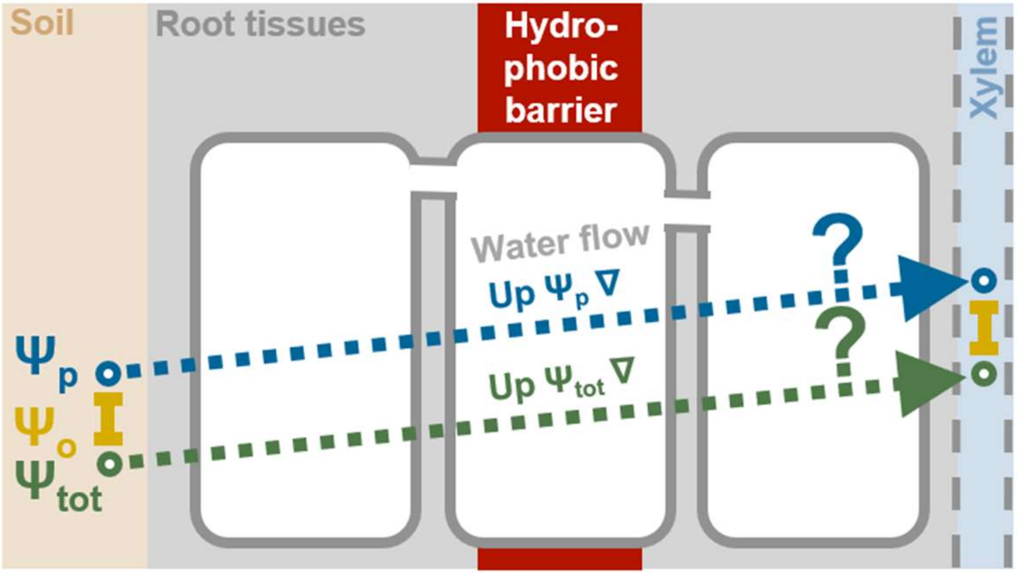
Root water uptake uphill of water potential gradients…



Did plants drop thermodynamics classes at school ?

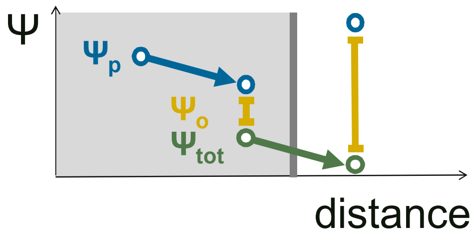
ISRR - Rooting 2021

Valentin Couvreur, Adrien Heymans, Guillaume Lobet, Malcolm Bennett & Xavier Draye

UCLouvain
University of Nottingham
JÜLICH Forschungszentrum

Current paradigm of water flow across root tissues

Water flow across
cell walls & membranes

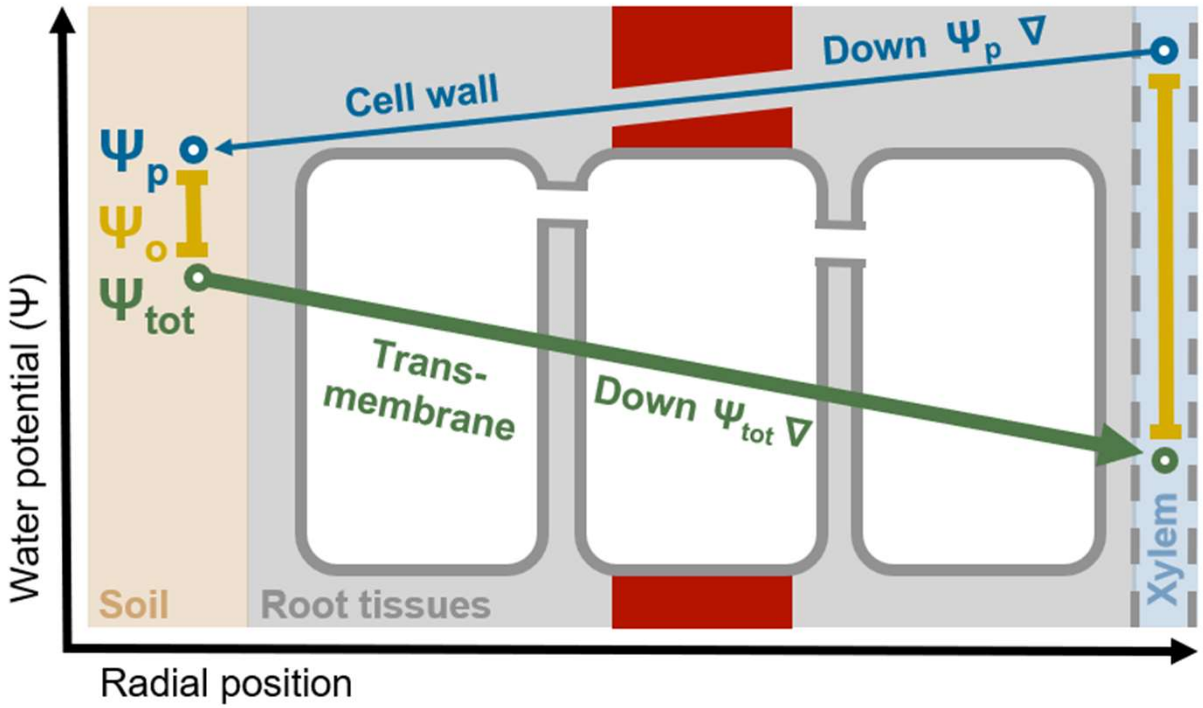


$$\Psi_{tot} = \Psi_p + \Psi_o$$

where

$$\Psi_o = -RT\,C_{os}$$

Root radial flow is analog to flow across a “big membrane”

