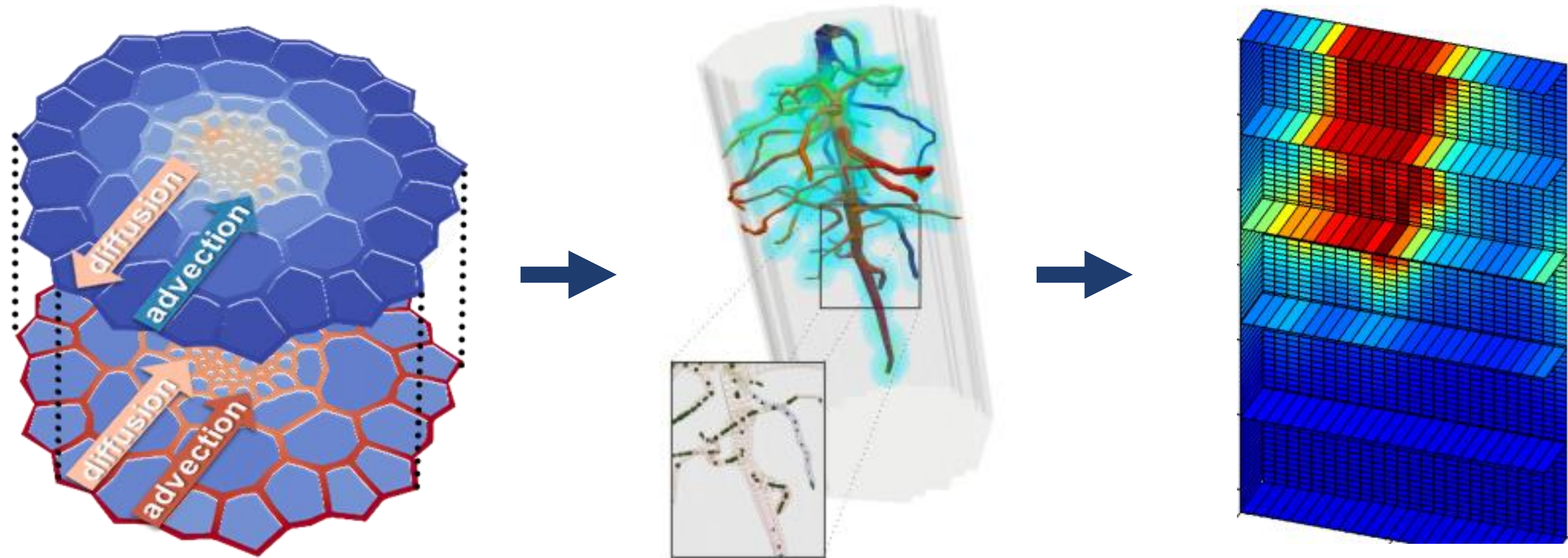


Emergent properties of root hydraulic anatomies



Valentin Couvreur, Guillaume Lobet, Adrien Heymans, Mathieu Javaux,
Jan Vanderborght, Malcolm J Bennett & Xavier Draye



HydroField 10/04/2024



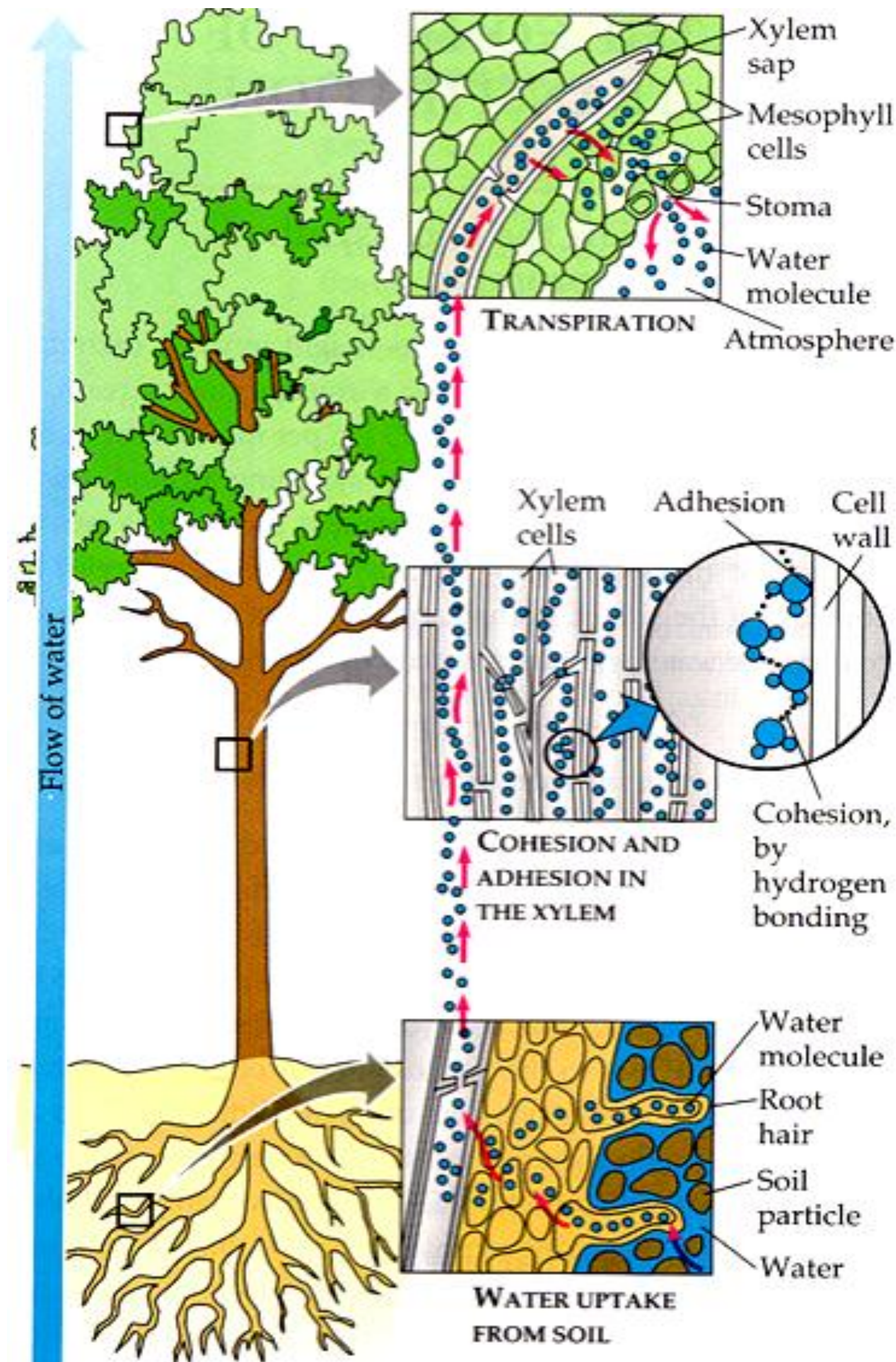
University of
Nottingham



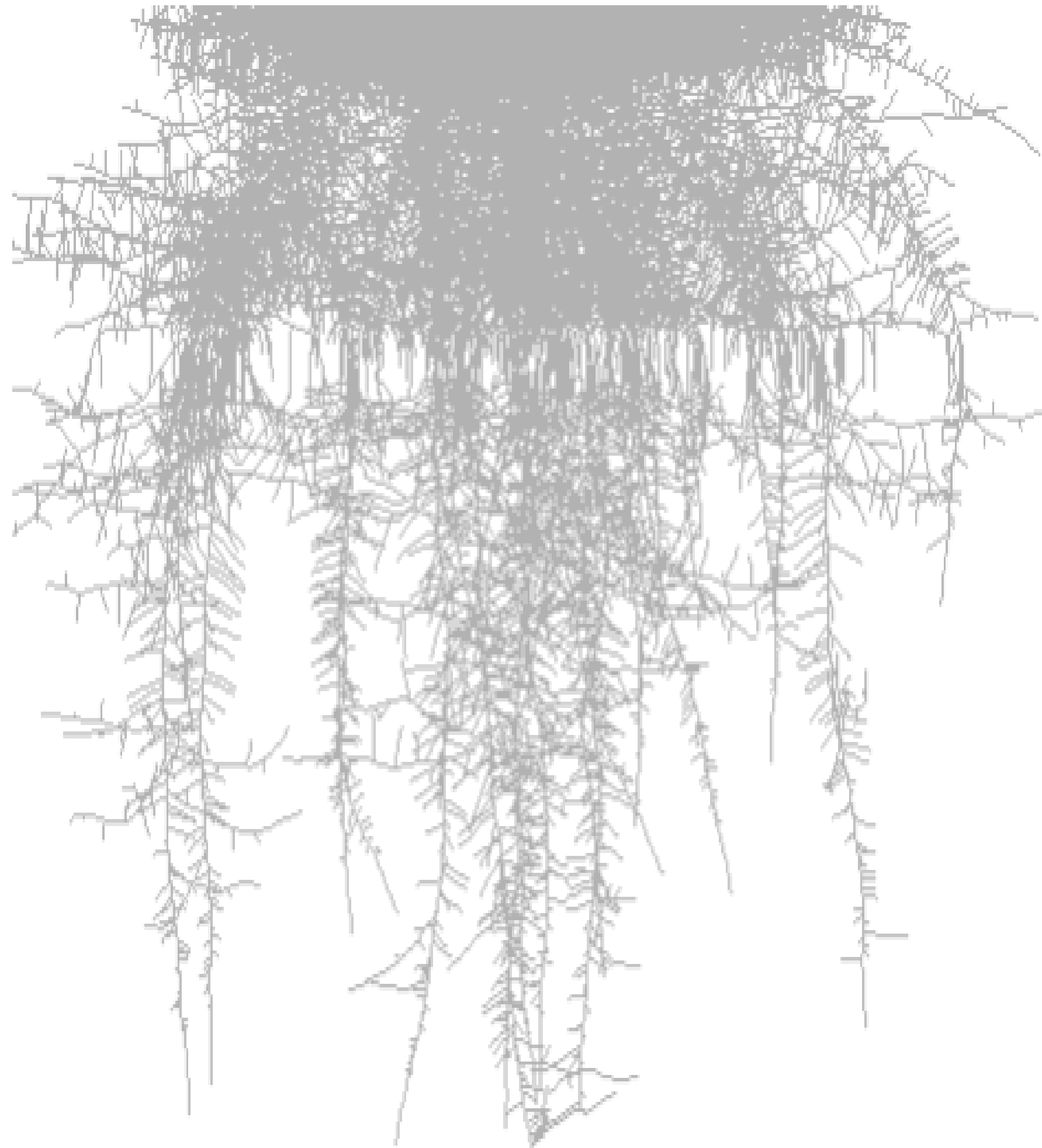
What drives water movement ?

$$F = K \cdot \Delta\Psi \quad (\text{van den Honert, 1948})$$

components ?
gravity matric
pressure osmotic



Modelling water flow in root hydraulic architectures

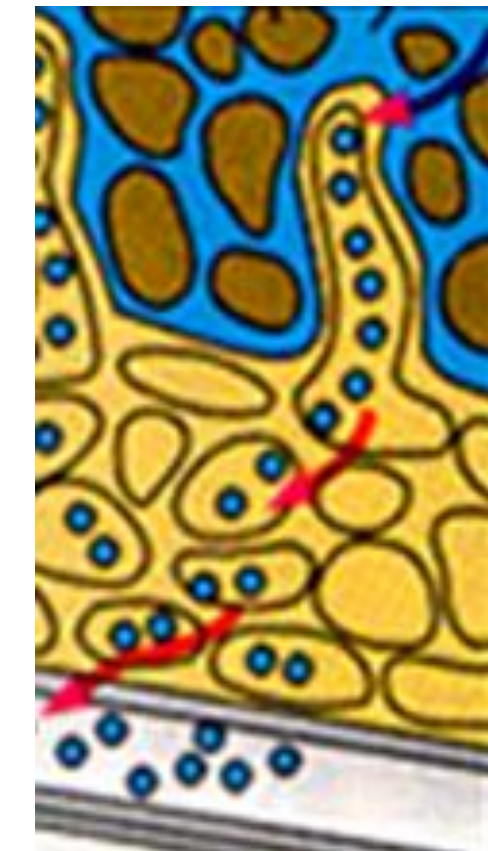


RootTyp (Pages et al., 1989)

$$F_x = -K_x \cdot \Delta\Psi_{\text{xylem}}$$



$$F_r = K_r \cdot (\Psi_{\text{soil}} - \Psi_{\text{xylem}})$$



Mass conservation

No capacitance

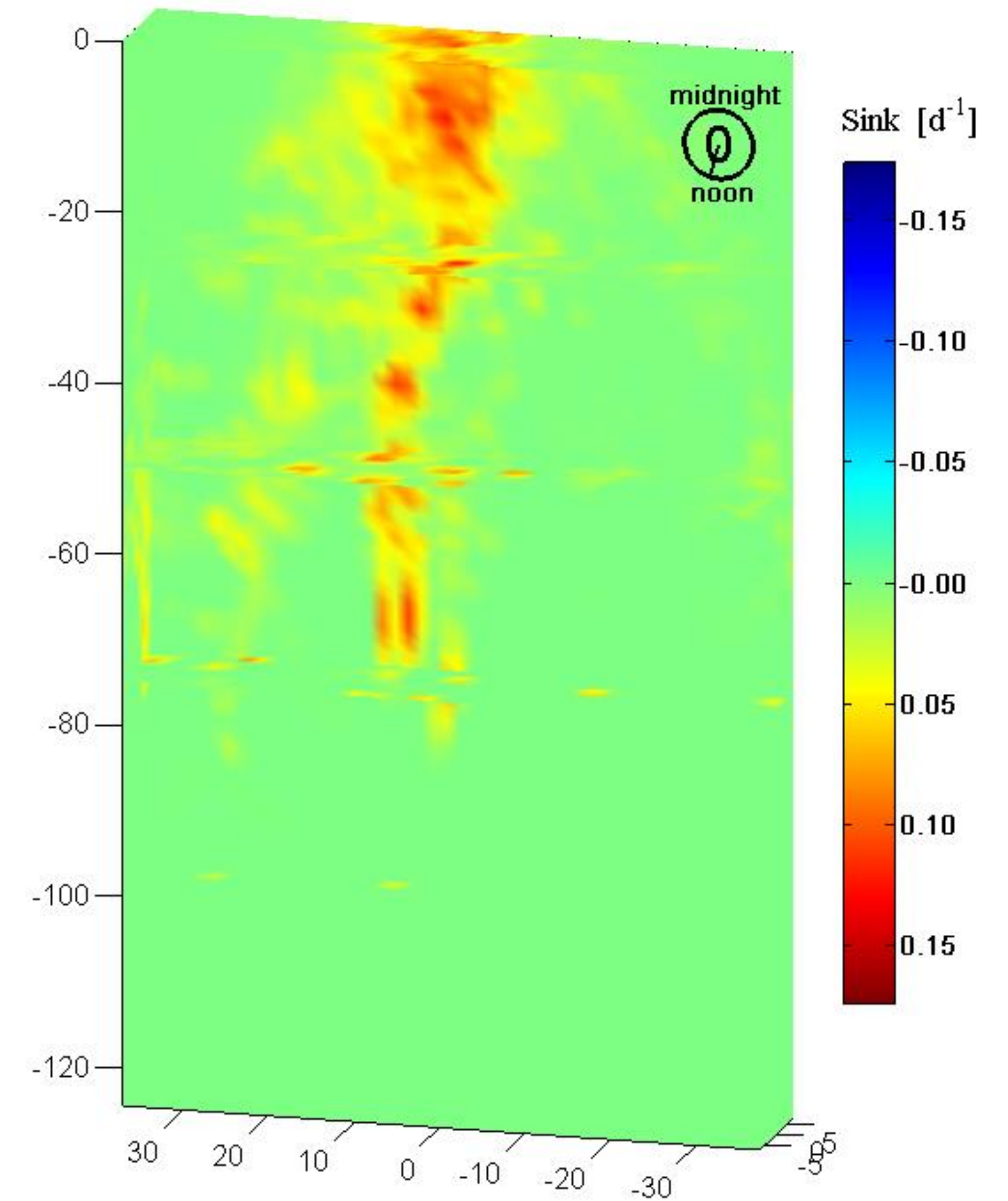
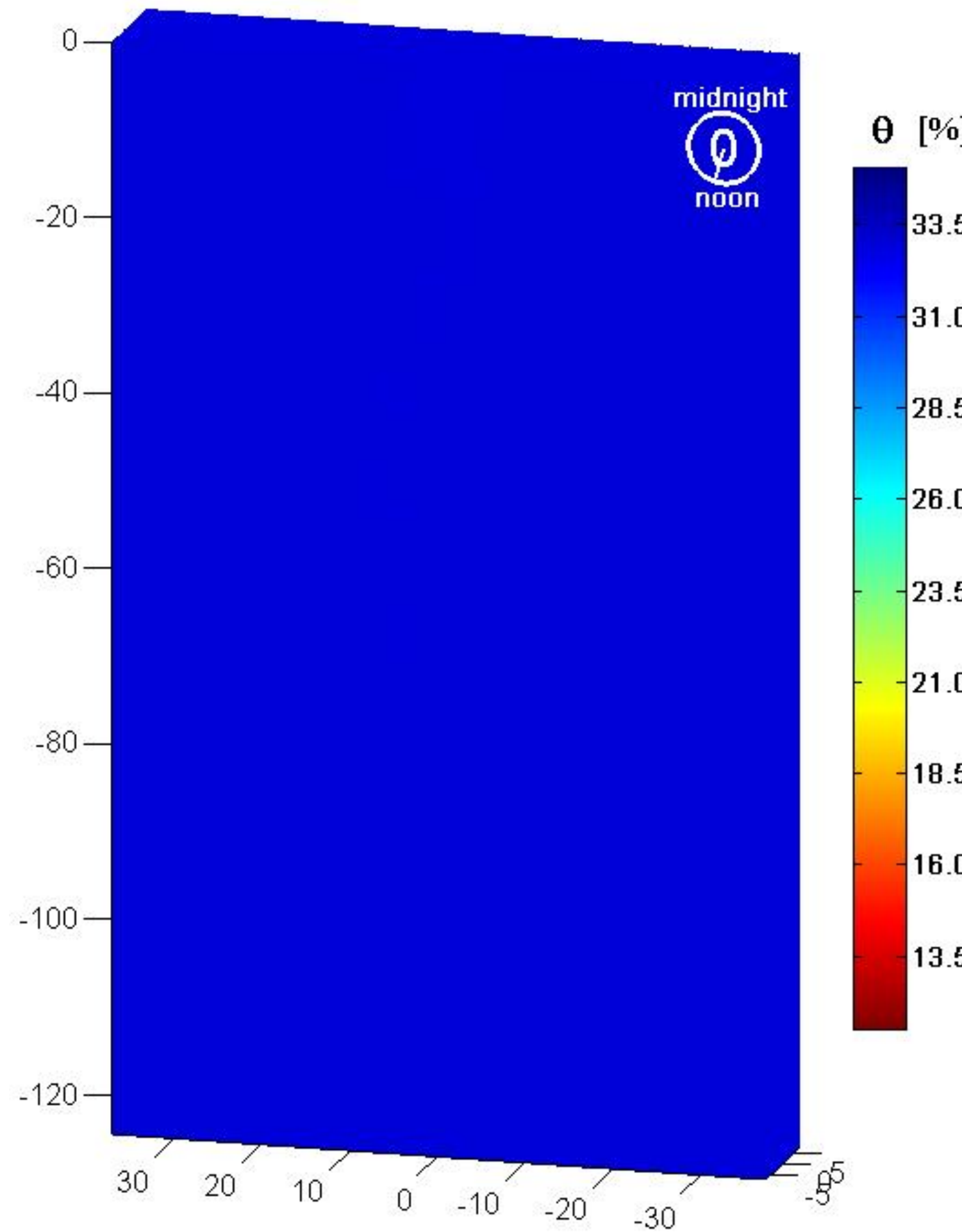
(Doussan et al., 1998)

Water flow simulations in soil & root hydraulic architectures

(Doussan et al., 2006; Javaux et al., 2008)



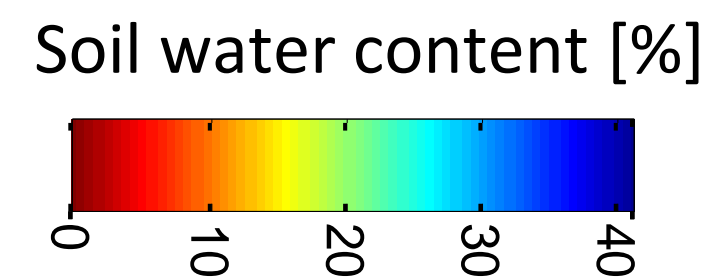
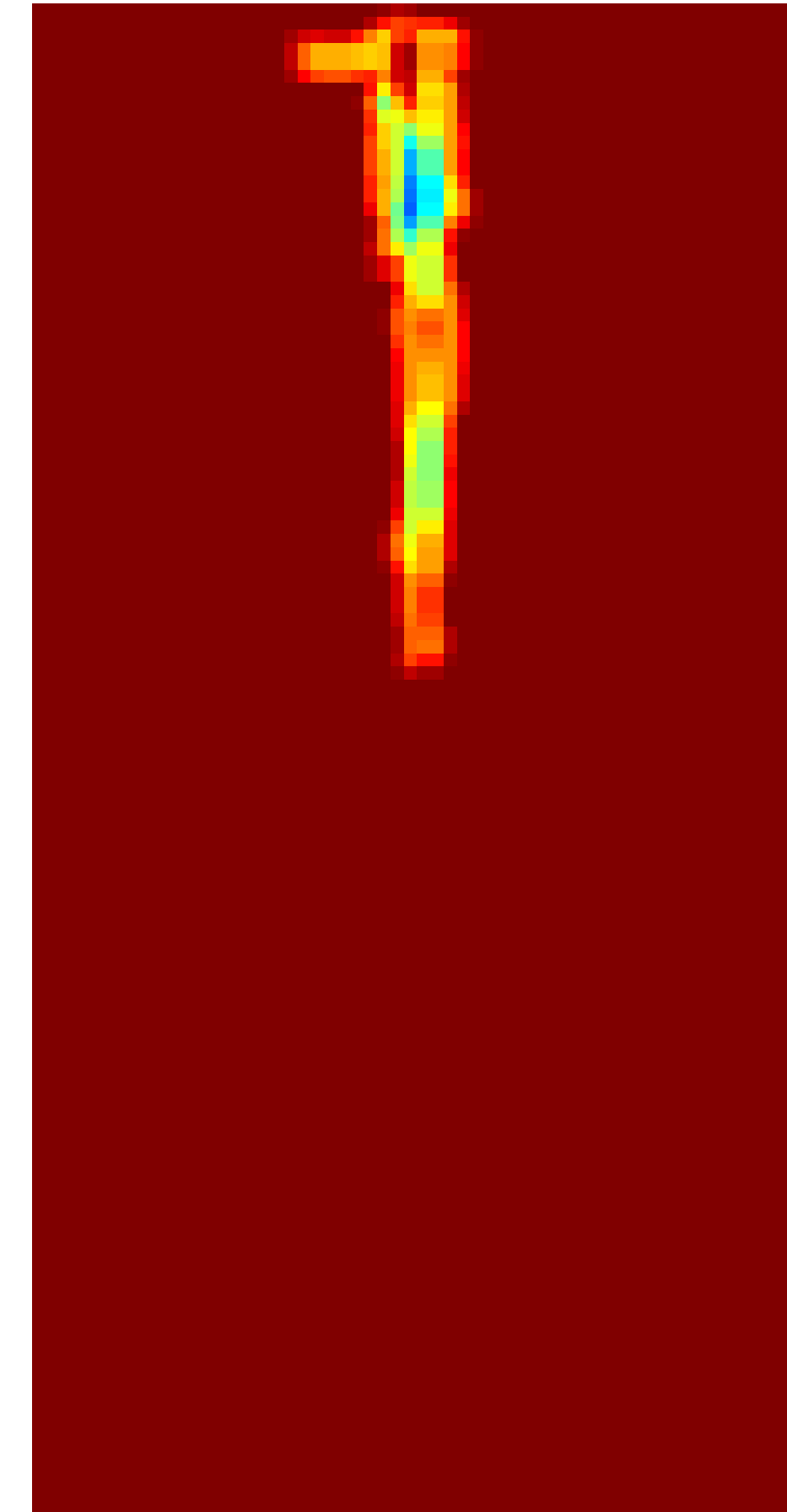
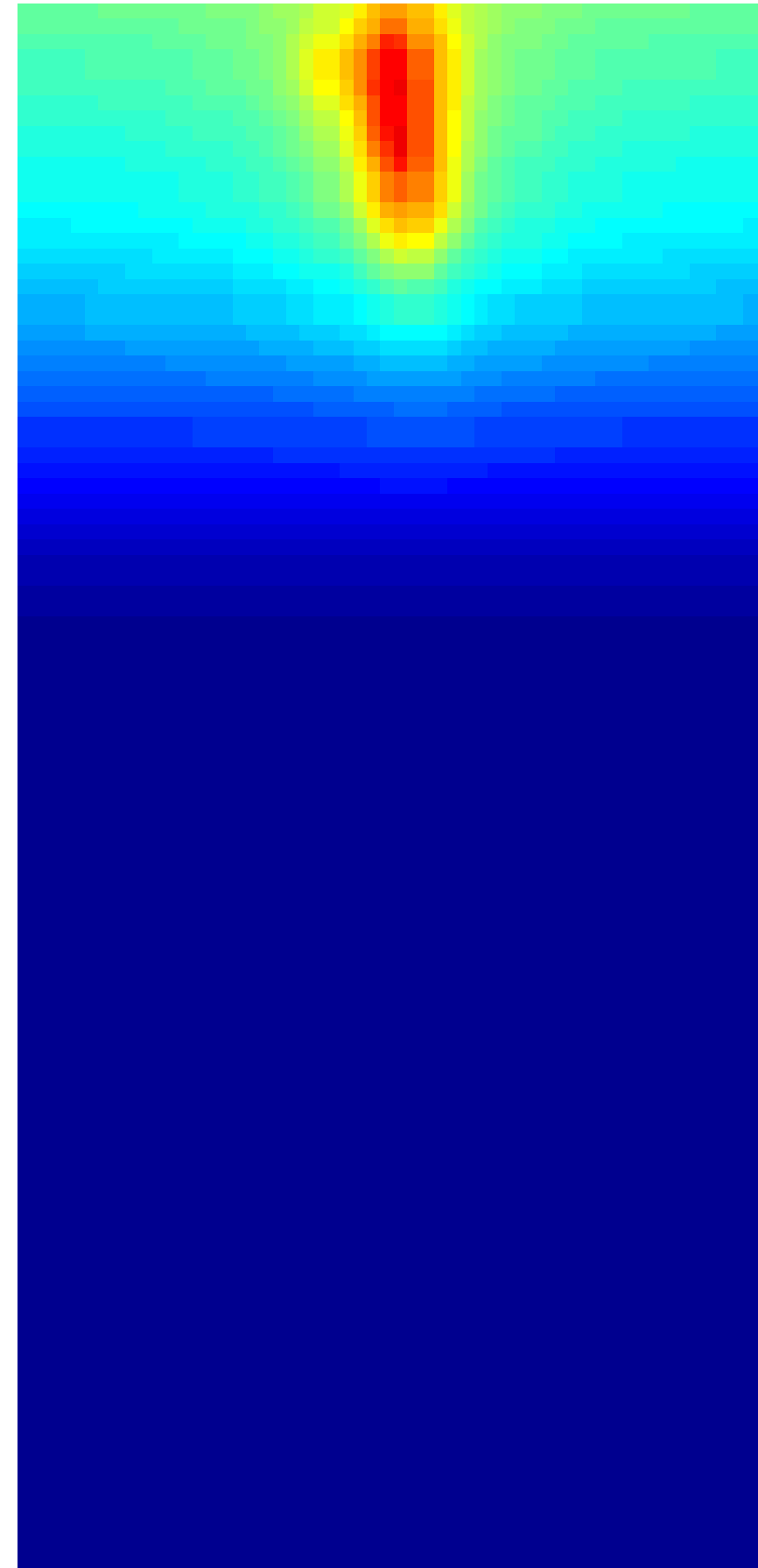
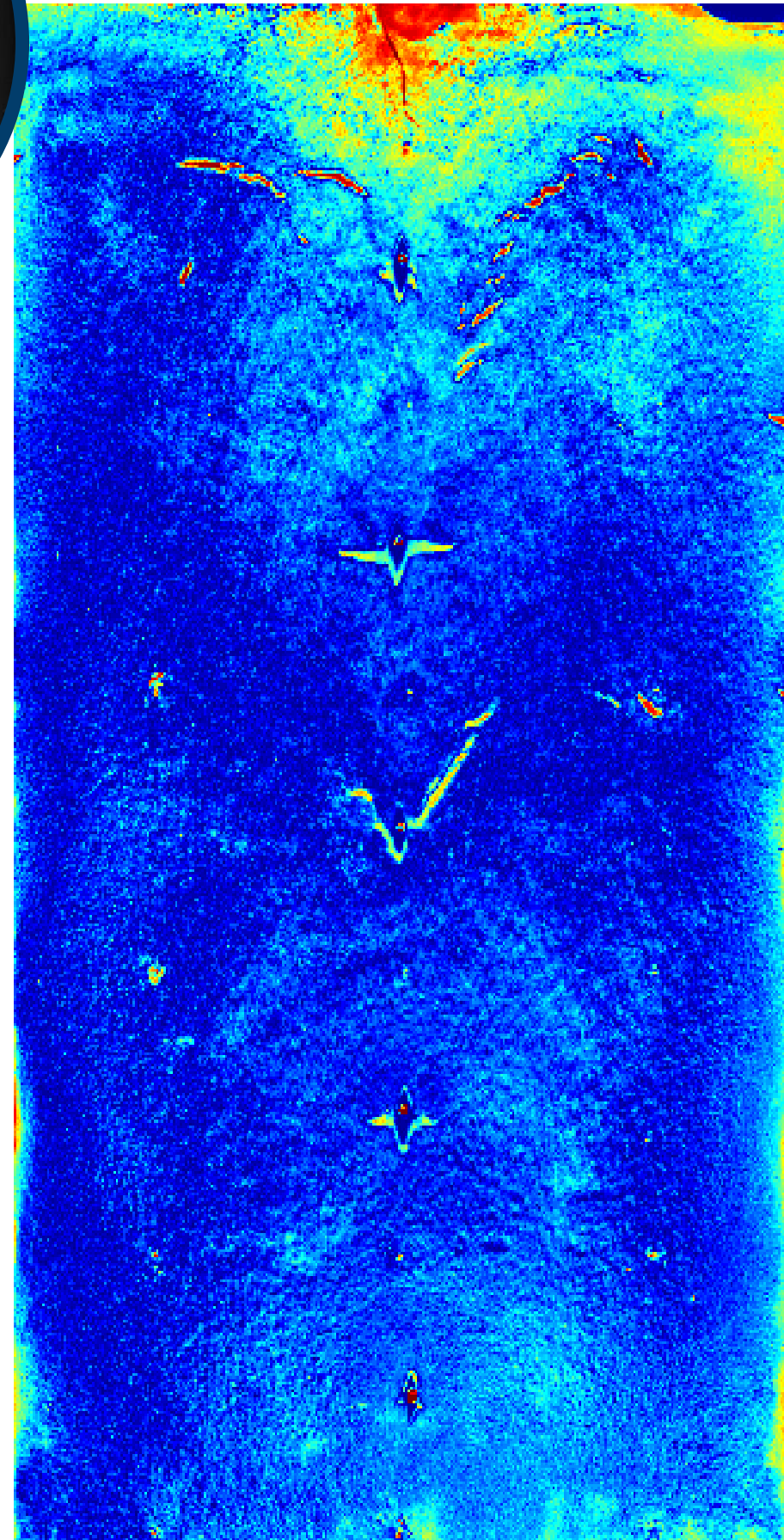
Complex system at play



Water uptake location is very plastic

Water uptake may occur where no soil water content change is visible

Models to facilitate interpretation of experimental observations



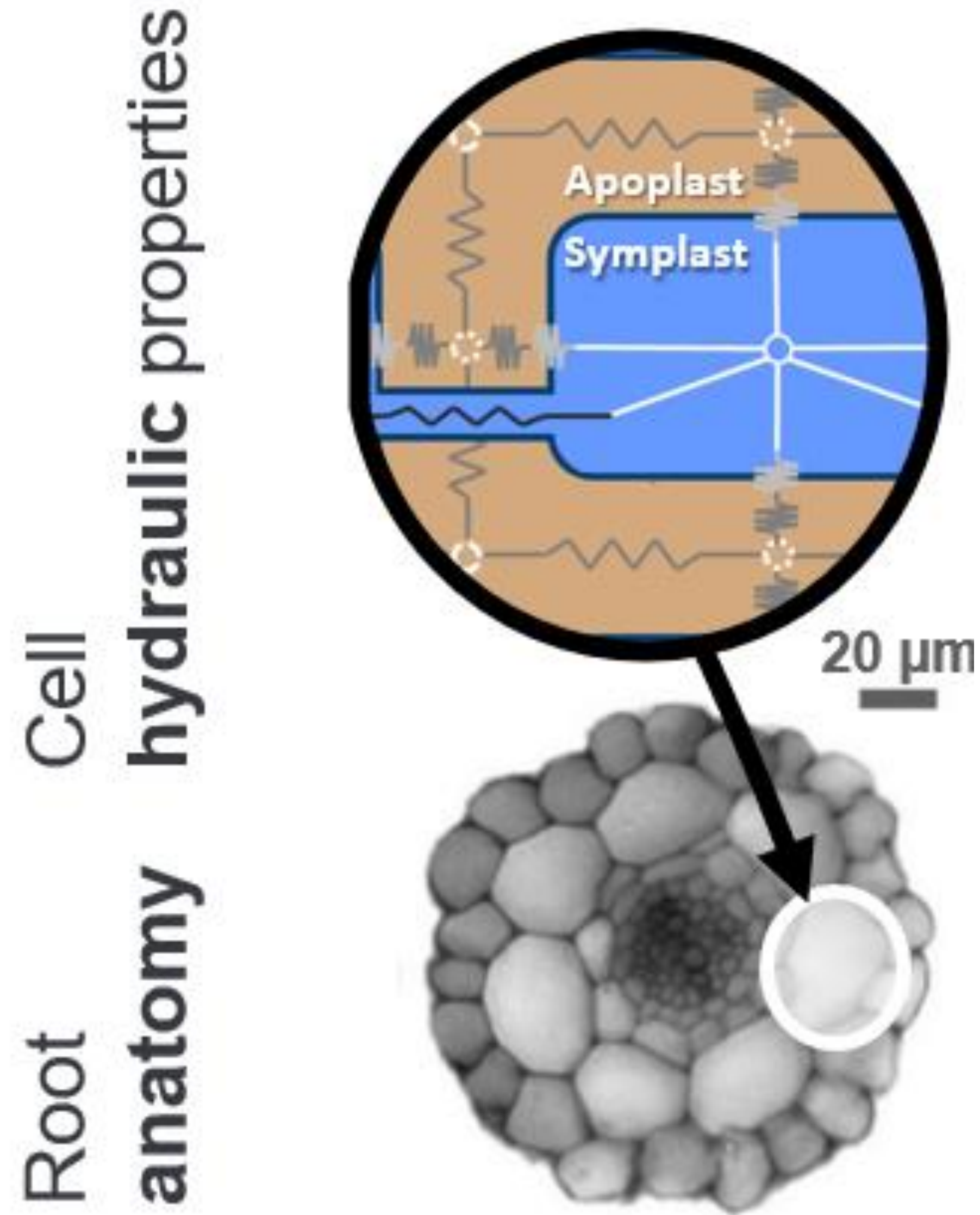
Water uptake location is very plastic

Water uptake may occur where no soil water content change is visible

The idea of modelling water flow in root hydraulic anatomies

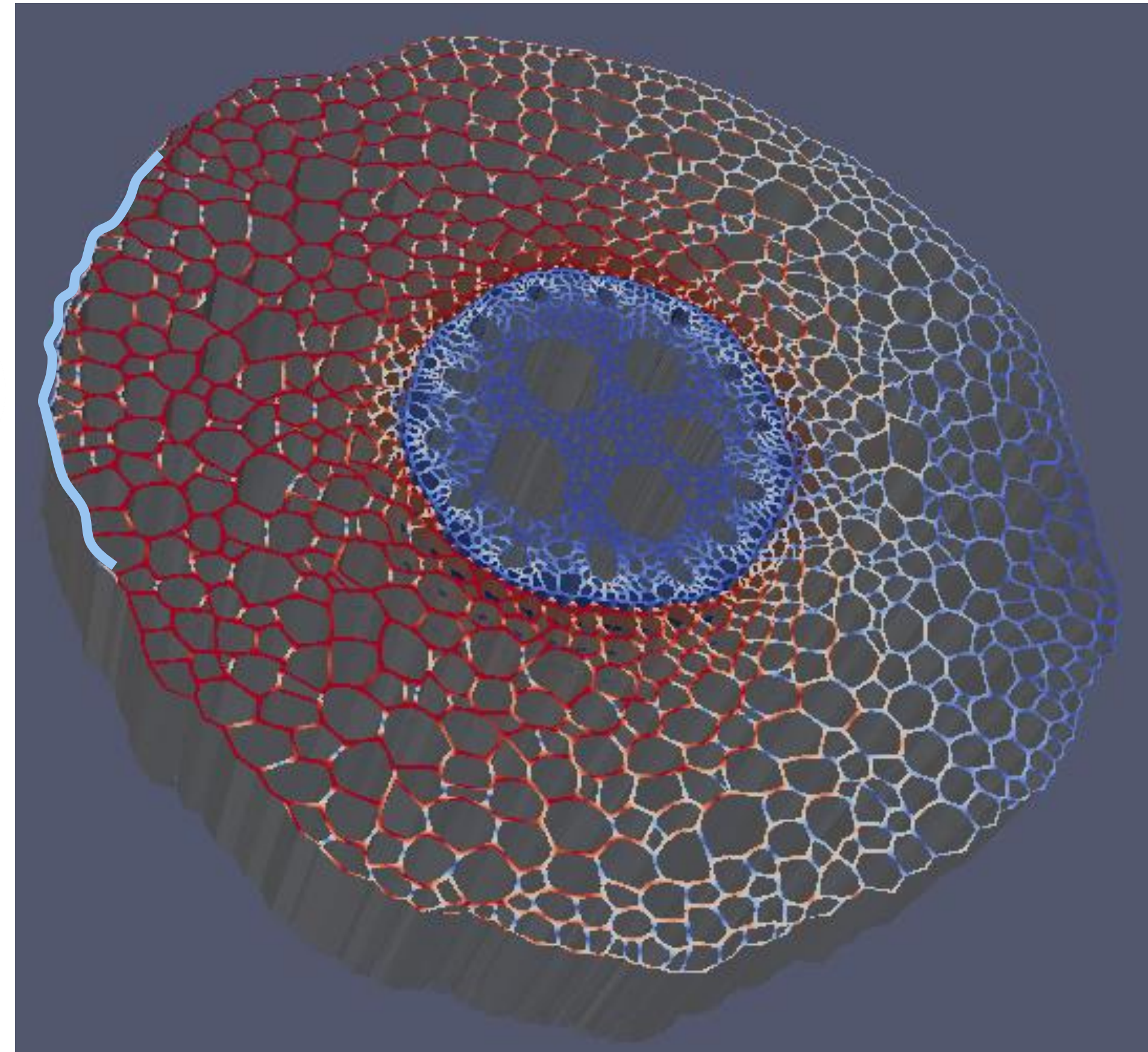


Xavier Draye



Water flow equations :

