Soil hydraulic constraints on transpiration

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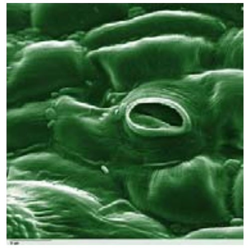
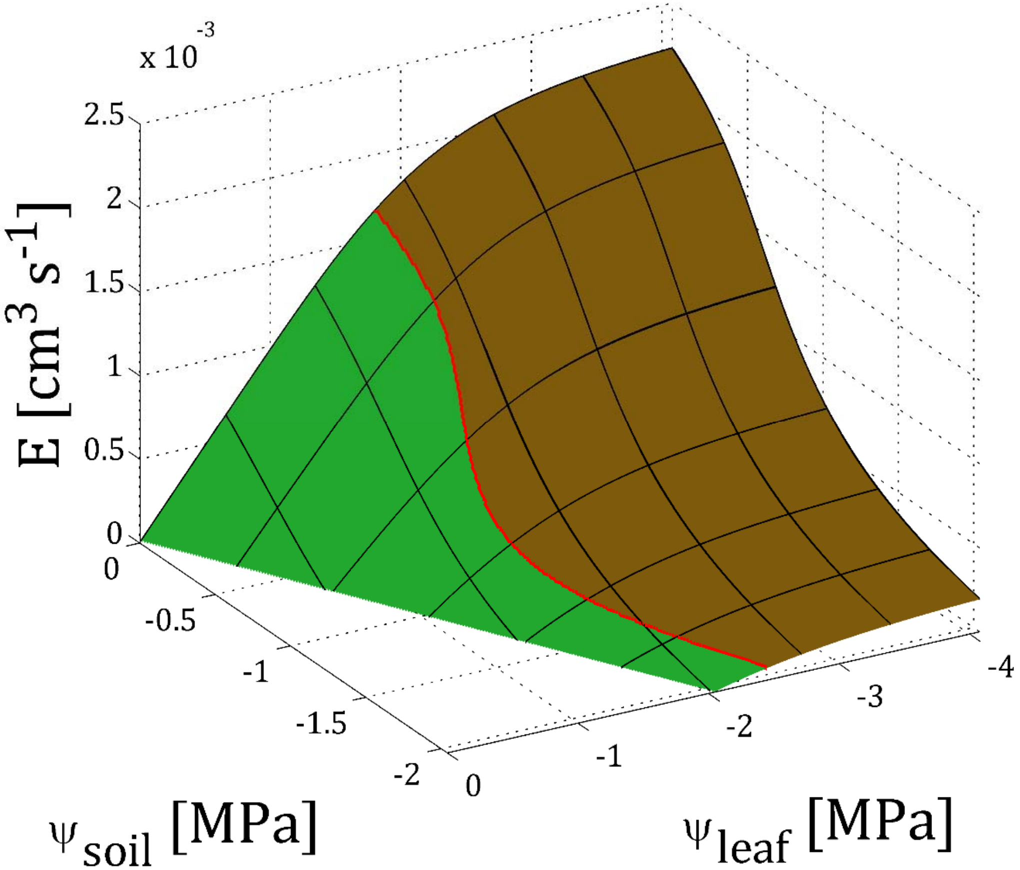




General question

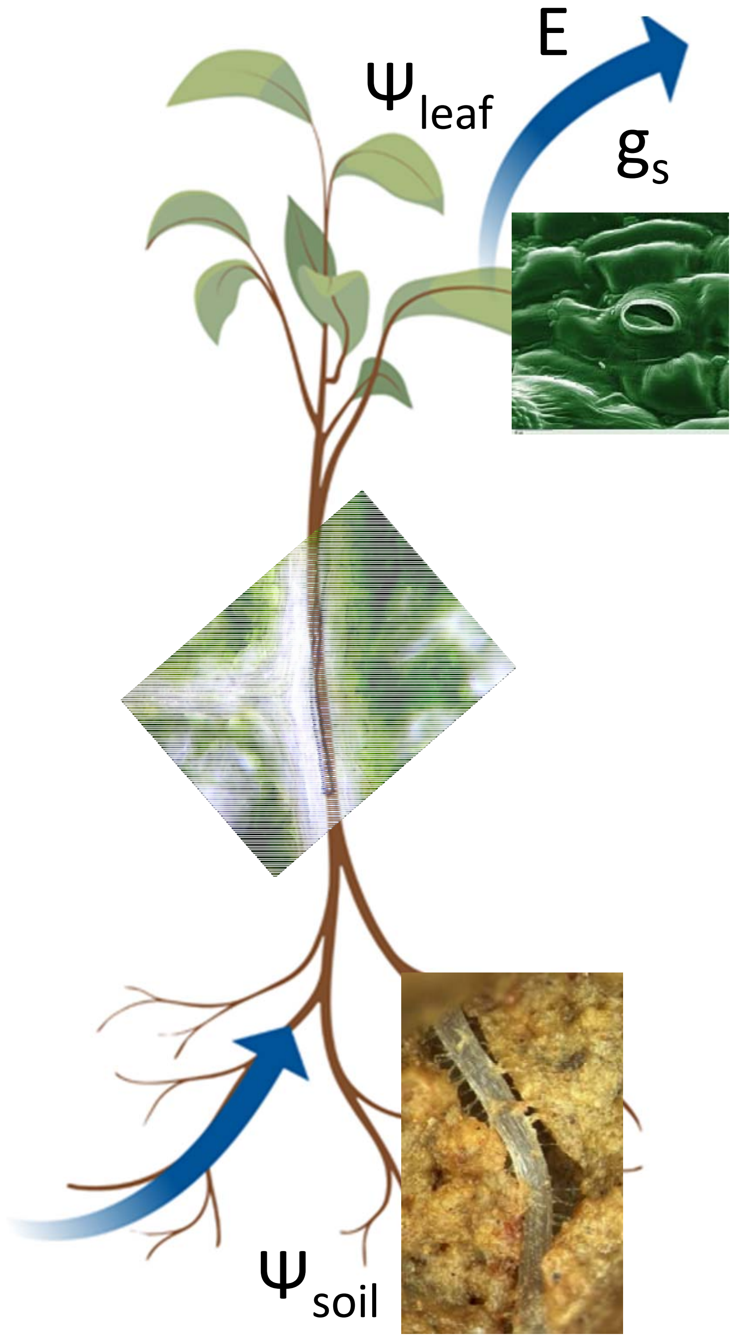
How does soil drying (Ψ_{soil}) impact transpiration (E) and leaf water potential (Ψ_{leaf})?

State of the art

As the soil dries, Ψ_{soil} decreases and so thus Ψ_{leaf}. Stomata regulation prevents that Ψ_{leaf} drops and that the xylem cavitates.

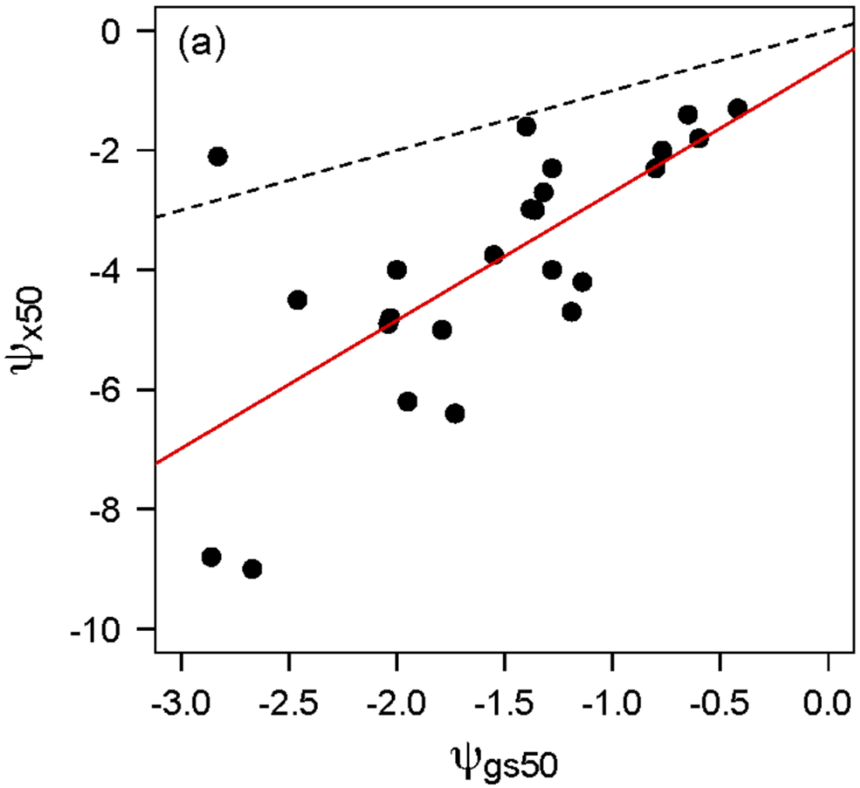
Stomatal conductance (g_s) depends on leaf water potential, via active and passive mechanisms (Brodribb & McAdam 2017; Buckley 2019) .

It was proposed that stomata close when the relationship between E and Ψ_{leaf} becomes not linear, due to xylem cavitation (Sperry and Love 2015).



But stomata close much before the xylem cavitates.

What mechanism allows stomata to respond to the decrease in xylem conductance, before this decrease occurs?



