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Stomatal control model to maximize plant photosynthesis, phloem transport and sugar usage

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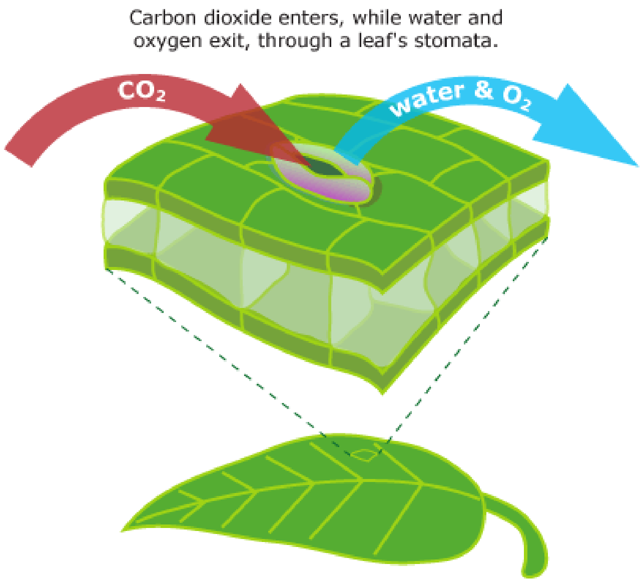
Four seasons of the northward landscape from the mast of the SMEAR II
https://www.atm.helsinki.fi/SMEAR/index.php/smear-ii

Introduction

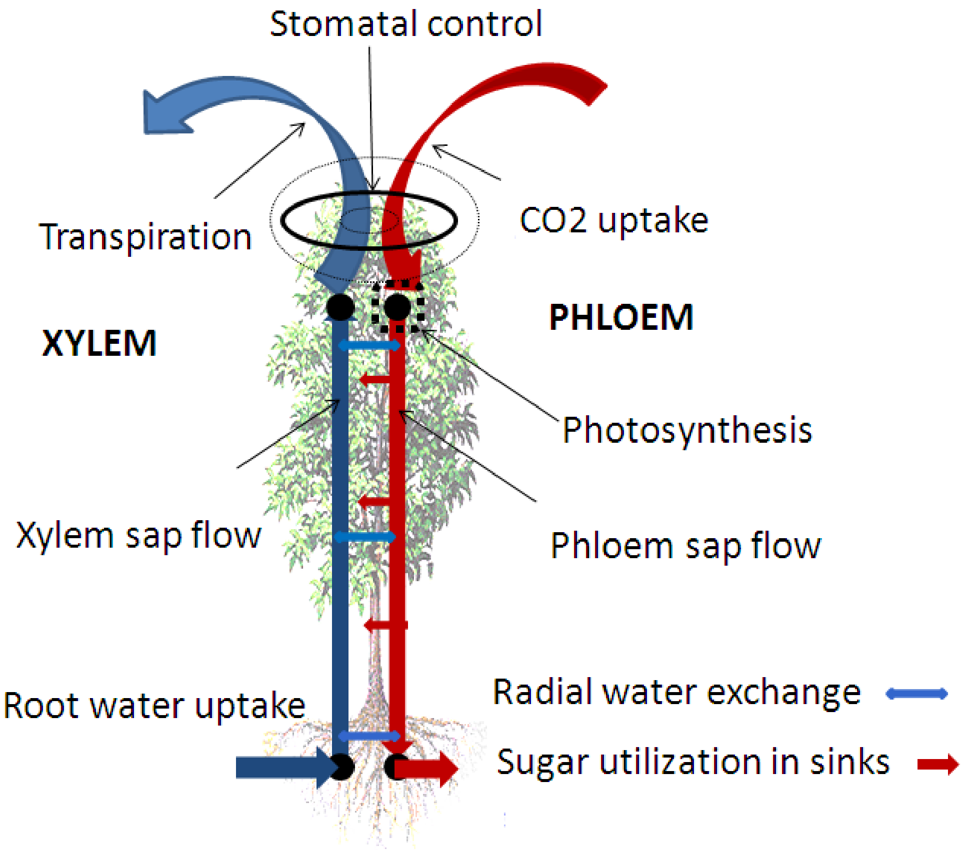
- Stomatal control models describe stomatal behavior as a function of environmental conditions (and empirical parameters).

- But yet we know that:
- Stomata react to changes in leaf water and carbohydrate status.
- Leaves are connected to other plant parts.



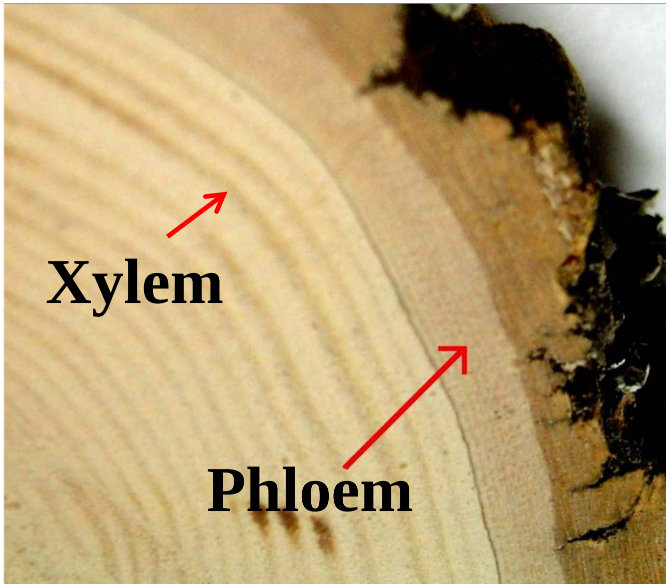
Introduction

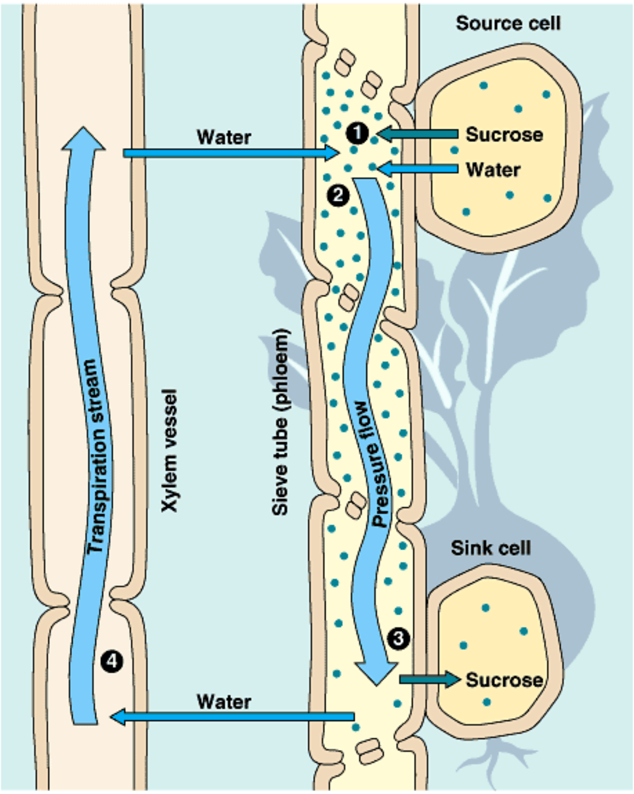
- All processes within a tree are somehow coupled to each other.
- Changes in source, sink or transport processes affects changes in all other processes.
- Can we try to understand stomatal behavior from whole tree level perspective?



Introduction

- Especially phloem transport links all tree processes: phloem transport from sources to sinks is dependent on both source and sink function, and on xylem water status.
- Change in any of these changes the osmotic concentration and turgor pressure and flow rate in phloem.





