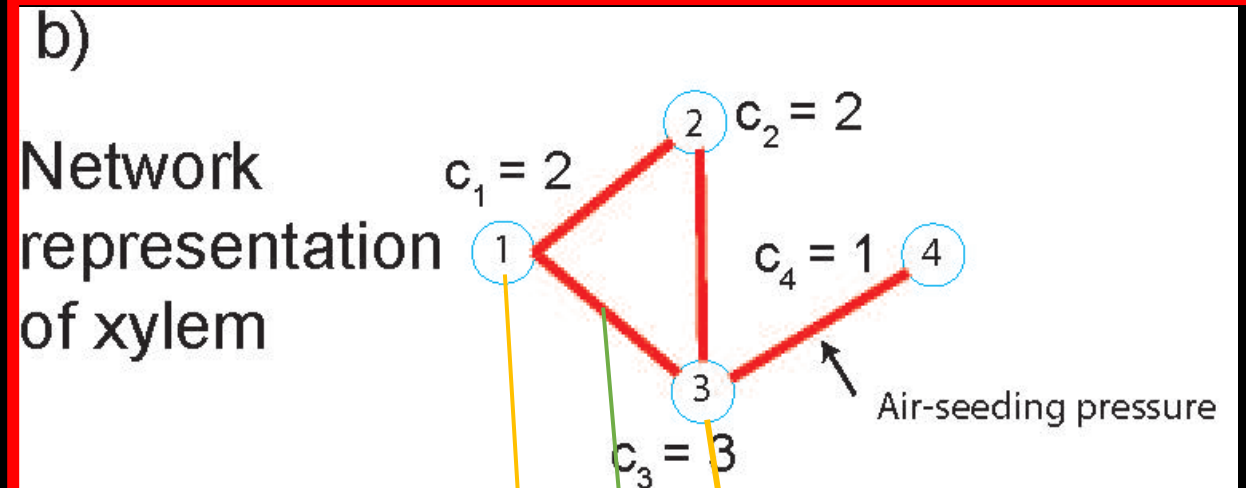
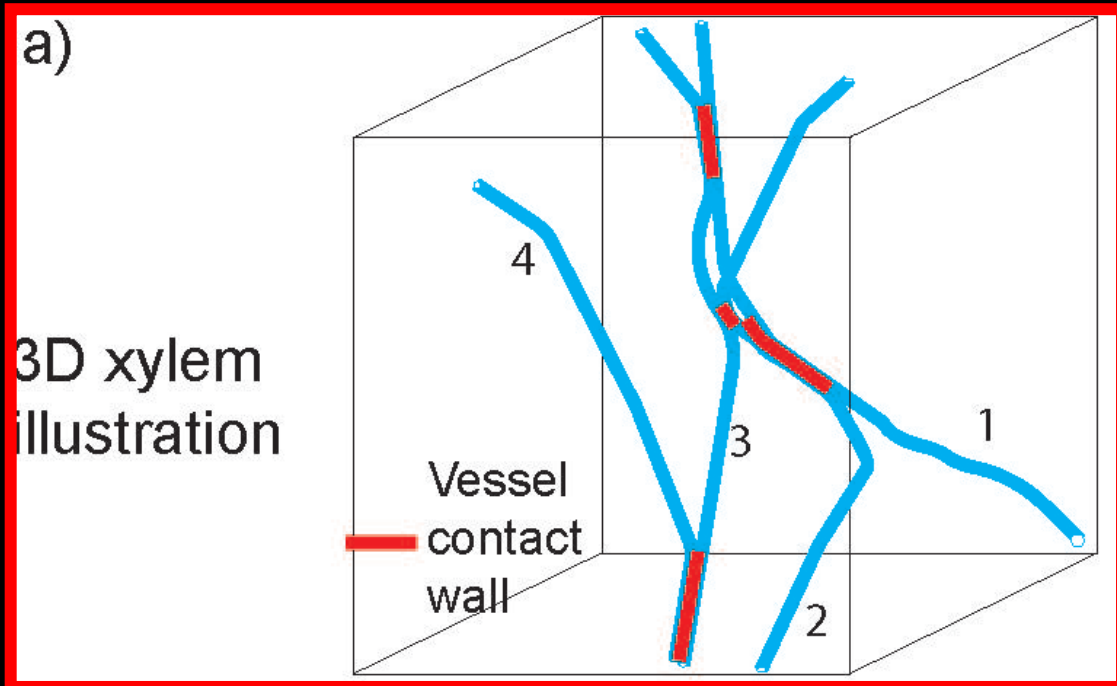
Example of 'network'-scale property