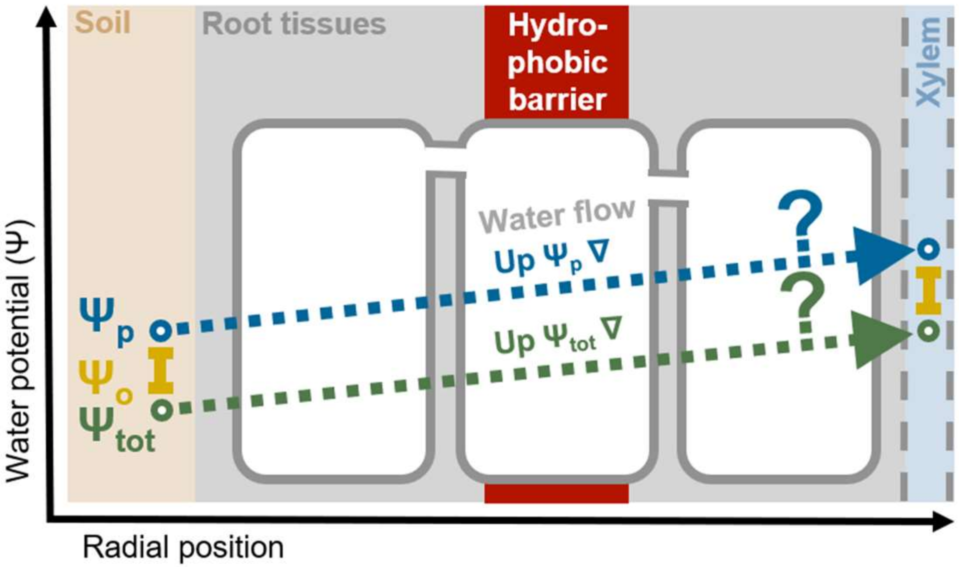


Osmotic Theories. The most satisfactory explanation of root pressure assumes that it is an osmotic process in which roots function as osmometers because of accumulation of solutes in the xylem sap.

(Kramer and Boyer, 1995)

The riddle of the uphill water flow

Observations under salt stress



Arrowleaf saltbush: Bai et al. (2007)

Maize: Miller (1985)
Zholkevich et al. (1990)
Enns et al. (2000)
Rowan et al. (2000)

In roots stressed to $\Psi_o = -0.3$ MPa, Ψ_x was always more positive than Ψ_o, and Ψ_x changed only slightly (ca. 0.05 MPa). Thus the adjustment in the roots which increased root pressure cannot be ascribed to Ψ_x, contradicting the osmotic-xylem-sap mechanism.

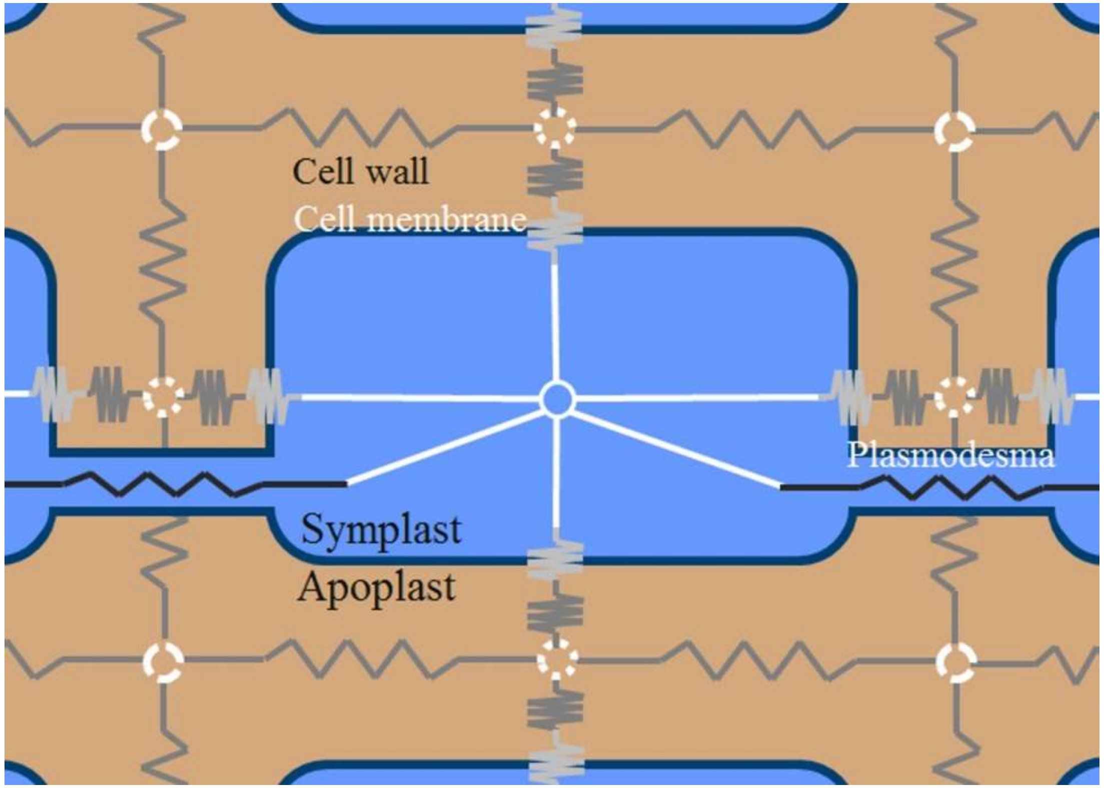
(Enns et al., 2000)

These reports constitute a serious challenge to the widely accepted theories in plant physiology on the mechanisms of how plant roots absorb water under salt stress and how root pressure is generated, because the phenomenon seemingly goes against the second law of thermodynamics

(Bai et al., 2007)

Cell level hydraulic model

Permeability of cell walls (Steudle and Boyer, 1985), membranes (Elhert et al., 2009), and plasmodesmata (Bret-Hart and Silk, 1994; Warmbrodt, 1985; Clarkson et al., 1987)



Flow principles:

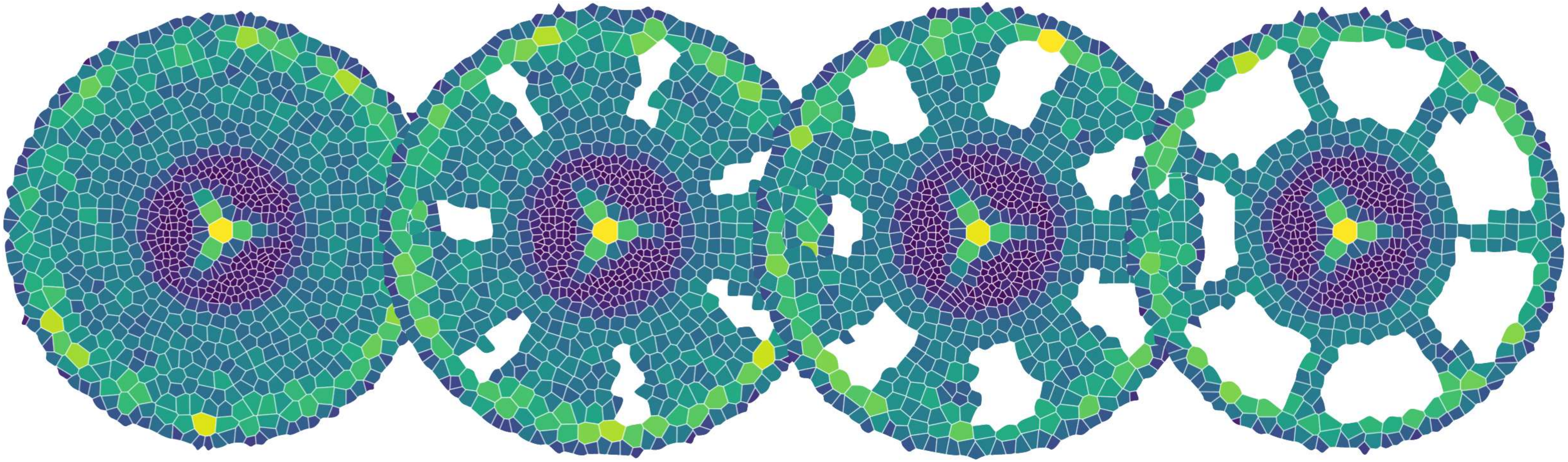
- Ψ_p driven in walls and plasmodesmata
- Ψ_{tot} driven flow across membranes