Anderegg et al. 2017 PLoS ONE

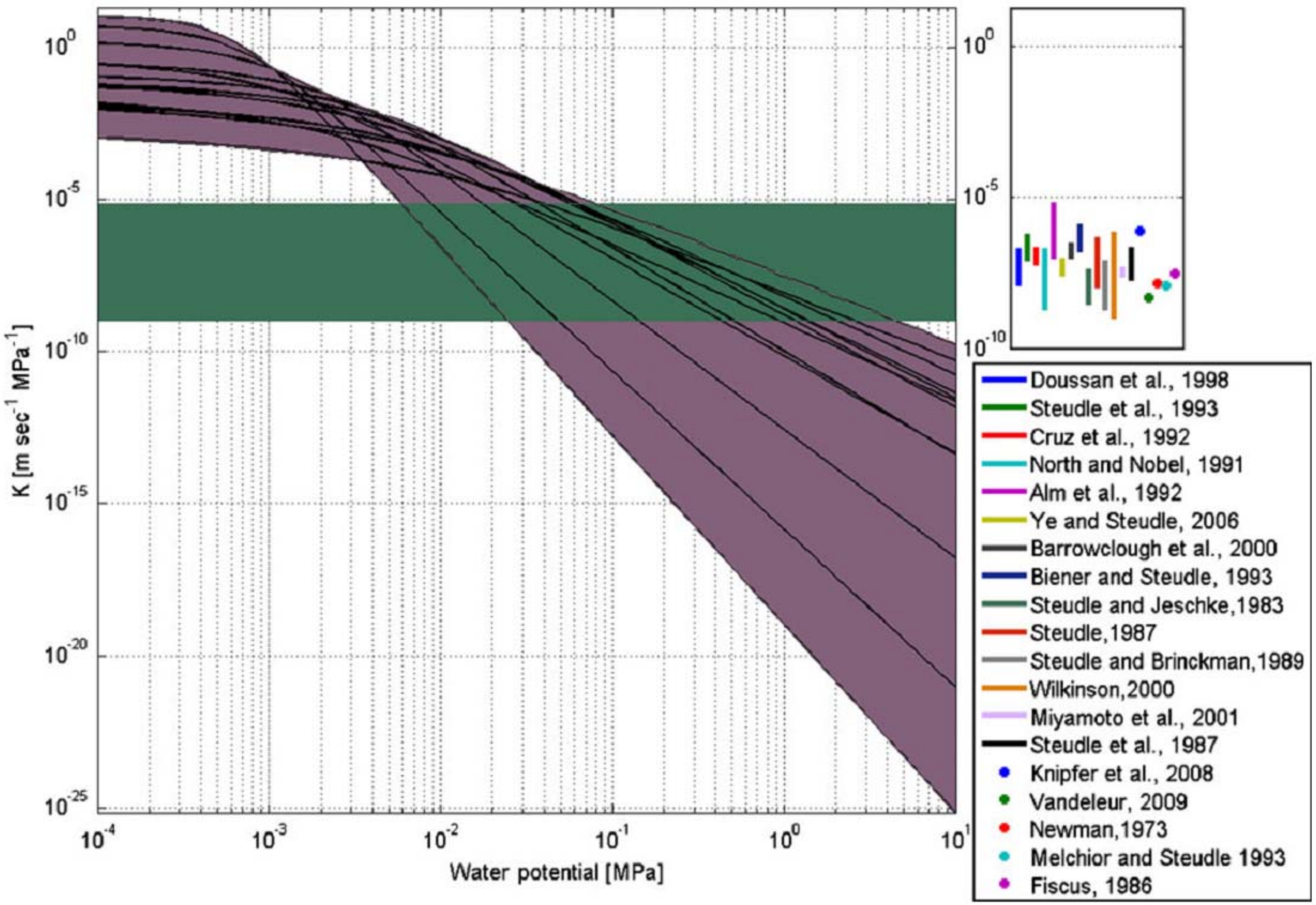
Hypothesis

Stomata close when $\Psi_{leaf}(E)$ becomes nonlinear, and this nonlinearity depends on the loss of soil hydraulic conductivity.
The loss of soil hydraulic conductivity, more than xylem vulnerability, drives stomatal response to soil drying.

Principles of water flow in soils

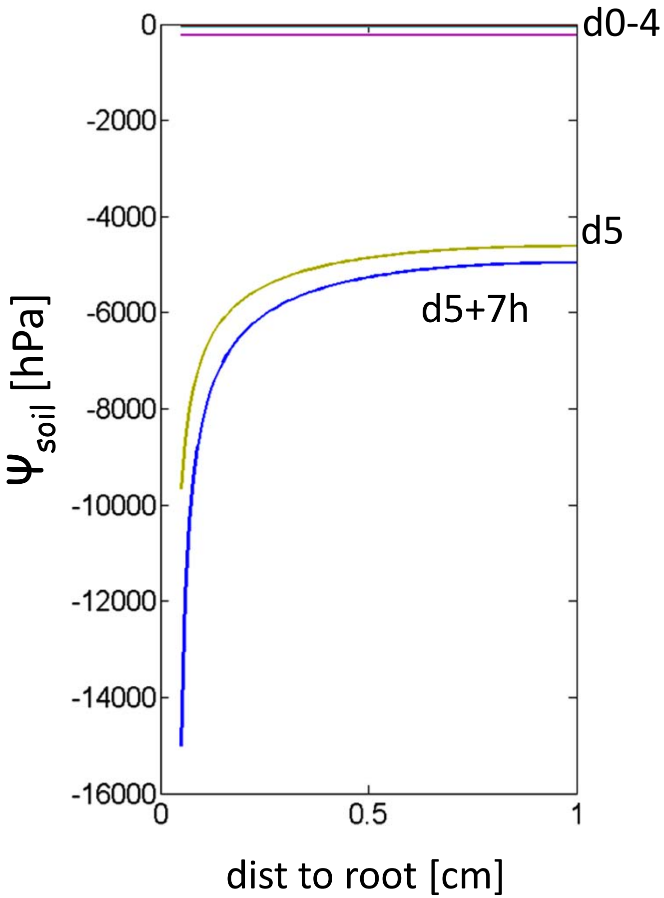
As the soil dries, ist hydraulic conductivity drops by >10 orders of magnitude.

Draye et al. 2010

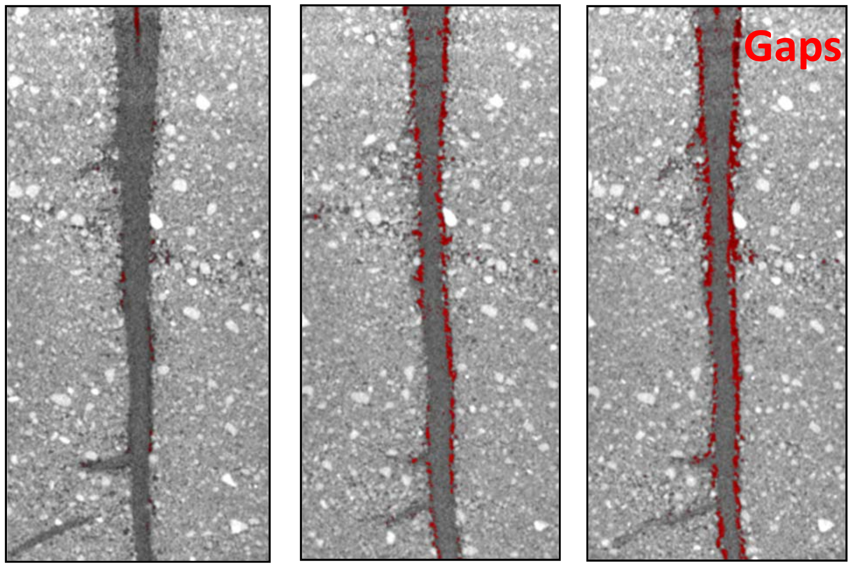


Principles of water flow in soils

Models predict a big drop in Ψ_{soil} around the roots (*Gardner 1960*).



Below this critical Ψ_{soil} the soil can no longer sustain the transpiration demand, roots shrink and lose contact to the soil.



Carminati et al. 2013

Principles of water flow in soils

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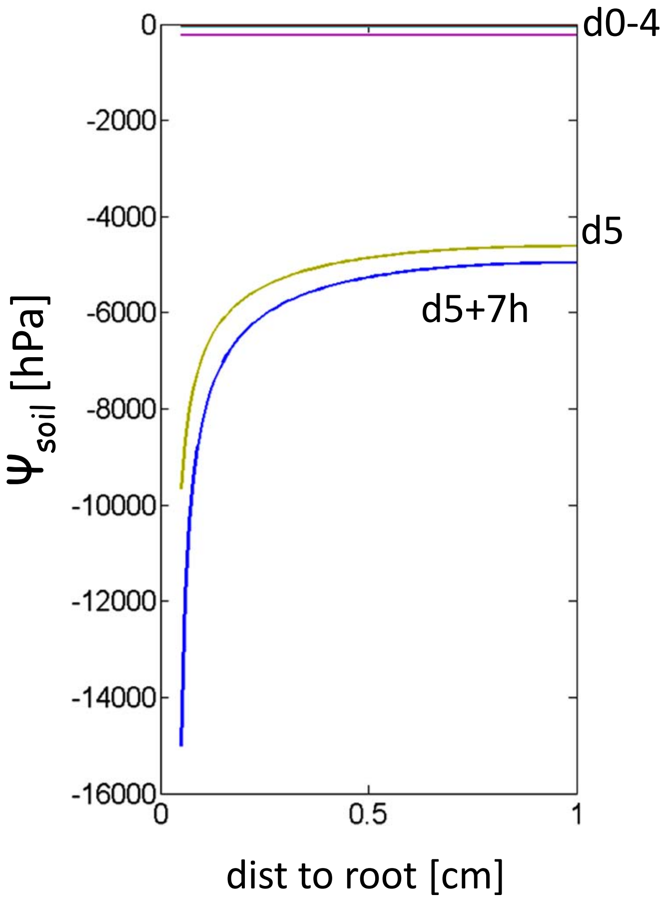