- $F = K \cdot \Delta\Psi$
- Mass conservation
- No capacitance



(Couvreur et al., 2018)

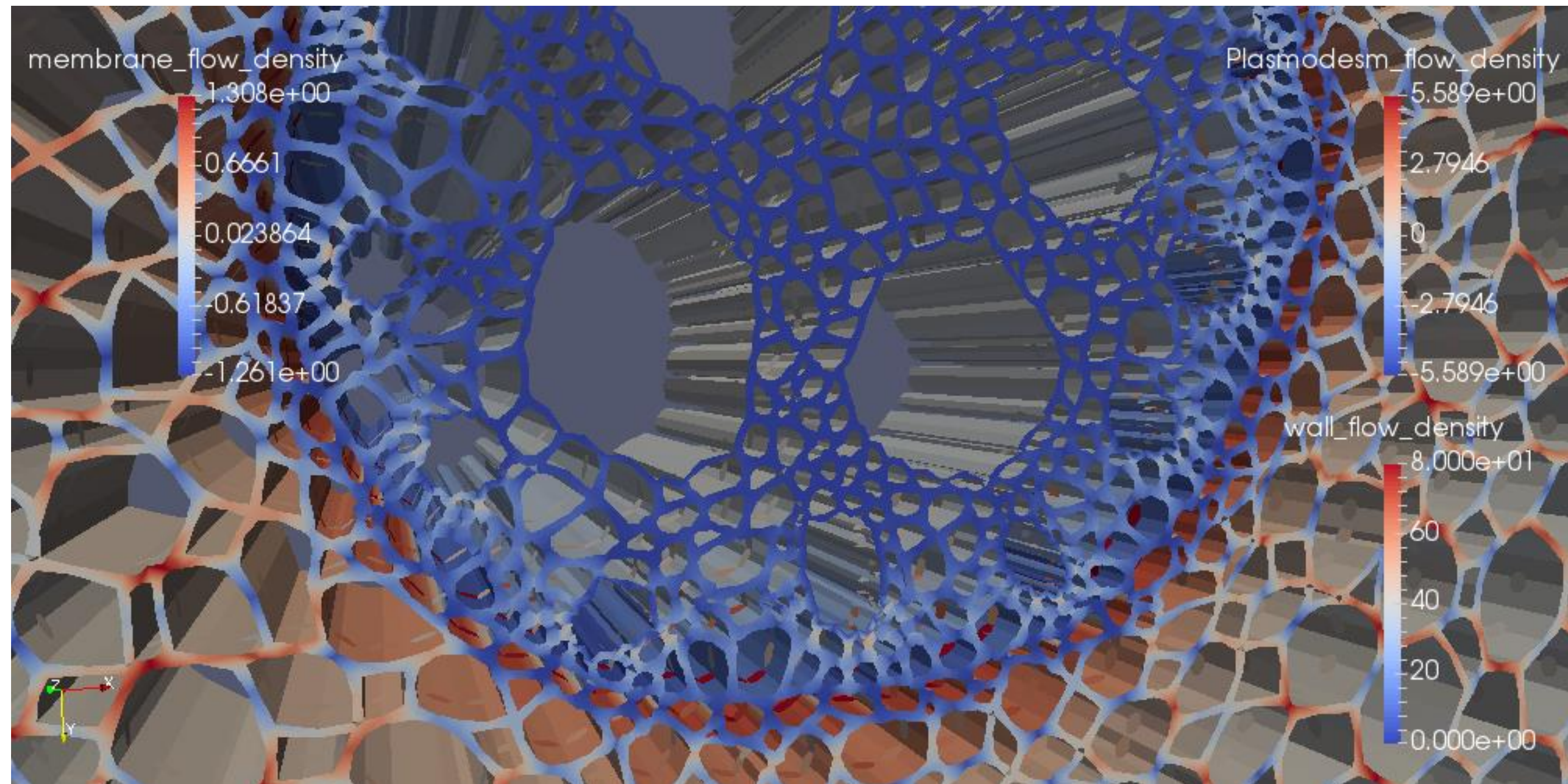
Exploration of water flow in hydraulic anatomies with MECHA

Boundary conditions: -0,01 MPa soil-root interface \longrightarrow -0.5 MPa xylem vessels

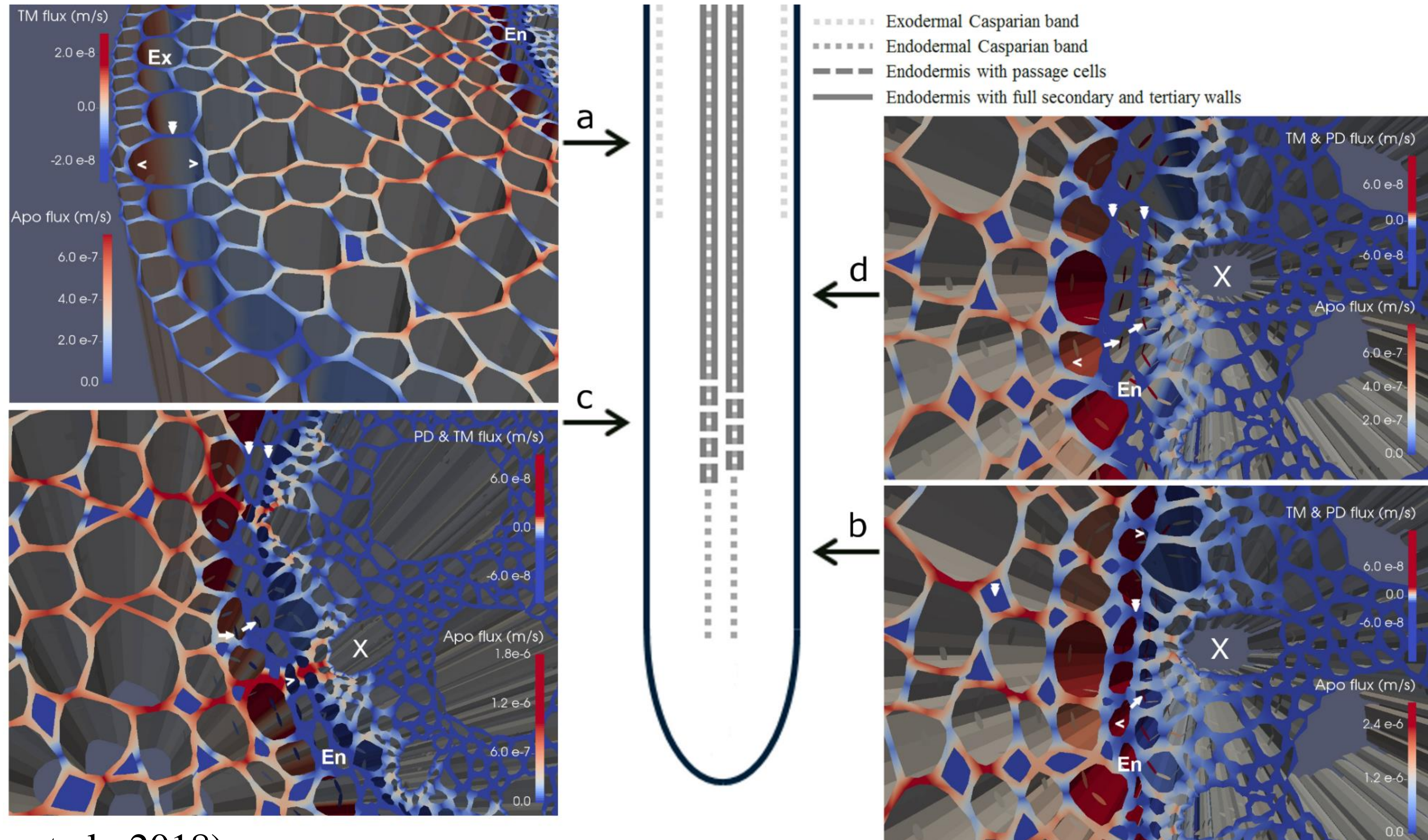
k_{wall} : 2E-2 cm/hPa/d (Steudle and Boyer, 1985)

k_{membrane} : 2E-4 + 4.5E-4 cm/hPa/d (Ehlert et al., 2009)

$k_{\text{plasmodesmata}}$: 2E-4 cm/hPa/d (Gunning and Robards, 1976) 6E-3 cm/hPa/d (Bret-Harte and Silke, 1994)

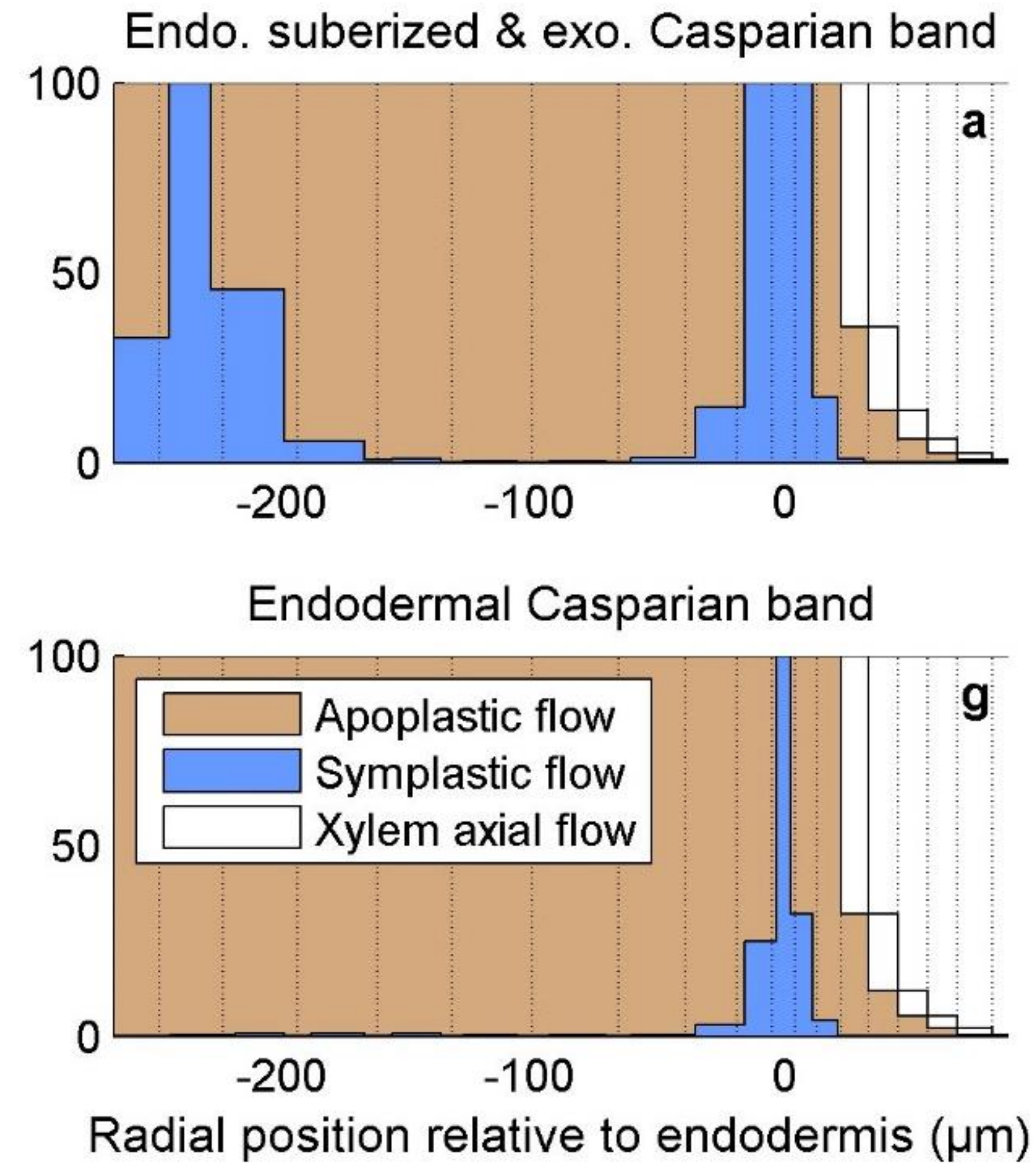
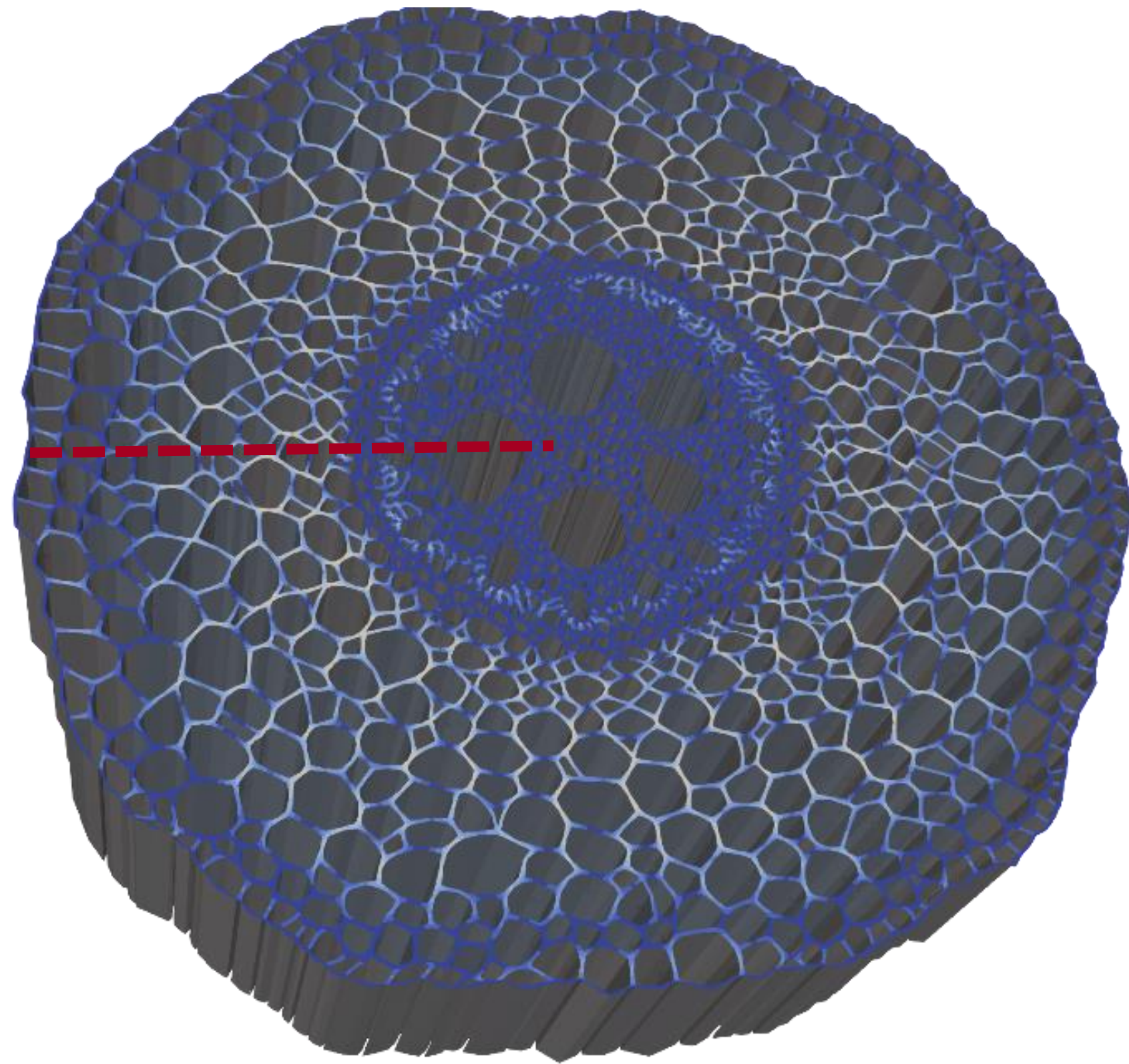


Exploration of water flow in hydraulic anatomies with MECHA

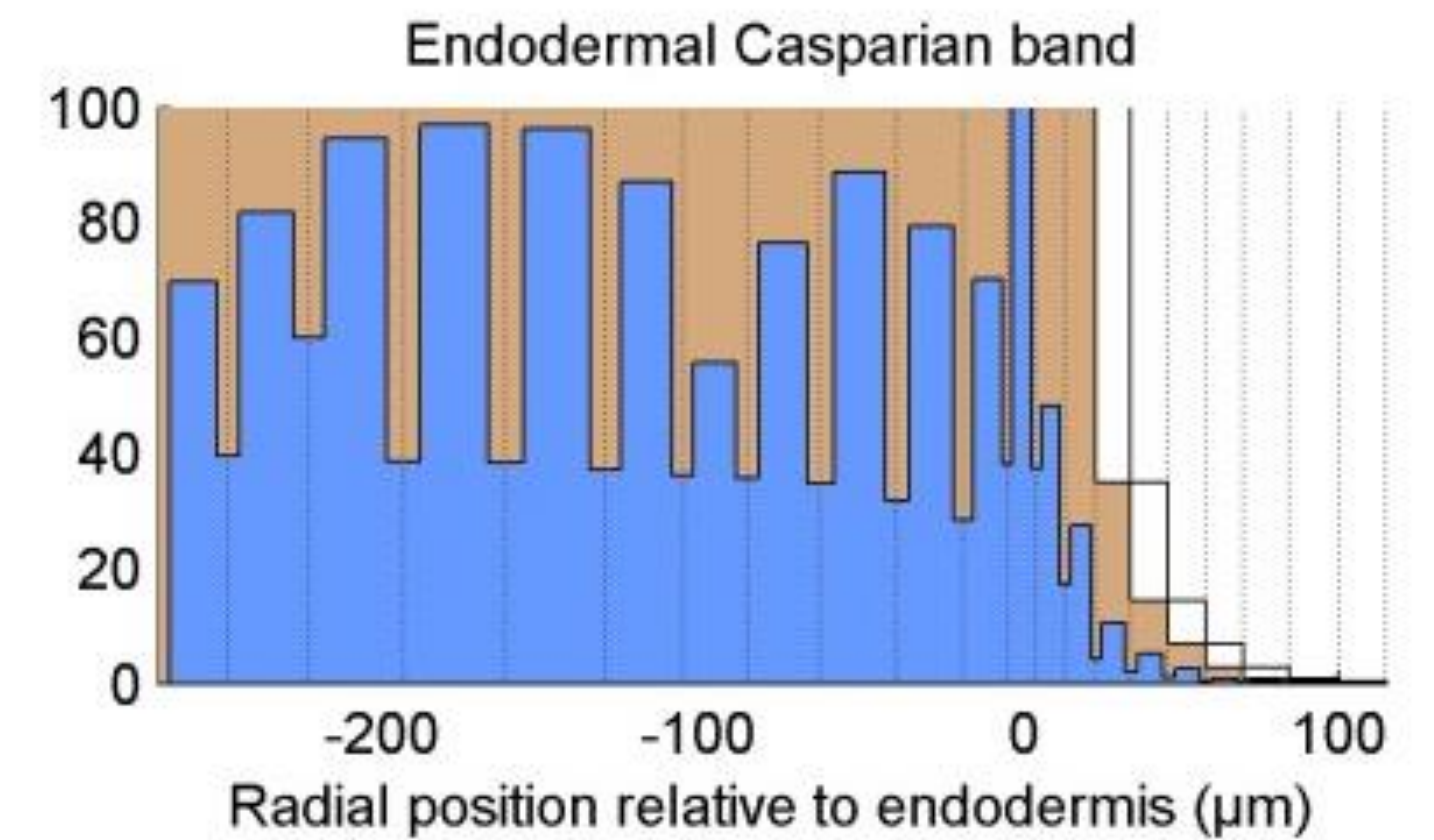
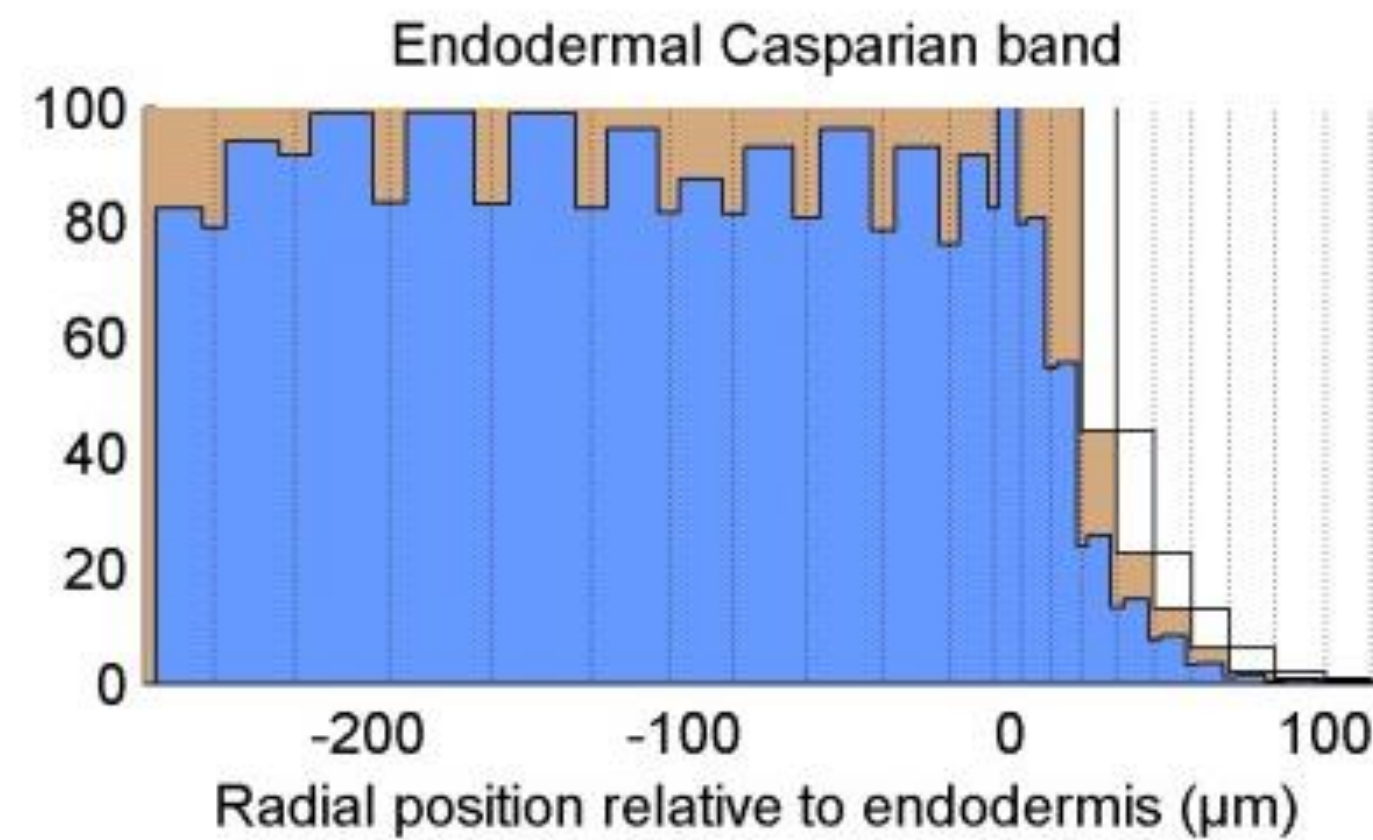
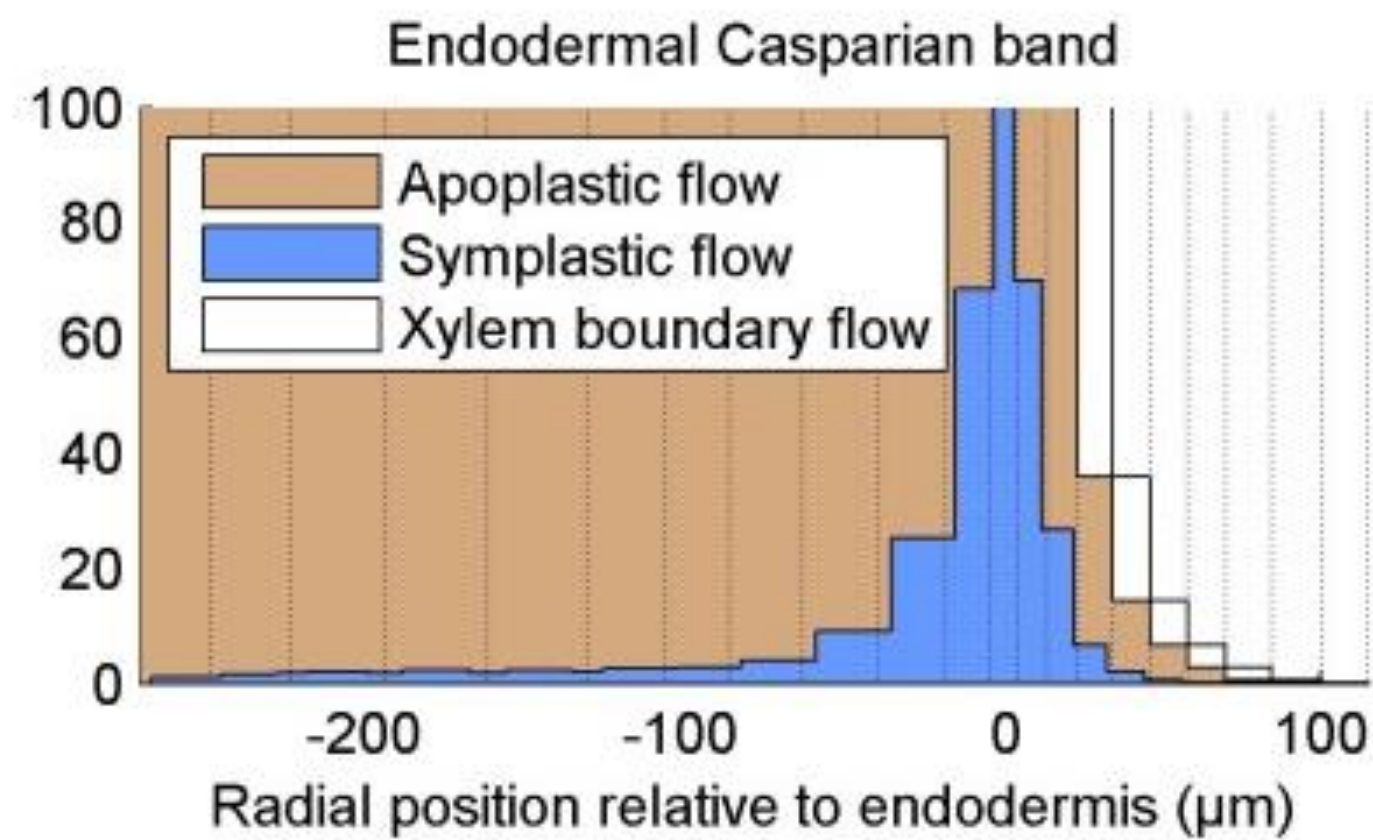
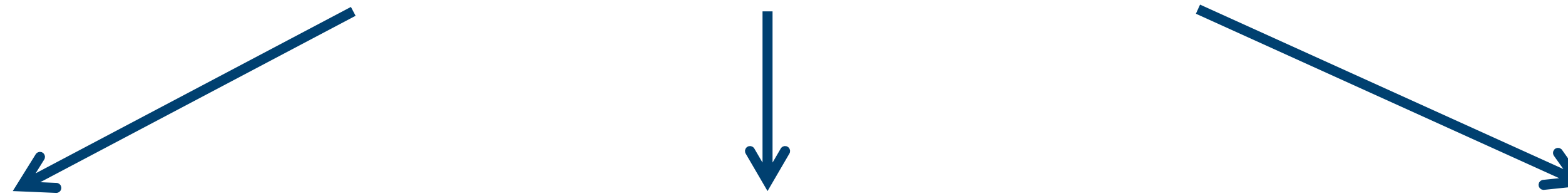
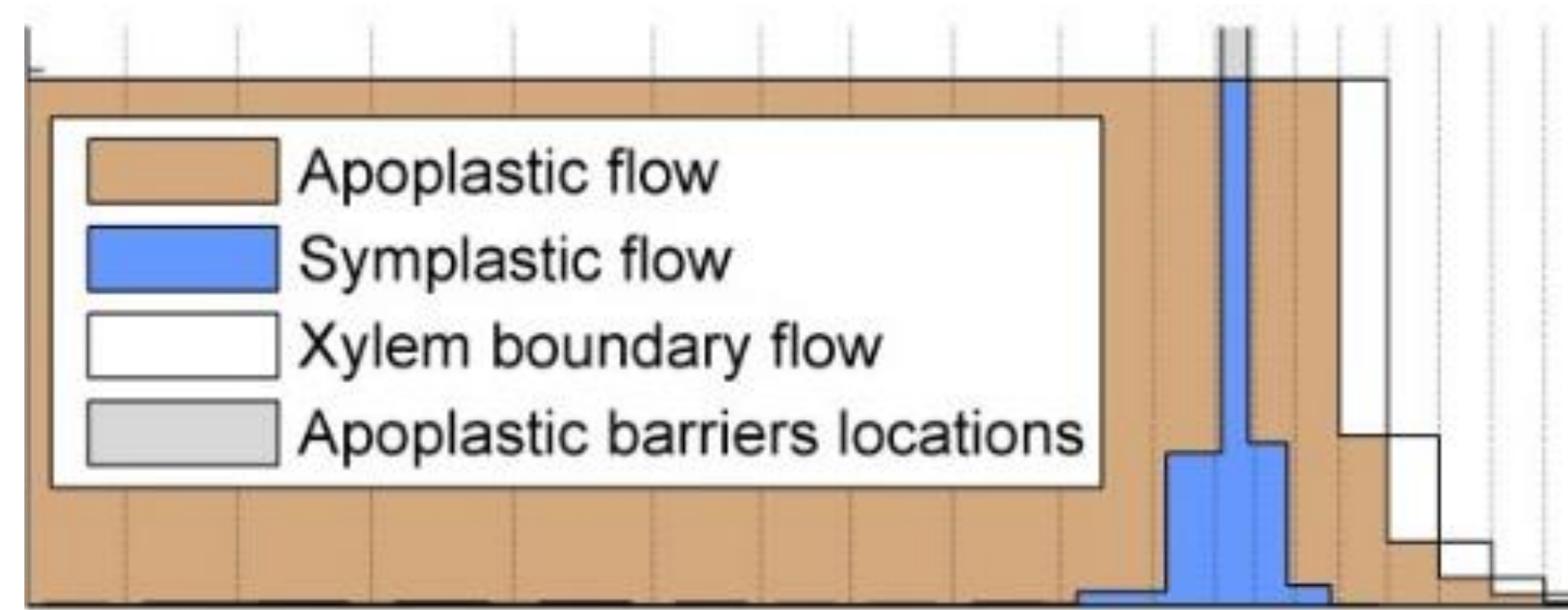


(Couvreur et al., 2018)

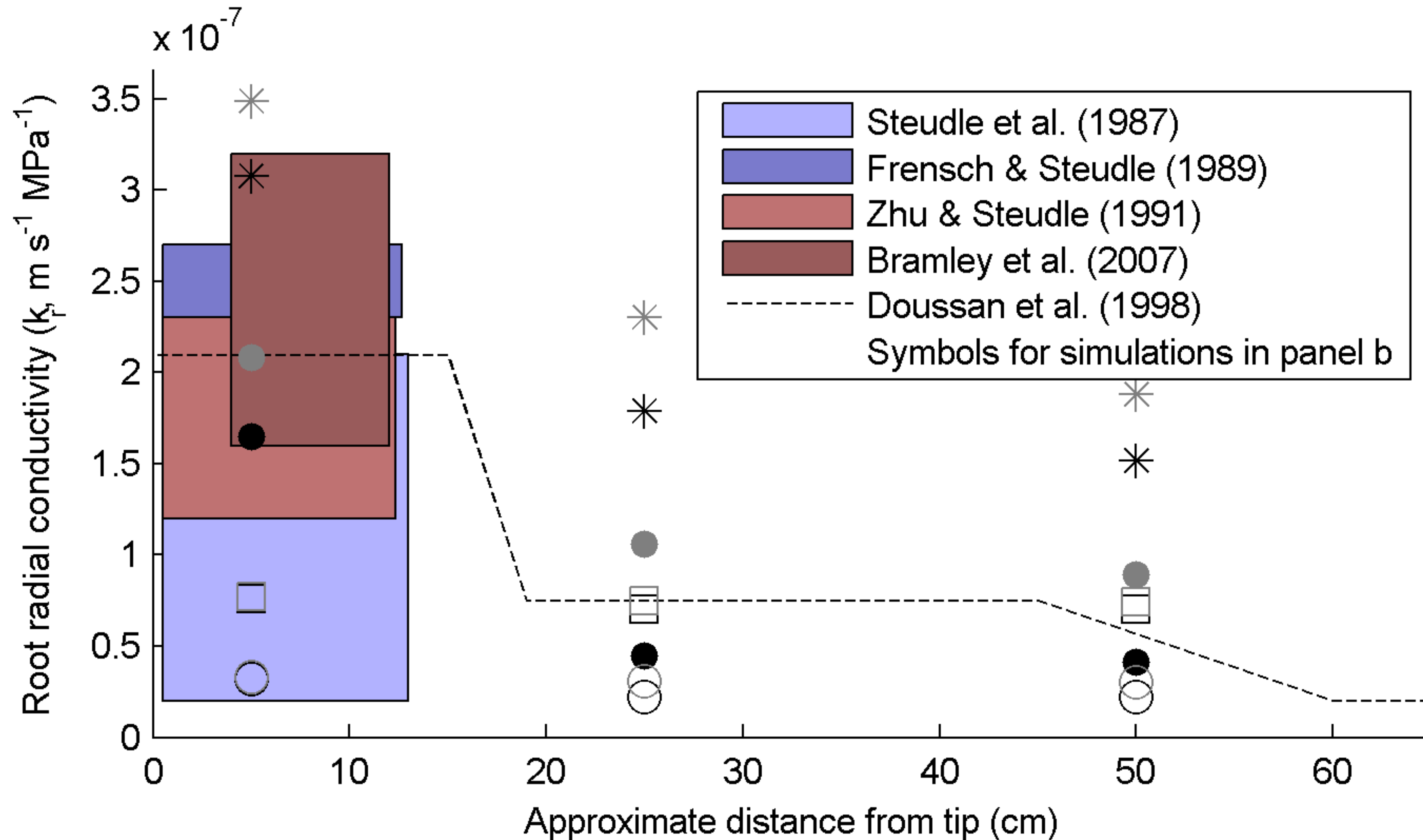
Condensed view of radial water flow pathways



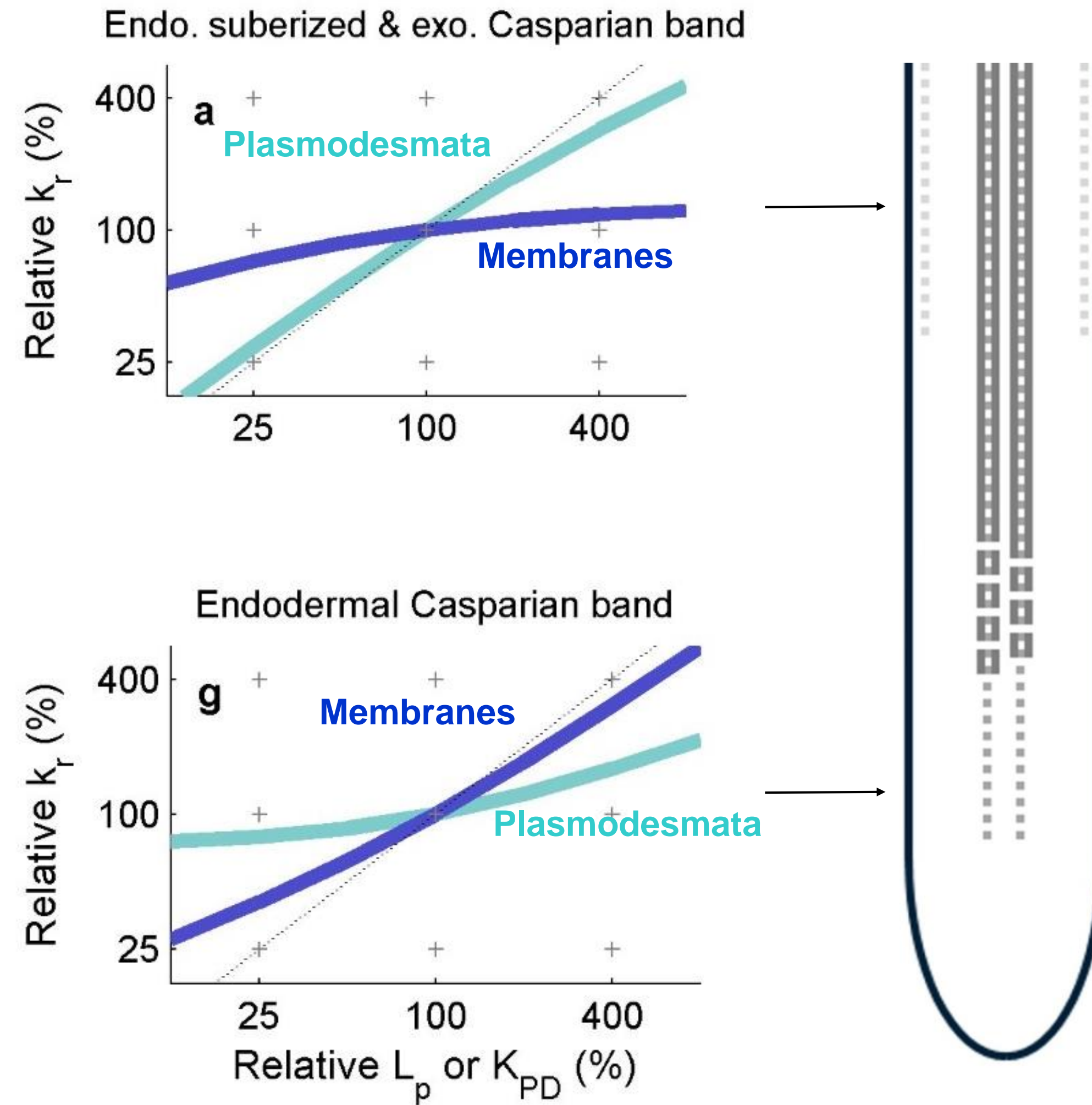
Quiz : Plasticity of radial water flow pathways



Radial conductivity is sensitive to cell-scale hydraulic properties



Which cell properties control root radial conductivity ?