Plasmod.: $2.0\ 10^{-4}$ cm hPa^{-1} d^{-1}
Membrane: $5.0\ 10^{-4}$ cm hPa^{-1} d^{-1}
Young root: $1.0\ 10^{-4}$ cm hPa^{-1} d^{-1}

Cell wall: 0.005 cm^2 hPa^{-1} d^{-1}
Silty clay: 0.5 cm^2 hPa^{-1} d^{-1}

GENERATOR OF ANY TYPE OF ROOT ANATOMY

- GRANAR -



XYLEM POLES / CORTEX / AERENCHYMA / …

Open Source

bit.ly/granar-root

Heymans et al, 2020

GRANAR, a Computational Tool to Better Understand the Functional Importance of Monocotyledon Root Anatomy

A map of cell osmotic potential

- Maize plants guttating at night
- Root bathing solution with low Ψ_{tot}
- Cell layers osmotic potential from snap-frozen roots

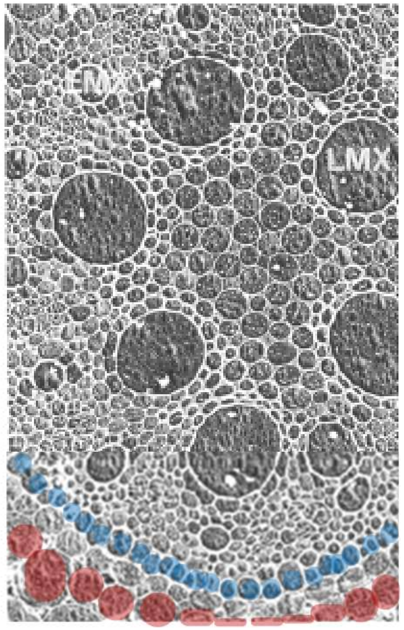
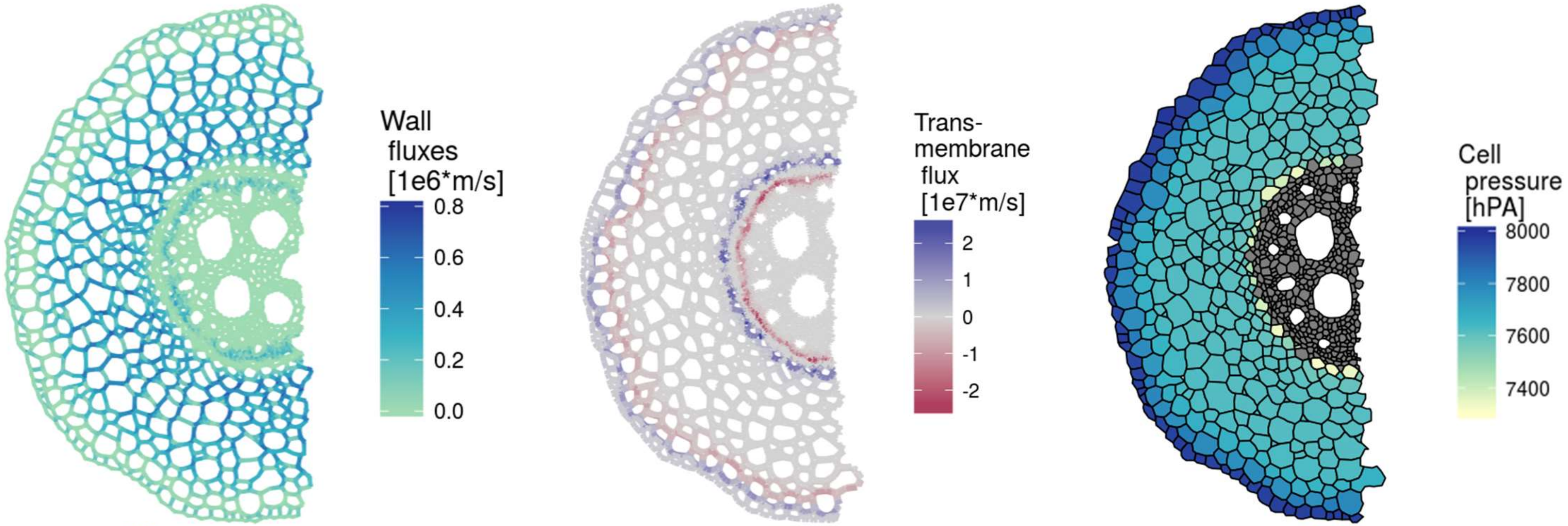


Table 5. Effect on water potentials of xylem sap and of cell vacuoles of adding 50 mM KNO_3 to the nutrient solution for 5 days (experiment 5)[a]

Treatment	Ψ_x (MPa)		Ψ_v (MPa)			
	LMX	EMX	XP	Pe	En	C
Control	–0.15	–0.15	–0.74	–0.50	–0.62	–0.80
KNO_3	–0.23	–0.21	–1.21	–0.92	–1.05	–1.26
$\Delta\Psi$[b]	0.08	0.06	0.47	0.42	0.43	0.46

(Enns et al., 2000)

MODELLING WATER FLOW AT THE ORGAN SCALE
- MECHA -



Open Source

mecharoot.github.io

Couvreur et al, 2018

Going with the Flow: Multiscale Insights into the Composite Nature of Water Transport in Roots[1][OPEN]