Lithocarpus densiflora *Quercus rubra*

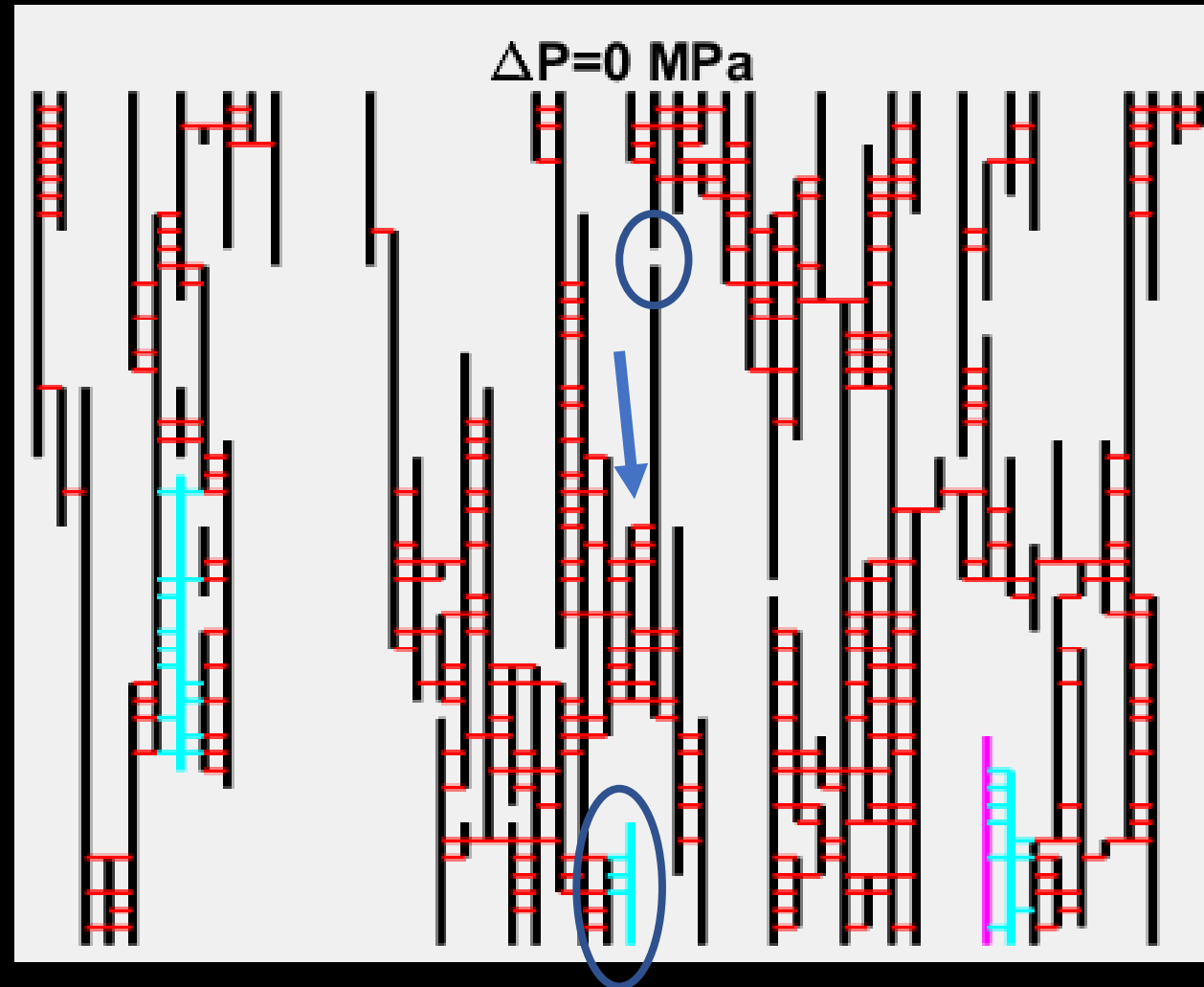


Nothofagus antarctica *Ulmus americana*

Tapping into graph theory: vessel connectivity

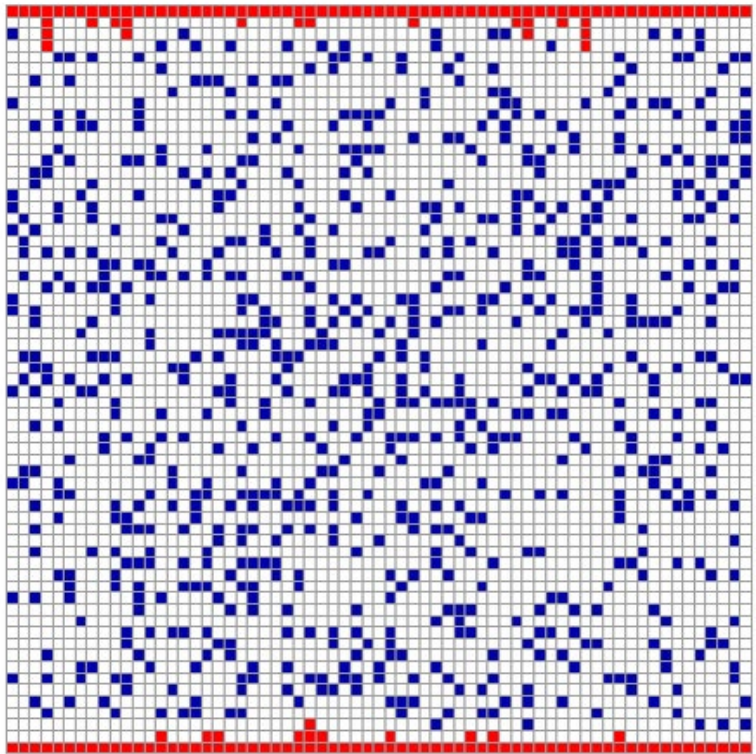


Increasing connectivity: a trade-off between redundancy and embolism spread speed