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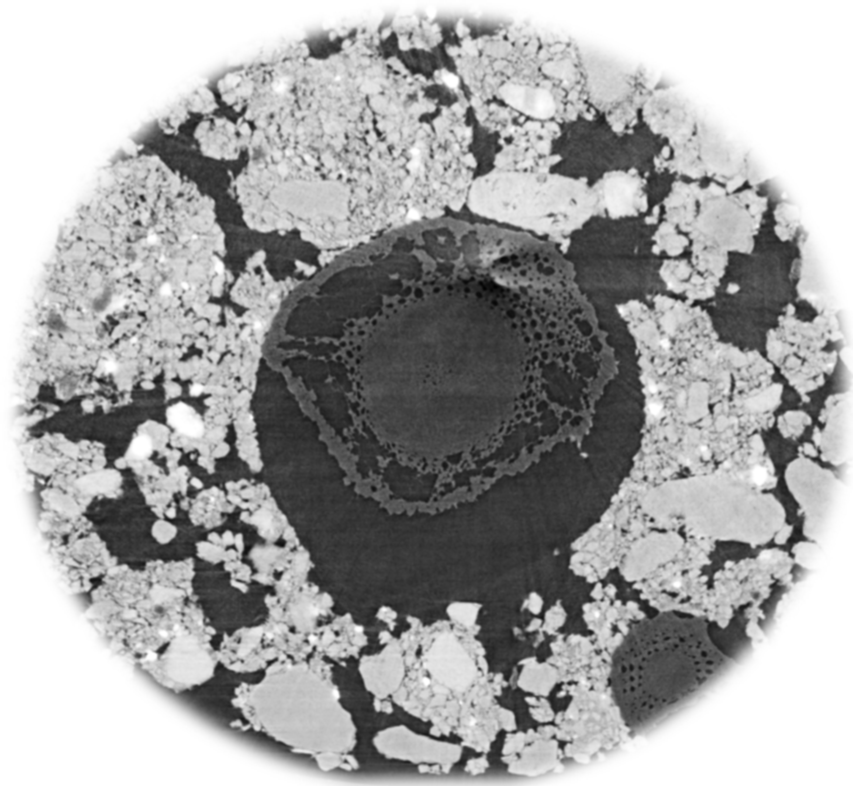
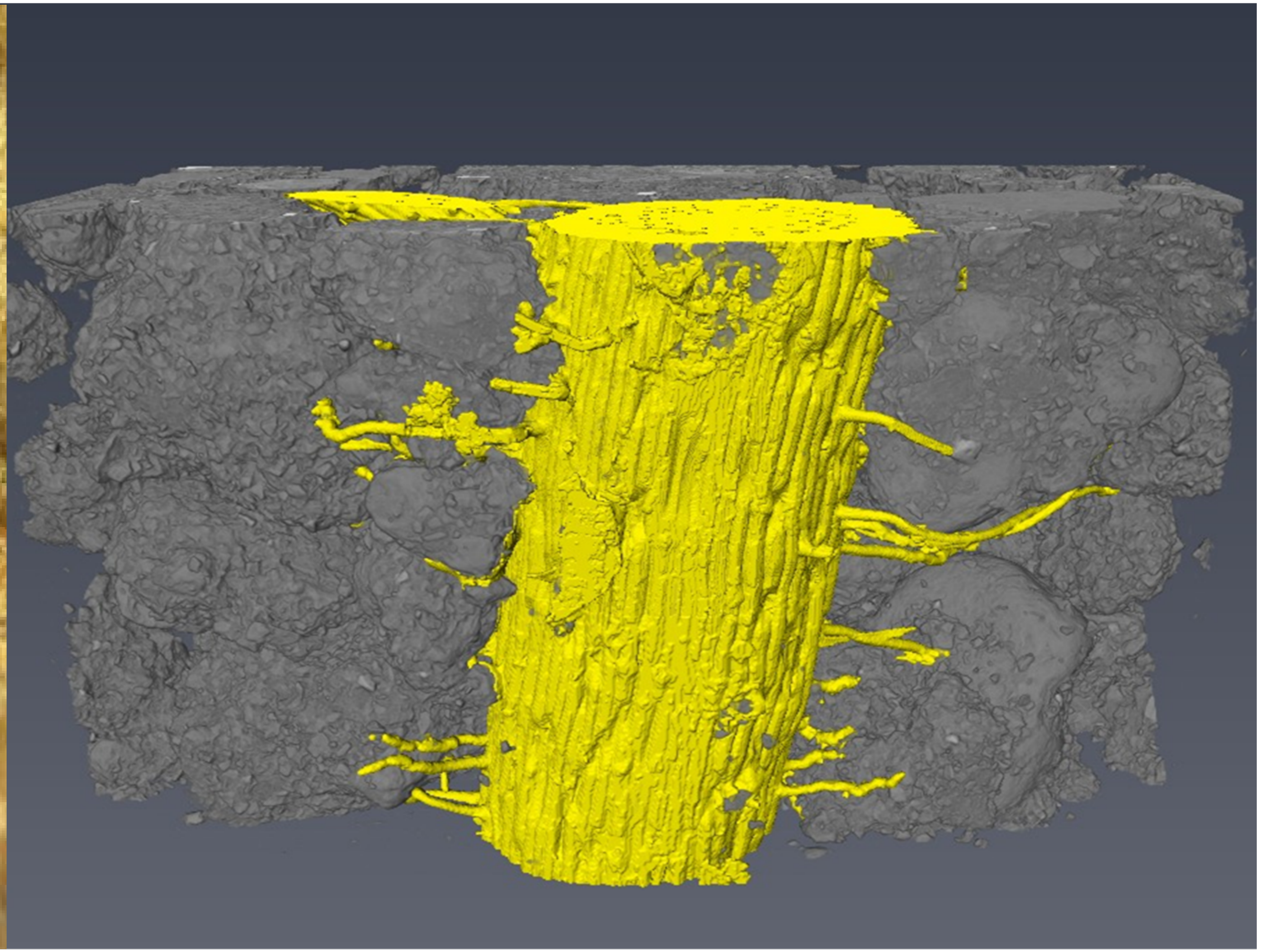
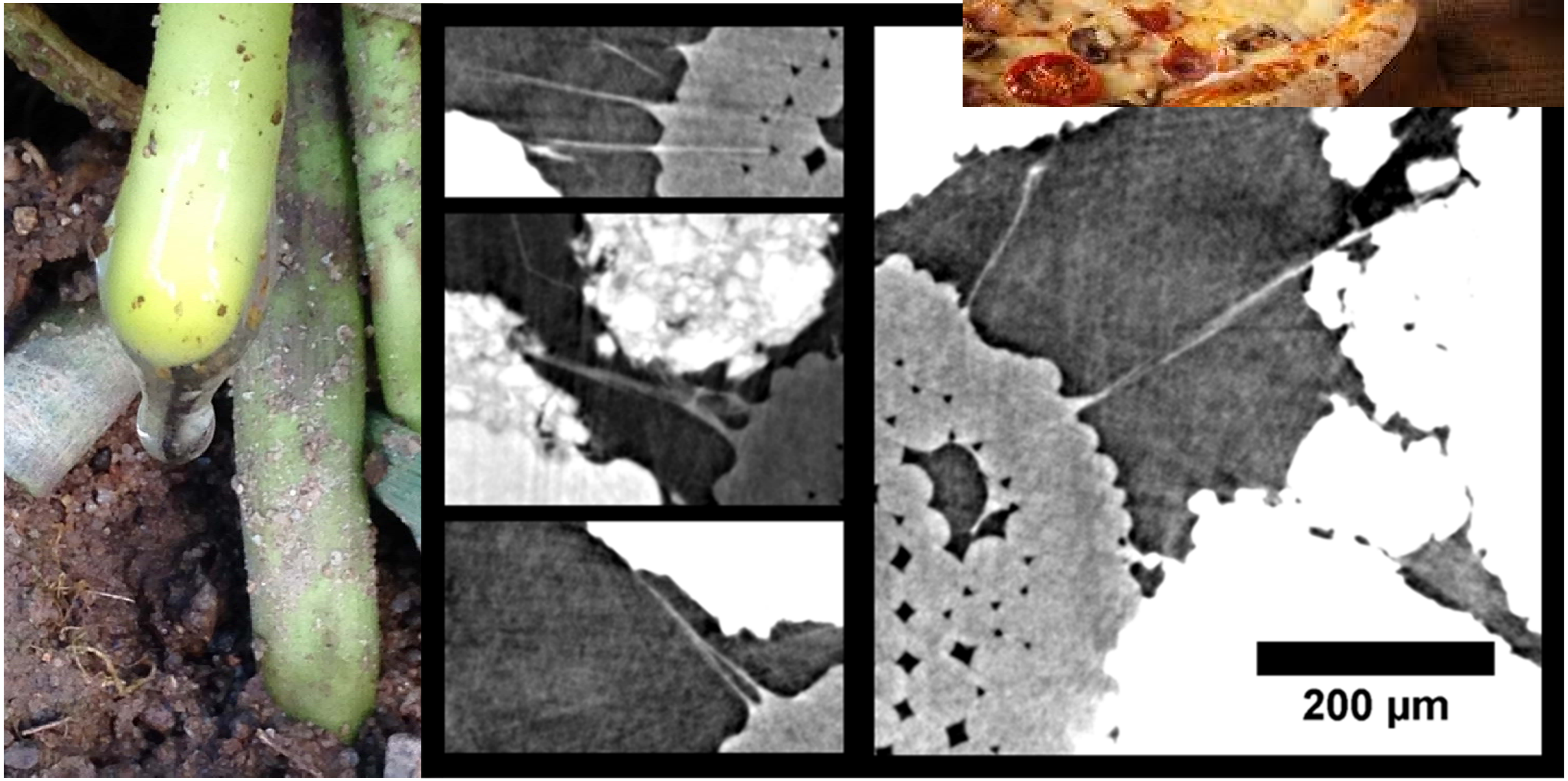


