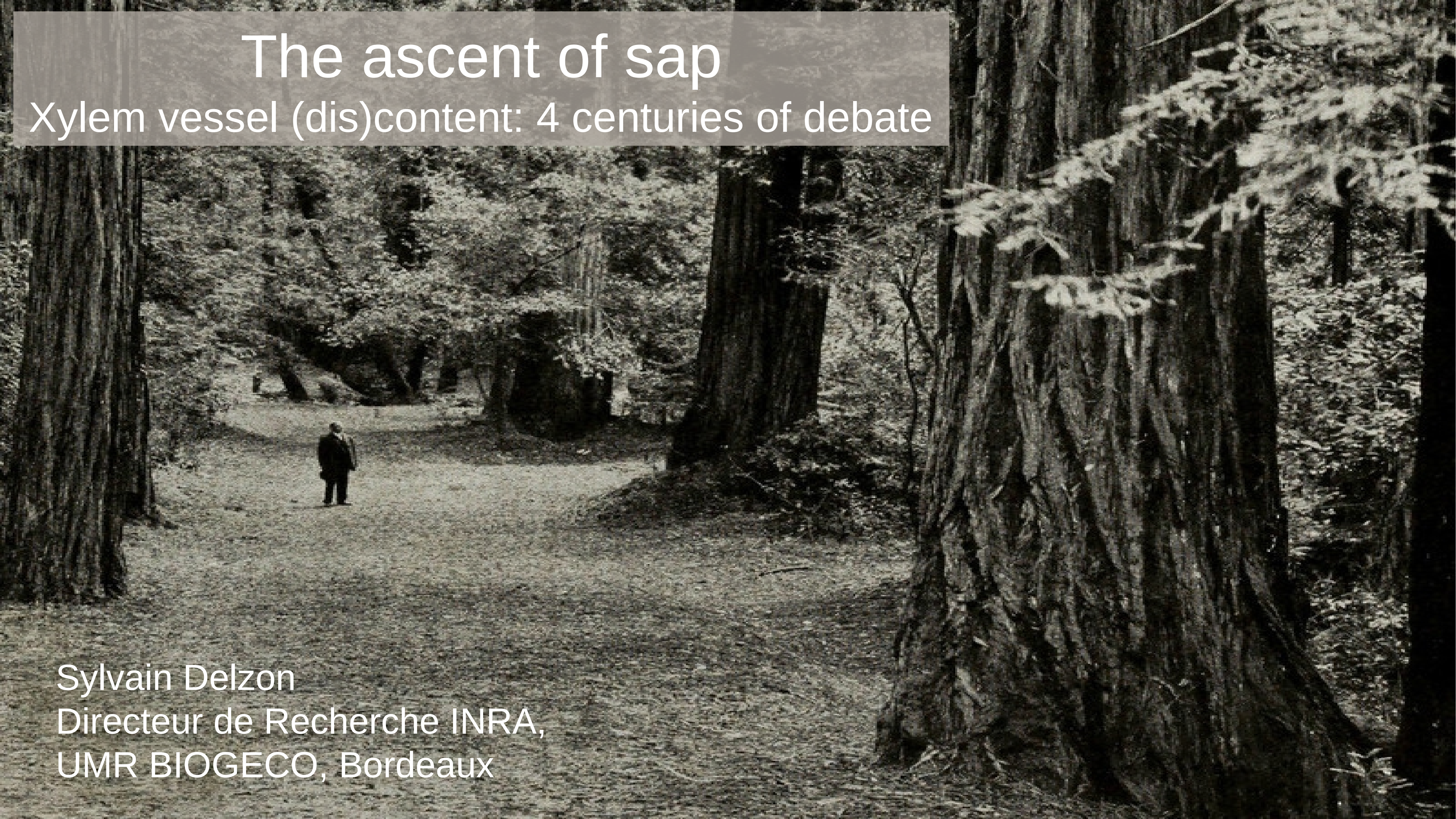
The ascent of sap

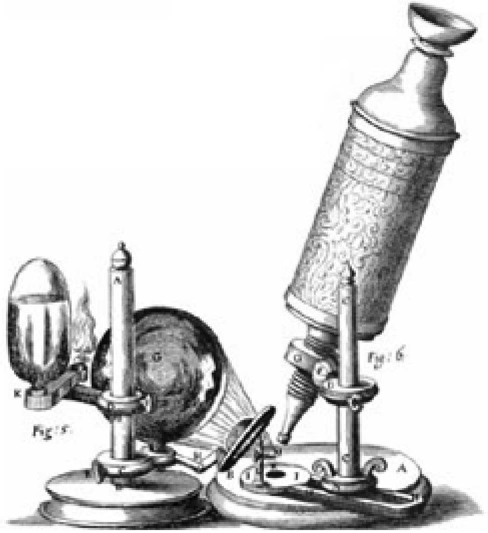
Xylem vessel (dis)content: 4 centuries of debate

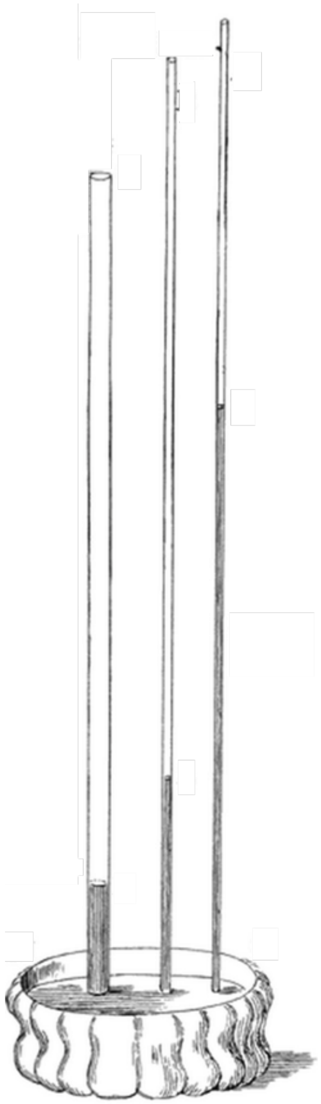


Sylvain Delzon
Directeur de Recherche INRA,
UMR BIOGECO, Bordeaux

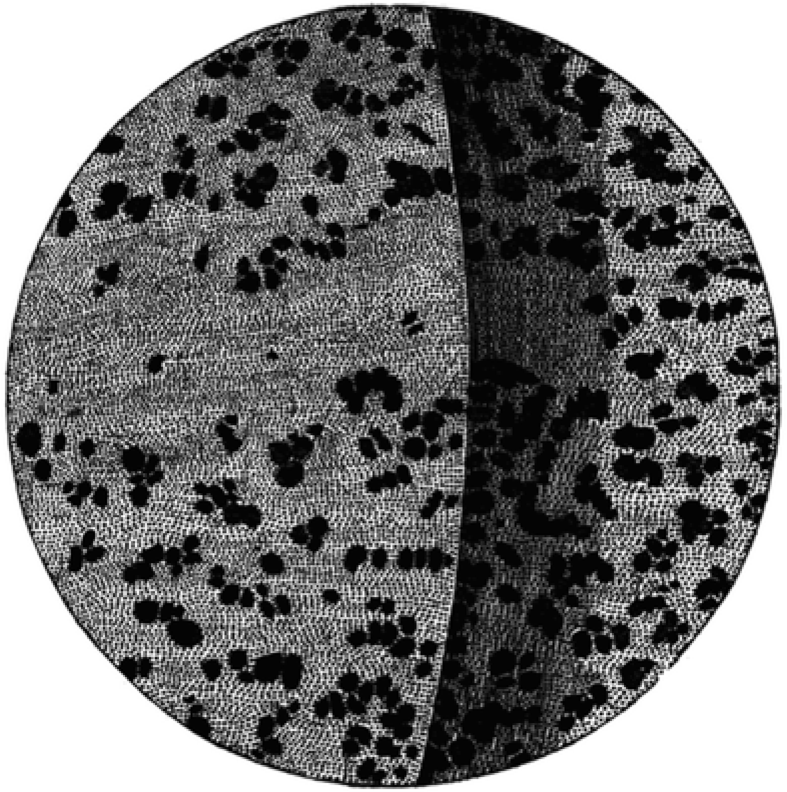
Robert Hooke

1635-1703





Wood contains pores (vessels)



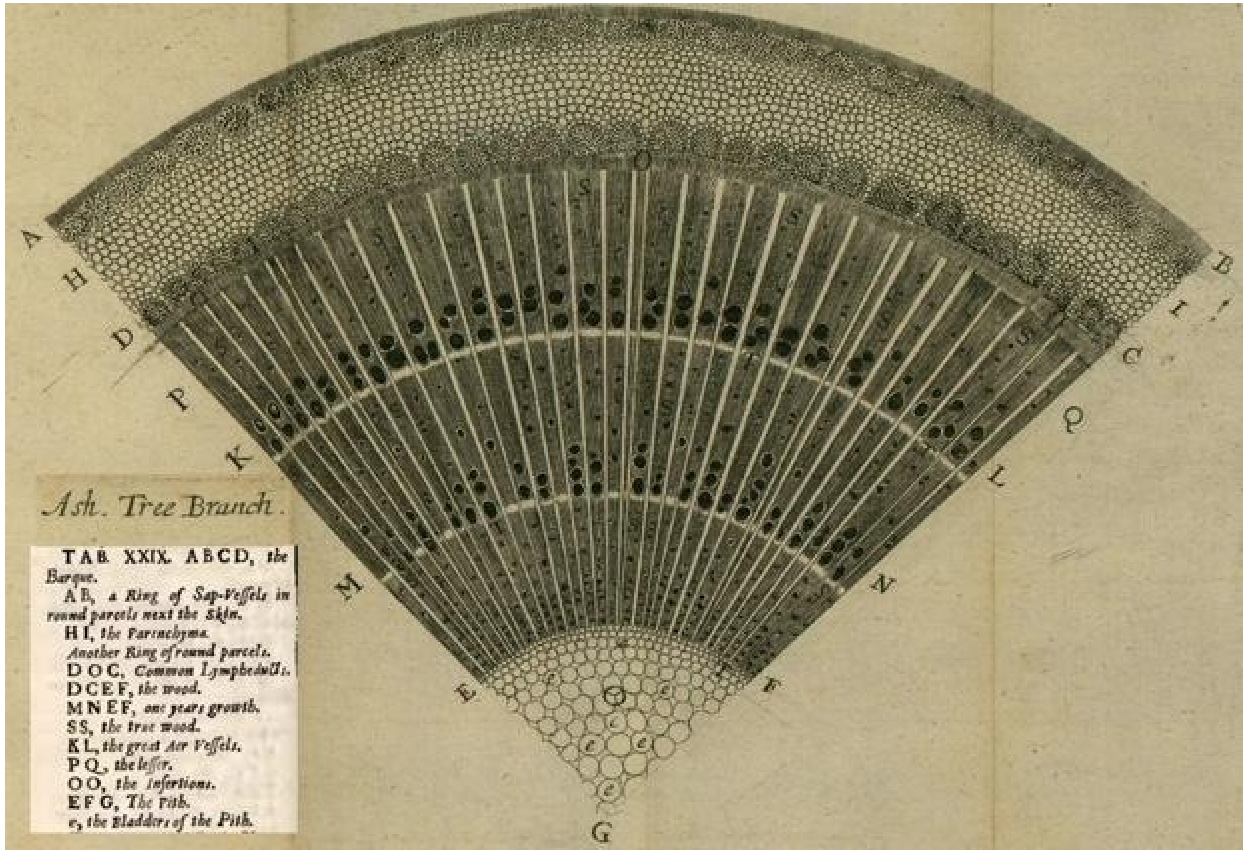
*« … the ascending of the Sap in Trees and Plants**, through their small, and some of them imperceptible pores*** » 1664

that transport ascending sap

Nehemiah Grew

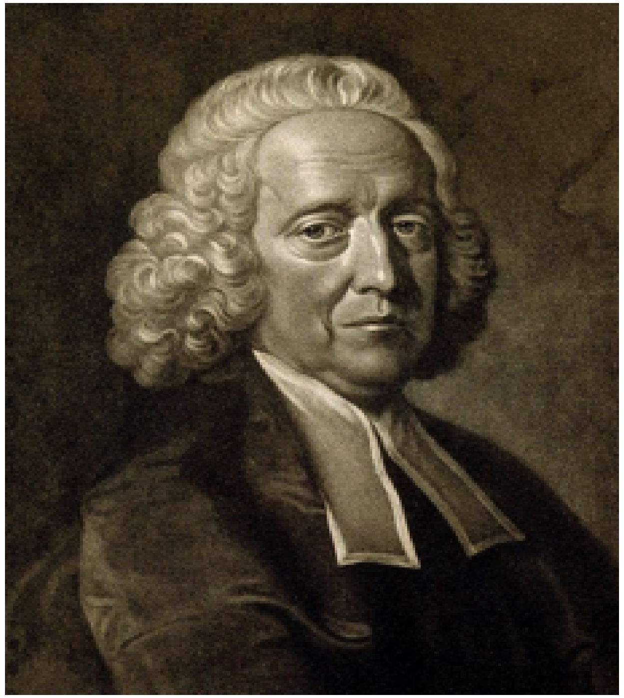
1641-1712

Wood contains trachea (“air-vessels”) that do not transport sap but air

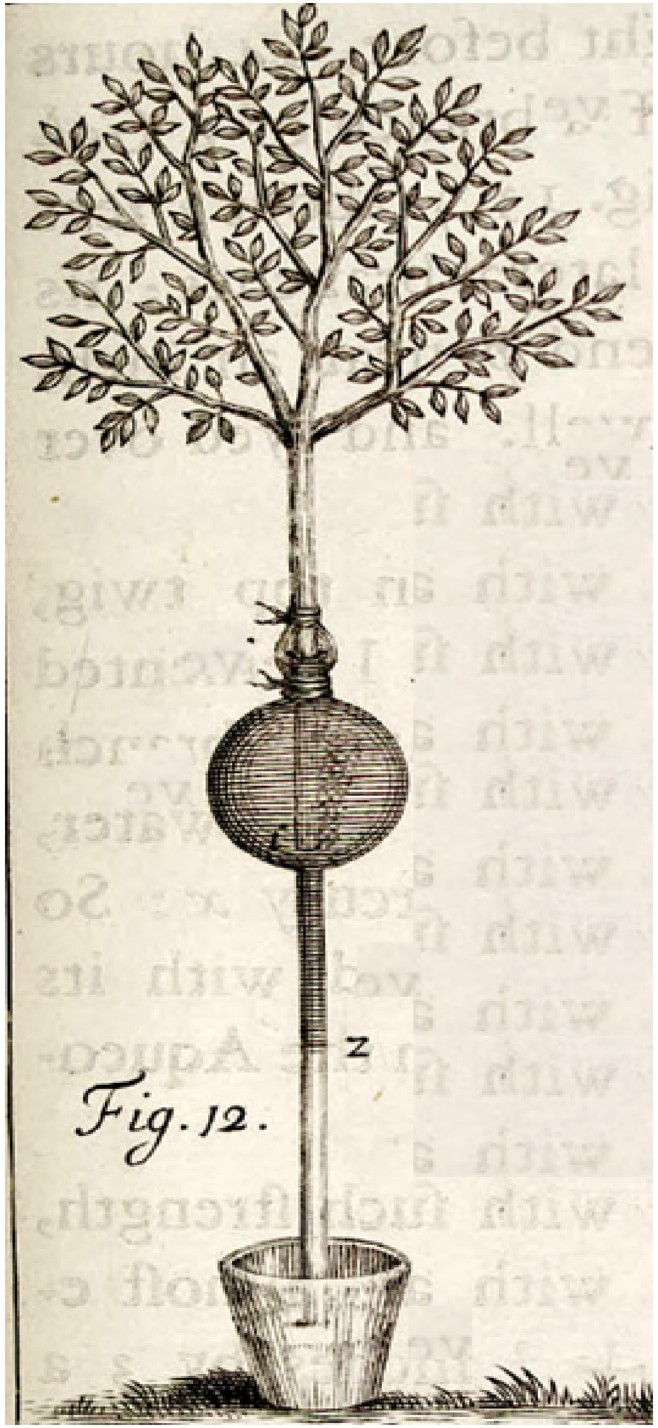


“Whence appears the ***Error of that so Common Opinion*** *that the sap always rises between the wood and the bark”.* Grew N. 1675. *The comparative anatomy of trunks*

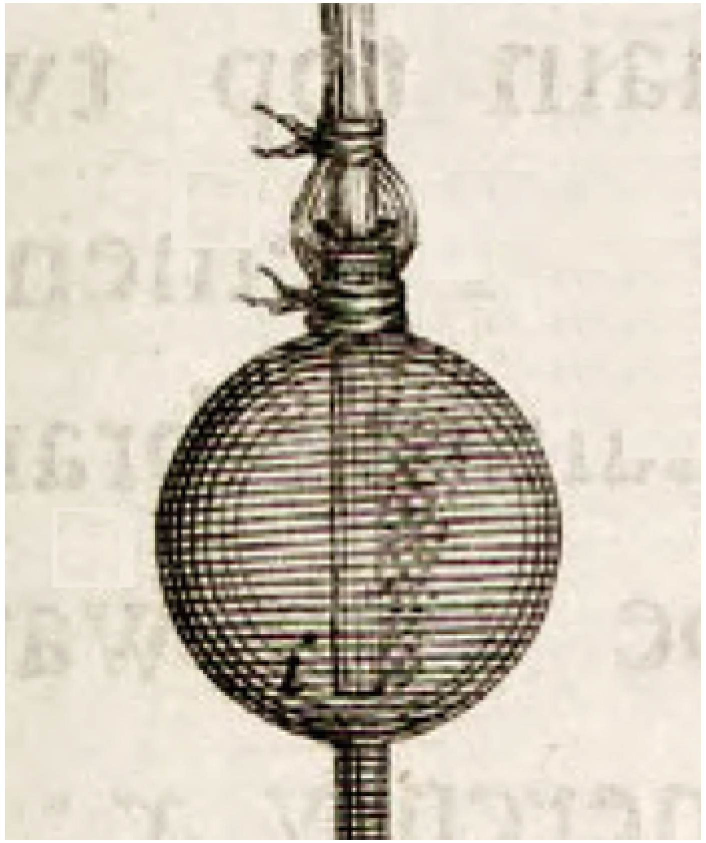
Stephen Hales
1677-1761



Sap is transported in the wood, not in the bark.

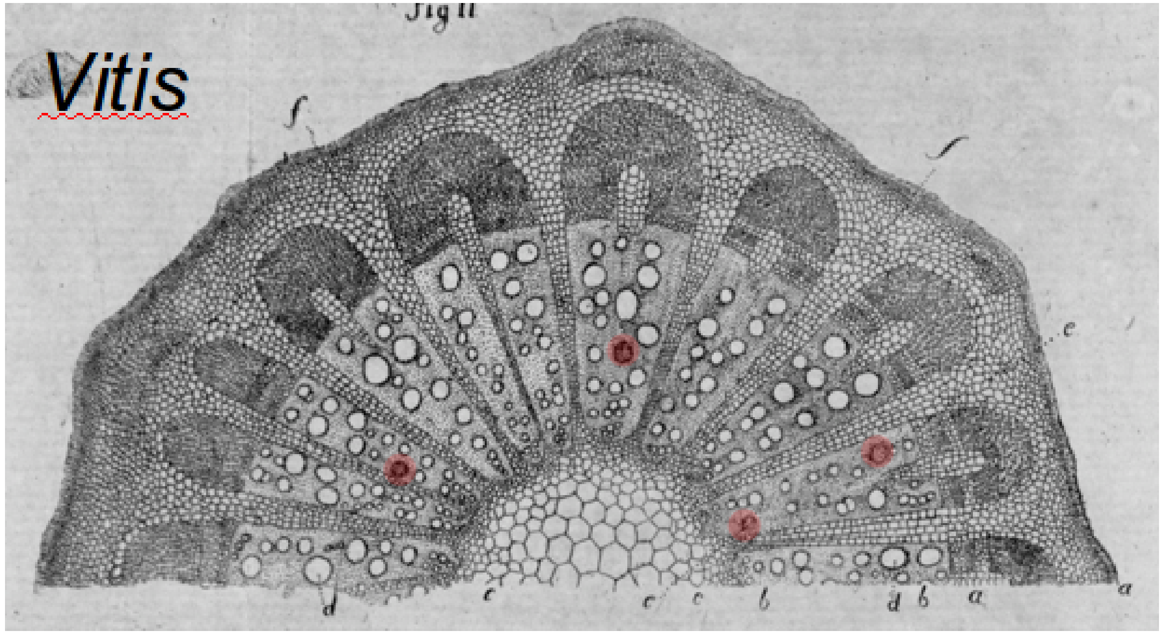


But vessels still transport air !



« [the air issued] into the water at the bottom of the stick (…) through the ***largest vessels of the wood****. Which observation corroborates Dr. Grew's and Malpighi's opinion that* ***they are air-vessels.*** » Hales 1727.

Georg Reichel
1727-1777

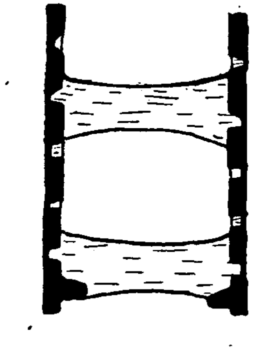


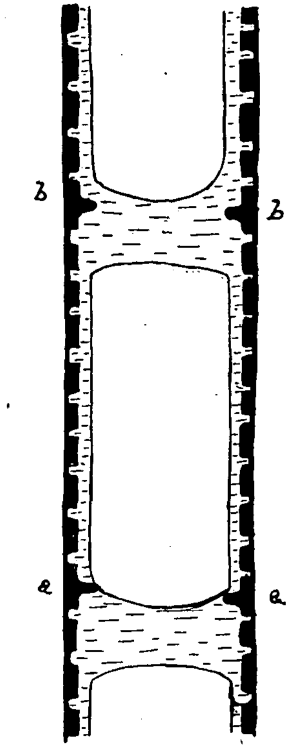
Xylem vessels transport sap

Julius Von Sachs

1832-1897

« Jamin's chain »



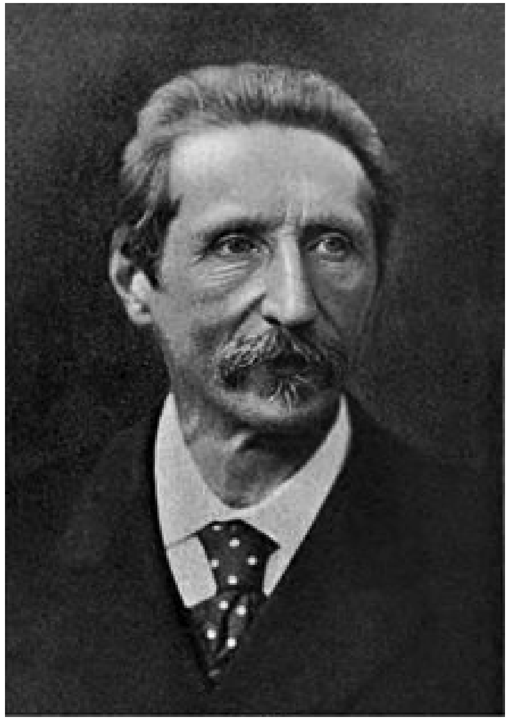


Ewart 1905

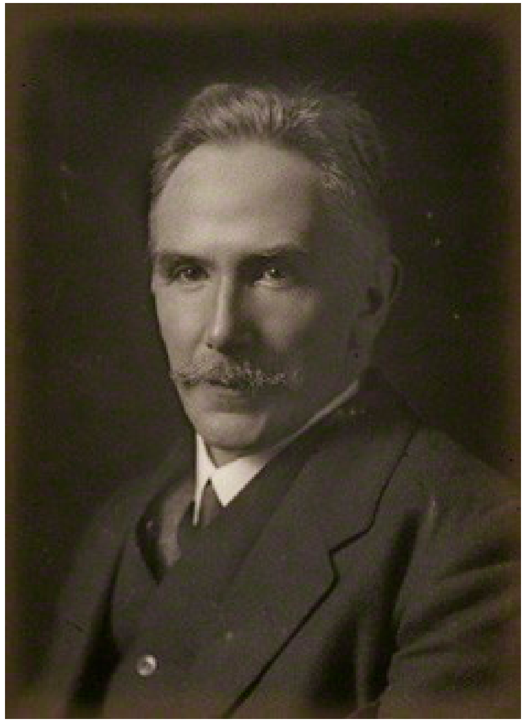
Xylem vessels are partially filled with water

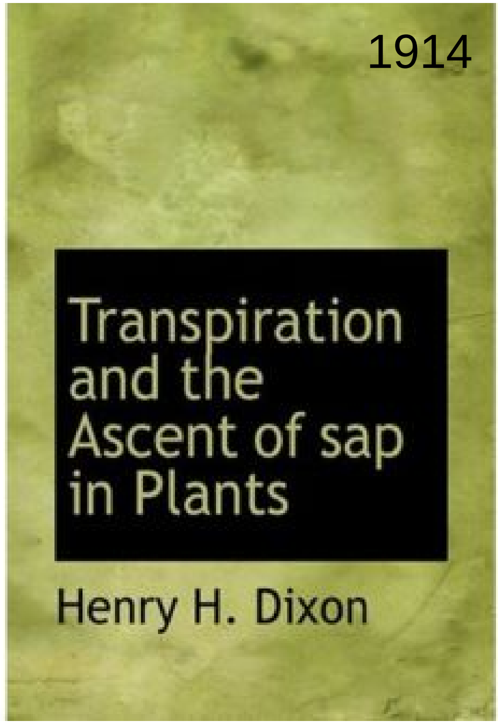
« At the time when **transpiration is going** on in the leaves, the cavities of the wood-cells and vessels of foliage-trees **are not filled with water**; rather, the wood-cells and vessels are only to a small extent filled with water, the vessels, however, being quite empty » (Sachs 1874).

E. Strasburger
1844-1912



Henry Dixon
1869-1953





Xylem vessel are full of sap. A prerequisite for the Cohesion-Tension theory.

Martin Canny

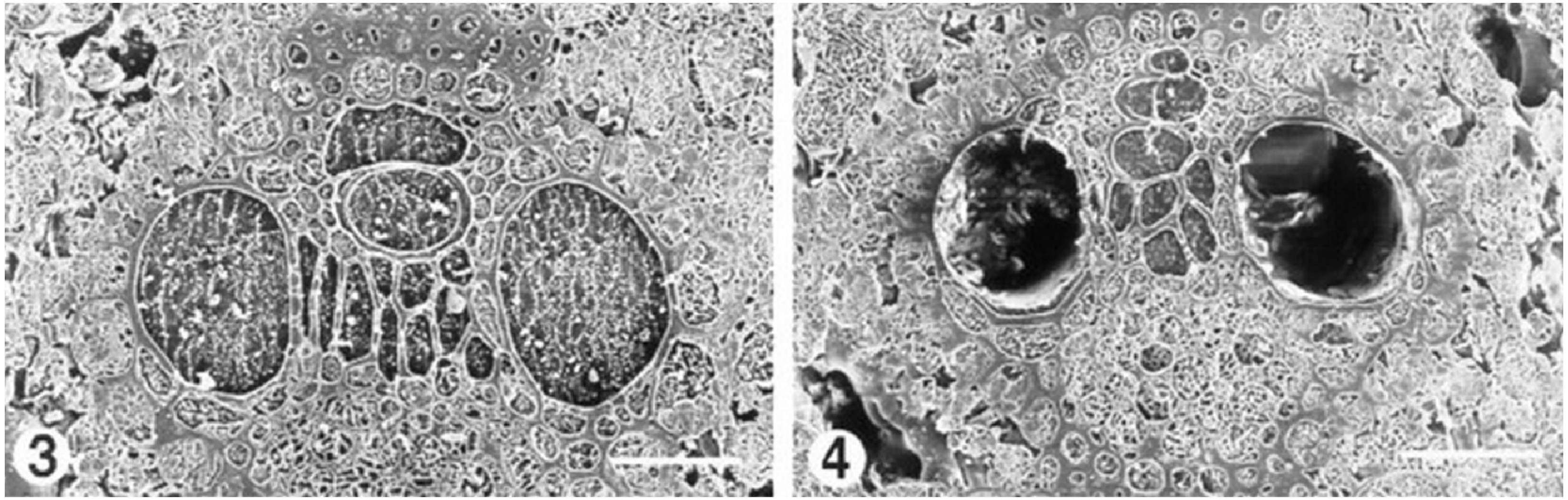
1931-2013

VESSEL CONTENTS DURING TRANSPIRATION
EMBOLISMS AND REFILLING[1]

1997

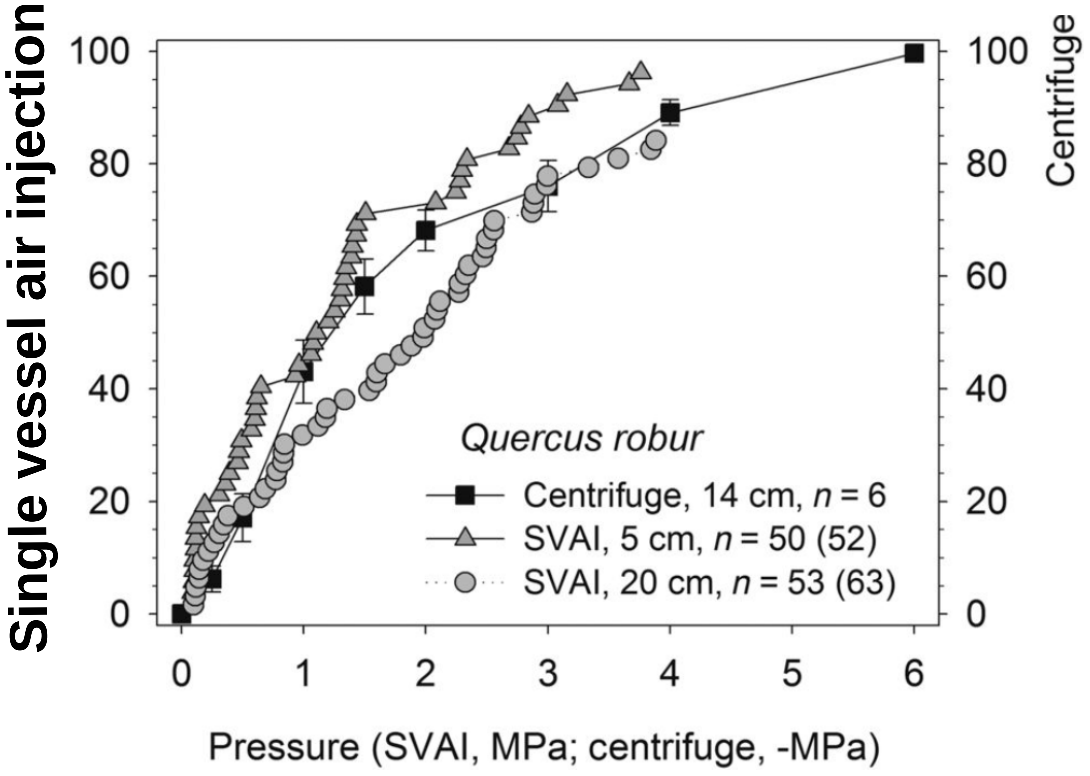
Cryo-SEM observations

morning | noon

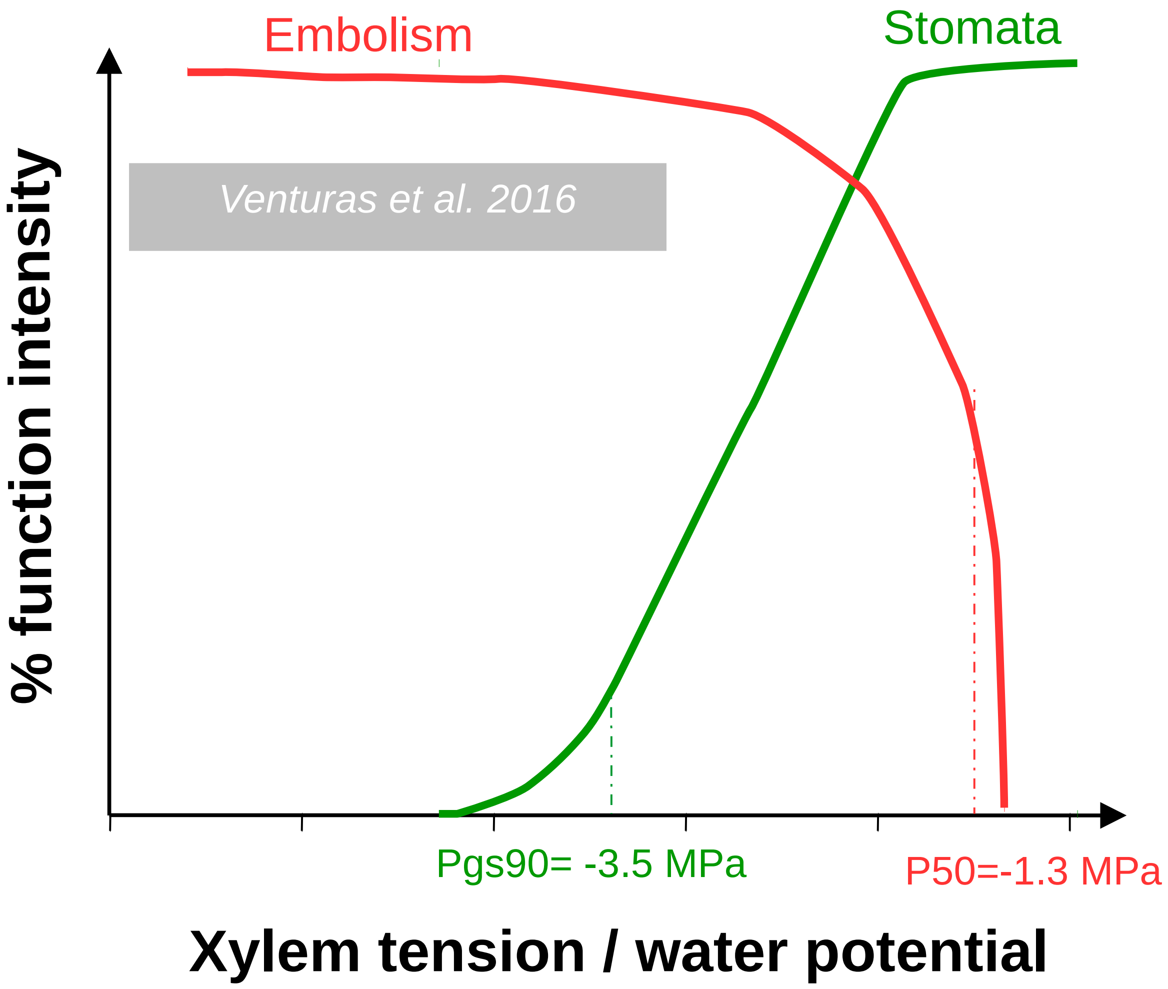


« The observations contradict at every point the assumptions of the Cohesion Theory and the evidence that has been used to support it. Water columns are weak, and are already much broken early in the day and full of air» Canny 1997