Not just “which” properties, but also “where”...

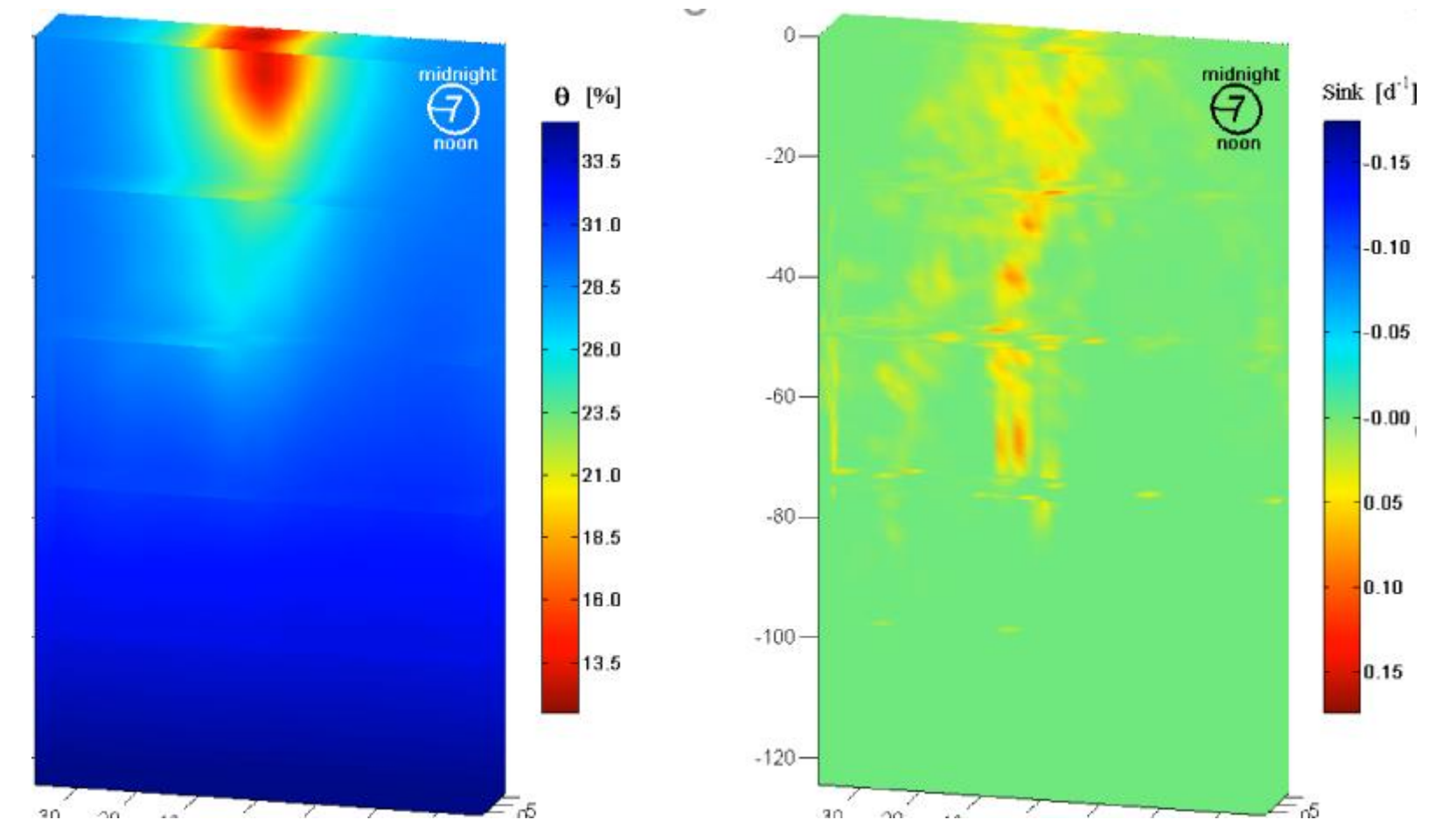
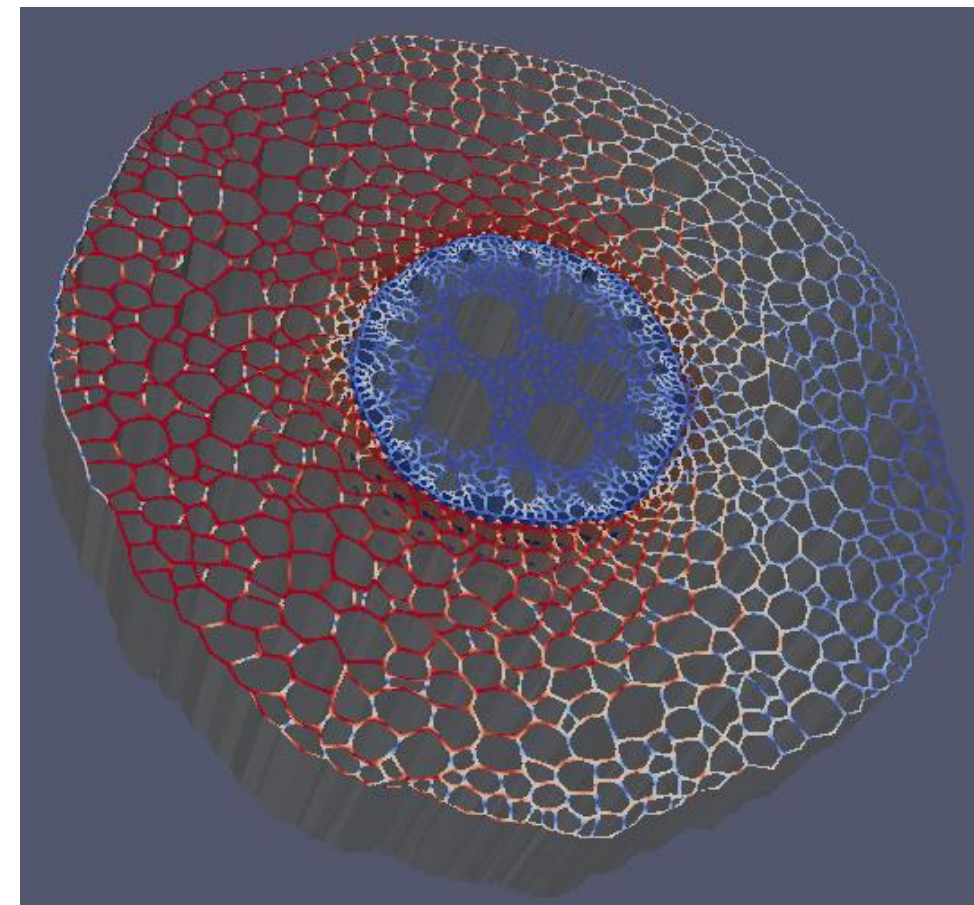
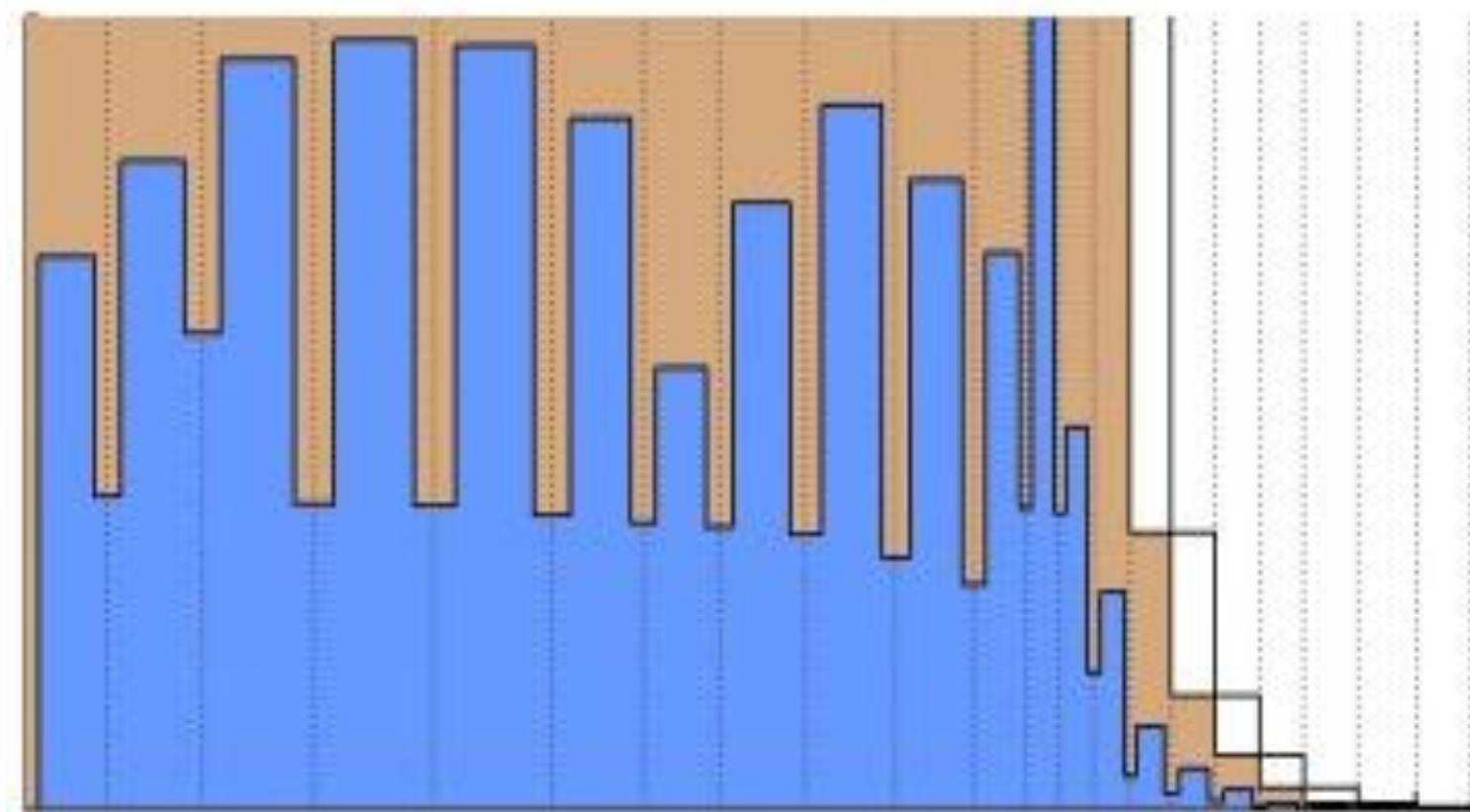
Take home messages → Station 1 : hydraulic networks behaviour

Hydraulic networks are complex systems

... already in simple models with constant conductivities and no capacitance

Structure (architecture / anatomy) and function (hydraulic conductivity) co-determine water flow

Redundancy of water pathways is key for plasticity of uptake under changing conditions

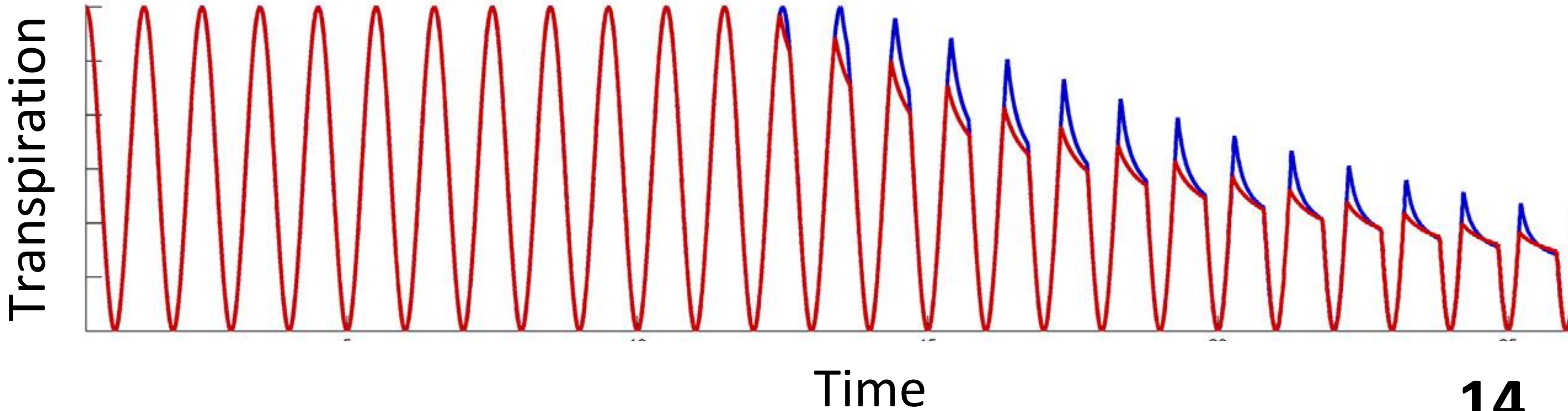
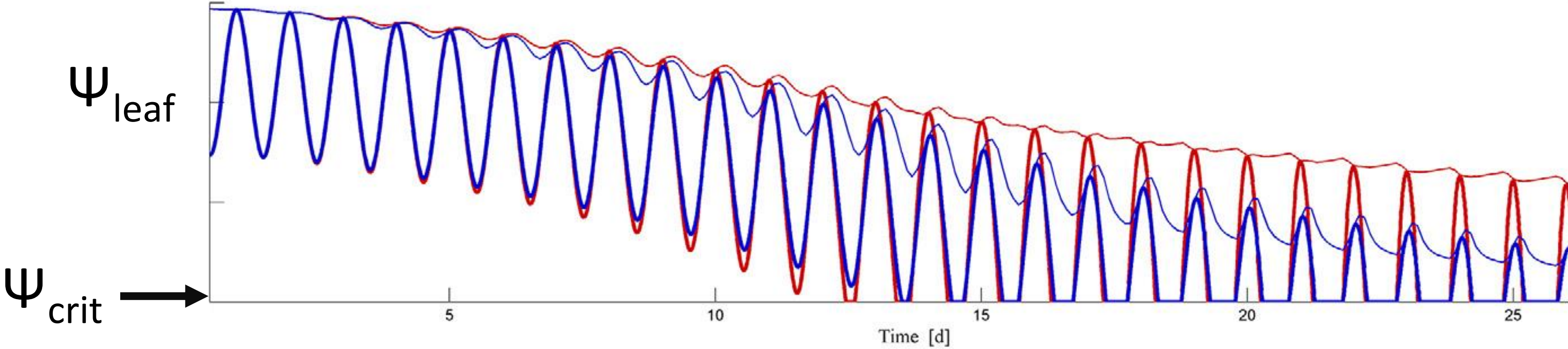
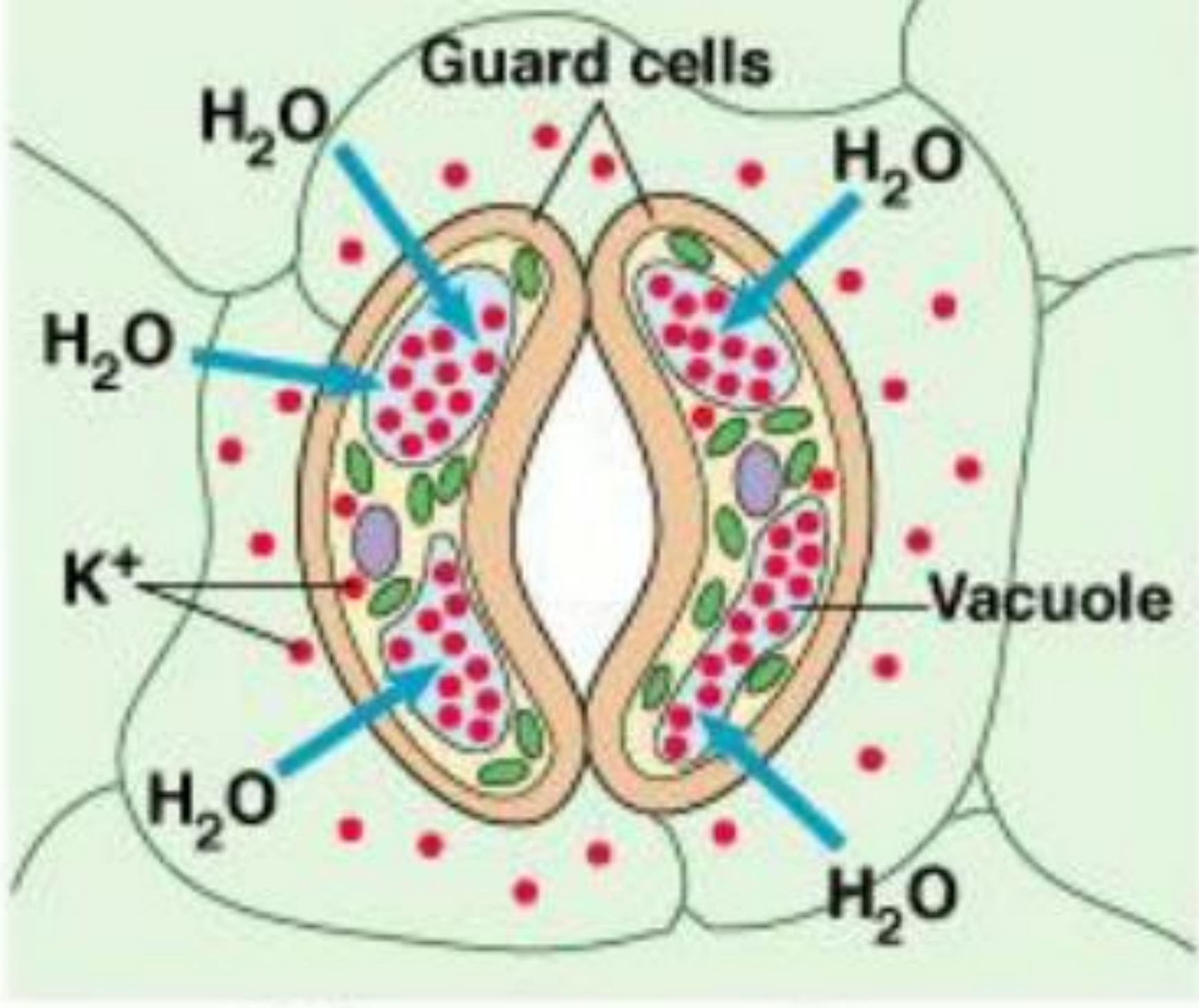


Let's dive into emergent properties !

Emergence may help describing complex phenomena in simple terms

Surprising macroscopic relations arising from elemental laws and properties are called “emergent”

→ e.g. isohydric control of transpiration



Emergence in Conway's « Game of life »

Elemental properties

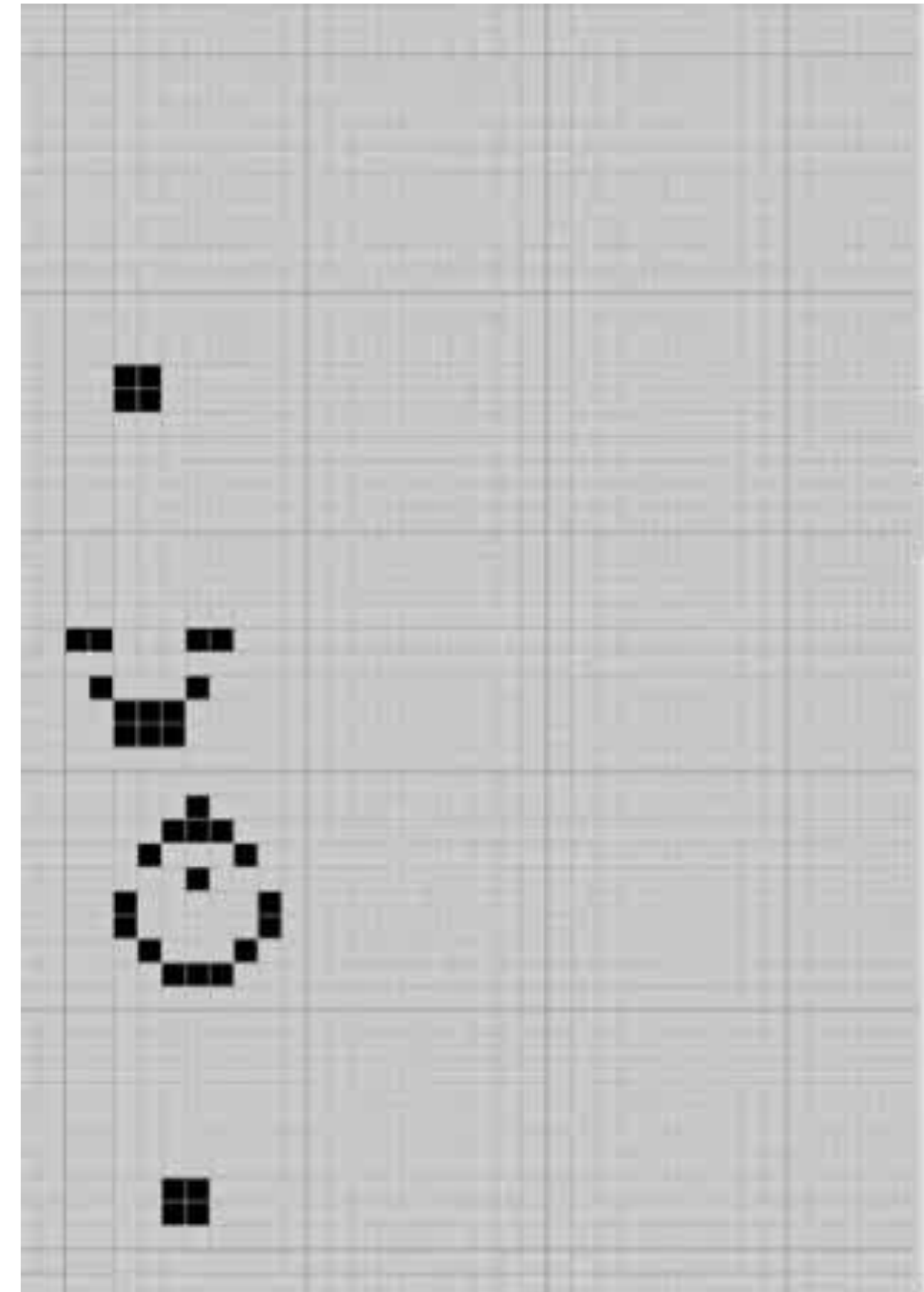
- Cells are either black (“alive”) or white (“dead”).
- Each cell is connected to its eight neighbouring cells.



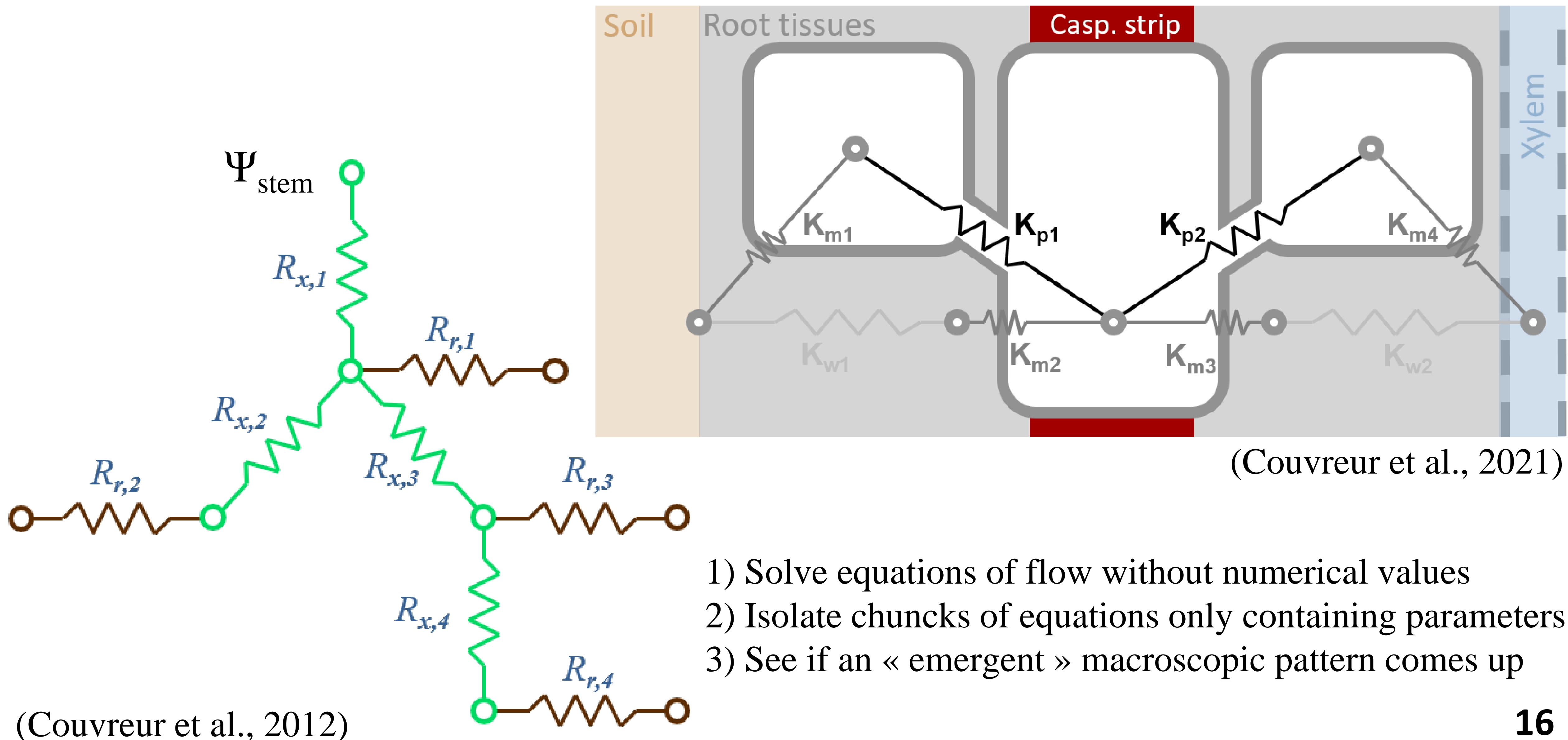
Elemental laws

- Living cells surrounded by 2 or 3 living cells stay alive.
- Dead cells surrounded by 3 living cells come back to life.

Macroscopic behaviour



Identifying emergent behaviours of hydraulic networks

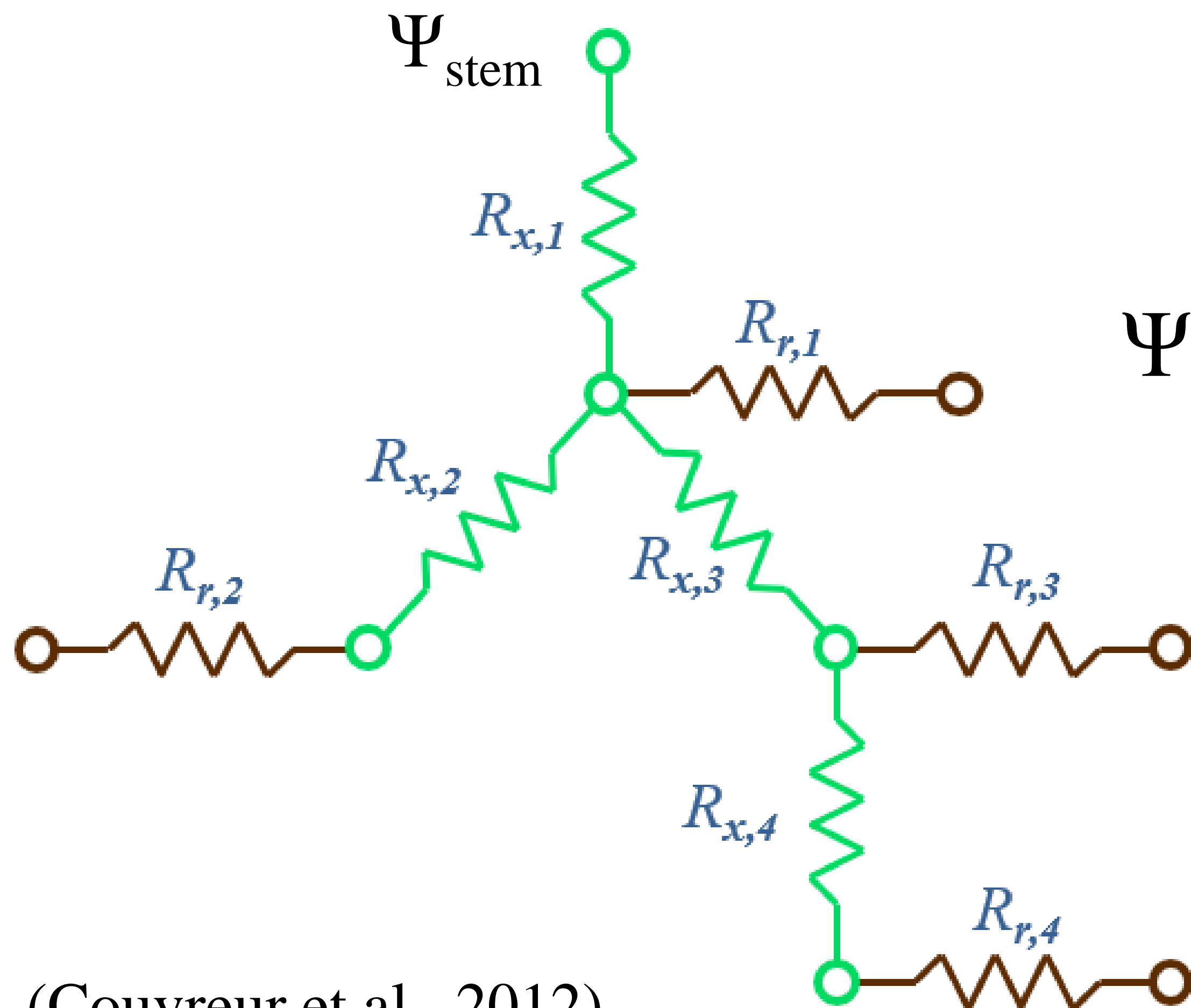


(Couvreur et al., 2021)

- 1) Solve equations of flow without numerical values
- 2) Isolate chunks of equations only containing parameters
- 3) See if an « emergent » macroscopic pattern comes up

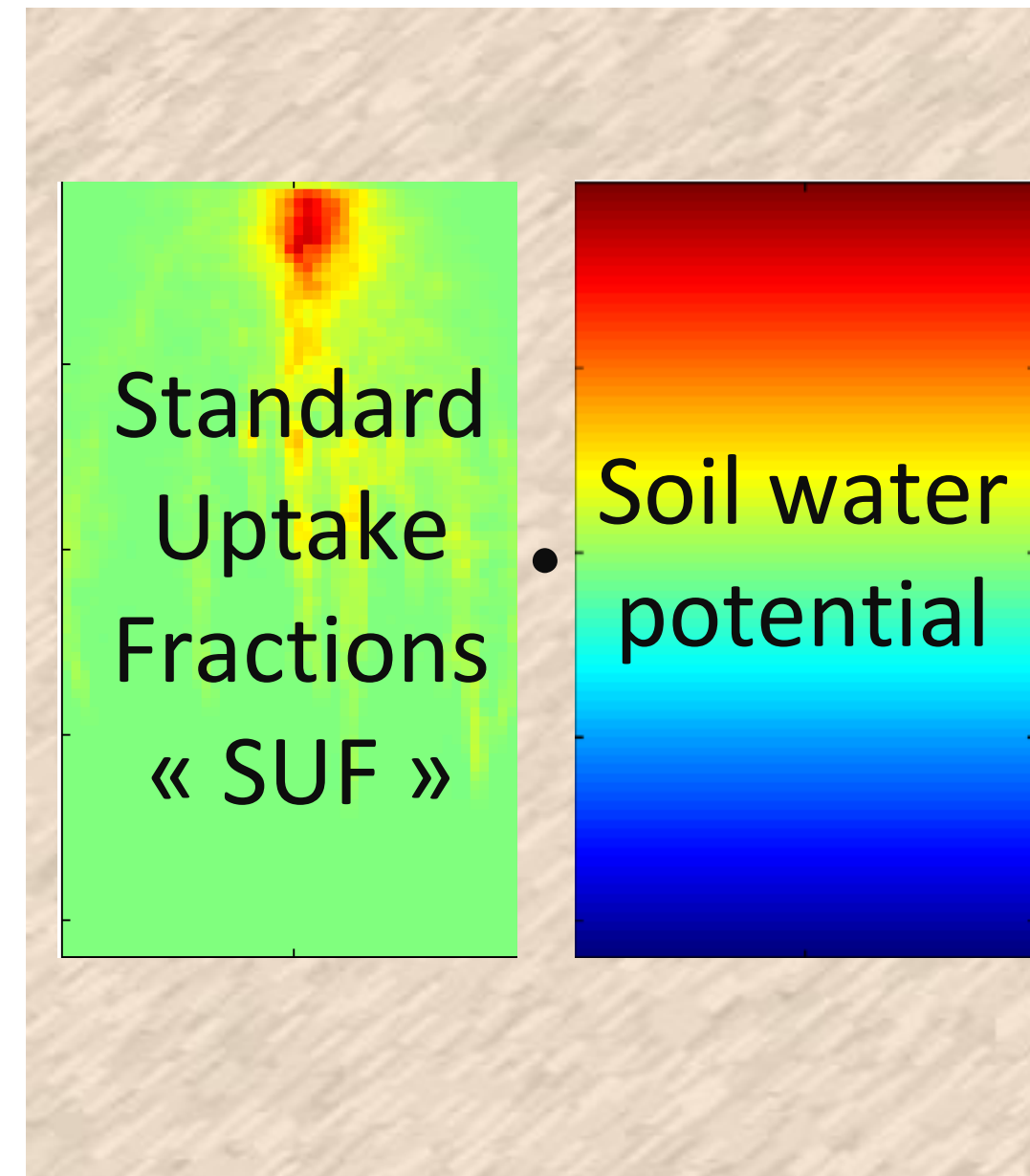
(Couvreur et al., 2012)