Percolation as a model of embolism spread in xylem

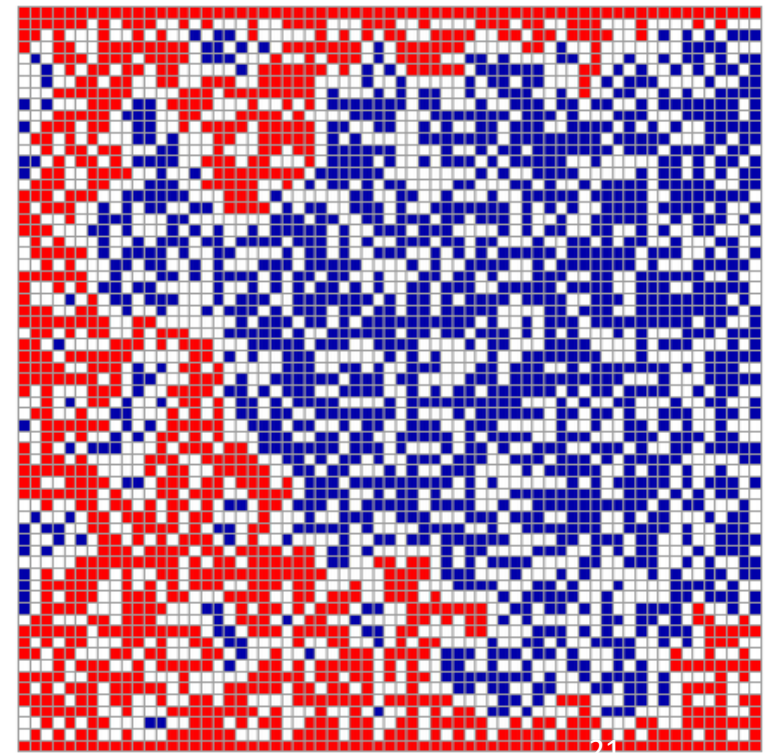
Probability = 0.2



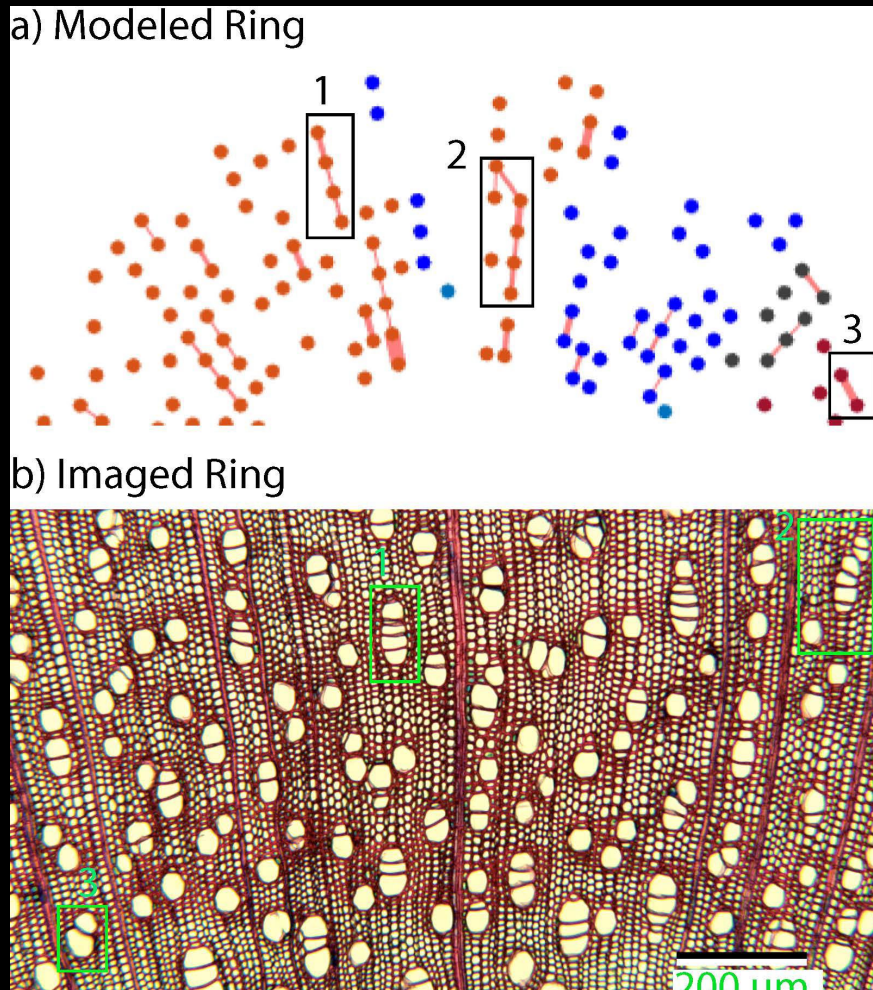
0.51



0.58



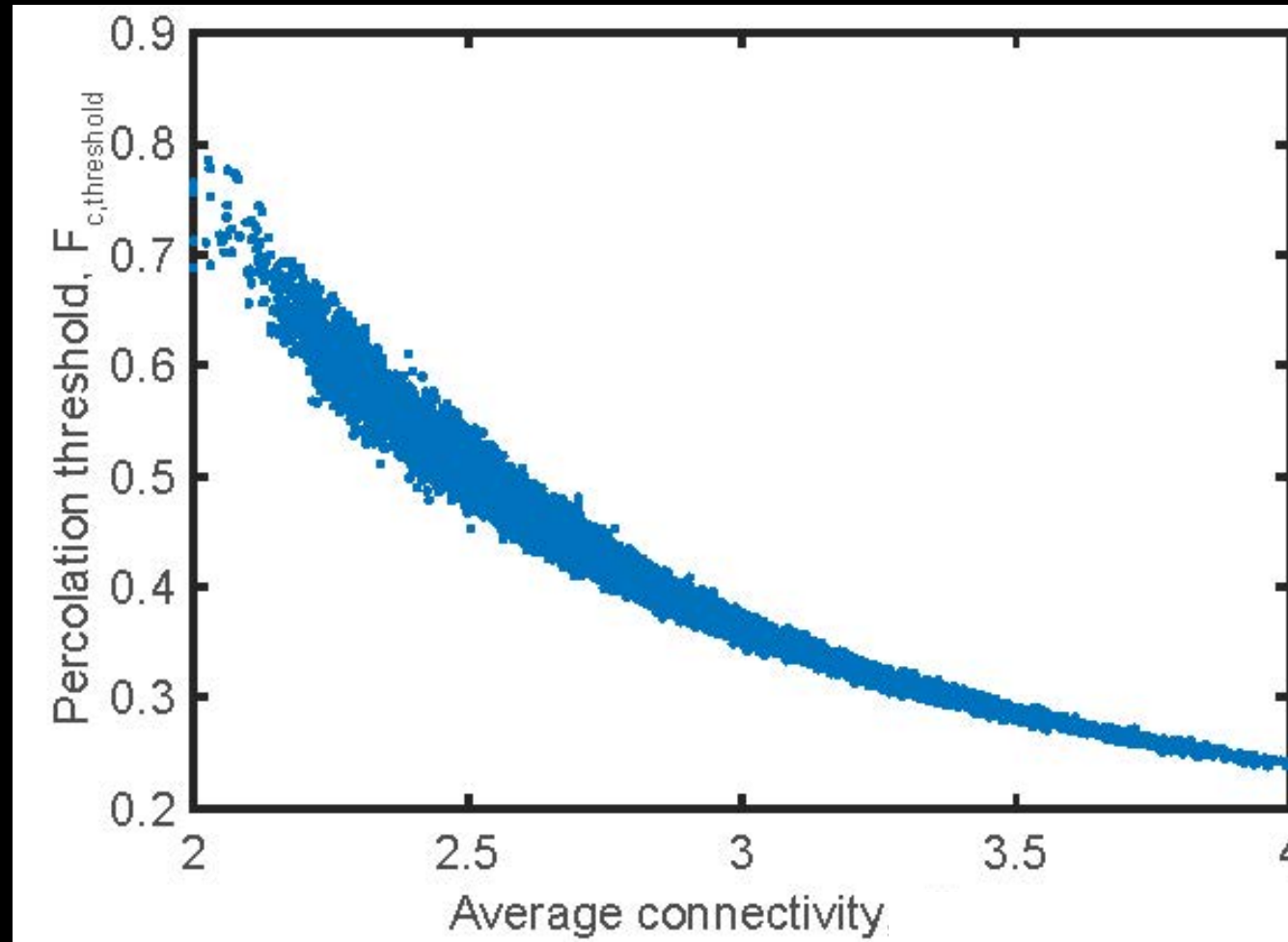
3D model to accurately represent plant porous media