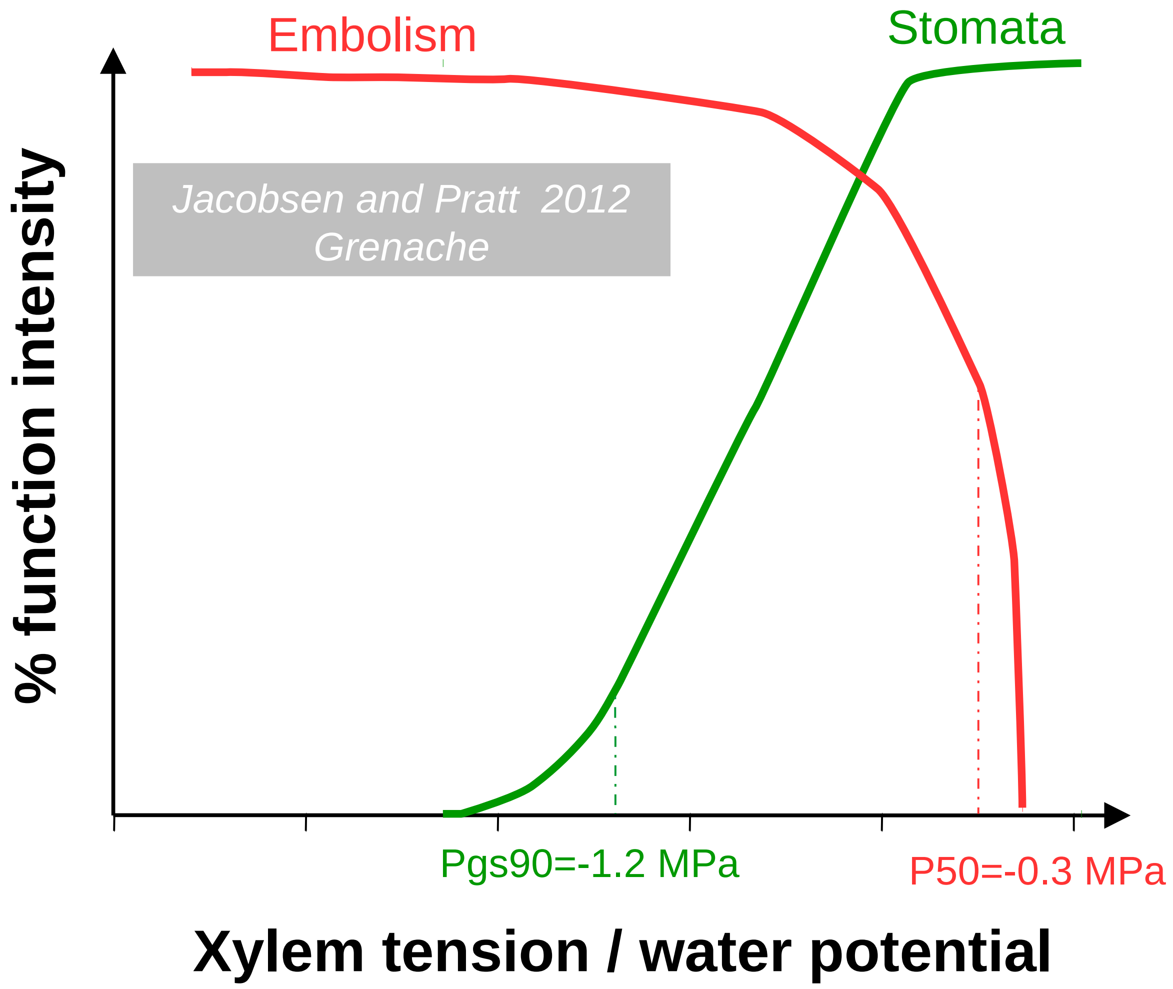
Numerous studies reported daily cycle of embolism formation and embolism repair in Quercus sp

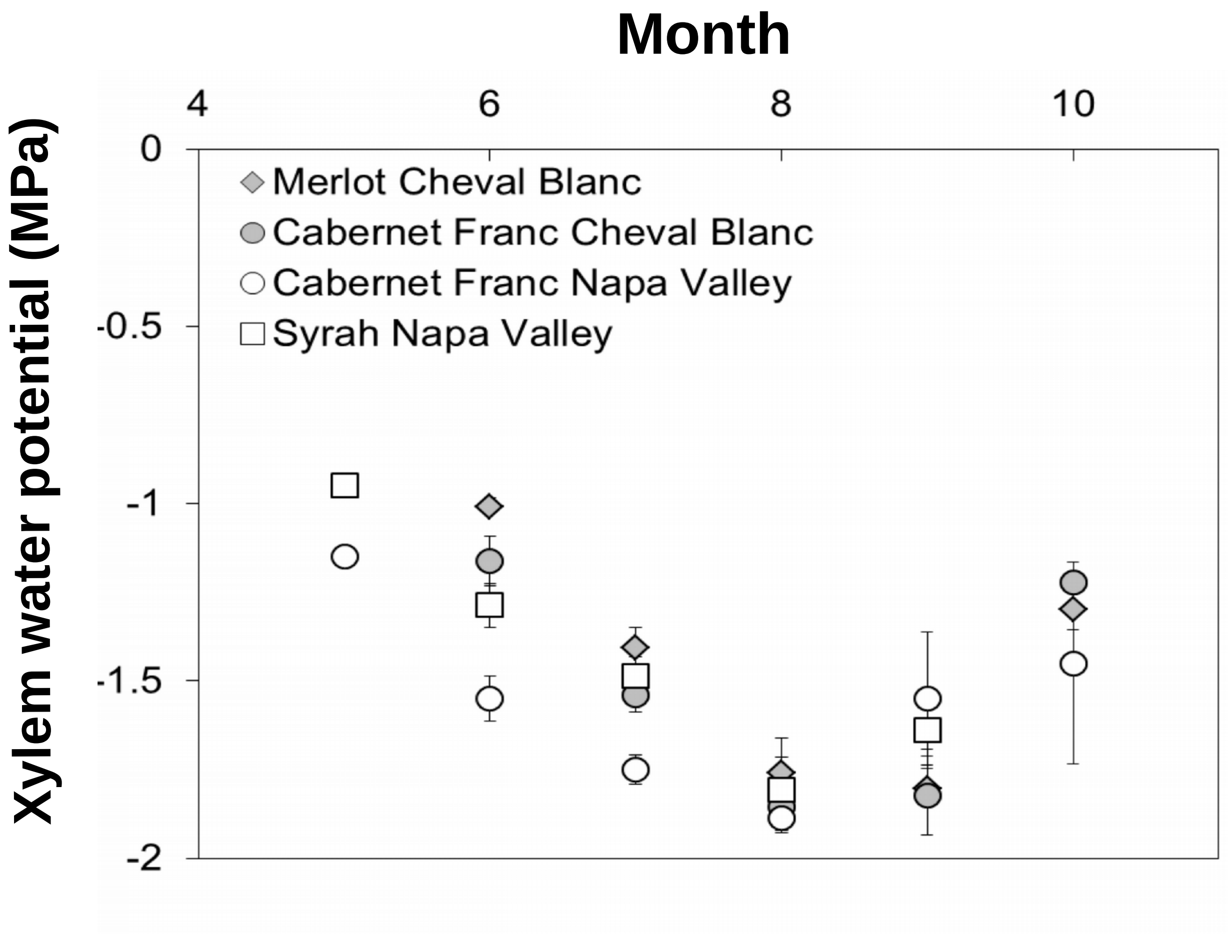


Venturas et al. 2016 TP



Do Vitis pipes cavitate in the early morning?

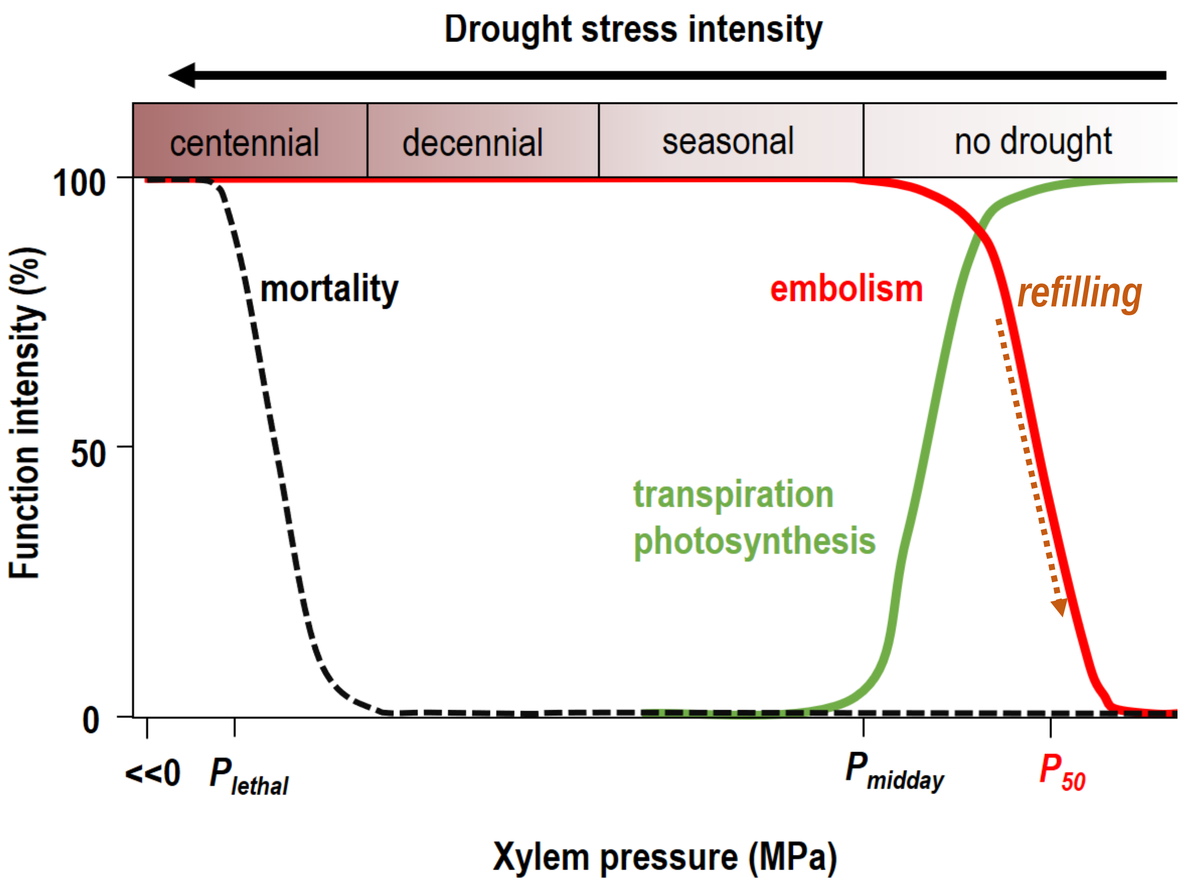


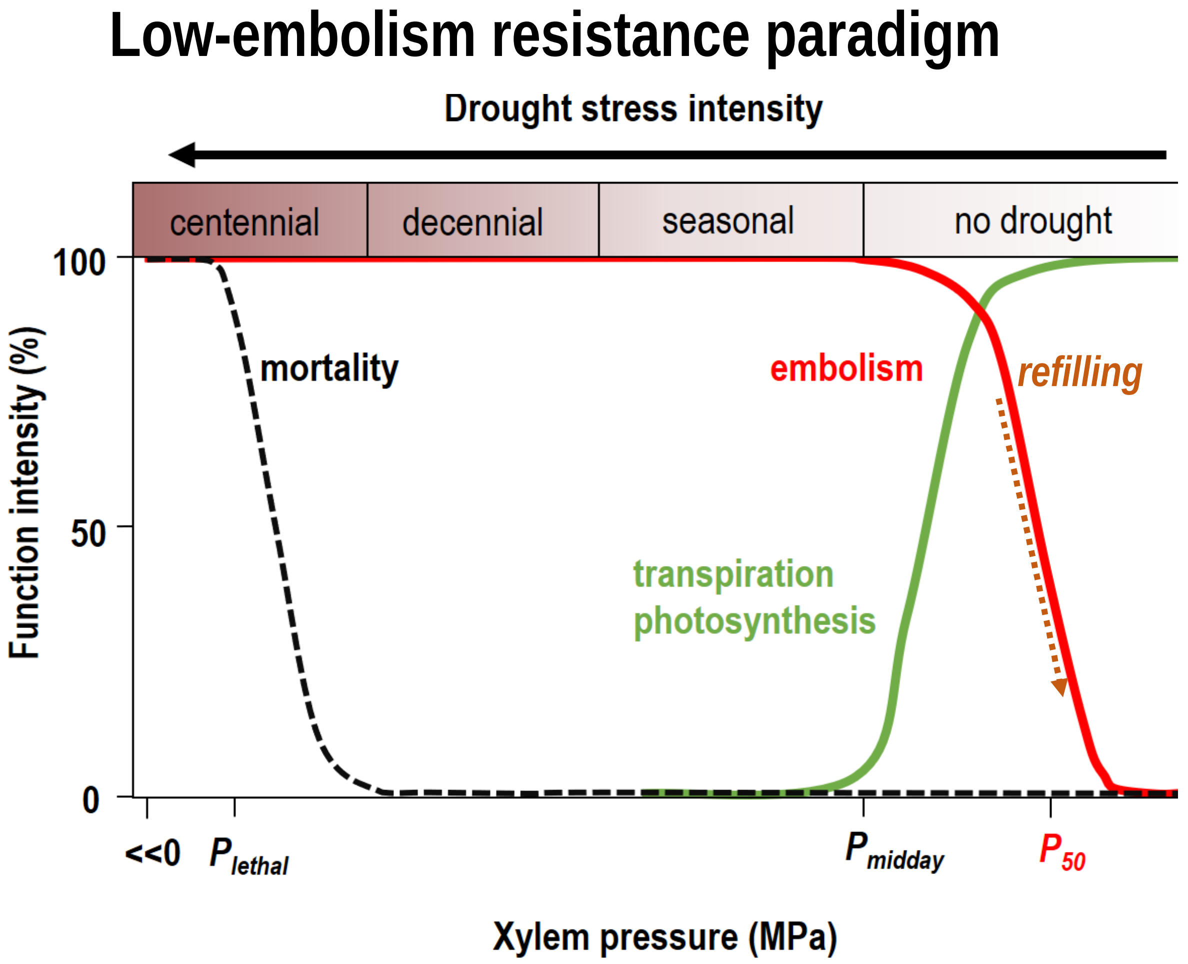


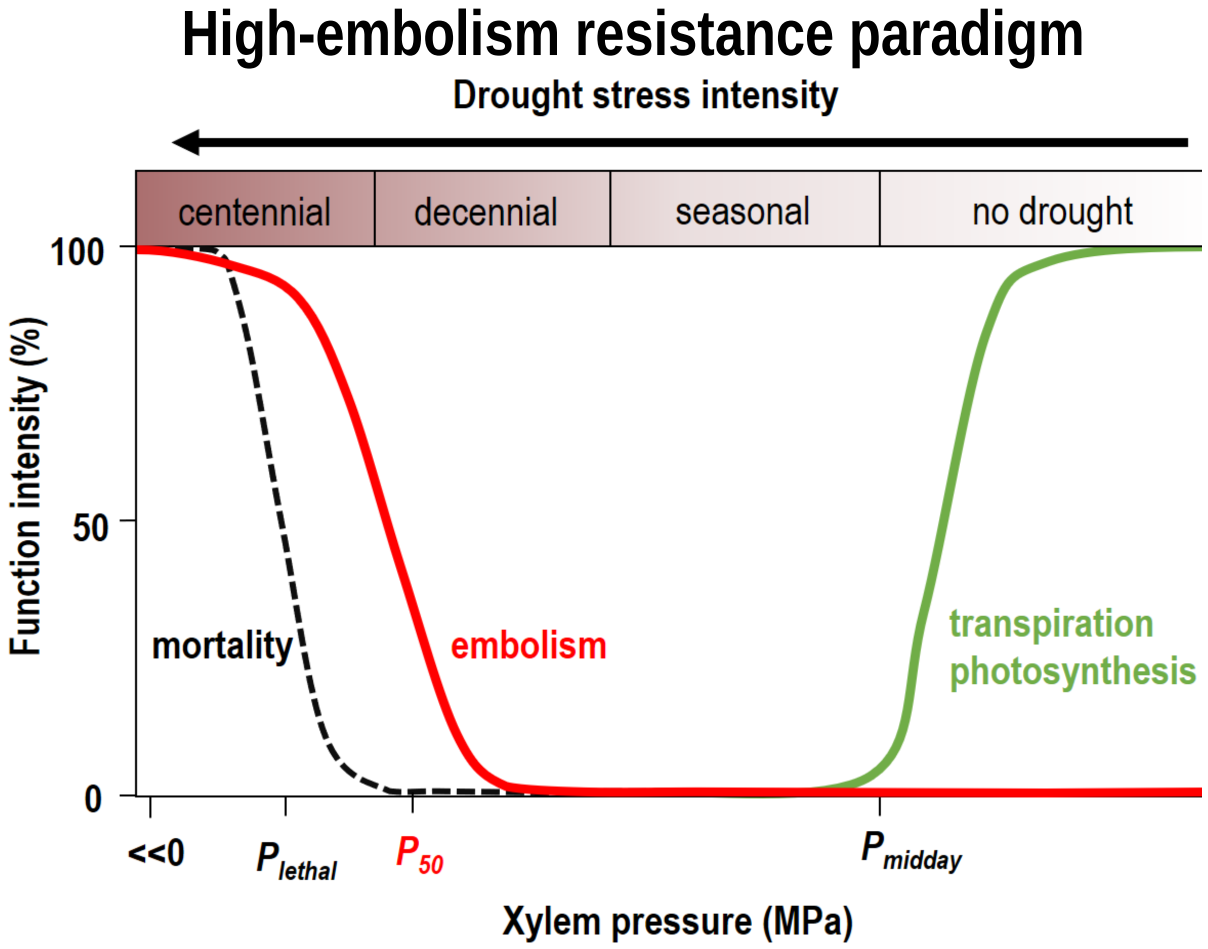
PSImin obtained over 24 yrs in the world's top wine regions

TWO PARADIGMS

Low-embolism resistance paradigm







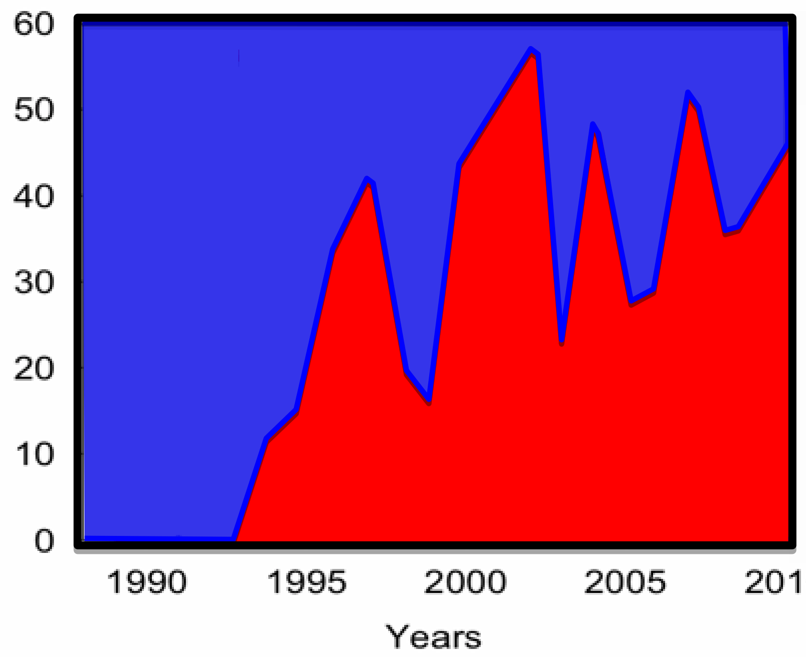
Non-invasive and less prone to artifacts methods are required

Some annoying facts…

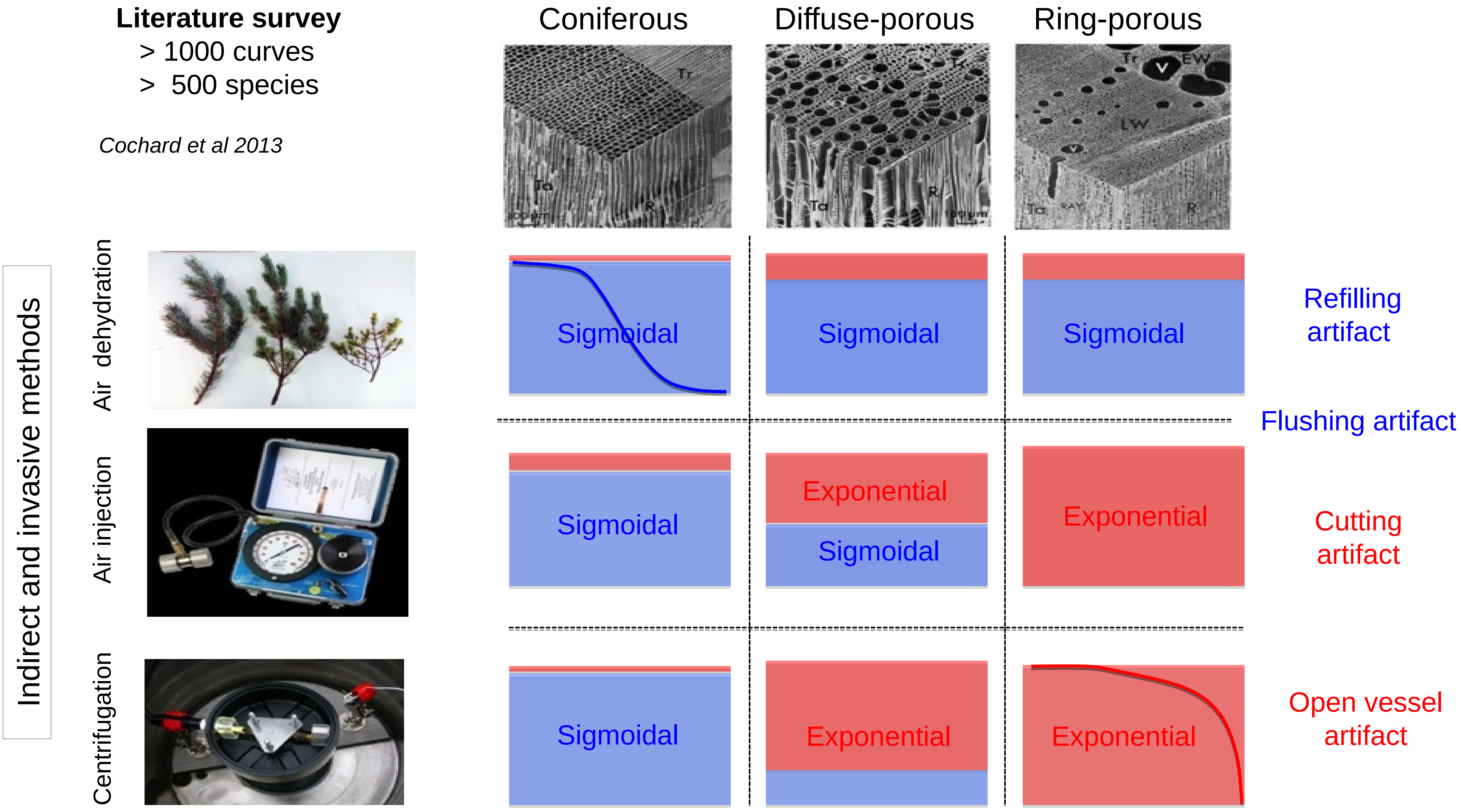
- The same species can display both low and high cavitation resistance behaviours
  Quercus spp, Fraxinus, Vitis, Olea, Robinia etc…

- Species tend to become more vulnerable and r-shaped with time (climate change?)

Highly cavitation-resistant species

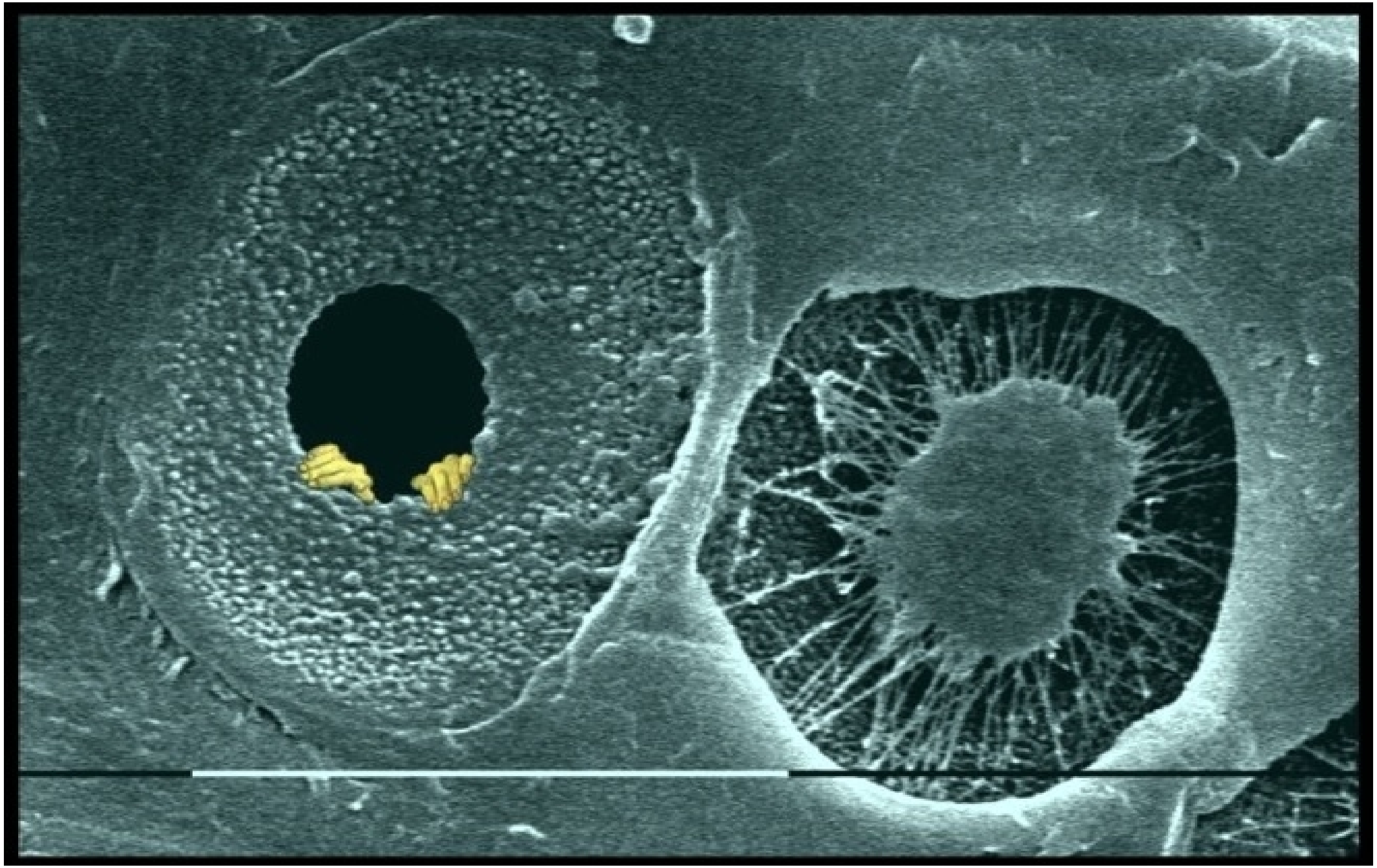


Low cavitation-resistant species

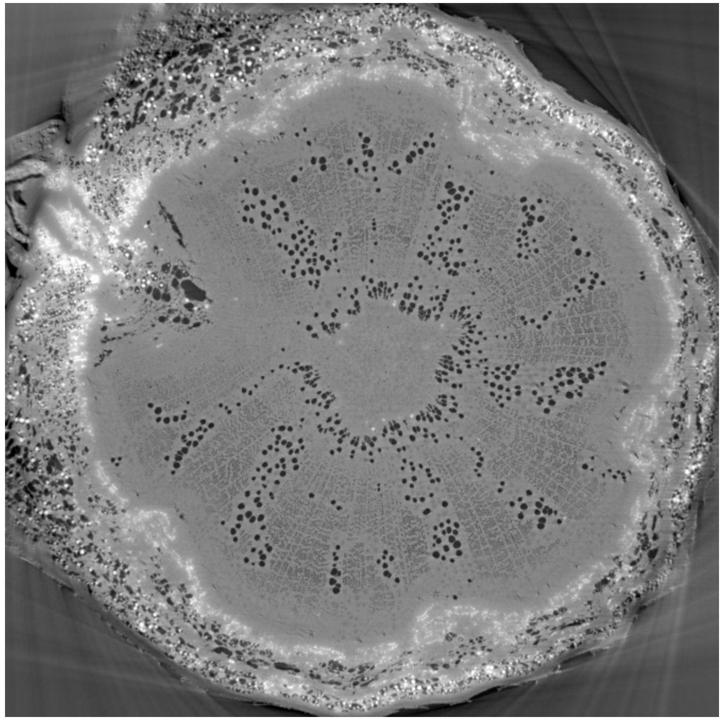


Literature survey
> 1000 curves
> 500 species
Cochard et al 2013
Coniferous
Diffuse-porous
Ring-porous
Indirect and invasive methods
Air dehydration
Air injection
Centrifugation
Sigmoidal
Sigmoidal
Sigmoidal
Refilling artifact
Flushing artifact
Sigmoidal
Exponential
Sigmoidal
Exponential
Cutting artifact
Sigmoidal
Exponential
Exponential
Open vessel artifact

The Pitfalls of indirect hydraulic methods

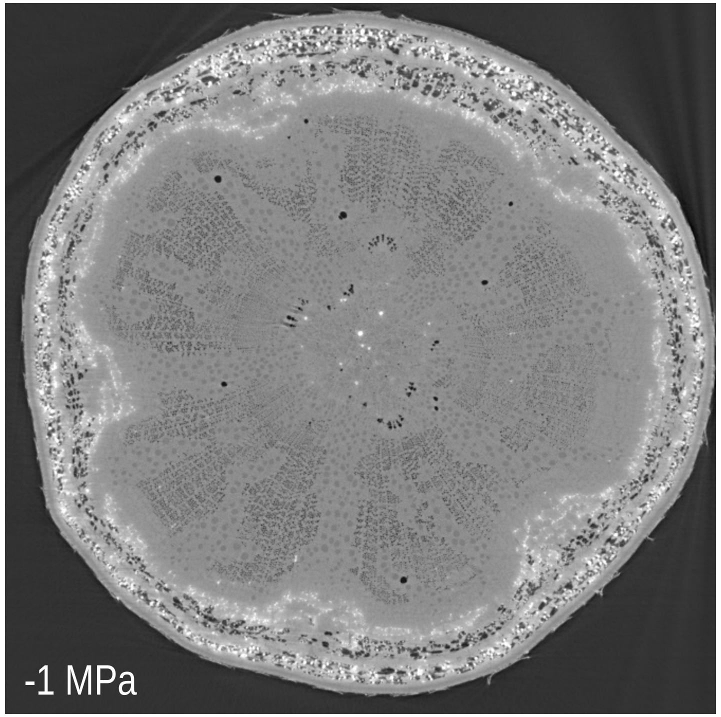


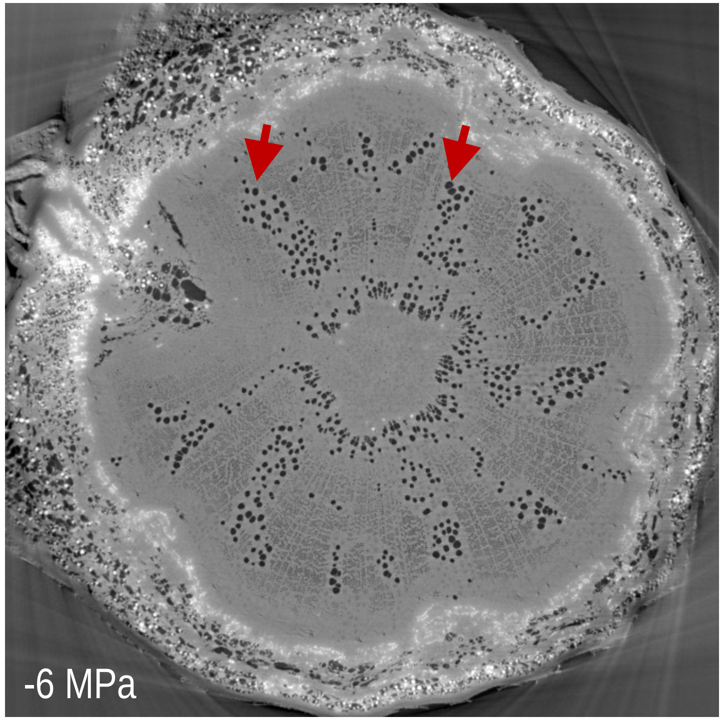
Story I: Do plants experience daily embolism and repair?