Dynamic modeling approach

- What if stomata would react in a way as to maximize instantaneous rate of phloem transport?
- (and ABA tranport from leaves)?

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Assimilate transport in phloem sets conditions for leaf gas exchange

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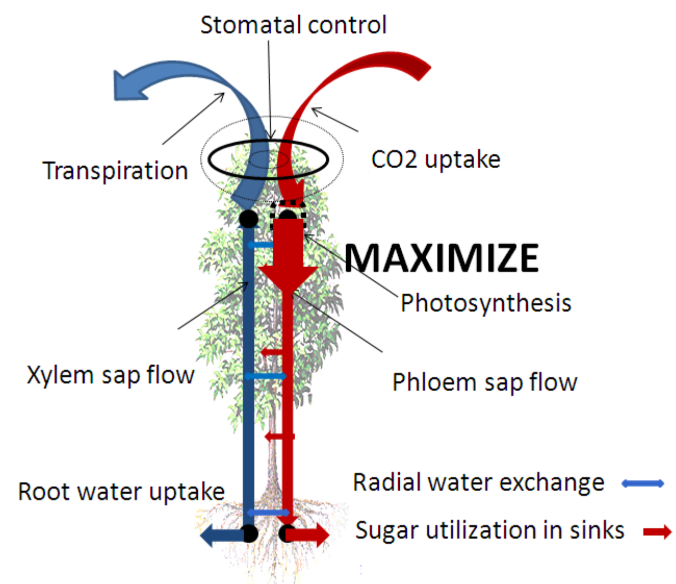

Dynamic modeling approach

- A dynamic model formulation yields reasoable results, but impossible to get analytical solution and solution is dependent on the time scale used.

High stomatal conductance when:
-High PAR
-Low VPD
-Good xylem conductance
-Good phloem conductance
-High soil water potential
-Low sugar concentration in sink
 (high utilization rate of sugars)

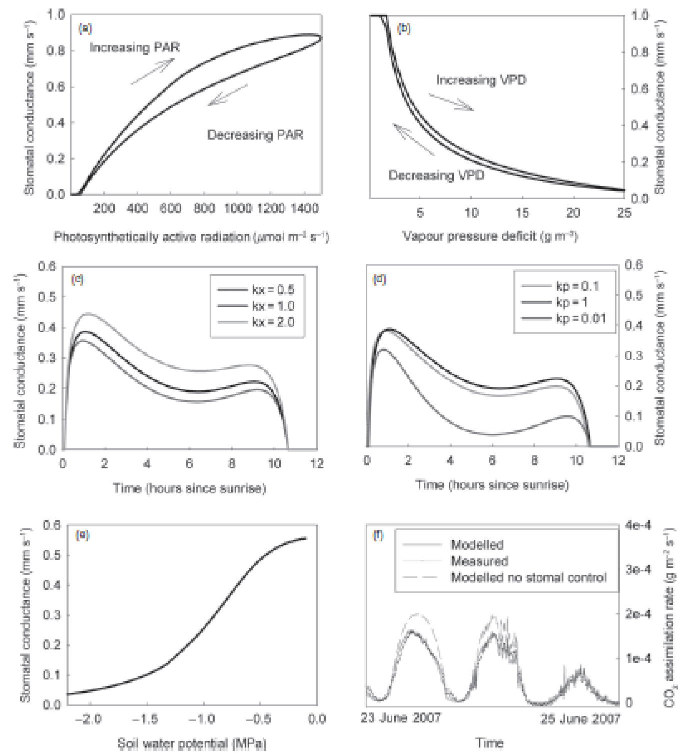

Figure 4. Stomatal conductance as a function of light (a) and vapour pressure deficit (VPD) (b), its daily pattern assuming sinusoidal light and temperature development with varying xylem conductance (kx) (m^2) (c), (base case solid black, halved xylem conductance dark grey and doubled phloem conductance light grey), and with varying phloem conductance (kp) (d) (base case solid black, one-tenth phloem conductance light grey and doubled phloem conductance dark grey), as a function of soil water potential (e) and comparison of measured (solid black), modelled (grey) and modelled without stomatal control (dashed grey) net assimilation rate for 3 d (22–24) in June 2007 at Hyytiala SMEAR II station (f).

Steady state approach

- Maximize whole tree metabolic rate?
- In steady state mebolic rate = photosynthesis rate = phloem transport rate = sink sugar utilization rate.


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Research paper

A steady-state stomatal model of balanced leaf gas exchange, hydraulics and maximal source–sink flux

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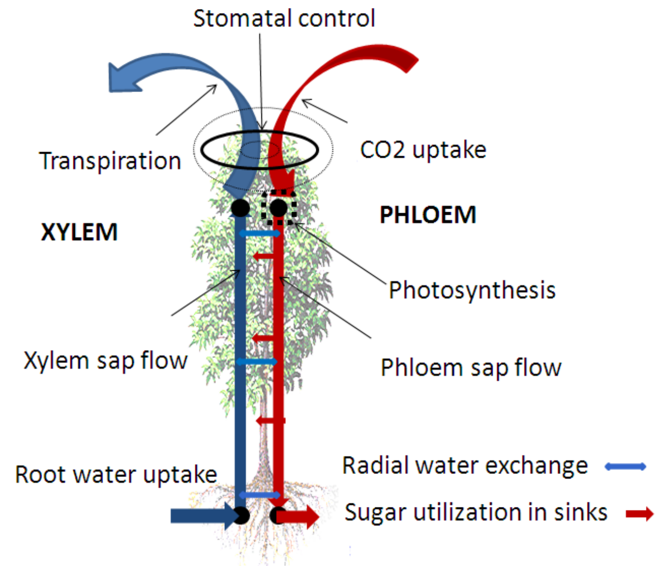
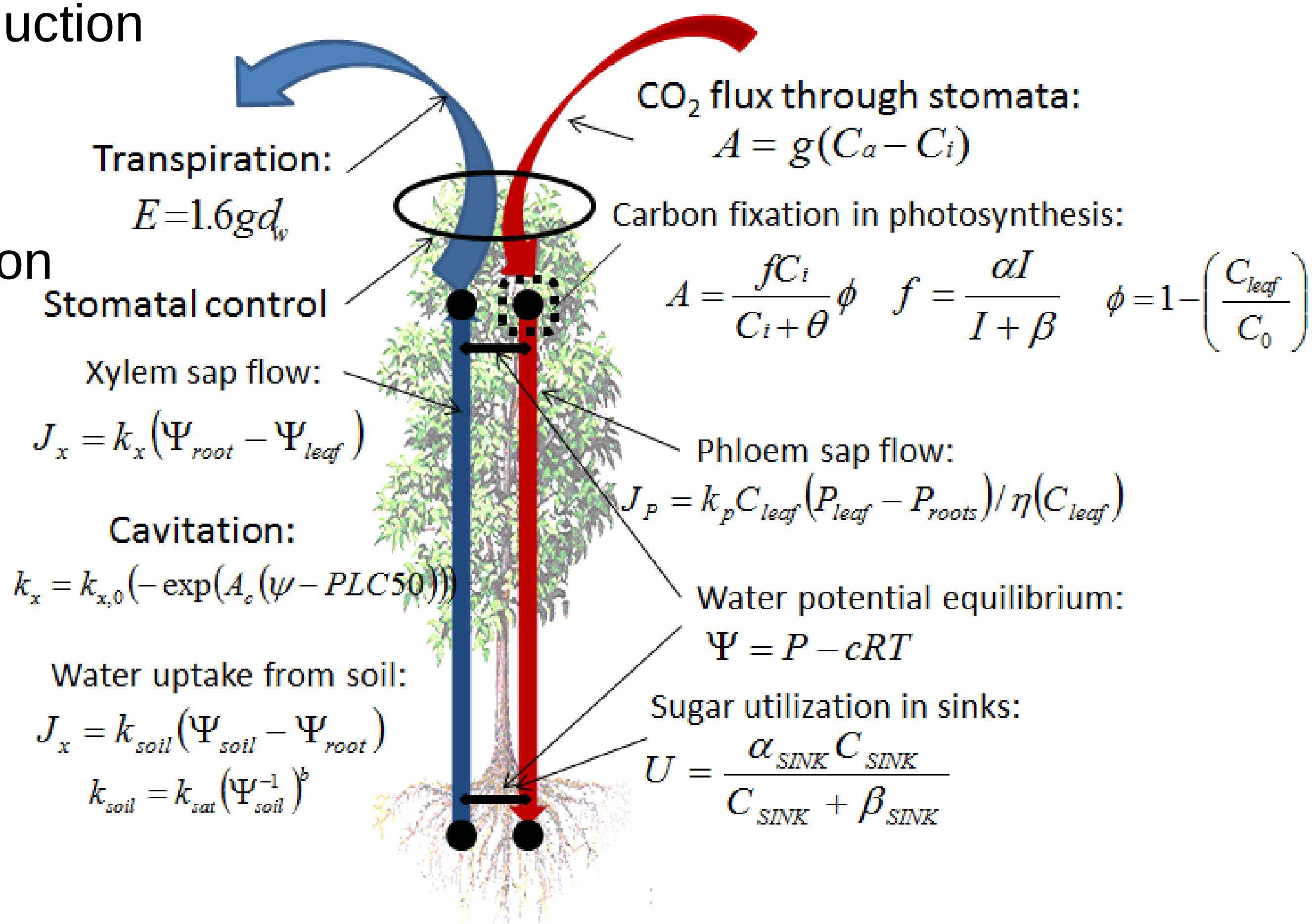