$$\text{Grouping Index, } GI = \frac{\# \text{ of conduits}}{\# \text{ of groups}}$$

Acer negundo (Boxelder)

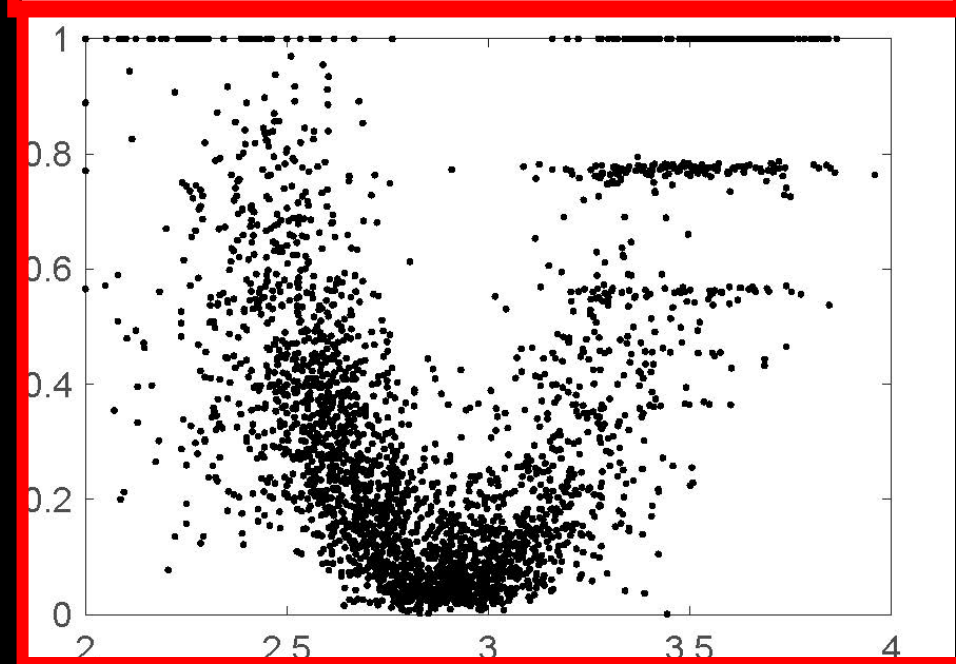
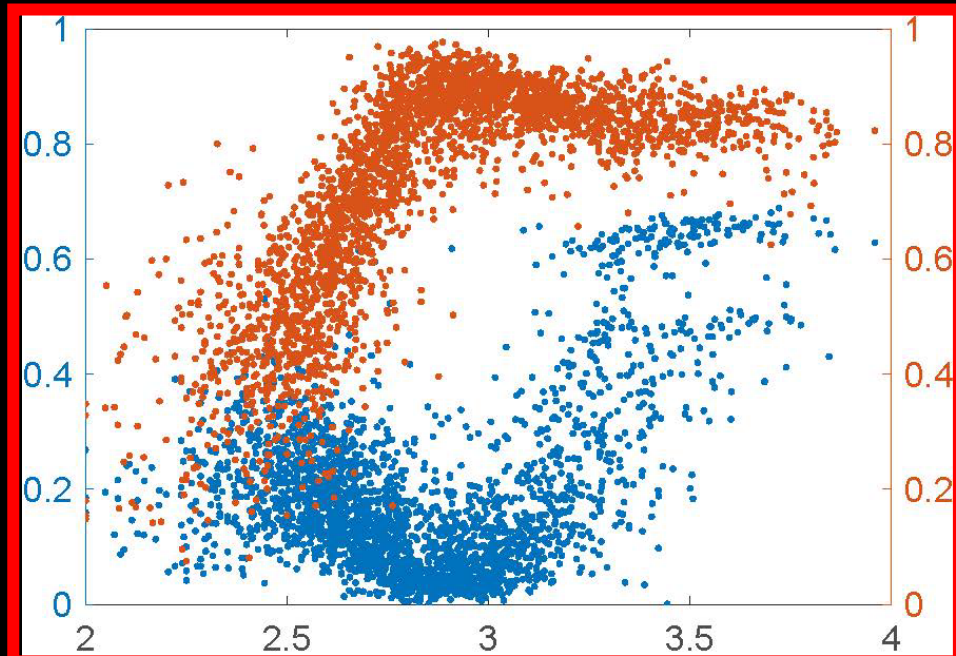
The percolation threshold declines as vessel connectivity increases = faster embolism spread