Dawn of a new cavitation research era: Direct, non-invasive, real time views of cavitation

Synchrotron technology





X-ray micro-CT scans

Source : http://sylvain-delzon.com/

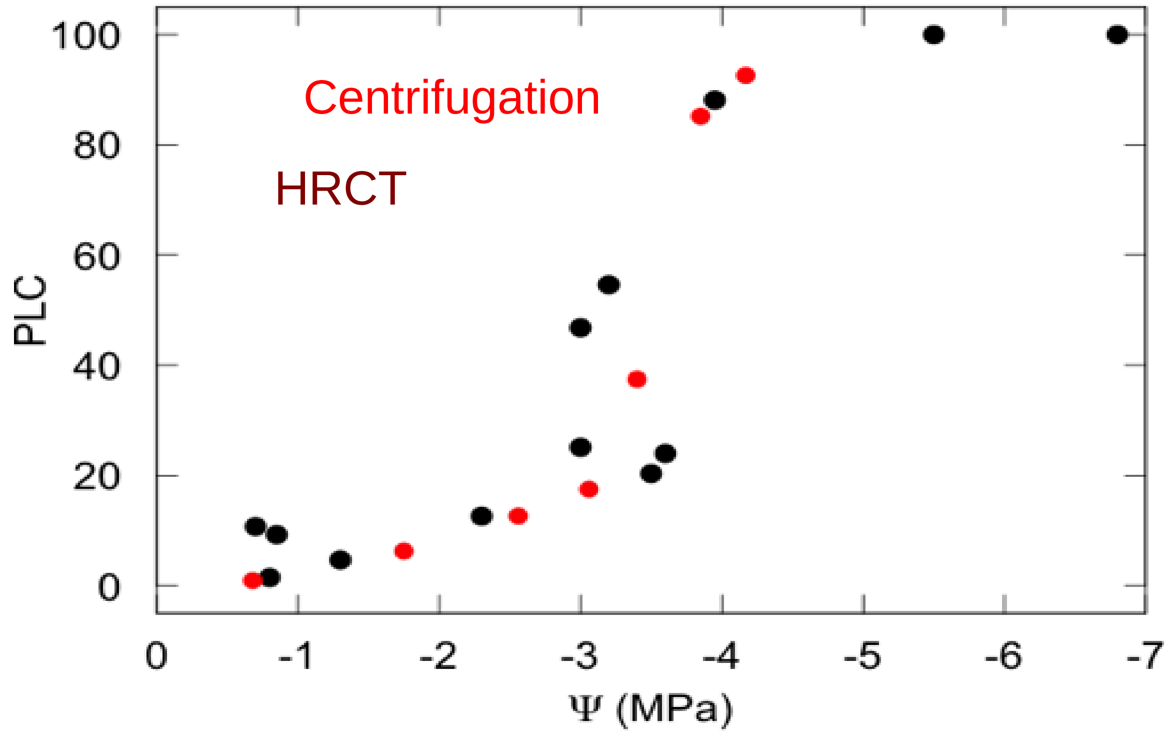
Torres *et al.* 2017 New Phytol

Torres *et al.* 2015 Plant Phys

Cochard *et al.* 2016 PC&E

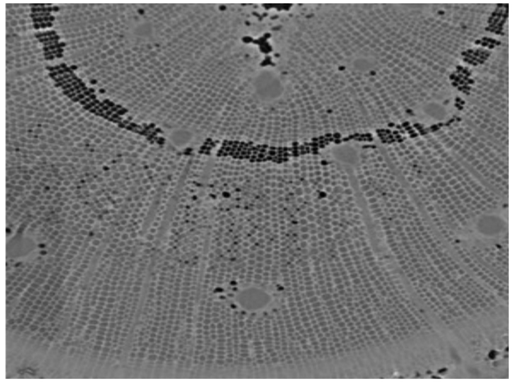
Pinus pinaster

coniferous

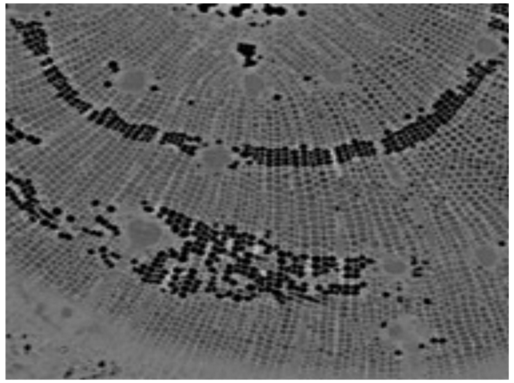


Choat et al. 2016

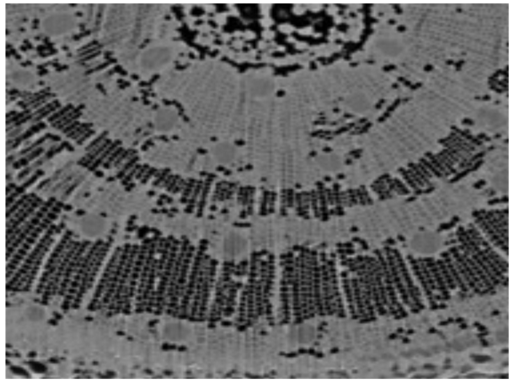
-0.8 MPa



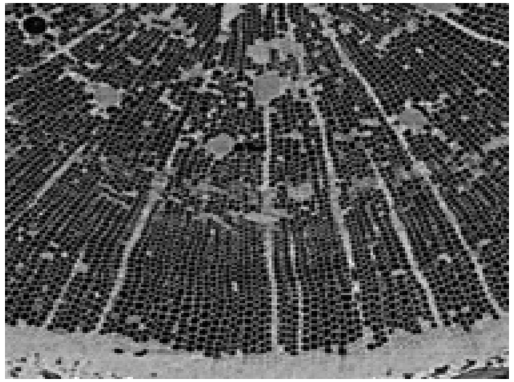
-1.3 MPa



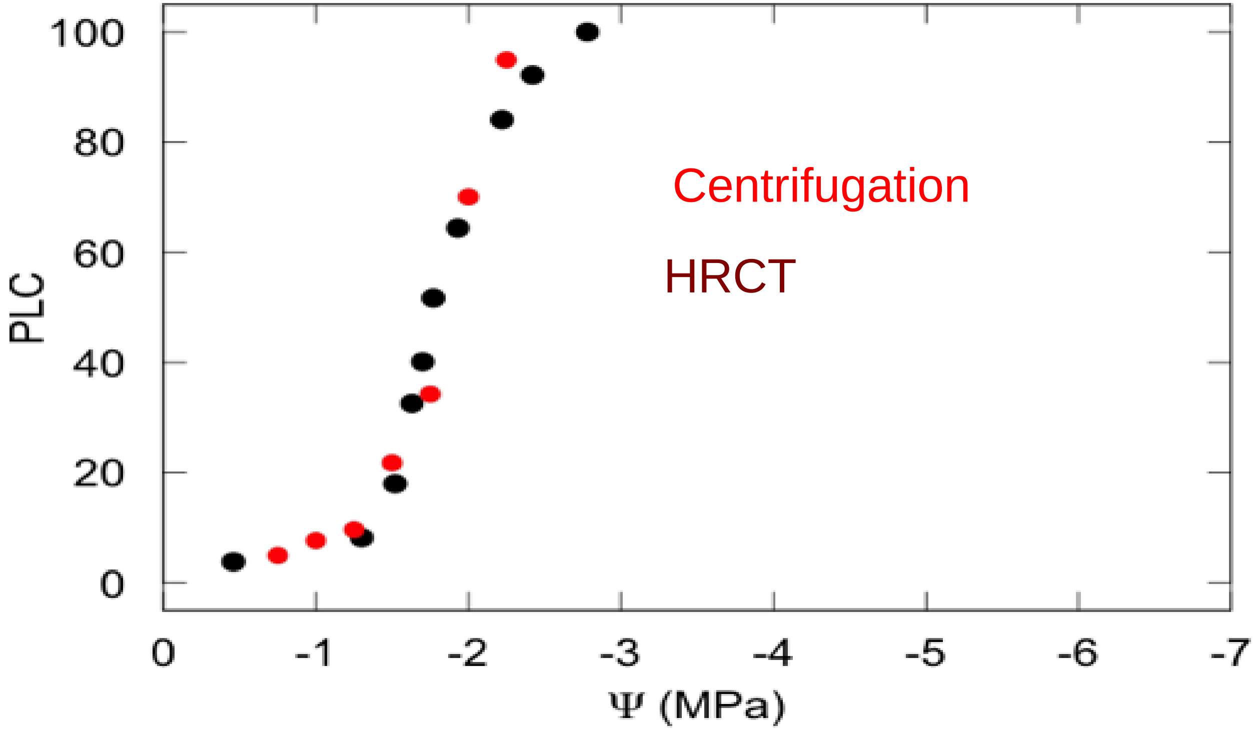
-3.0 MPa



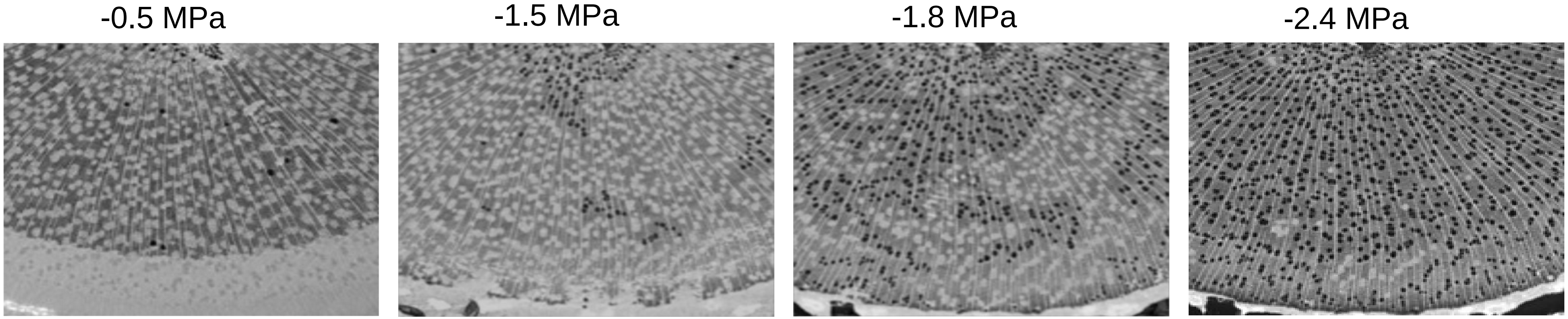
-6.8 MPa



Populus tremula x *alba*
diffuse-porous short-vesseled

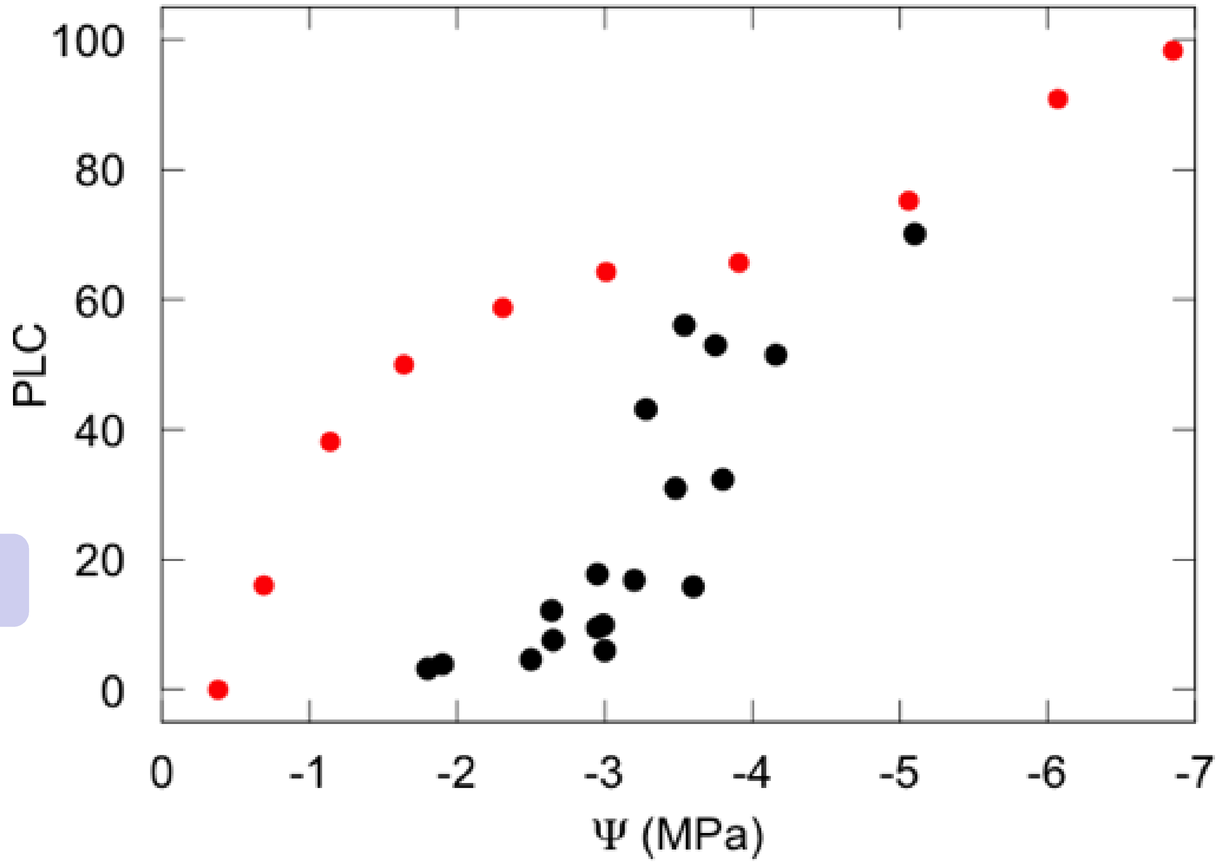


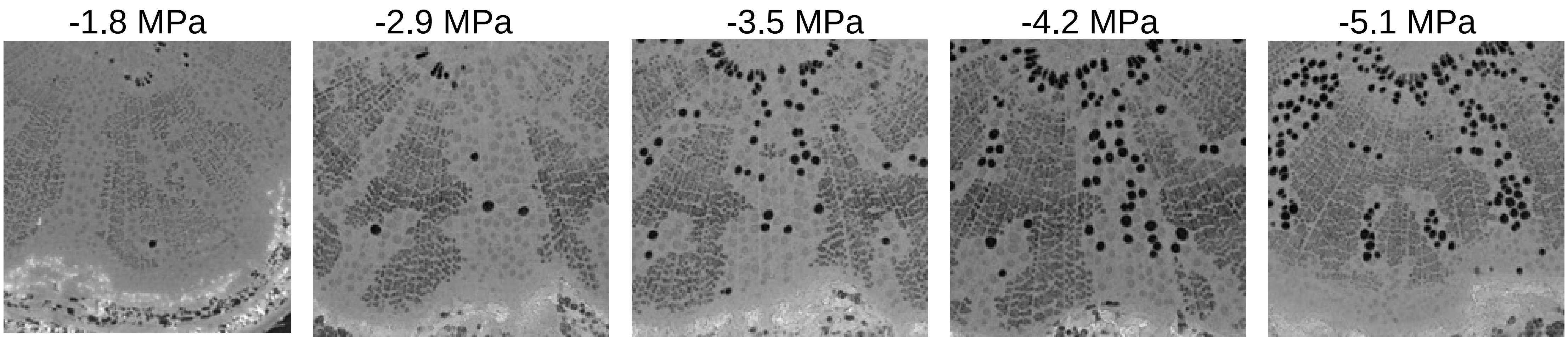
Choat et al. 2016



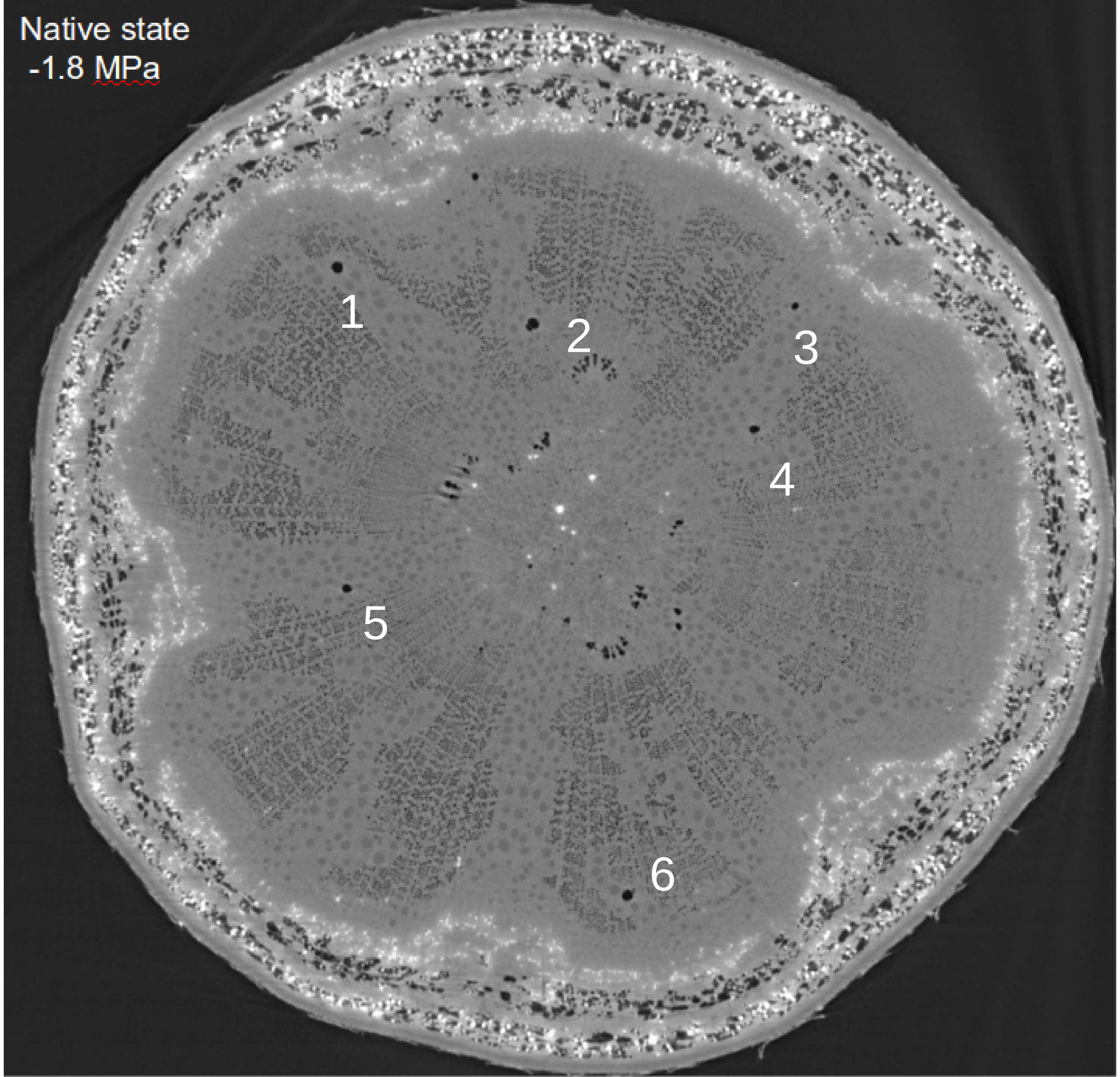
Quercus robur
ring-porous long-vesseled

Choat *et al.* 2016 Plant Phys

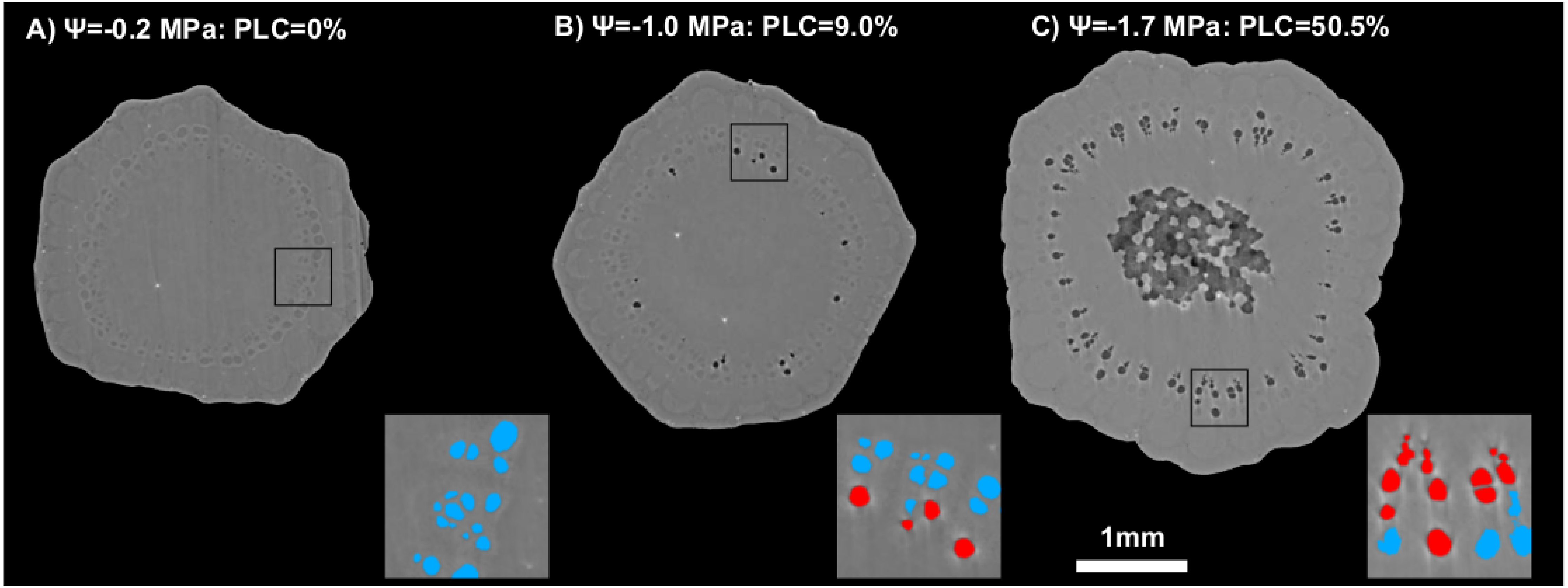




Cavitation is not routine in trees

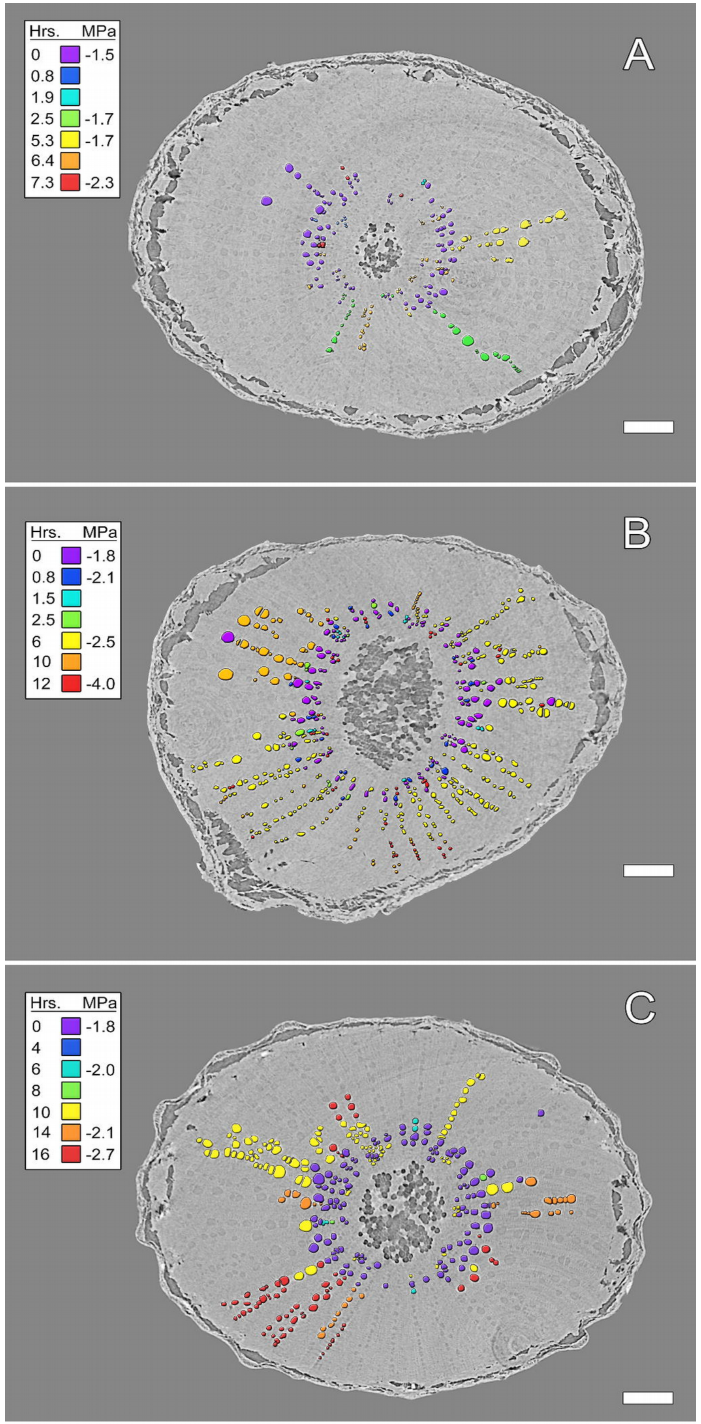


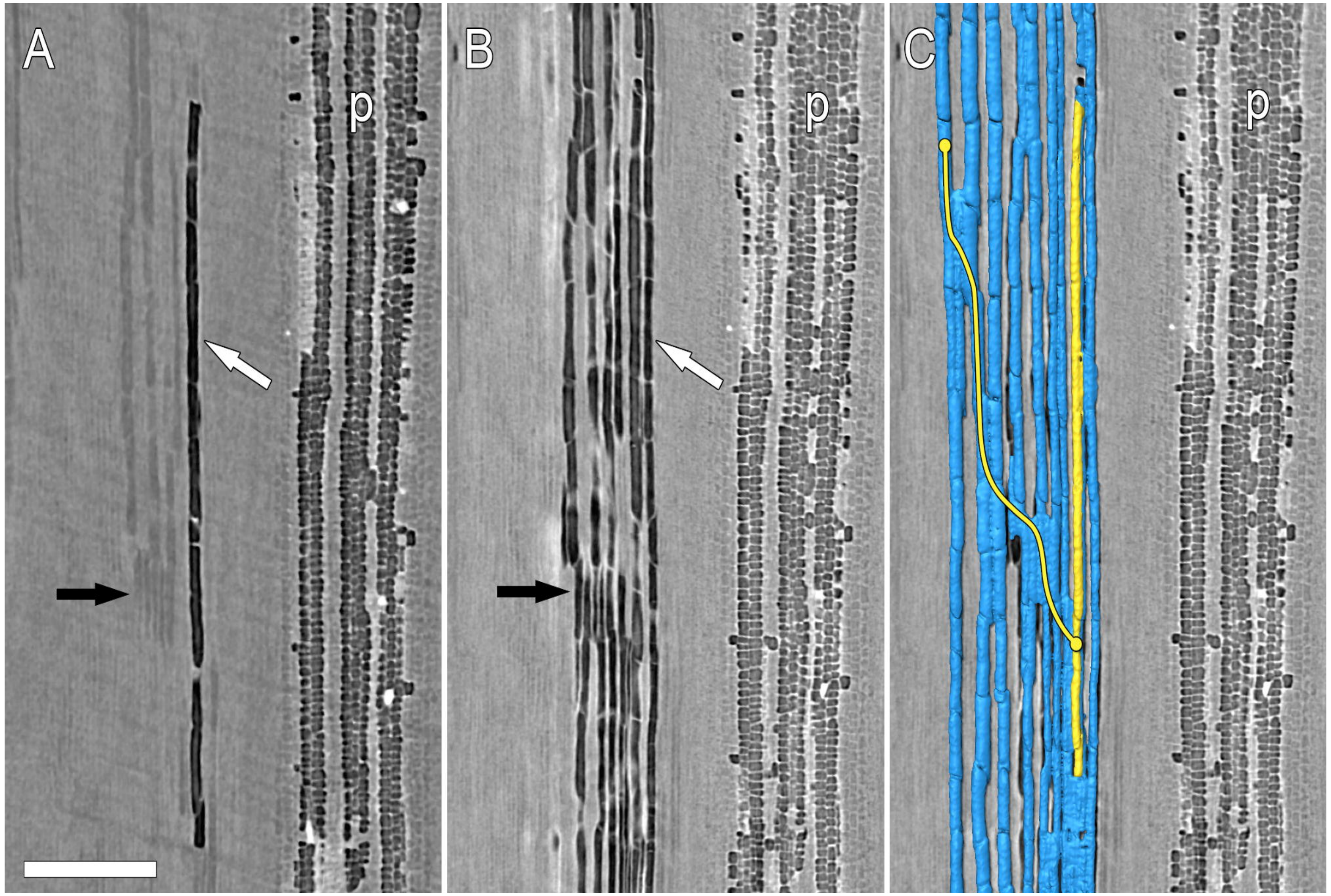
Vulnerability to embolism in Vitis



Charrier *et al.* 2016 Plant Phys

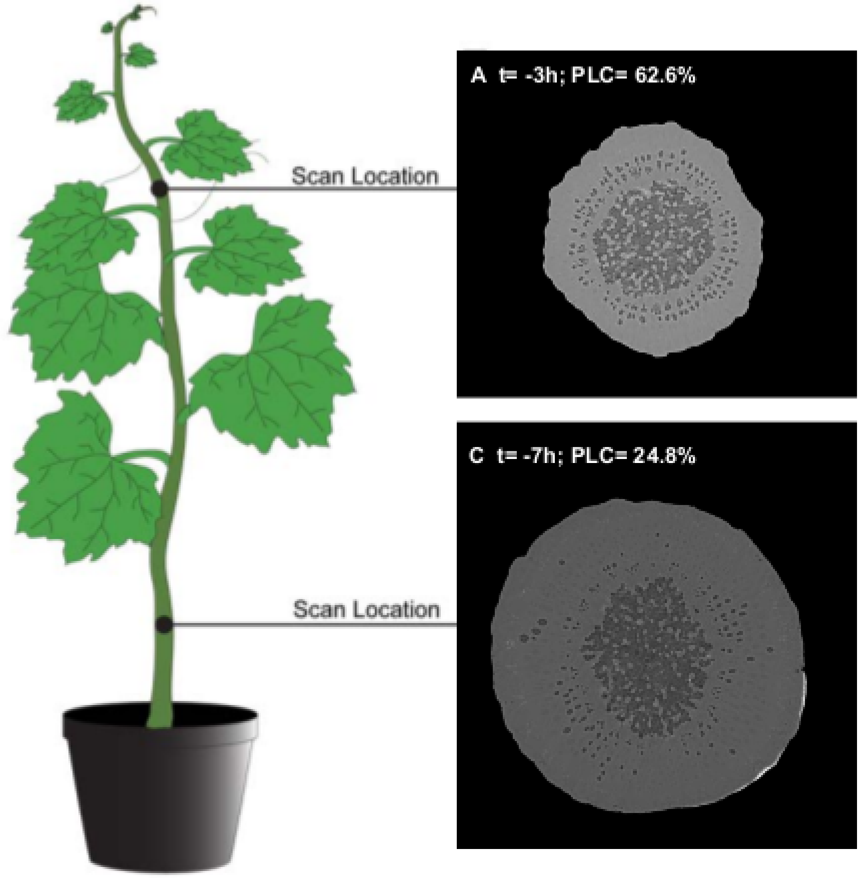
Embolism spread

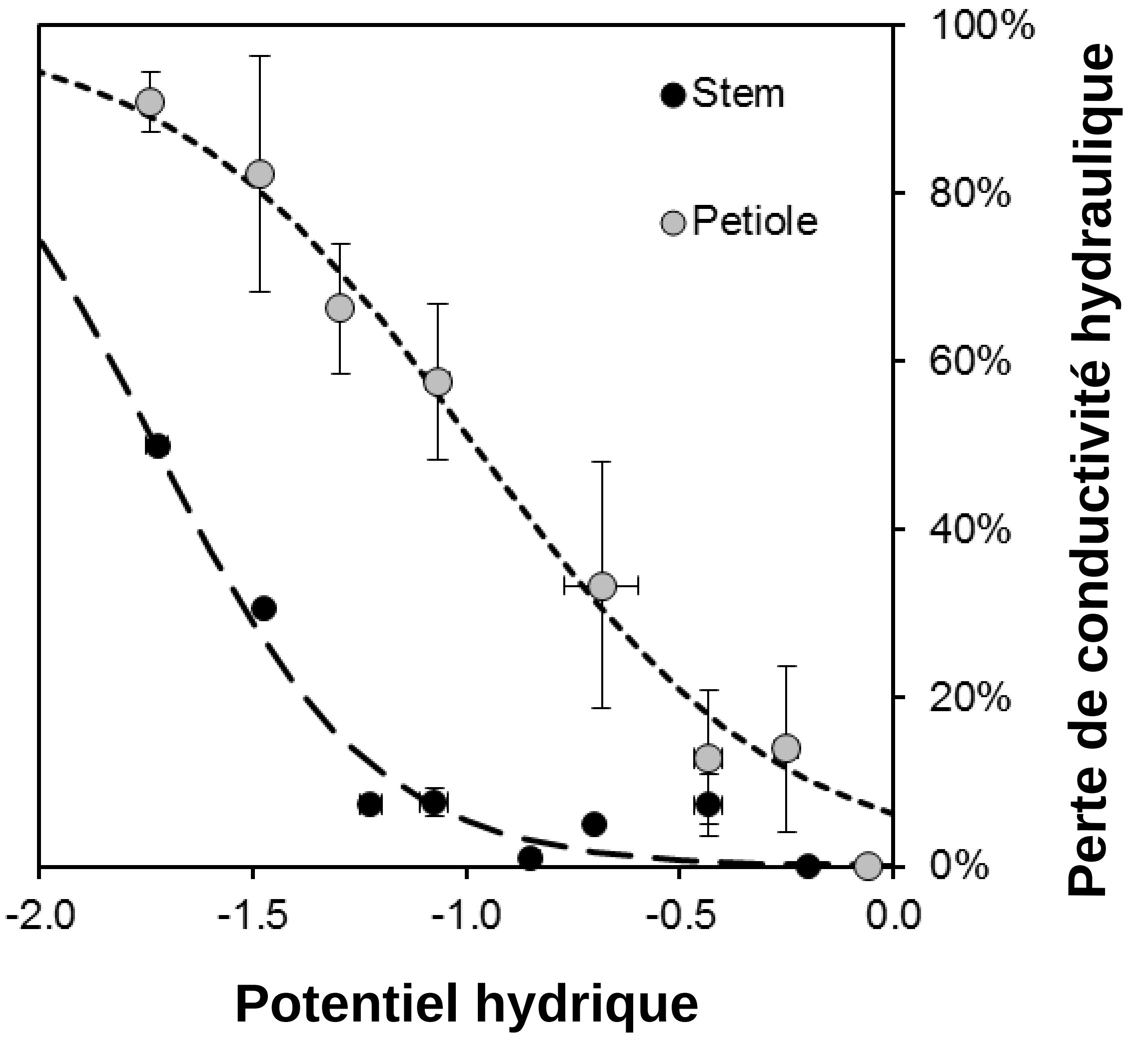




Brodersen et al. 2013

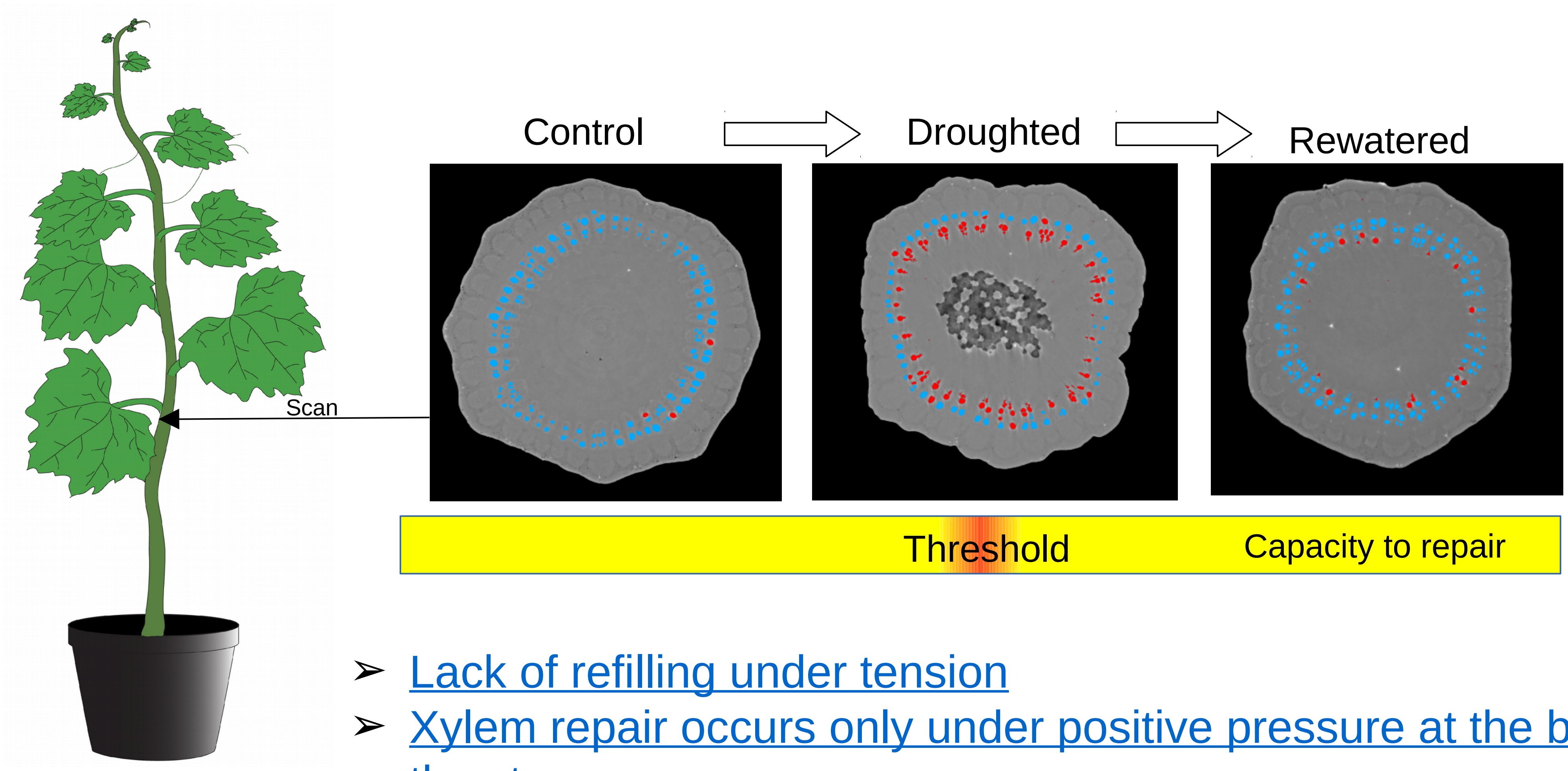
Significant hydraulic segmentation in Vitis





Charrier *et al.* 2016 Plant Phys

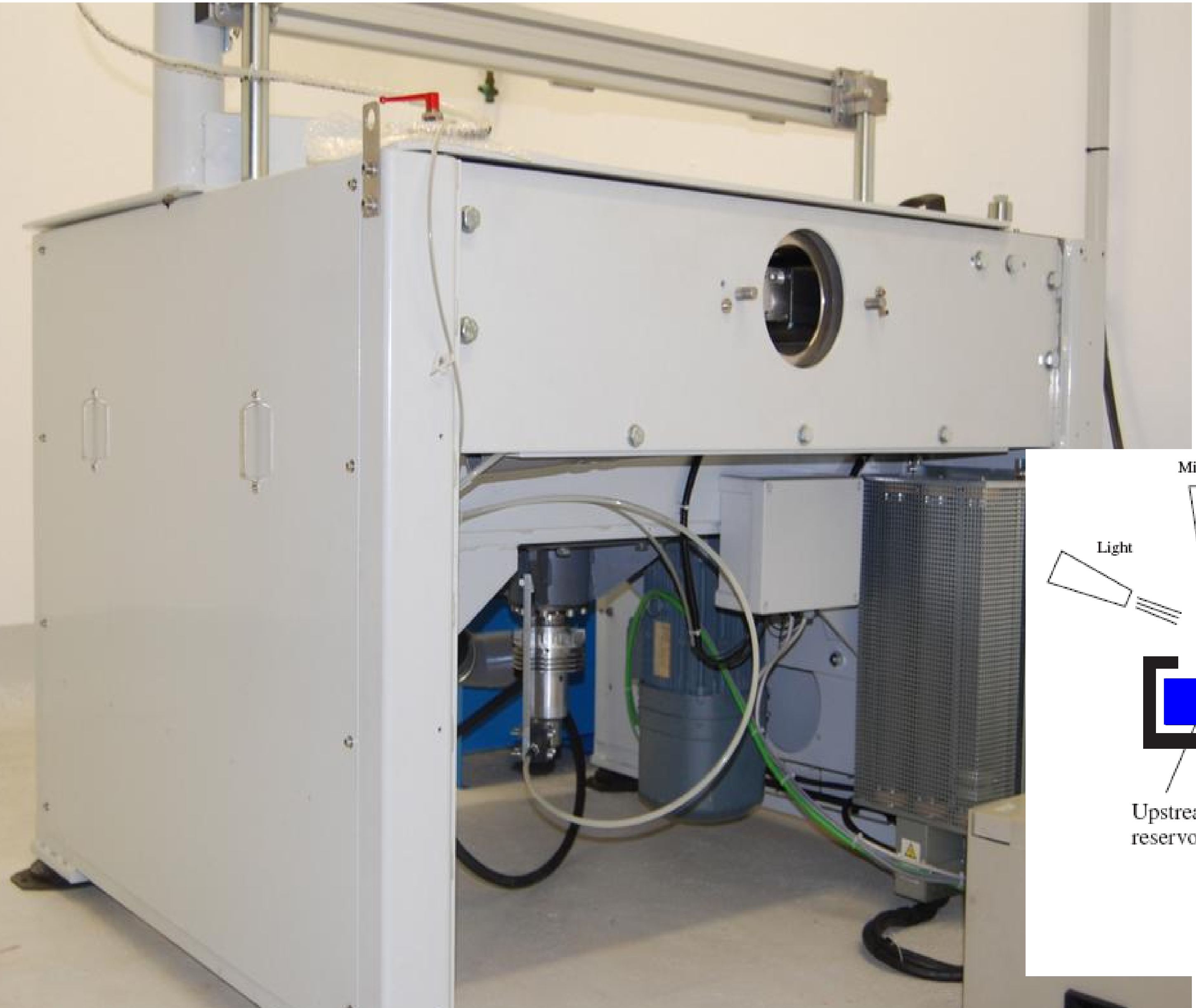
Refilling: Do we need a miracle?