photosynthesis rate
= phloem transport rate
= sink rate

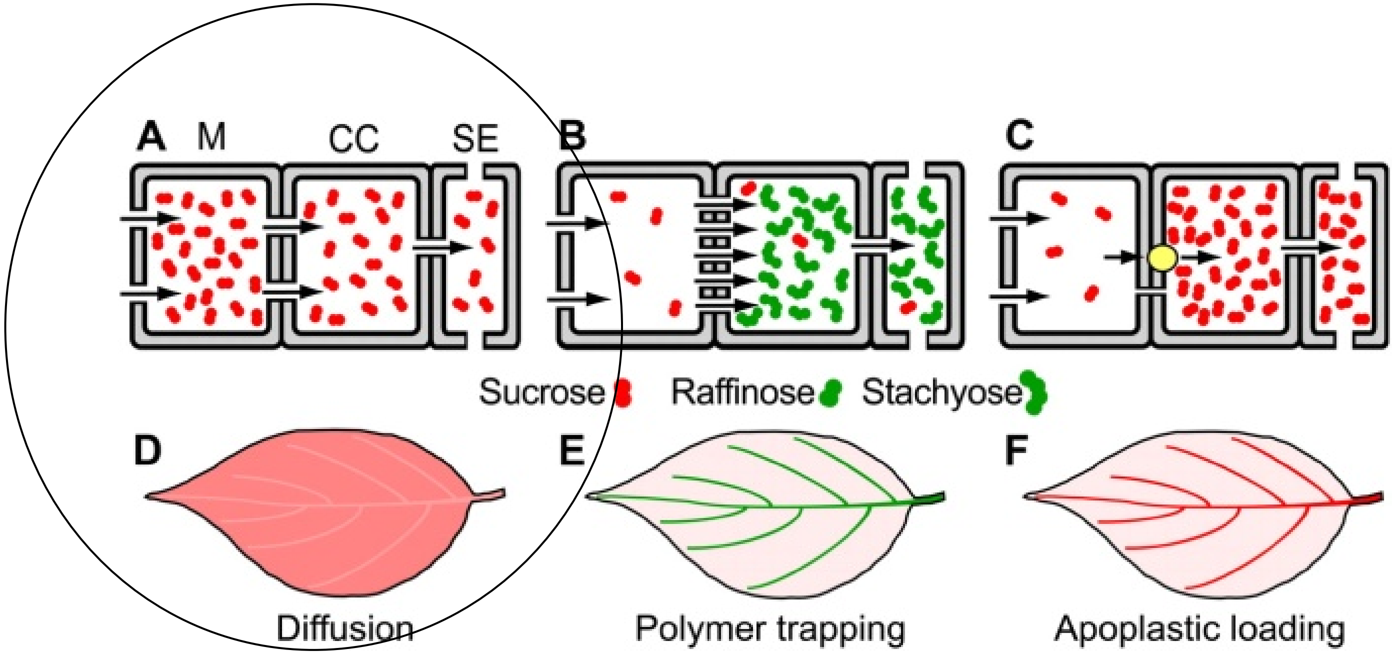
Steady state approach

- Description of different processes:
- Source sugar production
- Xylem transport
- Phloem transport
- Sink sugar utilization
- Transpiration
- Root water uptake



Source

- Sugar concentration in leaf mesophyll and phloem are tighly coupled in (most) trees species since phloem loading is passive by diffusion.
- It has been found in many studies that increasing leaf sugar concentration (connecte with e.g. drought, sink limitation) decreases photosynthesis rate for a given internal leaf CO2 concentration.



Source

- Increasing sugar concentration will cause a smaller photosynthesis rate for a given ci, light and temperature (this is an assumption, which is under test).
- Changes in mesophyll conductance or biochemistry of photosynthesis
- Opening causes c_i to increase, but photosynthesis rate for a given c_i to decrease.
- Maximum photosynthesis rate at an intermediate stomatal conductance

$$A = \frac{fC_i}{C_i + \theta}\phi \qquad f = \frac{\alpha I}{I + \beta} \qquad \phi = 1 - \left(\frac{C_{leaf}}{C_0}\right)$$

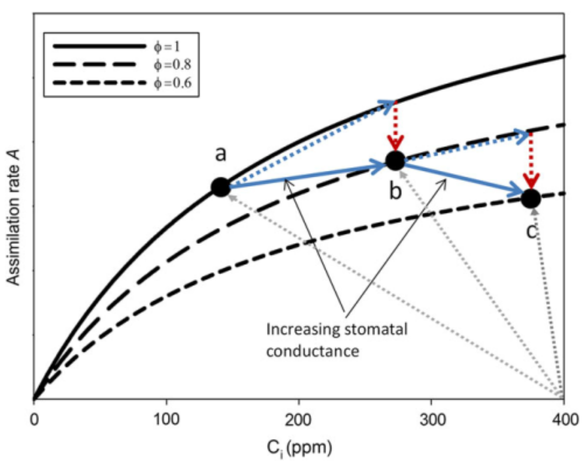
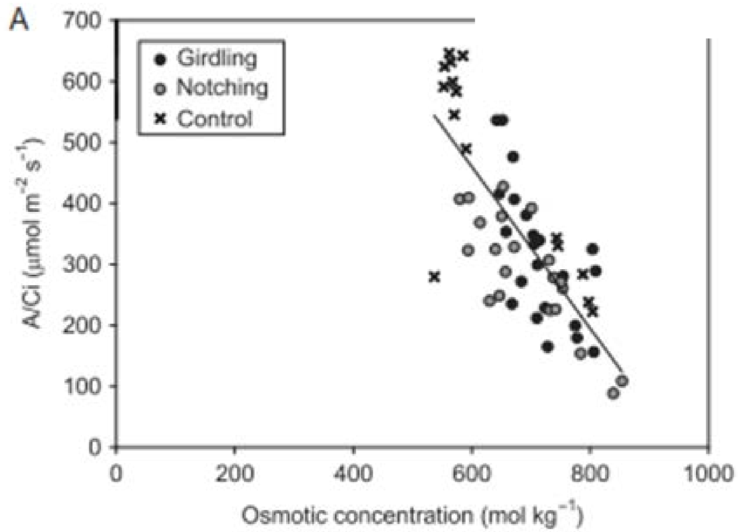


Figure 4. A schematic figure of the photosynthesis rate as a function of leaf internal CO_2 concentration C_i when ambient CO_2 concentration is held constant. Stomatal opening increases C_i and causes movement along any A–C_i curve ($\phi = 1$, $\phi = 0.8$ or $\phi = 0.6$) to the upper right diagonal direction. Stomatal opening simultaneously causes ϕ to decrease thus forcing a movement to a lower A–C_i curve. The grey dotted lines intersecting the x-axis at 400 ppm represent the supply functions of CO_2 through the stomata.

