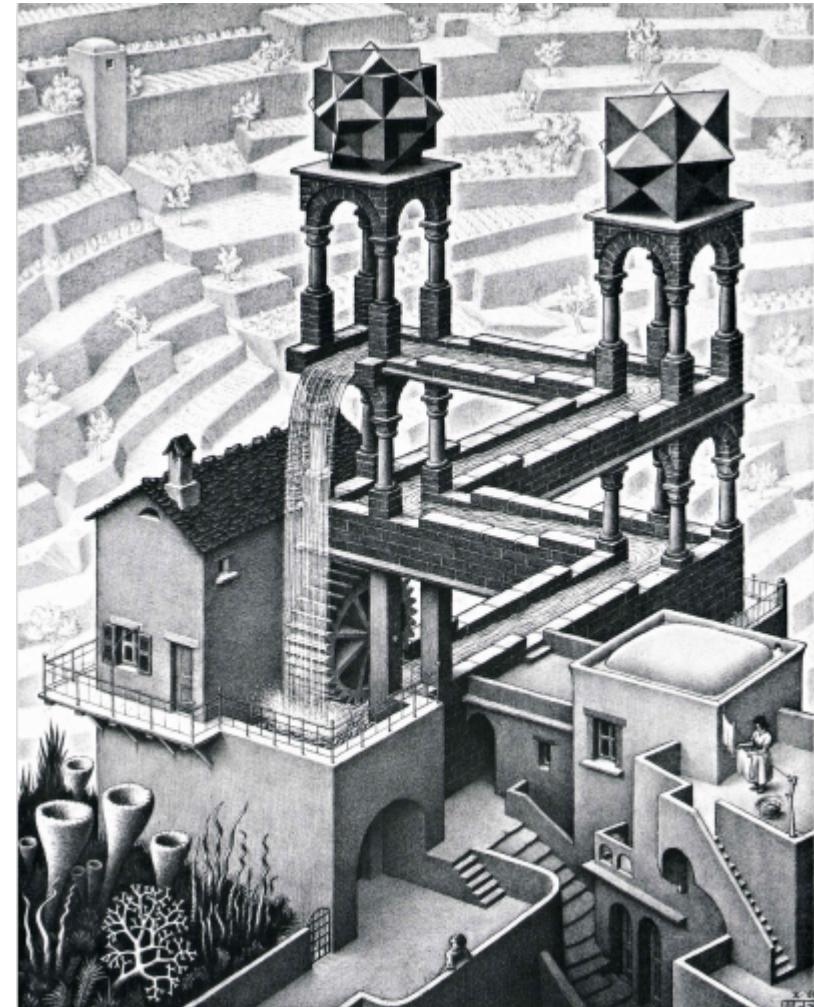


Forest water and energy balance (theory)

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Outline

1. Preliminary concepts
2. Forest water balance in medfate
3. Transpiration and photosynthesis under the basic model
4. Transpiration and photosynthesis under the advanced model
5. Plant drought stress and cavitation
6. Basic vs. advanced models: a summary of differences



M.C. Escher - Waterfall, 1961

1. Preliminary concepts

Water potential

The water potential, Ψ , is the potential energy of water relative to pure water under reference conditions. It quantifies the tendency of water to move from one area to another.

It has pressure units (e.g. MPa) and can be divided into different components:

$$\Psi = \Psi_{\Pi} + \Psi_p + \Psi_g + \Psi_m$$

The diagram illustrates the decomposition of water potential (Ψ) into four components. The equation $\Psi = \Psi_{\Pi} + \Psi_p + \Psi_g + \Psi_m$ is at the top. Below it, four lines point downwards to their respective labels: 'Osmotic potential (negative, living cells)' points to Ψ_{Π} ; 'Pressure (positive or negative)' points to Ψ_p ; 'Gravity (negative)' points to Ψ_g ; and 'Matric (negative, soils)' points to Ψ_m .