Model confirms 'redundancy- spread speed' trade-off of connectivity

Spread speed

Redundancy



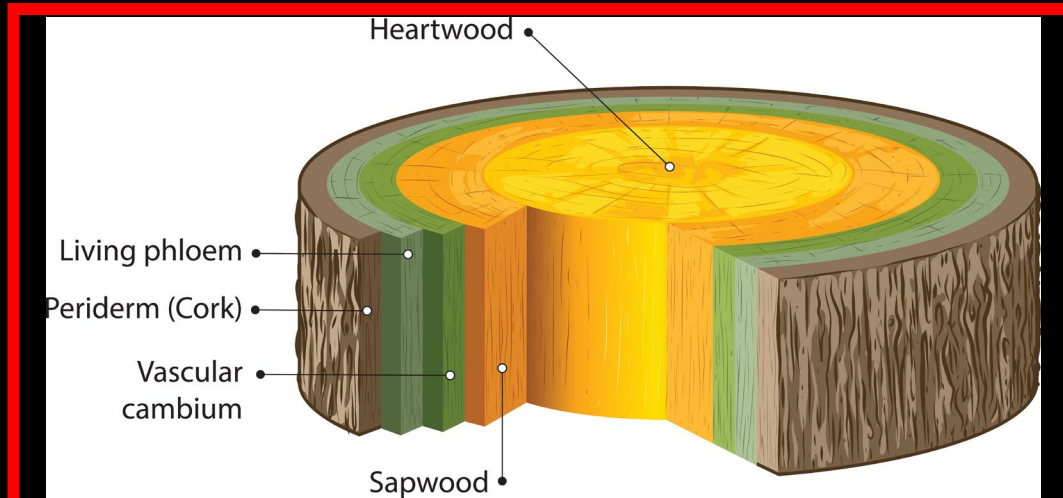
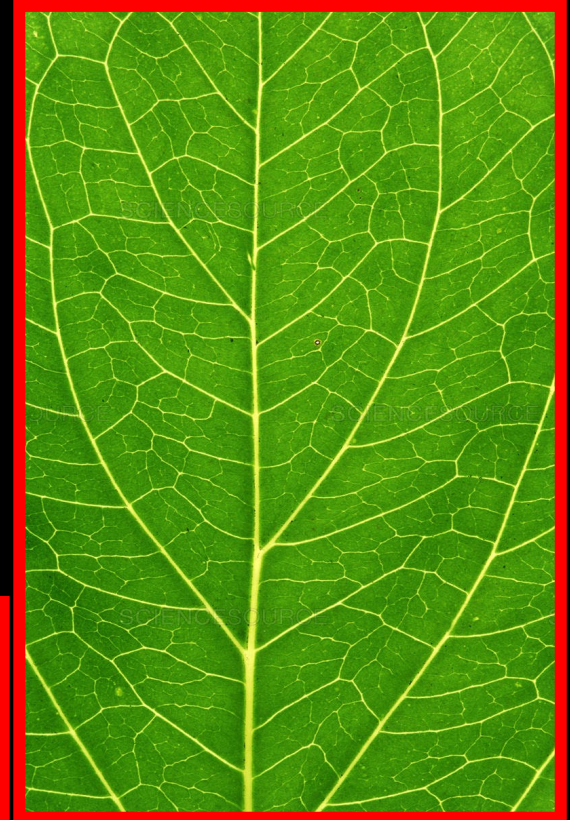
$$\frac{\text{spread speed}}{\text{Redundancy}}$$

Mrad et al. 2021
“The roles of conduit
redundancy and
connectivity in xylem
hydraulic functions”
In Review, New
Phytologist

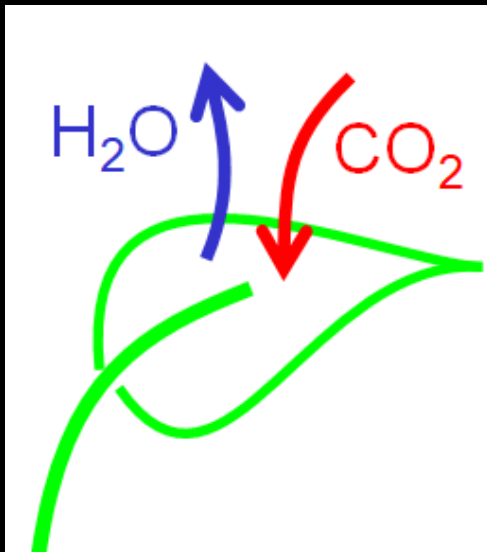
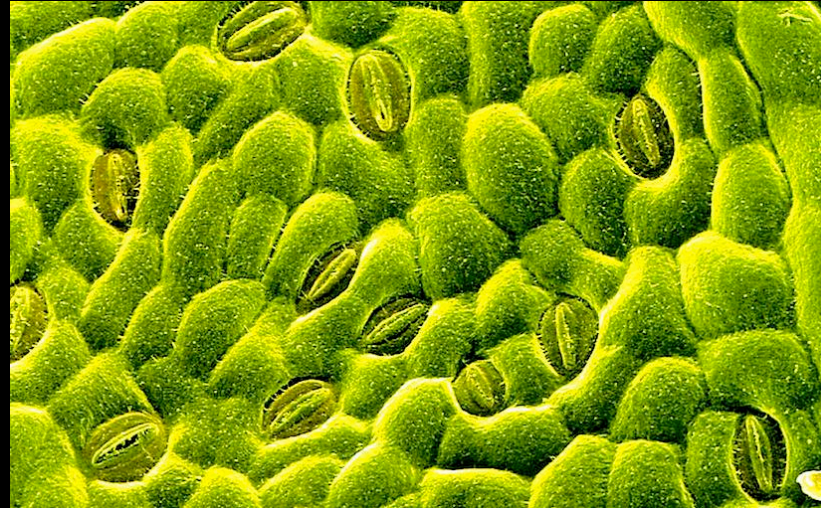
On their way to the leaf, water molecules overcome soil-root, sapwood, leaf resistances



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How do stomata, and photosynthesis, respond to lack of water?