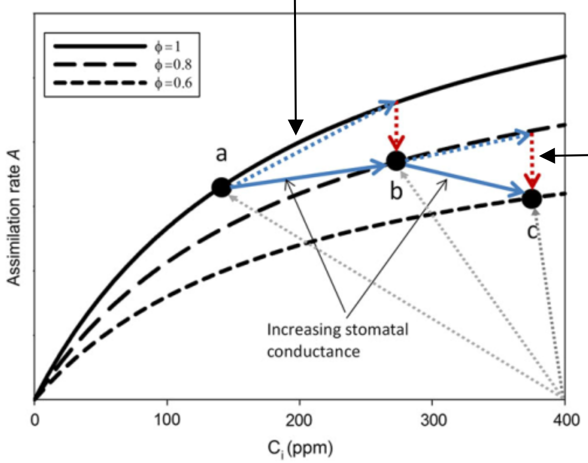


A is photosynthesis rate.
Ci is leaf internal CO2 conc
f is a function of light.
Cleaf is leaf osmotic conc.
C0 is leaf osmotic conc where A goes to zero.

Source

- How do structural and functional properties, as well as environmental conditions come into play in this scheme:

Dependent on e.g. photosynthetic parameters, light level, ambient CO2



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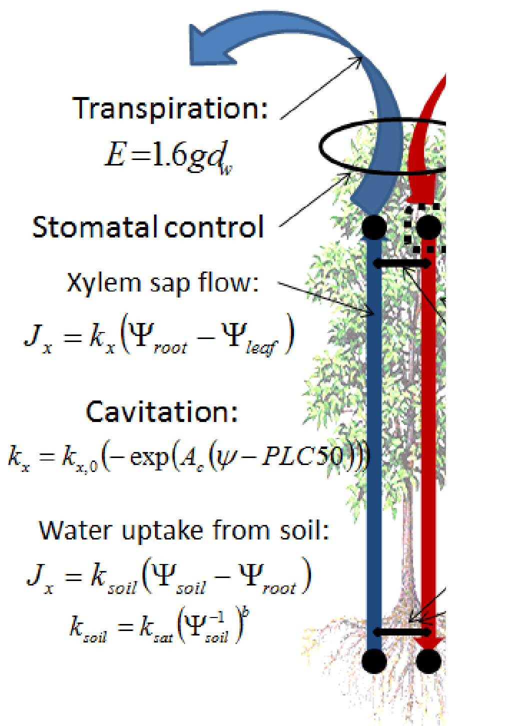
Depedent on e.g.:
VPD
Xylem conductance
Phloem conductance
Sink strength
Ambient CO2
Soil water potential

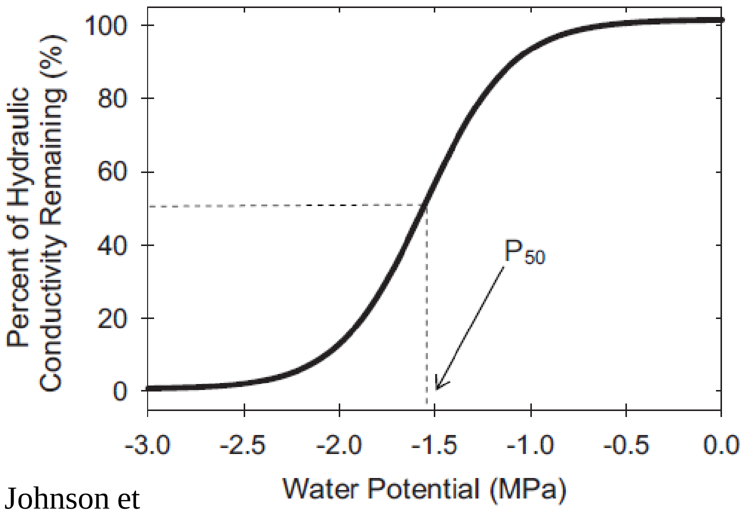
Xylem transport

- Leaf osmotic concentration and water potential are tightly correlated due to water pot. equilbrium and phloem transport.
- Decrease in water potential is higher for a given stomatal opening when VPD is high and hydraulic conductance from soil to leaf is low.

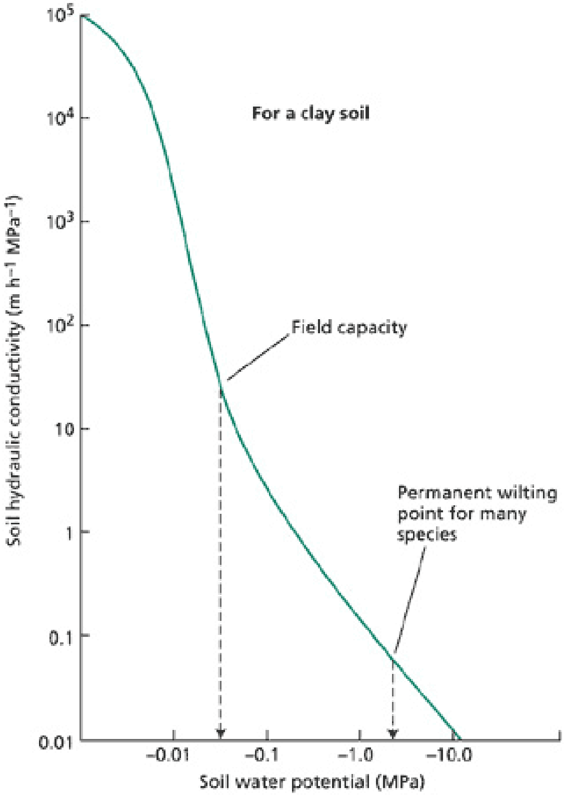


Xylem transport

- Soil conductance is dependent on soil water content.
- Xylem hydraulic is dependent on plant water content (and stomatal conductance).