But not all components are equally relevant in all contexts

Soil water retention curves

The *water retention curve* of a soil (or *soil moisture characteristic curve*) is the relationship between volumetric soil moisture content (θ in $m^3 \cdot m^{-3}$ of soil excluding rock fragments) and the corresponding soil water potential (Ψ , in MPa)

Two water retention curve models are available in **medfate**:

Saxton model:

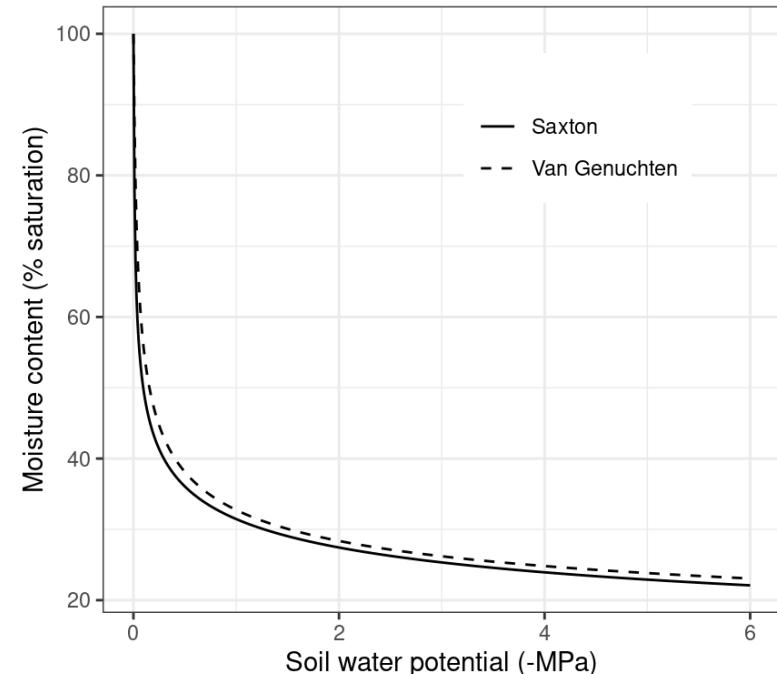
$$\theta(\Psi) = (\Psi/A)^{(1/B)}$$

where A and B depend on the texture and, if available, organic matter in the soil.

Van Genuchten model:

$$\theta(\Psi) = \theta_{res} + \frac{\theta_{sat} - \theta_{res}}{[1 + (\alpha \cdot \Psi)^n]^{1-1/n}}$$

where $\theta(\psi)$ is the water retention, θ_{sat} is the saturated water content, θ_{res} is the residual water content, α is related to the inverse of the air entry pressure, and n is a measure of the pore-size distribution.



Important

Parameters of the water retention curves can be calibrated empirically but are normally derived from soil texture and bulk density.

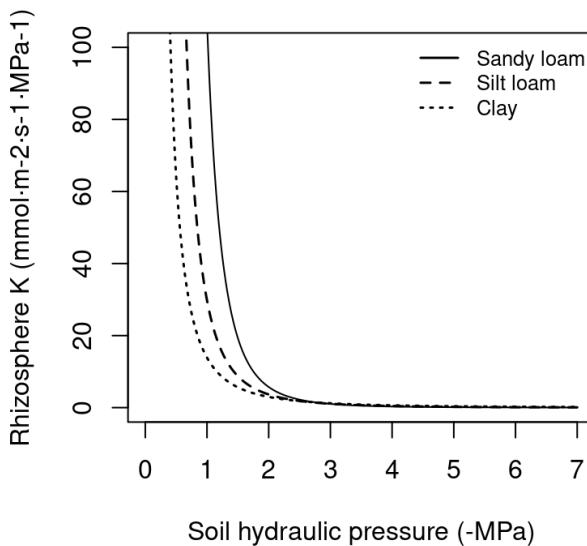
Hydraulic conductance and vulnerability curves

- **Hydraulic conductance k** is used to measure how much flow exists along a pathway segment (e.g. soil, stem, leaves, ...) for a given difference in water potential.
- Hydraulic conductance decreases when **air replaces water** in any segment.
- **Vulnerability curve** specifies the relationship between water potential, Ψ , and hydraulic conductance, k , of a given segment.

Rhizosphere

Conductance is modelled as a van Genuchten (1980) function:

$$k(\Psi) = k_{max} \cdot v^{(n-1)/(2 \cdot n)} \cdot ((1 - v)^{(n-1)/n} - 1)^2$$