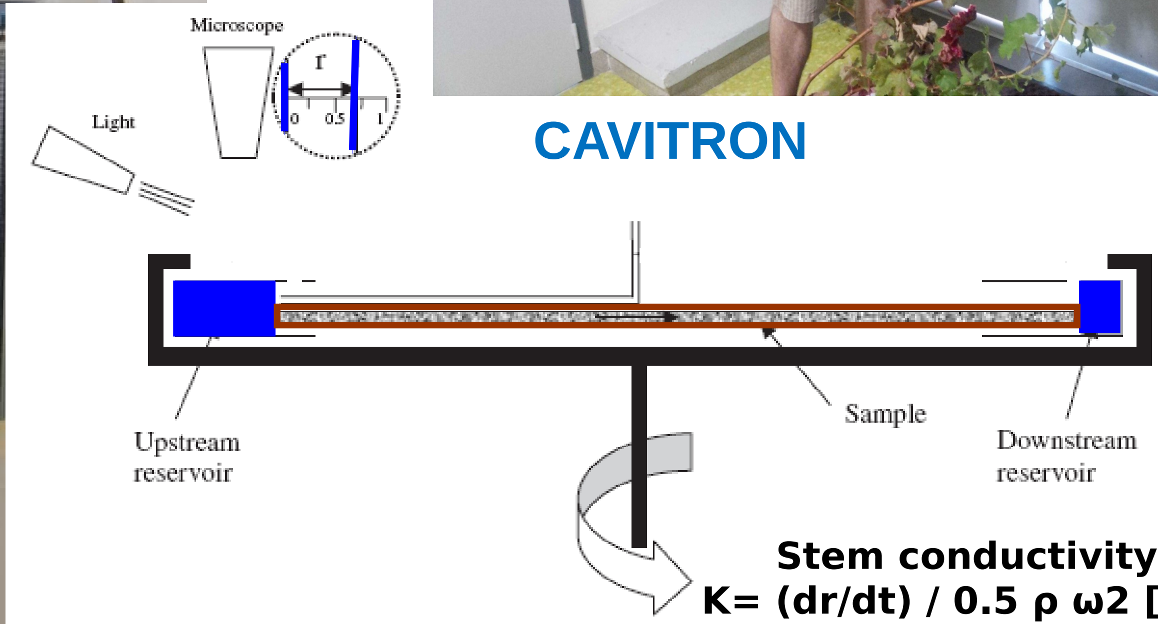
- ➢ Lack of refilling under tension
- ➢ Xylem repair occurs only under positive pressure at the base of the stem

Charrier *et al.* 2016 Plant Phys

A new prototype to measure long vesselled species: the MEGA-CAVITRON

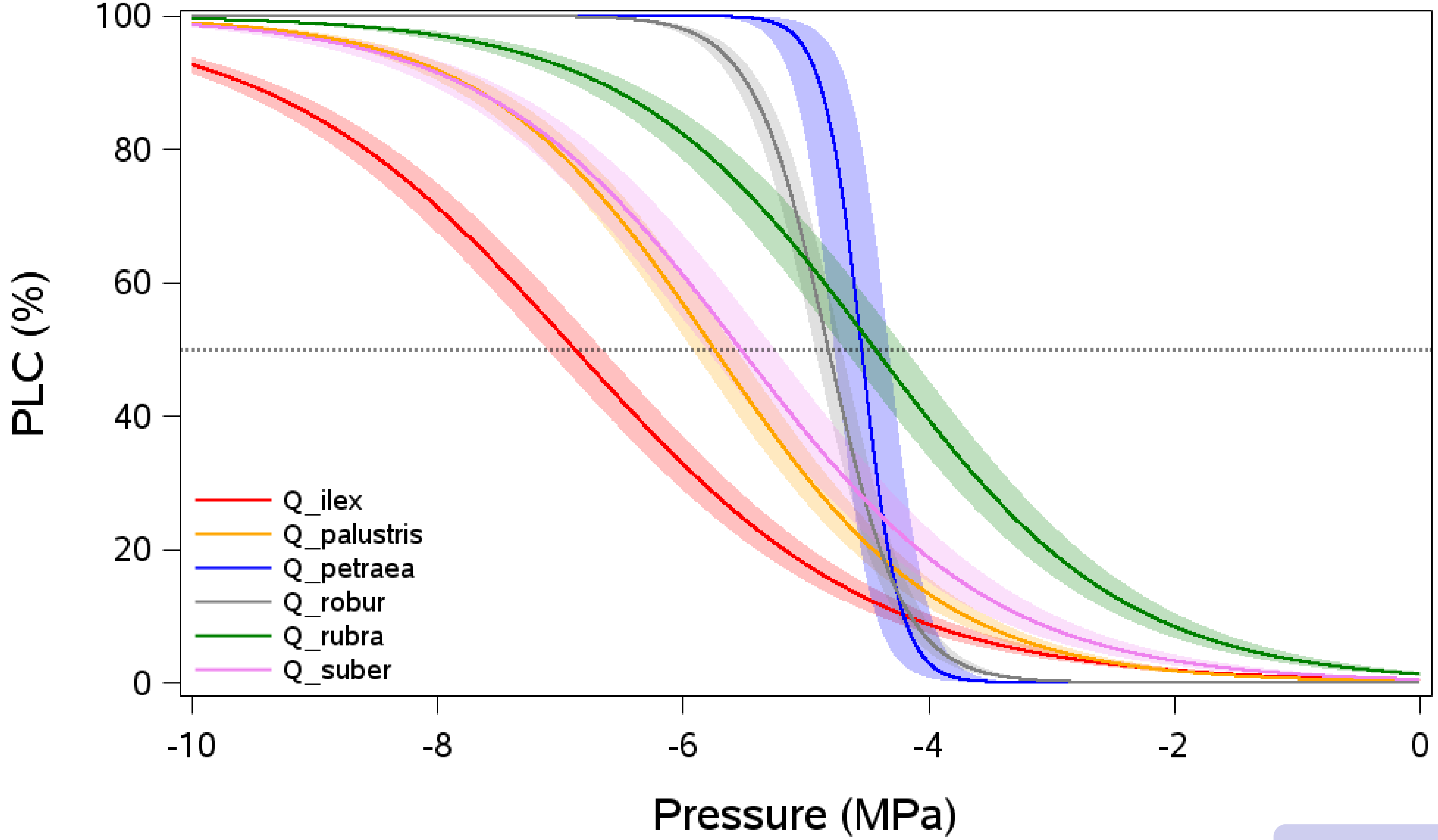


CAVITRON



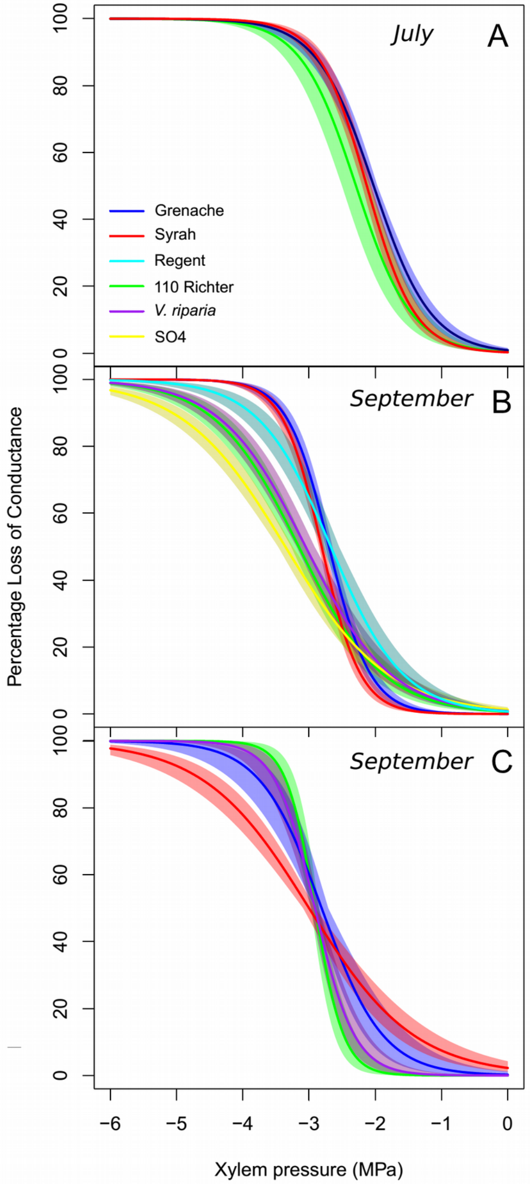
Stem conductivity:
K= (dr/dt) / 0.5 ρ ω2 [R2 – (R-r)2]

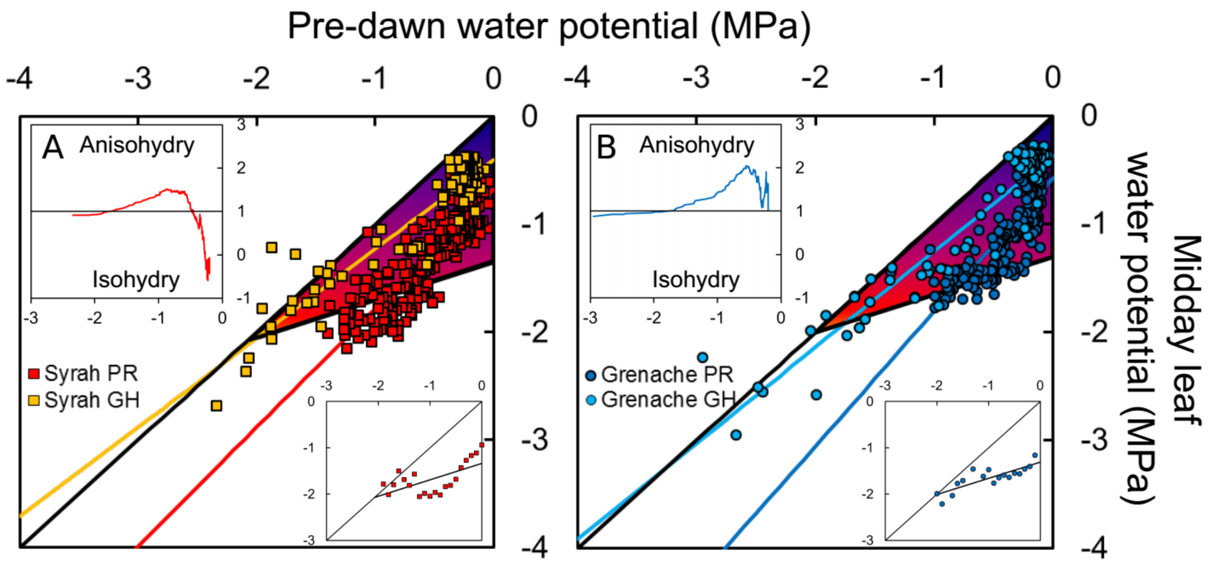
Cavitating the oaks of the world



Lobo *et al.* in prep

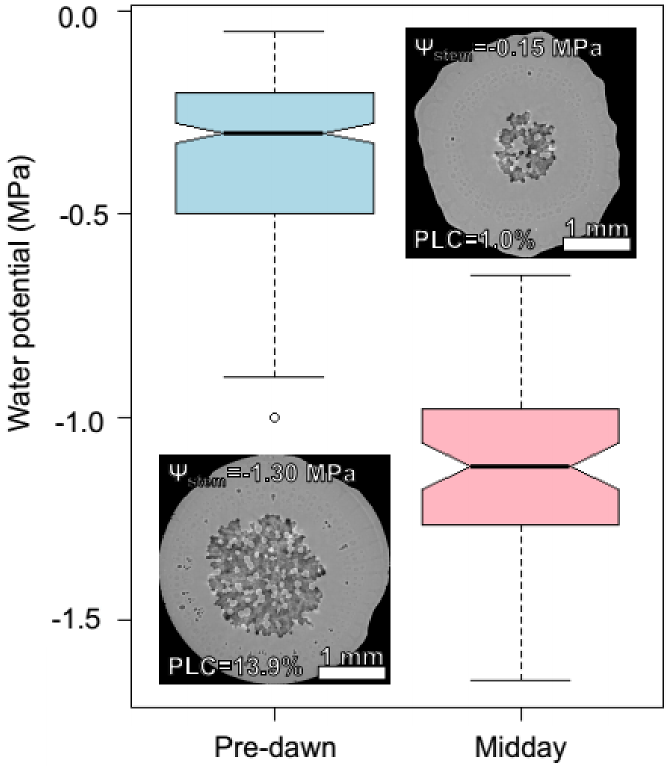
Vitis vinifera cv Grenache and Syrah have repeatedly been described as iso- and anisohydric, respectively





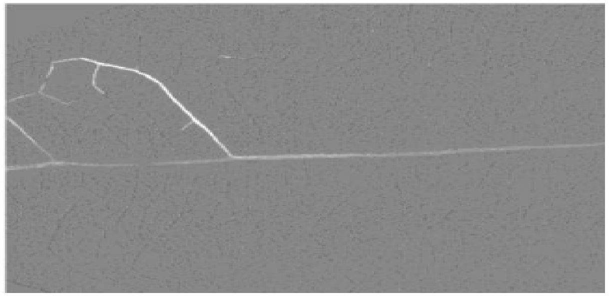
No differences in

1. embolism resistance, 2. water potential regulation, 3. stomatal regulation

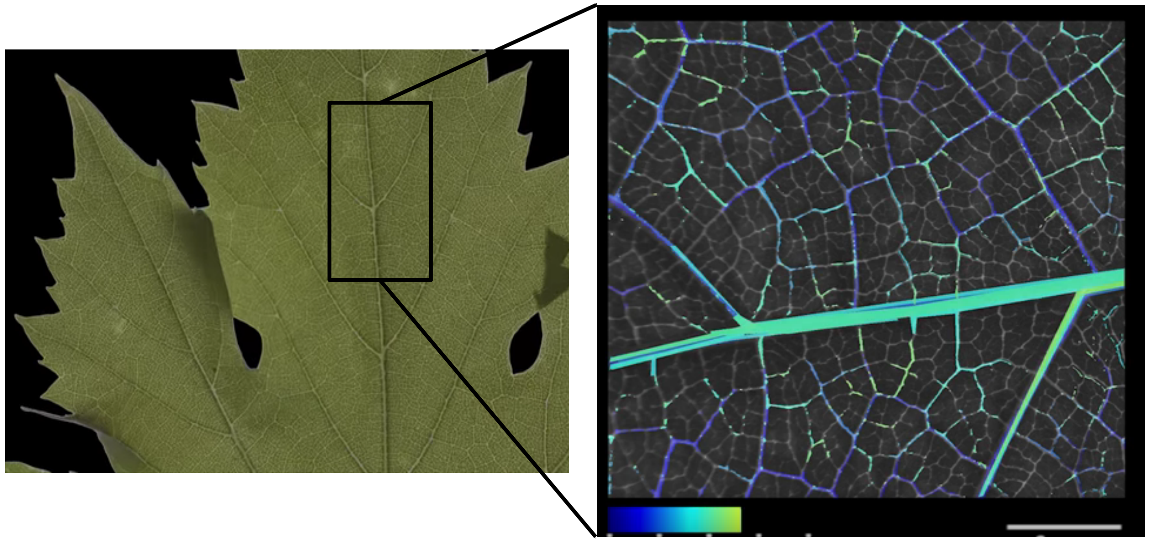


Deconstructing the iso/anisohydric concept ; Charrier *et al.* 2018

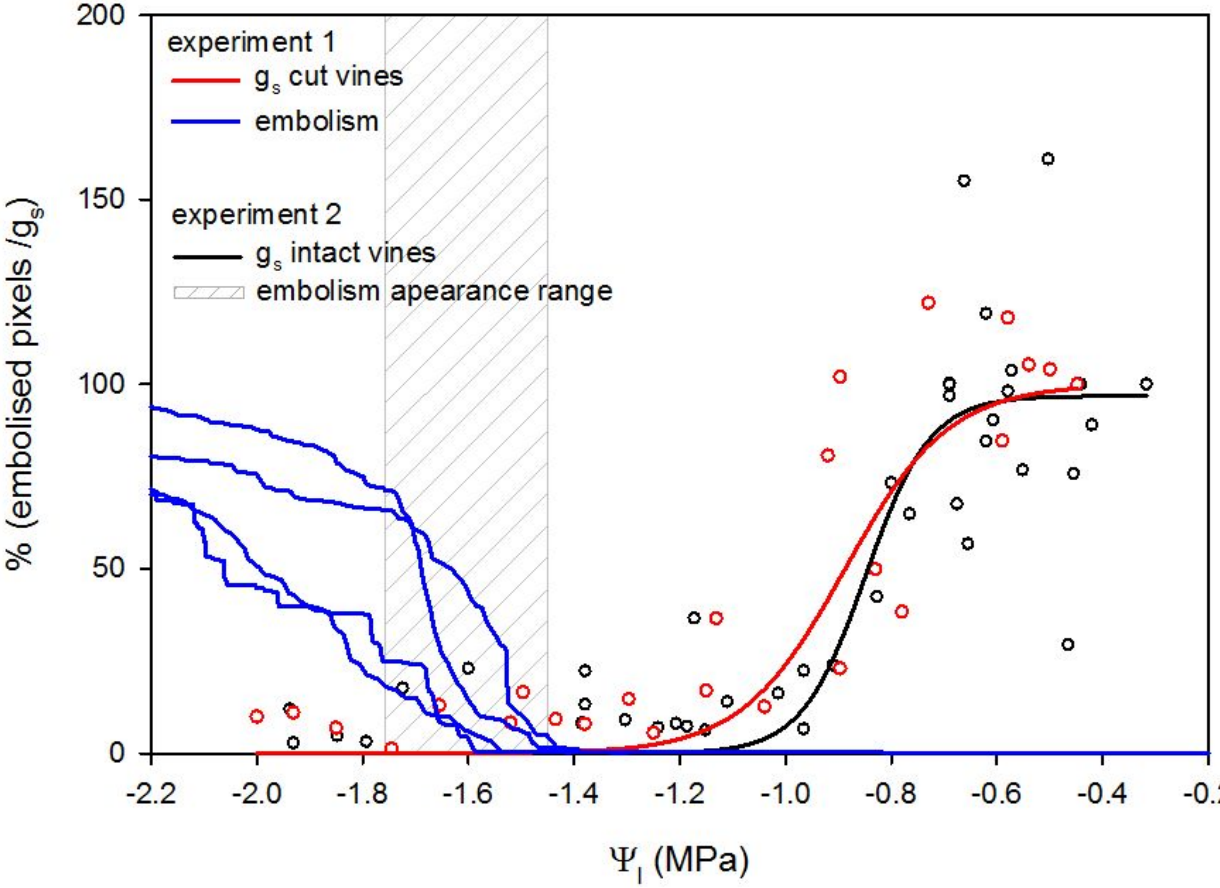
Visualizing embolism in leaves



Optical technique
(Brodribb *et al.* 2016 PNAS)

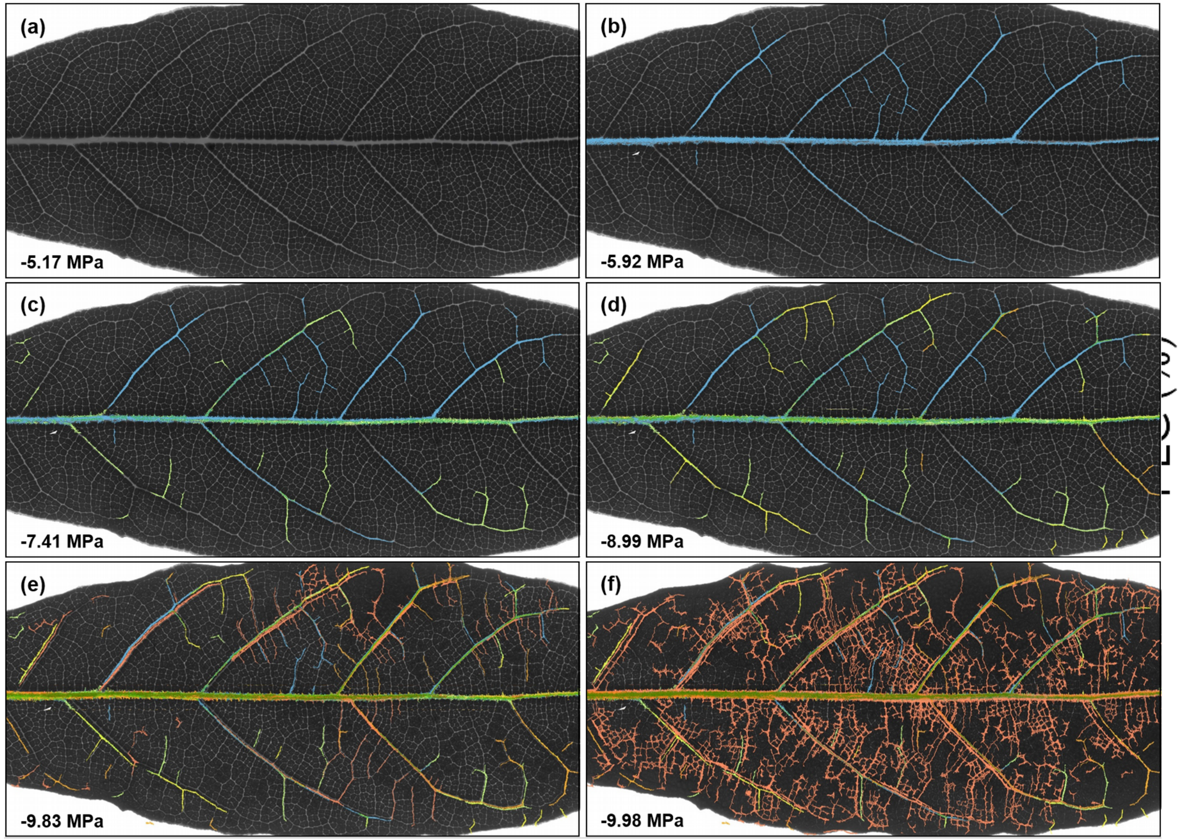


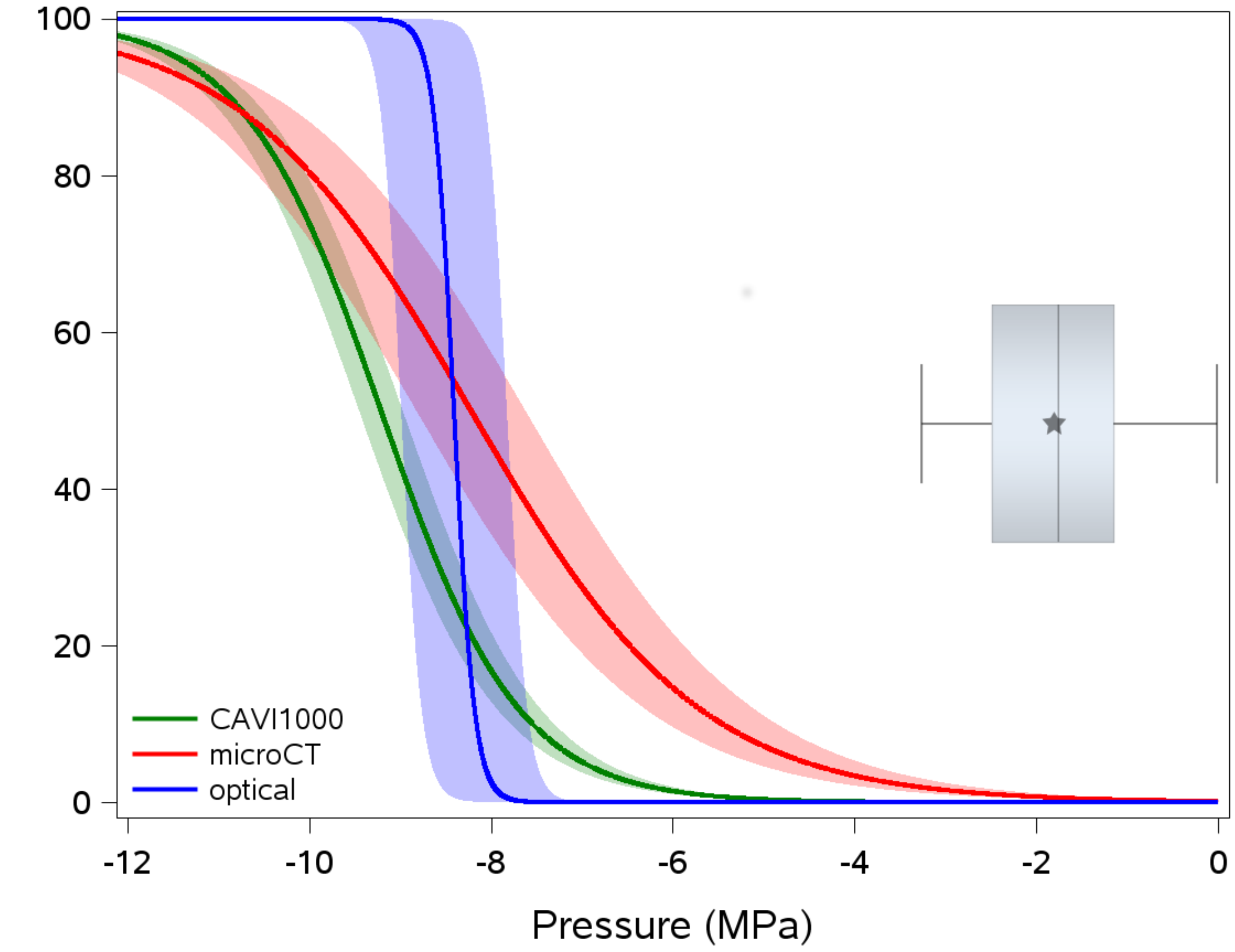
Hochberg et al. unpublished Harvard University



Leaf embolism always occurs after stomatal closure

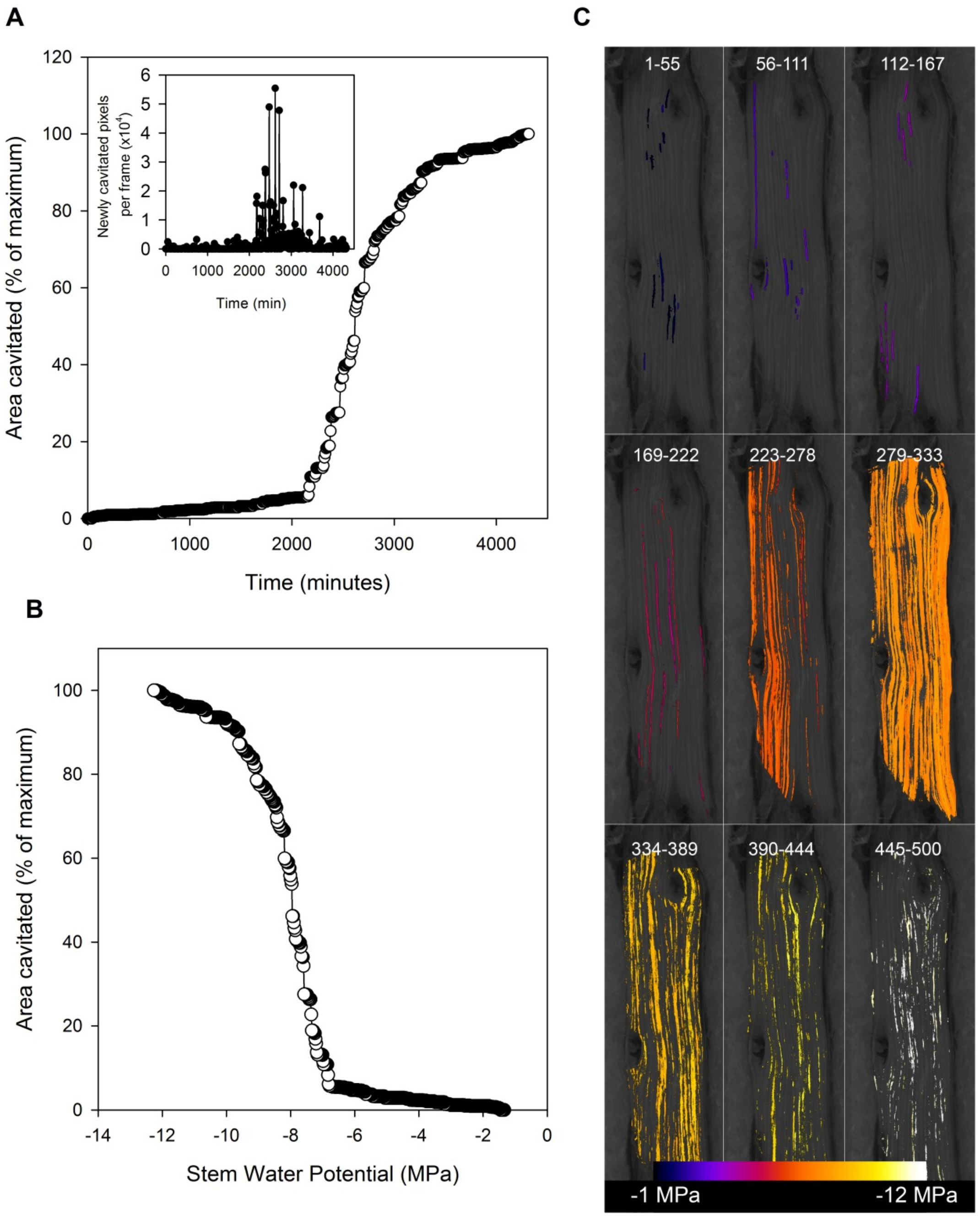
An inconvenient truth about xylem resistance to cavitation in the model species for refilling (*Laurus nobilis*).