Courtesy of Patrick Duddek

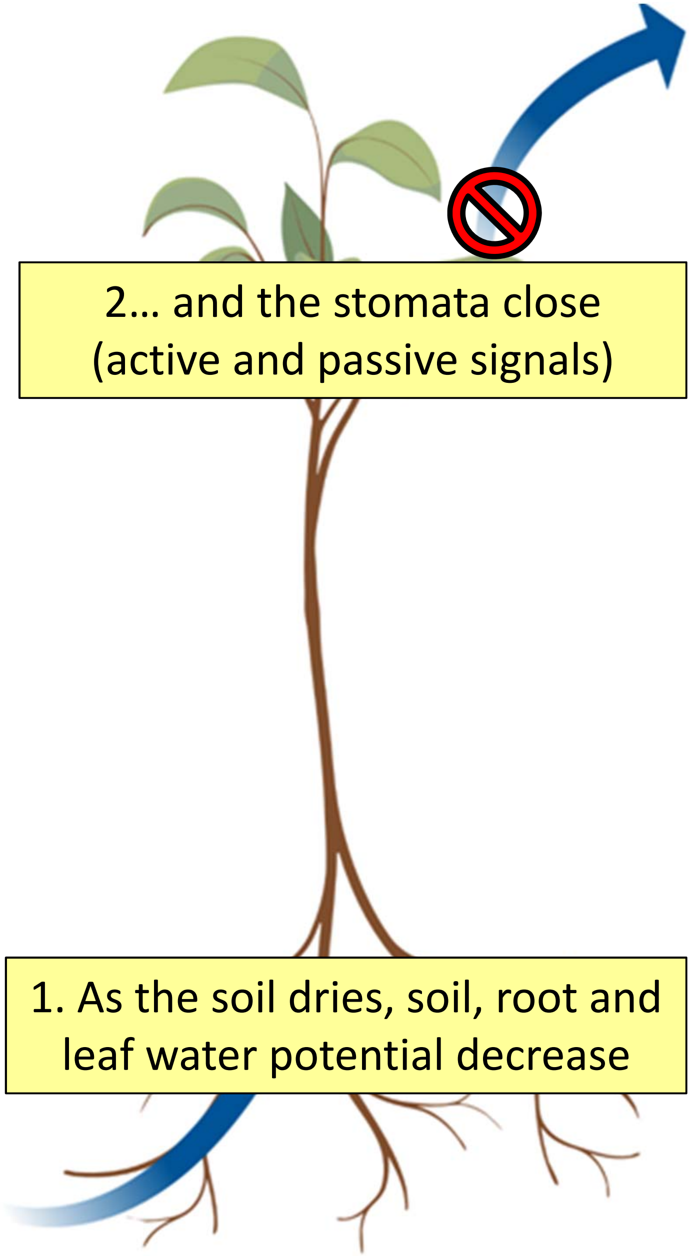
Root hairs connect roots to soil water

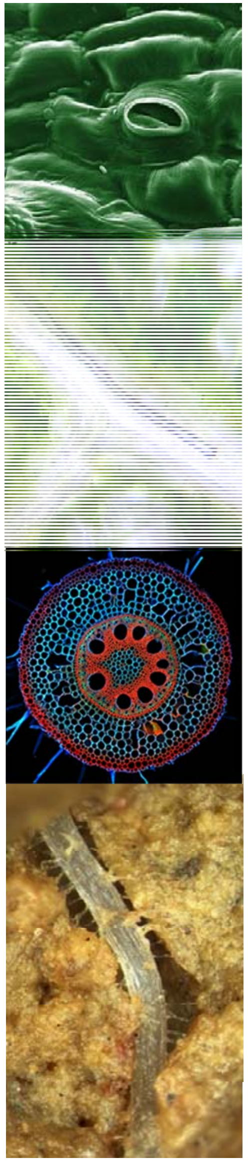


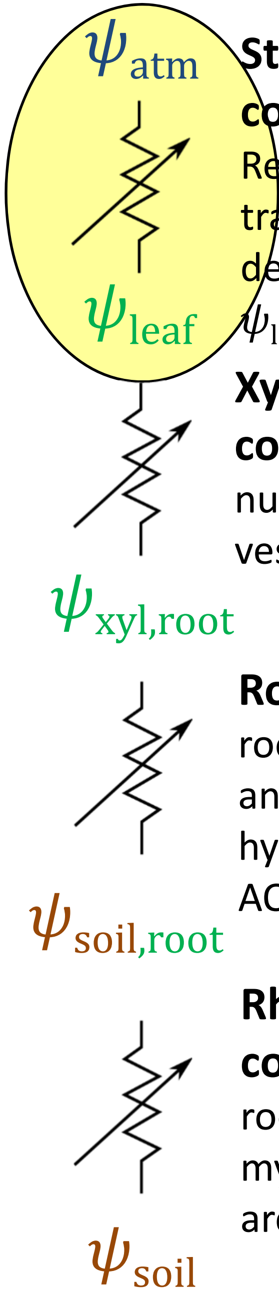
Mucilage connect roots



Principles of water flow in soil and plants







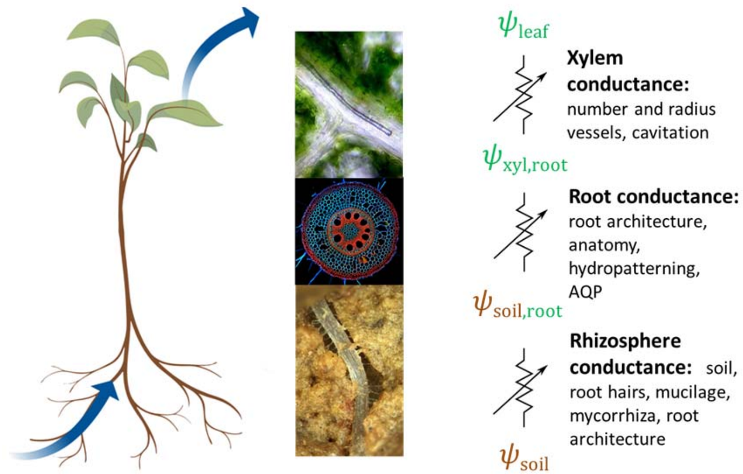
Stomatal conductance: Regulates transpiration, depends on ABA, ψ_{leaf}

Xylem conductance: number and radius vessels, cavitation

Root conductance: root architecture, anatomy, hydropatterning, AQP

Rhizosphere conductance: soil, root hairs, mucilage, mycorrhiza, root architecture

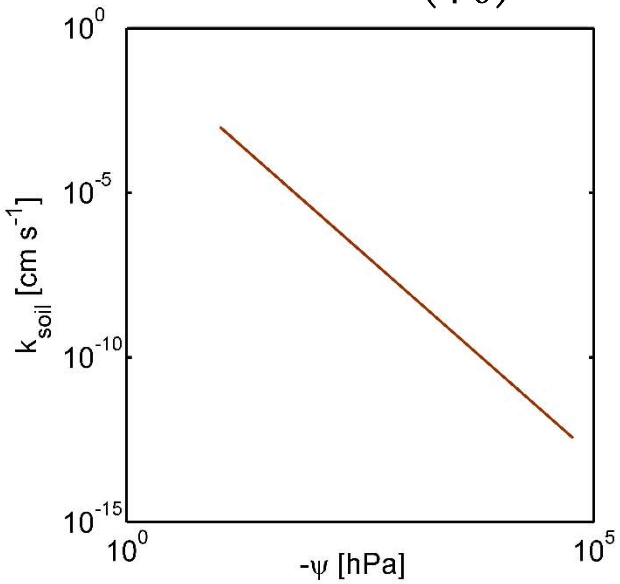
A simplified soil-plant hydraulic model



Soil

$$\frac{E}{2\pi r L} = -k_{soil}(\psi)\frac{\partial\psi}{\partial r}$$

$$k_{soil} = k_{sat}\left(\frac{\psi}{\psi_0}\right)^{\tau}$$



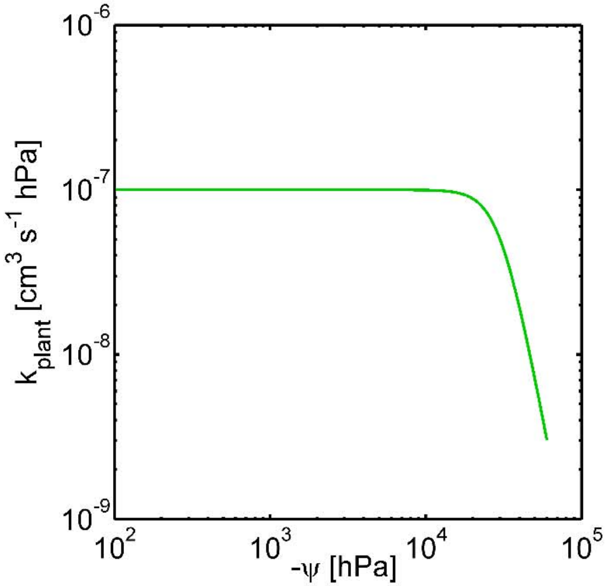
Roots

$$E = -K_{root}d\psi$$

Xylem

$$E = -K_x(\psi)(d\psi + dz)$$

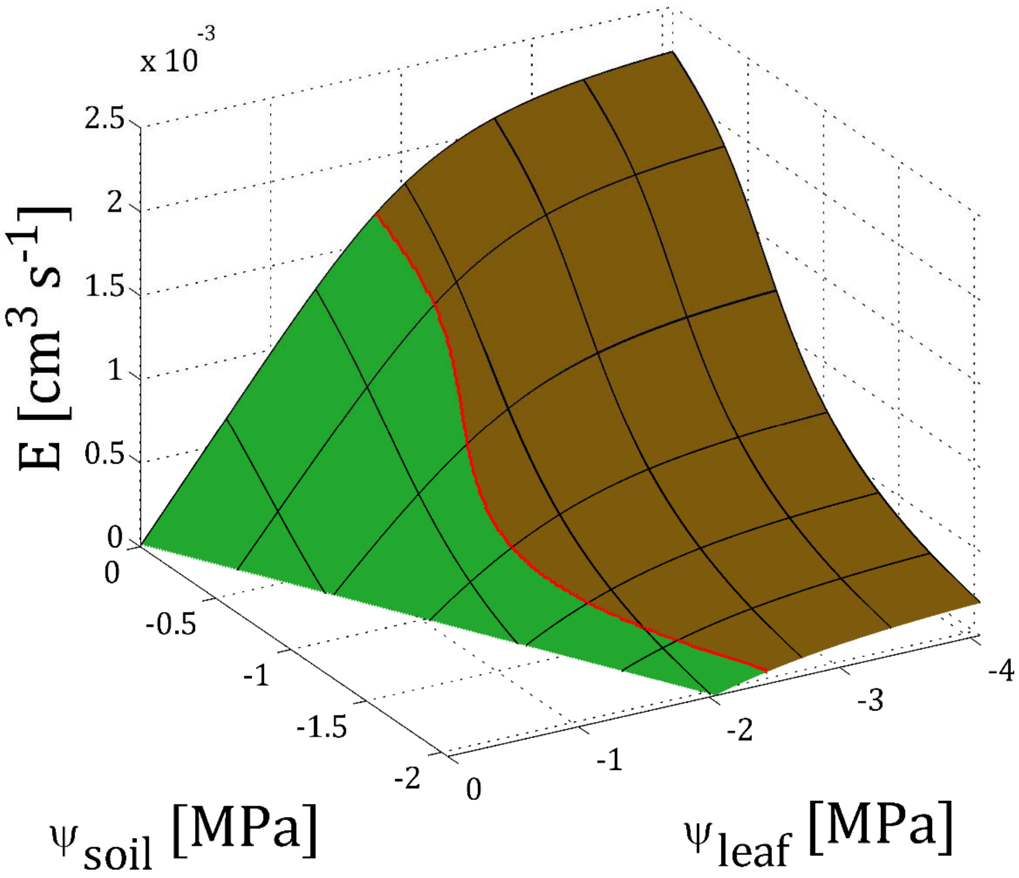
$$k_x = k_{max}\left(\frac{\psi}{\psi_{0x}}\right)^{\tau x}$$