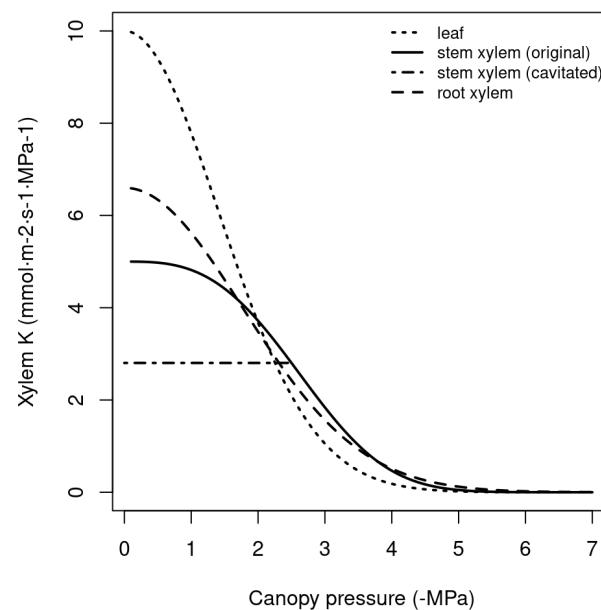


Xylem

Conductance is modelled using a **Weibull** or a **Sigmoid**:

$$k(\Psi) = k_{max} \cdot e^{-(\Psi/d)^c}$$

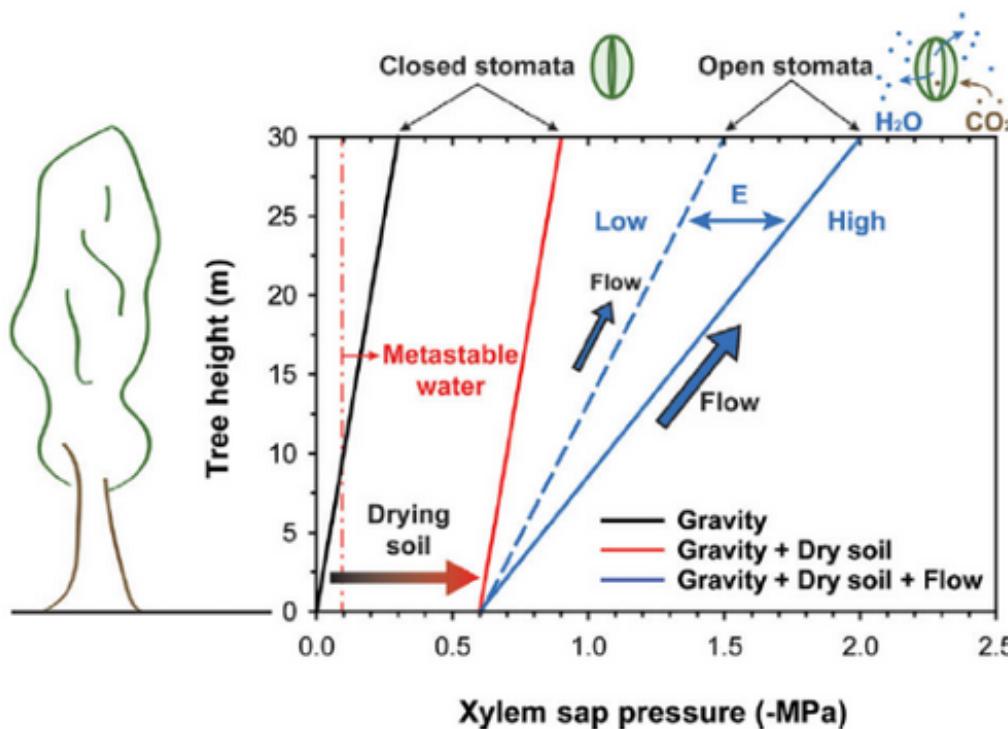
$$k(\Psi) = \frac{k_{max}}{1 + e^{(slope/25) \cdot (\Psi - \Psi_{50})}}$$