A simple and exact upscaled solution of stem water potential



$$\Psi_{\text{stem}} =$$

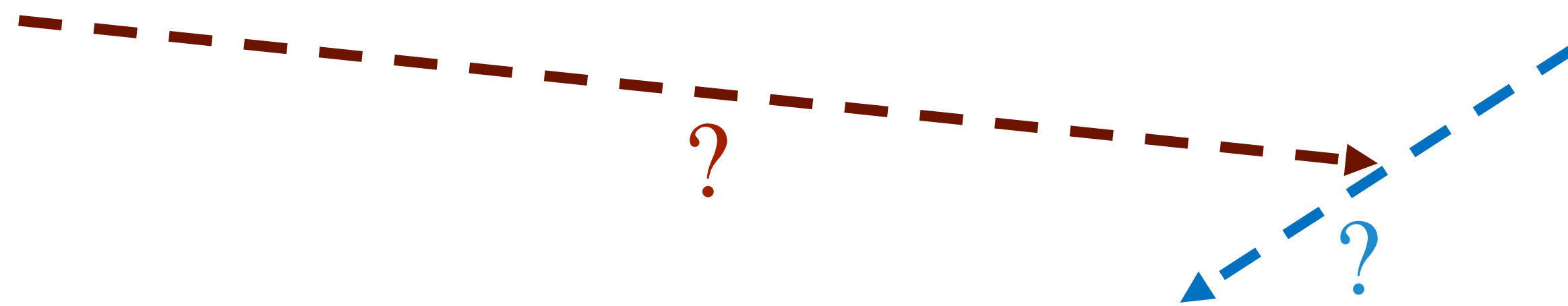
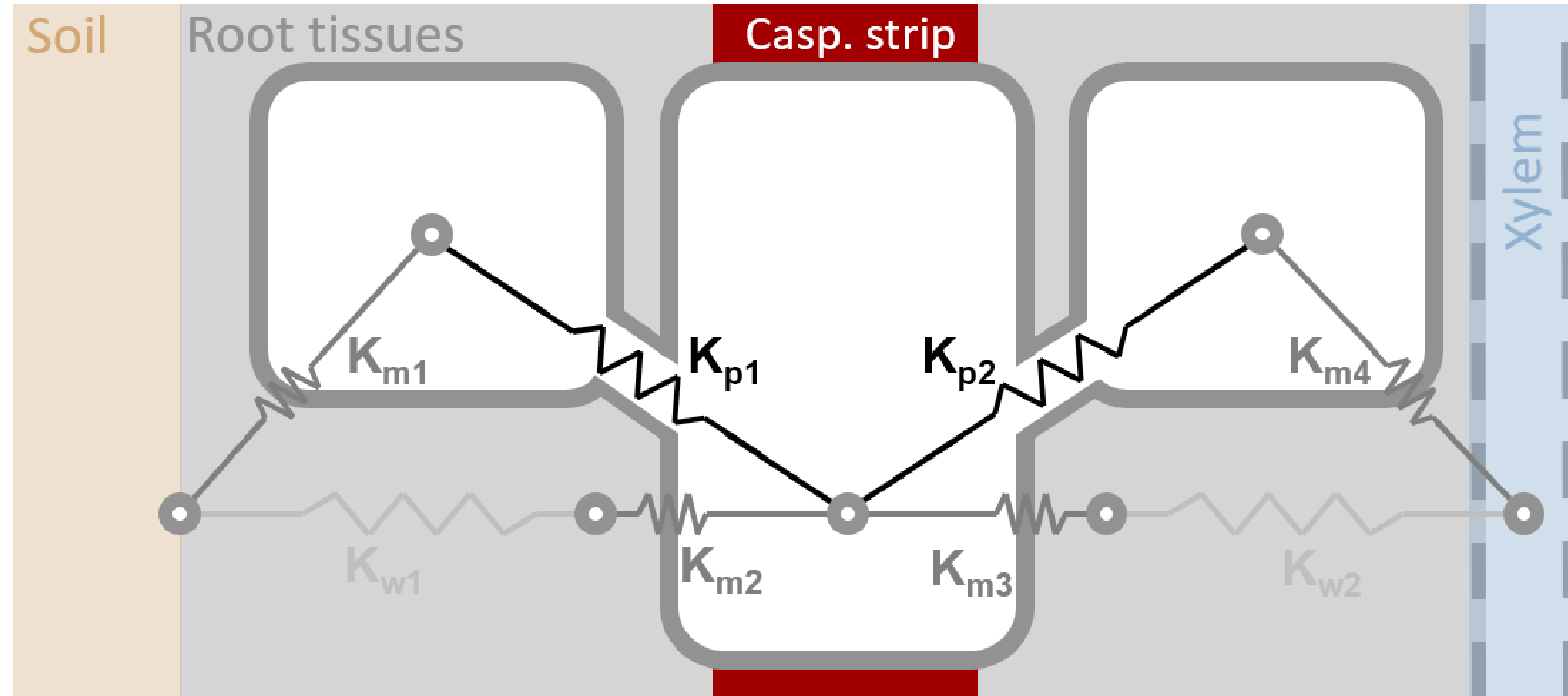
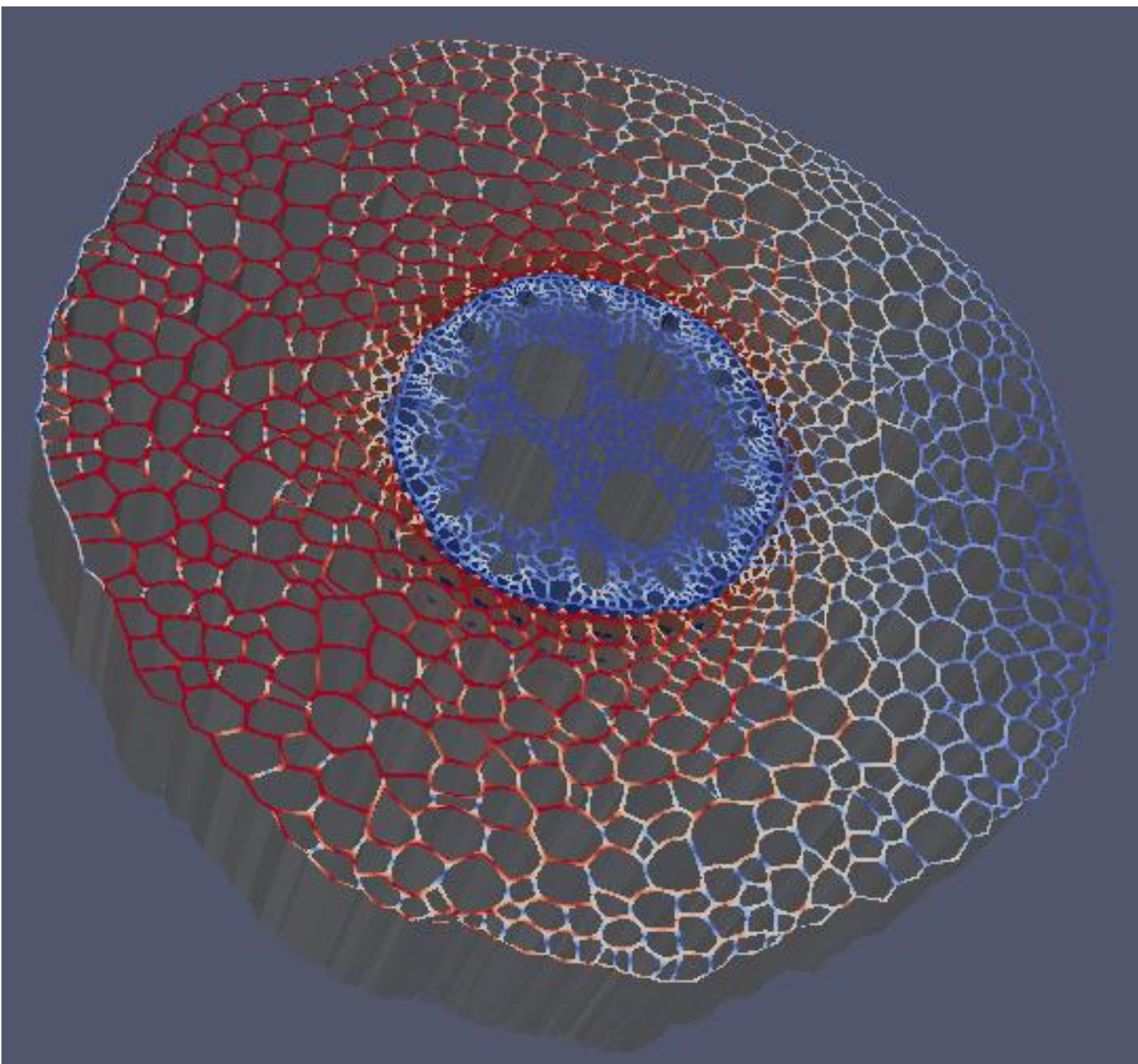
“Plant-sensed” soil
water potential



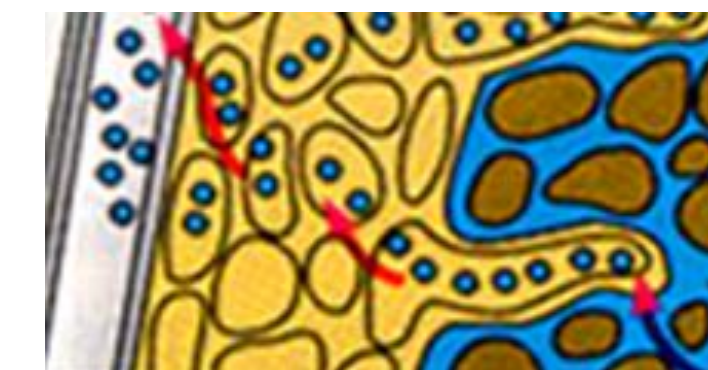
Frictions across
the root system

$$\frac{\text{Transpiration}}{K_{rs}}$$

Identifying emergent behaviours of hydraulic networks



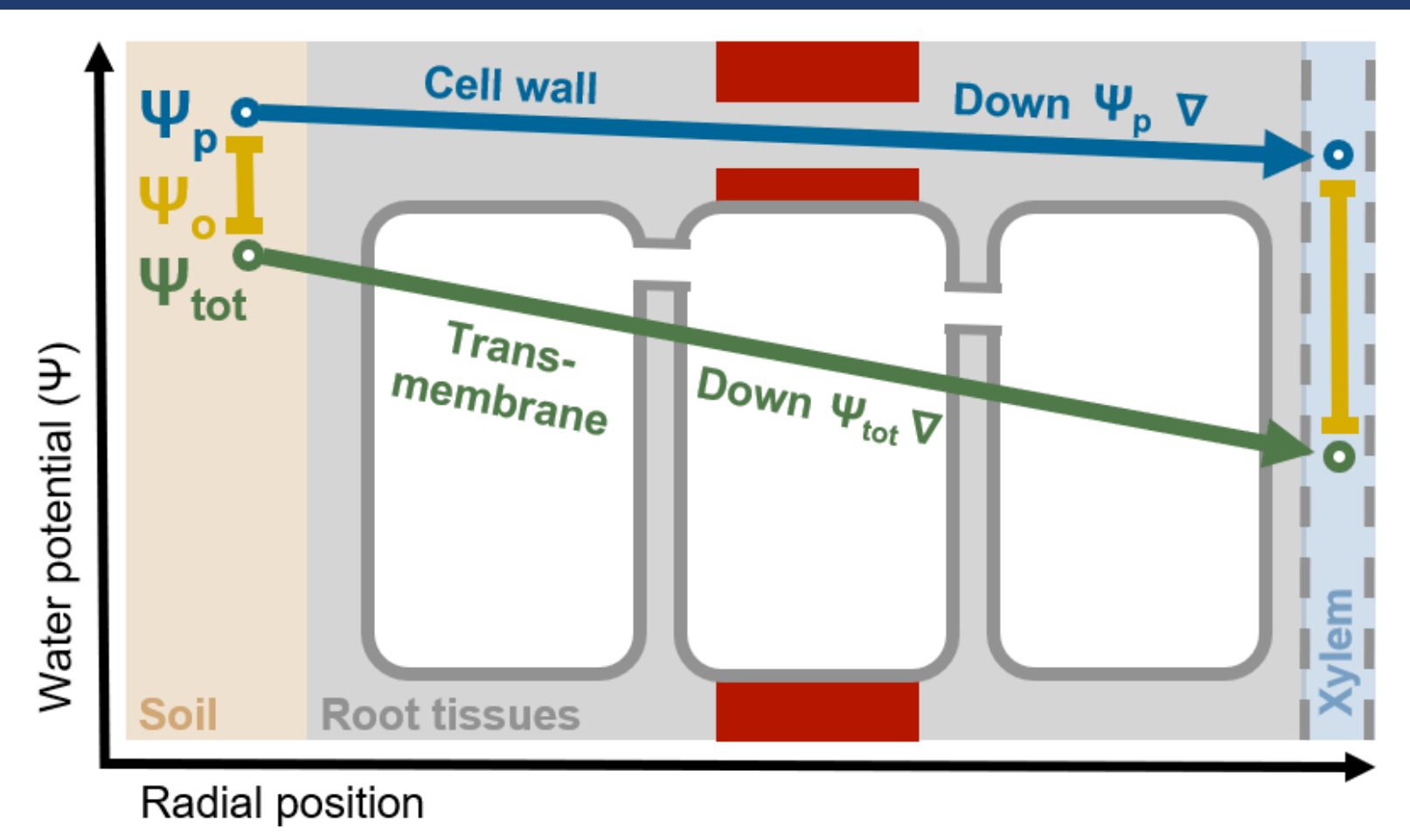
$$F_r = K_r \cdot (\Psi_{\text{soil}} - \Psi_{\text{xylem}})$$



THE PLANT WATER PUMP

Did vascular plants drop thermodynamics classes at school ... ?

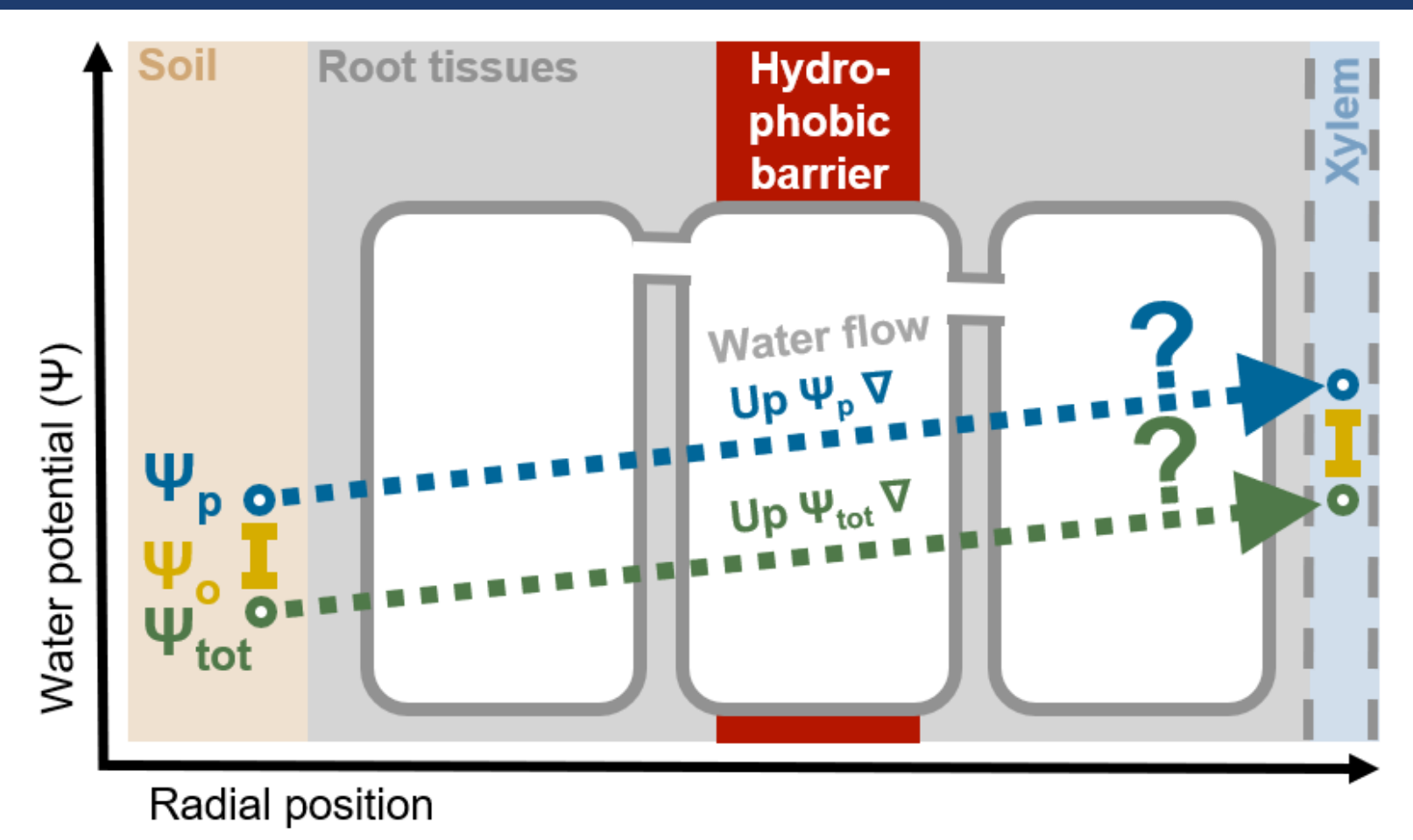
How water flow should be



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

(Kramer and Boyer, 1995)

What scientists observed



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)

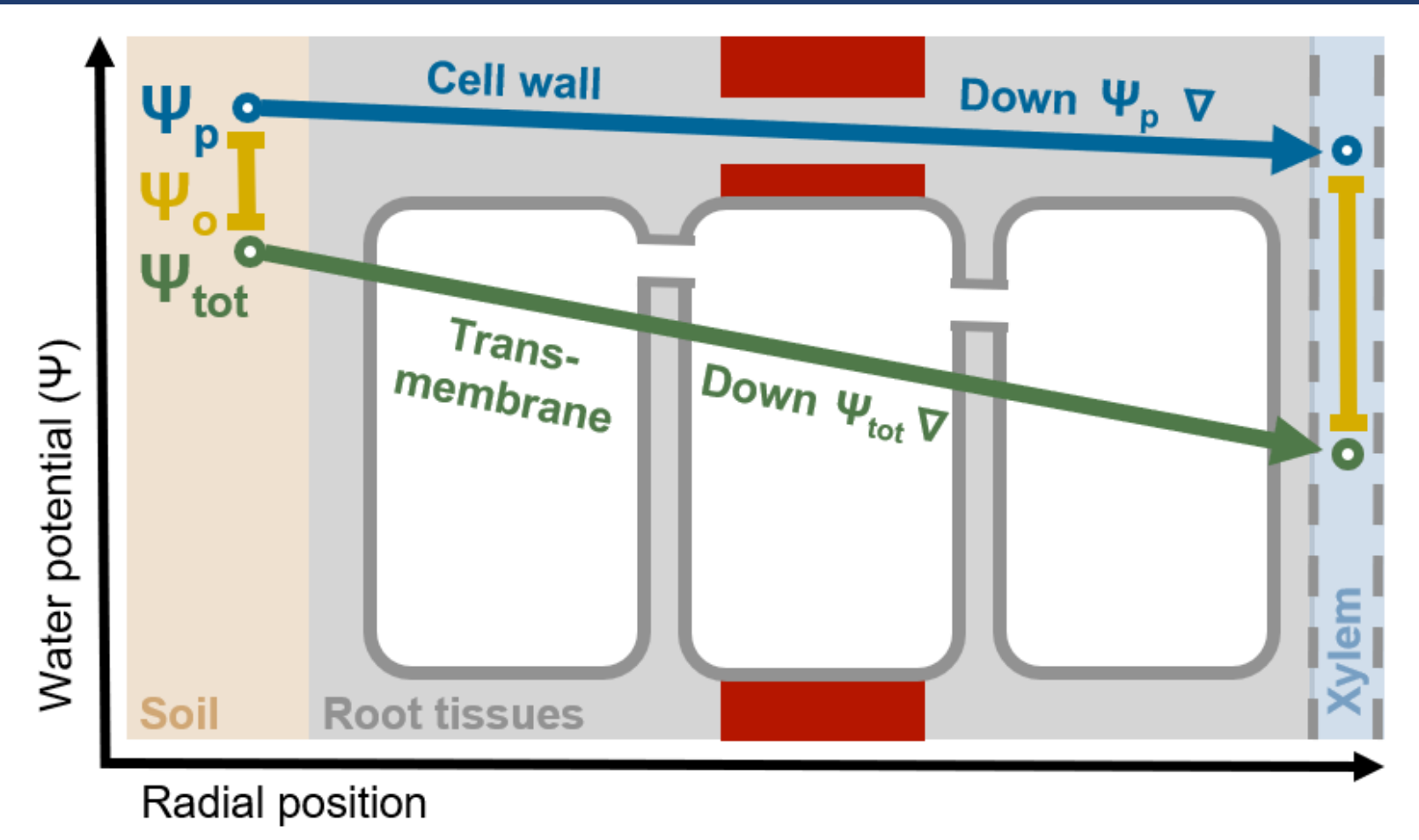
These reports constitute a serious challenge to the widely accepted theories in plant physiology on the mechanisms of how plant roots absorb water under salt stress and how root pressure is generated, because the phenomenon seemingly goes against the second law of thermodynamics

(Bai et al., 2007)

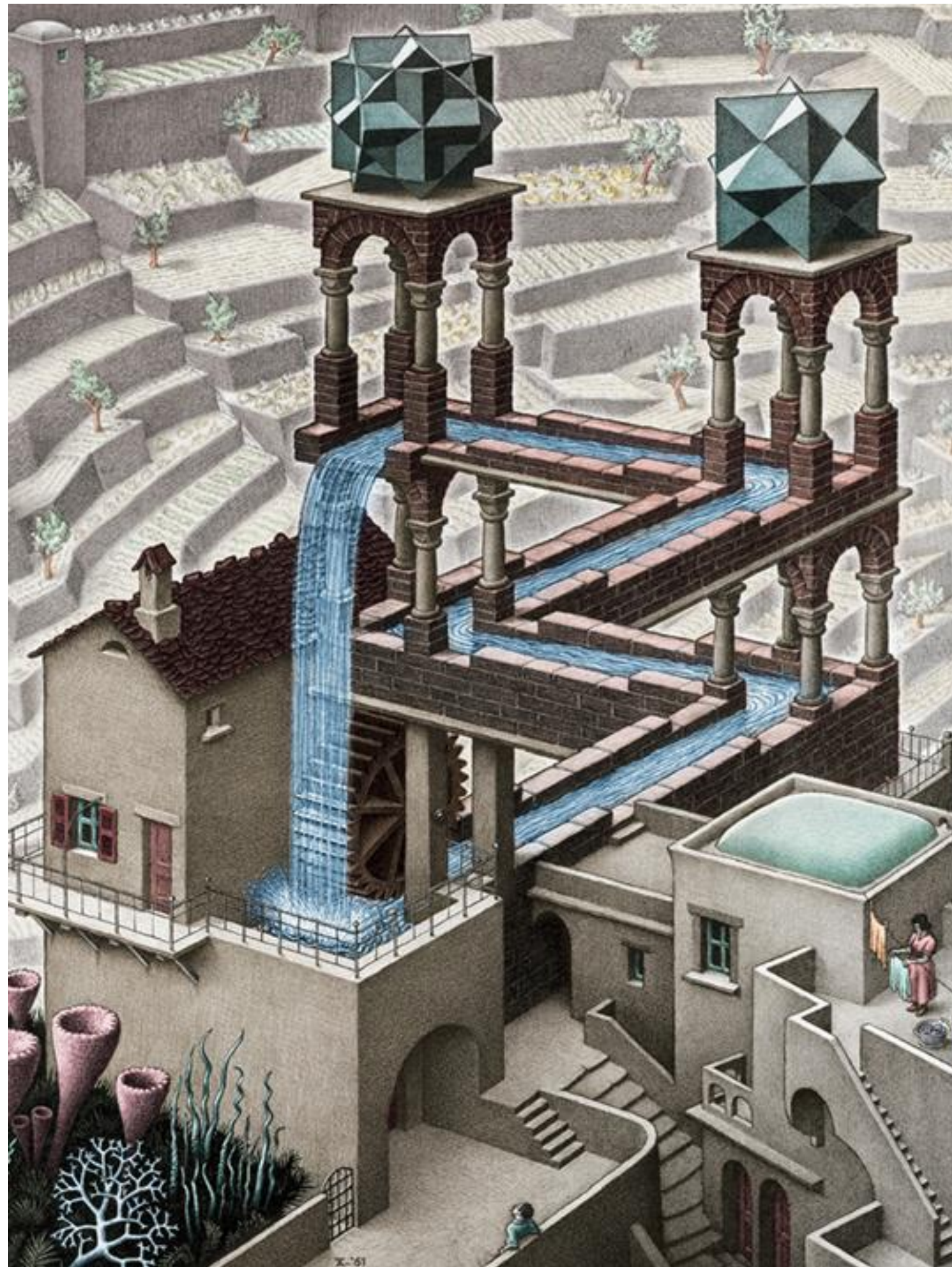
THE PLANT WATER PUMP

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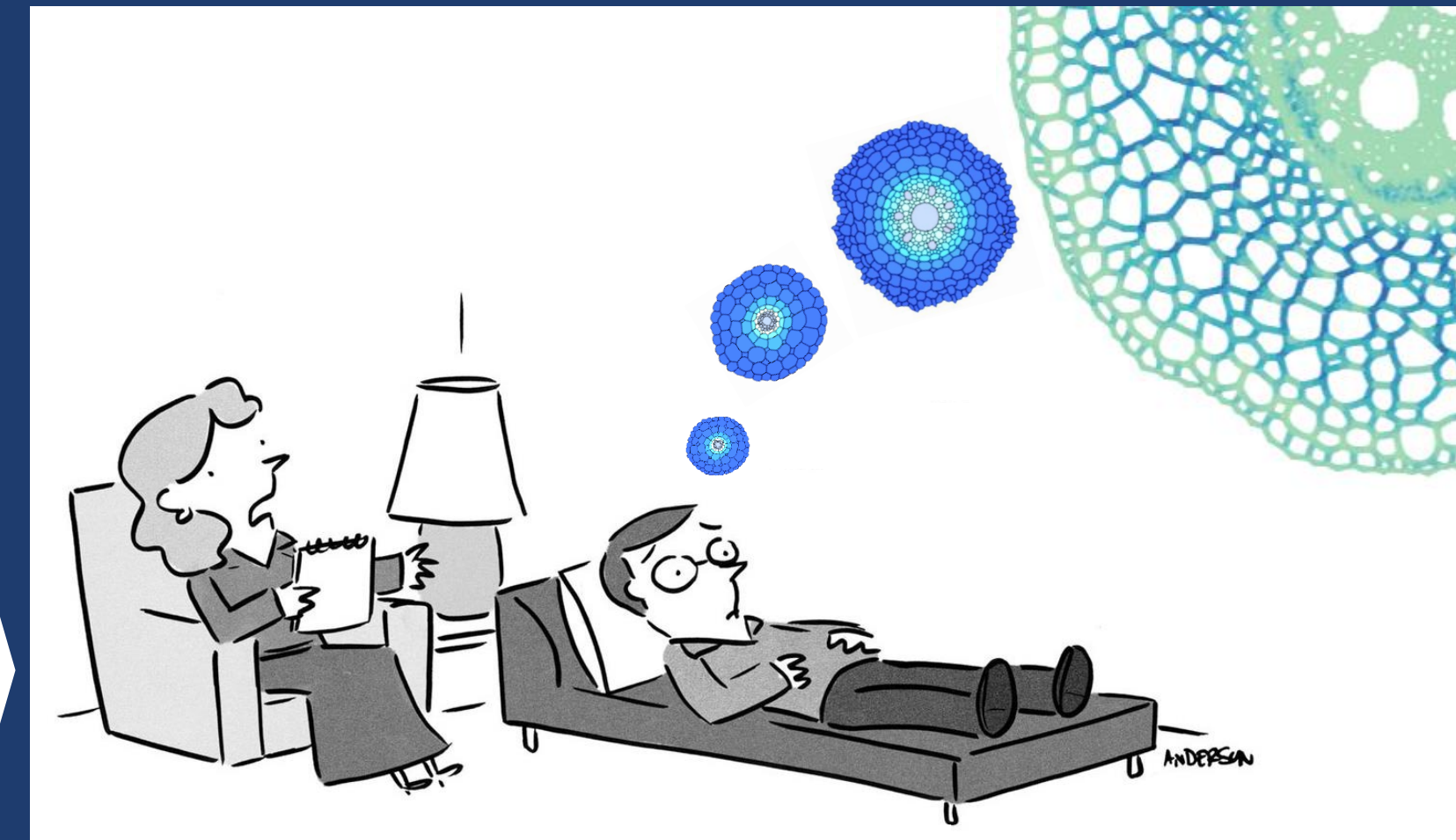
How water flow should be



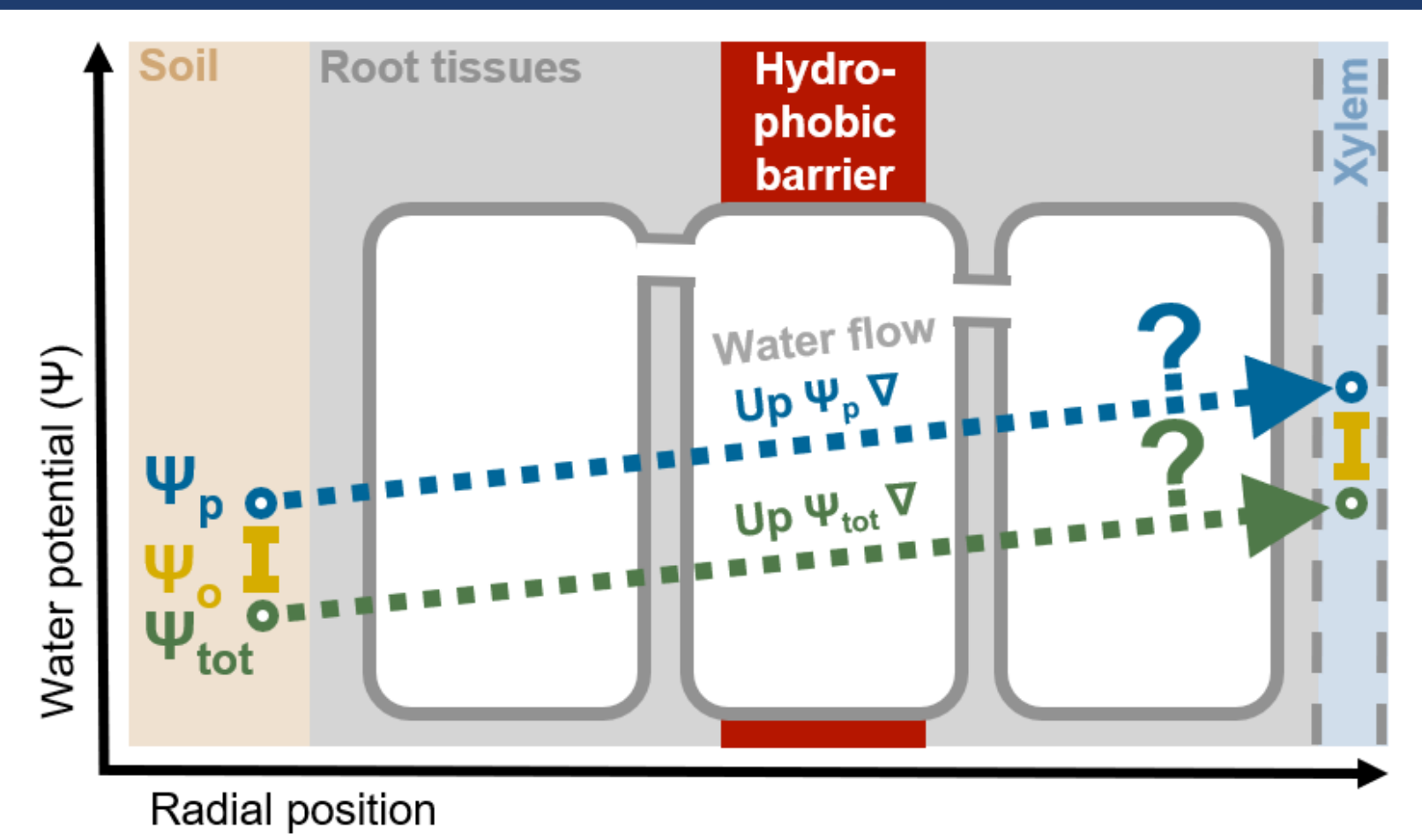
What it looked like



How we have been feeling



What scientists observed



How plants might have tricked us



A map of cell osmotic potential

- Maize plants guttating at night
- Root bathing solution with low Ψ_{tot}
- Cell layers osmotic potential by *Energy Dispersive X-Ray (EDX) microanalysis*

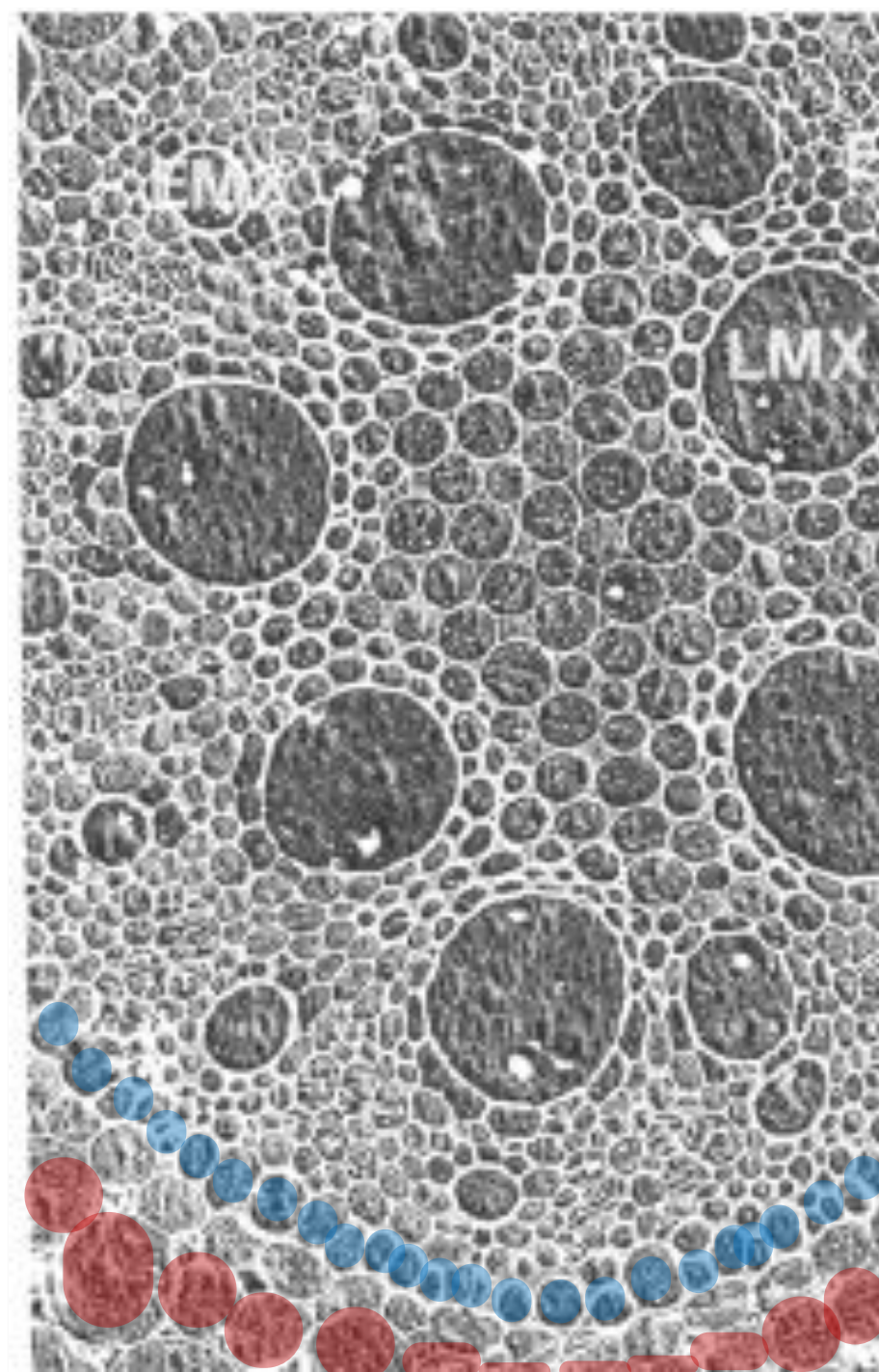


Table 5. Effect on water potentials of xylem sap and of cell vacuoles of adding 50 mM KNO_3 to the nutrient solution for 5 days (experiment 5)^a