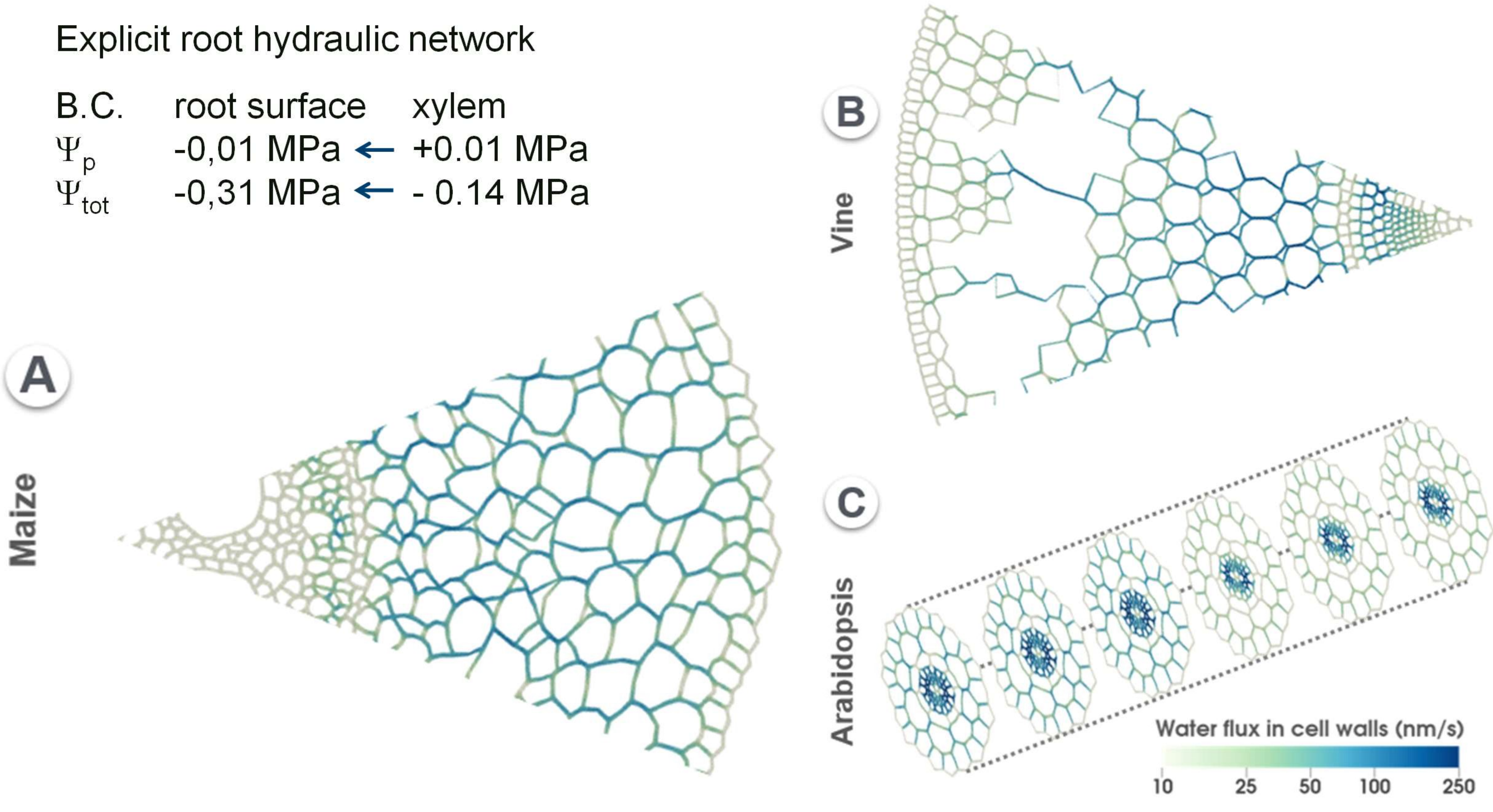
RADIAL CONDUCTIVITY

AXIAL CONDUCTIVITY

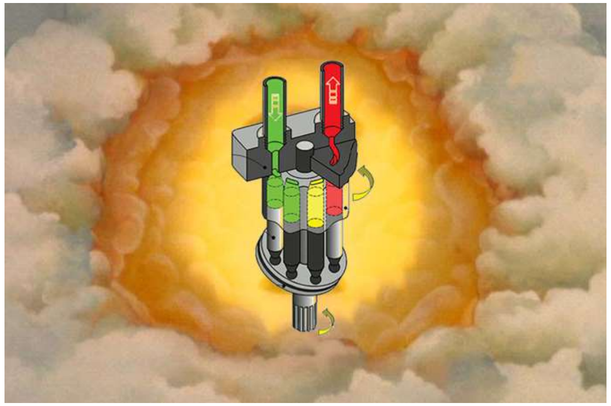
The quest for a water pump

Explicit root hydraulic network

B.C.	root surface		xylem
Ψ_p	-0,01 MPa	←	+0.01 MPa
Ψ_{tot}	-0,31 MPa	←	- 0.14 MPa