$K_{plant} = (1/K_{root} + 1/K_x)^{-1}$

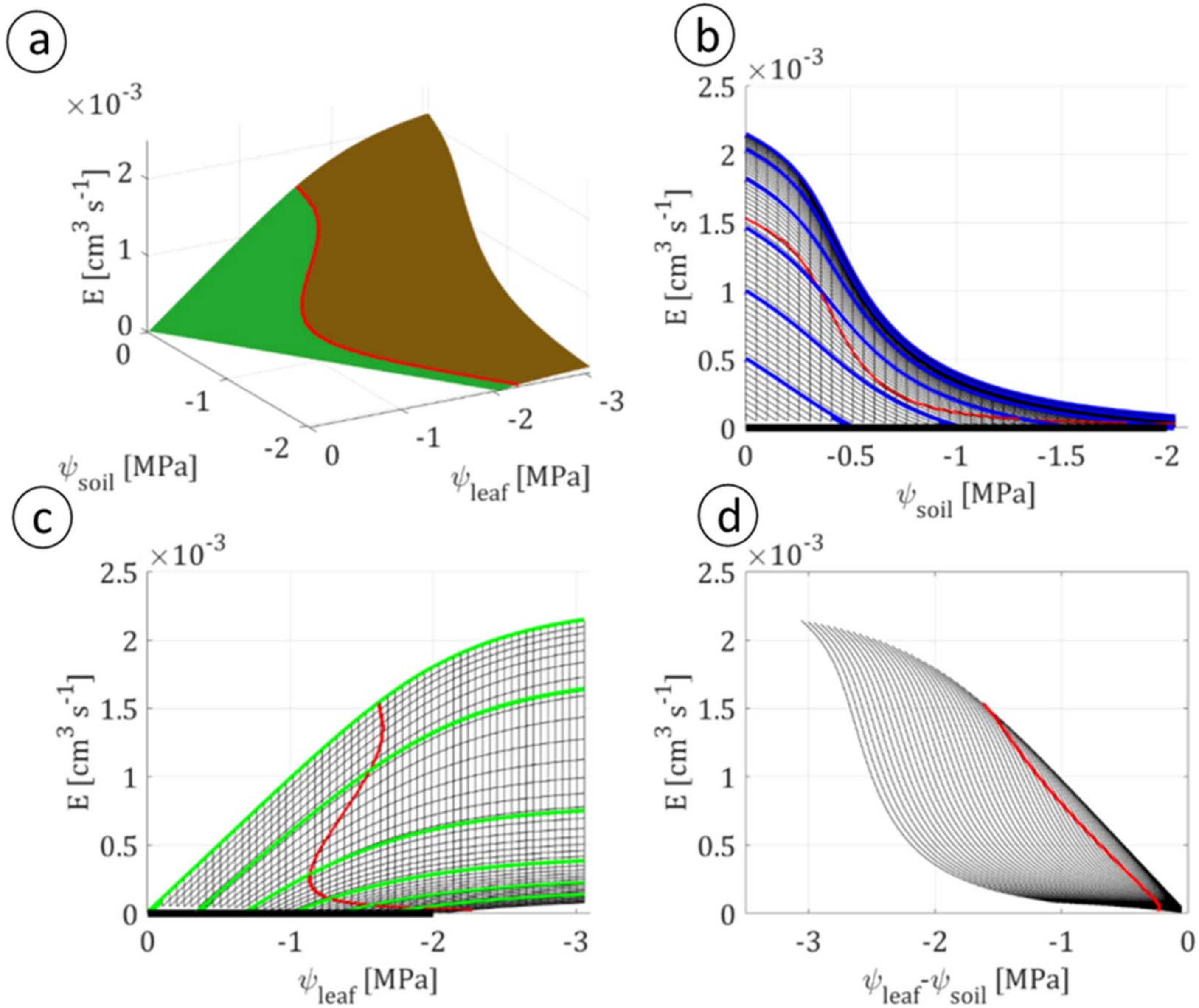
E transpiration
r root radius
z height
L active root length
Ψ hydrostatic/matric potential
k_{soil}, K_{root}, K_x soil, root and xylem conductvity

Physical constraints on water flow in soil and plants

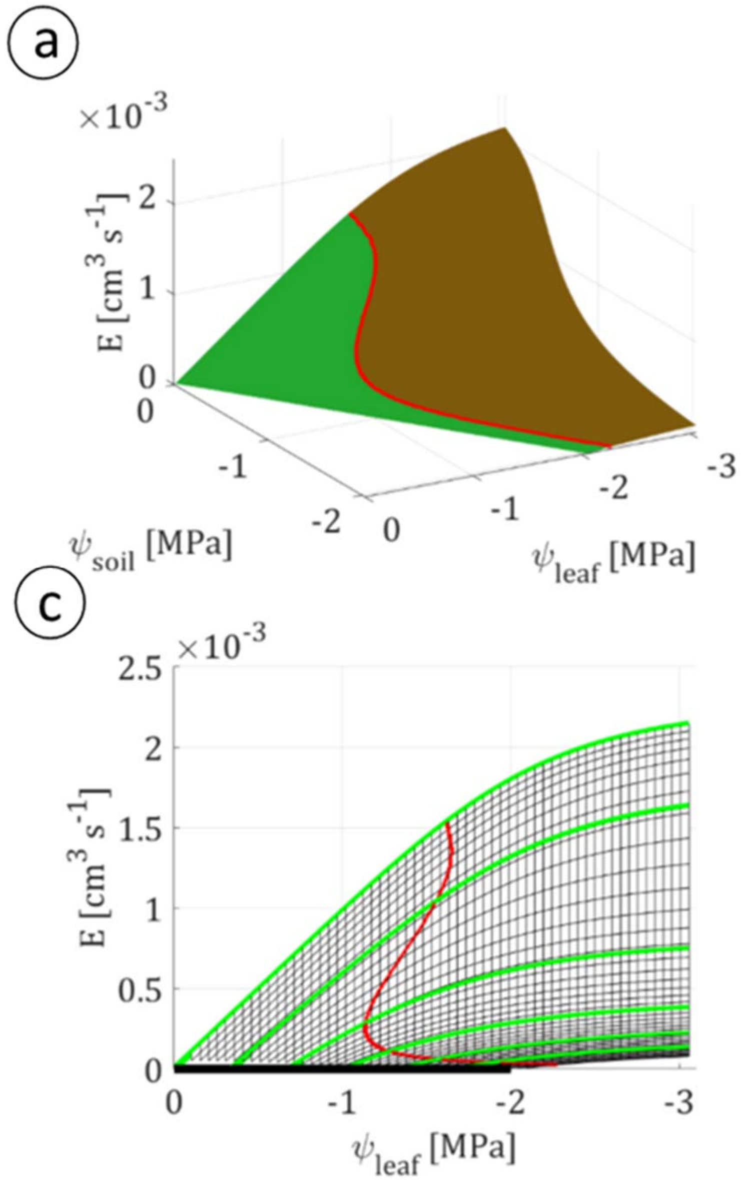


The red line marks the onset of hydraulic nonlinearity, when $\left.\frac{\partial E}{\partial \psi_{leaf}}\right|_{\psi_{soil}}$ starts to decrease.

Physical constraints on water flow in soil and plants



Physical constraints on water flow in soil and plants

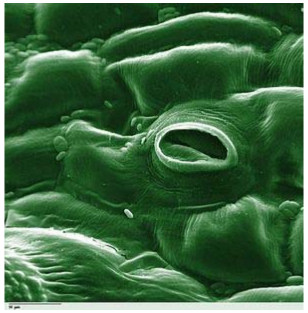


Beyond the **red line**, the water flow is not linear (=not *convenient*).

Hypothesis: plants do not cross the red line and stay in the linear part of the $E(\Psi_{leaf},\Psi_{soil})$ relation:

$$\left.\frac{\partial E}{\partial \psi_{leaf}}\right|_{\Psi_{soil}} \approx K_{plant}$$

Stomatal regulation



How could stomata respond to changes in $\frac{\partial E}{\partial \psi_{leaf}}$?

Hypothesis

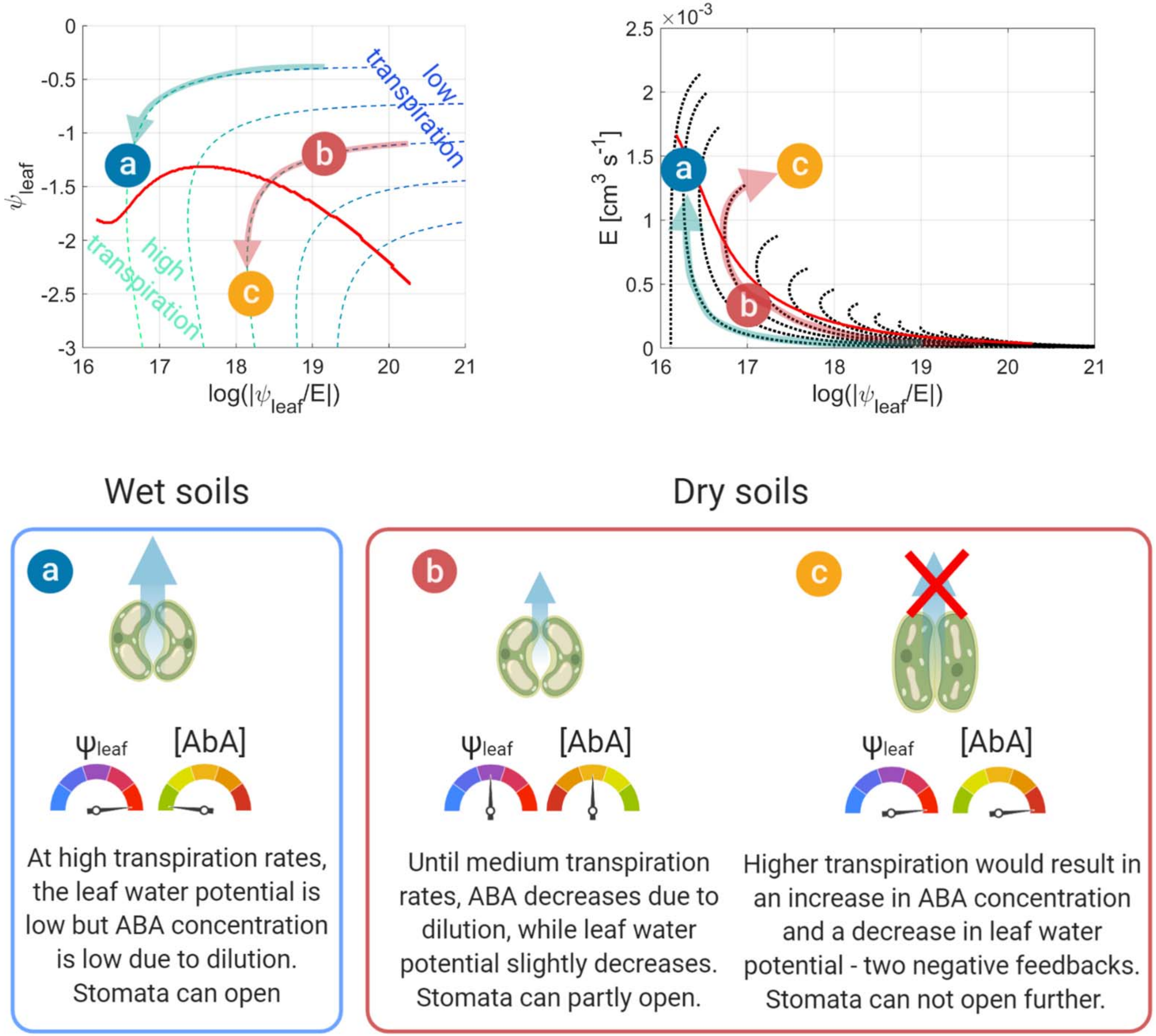
ABA production and dilution allows to maintain $\left.\frac{\partial E}{\partial \psi_{leaf}}\right|_{\Psi_{soil}} \approx K_{plant}$

Supporting argument

1. High concentration of ABA in the xylem $[ABA]_{xyl}$ triggers stomata closure.
2. ABA production increases with decreasing ψ_{leaf}.
3. ABA is diluted by water flow E.