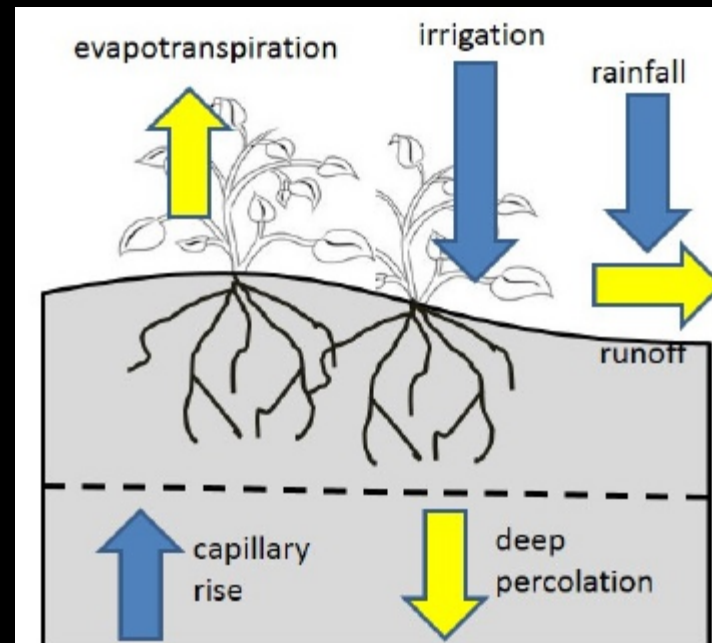
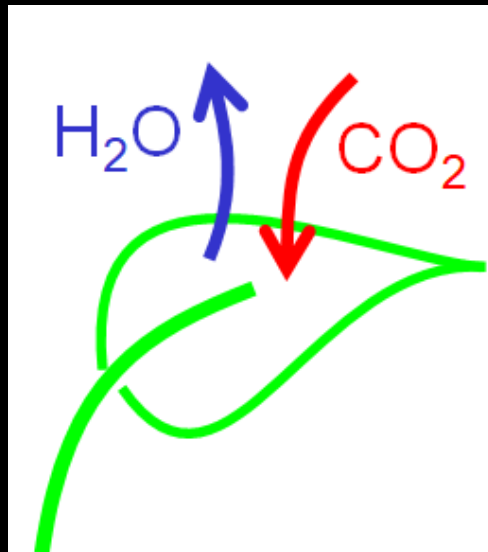
IX. *Observations on Stomata.*

By FRANCIS DARWIN, *F.R.S.*

Received May 31,—Read June 16, 1898.

The Hamiltonian mathematically represents the trade-off

$$H \left(g_s, x, \frac{dx}{dt}, \lambda, t \right) = A(g_s, t) - \lambda f_e \left(g_s, x, \frac{dx}{dt}, t \right)$$



Mrad et al. 2019 “A Dynamic Optimality Principle for Water Use Strategies Explains Isohydic to Anisohydric Plant Responses to Drought”
Frontiers in Forests and Global Change

Water-use strategy (WUS) as a “terminal” gain term

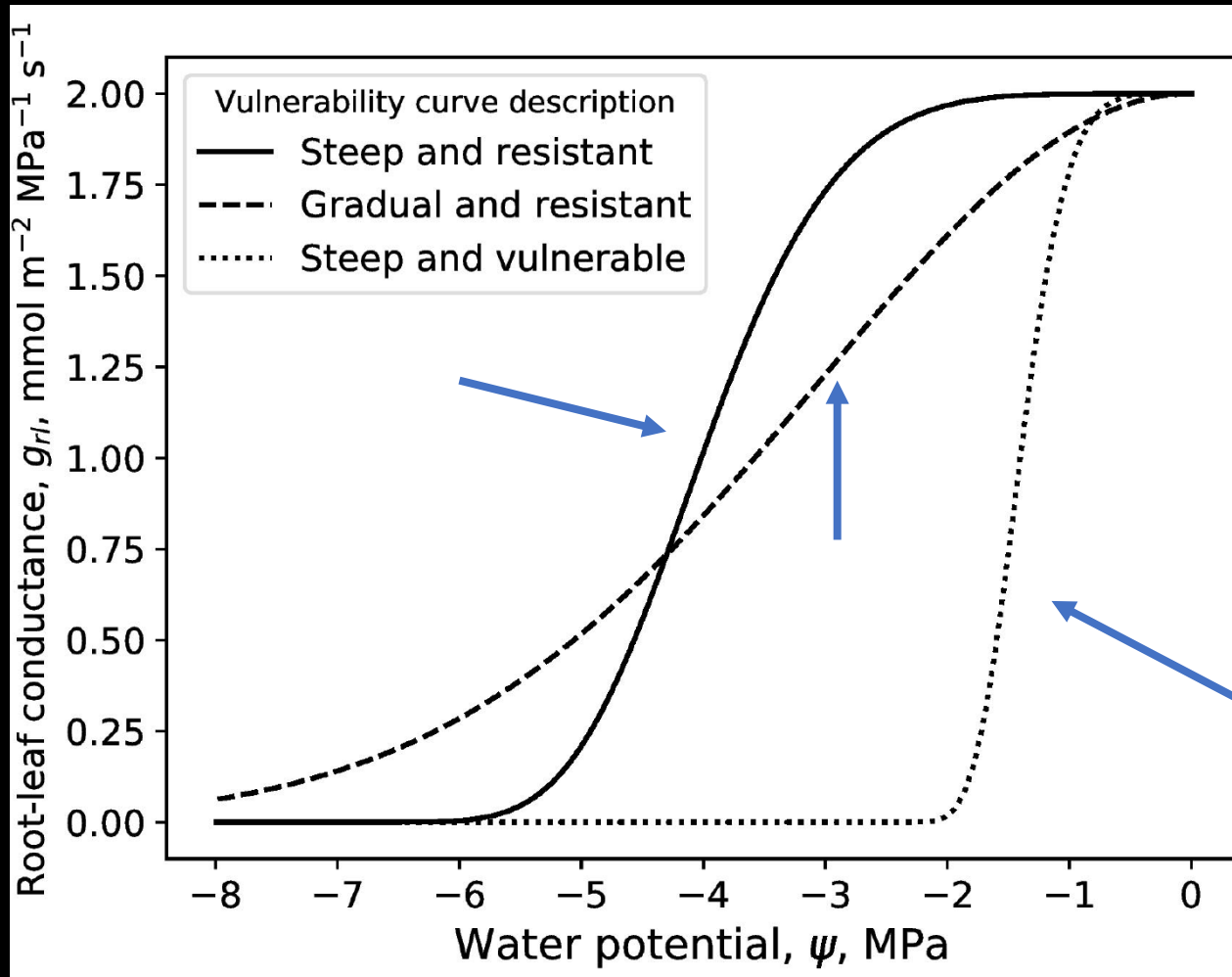
$$\int_0^T H \left(g_s, x, \frac{dx}{dt}, \lambda, t \right) dt + \mathbf{J_T}$$