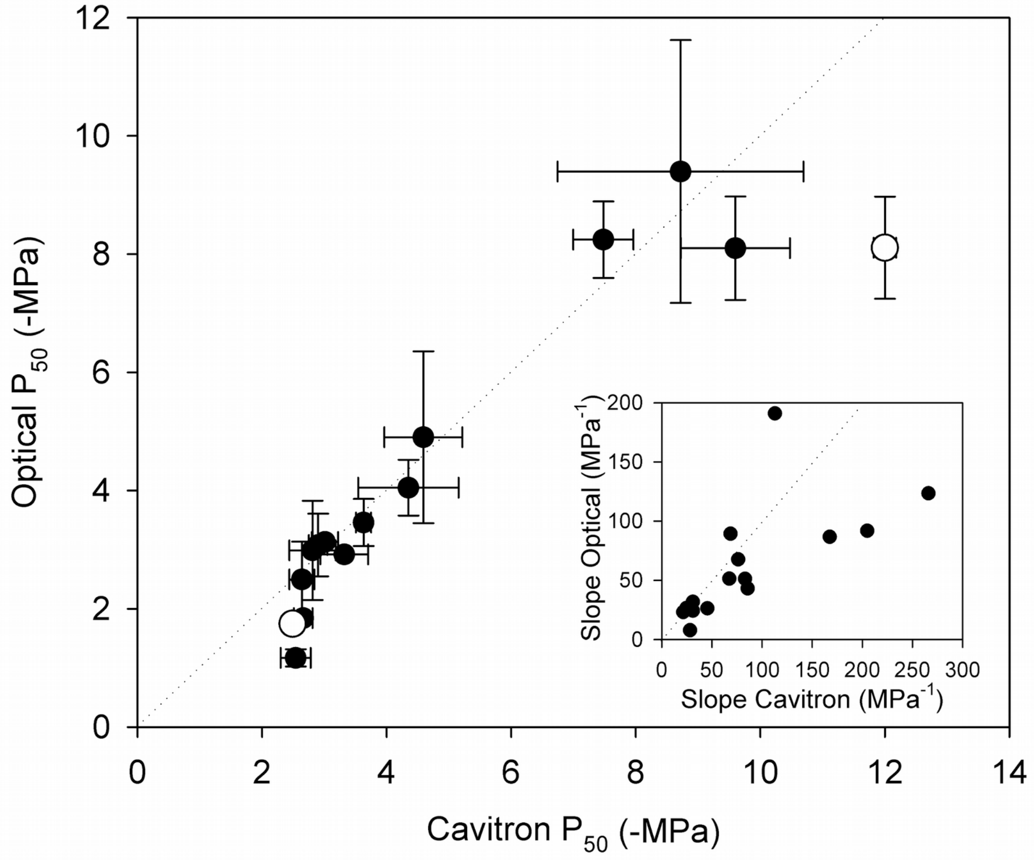




Lamarque et al. *2018*

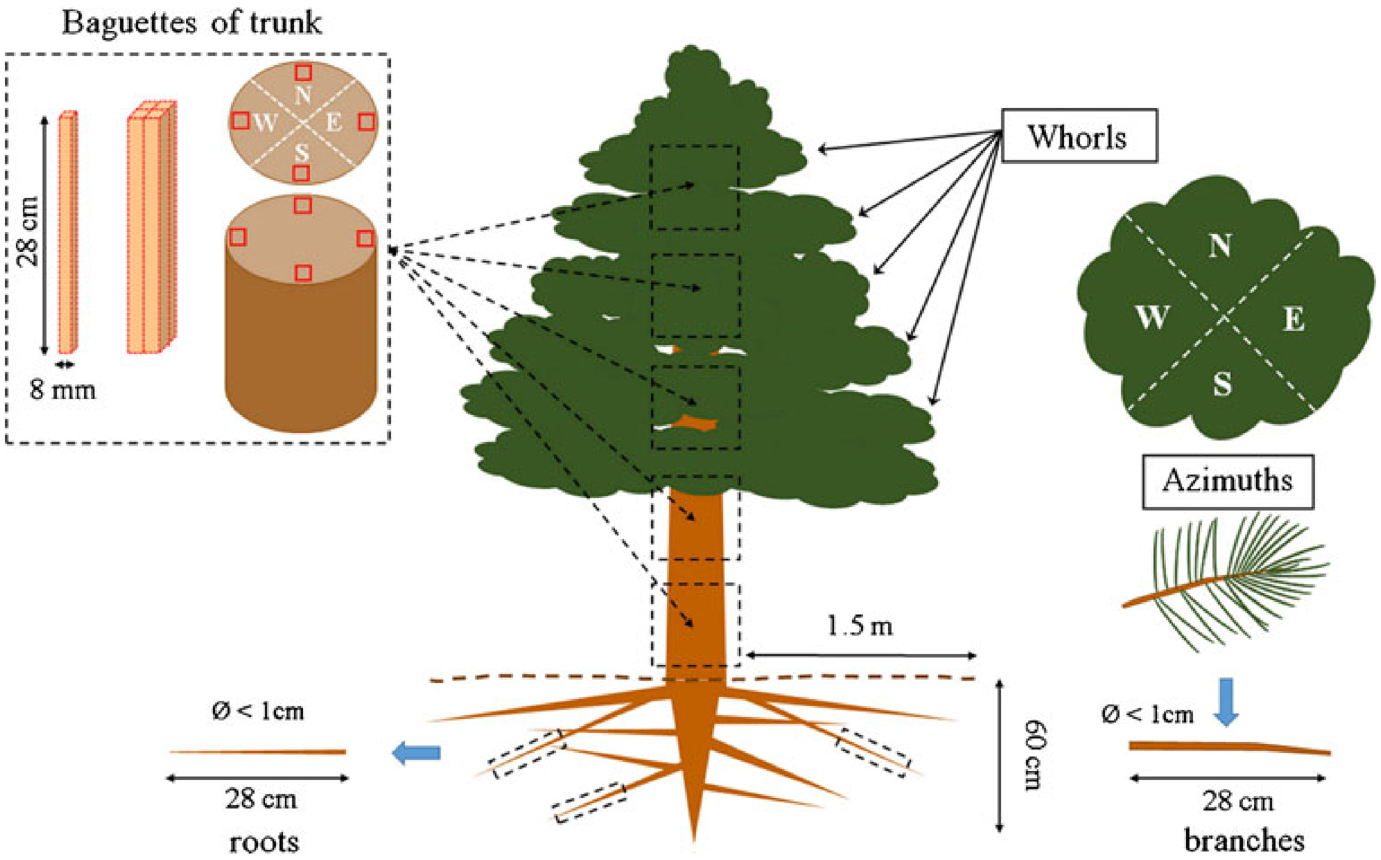
Stem embolism





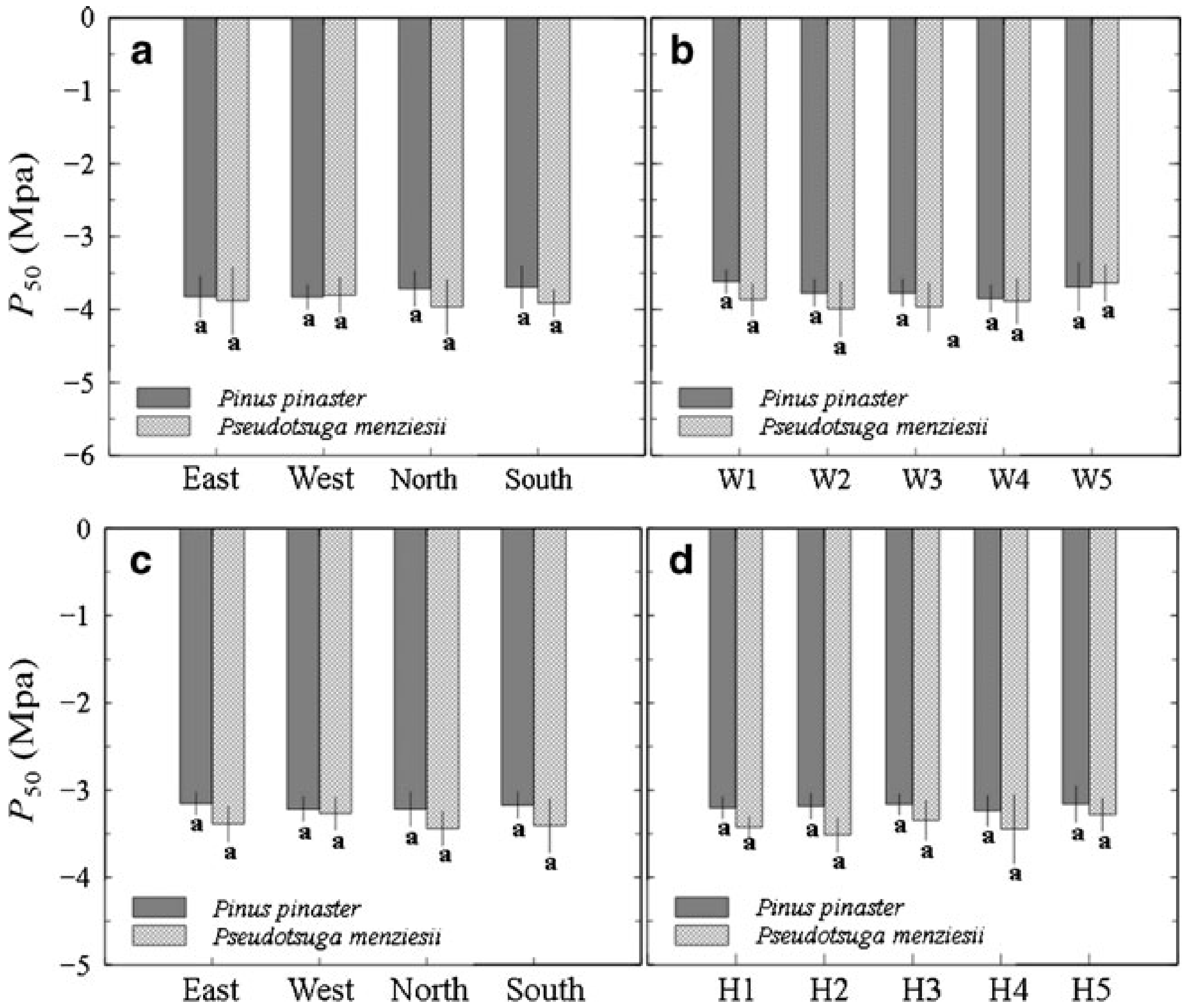
Brodribb, ..., Delzon *2018*

Within tree variability

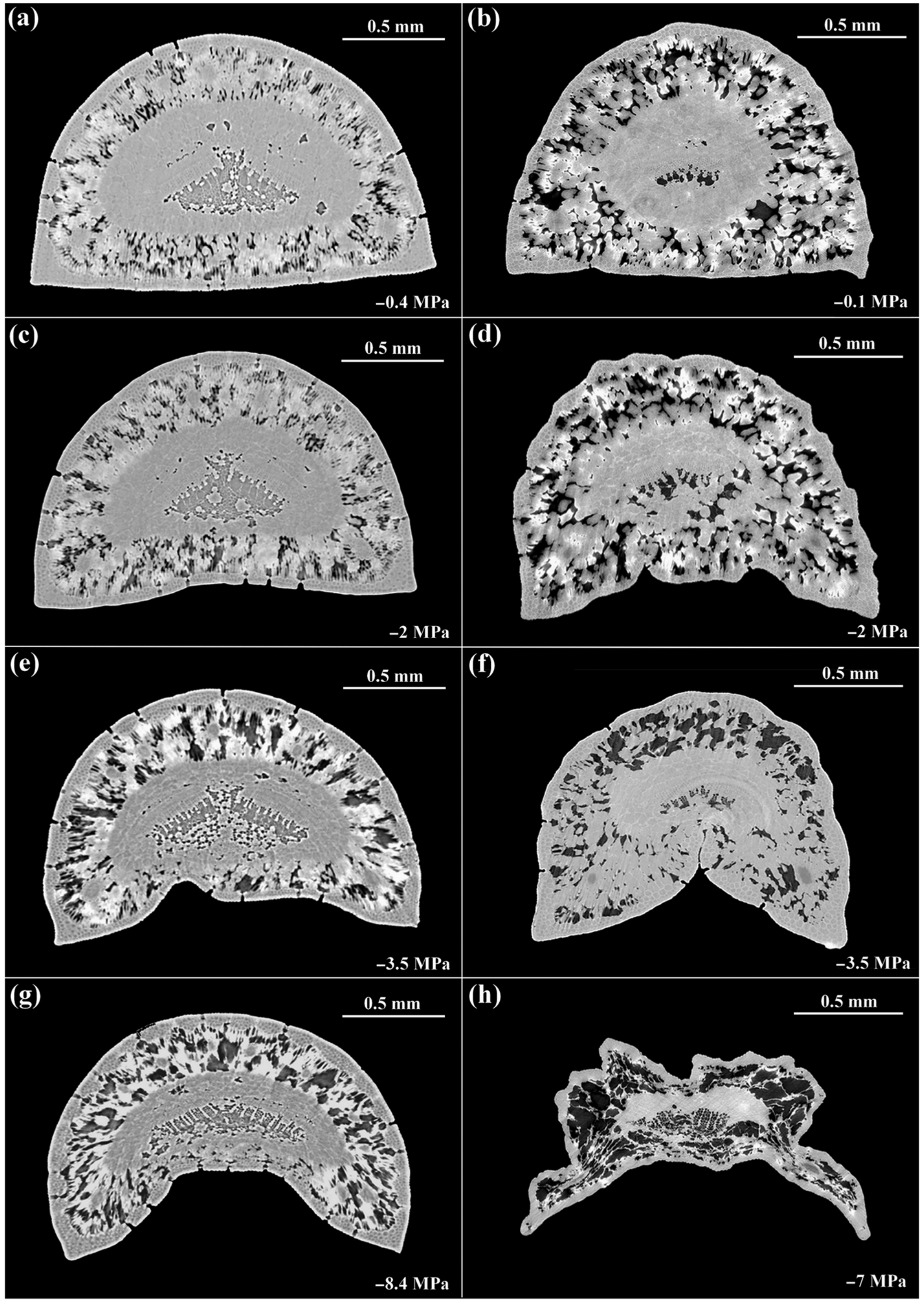


Bouche et al. 2016 *AFS*

No variability, no segmentation in conifer trees

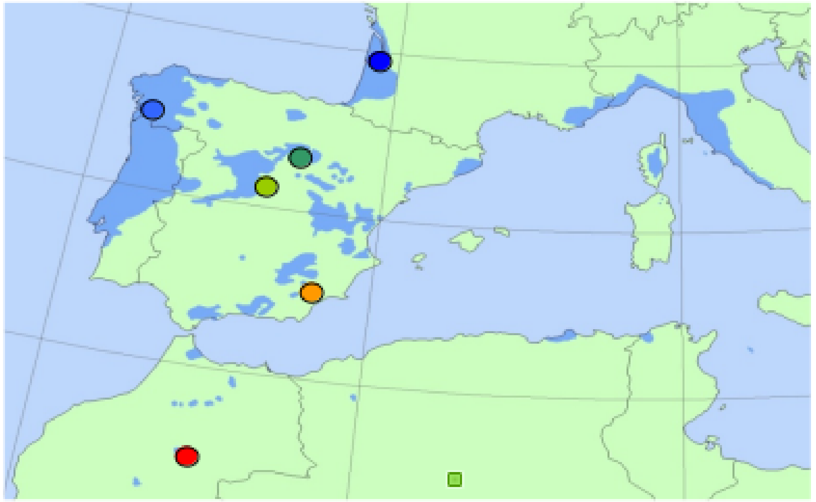


Bouche et al. 2016 *AFS*

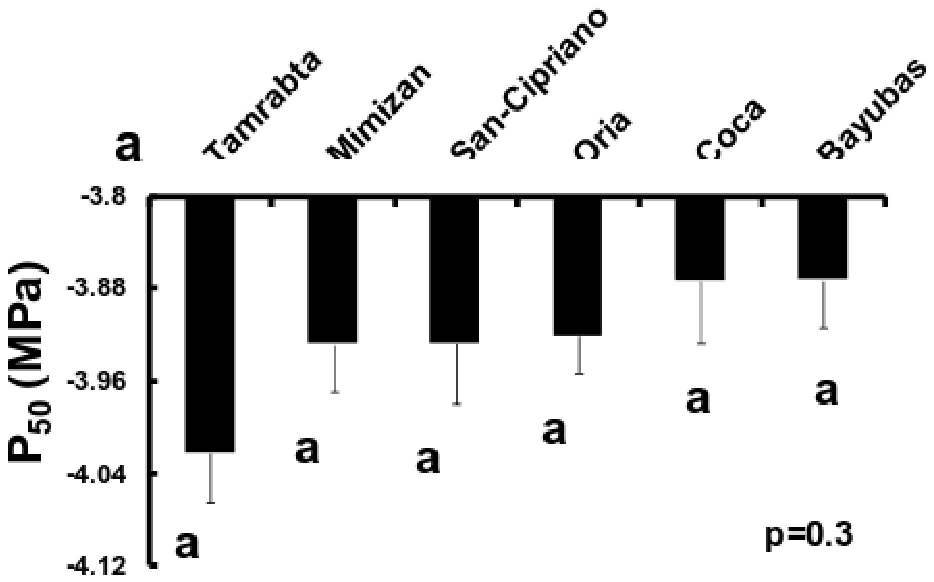


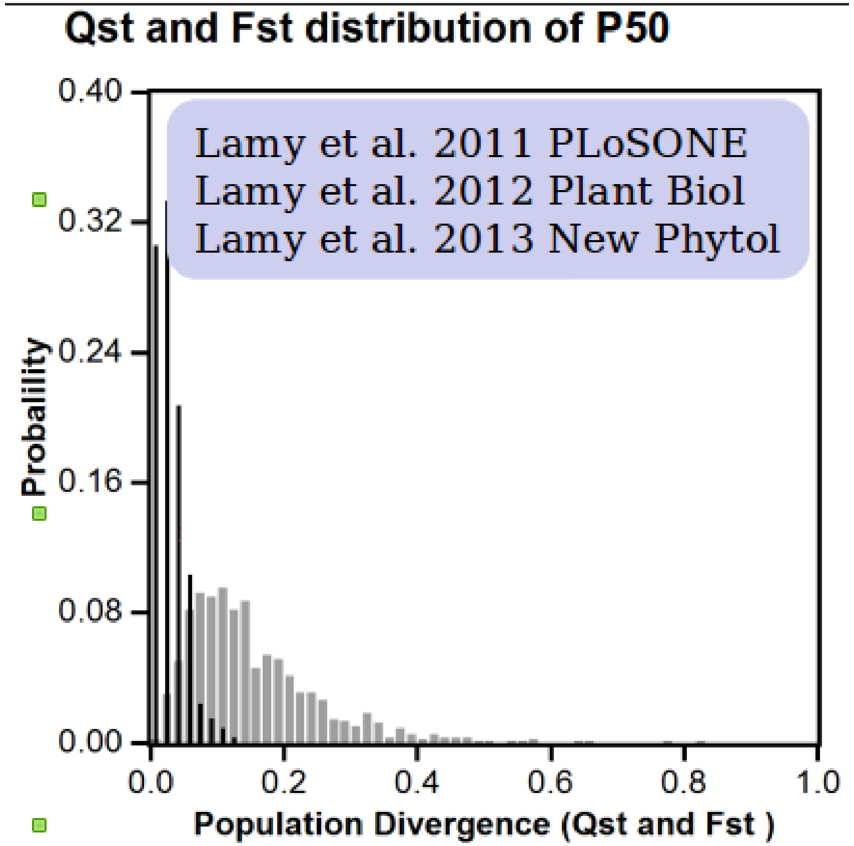
Bouche et al. 2015 *PC&E*

Intra-specific variability (Pinus pinaster)

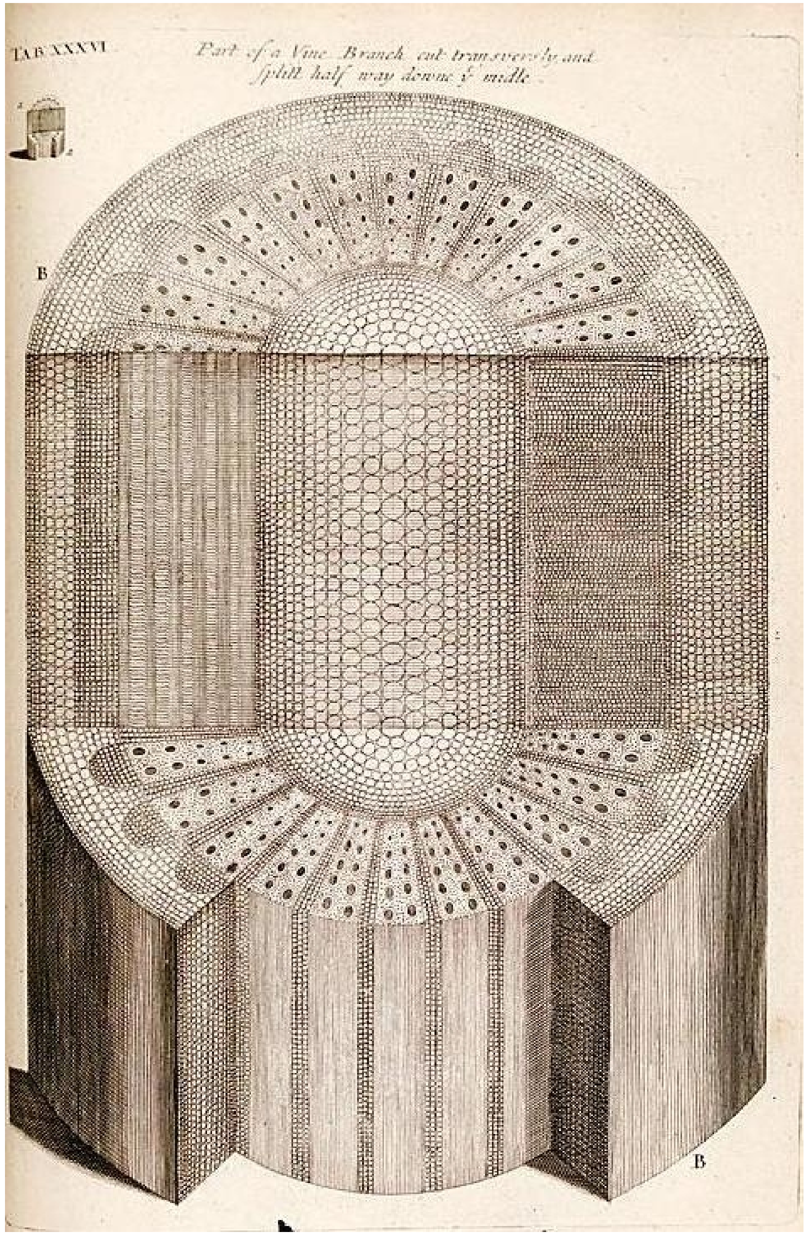


The QST<FST pattern can be interpreted as a canalization phenomenon or a consequence of uniform selection





Lack of genetic variation in cavitation resistance among populations across a species distribution range



Grew (1674) first microscopic observation

4 centuries later,

Badel *et al* (2014) X-ray micro-CT scan

similar observations but we must revisit the entire literature and switch to a high resistant paradigm:

1. Grapevine and oak are NOT highly vulnerable to embolism

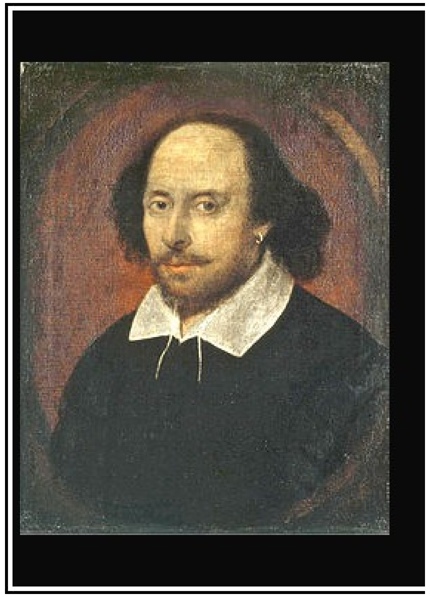
2. no evidence for xylem refilling under tension

3. lack of differences between varieties or populations

“I would fain die a dry death.”

William Shakespeare,

The Tempest Act i. Sc.1



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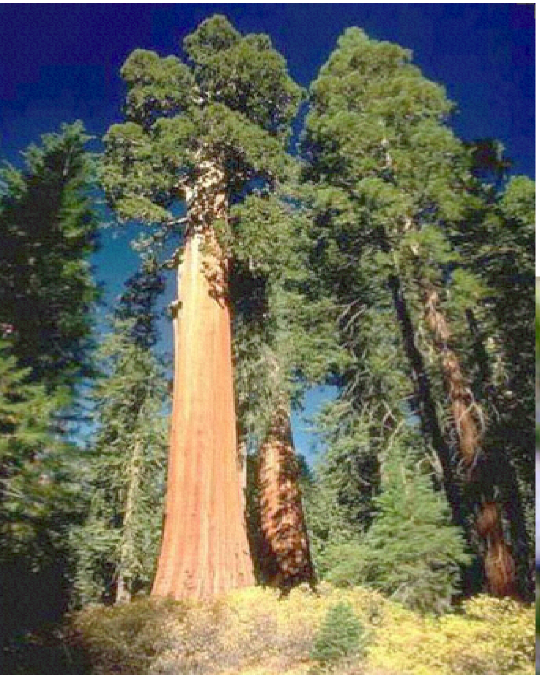
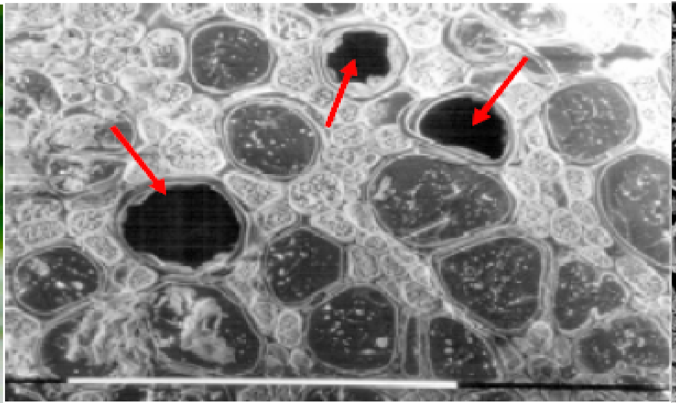
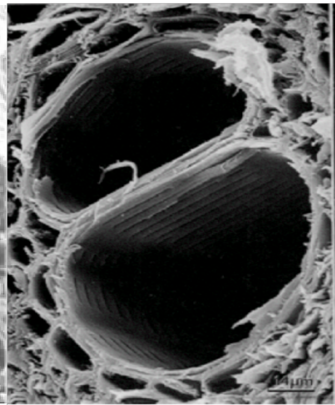
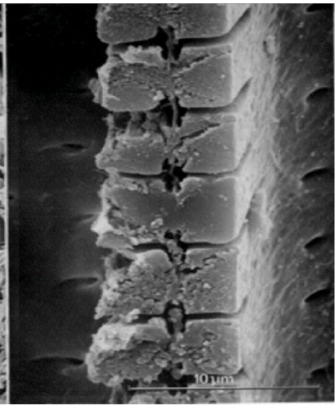
Sciences Technologies

Story II. Mechanisms of plants survival and mortality during drought

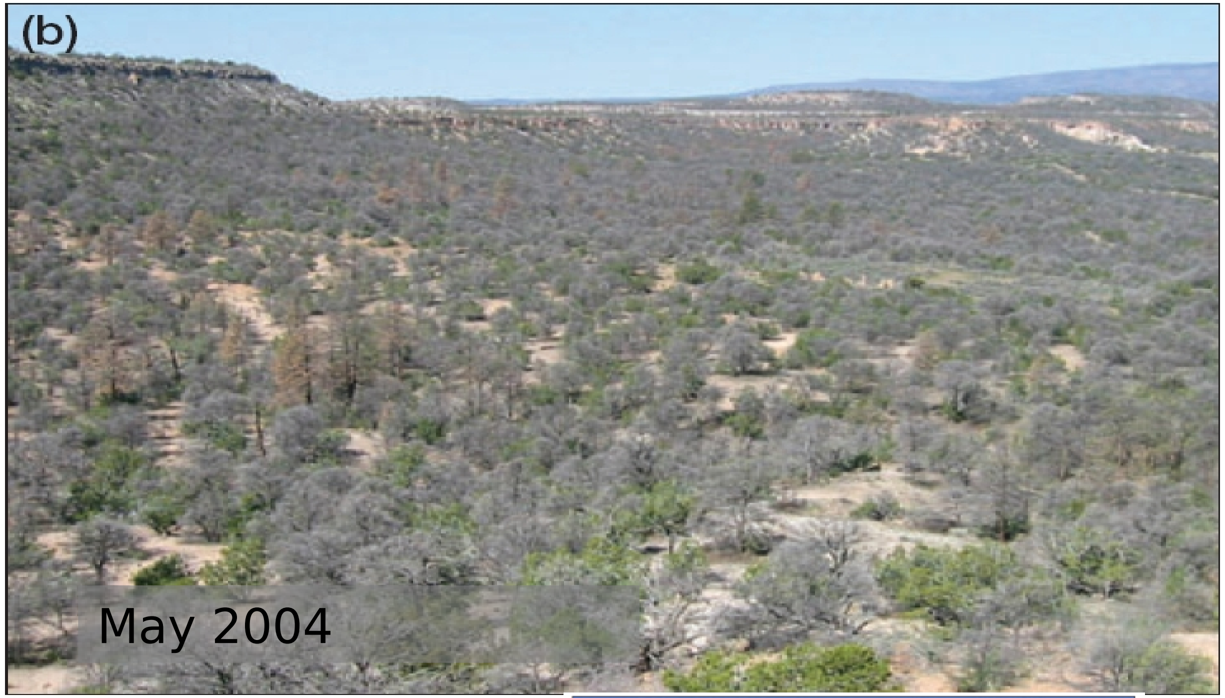








Drought-induced forest dieback



Breshears et al 2009

Juniperus monosperma

Pinus edulis

Why do some plants survive while others succumb to drought?

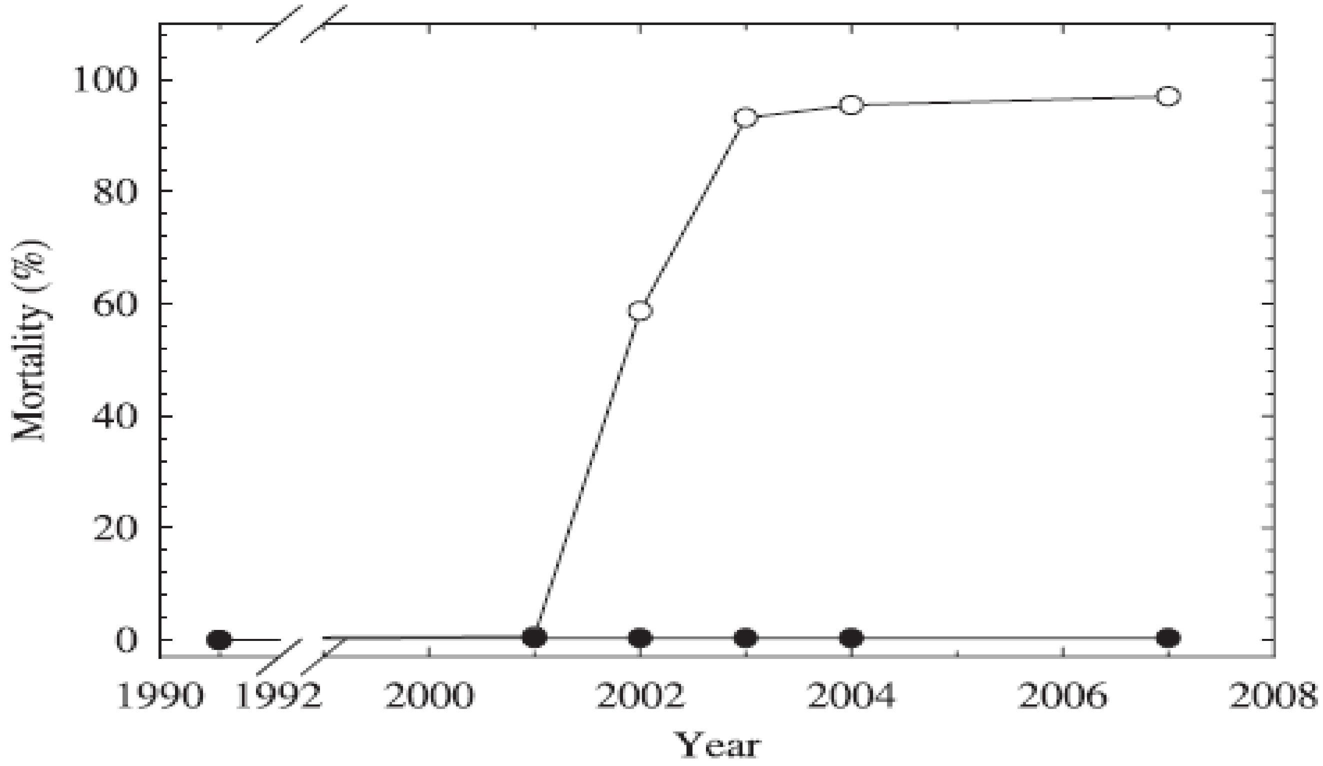


Fig. 2 Percentage mortality of piñon (open circles) and juniper (closed circles) trees at a 1.5 ha site, Mesita del Buey, near Los Alamos, New Mexico. For piñon, 16 of 484 trees survived (97% mortality), whereas for juniper, 559 out of 561 trees survived (< 1% mortality).

Why is predicting drought-induced mortality difficult?

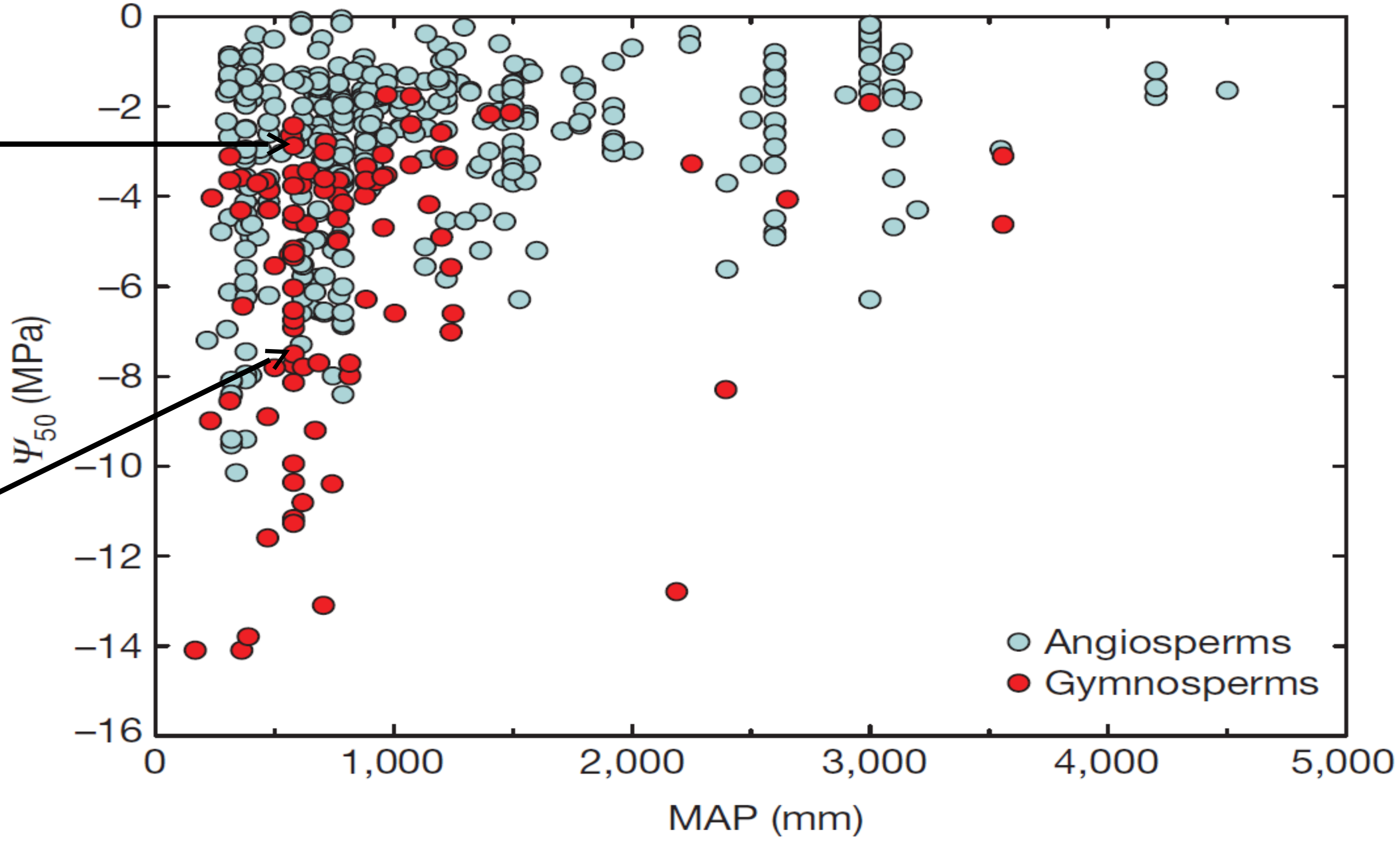
Too many ways to resist drought ⇒ no single trait is good enough

Acer monspessulanum

5% percentile of MAP (Spain) = 530 mm

Phillyrea latifolia

5% percentile of MAP (Spain) = 605 mm



Choat et al. (Nature 2012)

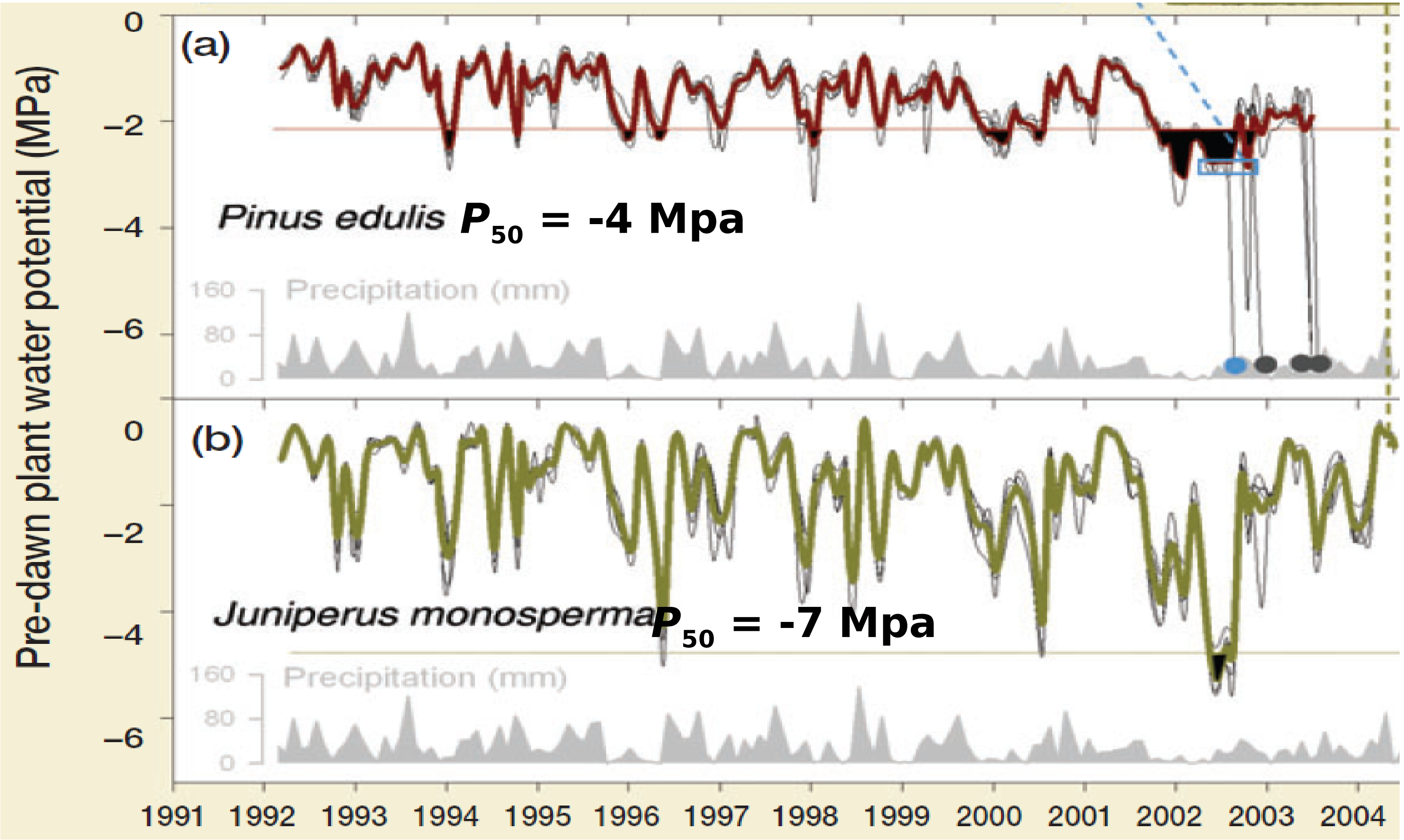
Les types de réponse à la contrainte hydrique: plusieurs manières de résister à la sècheresse

Resistance

- Escape
  - Phénologie
  - (ex: annuelles) éphémérophytes
- Exposition au Stress (ex: pérennes)
  - Avoidance
    - -*Water savers*
      - régulation stomatique
      - osmorégulation
      - stockage hydrique
      - (ex: cactées, pinacées,)
    - -*Water spenders*
      - enracinement profond
      - (ex: mesquite tree)
  - Tolerance
    - - Xylem resistance (ex: Juniperus)
    - - protoplasme resistance (ex:plantes reviviscentes, Lichen)