→ $[ABA]_{xyl}$ increases with increasing $\frac{-\psi_{leaf}}{E}$.

Stomatal regulation



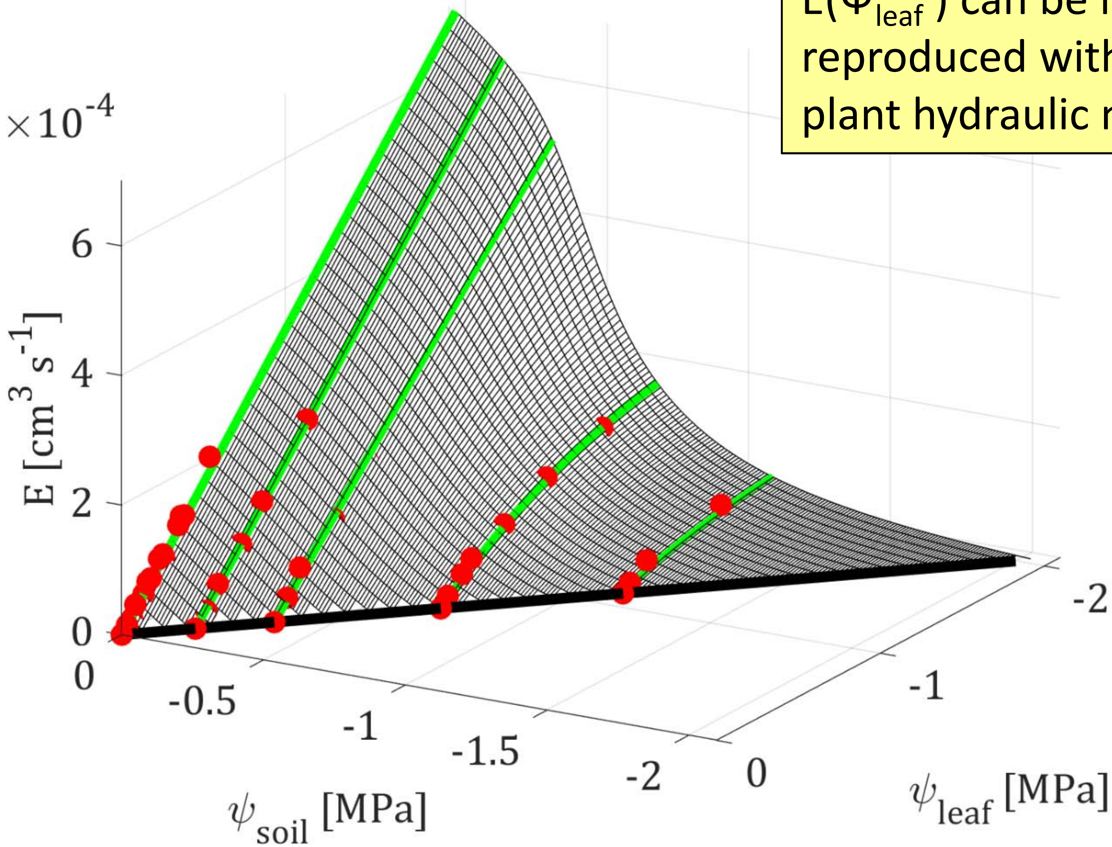
$\frac{\partial g_s}{\partial [ABA]_{xyl}} > 0$ is not sustainable, because an increase in stomata conductance is associated with an increase in $[ABA]_{xyl}$, which triggers a stomata closure. This mechanism would allow for plants to stay in the linear part of E (Ψ_{leaf},Ψ_{soil}).

Experimental evidences

Journal of Experimental Botany, Vol. 31, No. 120, pp. 333–345, February 1980

The Transport of Water from Soil to Shoot in Wheat Seedlings

J. B. PASSIOURA



$E(\Psi_{leaf})$ can be measured and reproduced with a simple soil-plant hydraulic model.

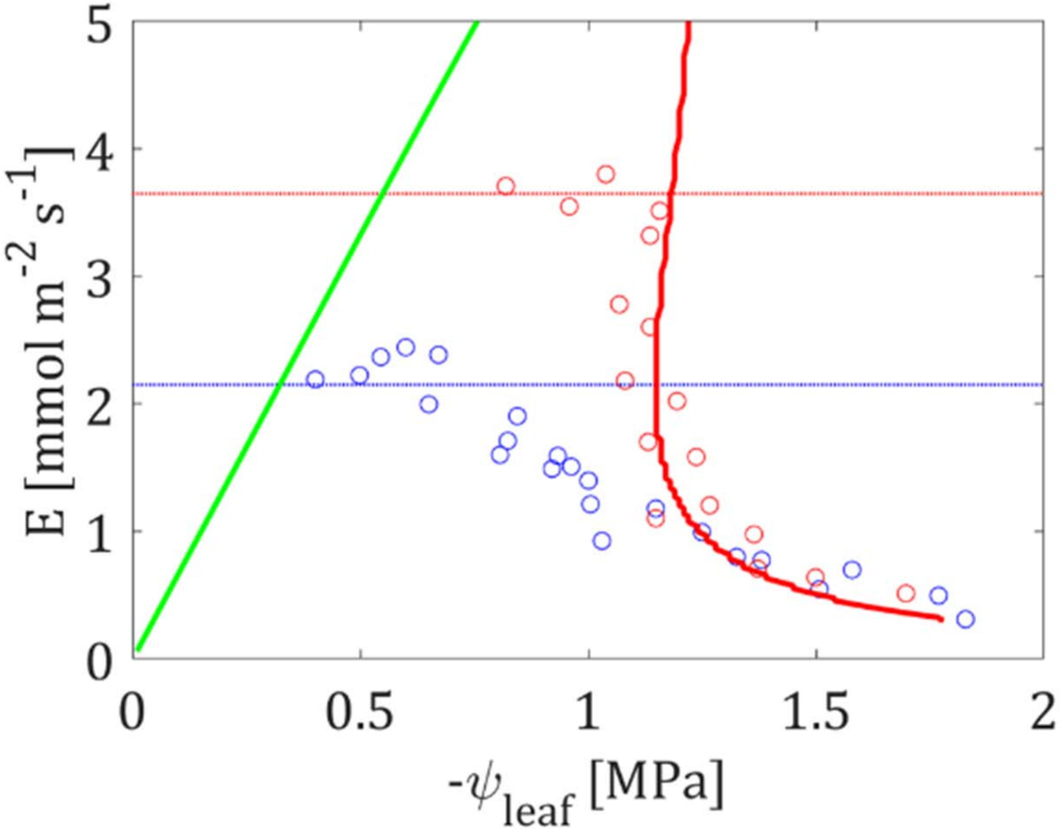
Experimental evidences

The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content

III. In the sclerophyllous woody species *Nerium oleander*

T. Gollan[1], N.C. Turner[1,2], and E.-D. Schulze[1]

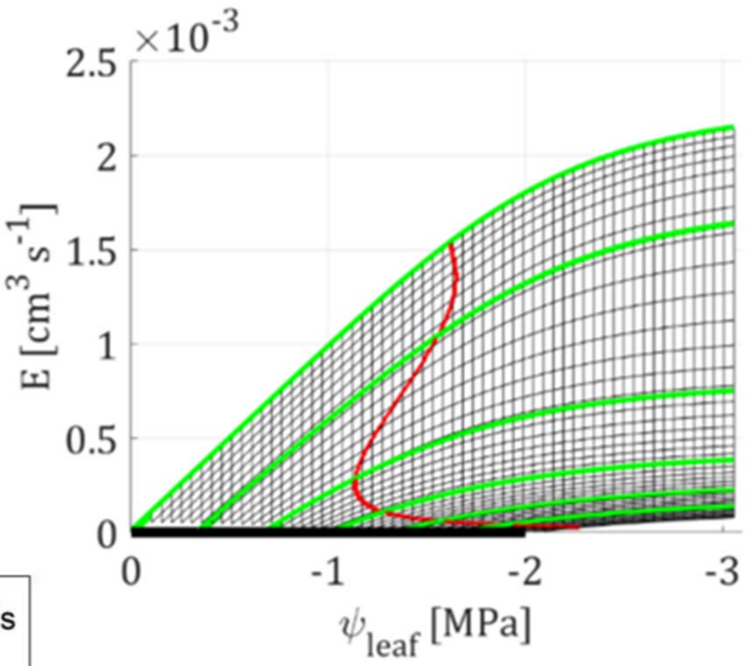
[1] Lehrstuhl für Pflanzenökologie, Universität Bayreuth, Postfach 3008, D-8580 Bayreuth, Federal Republic of Germany
[2] CSIRO Dryland Crops and Soils Research Program, Private Bag, P.O., Wembley, W.A. 6014, Australia

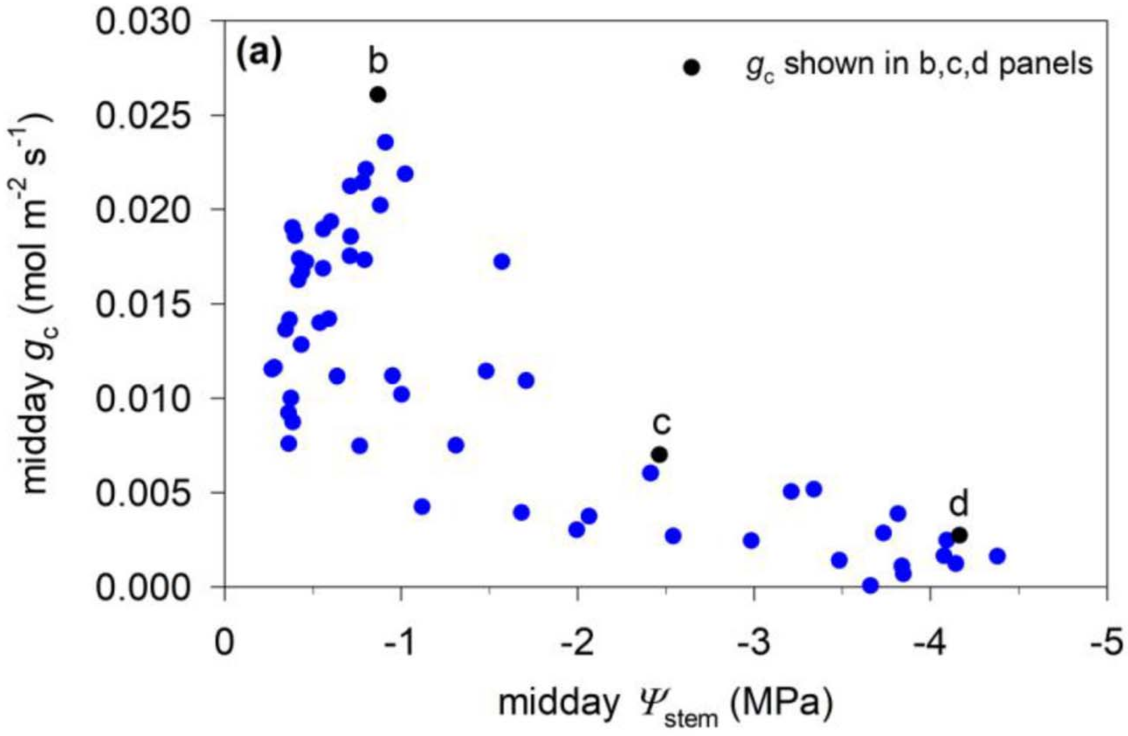


Transpiration of plants in drying soils follows the onset of hydraulic nonlinearity.