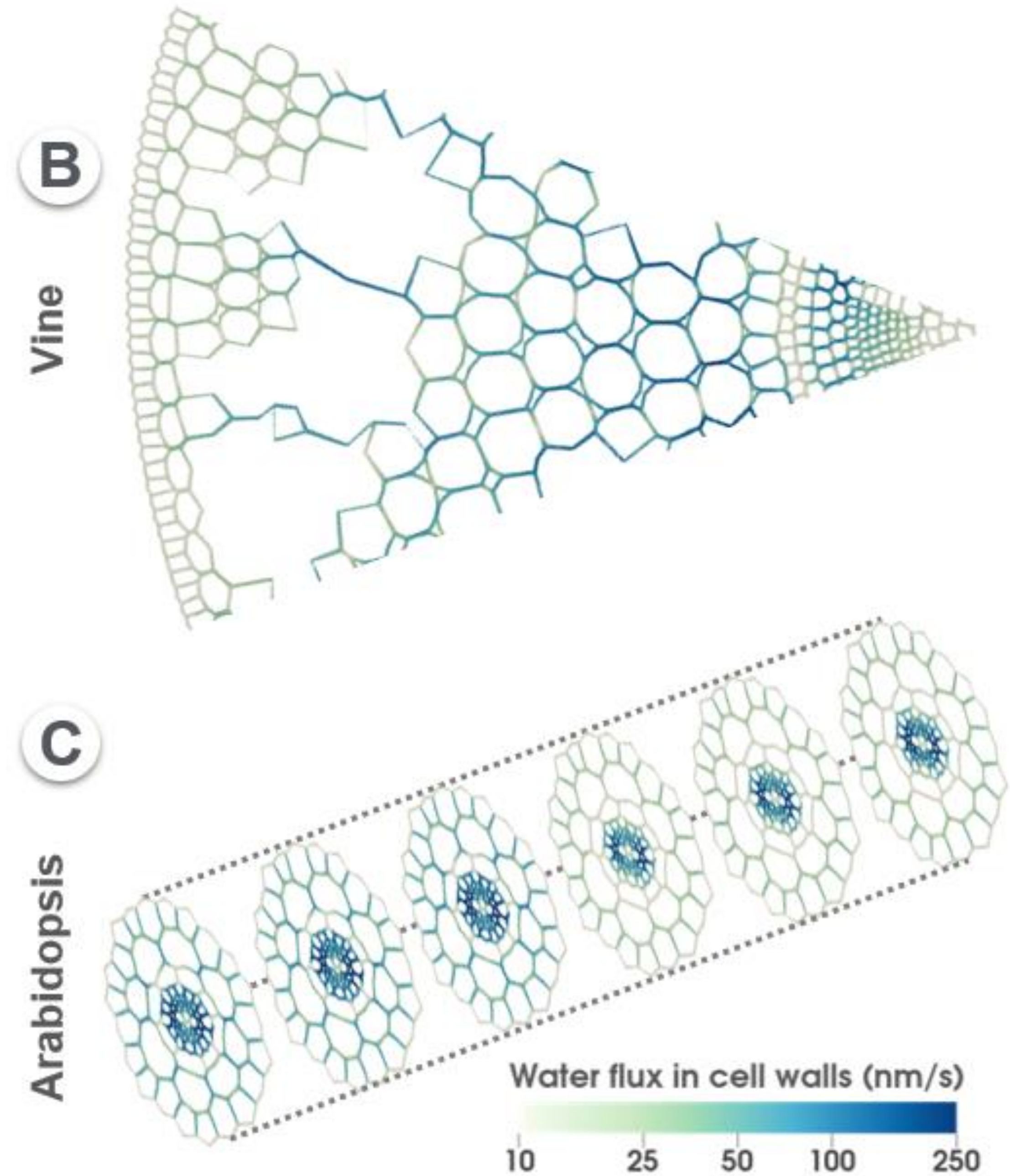
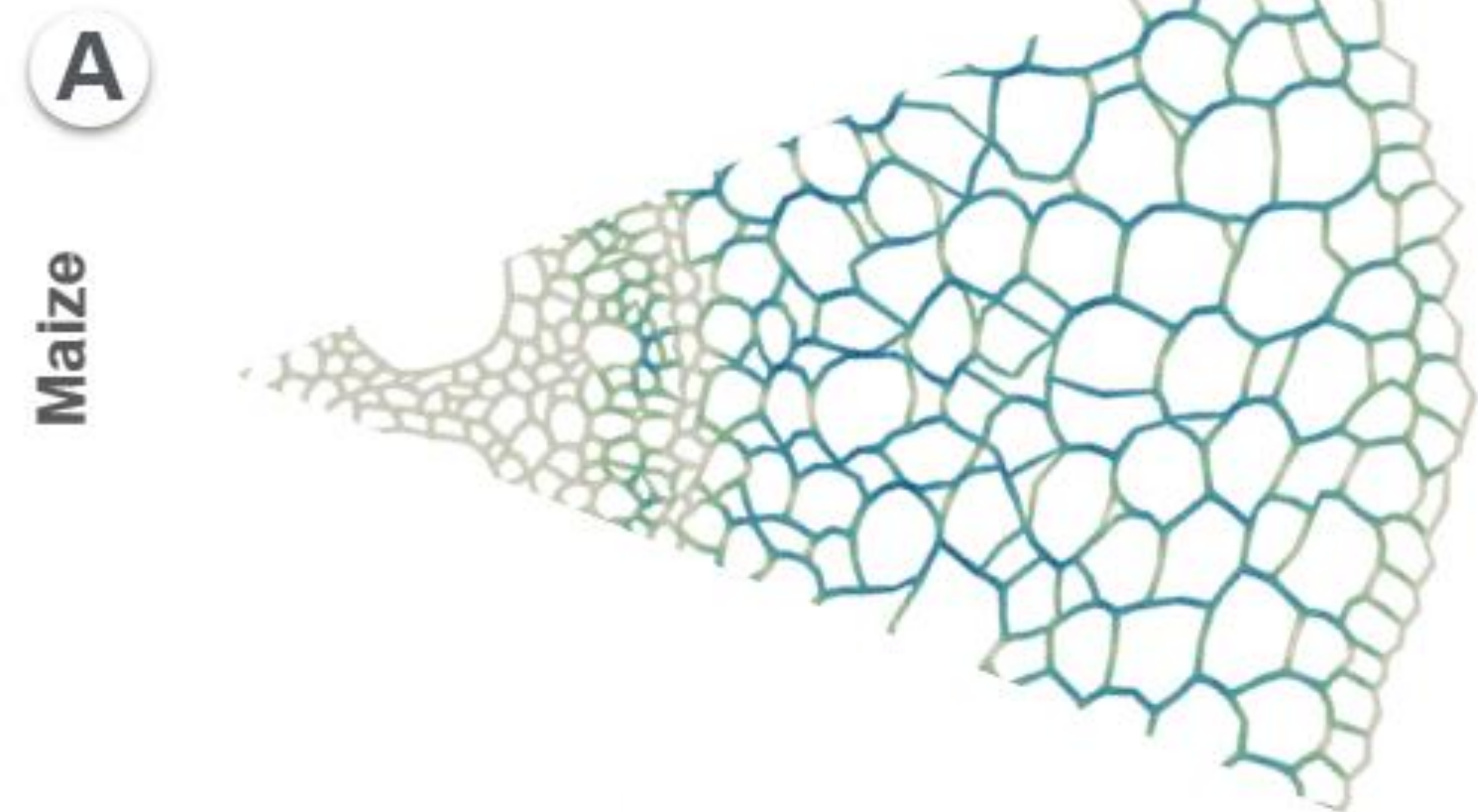
Treatment	Ψ_x (MPa)		Ψ_v (MPa)			
	LMX	EMX	XP	Pe	En	C
Control	-0.15	-0.15	-0.74	-0.50	-0.62	-0.80
KNO_3	-0.23	-0.21	-1.21	-0.92	-1.05	-1.26
$\Delta\Psi^b$	0.08	0.06	0.47	0.42	0.43	0.46

(Enns et al., 2000)

The quest for a water pump

Explicit root hydraulic network

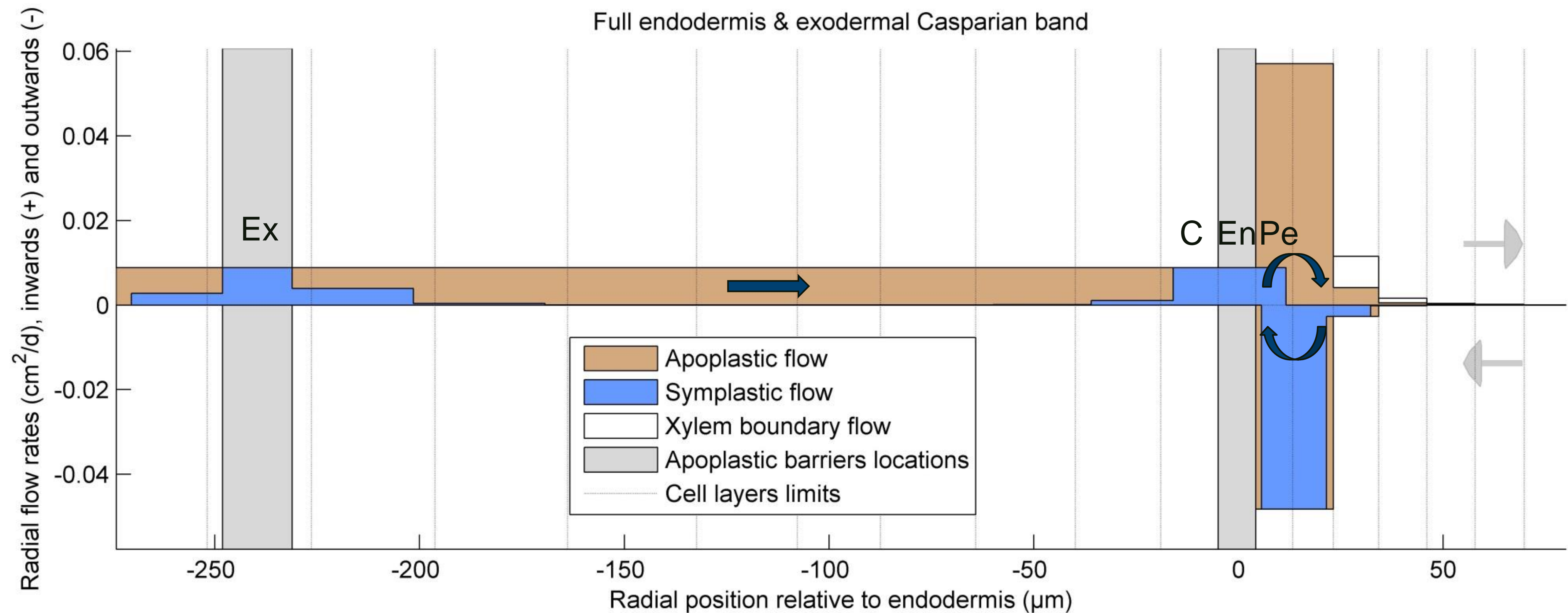
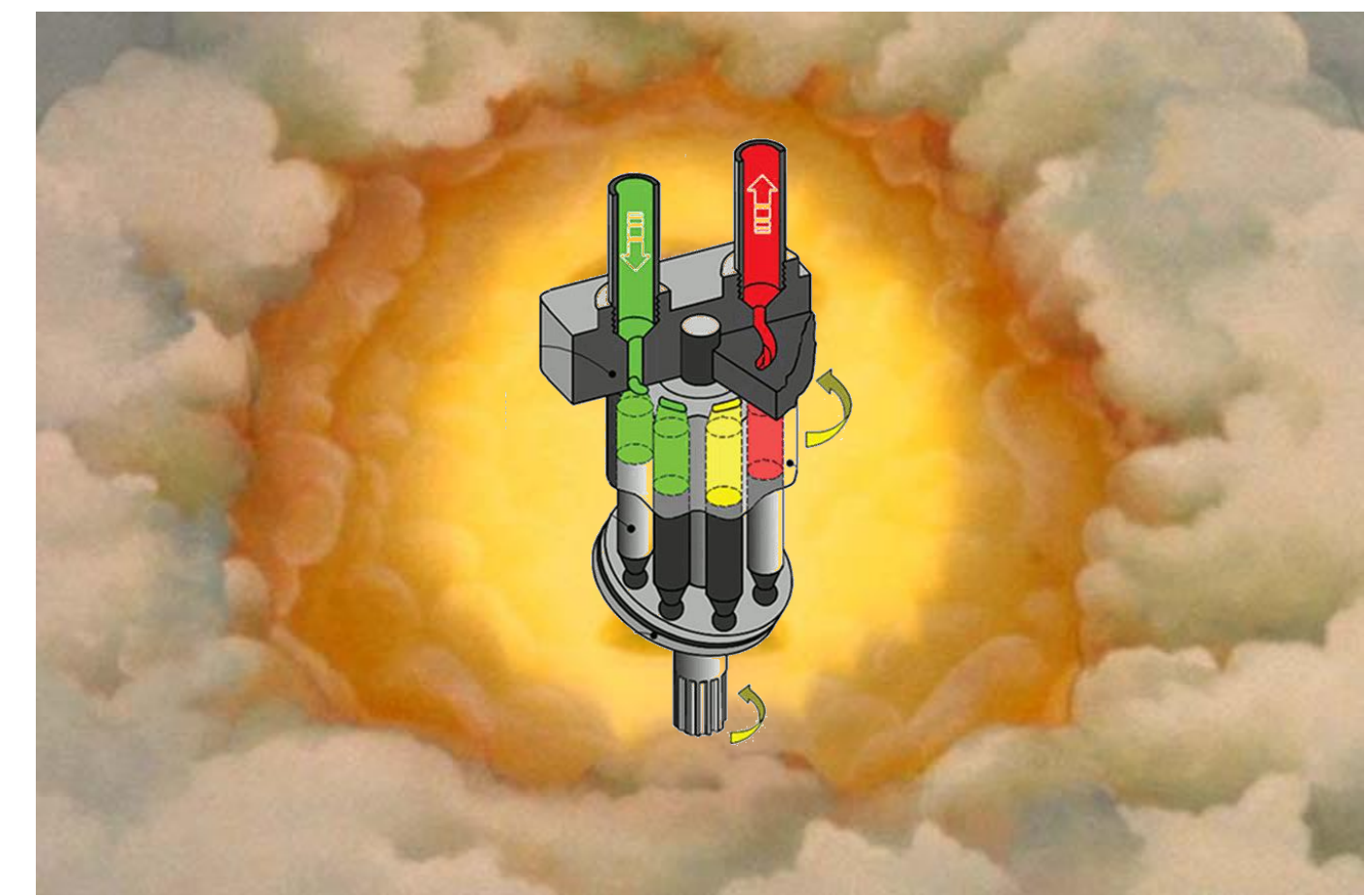
B.C.	root surface	xylem
Ψ_p	-0,01 MPa ←	+0.01 MPa
Ψ_{tot}	-0,31 MPa ←	- 0.14 MPa



The quest for a water pump

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

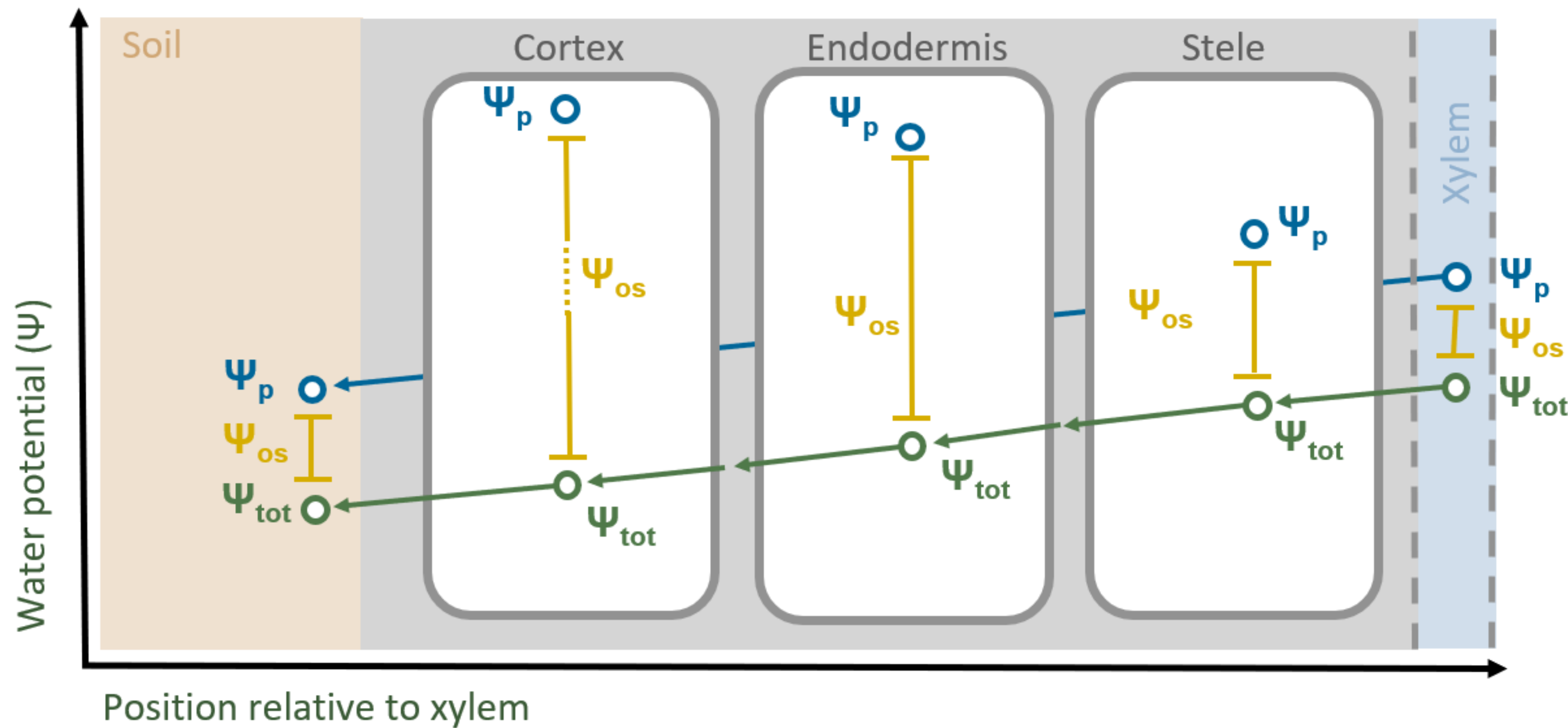


Flow against $\Delta\Psi_{tot}$ happens in both the explicit model & experiments !

Understanding the water pump

Building a water pump from scratch:

- 3 cells
- A cellular Ψ_{os} gradient

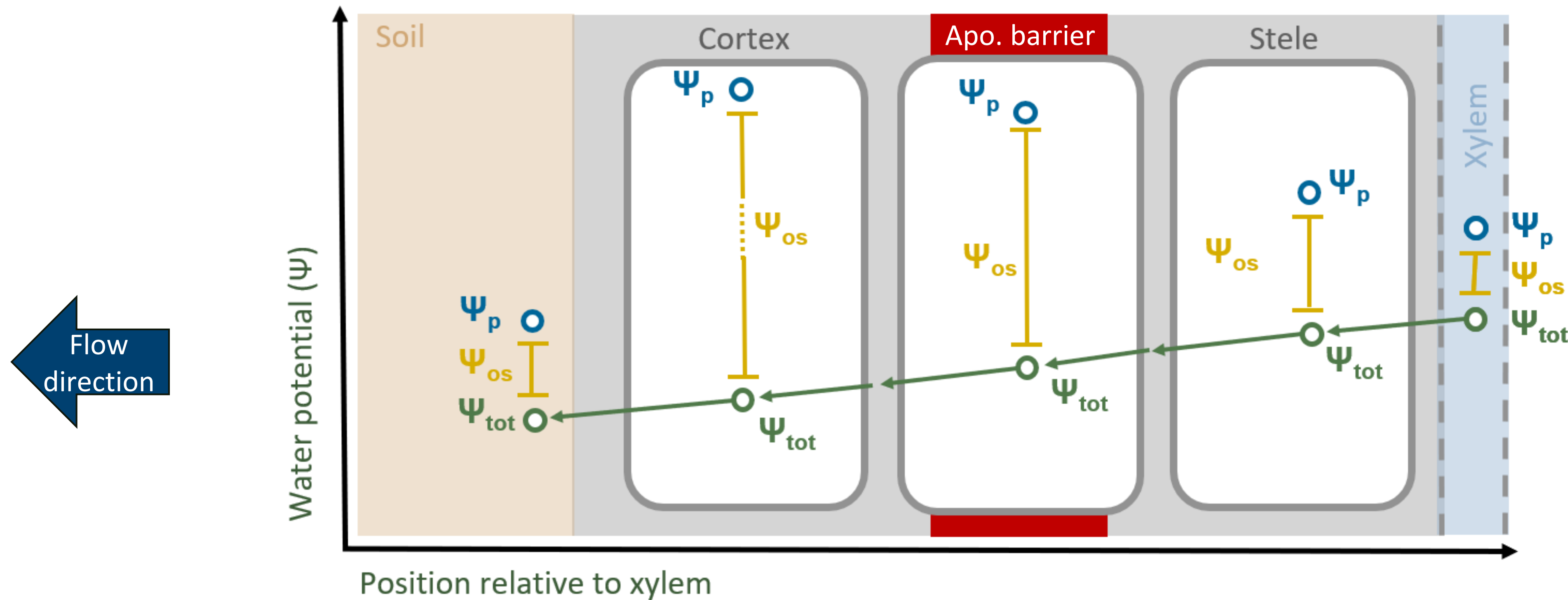


Cell Ψ_p decreases to the right but cell Ψ_{tot} increases to the right

Understanding the water pump

Building a water pump from scratch:

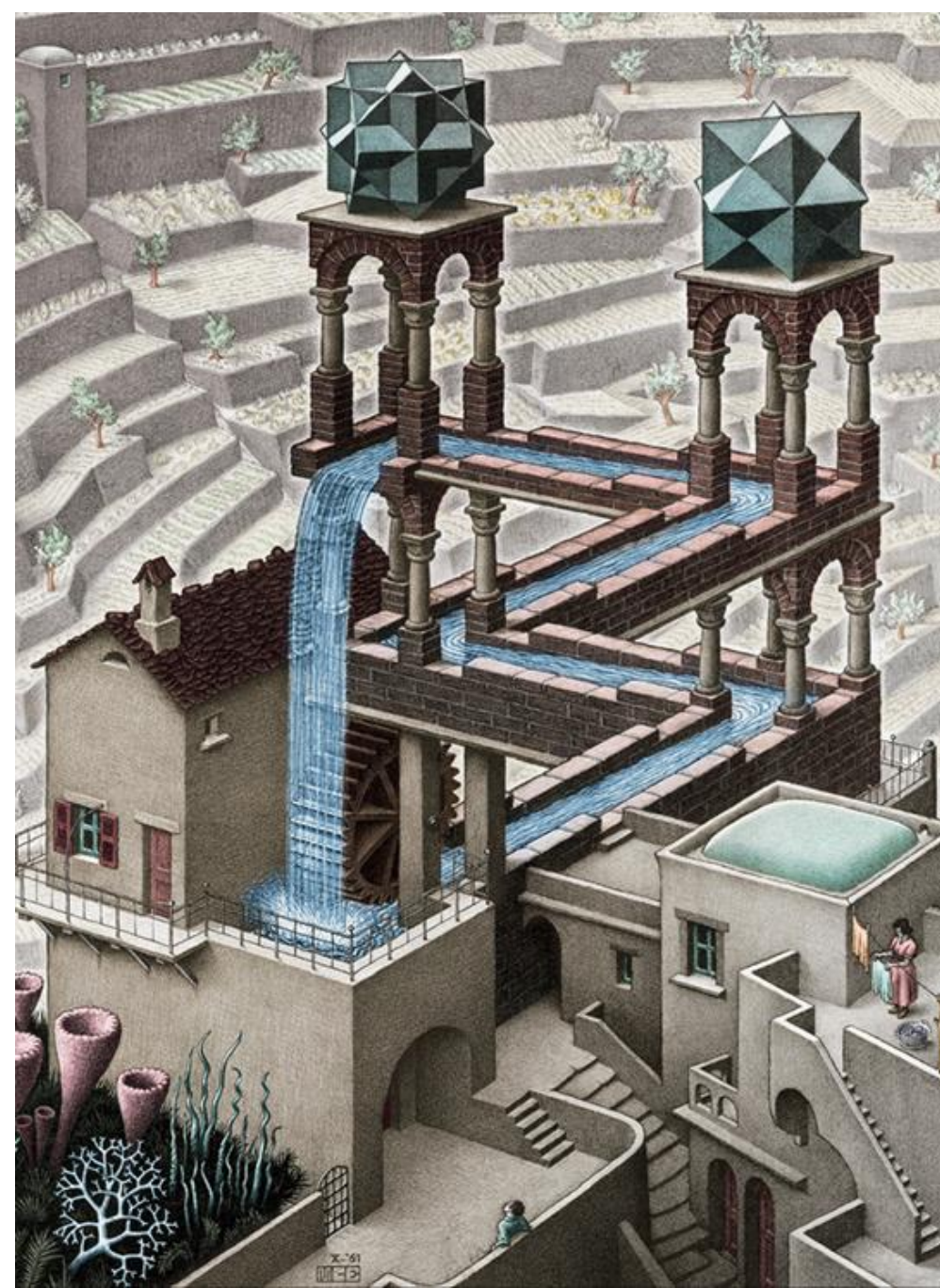
- 3 cells
- A cellular Ψ_{os} gradient
- An apoplastic barrier



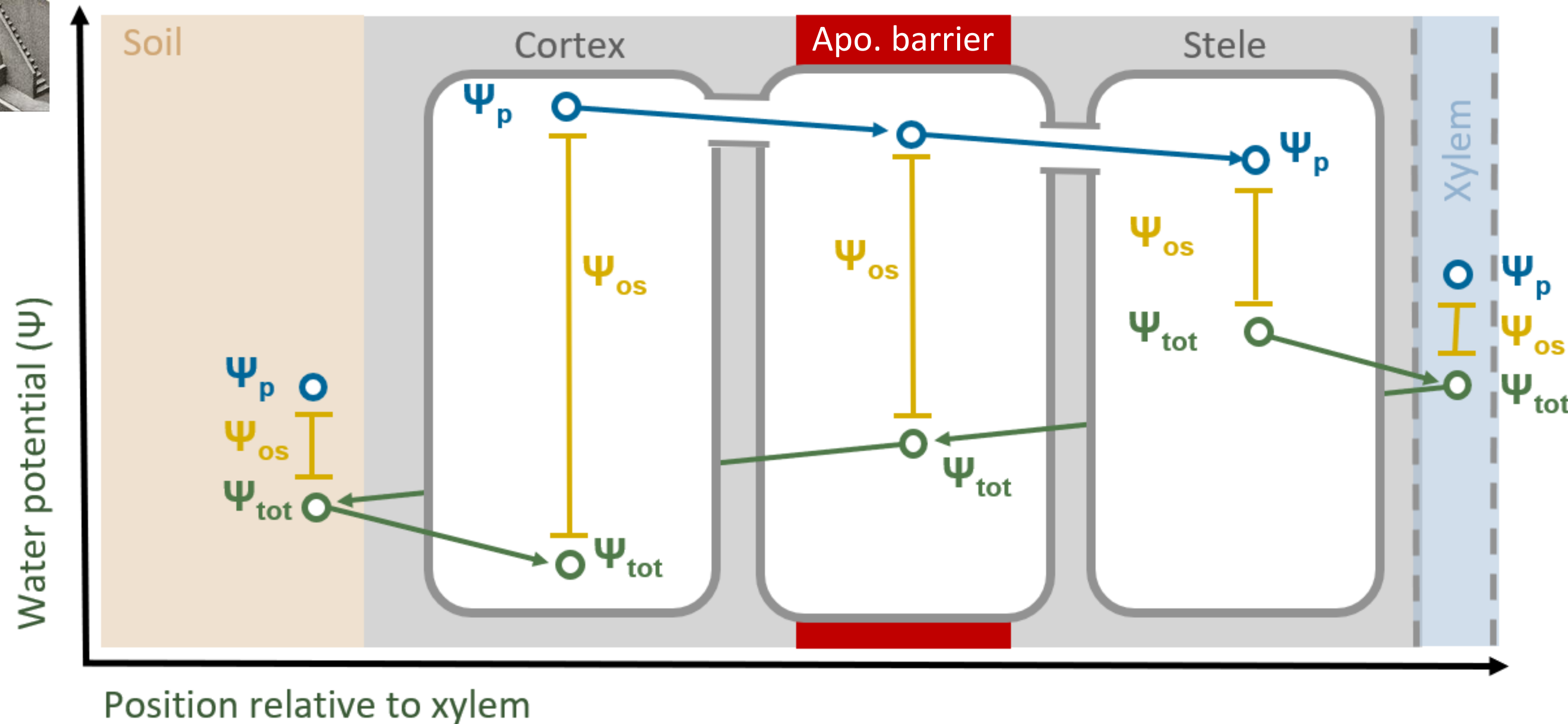
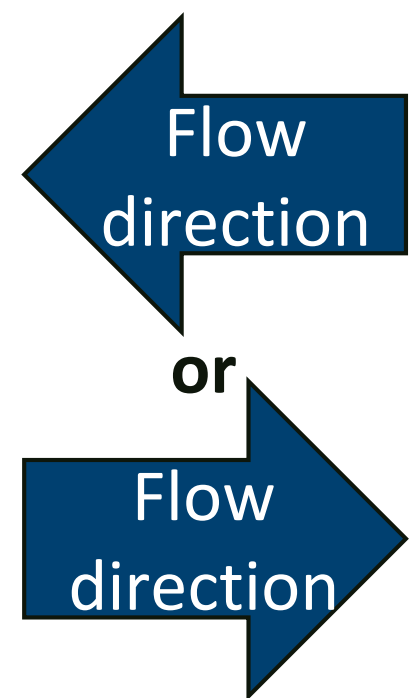
Understanding the water pump

Building a water pump from scratch:

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



Credits: M.C. Escher



Water flow is pressure-driven in plasmodesmata

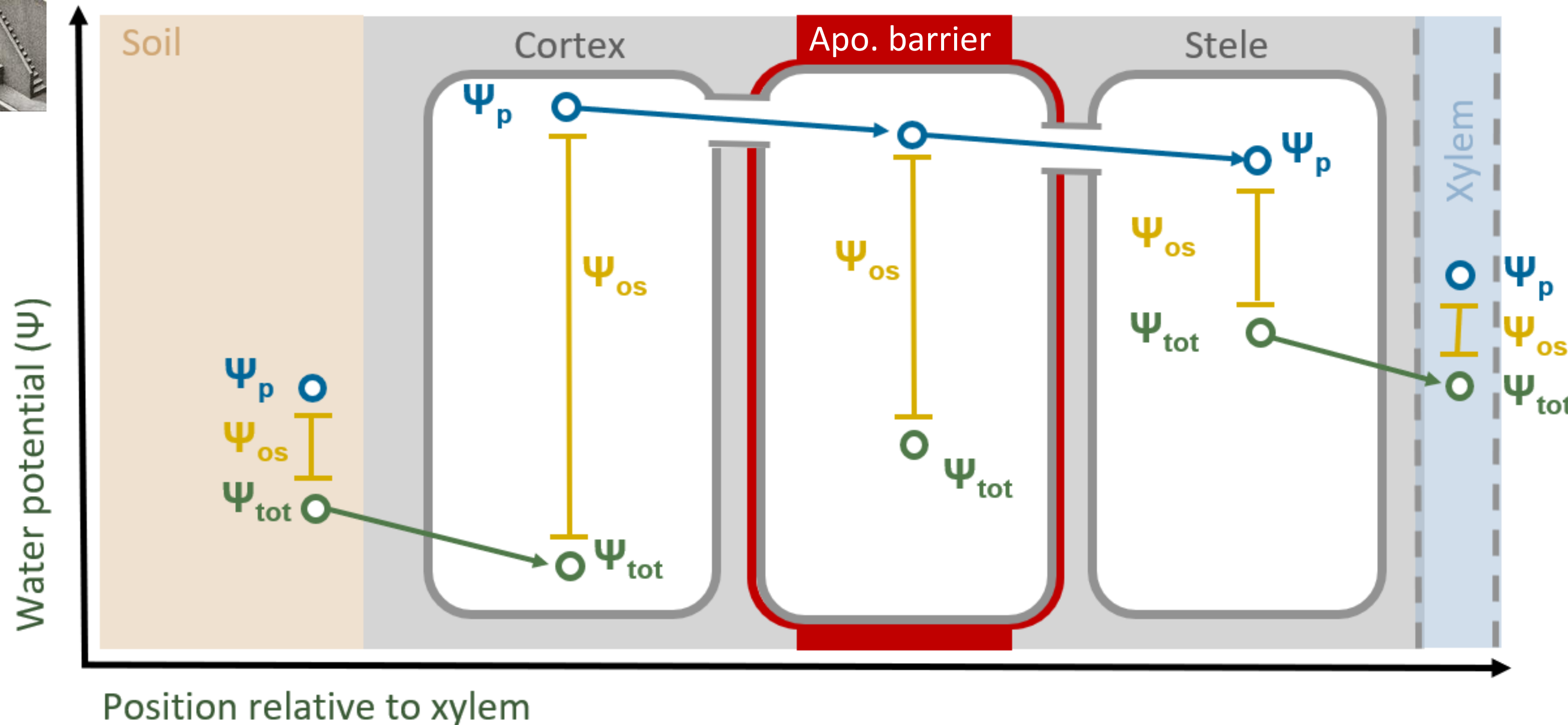
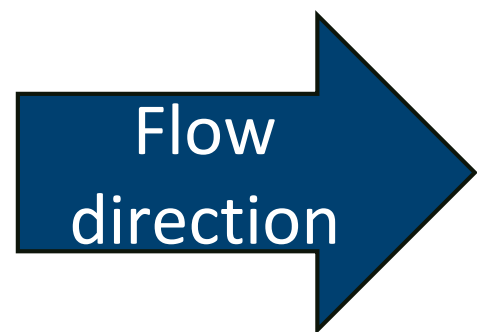
Understanding the water pump

Building a water pump from scratch:

- 3 cells
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- An apoplastic barrier
- Plasmodesmatal connections



Credits: M.C. Escher

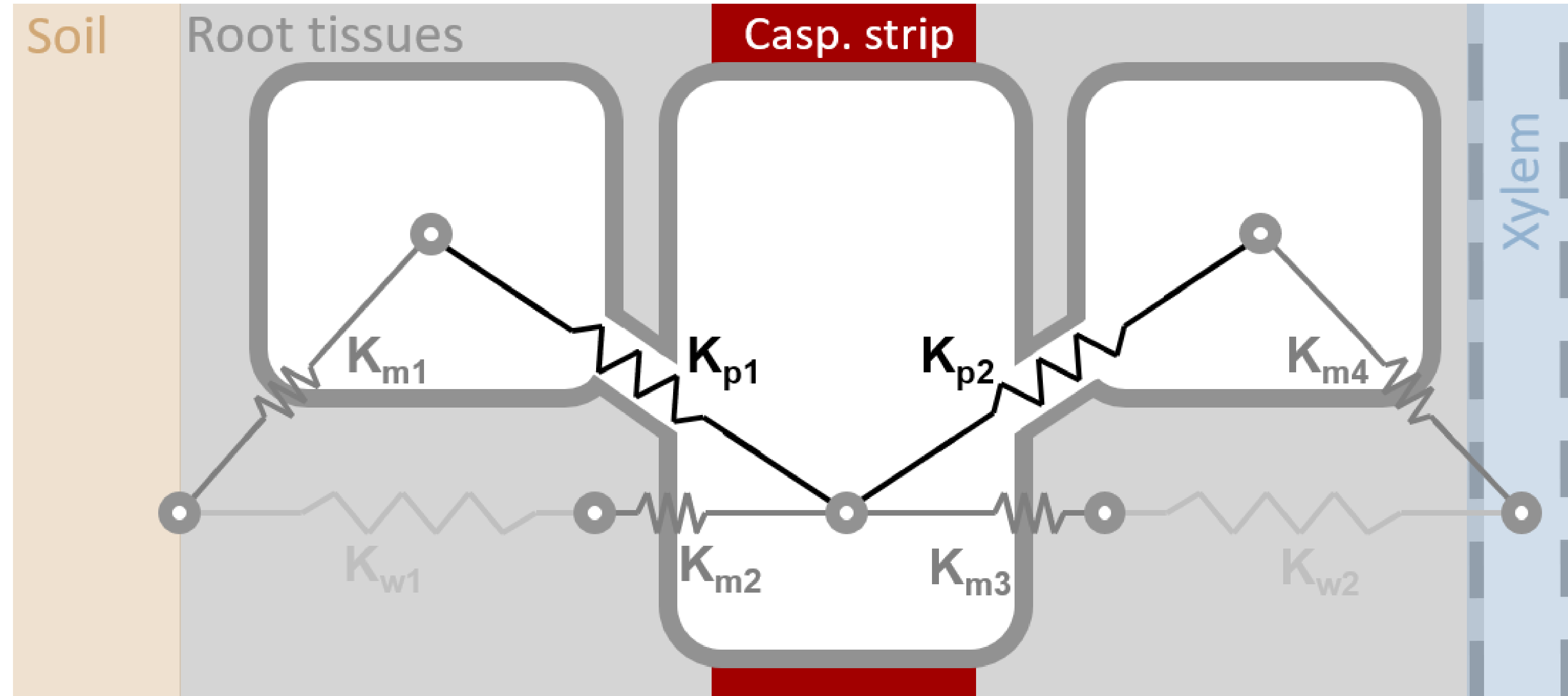
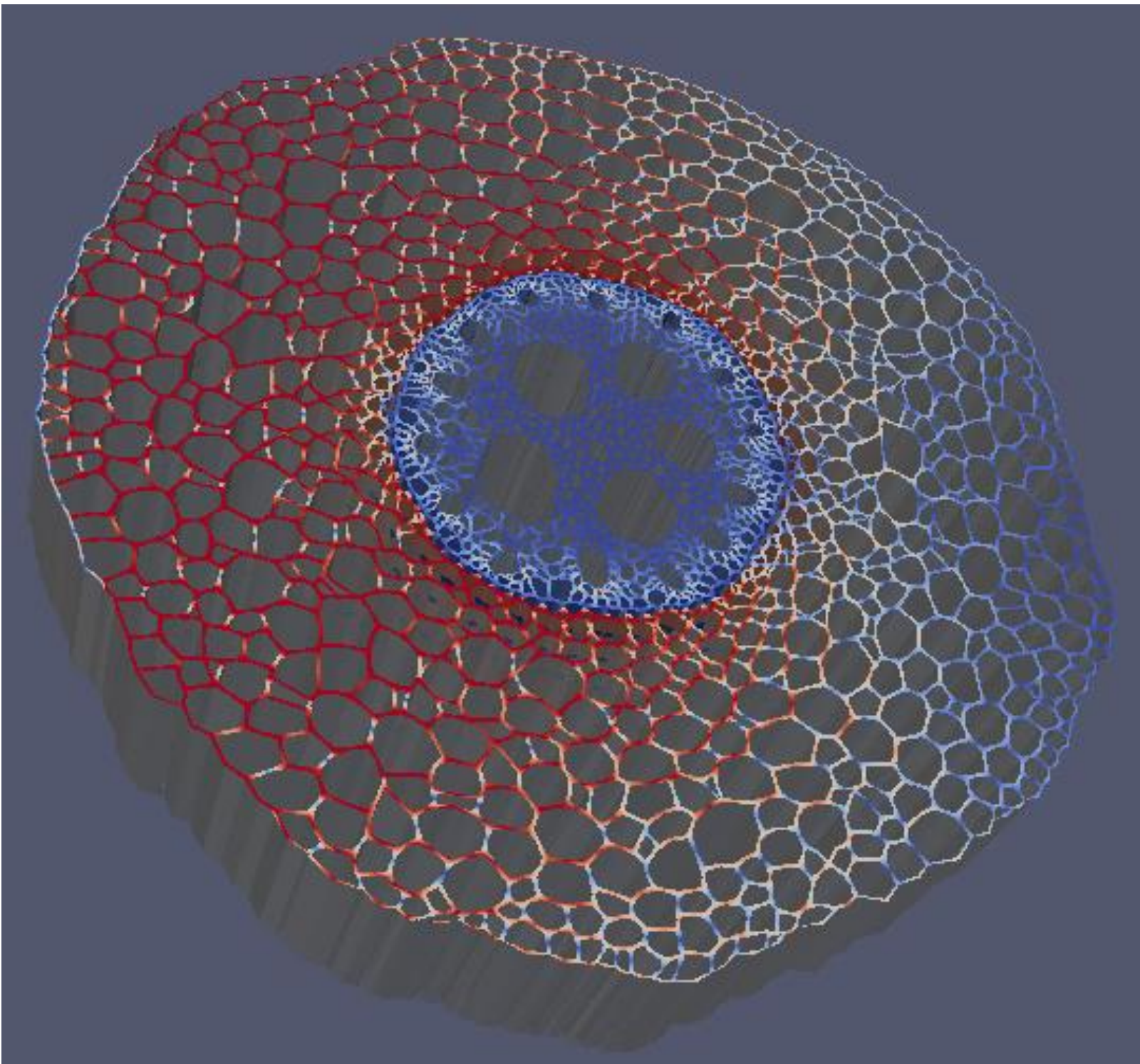