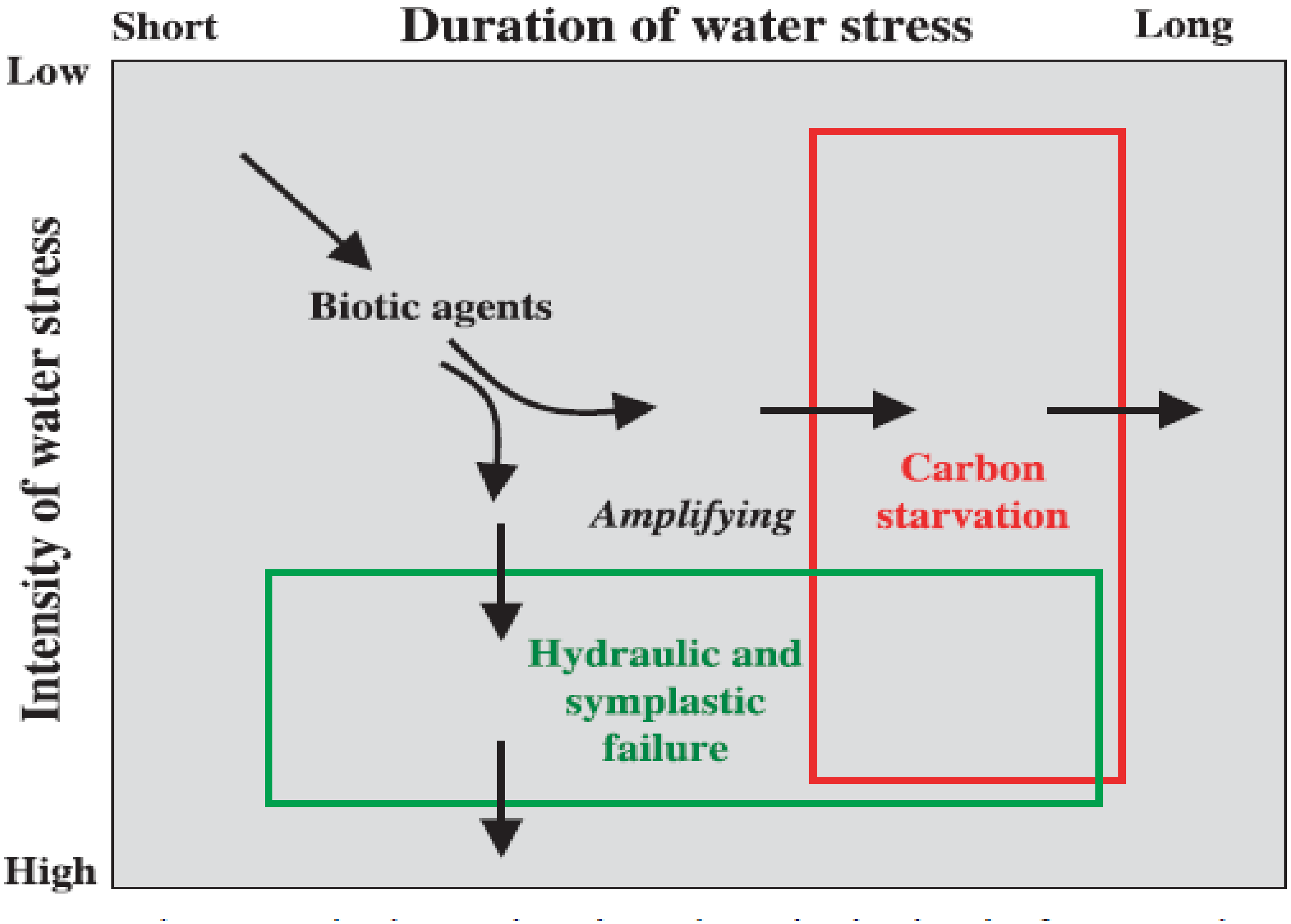
Drought-induced forest dieback

Breshears et al 2009 Linton et al 1998



Mortality by hydraulic failure *per se?*

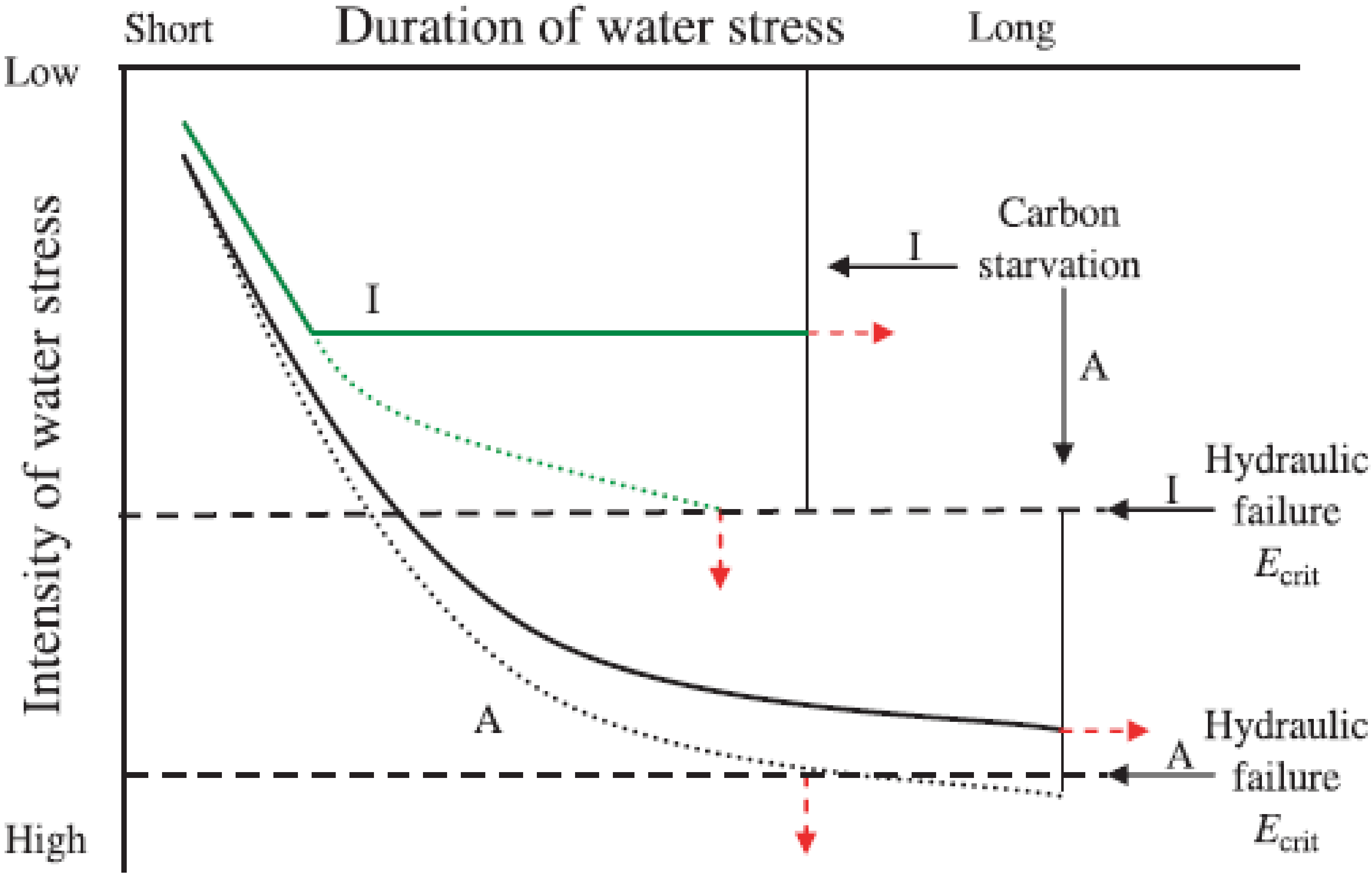
Hypotheses on mechanisms of drought-related mortality related to the intensity and duration of water stress



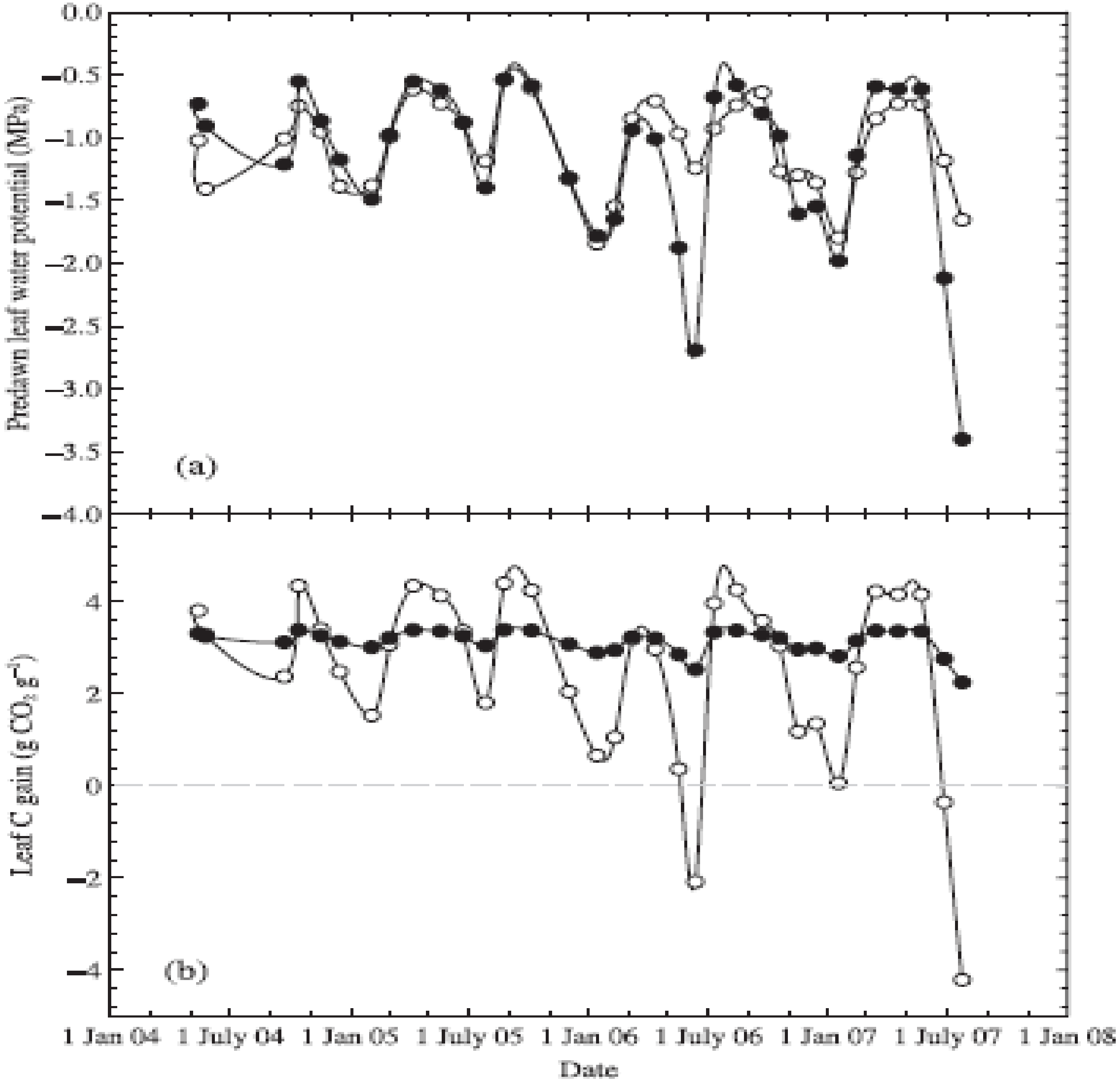
What do I need to do?

1. add water
2. add sugar

Theoretical predictions of the mechanisms of drought-related mortality for species utilizing isohydric vs anisohydric regulation of water potential.

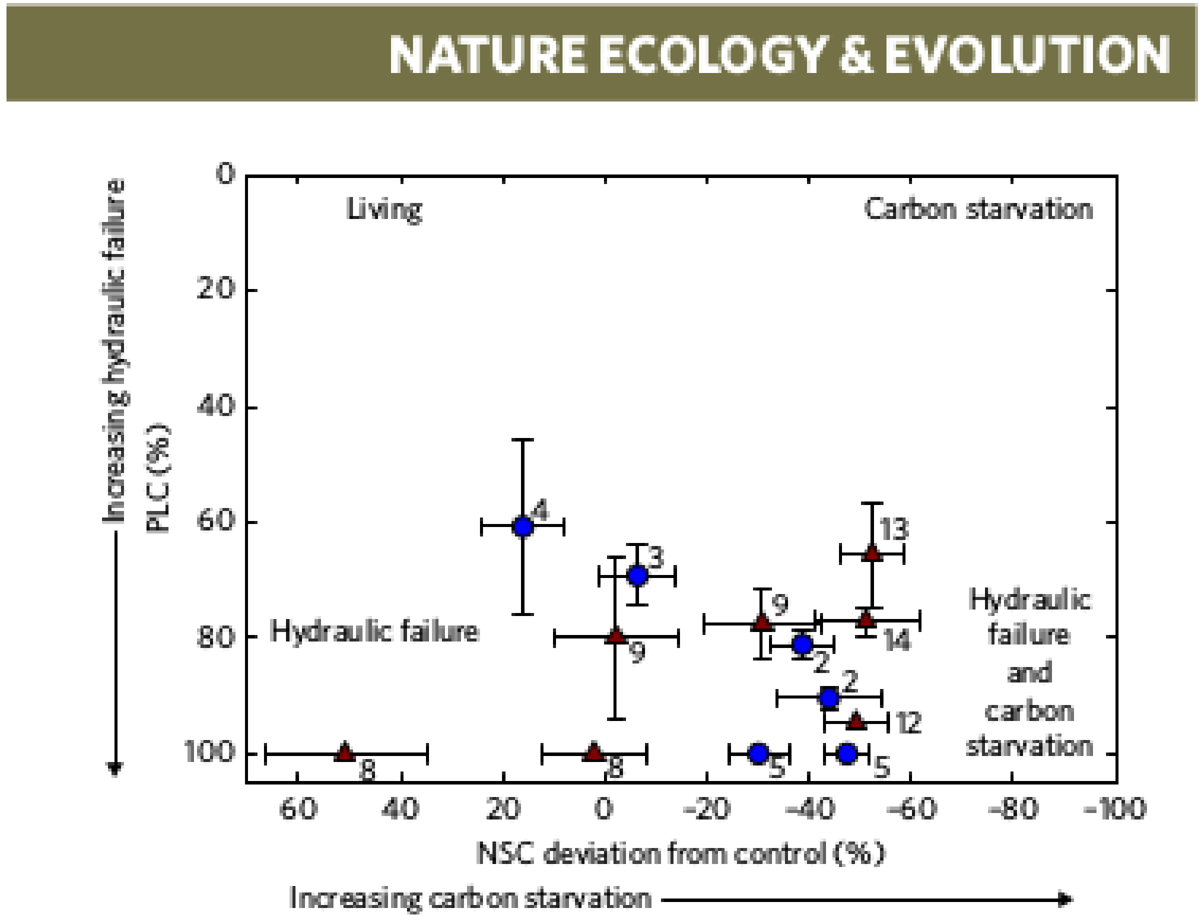


Carbon starvation



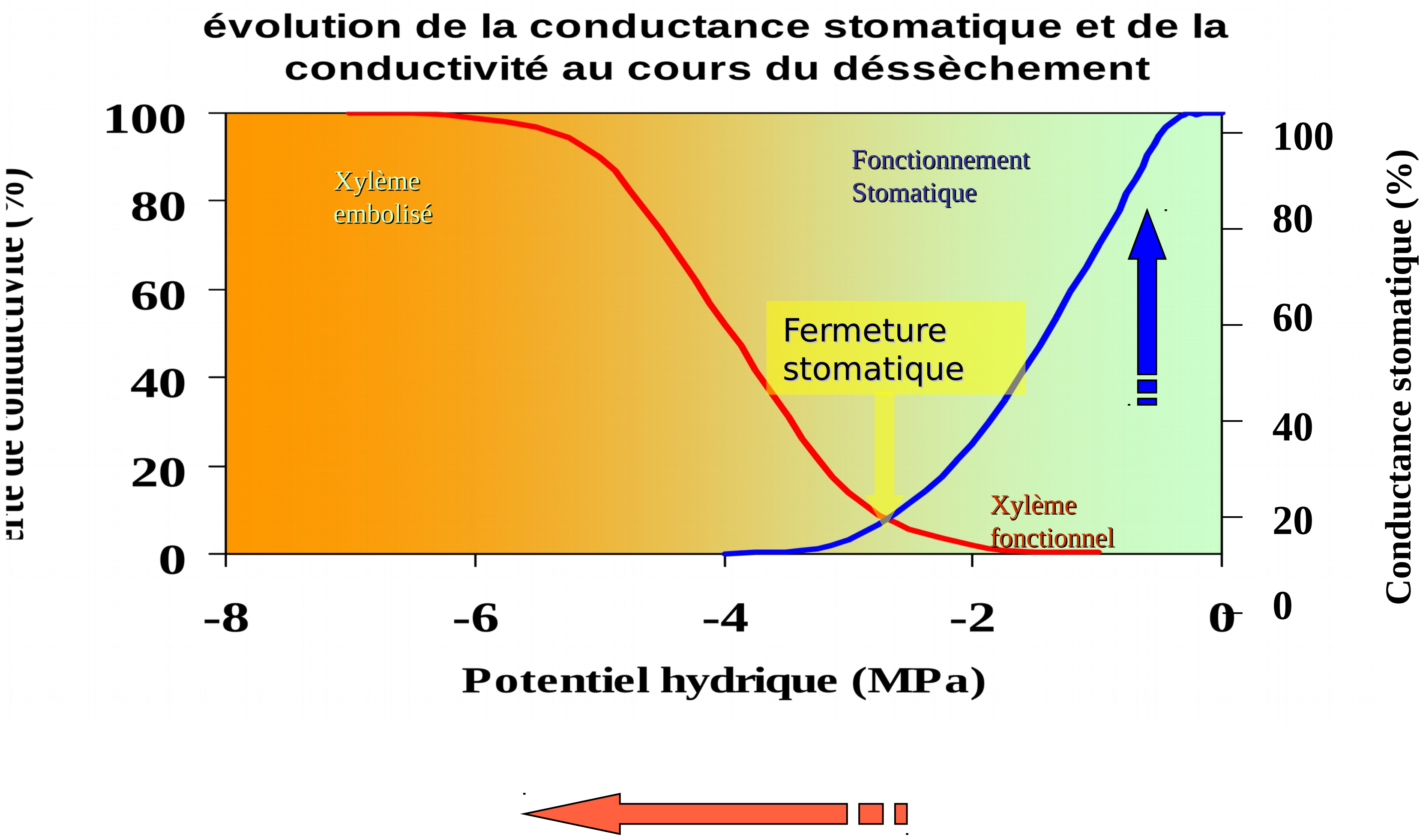
Three years of monthly observations of predawn water potential of piñon (open circles) and juniper (closed circles) from Mesita del Buey, Los Alamos, New Mexico.

We found that tree mortality from drought was always associated with substantial loss of hydraulic function and that lower NSCs at mortality were not universal

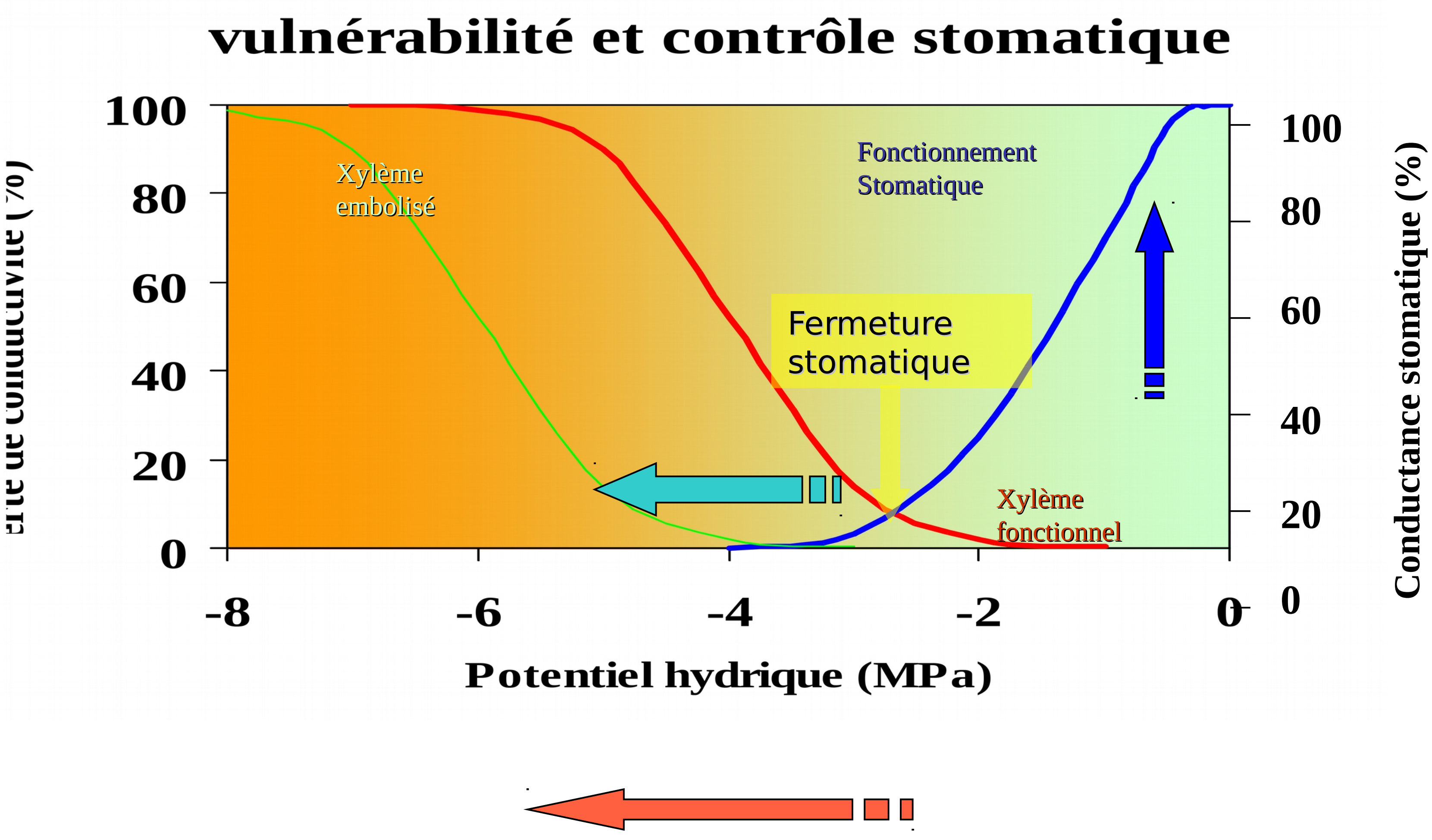


Adams et al. 2017

Vulnérabilité à la cavitation et contrôle stomatique



Vulnérabilité à la cavitation et contrôle stomatique



La réponse à la contrainte hydrique

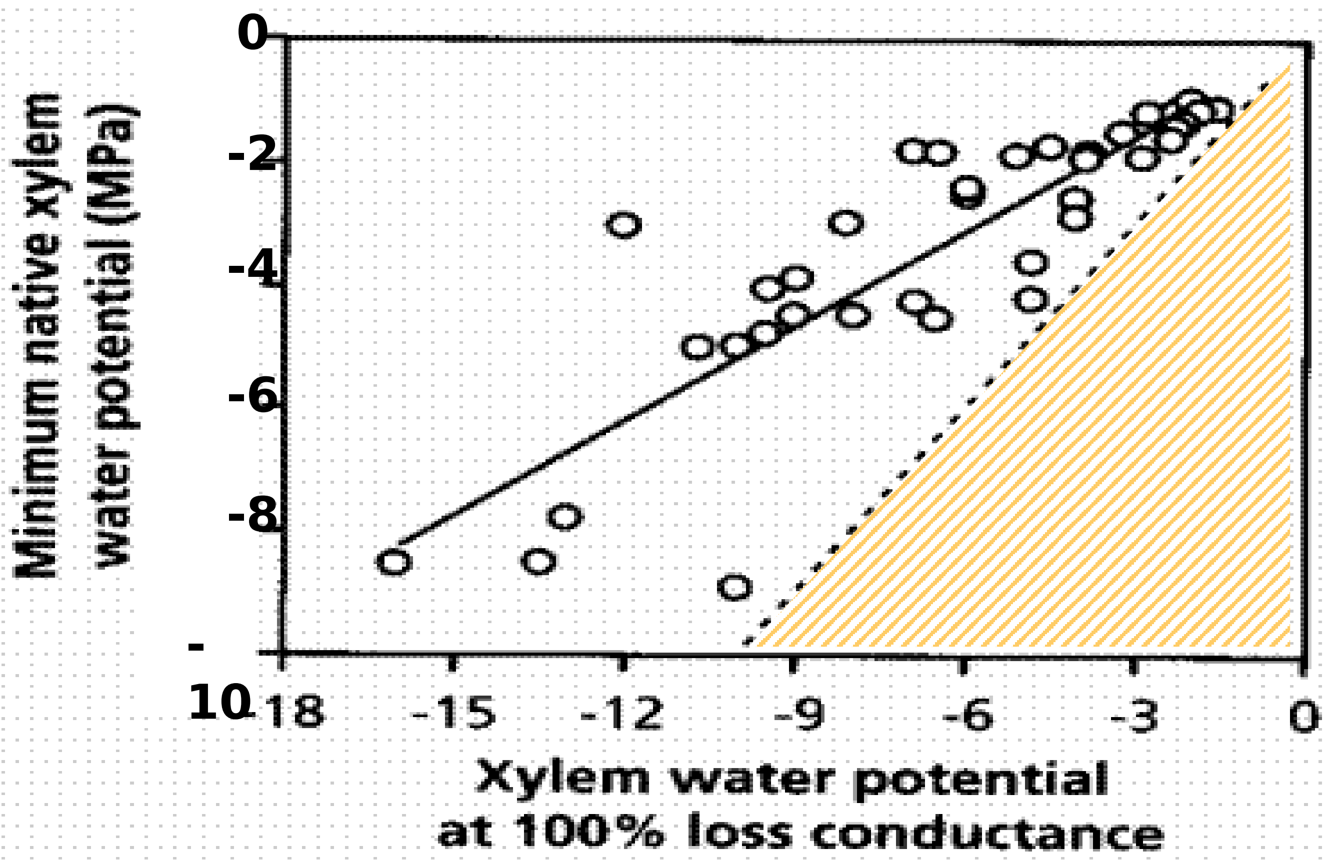
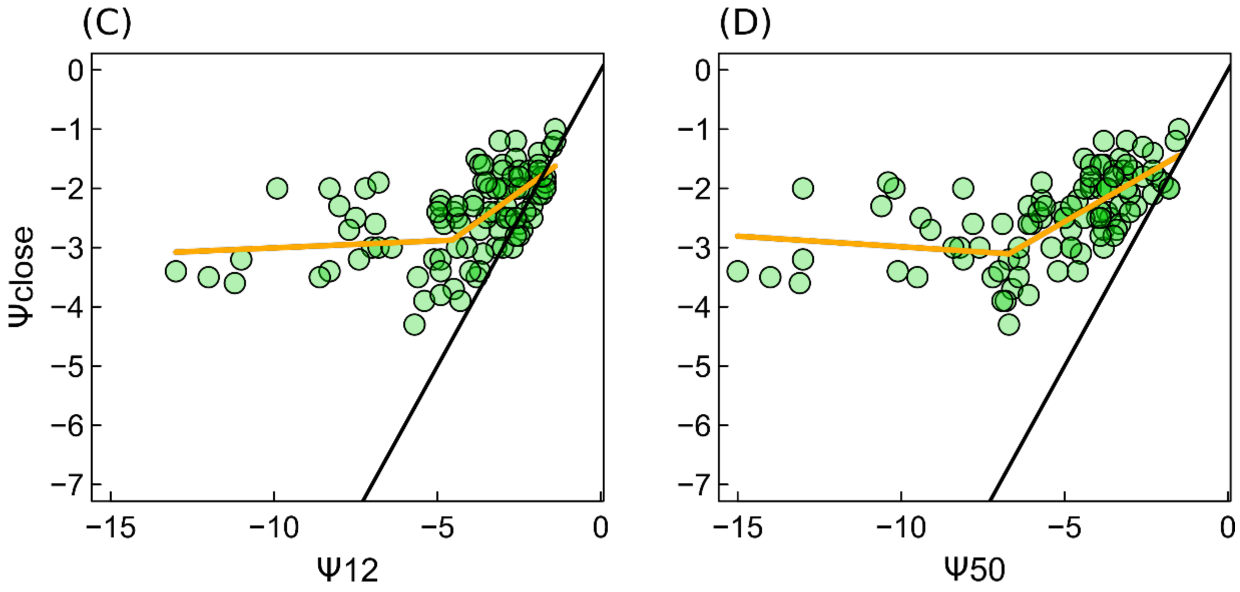


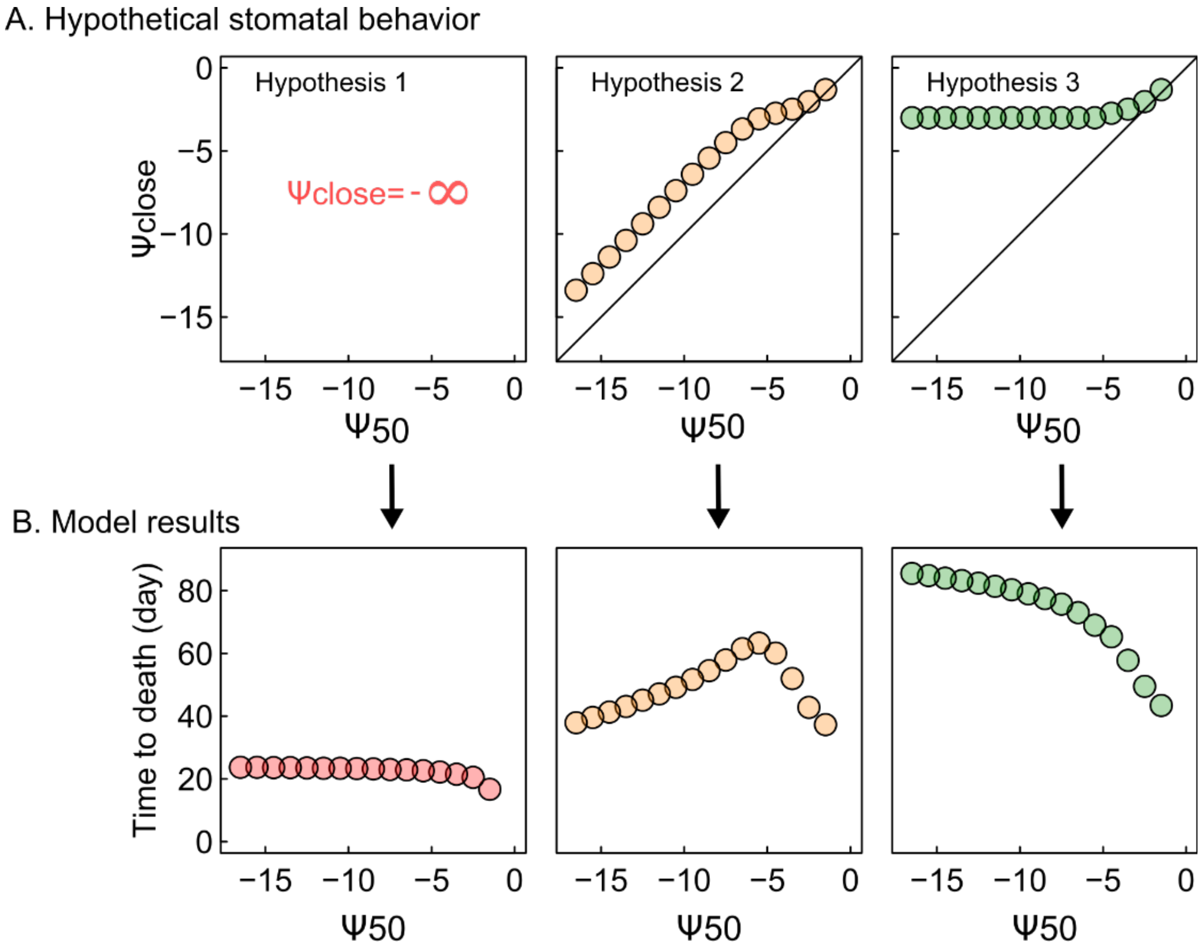
FIGURE 20. Xylem pressure required to induce 100% cavitation versus minimum pressure observe in the field. Dashed line indicates 1:1 relationship. Each point is a different species (Sperry 1995). Copyright Academic Press, Ltd.