where

$$\mathbf{J_T} = \Lambda x(T)$$

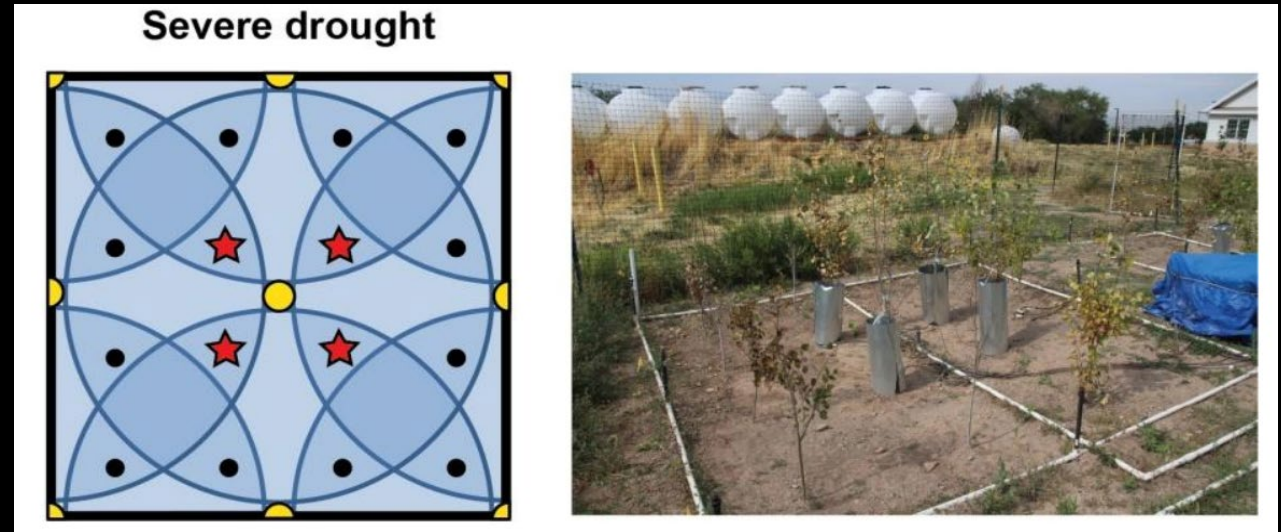
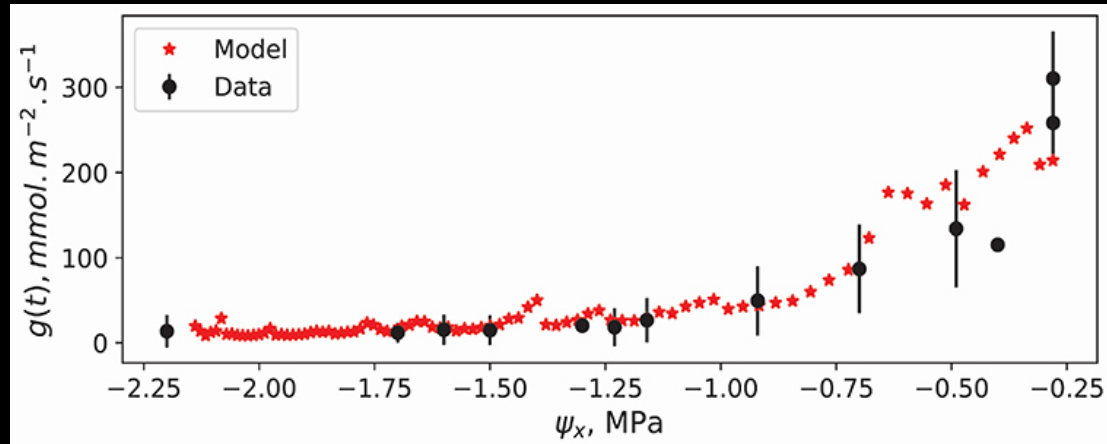
High Λ = conservative WUS
Low Λ = aggressive WUS

A limit to transpiration is enforced using soil-stem-leaf Vulnerability Curves



Mrad et al. 2019 “A Dynamic Optimality Principle for Water Use Strategies Explains Isohydric to Anisohydric Plant Responses to Drought”
Frontiers in Forests and Global Change