Pump “upgrade”
with suberin
lamellae

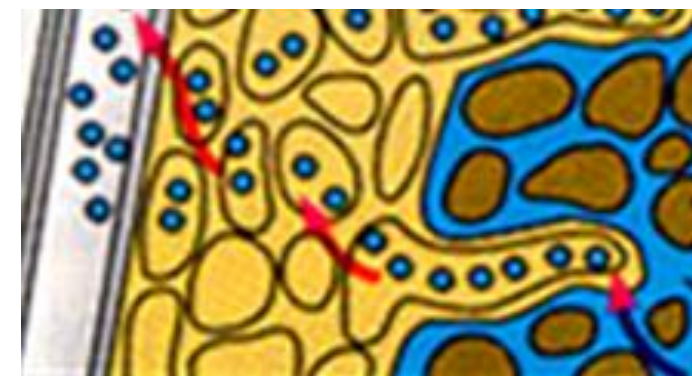
No need to load
solute in the
xylem

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

Identifying emergent behaviours of hydraulic networks



$$F_r = K_r \cdot (\Psi_{p,soil} - \Psi_{p,xylem} + [\overline{\Psi_{o,soil}} - \overline{\Psi_{o,xylem}}] - [\overline{\Psi_{o,cortex}} - \overline{\Psi_{o,stele}}])$$



Take home messages → Station 2 : emergent properties

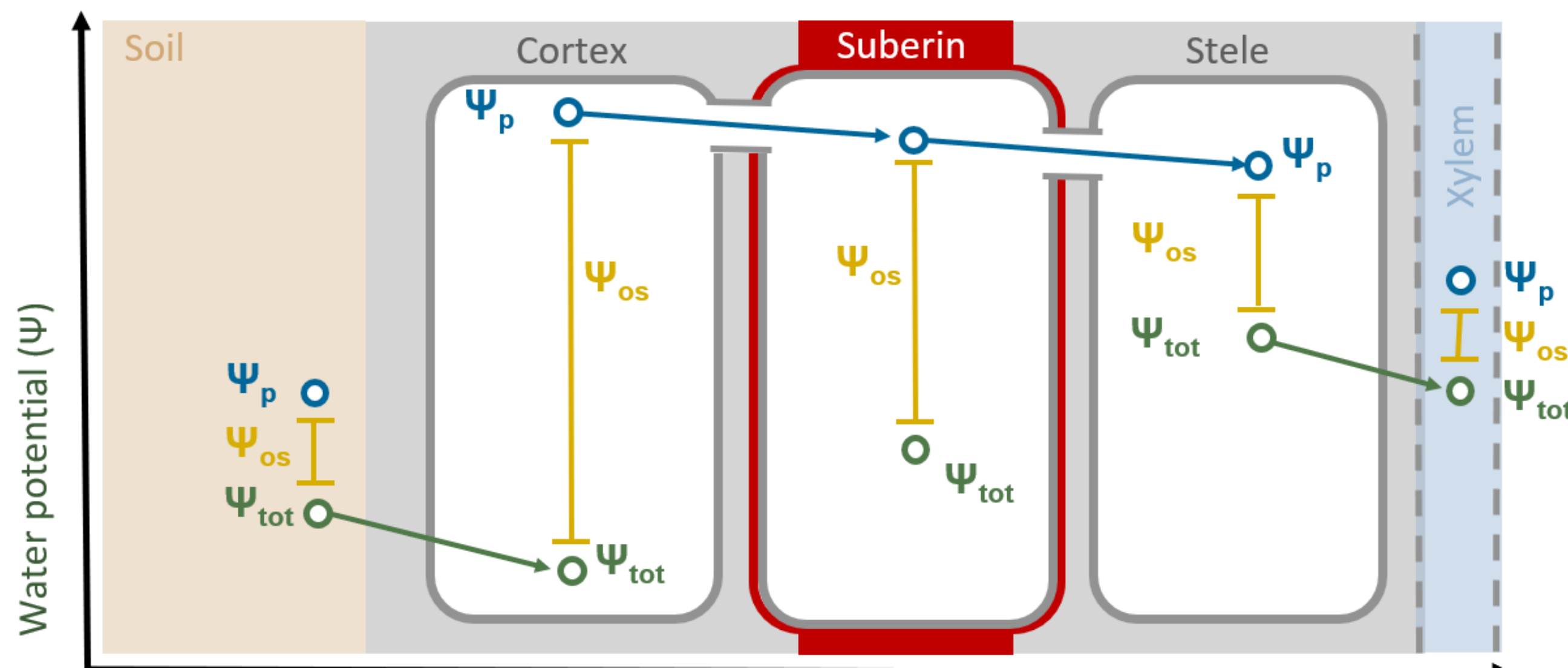
Simple upscaled solutions of water flow emerge in complex hydraulic networks !

$$F_r = K_r \cdot (\Psi_{p,soil} - \Psi_{p,xylem} + [\Psi_{o,soil} - \Psi_{o,xylem}] - [\Psi_{o,cortex} - \Psi_{o,stele}])$$

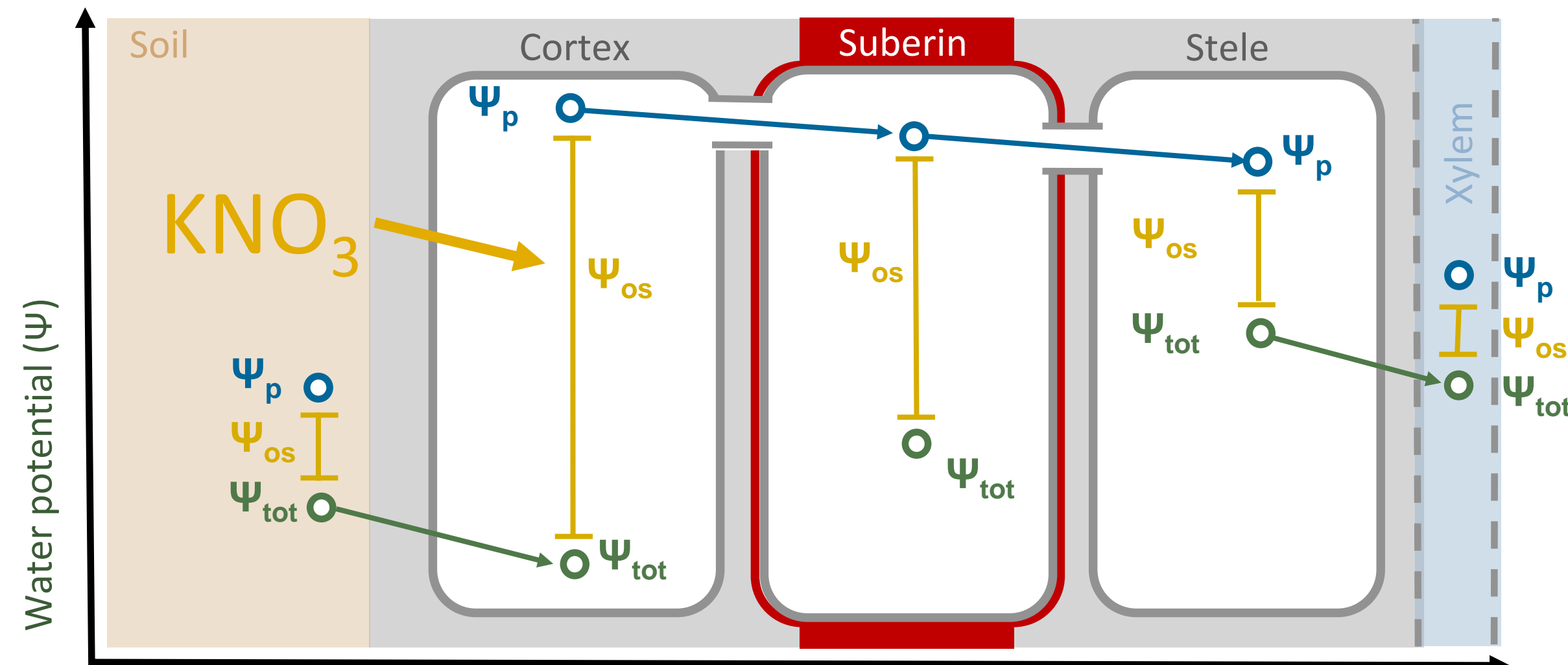
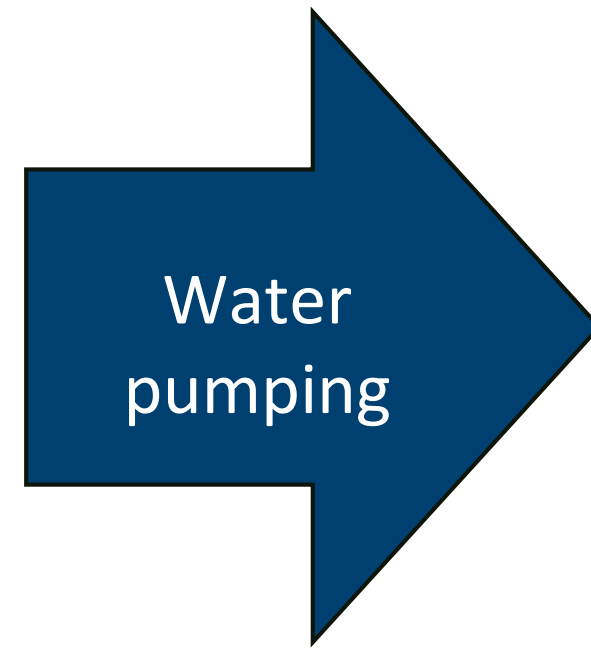
Solute mobility in hydraulic anatomies may generate several surprising emergent behaviours ...

Solute gradients across living cells could explain surprising observations of water pumping

The water pump requires plasmodesmata & improves with suberin deposition

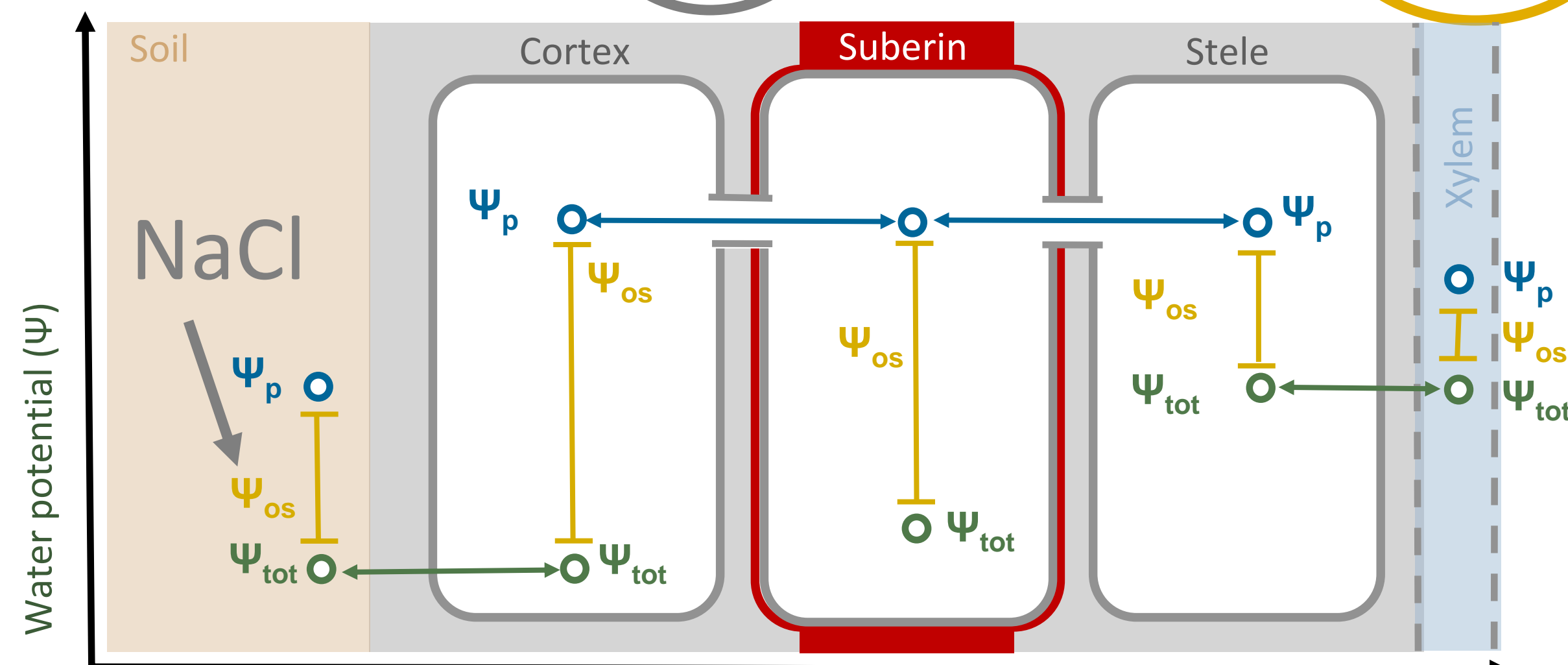


Root specific affinity for solute will directly affect water pumping



Position relative to xylem

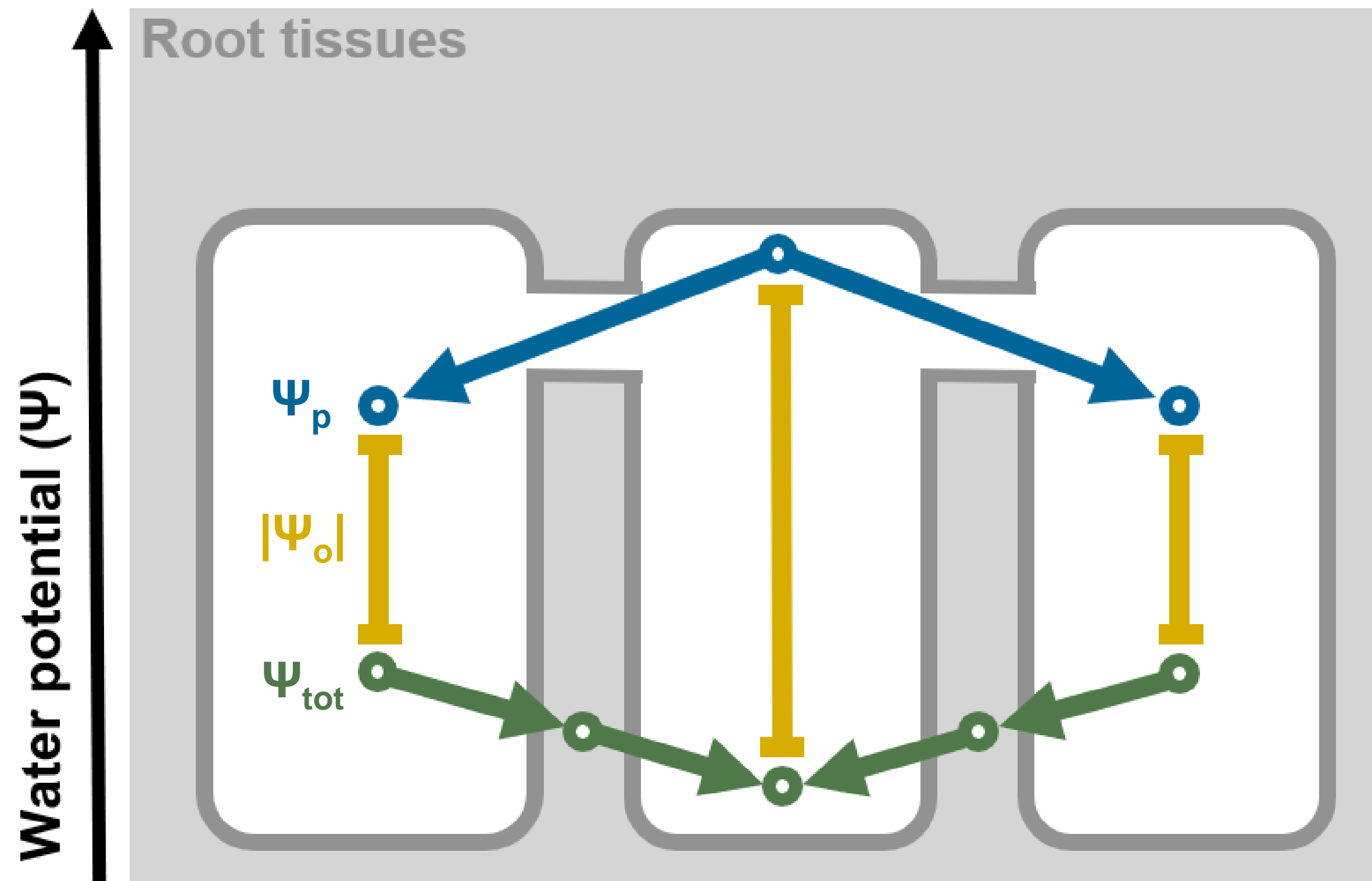
$$F_r = K_r \cdot (\Psi_{p,soil} - \Psi_{p,xylem} + \Psi_{o,soil} - \Psi_{o,xylem} - \Psi_{o,cortex} + \Psi_{o,stele})$$



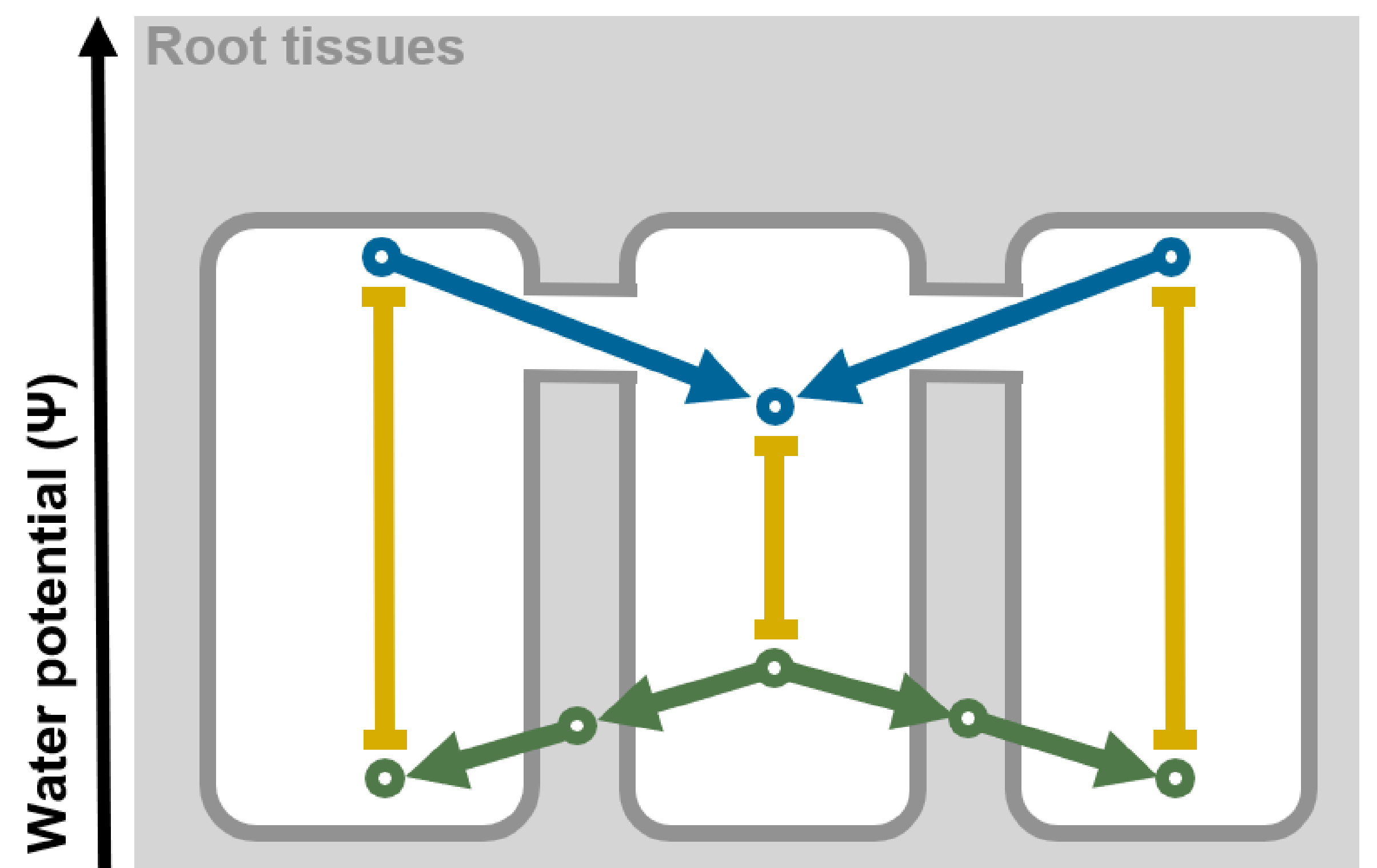
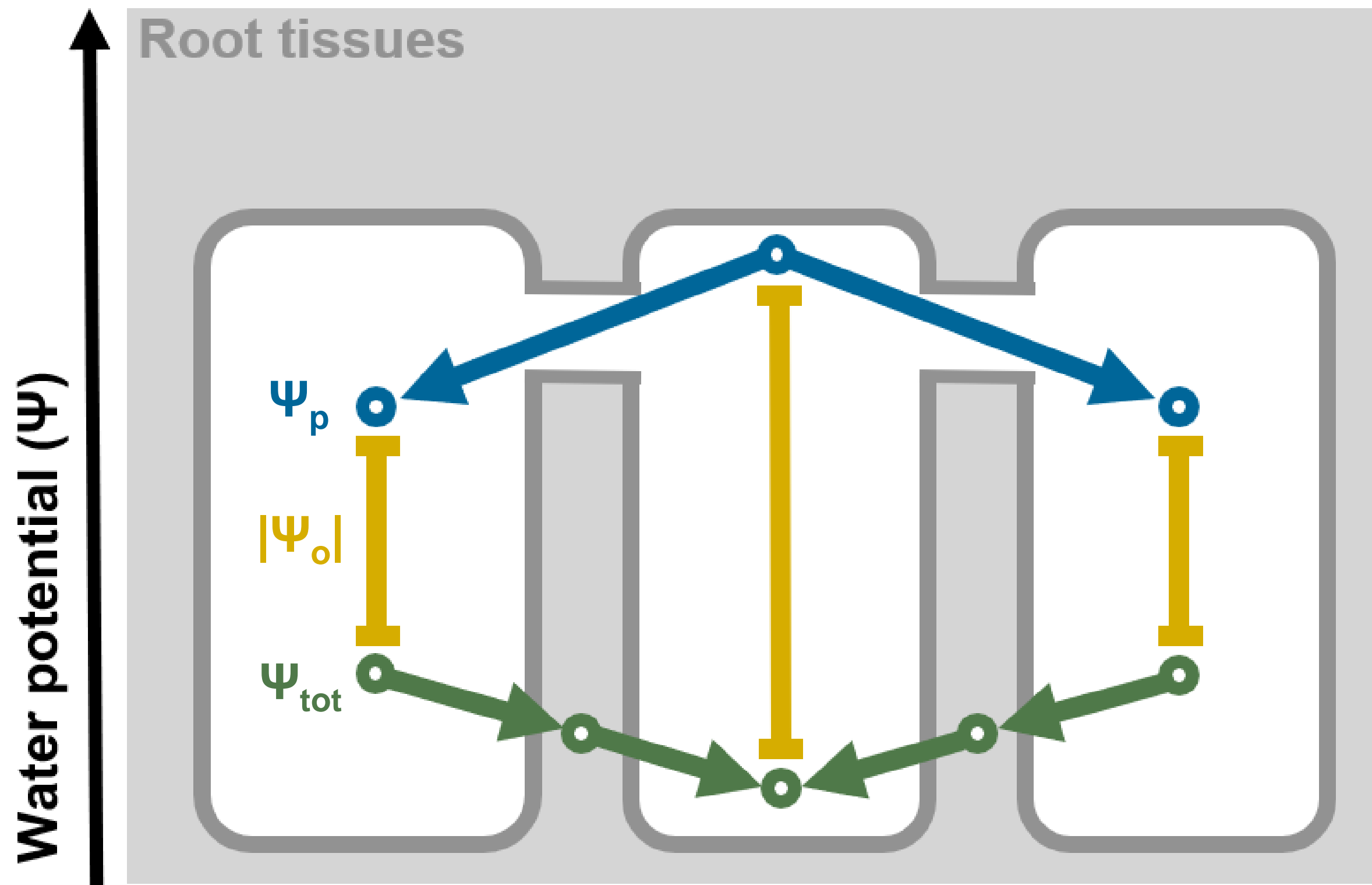
Position relative to xylem



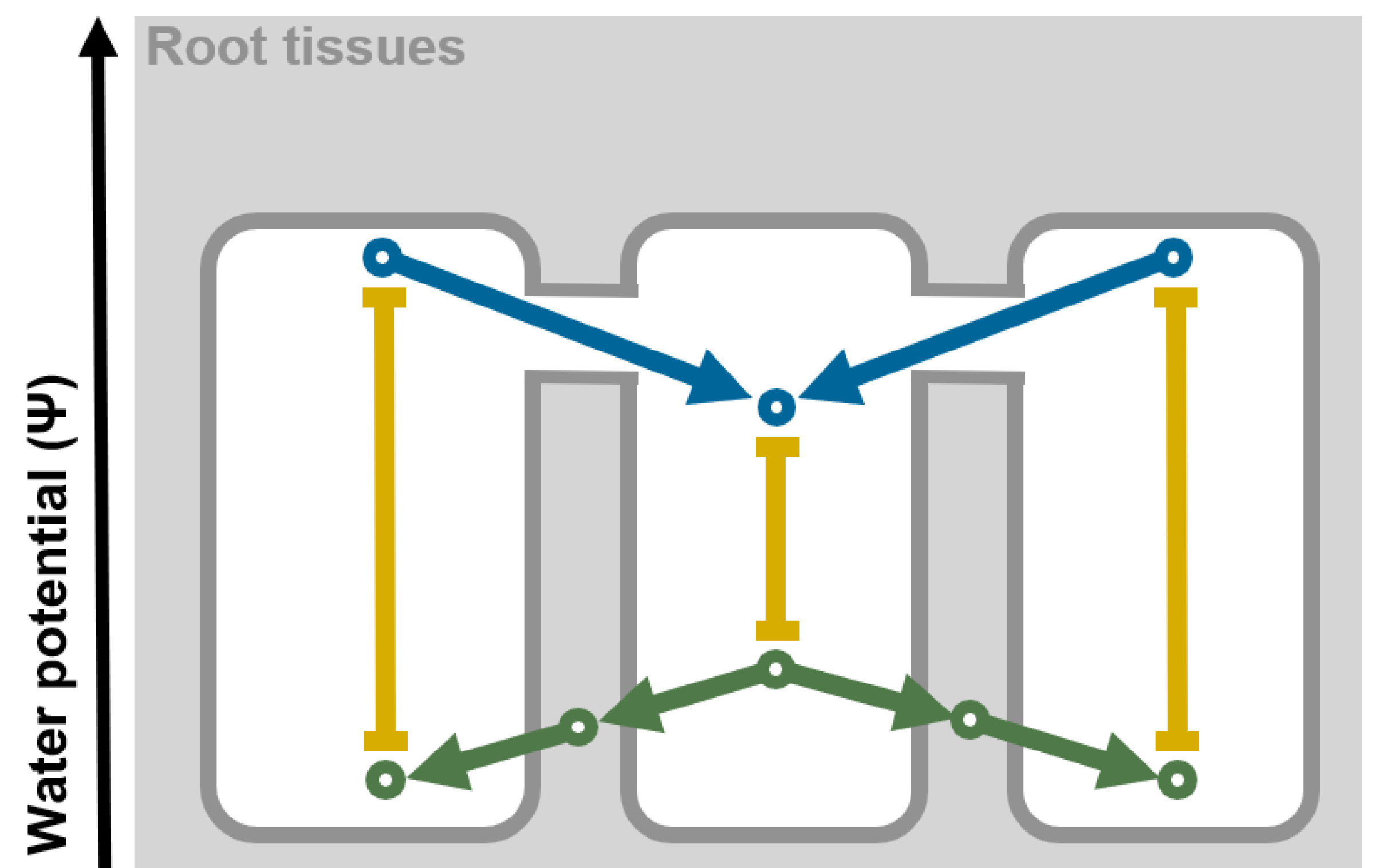
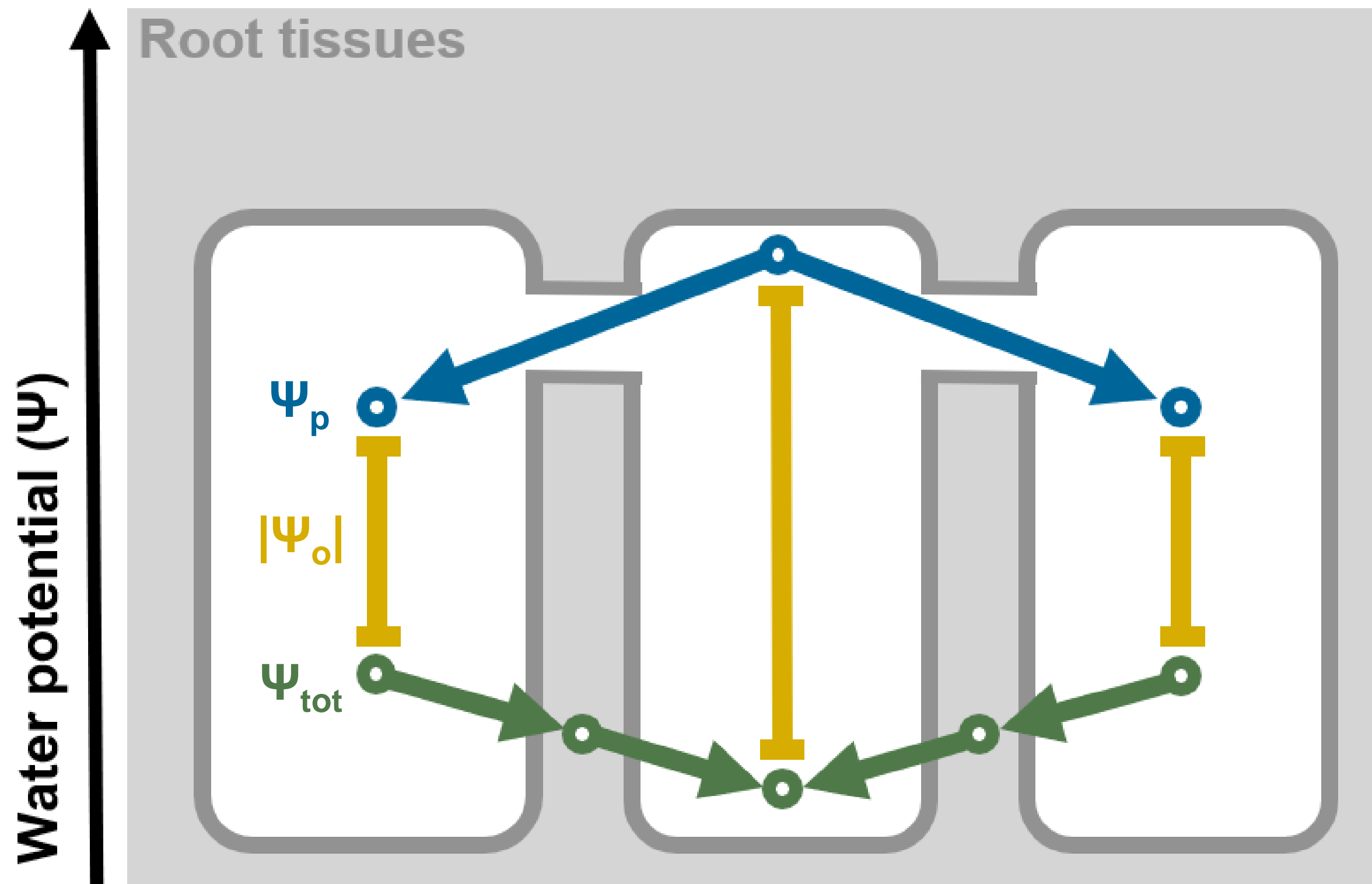
Food for thoughts ...



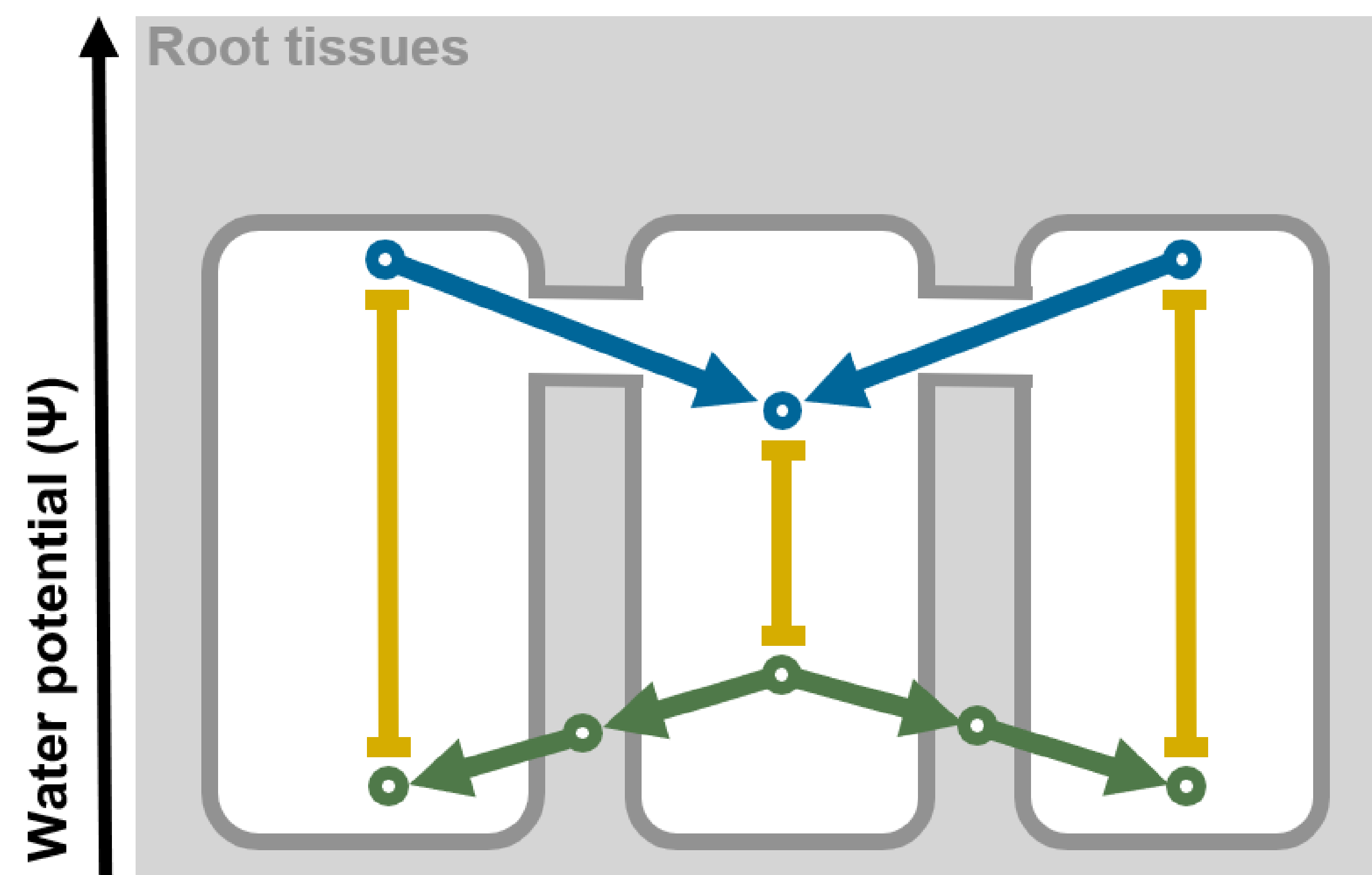
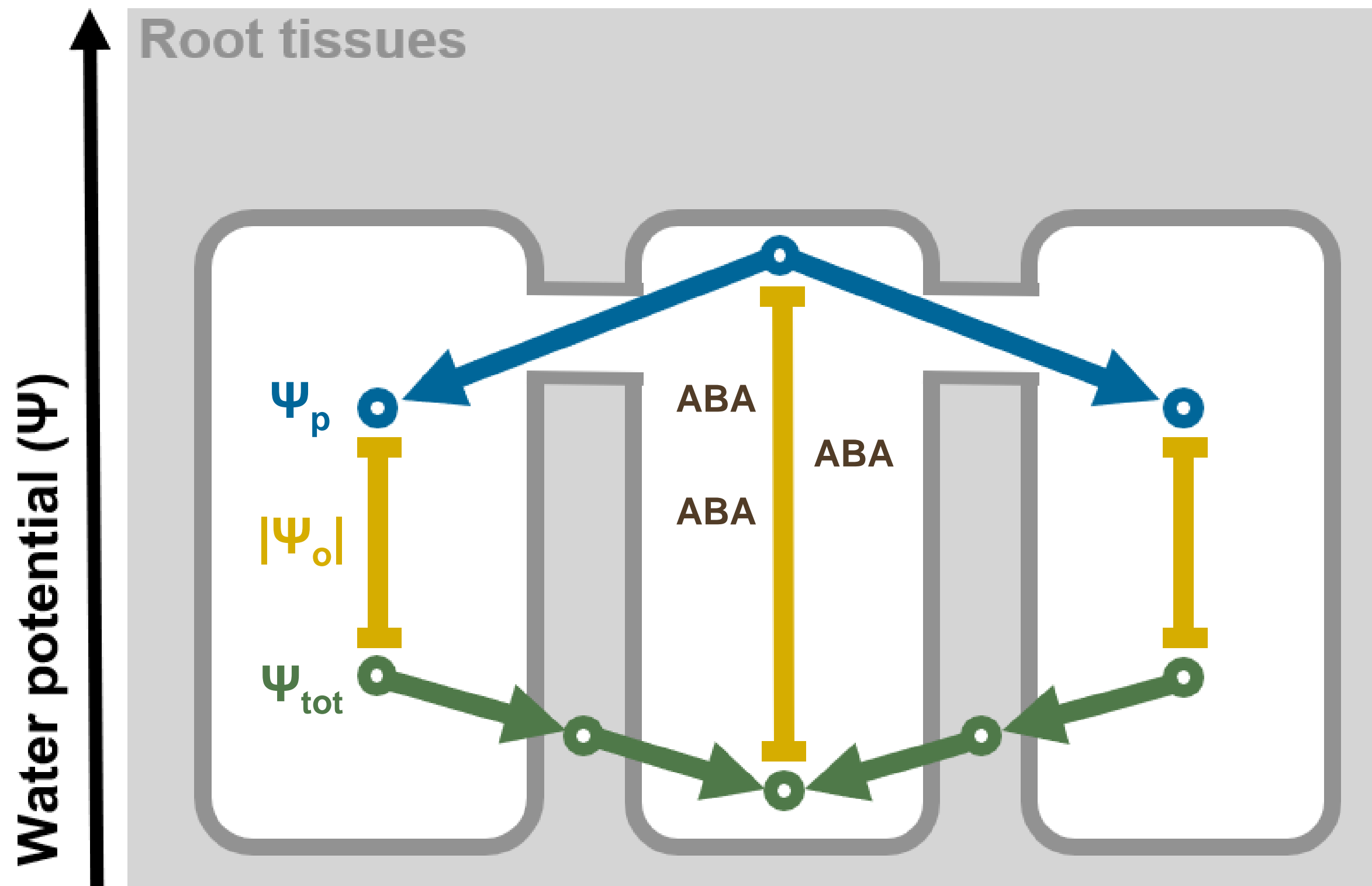
Food for thoughts ...