Species from dry habitats, which experience negative water potentials for months operate with a much larger safety margin (Sperry 1995)

Plant resistance to drought relies on early stomatal closure

160 species; all measured in our lab

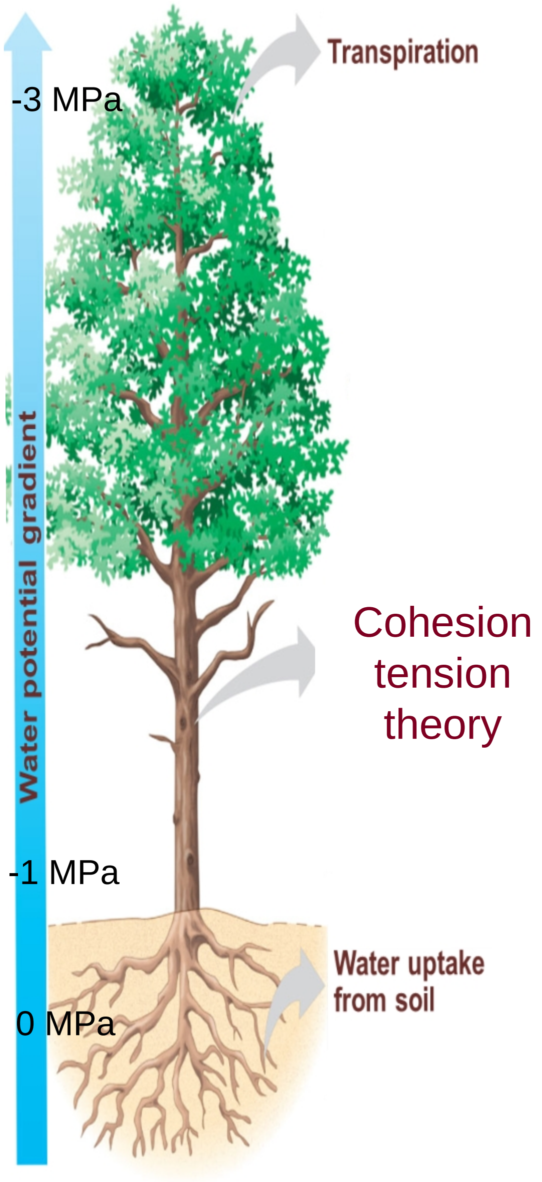


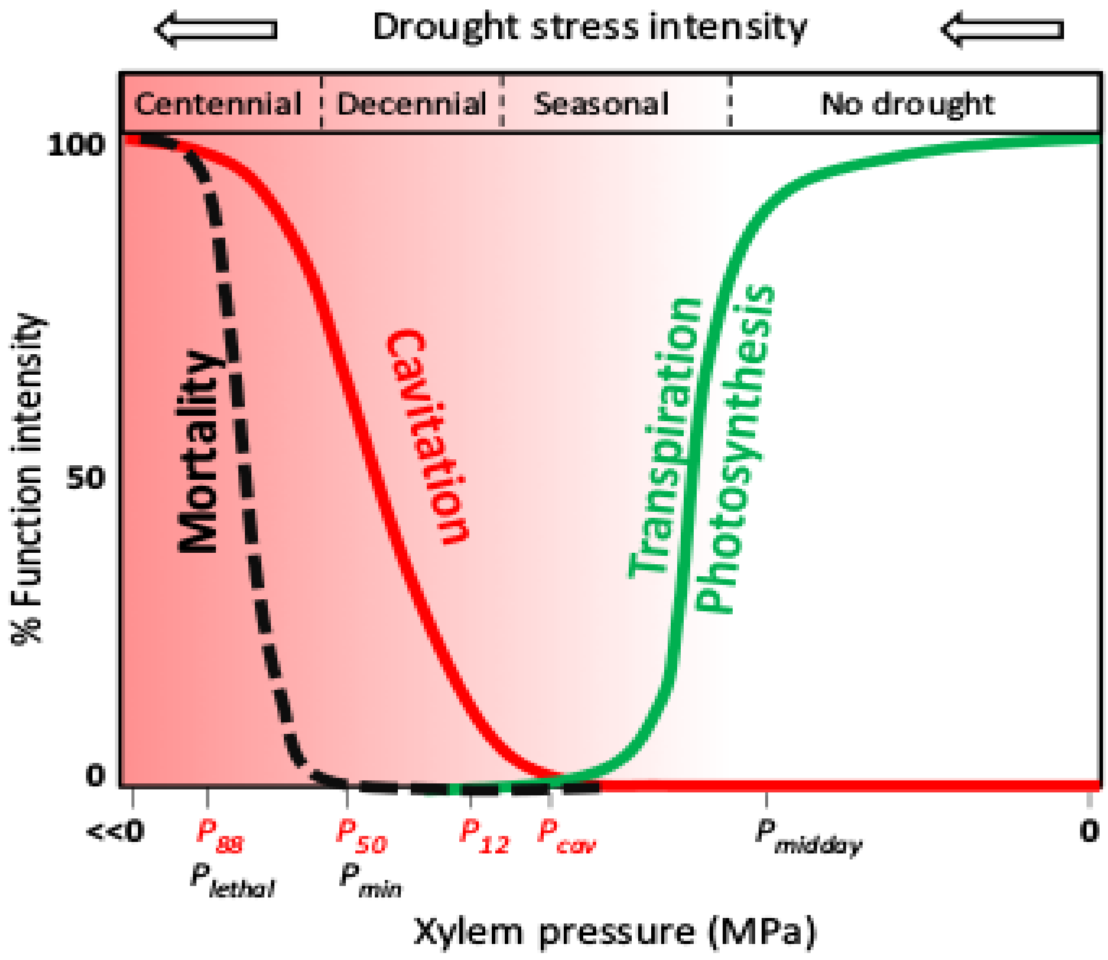


Martin St-Paul, Delzon and Cochard
Ecol Letters in revision

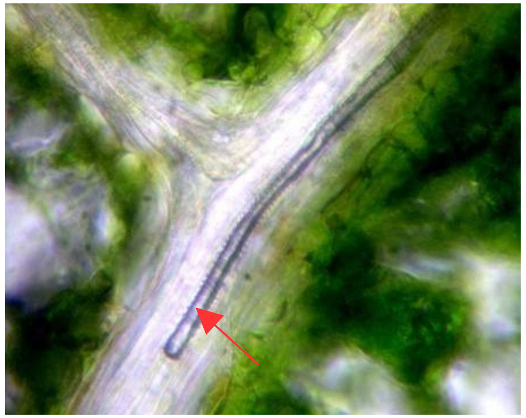
Hydraulic water transport and failure

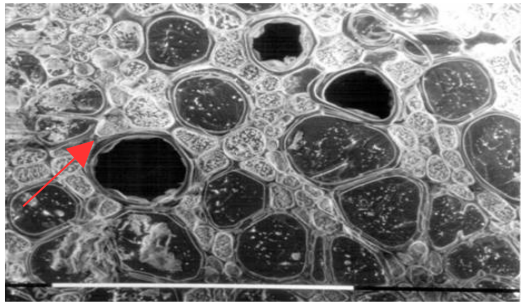
"I would fain die a dry death."
William Shakespeare, The Tempest





Delzon & Cochard 2014 New Phytol





Embolised vessels

Choat *et al.* 2012 Nature

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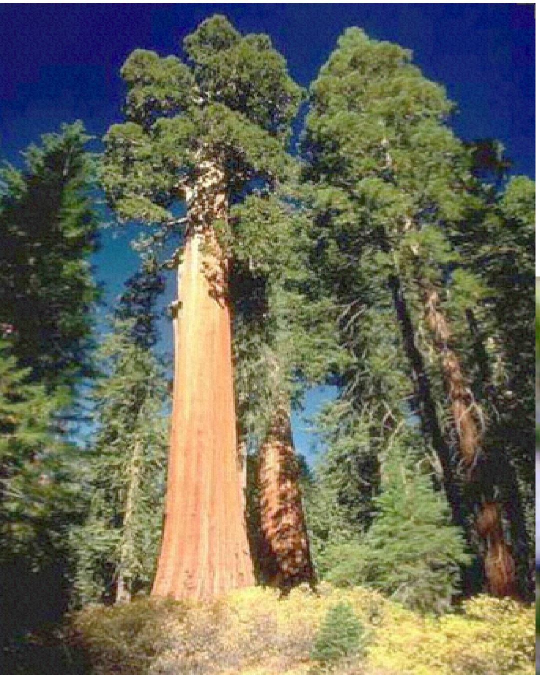
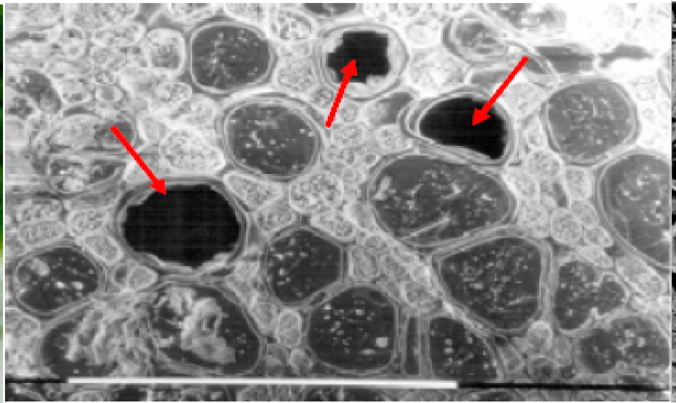
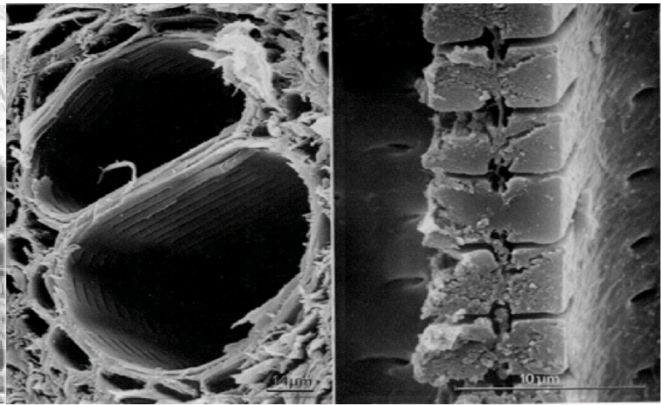
Story III. Cavitation resistance, survival and species distribution?



1. Survival and cavitation resistance

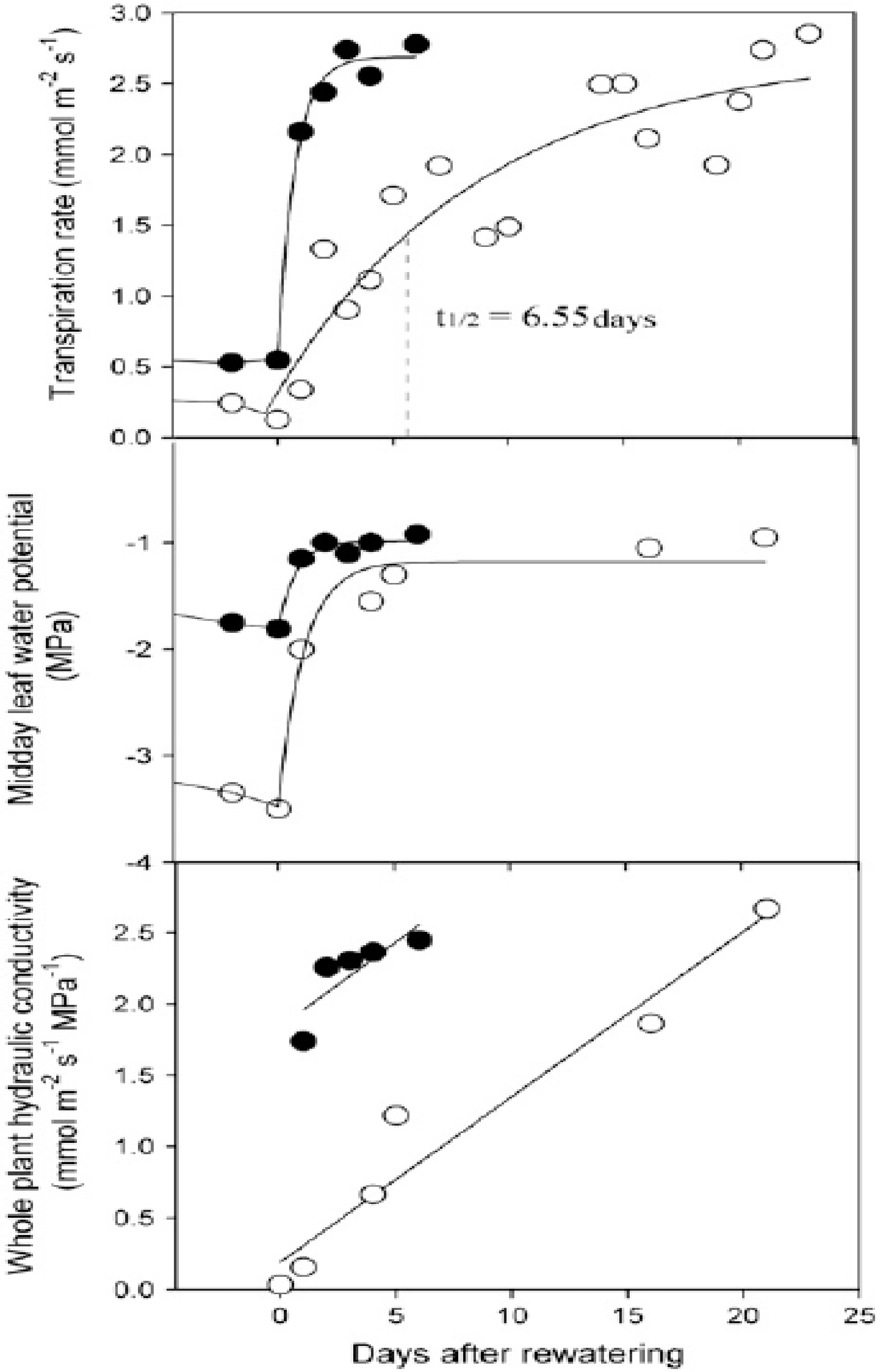
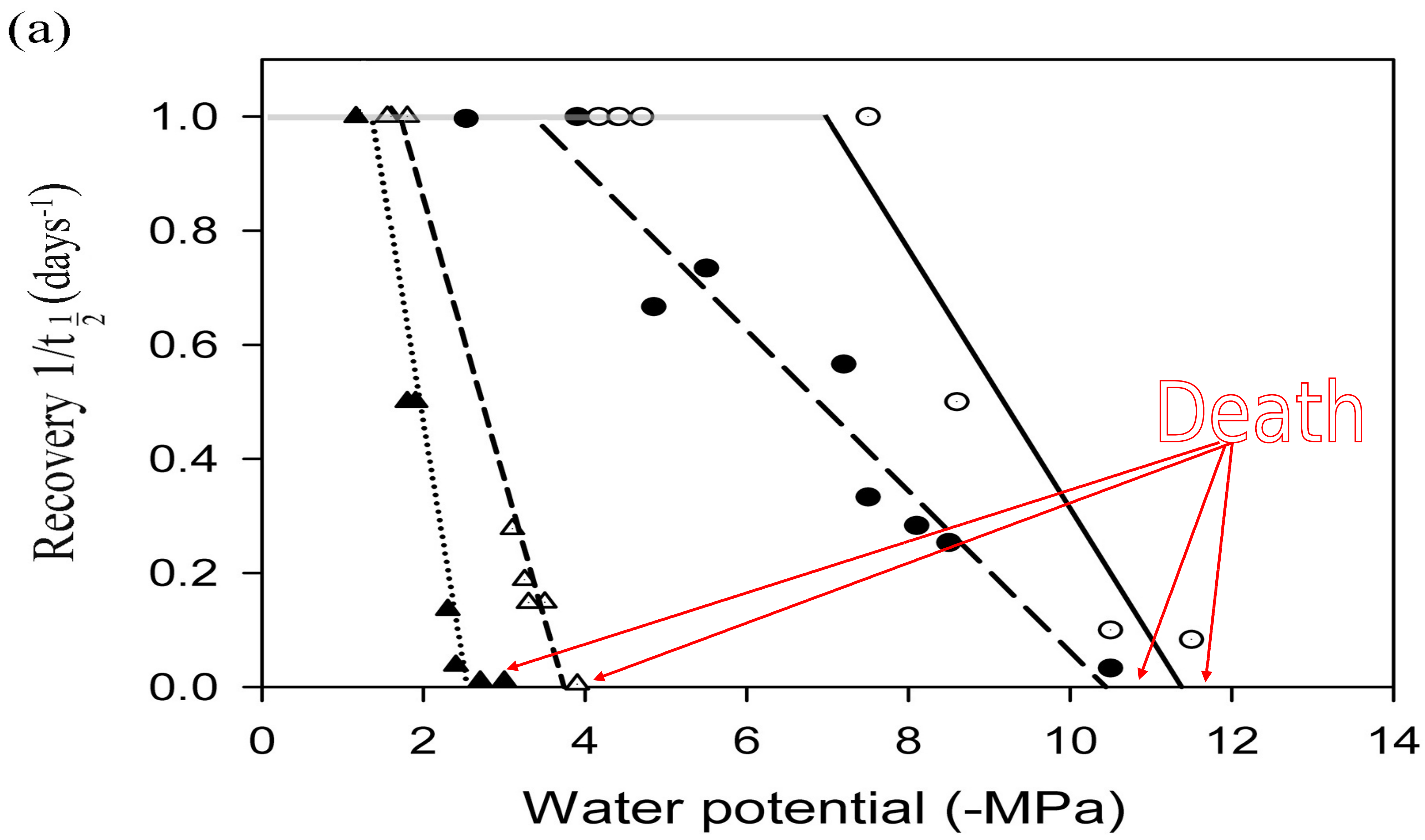
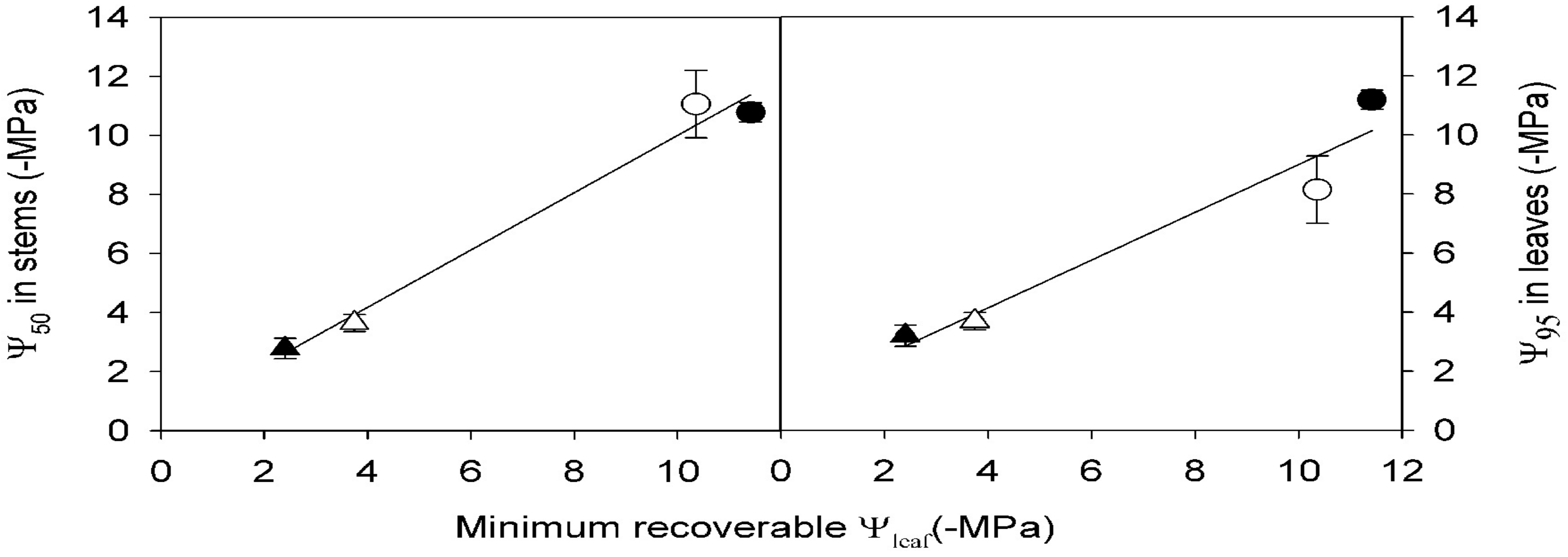


Figure 4. An example of recovery from mild (black circles) and severe (white circles) water stress in rewatered plants of *L. franklinii*. The mildly stressed plant shows a minimal reduction of K_{plant} and is able to rapidly recover leaf hydration and gas exchange. By contrast the severely stressed plant experiences profound depression of K_{plant} that recovers slowly, thus limiting gas-exchange recovery, which has a $t_{1/2}$ of



Brodribb & Cochard 2009 PP

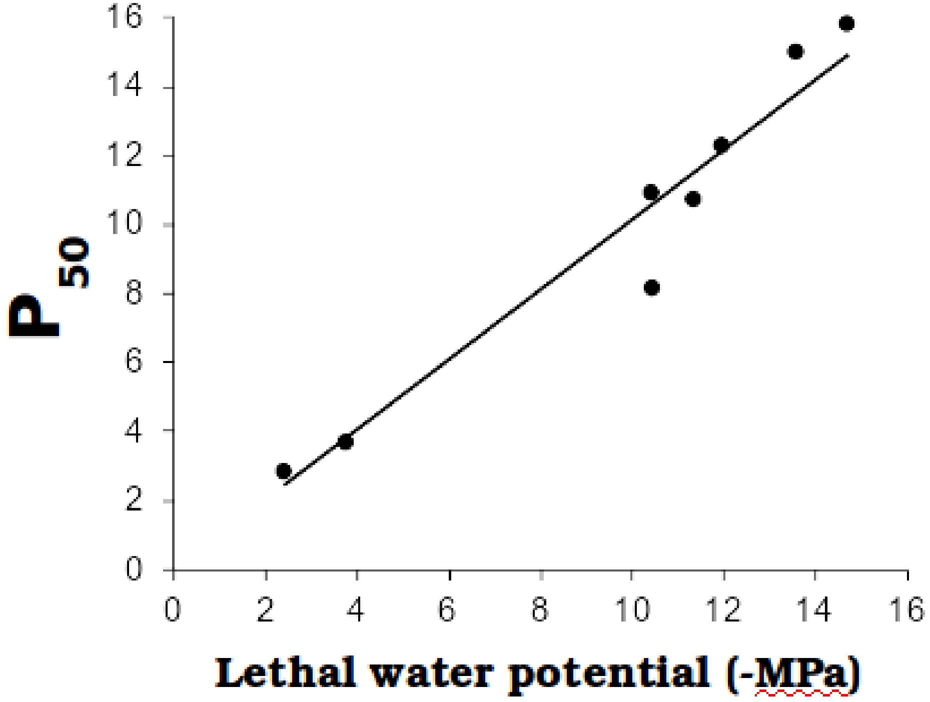
In conifers



Brodribb & Cochard 2009 PP

Thresholds for hydraulic failure depend on plant type but are well defined

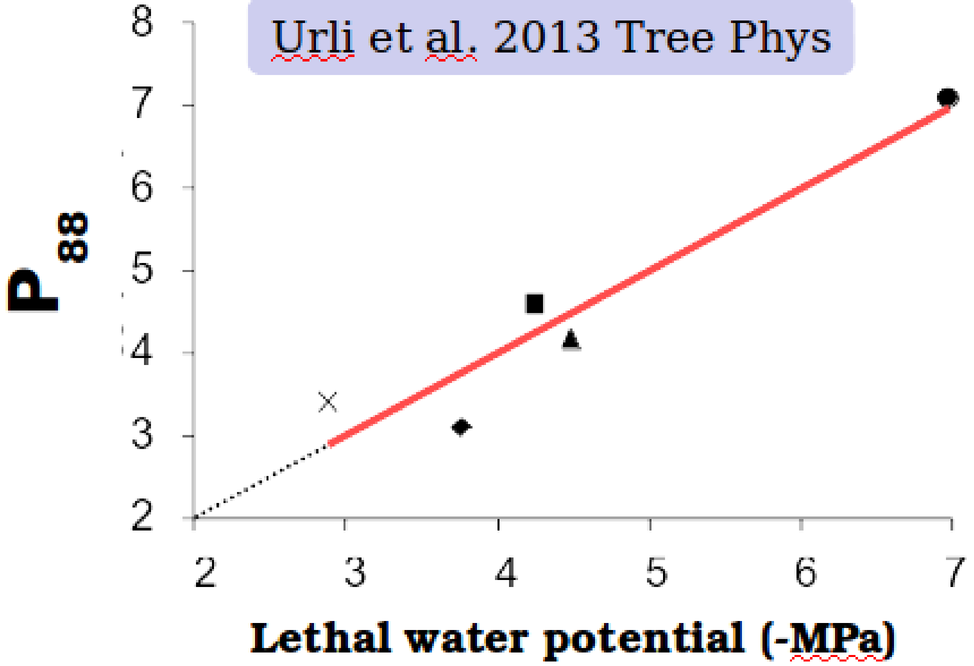
Conifers



Brodribb et al. 2010 New Phytol

Angiosperms

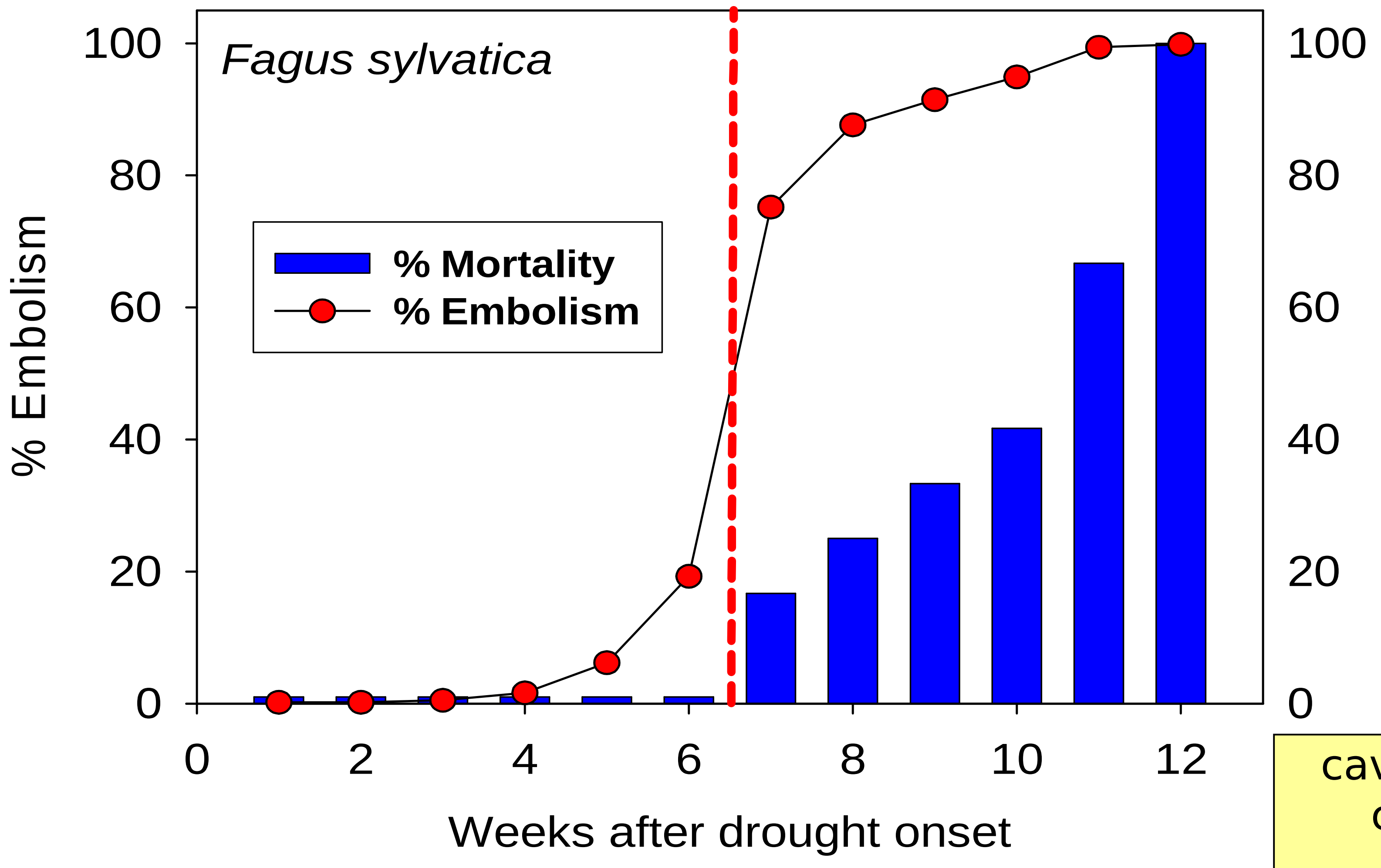
Urli et al. 2013 Tree Phys



Different xylem embolism thresholds for catastrophic hydraulic failure

Cavitation resistance correlates with species drought resilience/survival

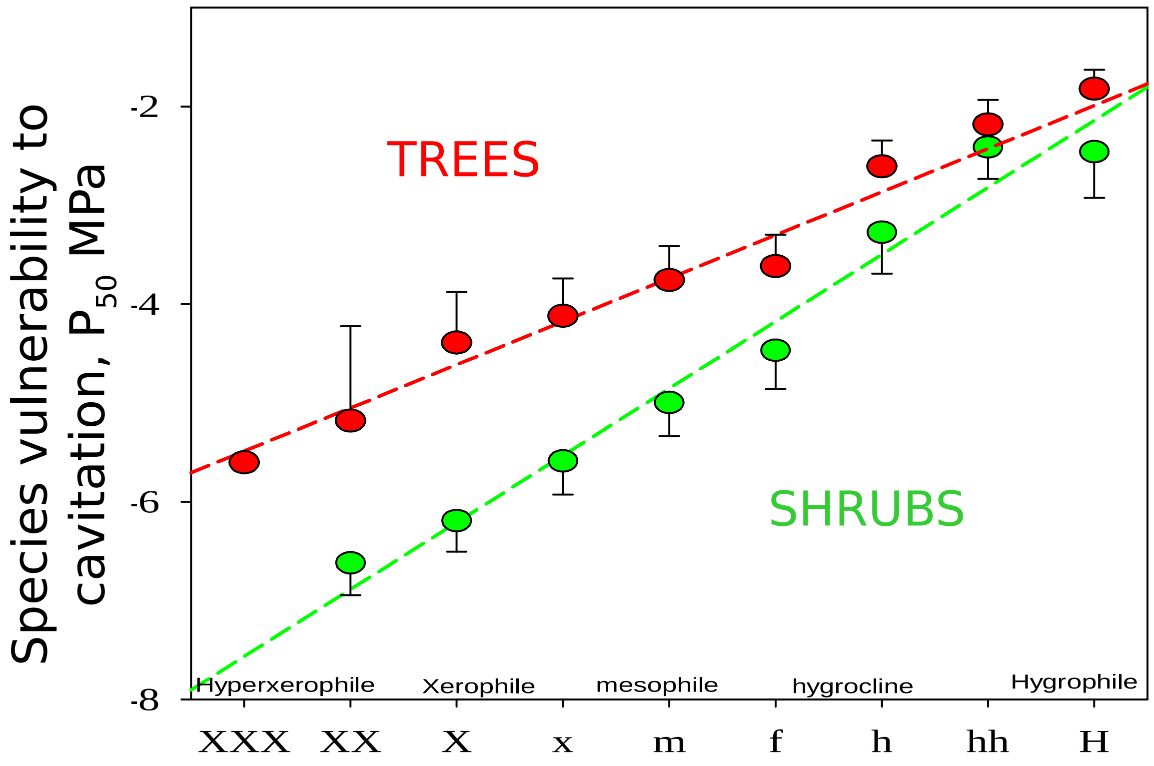
Barigah & Cochard, unpublished



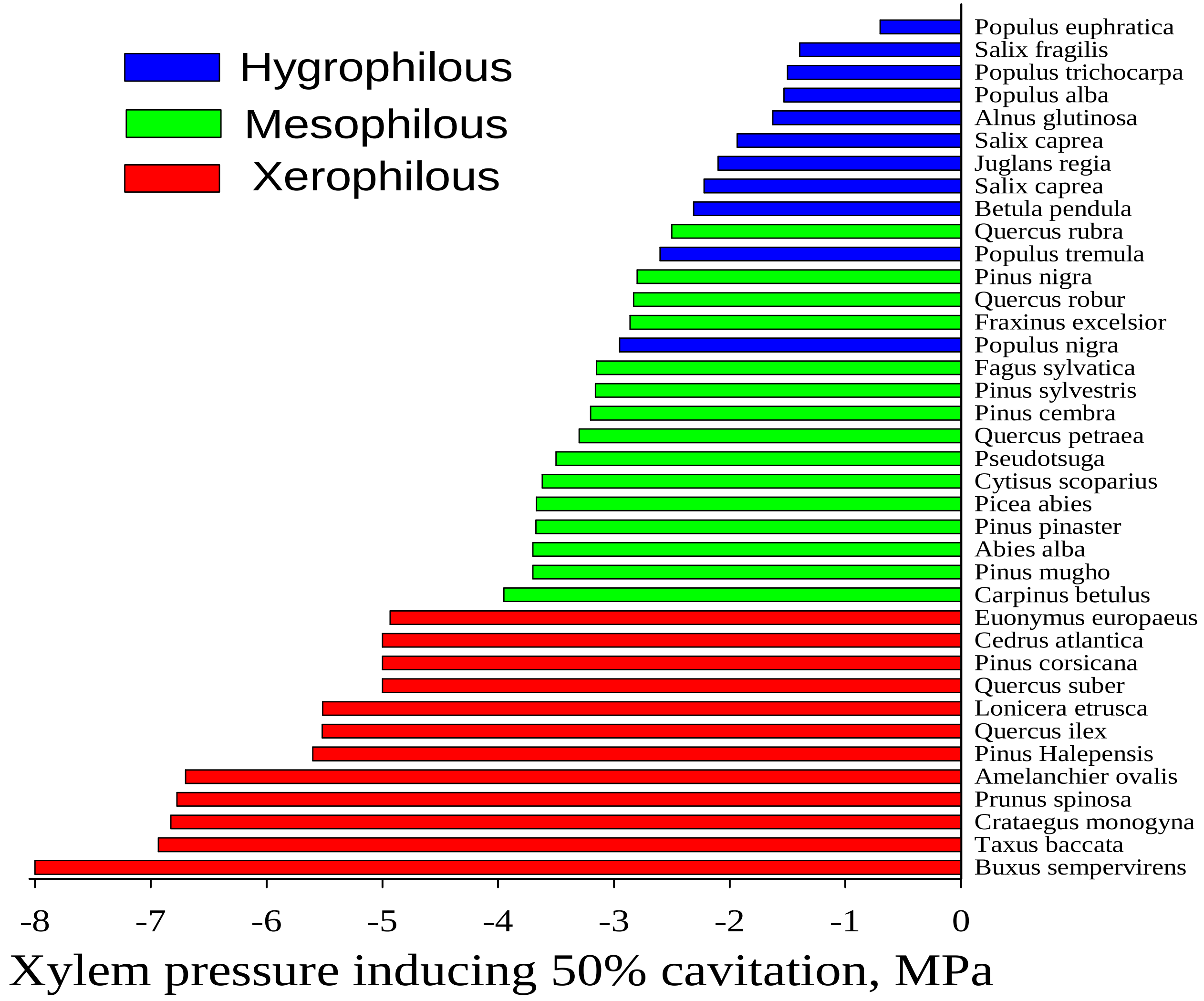
Dry till death experiment

cavitation resistance seems a good criterion for screening drought tolerance

Cavitation resistance correlates with species ecological preferences



Species ecological preference, as measured by plant ecologist (Rameau et al)



Cochard et al, unpublished

Cavitation resistance versus vegetation type

Vulnérabilité du système conducteur à l'embolie liée à la sécheresse : Ψ_{50}

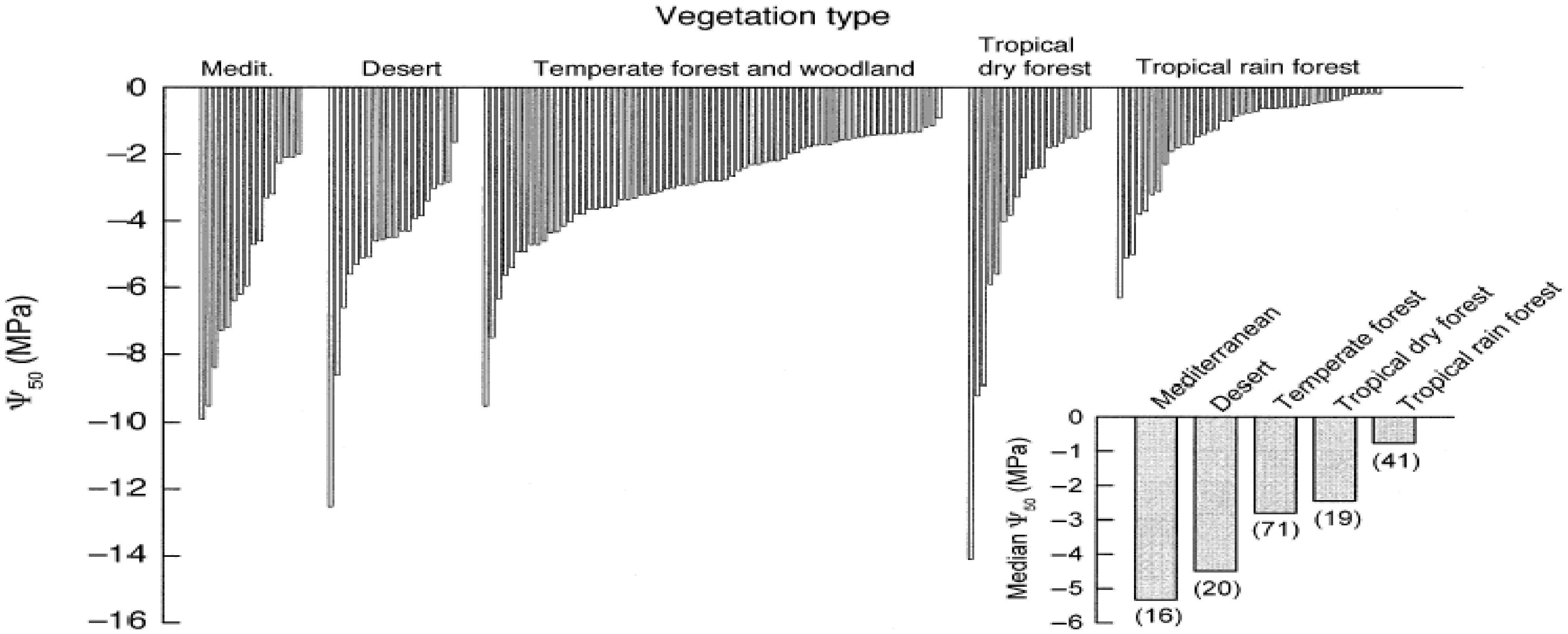


FIG. 1. The distribution of vulnerability to water-stress-induced cavitation (as determined by xylem tension at which 50% cavitation occurred [Ψ_{50}]) for the species used in this database, ranked by magnitude within five vegetation types. The median Ψ_{50} for each vegetation type, along with the sample size for that group, is shown in the inset.