Johnson et al. 2012



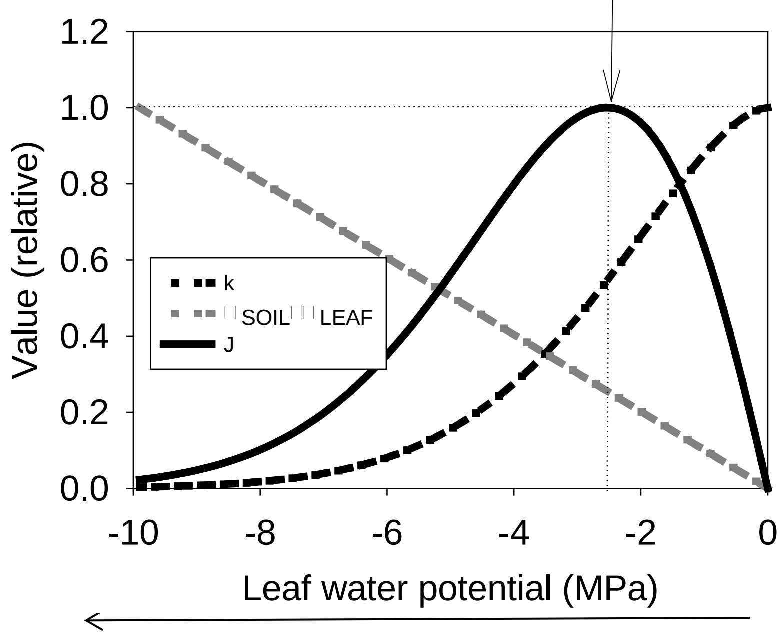
Embolism and stomatal control

- Due to embolism, there is a maximum water transport rate that can be sustained with a given xylem structure.
- The maximum water transport rate is achieved when some embolism is allowed.
- This maximum water transport is not necessarily the solution to maximing metabolic rate.

Maximum possible water flow/ transpiration rate

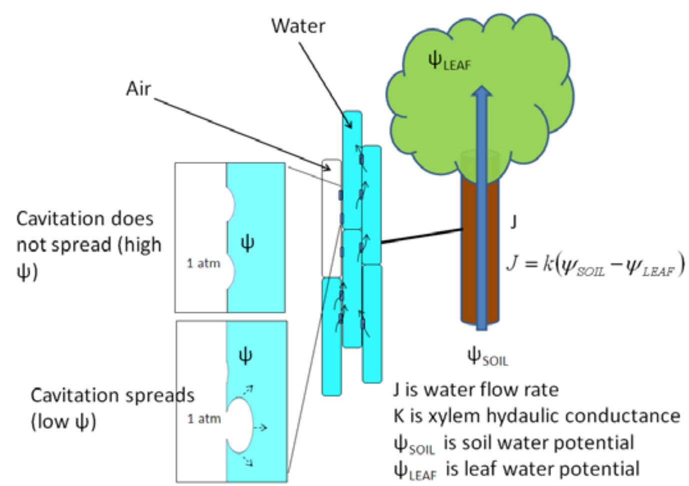
$$J = k(\psi)(\psi_{SOIL} - \psi_{LEAF})$$

conductance — Driving force



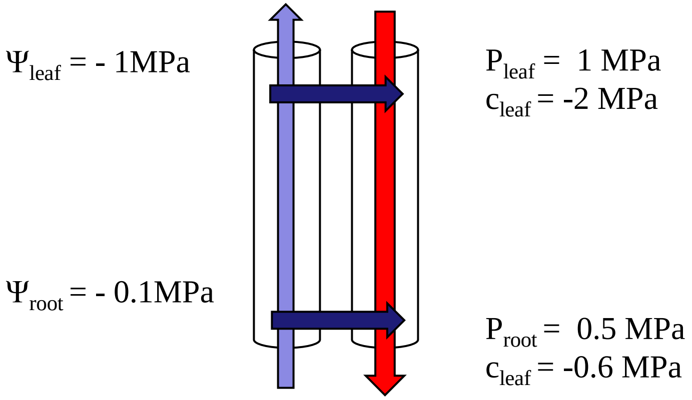
Driving force increases

Conductance decreases



Phloem transport

- Phloem is at water potential equilibrium with xylem at each location → water potential and phloem osmotic concentration are tightly coupled.



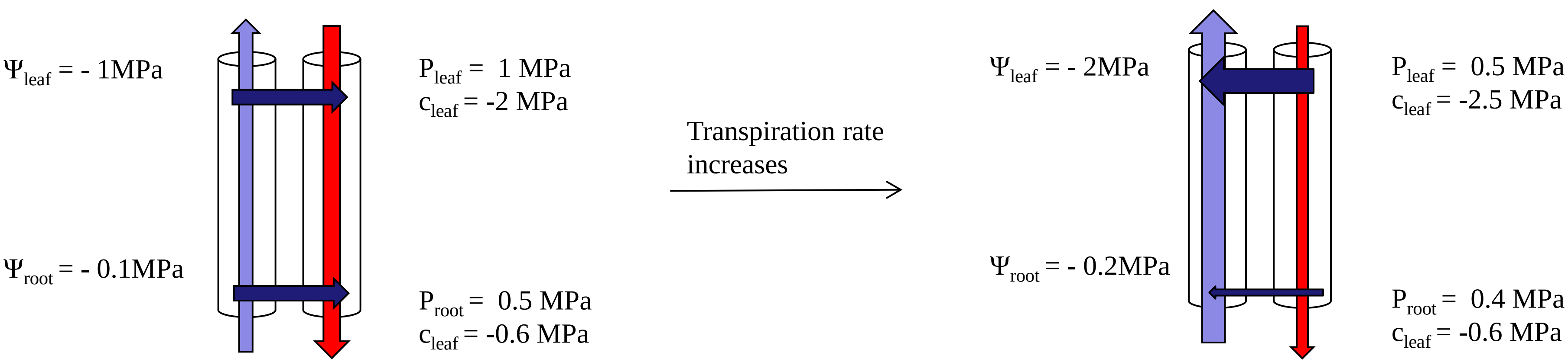
Phloem transport is affected by xylem transport, a modeling example

- What happens e.g. when transpiration rate increases:

  ψ_{leaf} and ψ_{root} decrease and $\psi_{root} - \psi_{leaf}$ increase

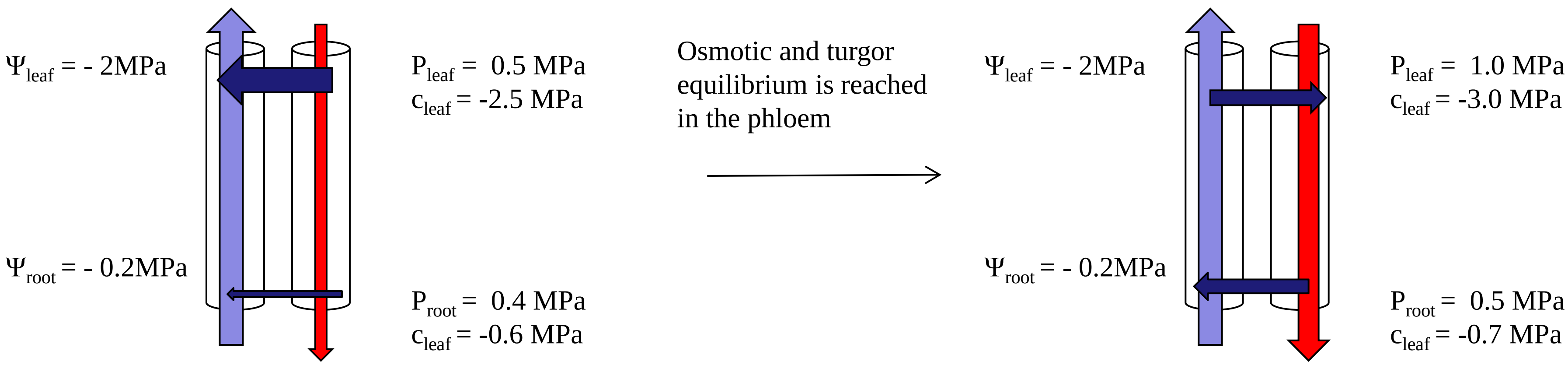
  Xylem draws water from the phloem, and more at the source in relation to sink

  Phloem turgor and its gradient decreases and phloem flow slows down.