The quest for a water pump



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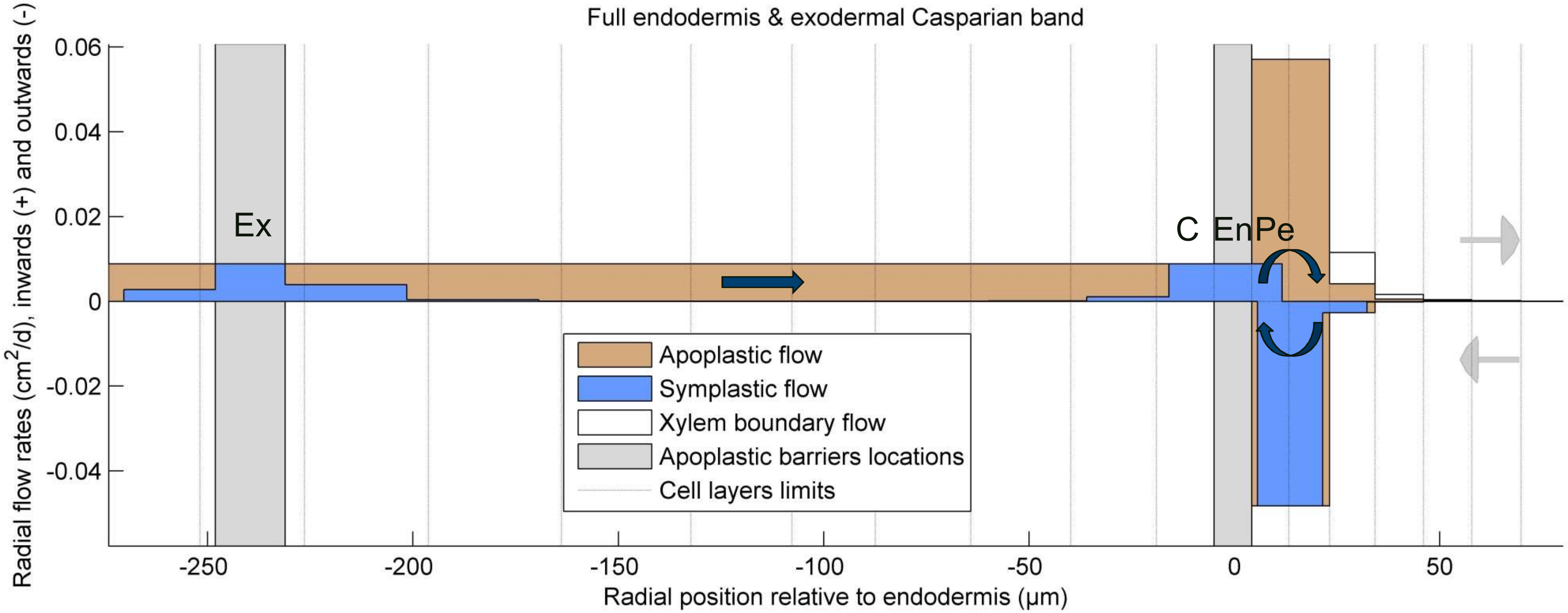
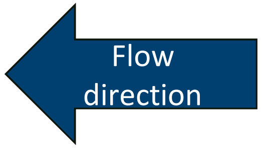
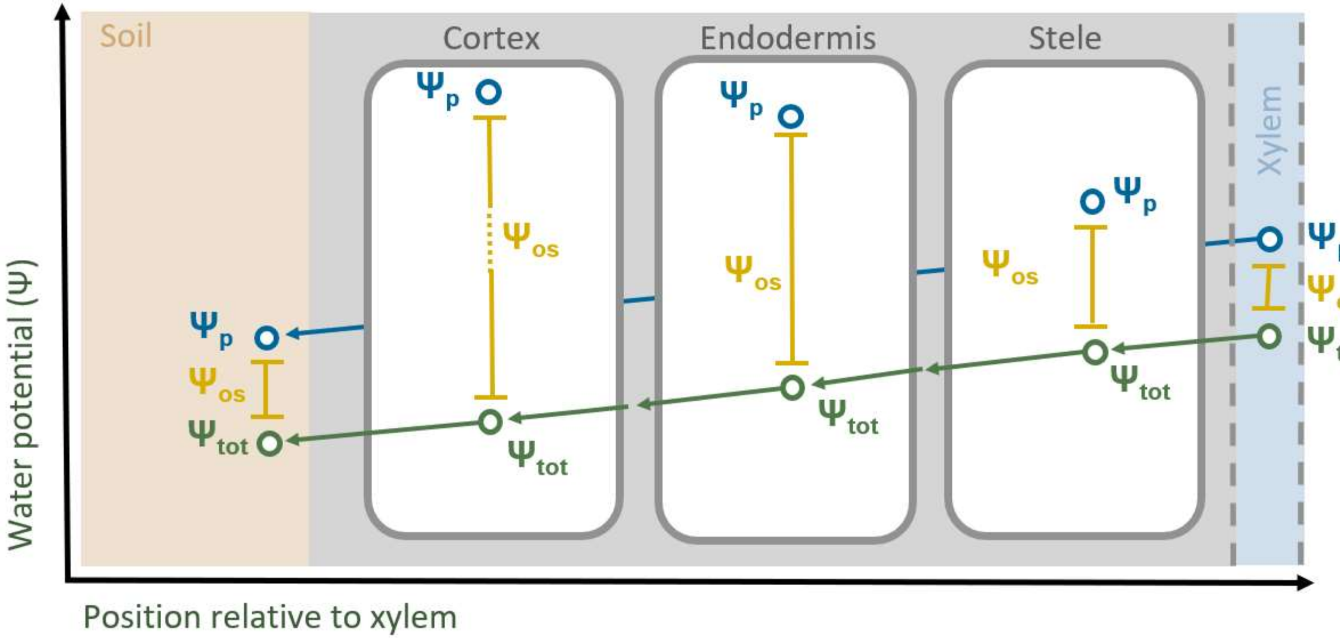


Flow against $\Delta\Psi_{tot}$ happens in both the explicit model & experiments !