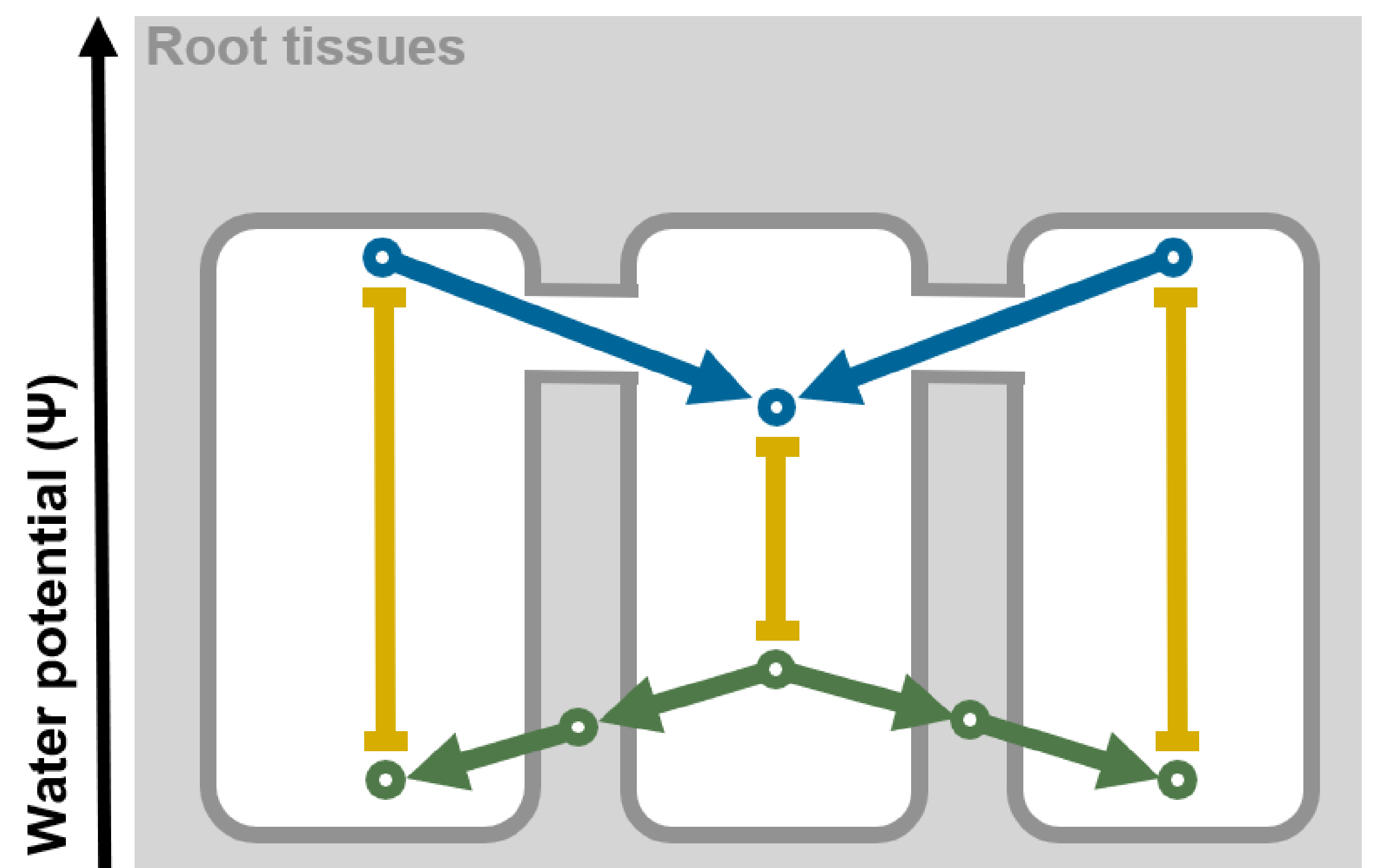
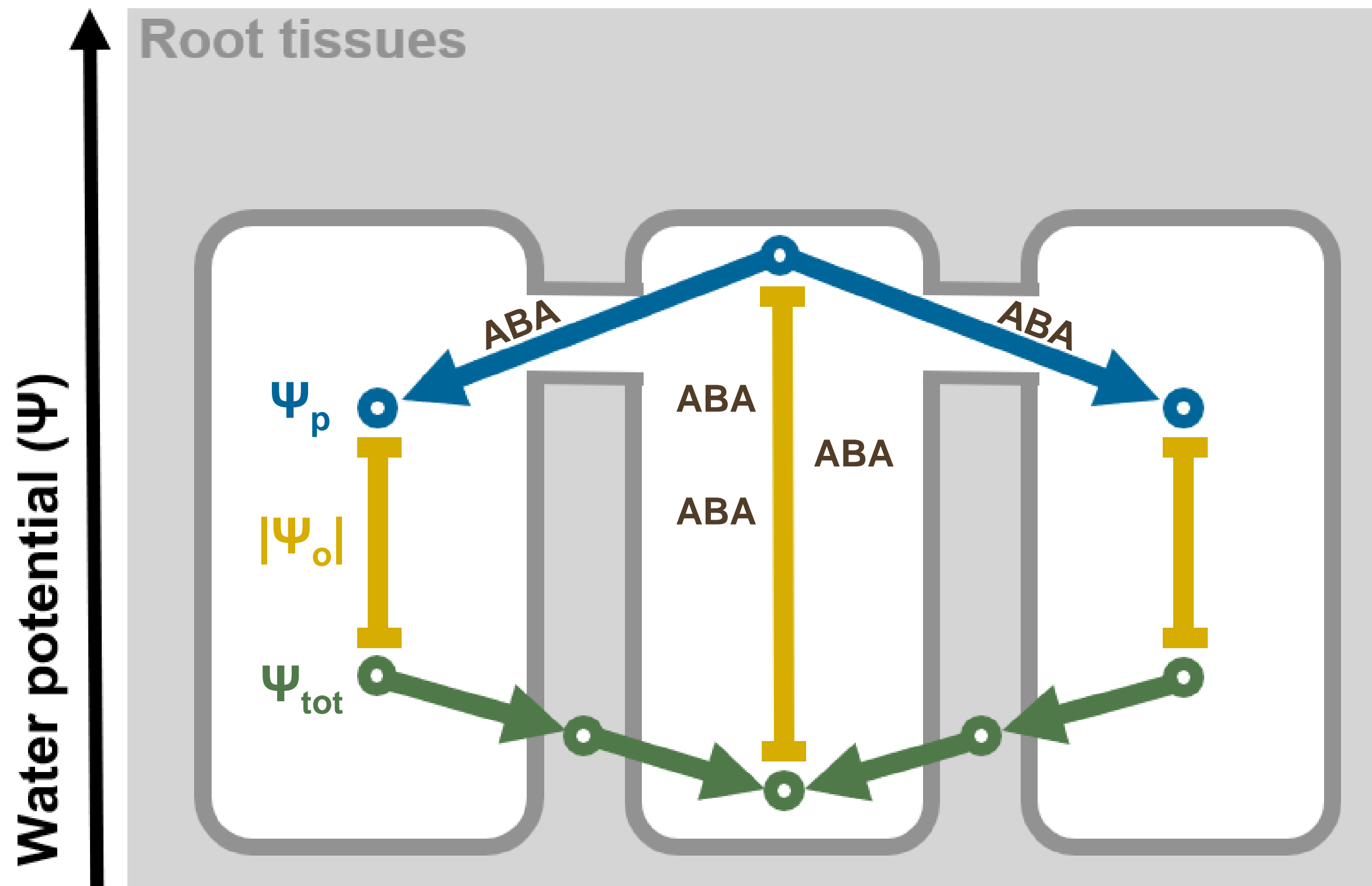
Food for thoughts ...



Food for thoughts ...

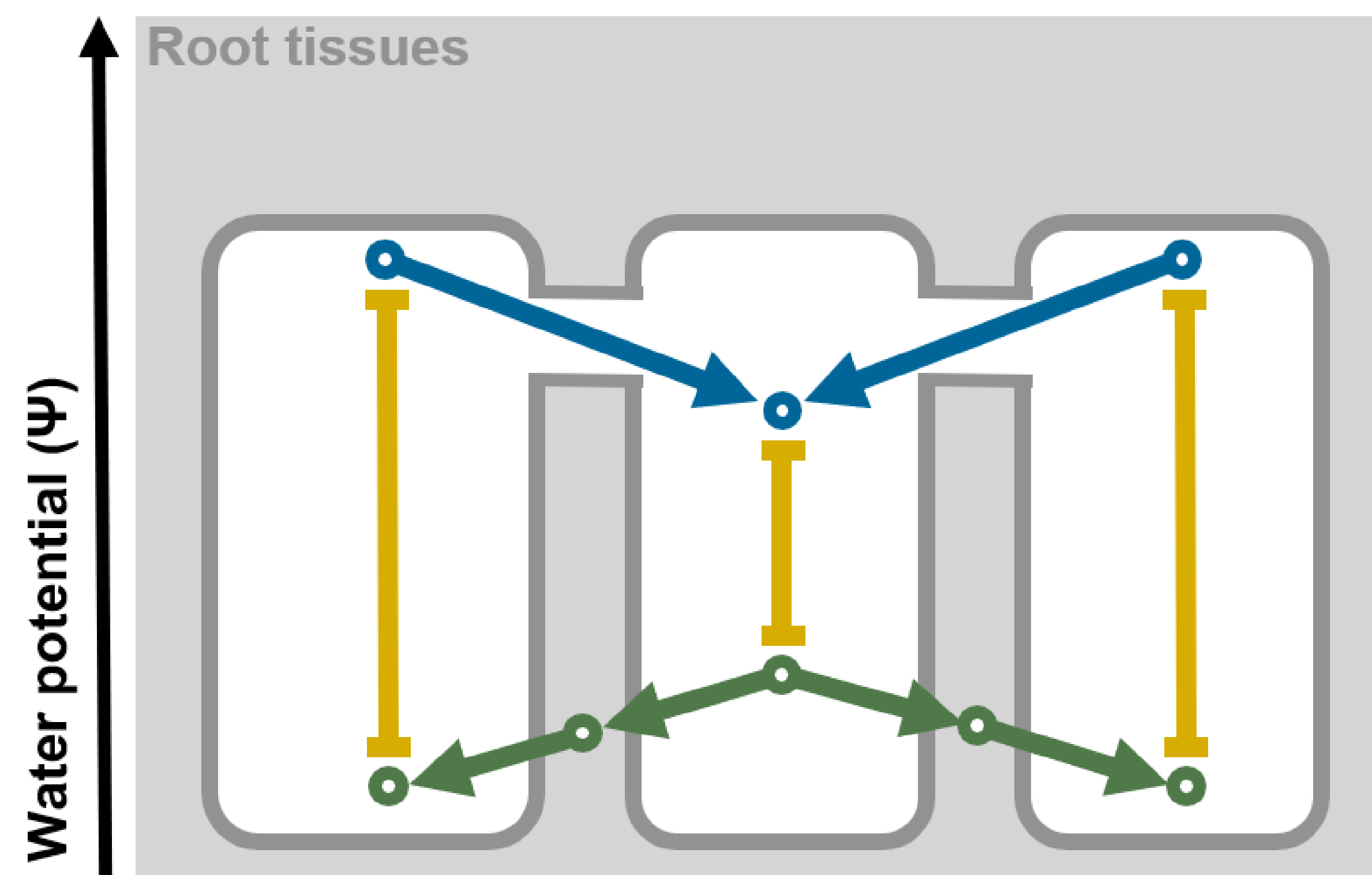
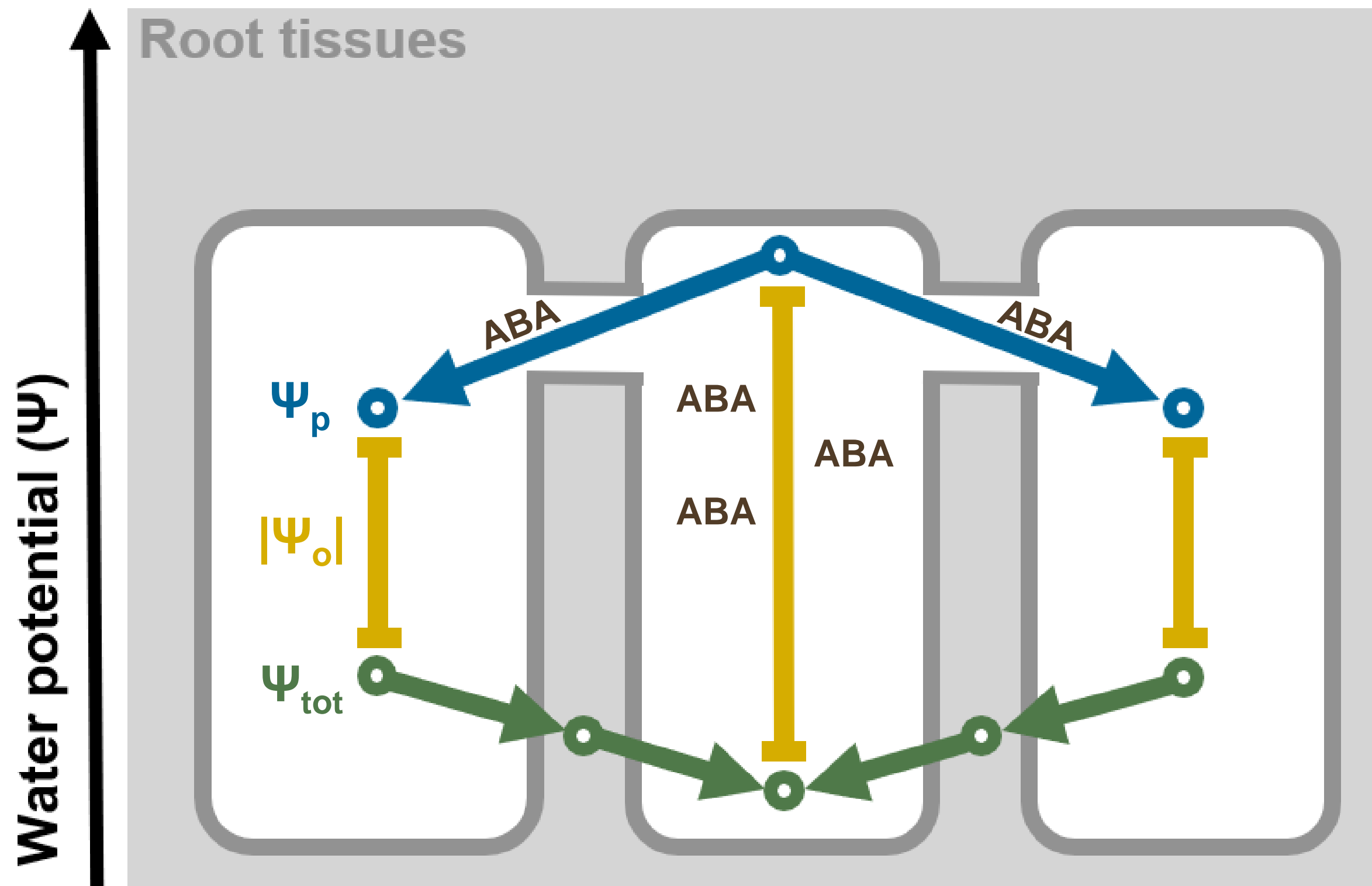


Food for thoughts ...



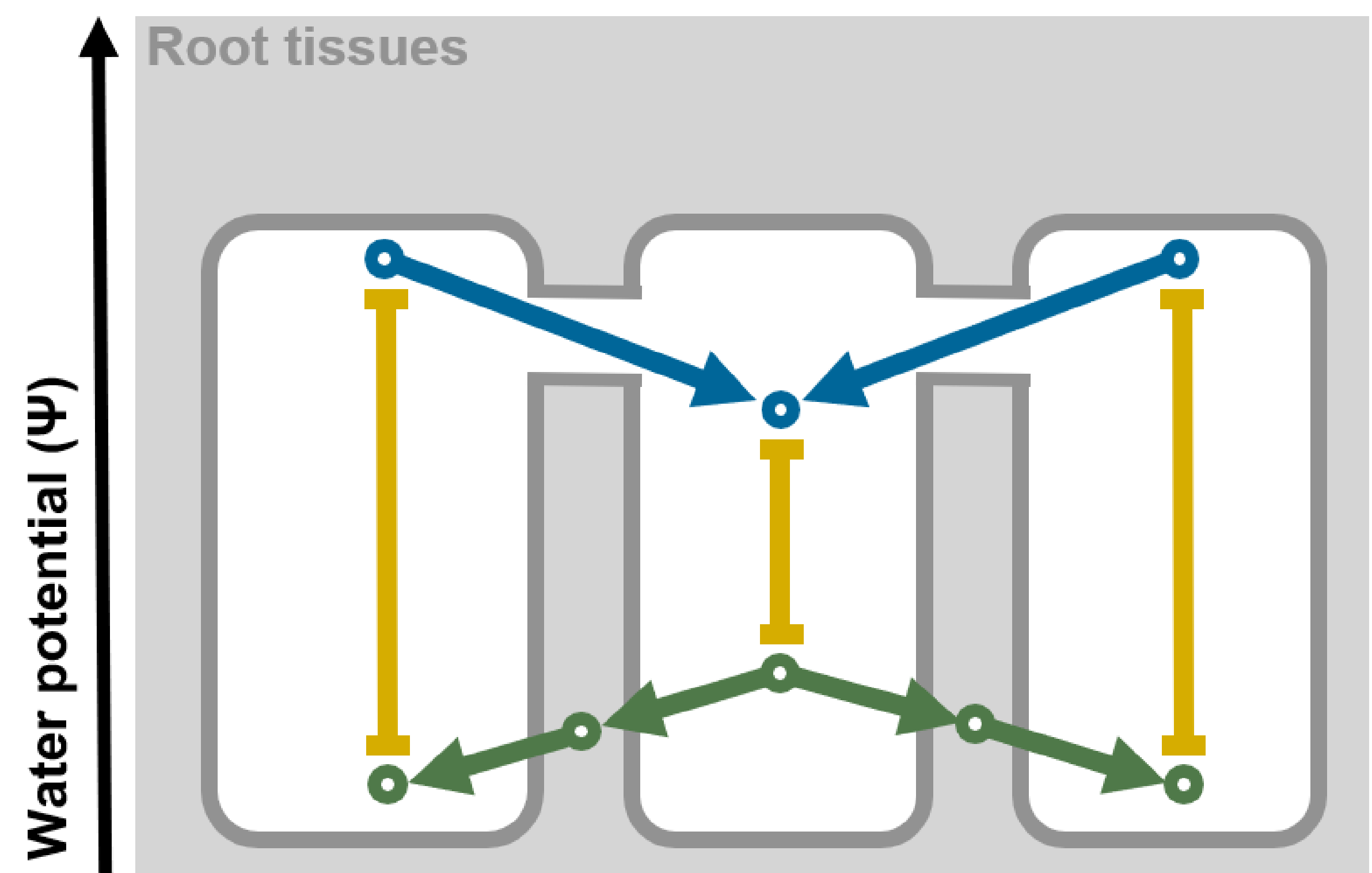
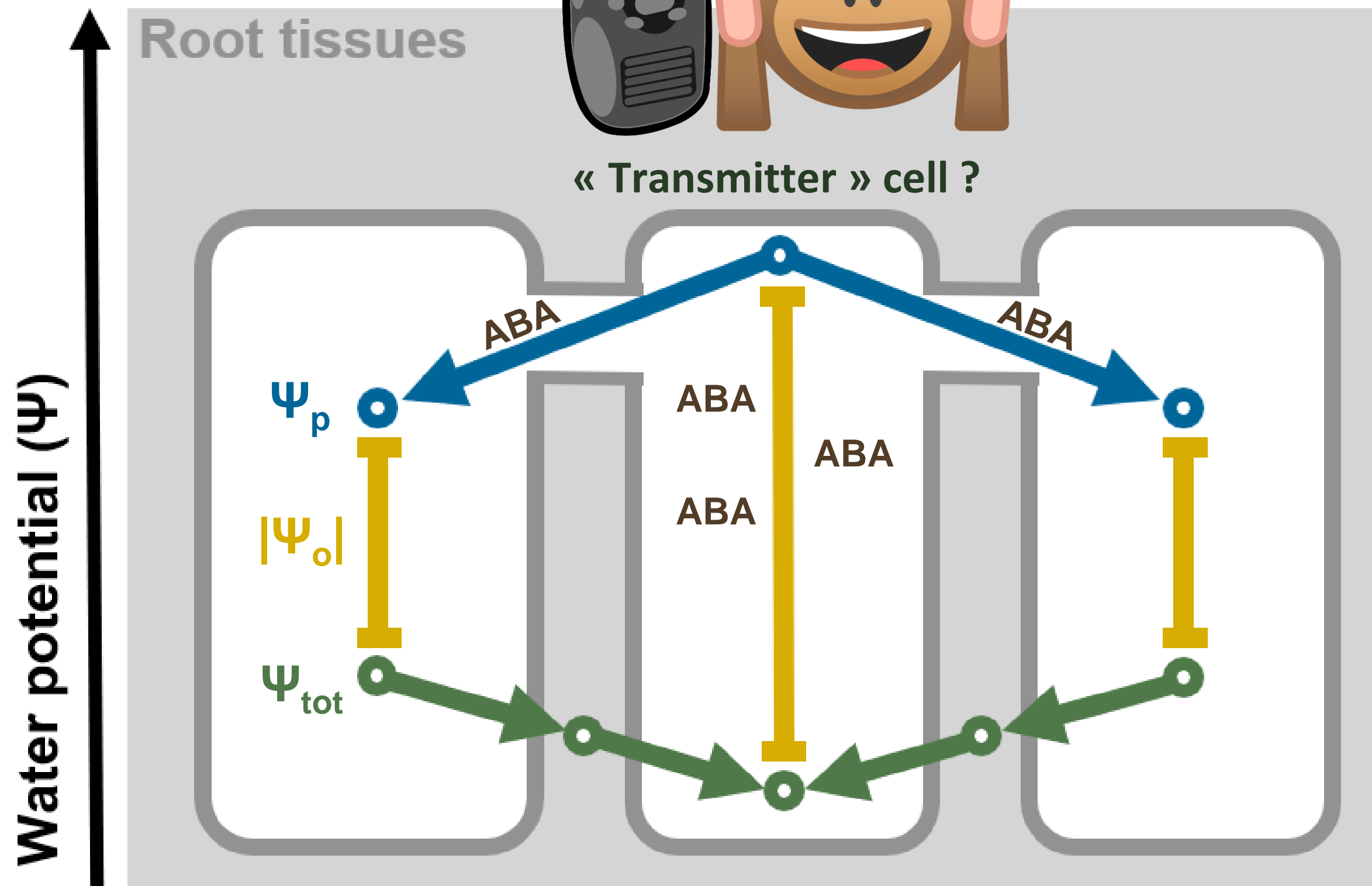
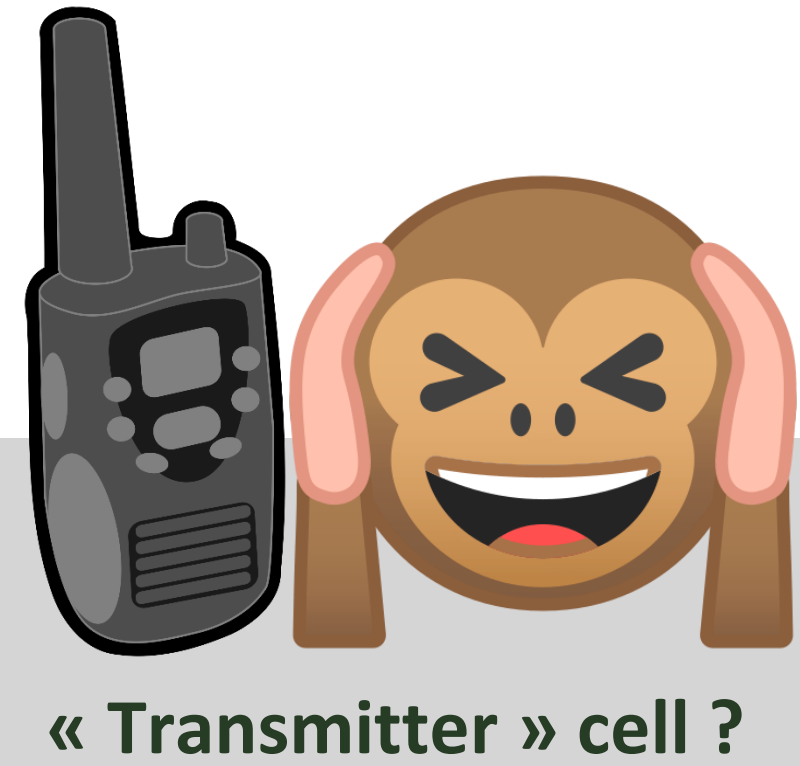
Food for thoughts ...

... the walkie-talkie analogy of symplastic communication



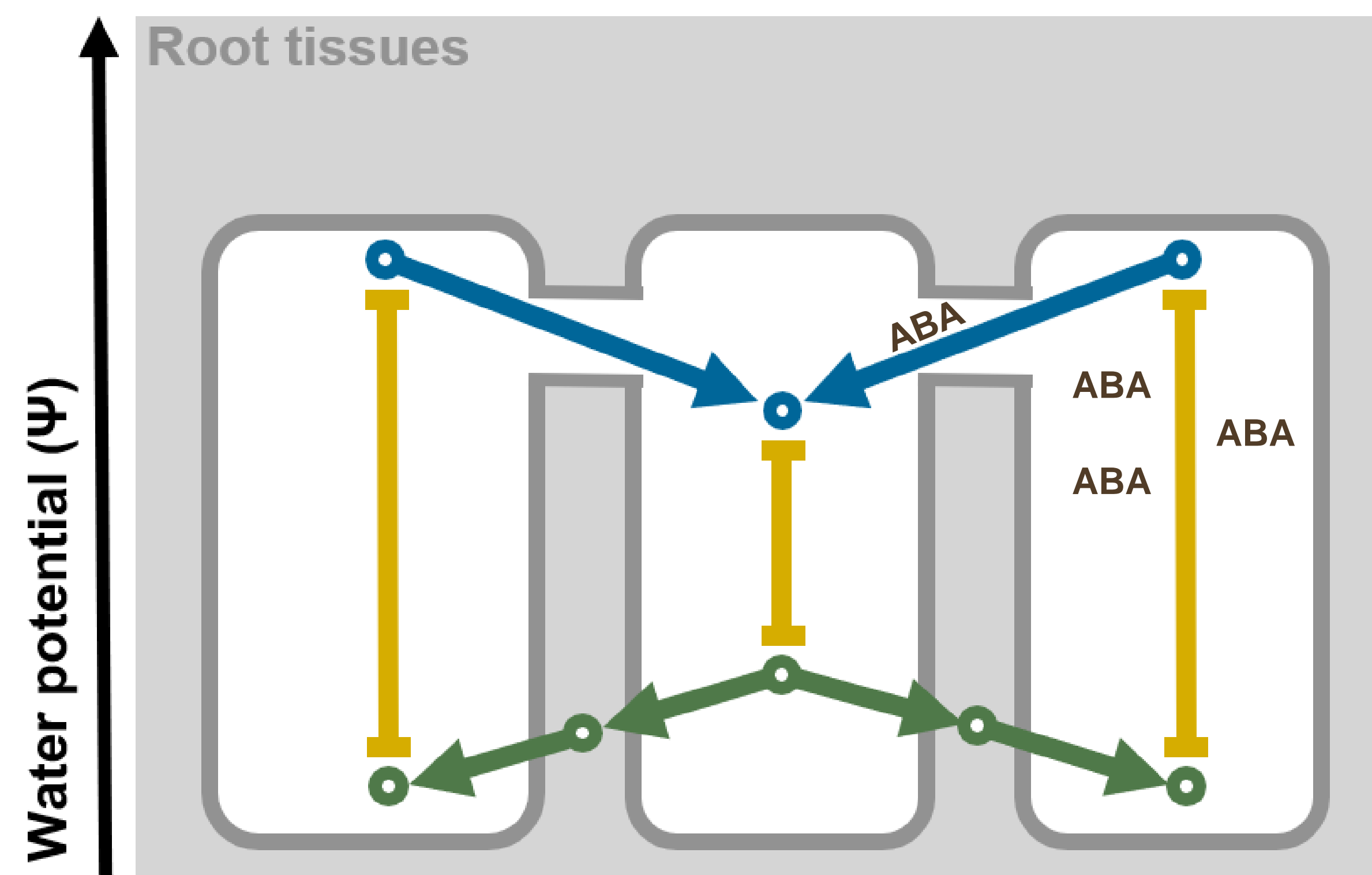
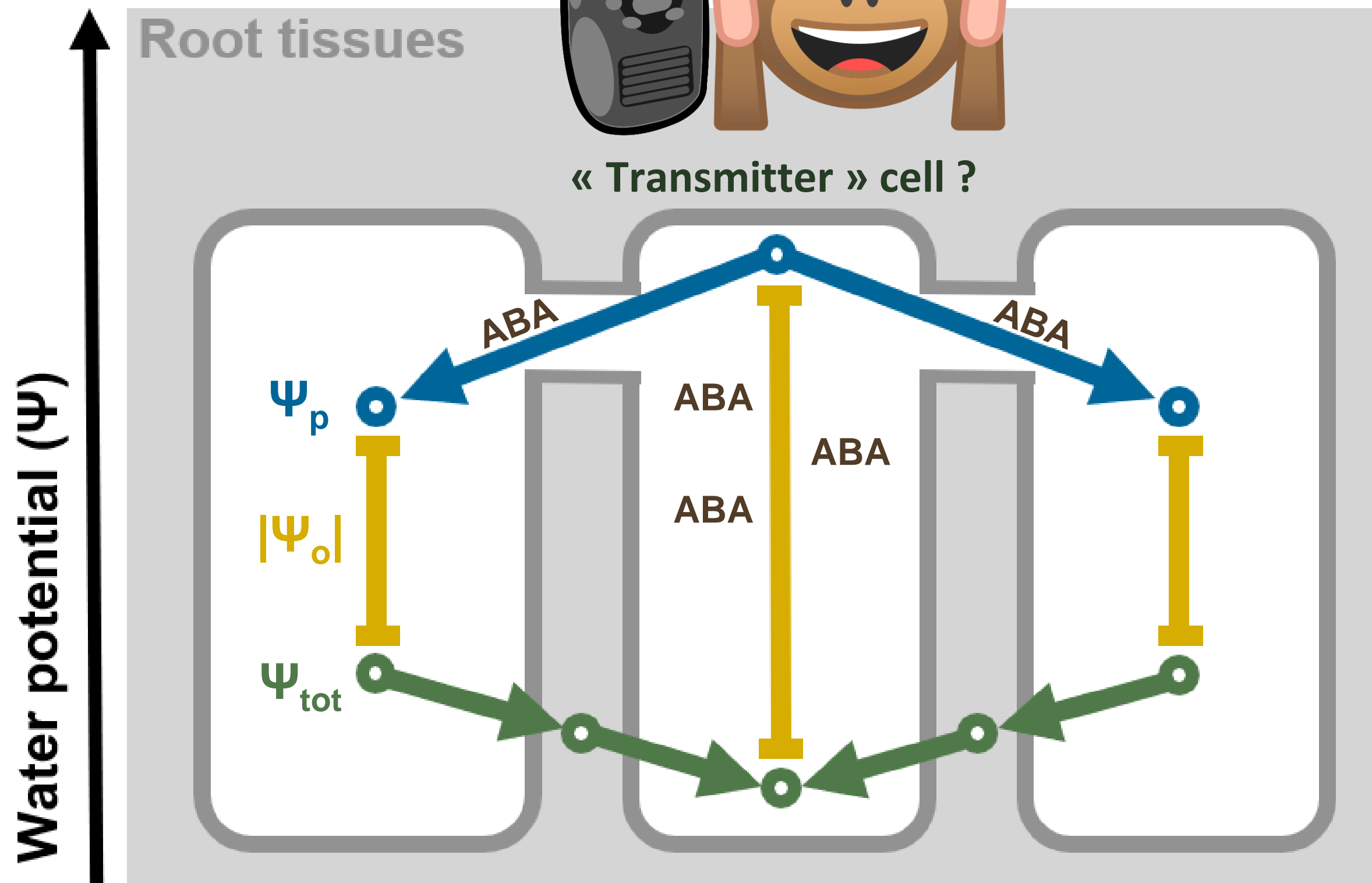
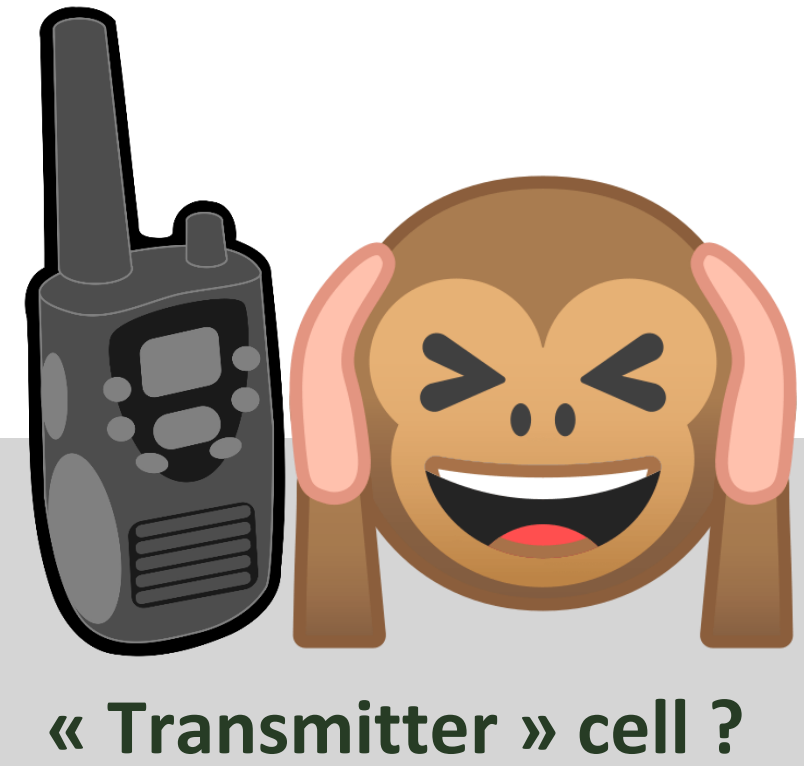
Food for thoughts ...