The model reproduces an 87-day dry-down for 16 Aspen saplings



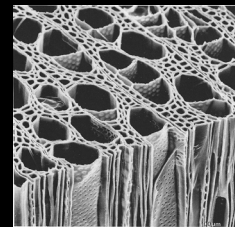
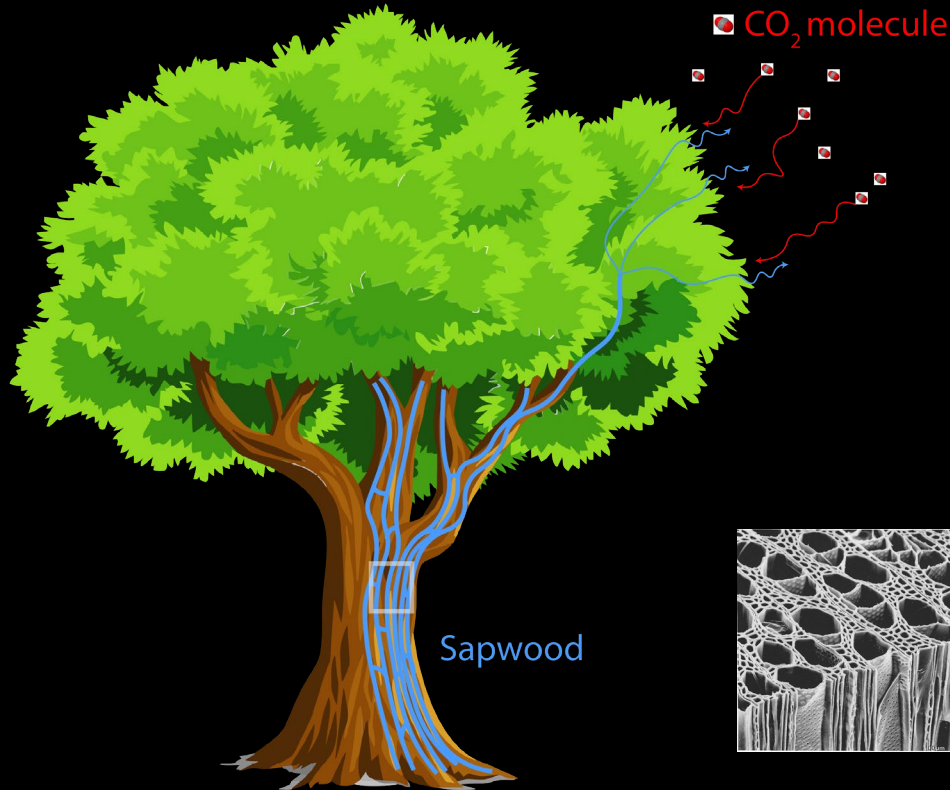
Venturas, M. D., et al. *New Phytologist* (2018)

The end



PNAS

Proceedings of the National Academy of Sciences of the United States of America



Sapwood



@mradassaad

[https://github.com/mradassaad/Xylem_Network_](https://github.com/mradassaad/Xylem_Network_Matlab)

Matlab

Recovering the Metabolic, Self-Thinning, and Constant Final Yield Rules in Mono-Specific Stands

Assaad Mrad^{1*}, Stefano Manzoni^{2,3}, Ram Oren^{1,4}, Giulia Vico⁵, Magnus Lindh² and Gabriel Katul^{1,6}

Peak grain forecasts for the U.S. High Plains amid withering waters

Assaad Mrad¹, Gabriel G. Katul¹, Delphis F. Levia^{2,3}, Andrew J. Guswa⁴, Elizabeth W. Boyer⁵, Michael Bruen⁶, Darryl E. Carlyle-Moses⁷, Rachel Coyte¹, Irena F. Creed⁸, Nick van de Giesen⁹, Domenico Grasso¹⁰, David M. Hannah¹¹, Janice E. Hudson², Vincent Humphrey¹², Shin'ichi Iida¹³, Robert B. Jackson¹⁴, Tomo'omi Kumagai¹⁵, Pilar Llorens¹⁶, Beate Michalzik¹⁷, Kazuki Nanko¹³, Catherine A. Peters¹⁸, John S. Selker¹⁹, Doerthe Tetzlaff^{20,21}, Maciej Zalewski²², and Bridget R. Scanlon²³

A network model links wood anatomy to xylem tissue hydraulic behaviour and vulnerability to cavitation

Assaad Mrad¹ | Jean-Christophe Domec^{1,2} | Cheng-Wei Huang³ | Frederic Lens⁴ | Gabriel Katul¹

A Dynamic Optimality Principle for Water Use Strategies Explains Isohydric to Anisohydric Plant Responses to Drought

Assaad Mrad^{1*}, Sanna Sevanto², Jean-Christophe Domec^{1,3}, Yanlan Liu¹, Mazen Nakad¹ and Gabriel Katul^{1,4}

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- Mrad, Assaad, et al. "A network model links wood anatomy to xylem tissue hydraulic behaviour and vulnerability to cavitation." *Plant, cell & environment* 41.12 (2018): 2718-2730.
- Mrad, Assaad, Sanna Sevanto, Jean-Christophe Domec, Yanlan Liu, Mazen Nakad, & Gabriel Katul. 2019. "A Dynamic Optimality Principle for Water Use Strategies Explains Isohydic to Anisohydric Plant Responses to Drought." *Frontiers in Forests and Global Change* 2 (August): 49
- Mrad, Assaad, et al. "Recovering the Metabolic, Self-Thinning, and Constant Final Yield Rules in Mono-Specific Stands." *Frontiers in Forests and Global Change* 3 (2020): 62.
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- Wang, Yujie, et al. "A theoretical and empirical assessment of stomatal optimization modeling." *New Phytologist* (2020).