Maherali et al, 2004

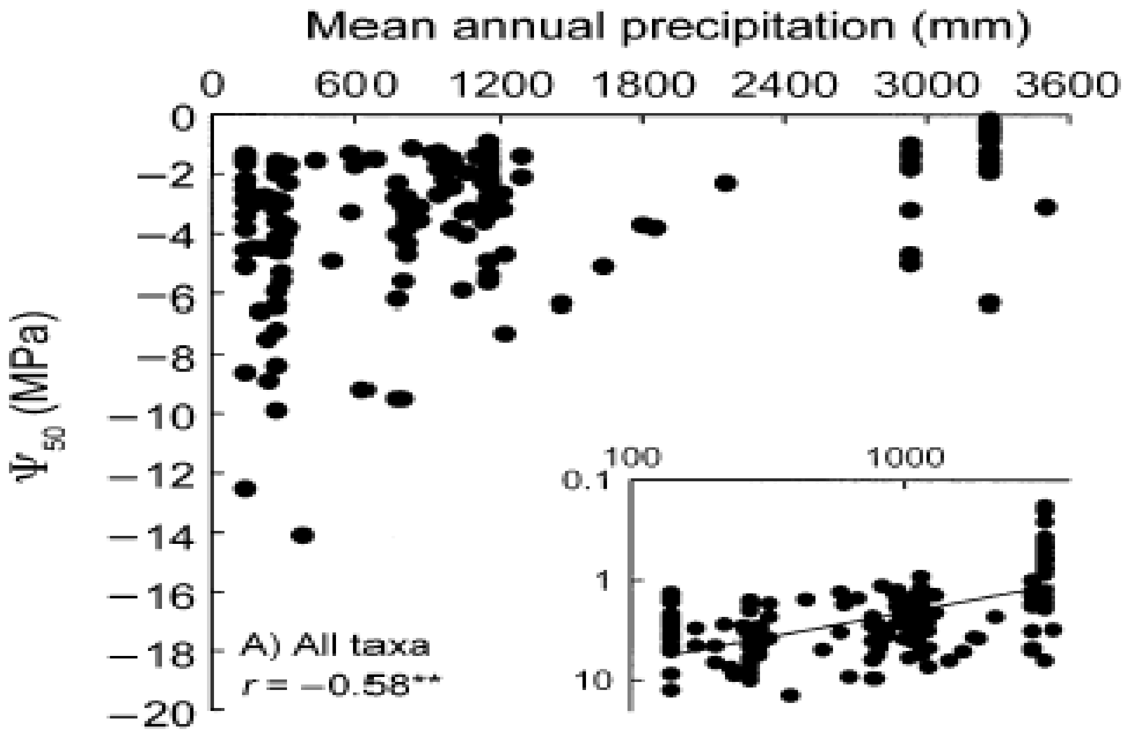
Implications

inter-specific level

A relatively large number of species can now be screened.

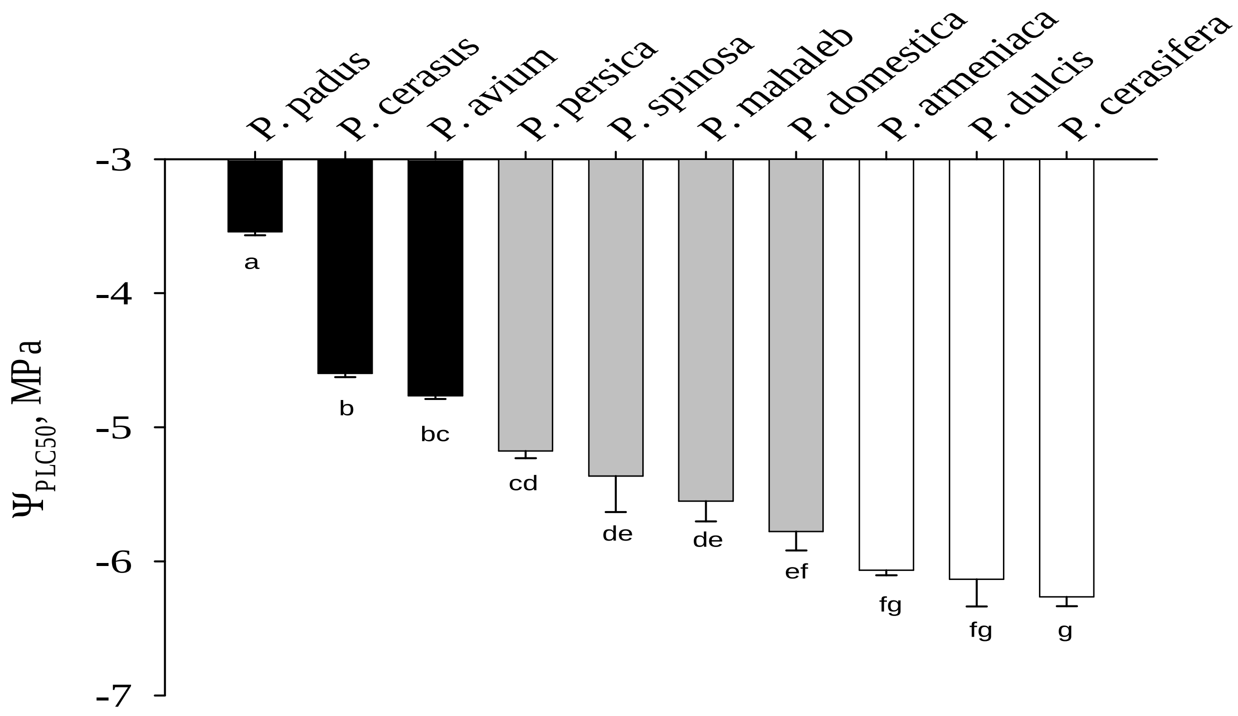
162 species

(angiosperms and gymnosperms)



Maherali et al 2004 *Ecology*

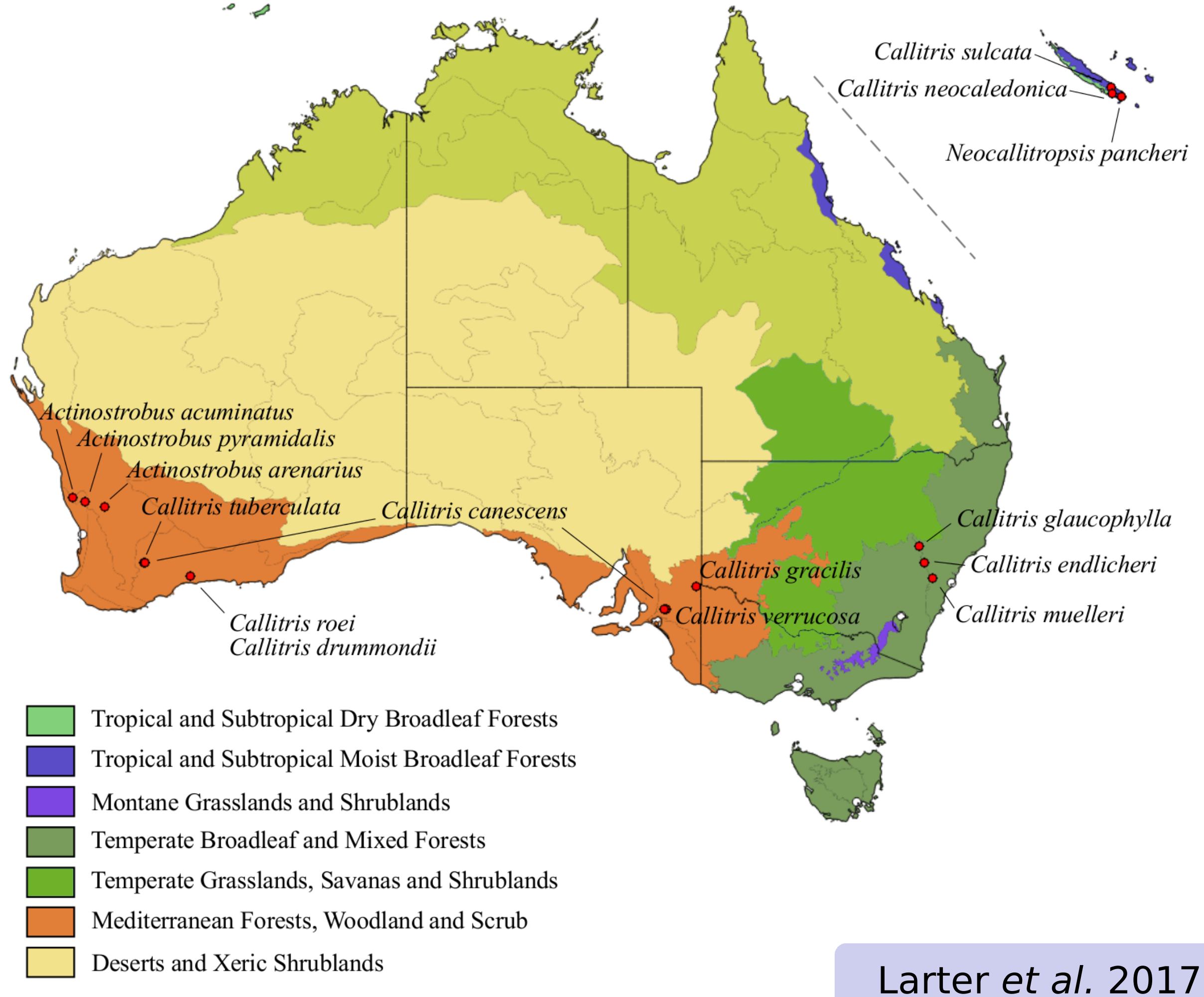
10 species within the genus Prunus

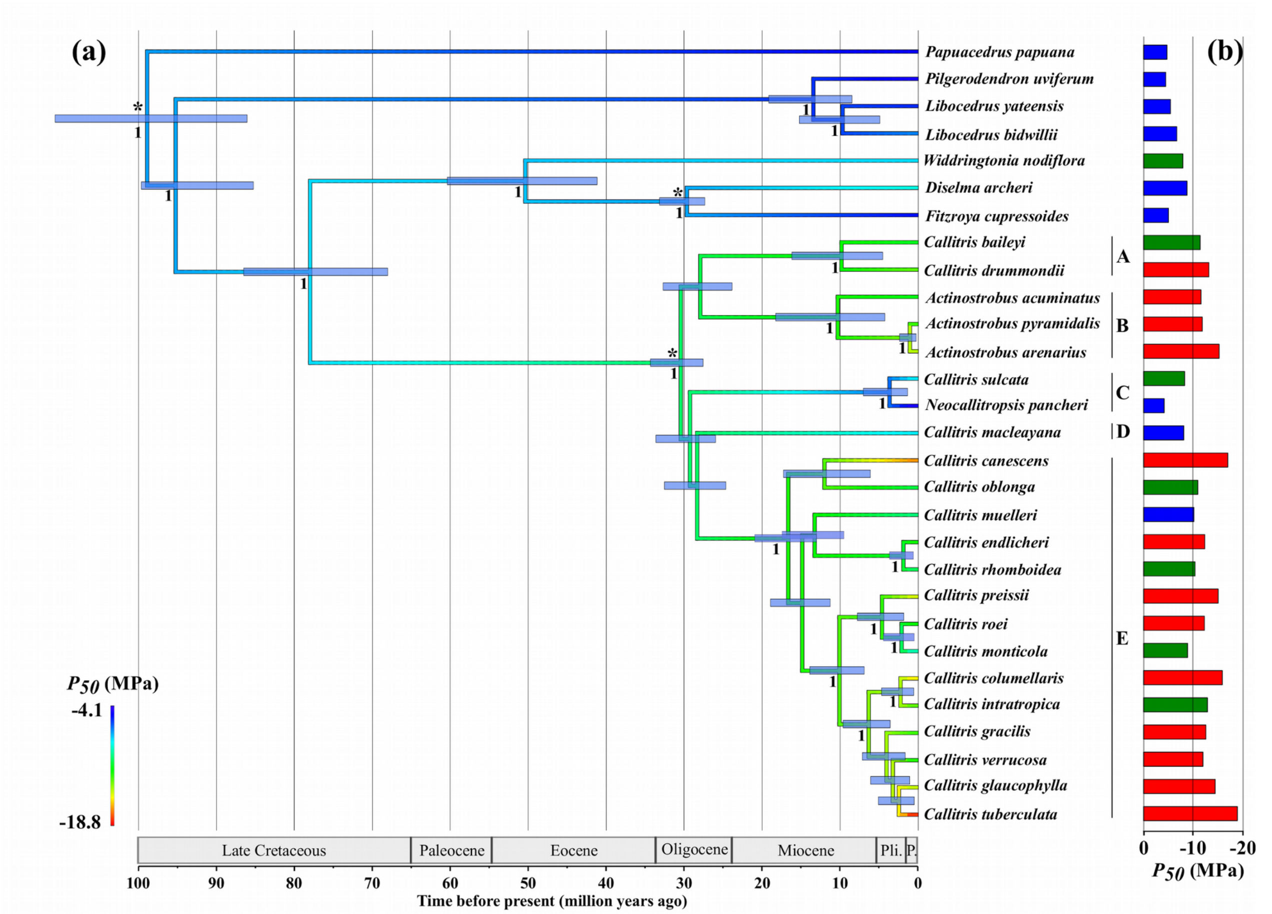


Cochard et al *submitted to Plant Cell Environment*

Aridity drives the evolution of extreme embolism resistance

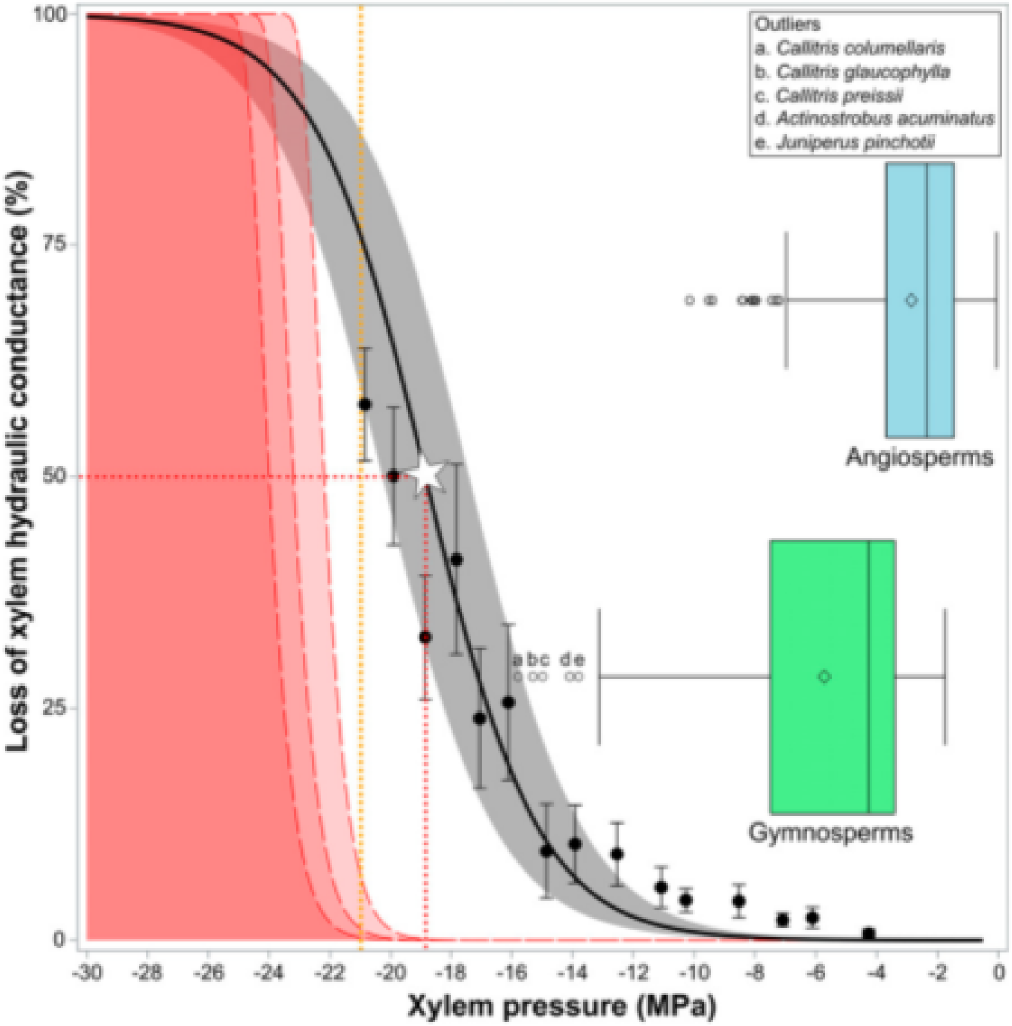
The case study of the conifer genus *Callitris*



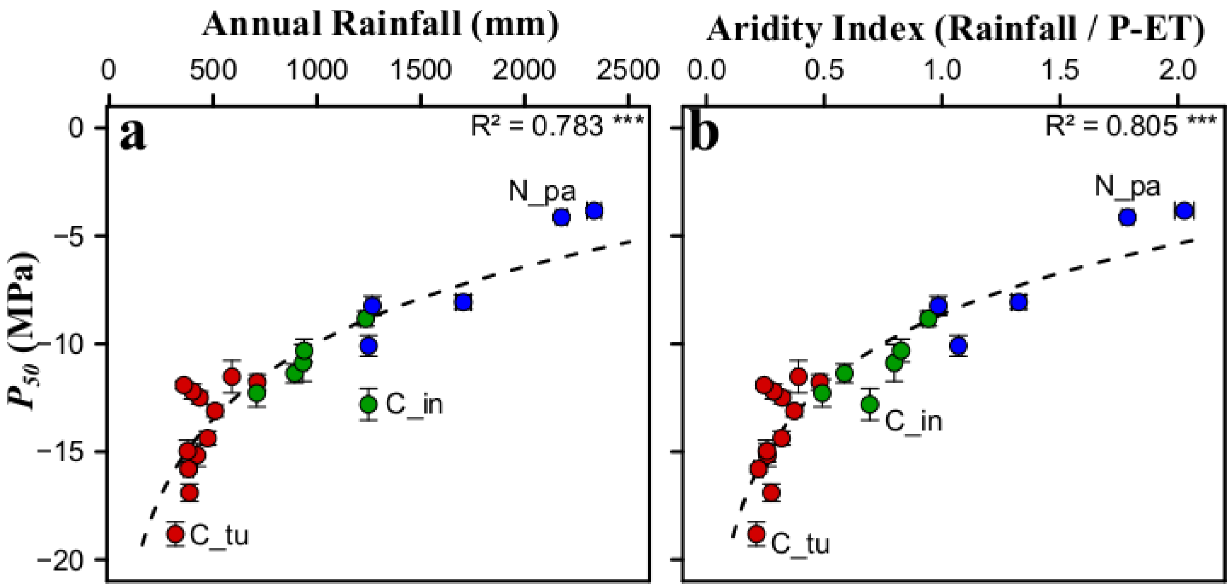


Larter *et al.* 2017 New Phytol

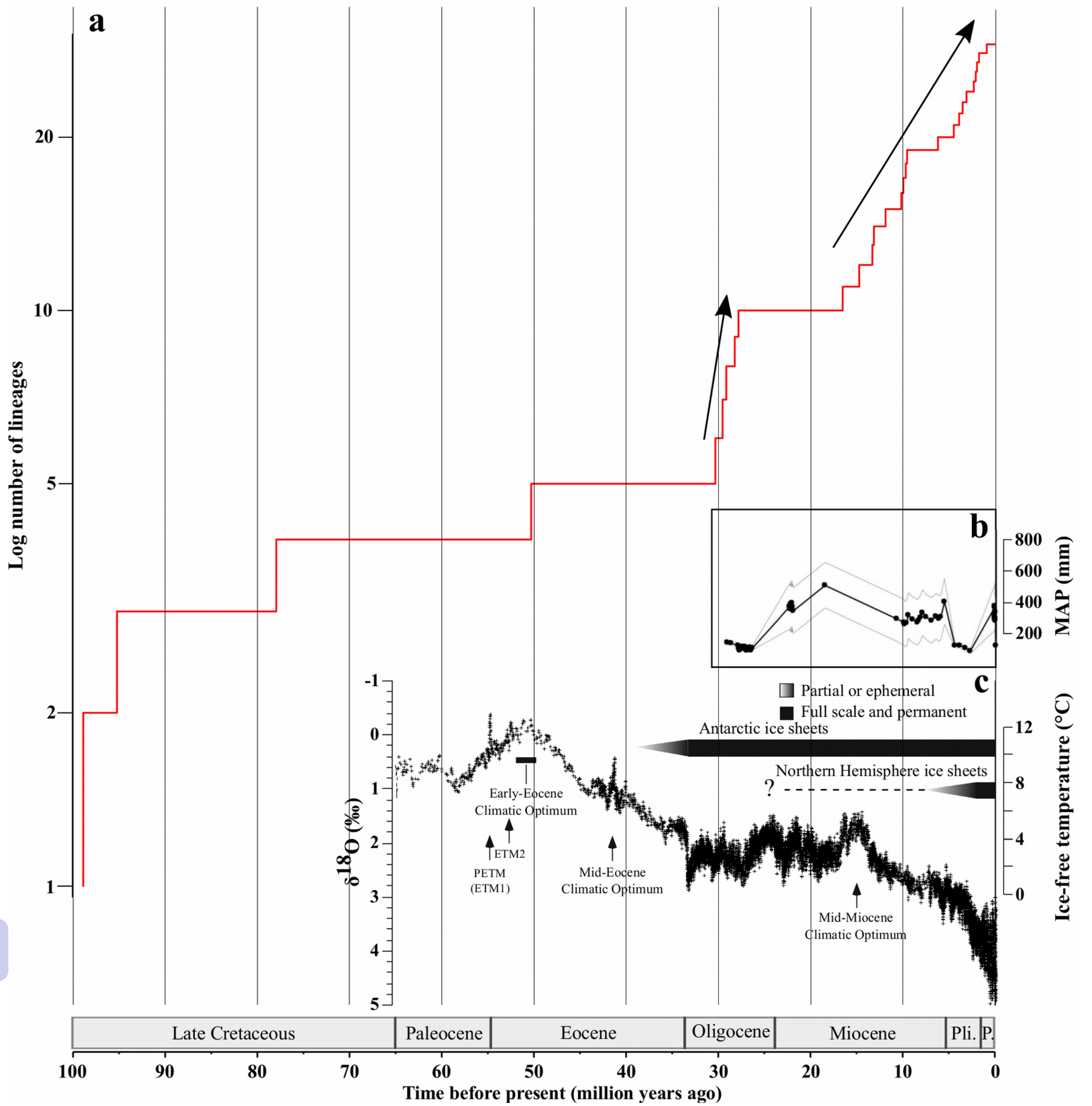
Extreme Aridity Pushes Trees to Their Physical Limits



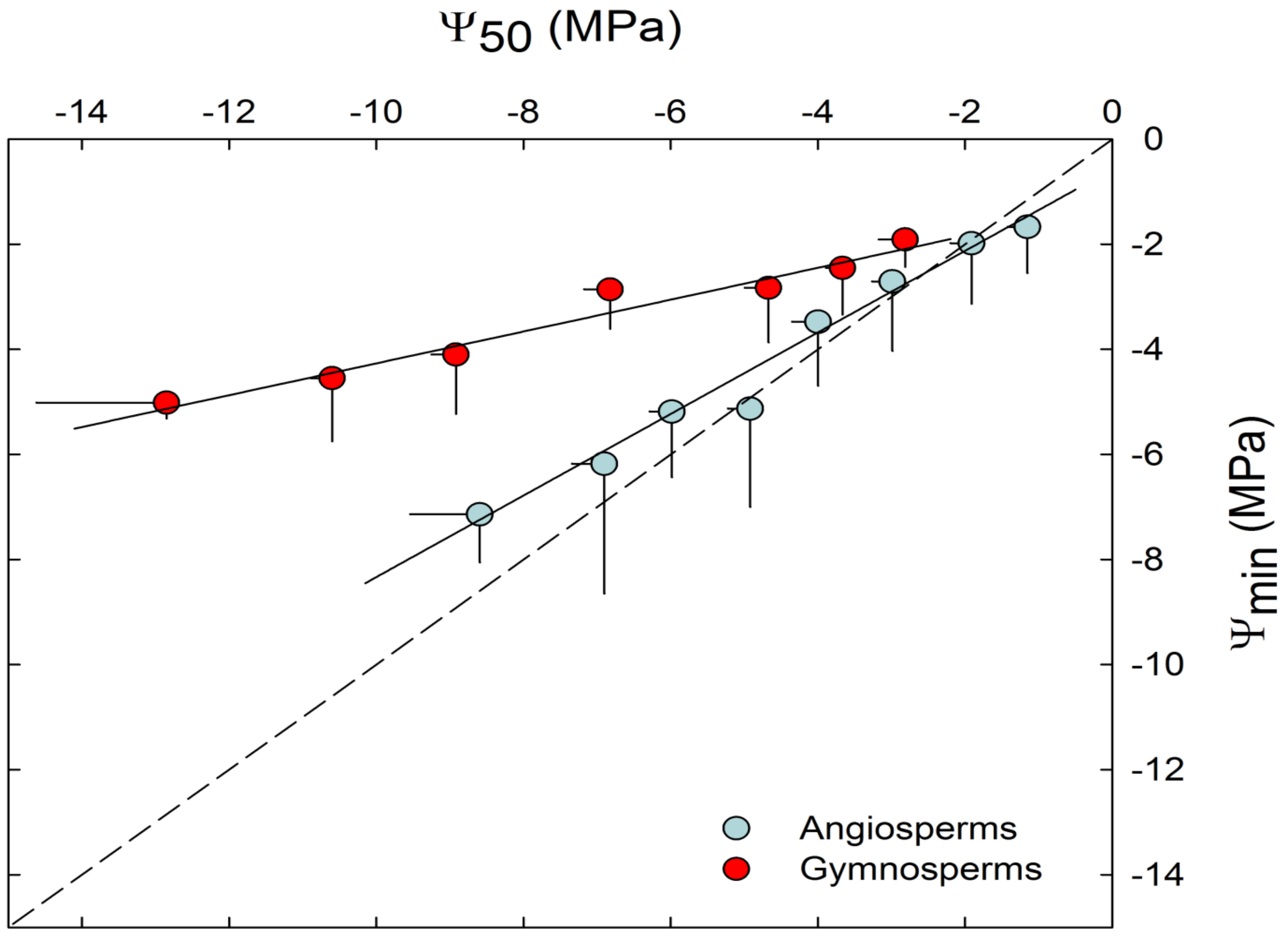
Aridity drives the evolution of extreme embolism resistance



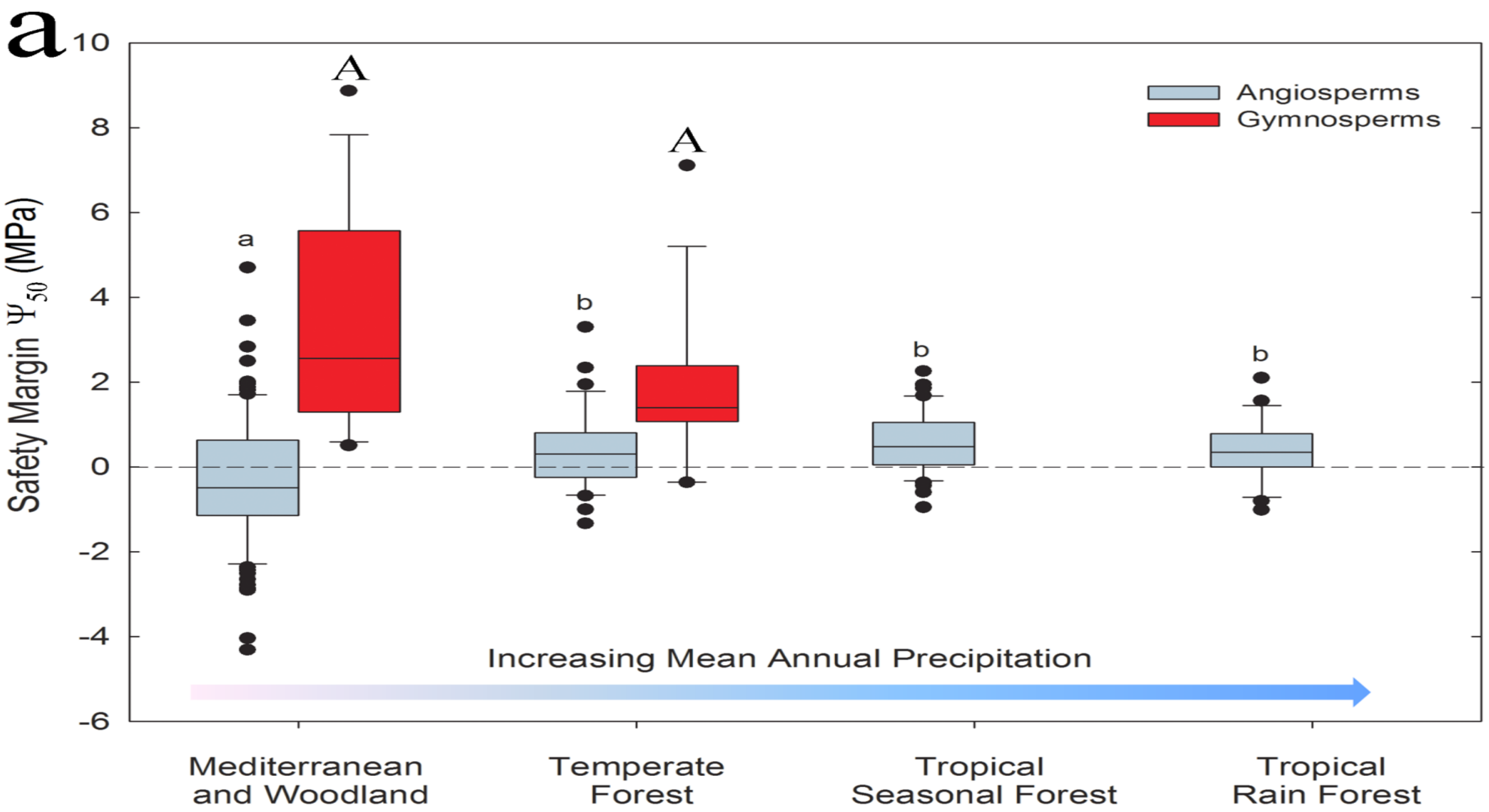
Larter *et al.* 2017 New Phytol



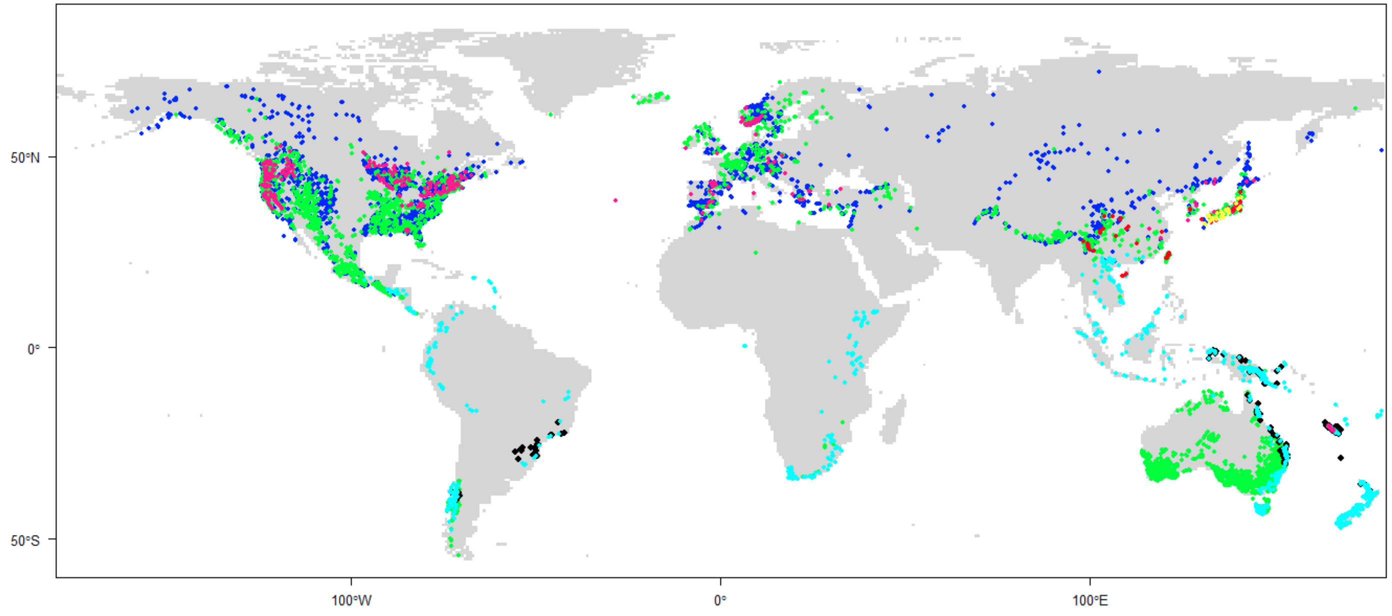
Minimum xylem pressure (Ψ_{min}) as a function of embolism resistance (Ψ_{50}) for 191 angiosperm and 32 gymnosperm species. The dashed line indicates the 1:1 line. The safety margin is the distance between each point and this line. Points were binned in 1.0 MPa increments for Ψ_{50}.



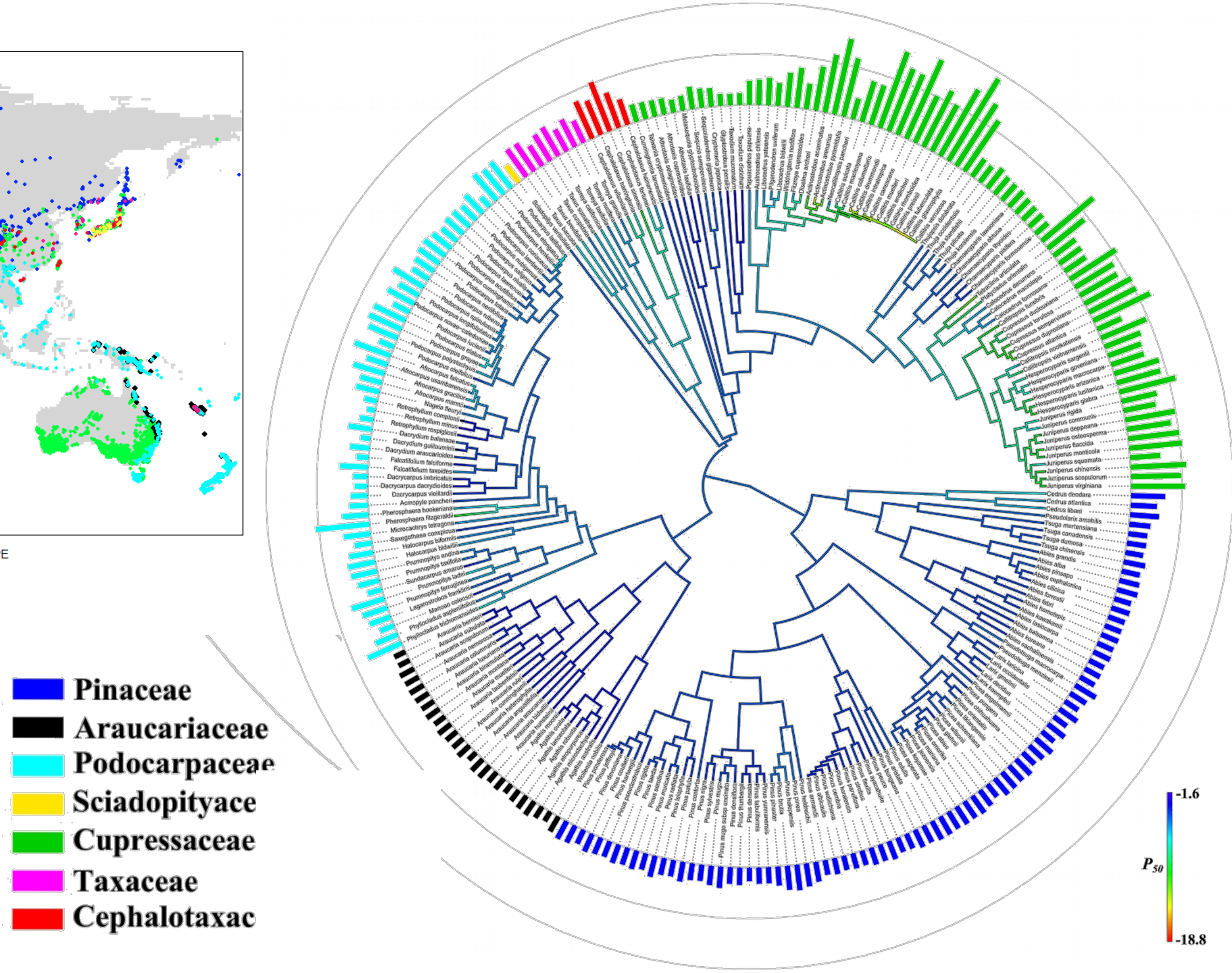
Box plot of hydraulic safety margins for angiosperm and gymnosperm species across major forest biomes. The Ψ_{50} (Ψ_{min} – Ψ_{50}) safety margin is shown in Fig. 2a



Assess ecological and evolutionary drivers in vulnerability to cavitation globally



Half of the world conifers
(285 species; all measured in our lab)



The synchrotron world tour team

The sherpas of plant hydraulics

Ice Charrier

M Torres

Pim Lamarque

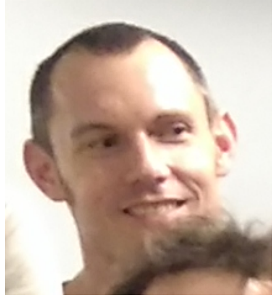
E Badel

N Martin

R Burlett

N Lenoir

A King



H Cochard

S Delzon

S Jansen

B Choat

G Gambetta