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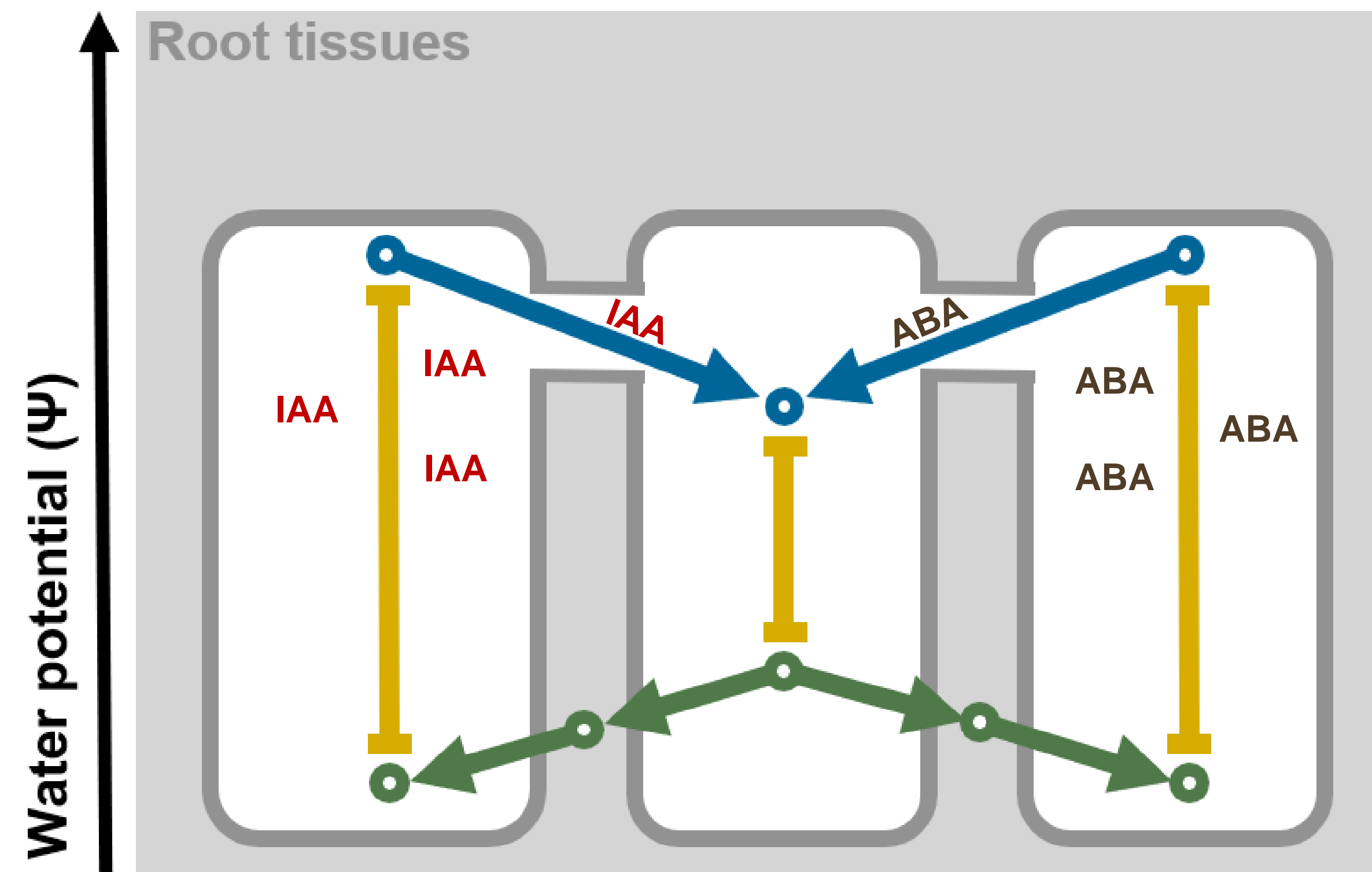
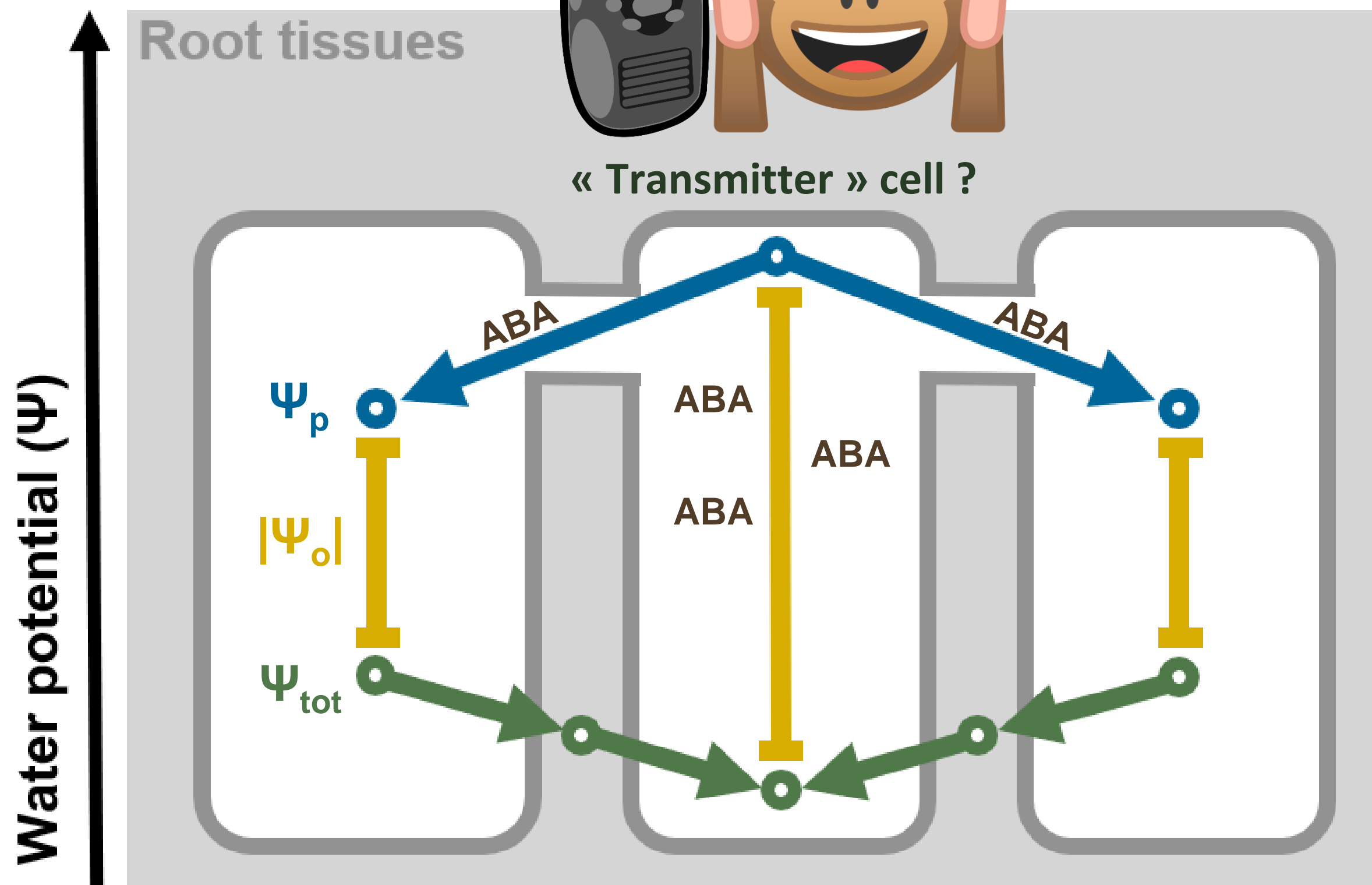


Food for thoughts ...

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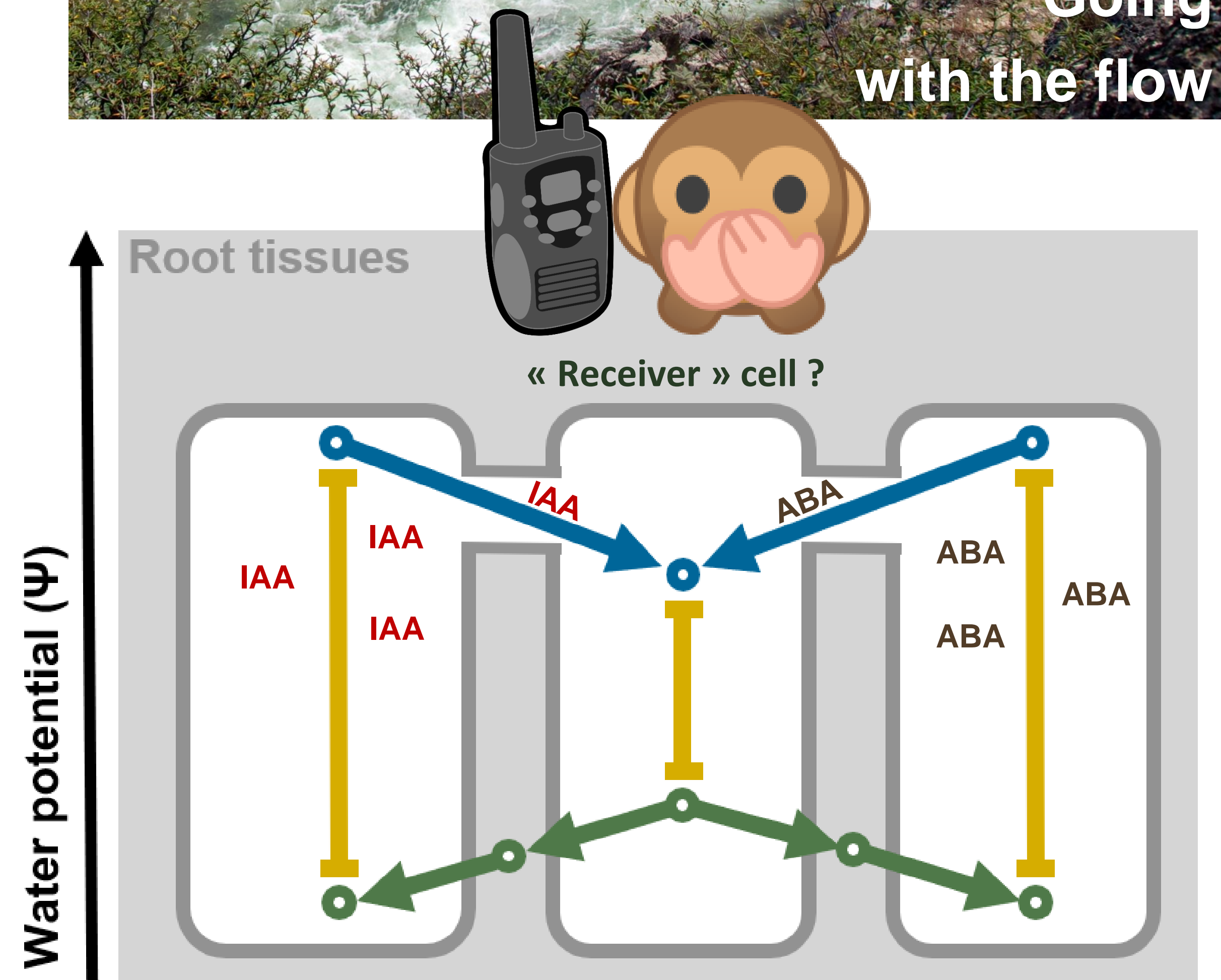
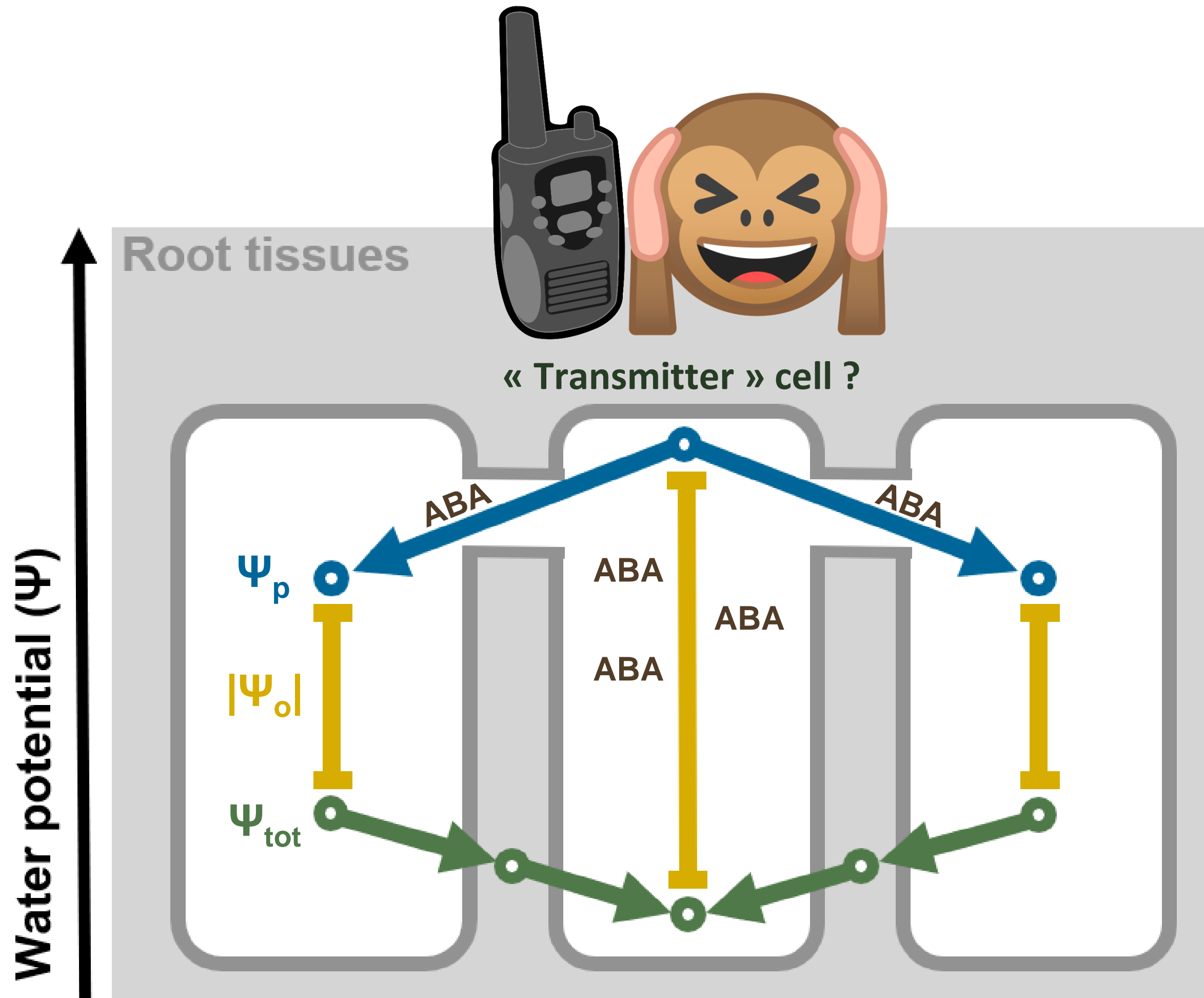
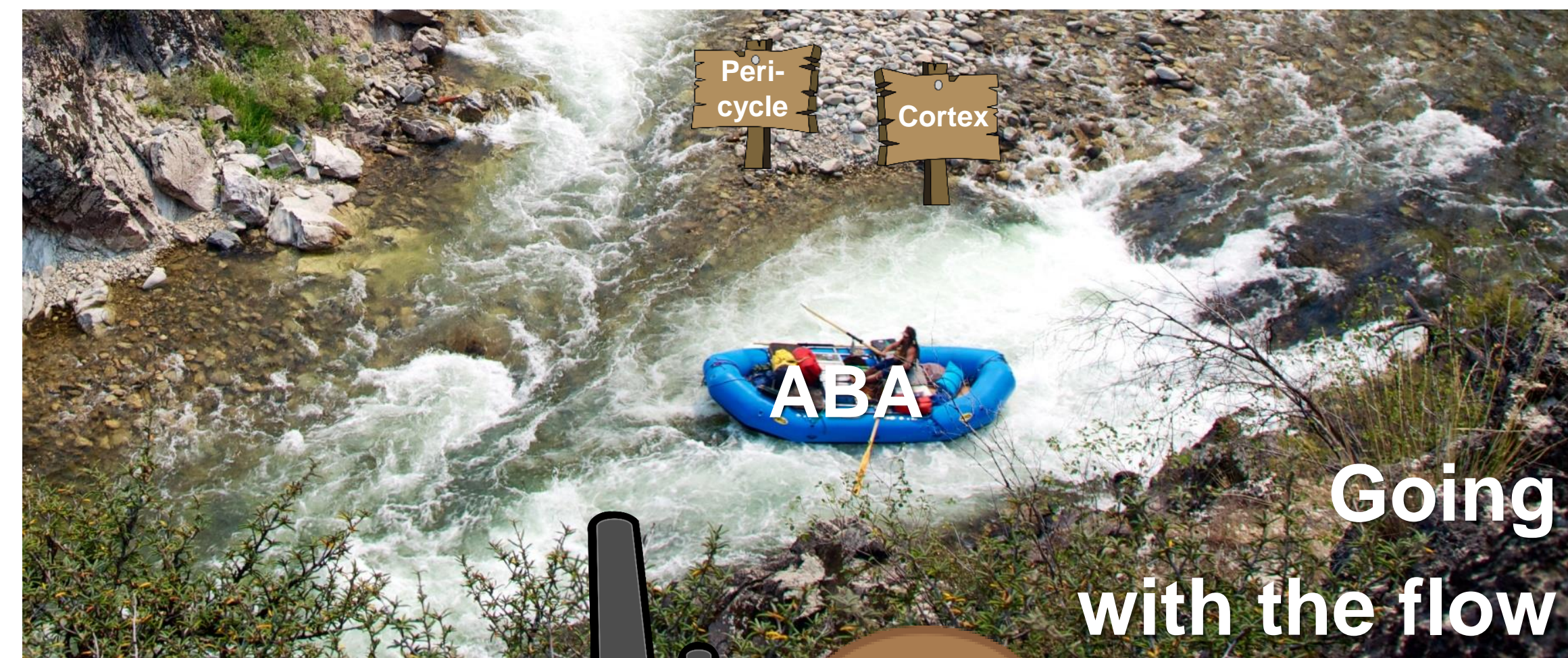


« Transmitter » cell ?

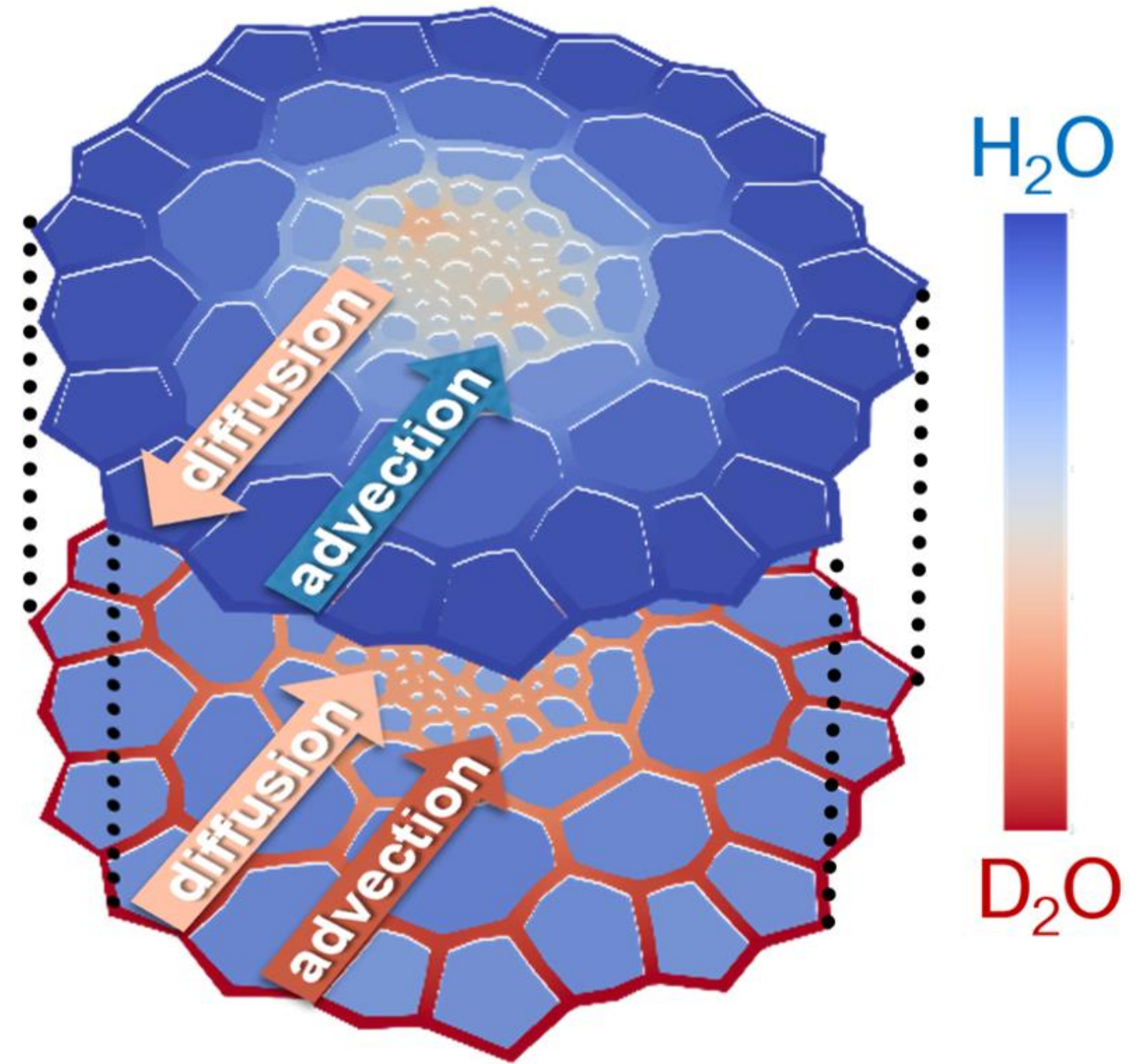
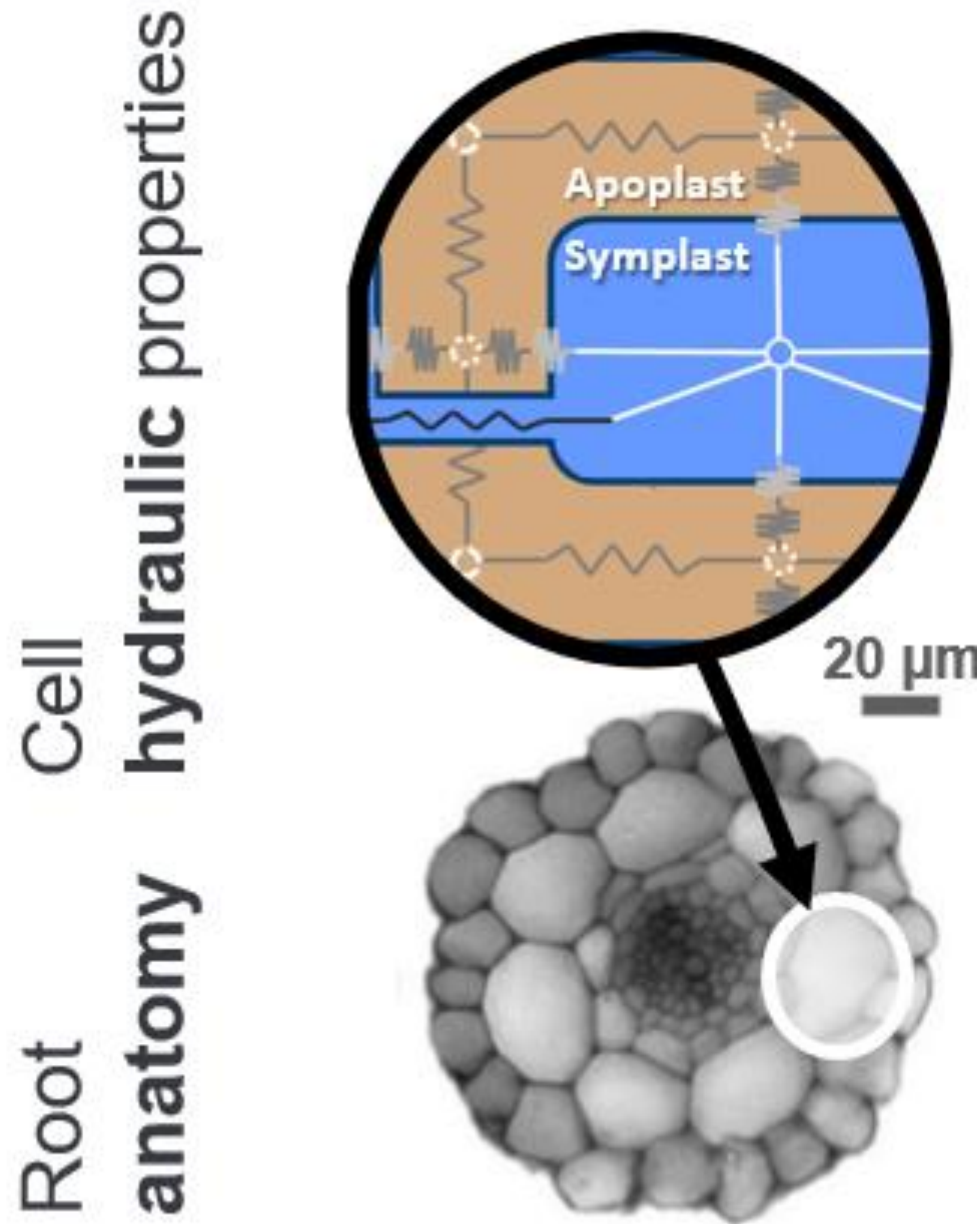


Food for thoughts ...

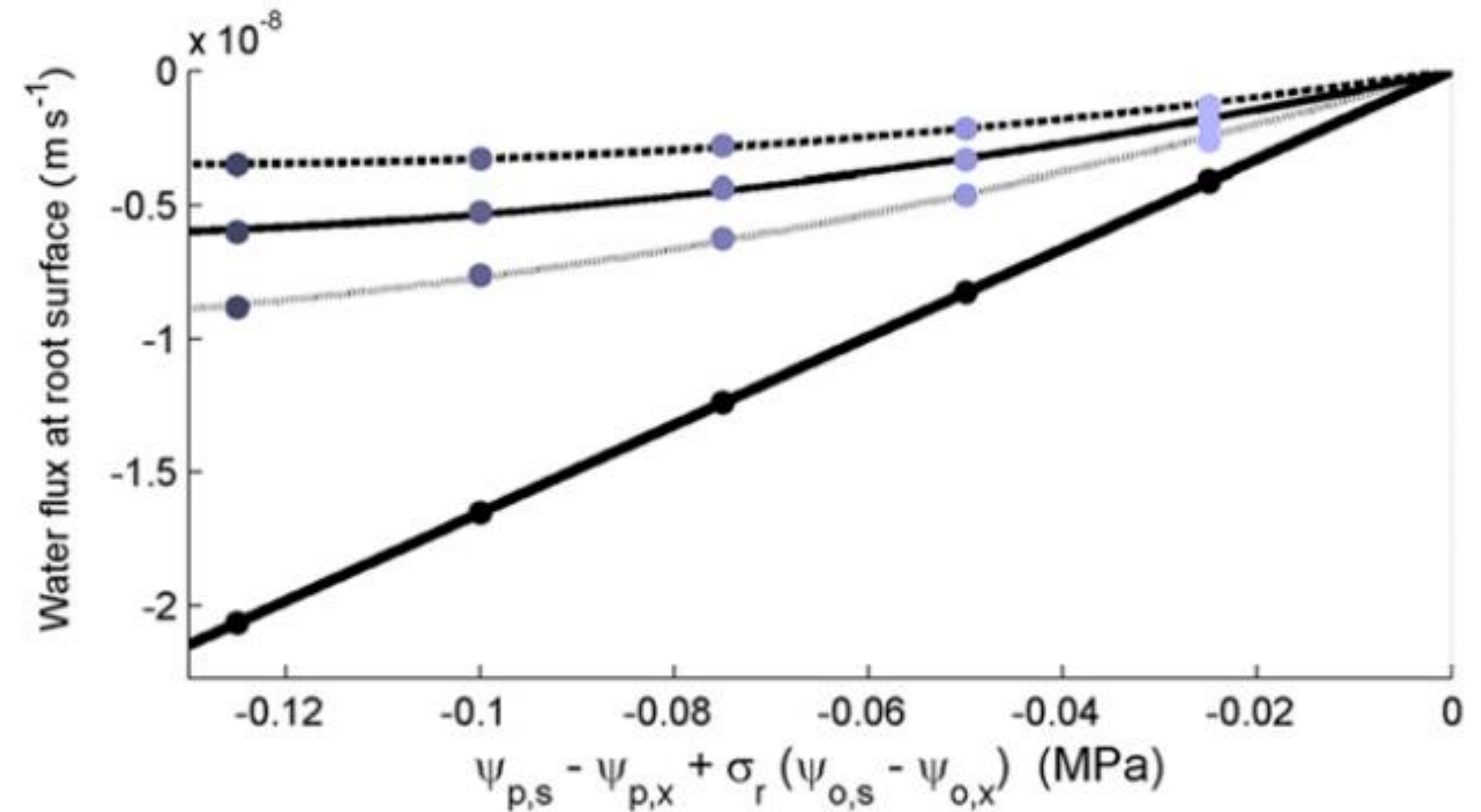
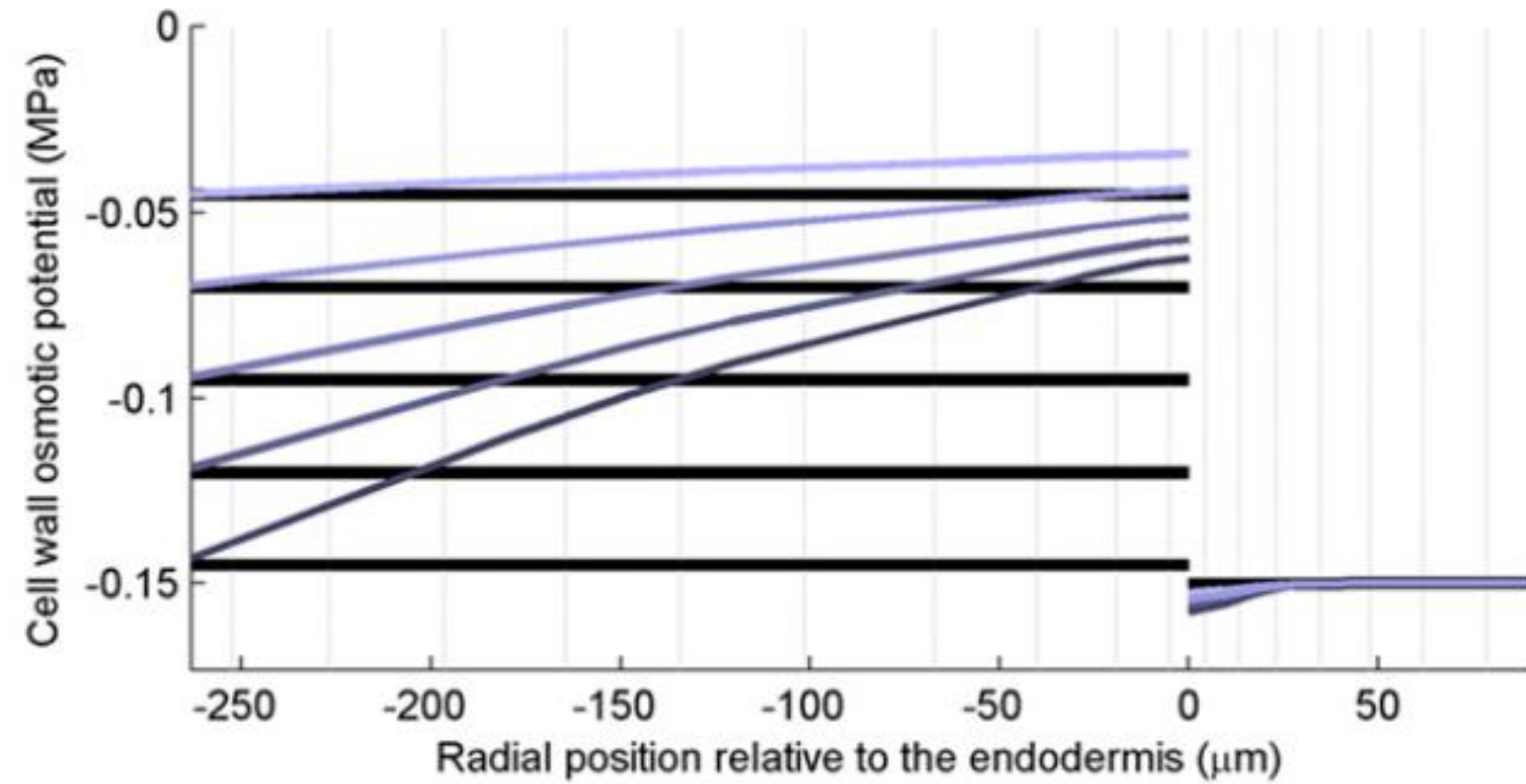
... the walkie-talkie analogy of symplastic communication



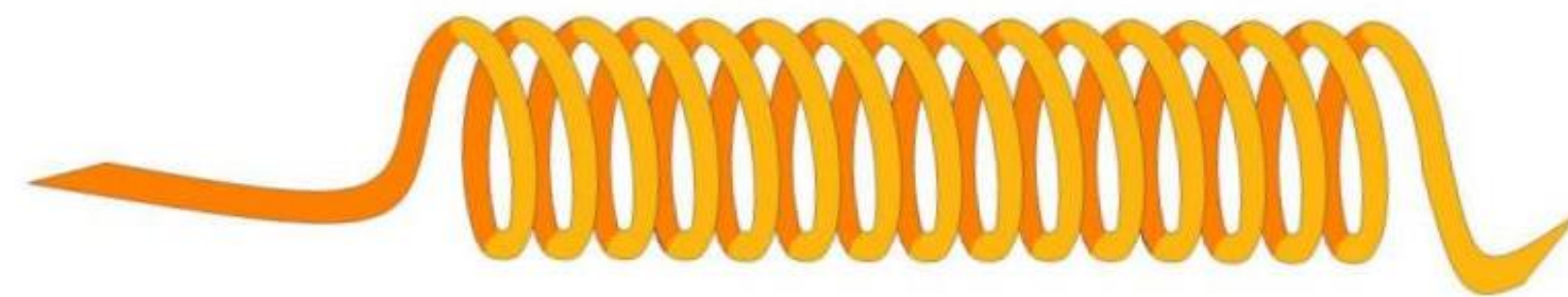
Solute advection-diffusion in root hydraulic anatomies



Effective root conductivity varies with water potential gradient



Would solute distribution act like an inductance limiting variations of flow across roots ?



Take home messages → Station 3 : emergent properties

Simple upscaled solutions of water flow emerge in complex hydraulic networks !

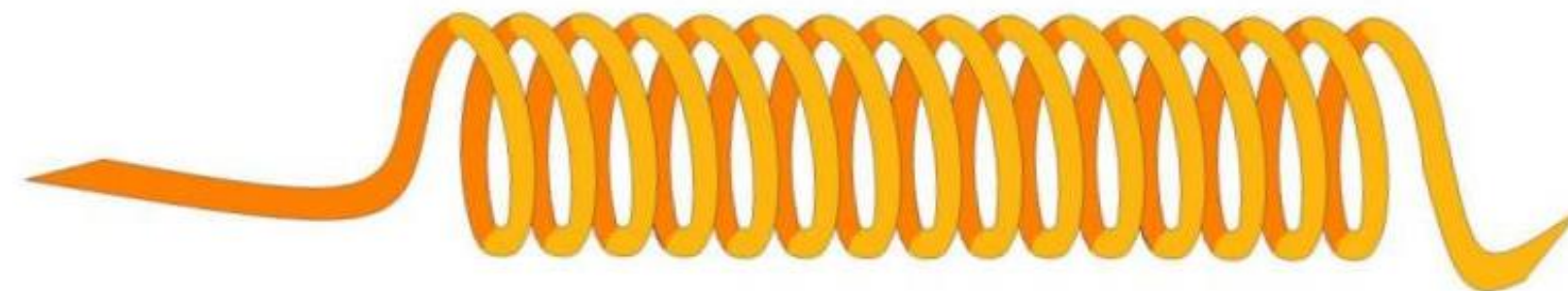
Solute mobility in hydraulic anatomies may generate several surprising emergent behaviours ...

Solute gradients across living cells could explain surprising observations of water pumping

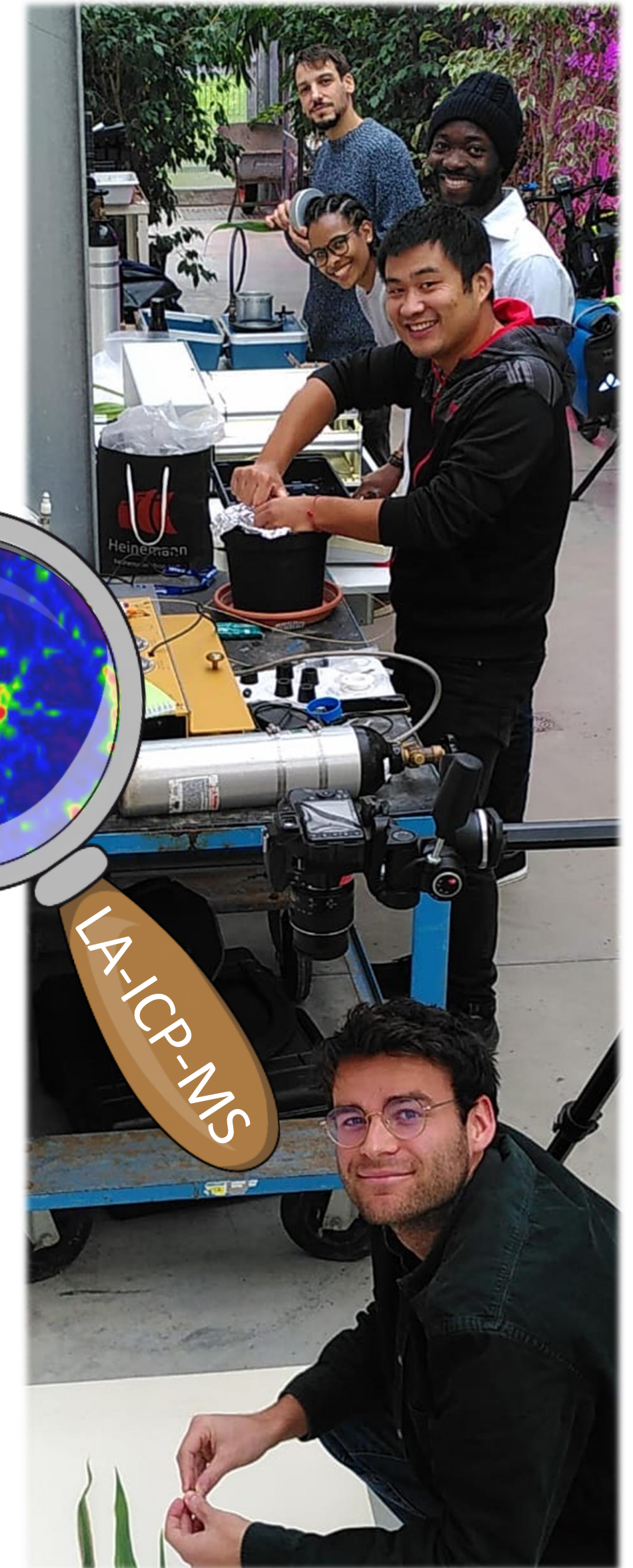
The water pump requires plasmodesmata & improves with suberin deposition

The water pump could be spontaneously (de)activated by (un)favorable solutes

Solute gradients in the apoplast could act as an « inductance » opposing water uptake fluctuations



A long way from models to measurements, and back again !



THANK YOU



FOR YOUR ATTENTION!



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Jan Vanderborght



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Adrien Heymans



Valentin Couvreur



Guillaume Lobet



Xavier Draye



Malcolm Bennett