Experimental evidences

Rodriguez-Domiguez & Brodribb,
New Phytologist, 2019

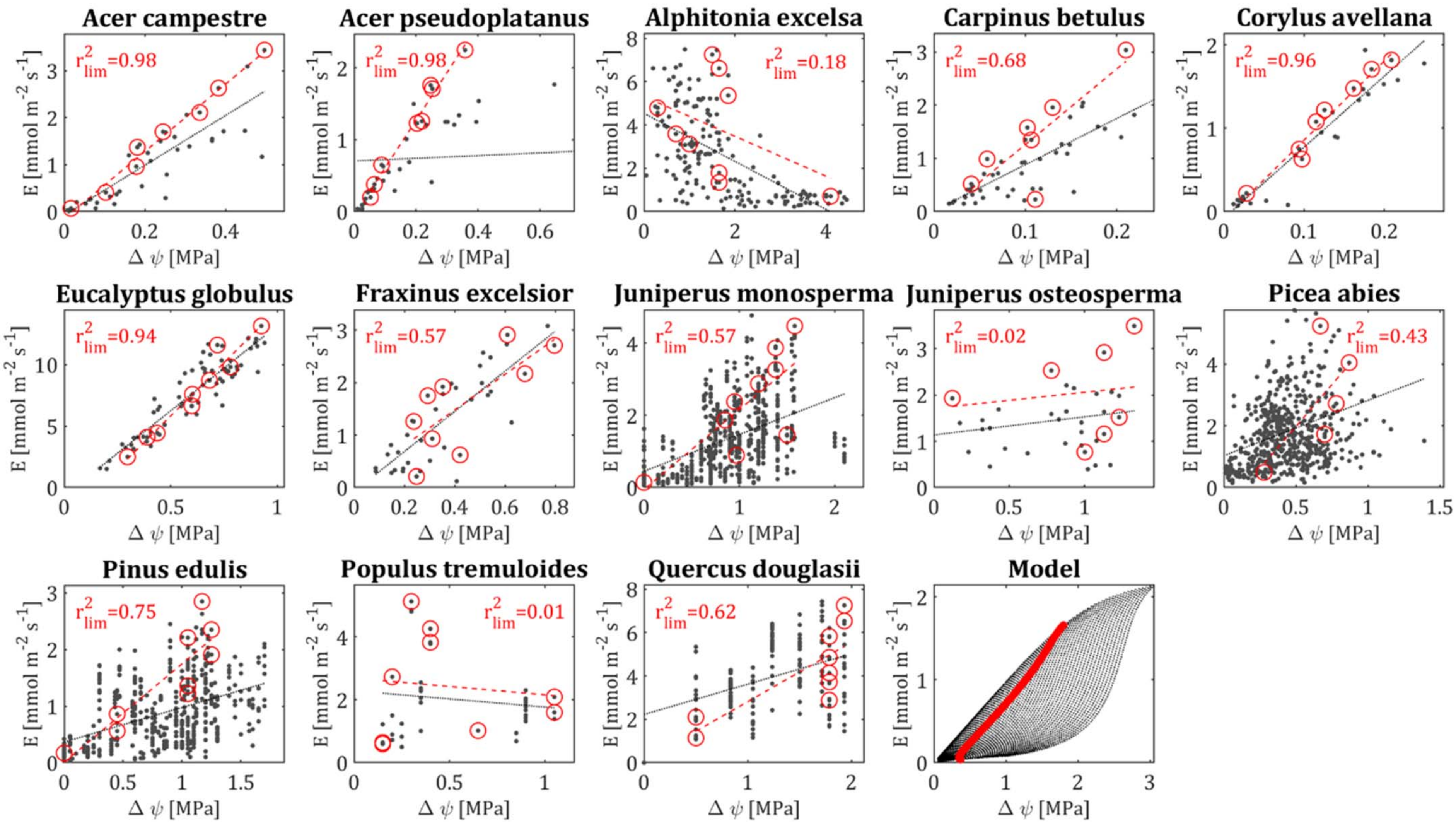




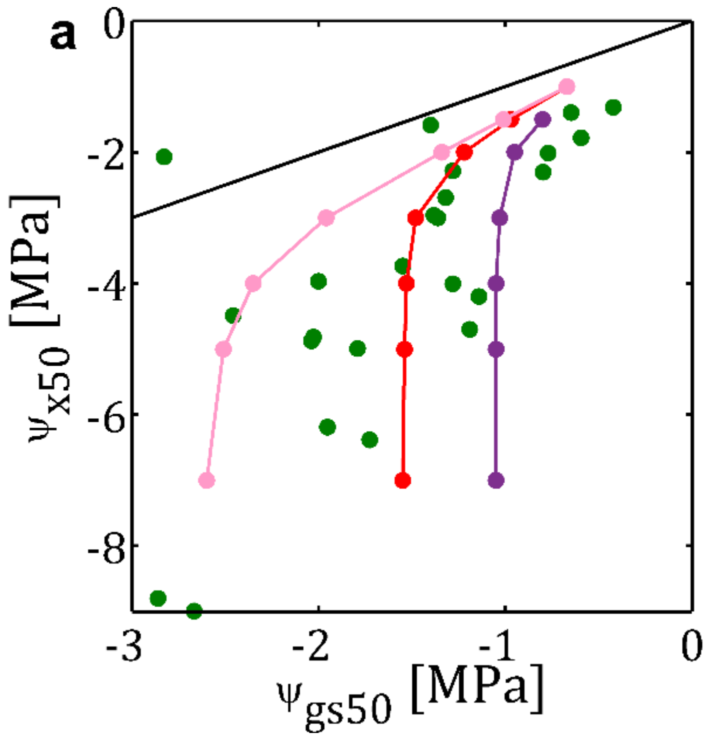
Expected and measured relationships between leaf water potential and stomatal conductance show a very similar behaviour.

Experimental evidences

meta analysis by Anderegg et al. 2017 PLoS ONE



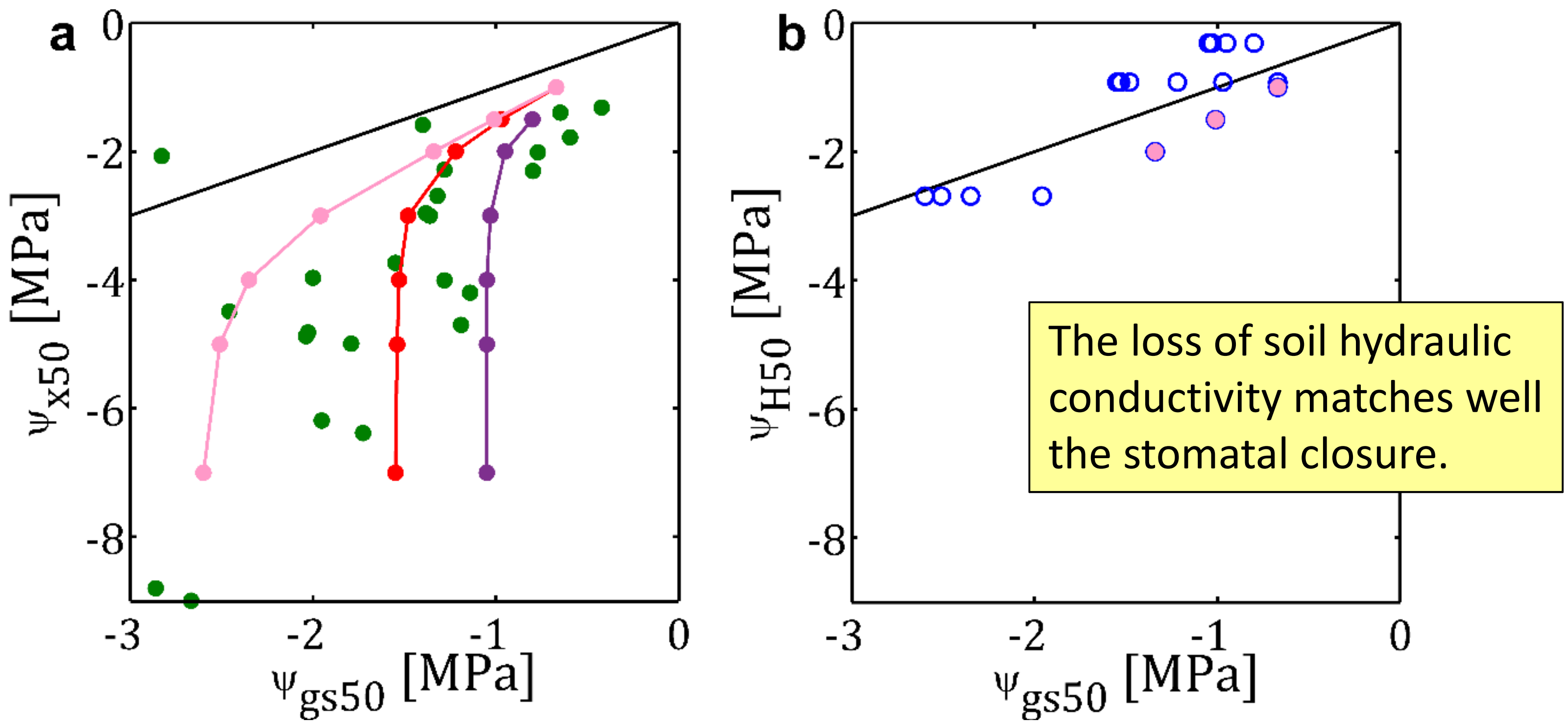
Soil versus xylem vulnearbility



Green circles from Anderegg et al. 2017. Pink, red and purple lines and circles are simulations with varying root lengths (pink L=500 cm, red L=2500 cm and purple L=12500 cm).