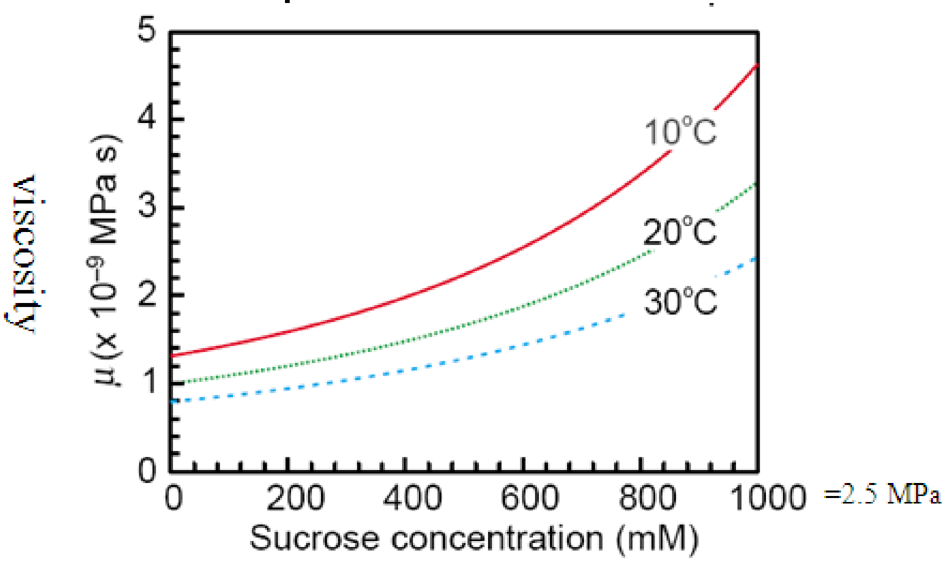
Phloem transport is affected by xylem transport, a modeling example

- Decreased phloem flow rate starts to increase sugar concentration in the source phloem.
- A new steady state phloem transport is reached when phloem flow rate increases to the level of sugar loading rate.



Phloem transport

- Phloem hydraulic conductance determines the pressure loss (coupled to sugar concentration) in phloem.
- Phloem conductance changes with viscosity (function of temperature and sugar concentration).
- Similarly to xylem transport, there is a maximum possible phloem transport rate.



Thompson 2006

Phloem sap flow:

$$J_P = k_p C_{leaf}\left(P_{leaf} - P_{roots}\right)/\eta\left(C_{leaf}\right)$$

Water potential equilibrium:

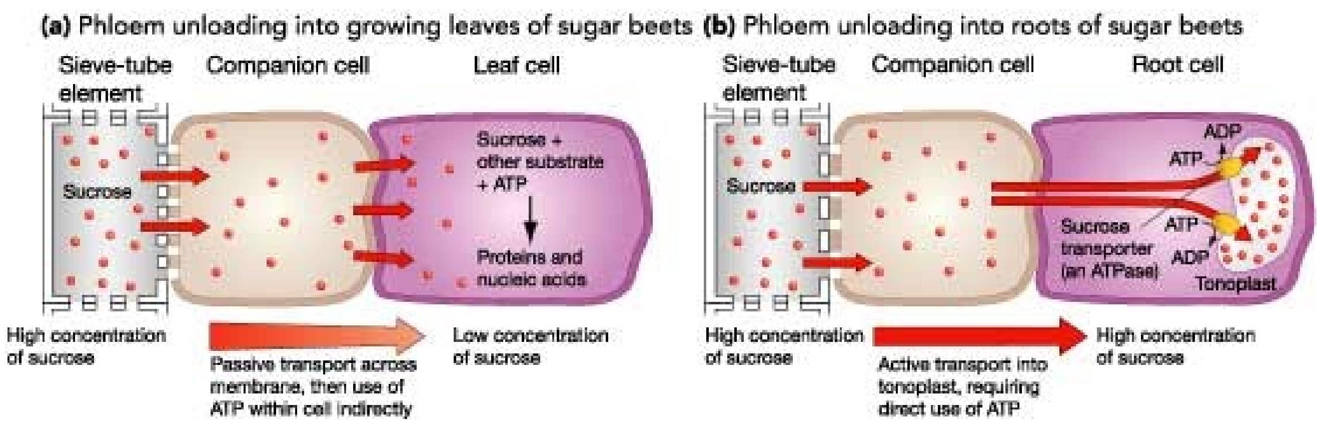
$$\Psi = P - cRT$$

Sink sugar utilization

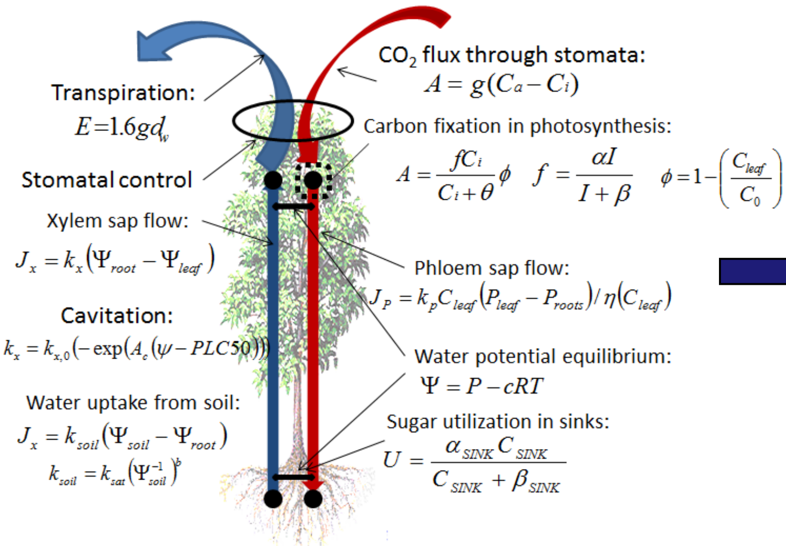
- Sugar usage rate is determined by sink strenght and phloem sugar concentration C_{sink}(or turgor pressure which is connected to concentration).
- Sink strength α_{sink} is dependent on temperature, hormonal growth.

Sugar utilization in sinks:

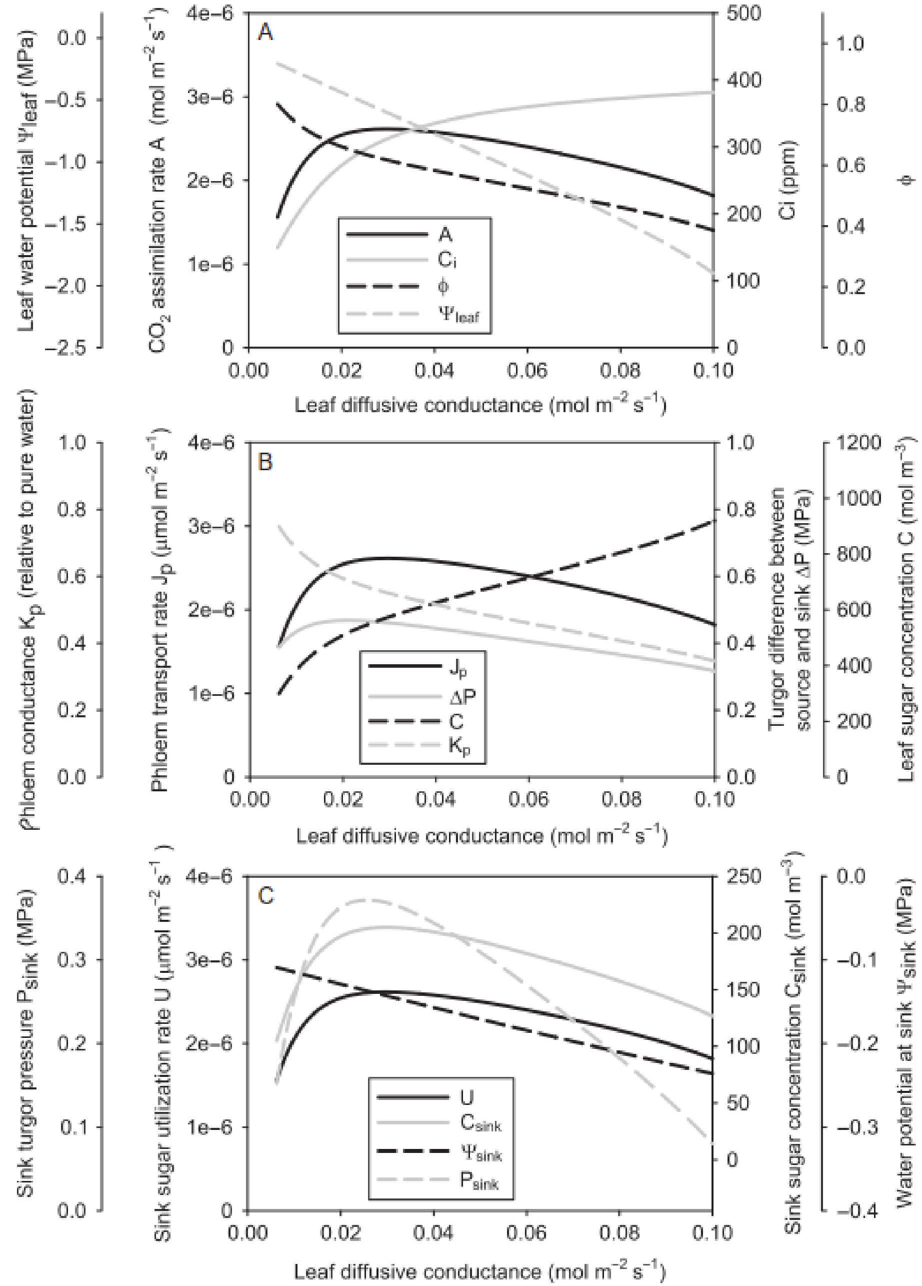
$$U = \frac{\alpha_{SINK} C_{SINK}}{C_{SINK} + \beta_{SINK}}$$



Example



Transpiration:
E=1.6gd_w
Stomatal control
Xylem sap flow:
J_x = k_x(Ψ_root − Ψ_leaf)
Cavitation:
k_x = k_x,0(−exp(A_c(ψ − PLC50)))
Water uptake from soil:
J_x = k_soil(Ψ_soil − Ψ_root)
k_soil = k_sat(Ψ_soil^−1)^b
CO2 flux through stomata:
A = g(Ca − Ci)
Carbon fixation in photosynthesis:
A = fCi/(Ci + θ) φ   f = αI/(I + β)   φ = 1 − (C_leaf/C_0)
Phloem sap flow:
J_P = k_p C_leaf (P_leaf − P_roots)/η(C_leaf)
Water potential equilibrium:
Ψ = P − cRT
Sugar utilization in sinks:
U = α_SINK C_SINK / (C_SINK + β_SINK)

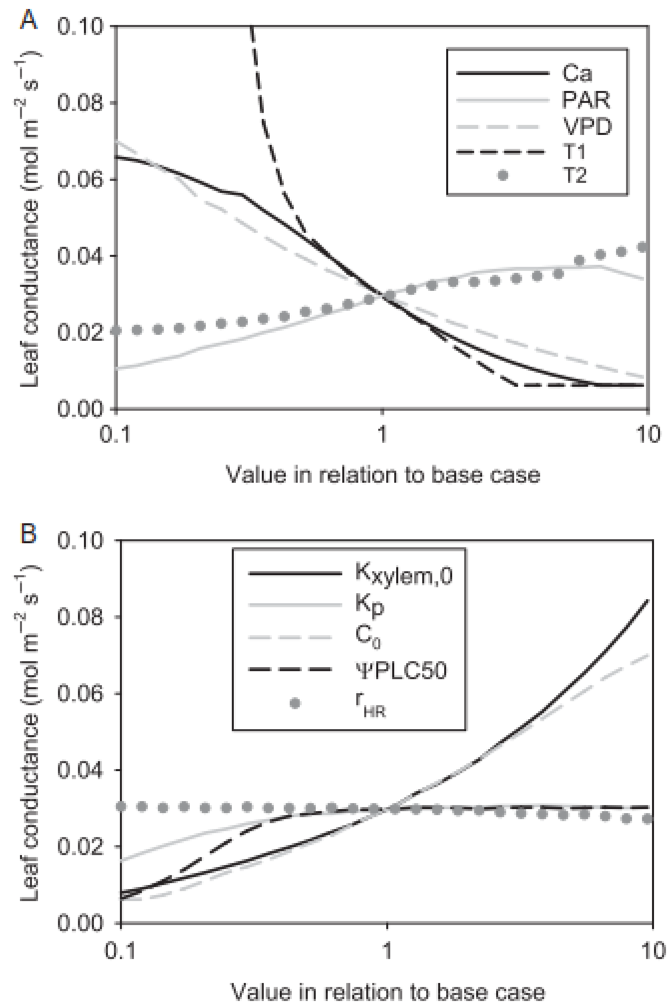


A
B
C
Leaf diffusive conductance (mol m−2 s−1)
Leaf water potential Ψleaf (MPa)
CO2 assimilation rate A (mol m−2 s−1)
Ci (ppm)
φ
A
Ci
φ
Ψleaf
Phloem conductance Kp (relative to pure water)
Phloem transport rate Jp (µmol m−2 s−1)
Turgor difference between source and sink ΔP (MPa)
Leaf sugar concentration C (mol m−3)
Jp
ΔP
C
Kp
Sink turgor pressure Psink (MPa)
Sink sugar utilization rate U (µmol m−2 s−1)
Sink sugar concentration Csink (mol m−3)
Water potential at sink Ψsink (MPa)
U
Csink
Ψsink
Psink

Results

- We can reproduce the well known trends of stomatal control to:
  - Ambient CO2 concentration
  - Light
  - VPD

  - Xylem conductance
  - Phloem conductance
  - Vulnerability to cavitation
  - Sink strength



Results

- Stomatal and non-stomatal limitations to photosynthesis are tightly correlated:
- Non-stomatal limitations to photosynthesis are coupled to stomatal action.
- Stomata react to non-stomatal limitations to maximize metabolic rate.