Understanding the water pump

Building a water pump from scratch:
- 3 cells
- A cellular Ψ_{os} gradient

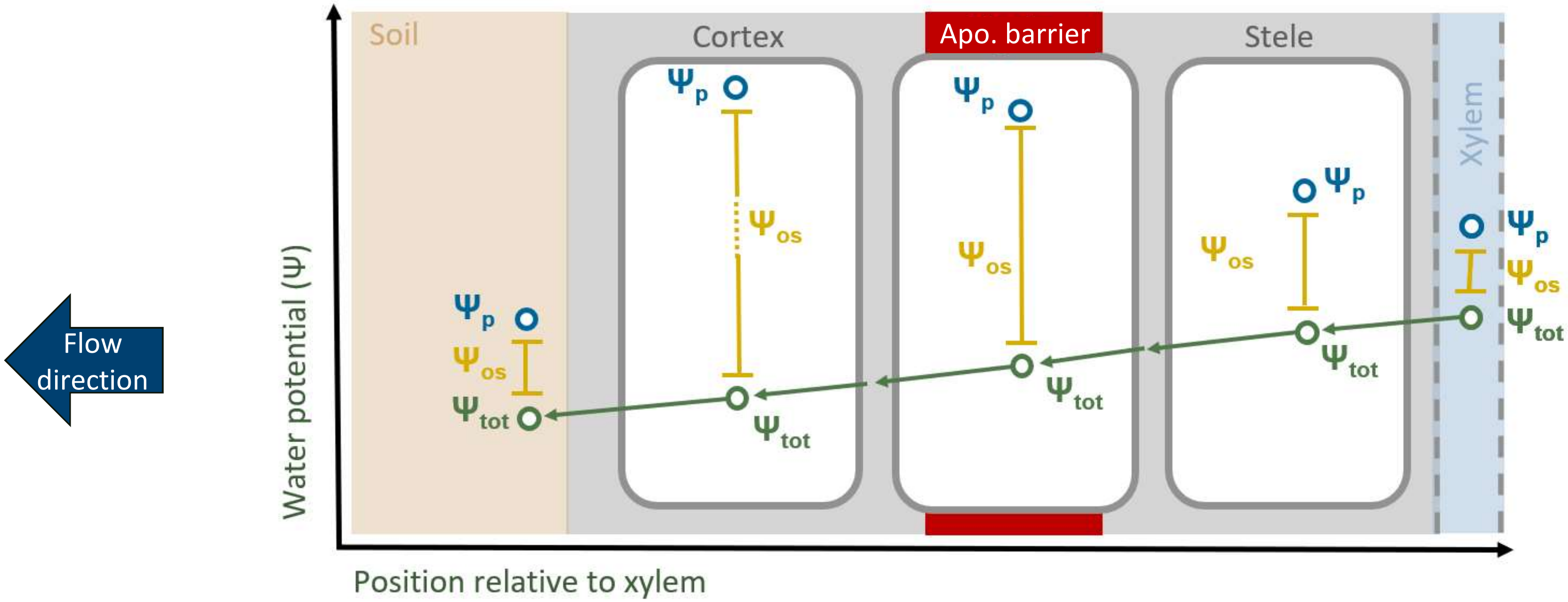




Cell Ψ_p decreases to the right but cell Ψ_{tot} increases to the right

Understanding the water pump

Building a water pump from scratch:
- 3 cells
- A cellular Ψ_{os} gradient
- An apoplastic barrier

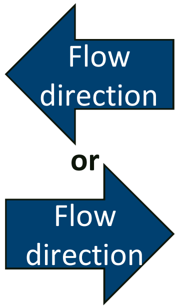


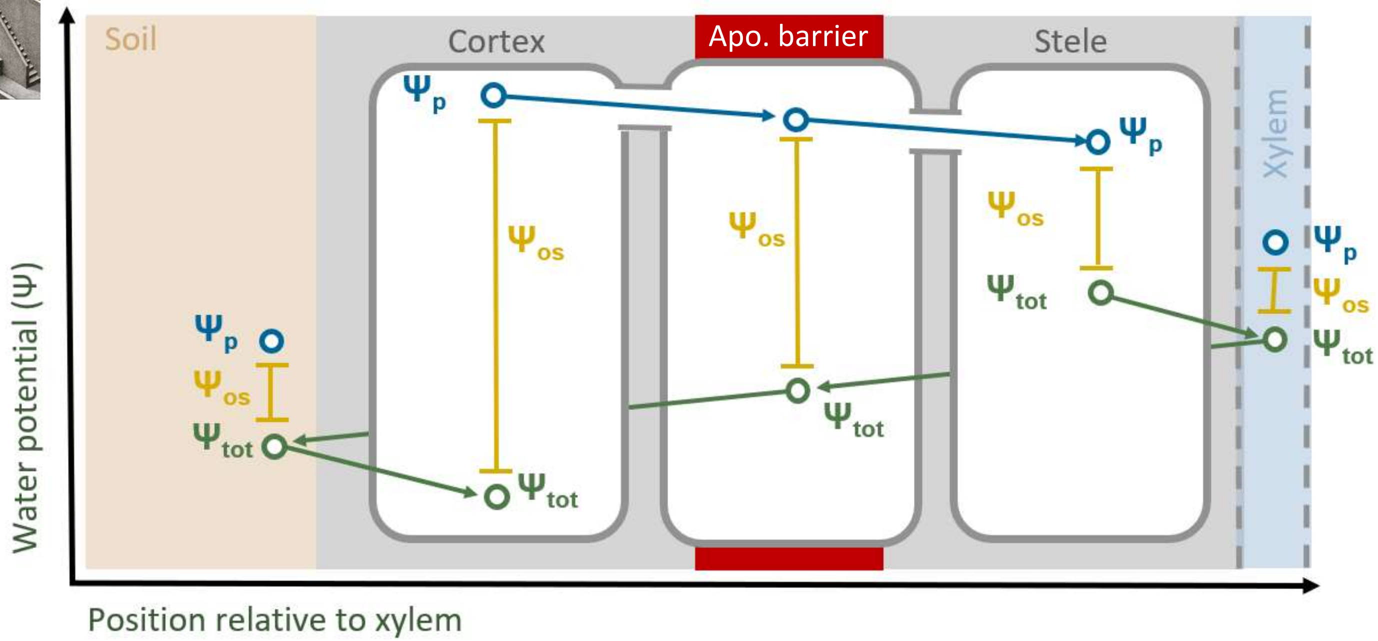
Understanding the water pump

Credits: M.C. Escher

Building a water pump from scratch:

- 3 cells
- A cellular Ψ_{os} gradient
- An apoplastic barrier
- Plasmodesmatal connections





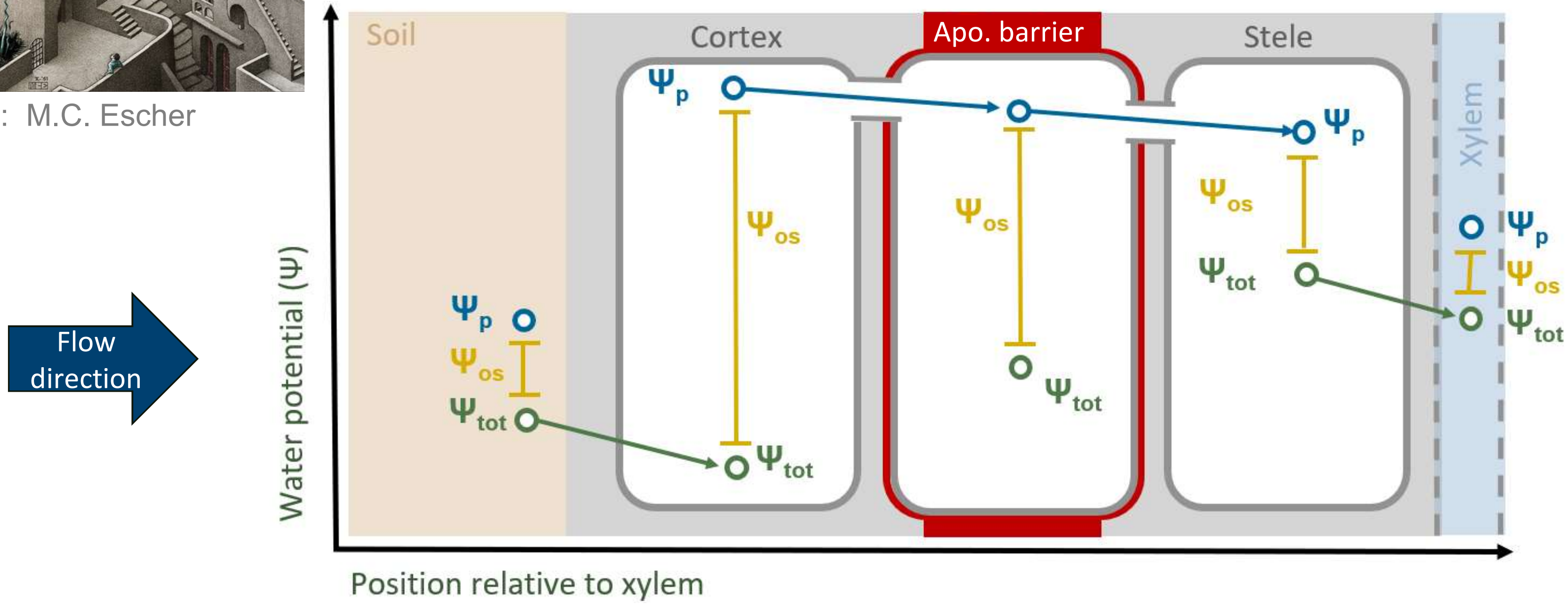
Water flow is pressure-driven in plasmodesmata