Loss in soil hydraulic can explain the stomata closure before the xylem cavitates.

Soil versus xylem vulnearbility



Definitions

ψ_{H50}: the maximum between ψ_{x50} and ψ_{s50}

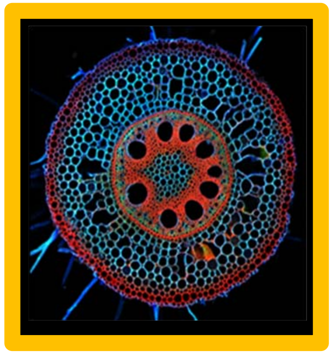
ψ_{s50}: the lowest soil matric potential at which 50% of the potential transpiration can be sustained by soil water flow.

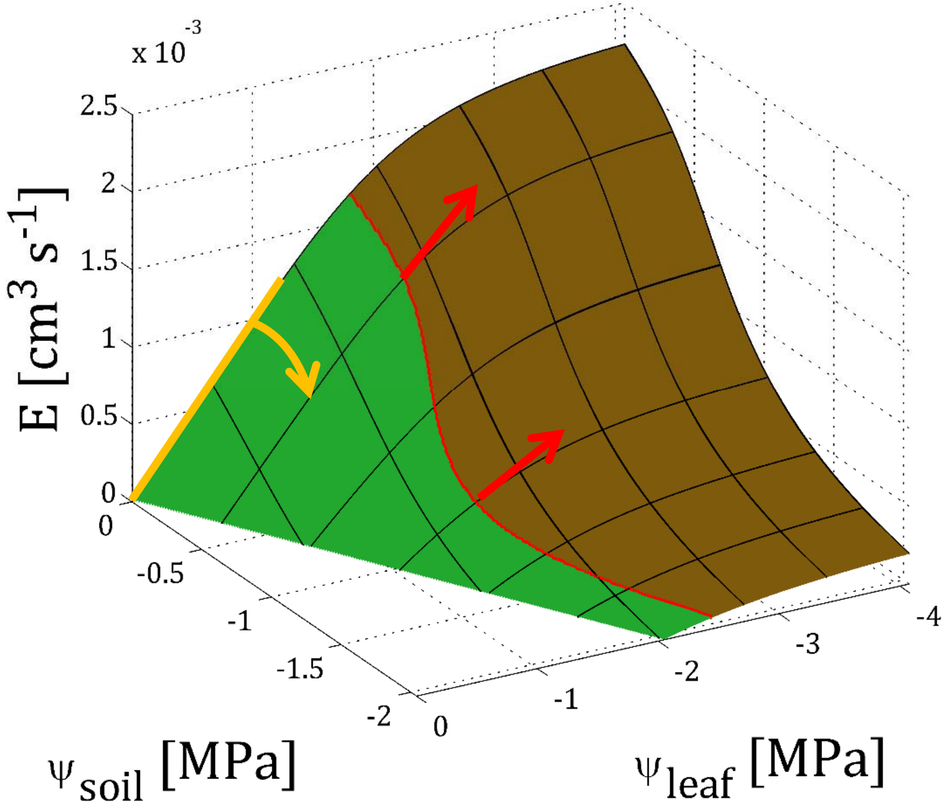
The blue circles are simulations corresponding to the pink, red and purple circles, whose ψ_{x50} is shown in (a). For the circles filled in pink $\psi_{H50} = \psi_{x50}$.

Belowground responses to soil drying:

Root hydraulic plasticity

Anatomical barrier or AQP regulations





Root growth

Root hairs

Mucilage

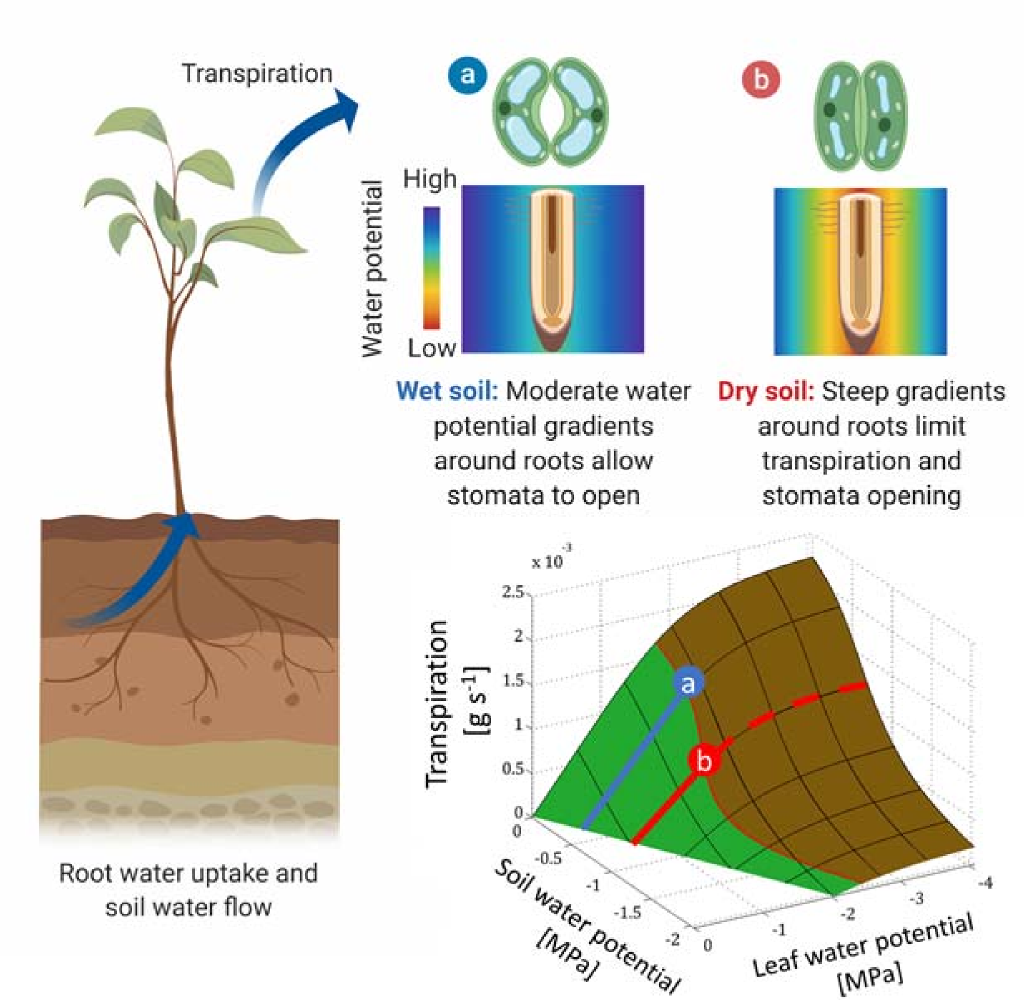
Plants can respond to soil drying not only by closiong stomata, but aslo by changing their hydraulic conductance.

Conclusions

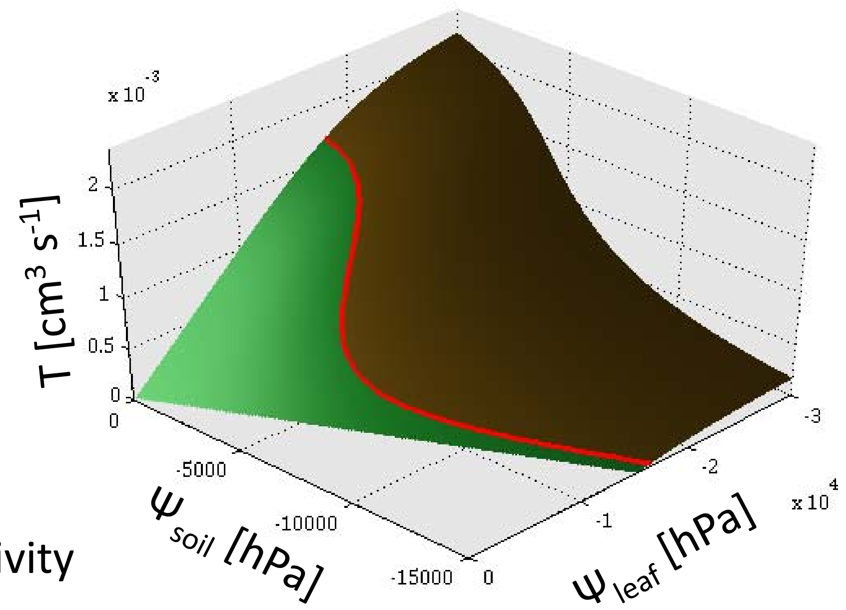
The loss of soil hydraulic conductivity around roots triggers the closure of stomata in a predictable way.

A hormonal signal diluted by transpiration allows for maintaining a linear relationship between transpiration and leaf water potential.

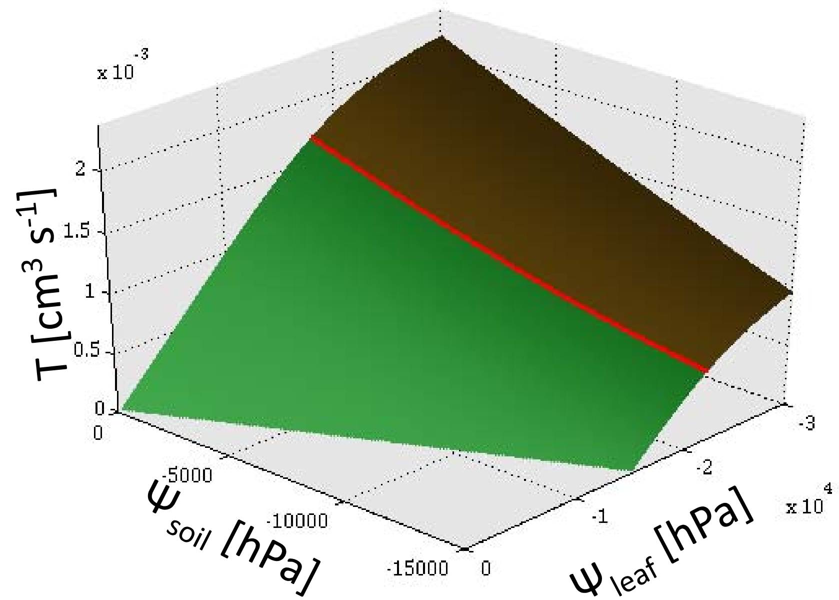
On a longer time scale (days-weeks) root plasticity can attenuate the drops in water potential around the roots.



Xylem or soil vulnerability



No drop in soil conductivity (e.g. large root surface)



No xylem cavitation