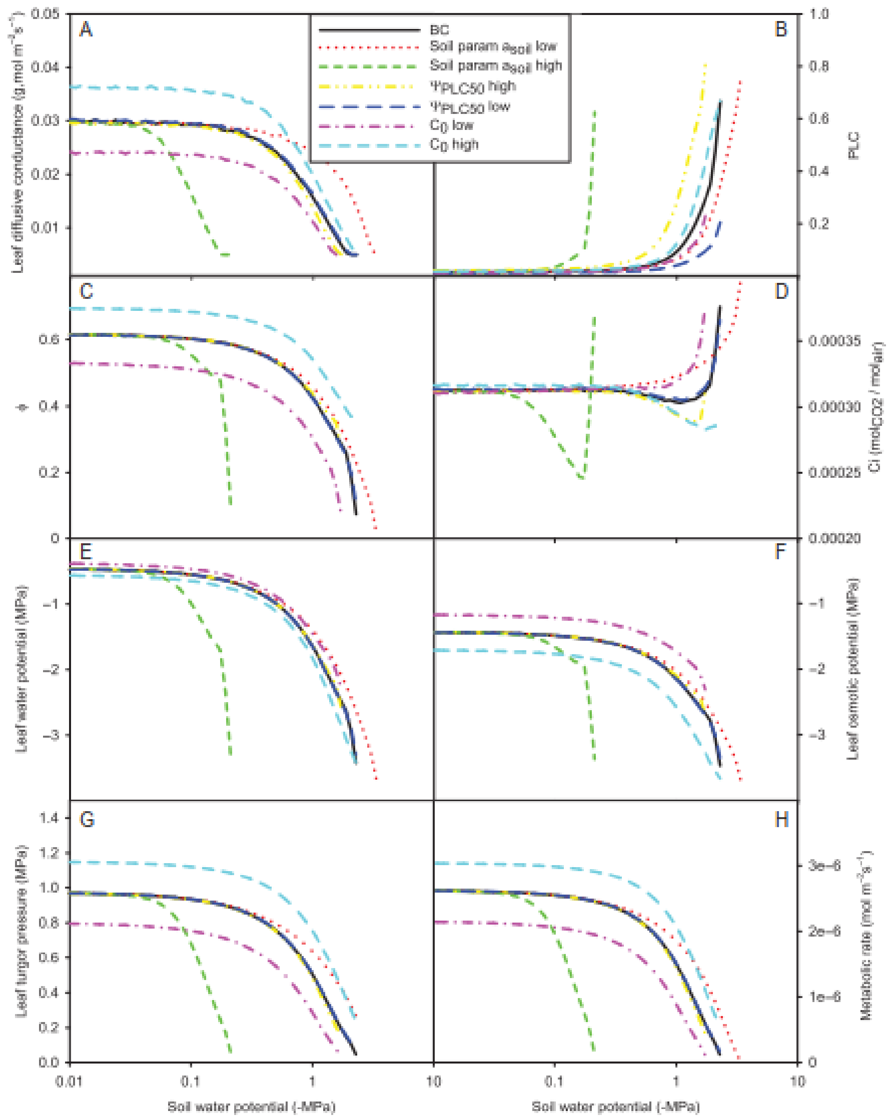


Figure 6. Model behaviour when soil water potential is decreased: (A) leaf diffusive conductance, (B) loss of xylem hydraulic conductance due to cavitation (PLC), (C) ϕ, (D) leaf internal CO_2 concentration, (E) leaf water potential, (F) leaf osmotic pressure, (G) leaf turgor pressure and (H) metabolic rate. 'BC' is for the base case simulation, 'soil param a_{soil} low' means parameterization with a_{soil} = 0.66 × base case value (soil hydraulic conductance is less sensitive to soil water potential), 'soil param a_{soil} high' means parameterization with a_{soil} = 1.2 × base case value (soil hydraulic conductance is more sensitive to soil water potential), 'ψ_{PLC50} low' means parameterization ψ_{PLC50} = 0.5 × base case value, 'ψ_{PLC50} high' means parameterization ψ_{PLC50} = 2 × base case value, 'C_0 low' means parameterization with C_0 = 0.5 × base case value, 'C_0 high' means parameterization with C_0 = 2 × base case value.

Results

- Empirical coefficient (g_1) of stomatal control models (Ball-Berry, Leuning) can be explained by soil to leaf hydraulic conductance (and sink strength, phloem condutance, vulnerability to cavitation)

$$g = g_0 + g_1 \frac{A}{\sqrt{d_w} C_a}$$

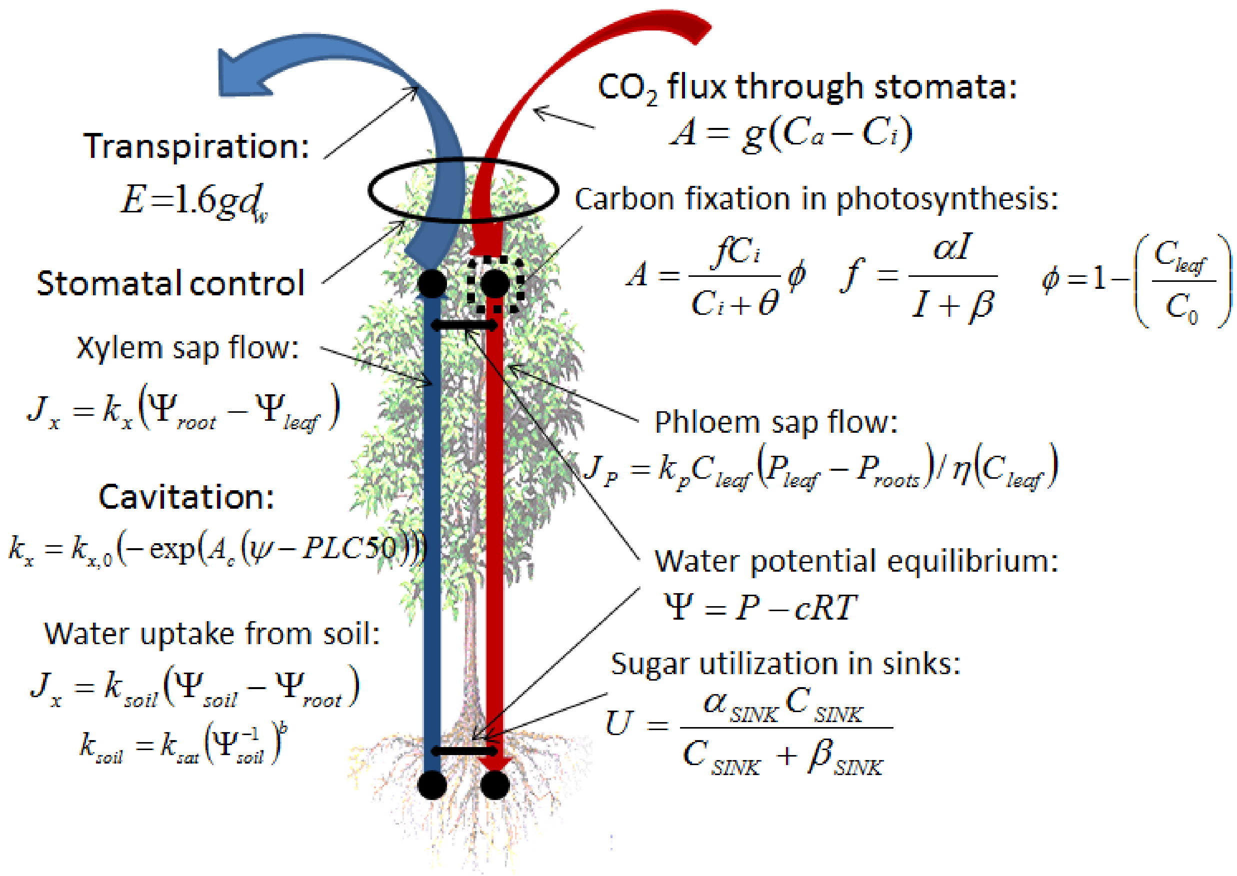
A is photosynthesis rate
dw is VPD
Ca is ambient CO2 concentration
g1 is empirical coefficient

- ”Cost of water” λ in optimal stomatal control models can be explained by soil to leaf hydraulic conductance (and sink strength, phloem condutance, vulnerability to cavitation)

$$g = \left(\sqrt{\frac{C_a}{\lambda d_w}} - 1 \right) f = \left(\sqrt{\frac{C_a}{\lambda d_w}} - 1 \right) \frac{\alpha I}{I + \beta}$$

Analytical solution

- Forget about carbon side, and make photosynthesis respond to leaf water potential.



Thank you

- Angi’s turn.

A theoretical framework linking processes, environmental drivers, structural and functional properties and internal tree state