Credits: M.C. Escher

Understanding the water pump

Building a water pump from scratch:

- 3 cells
- A cellular Ψ_{os} gradient
- An apoplastic barrier
- Plasmodesmatal connections

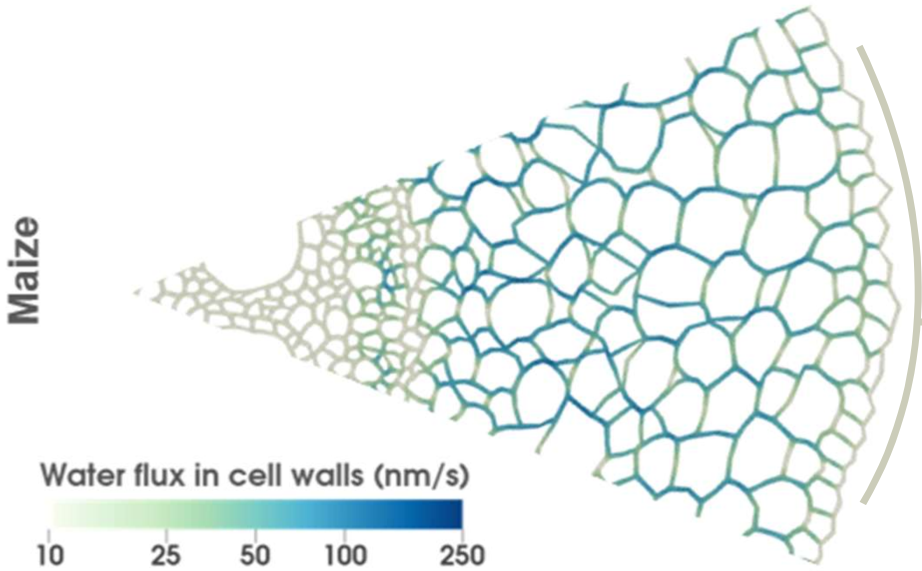


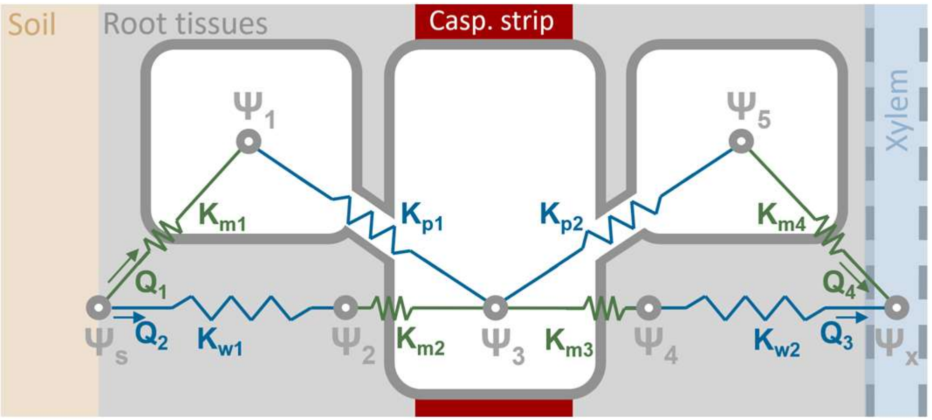
Pump "upgrade" with suberin lamellae

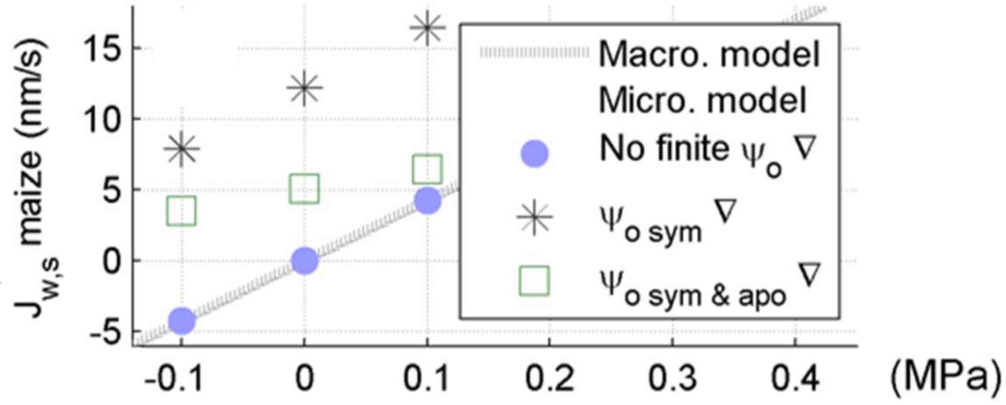
No need to load solutes in the xylem

Maintaining the osmotic gradient has a cost (no perpetual movement)

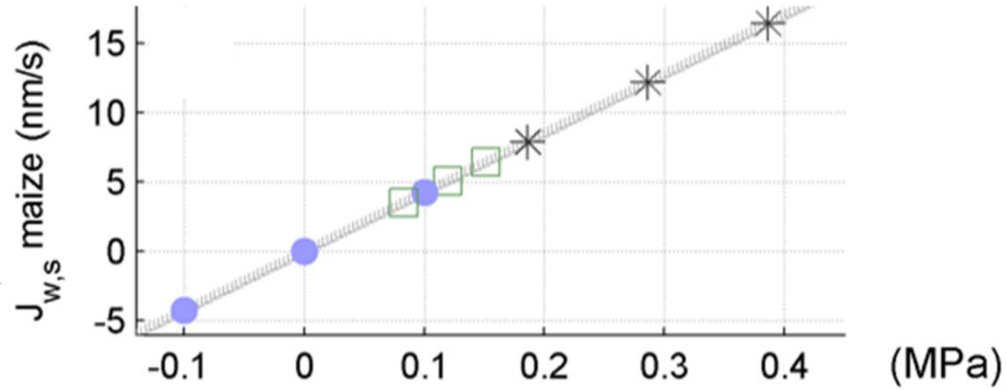
Integrating water flow principles across scales







Mainstream driving force $\boxed{\psi_{p,s} - \psi_{p,x} + \sigma_r (\psi_{o,s} - \psi_{o,x})}$

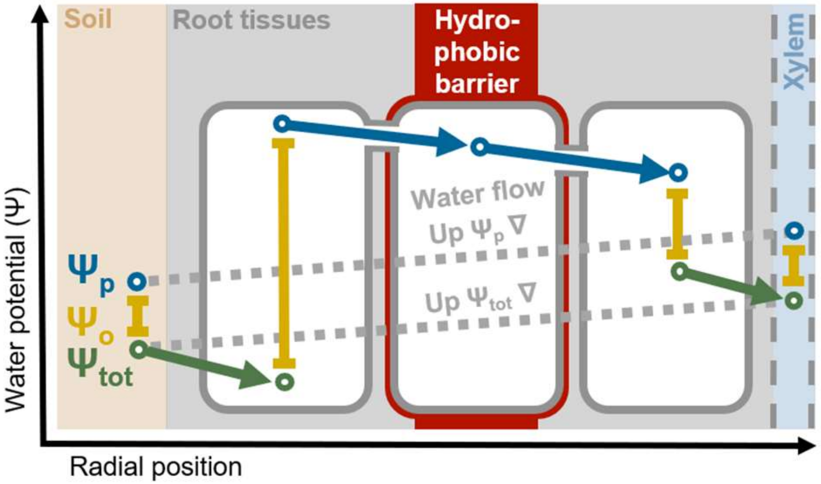


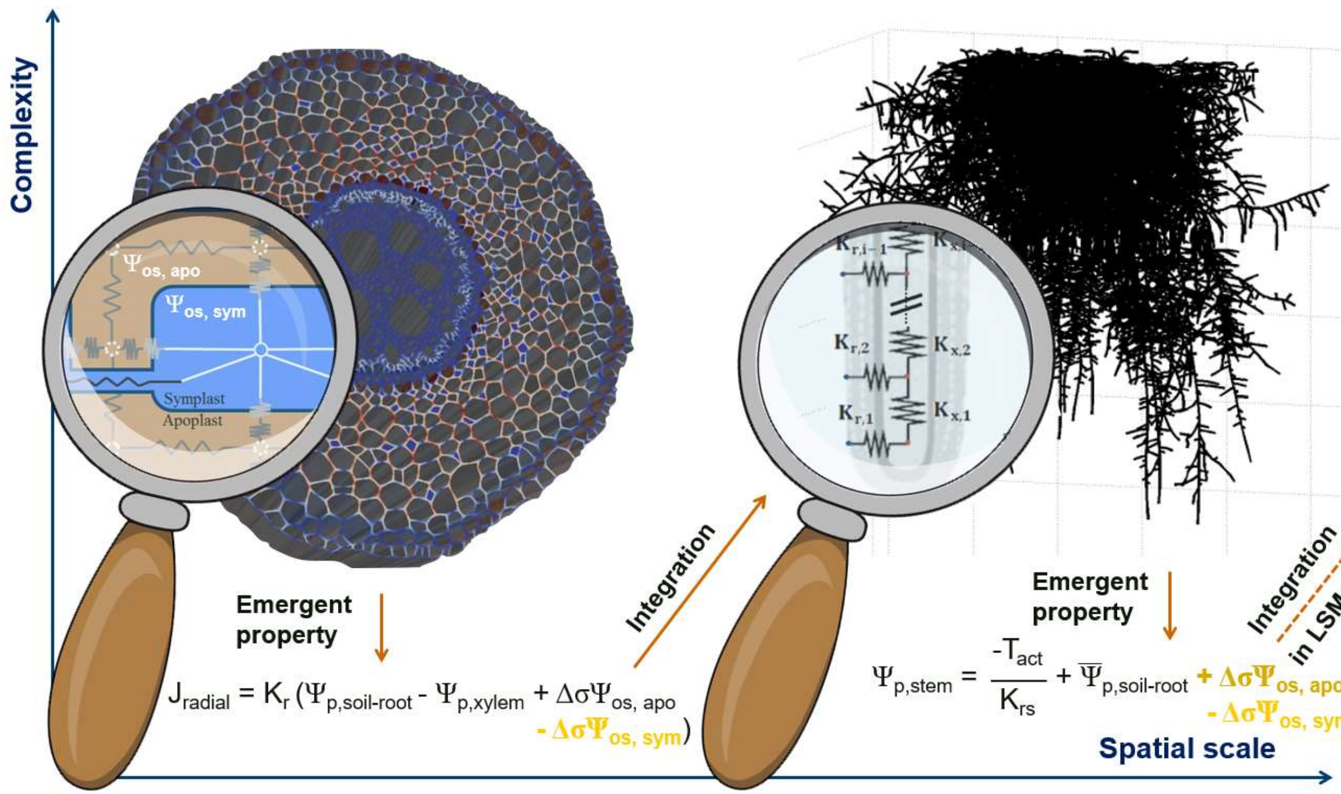
Upscaled driving force $\boxed{\psi_{p,s} - \psi_{p,x} + \sigma_r (\Delta\psi_{o,sym\ eq} - \Delta\psi_{o,apo\ eq})}$

Conclusions

1. New mechanistic theory consistent with experimental observations to solve the riddle of the “uphill water flow”

2. Its upscaled expression generalizes the paradigm of radial water flow by including osmotic gradients across living cells





Perspectives

Quantitative validation of the impact of symplastic water pumping on Ψ_{stem}

How do Ψ_o gradients in the symplast respond to water stress ?

What is the mechanism maintaining Ψ_o gradients in the symplast ?

THANK YOU FOR YOUR ATTENTION! ☺

Funding

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