Water potential drop in plants

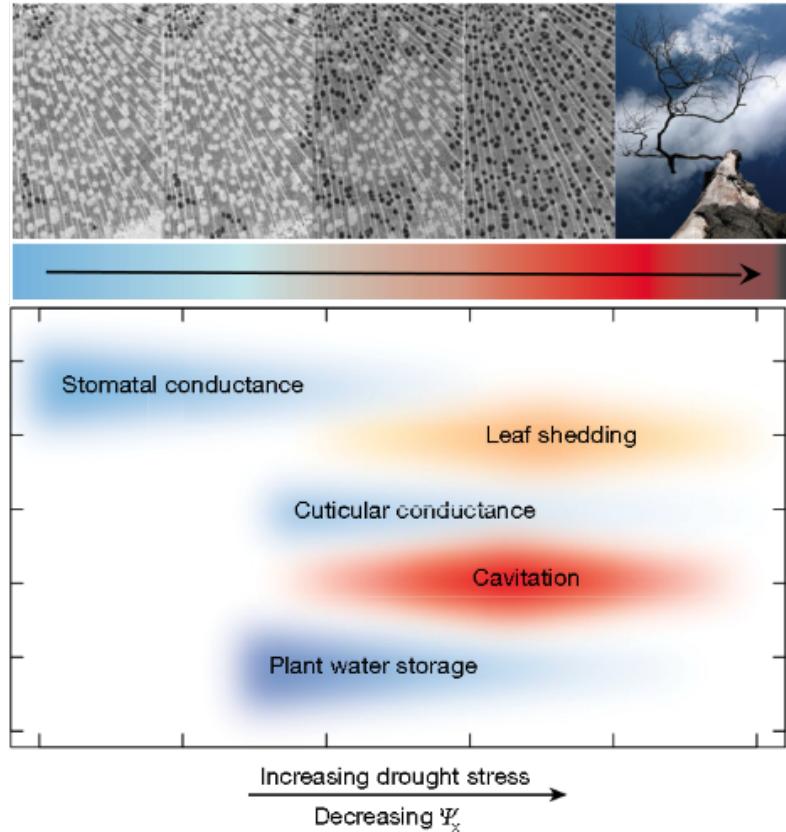
When stomata are closed (e.g. pre-dawn), plant leaf water potential is assumed to be in equilibrium with the water potential in the rhizosphere (neglecting gravity effects).

When stomata are open, a larger transpiration flow (E) implies (in steady state) a larger drop in water potential along the transpiration pathway ¹:



Drought impacts on plants

The decrease in soil water potential caused by drought has multiple effects on plants ¹, with some processes ceasing to occur and others becoming important or being promoted, depending on the plant response strategy ².



Process or variables affected	Reduction in tissue water potential ψ and turgor P
Cell growth	— - -
Growth respiration	— - -
ABA release	— - - - -
Stomatal conductance /transpiration	- - - - -
Leaf energy budget	- - - - -
Photosynthesis	- - - - -
Xylem cavitation	- - - - -
Root disconnection from soil	- - - - -
Maintenance respiration	- - - - -
NSC transport	- - - - -
Leaf turgor loss	- - - - -
Leaf shedding	- - - - -
Plant mortality	- - - - -

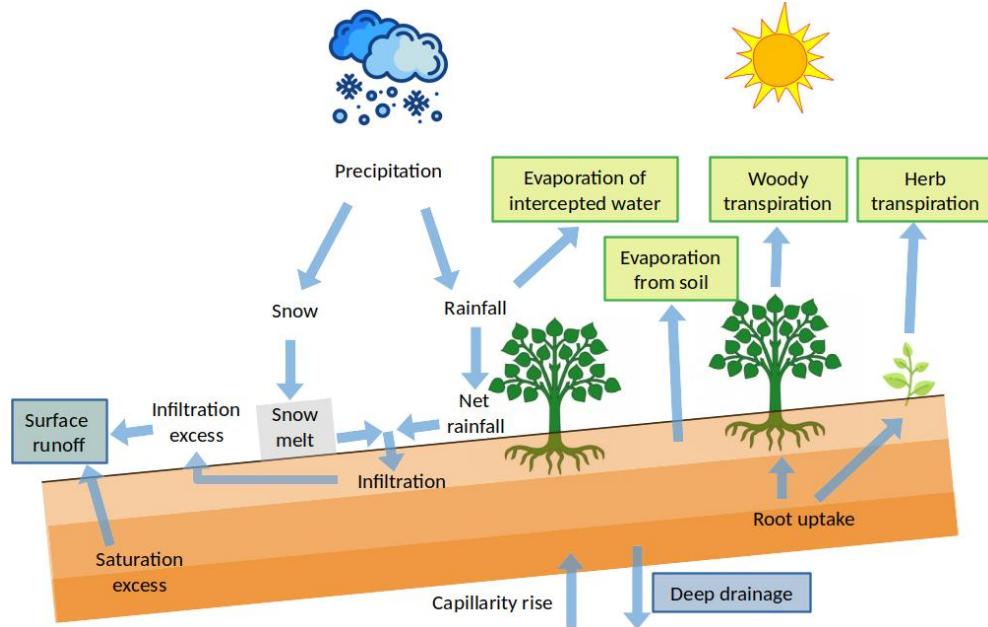
1. Choat et al. (2018) Nature, 558, 531-539.

2. Fatichi et al. (2016) Wiley Interdisciplinary Reviews: Climate Change, 7, 227-262.

2. Forest water balance in medfate

Water balance components

The water balance models in available in medfate simulate the following vertical water flows in a given forest stand.



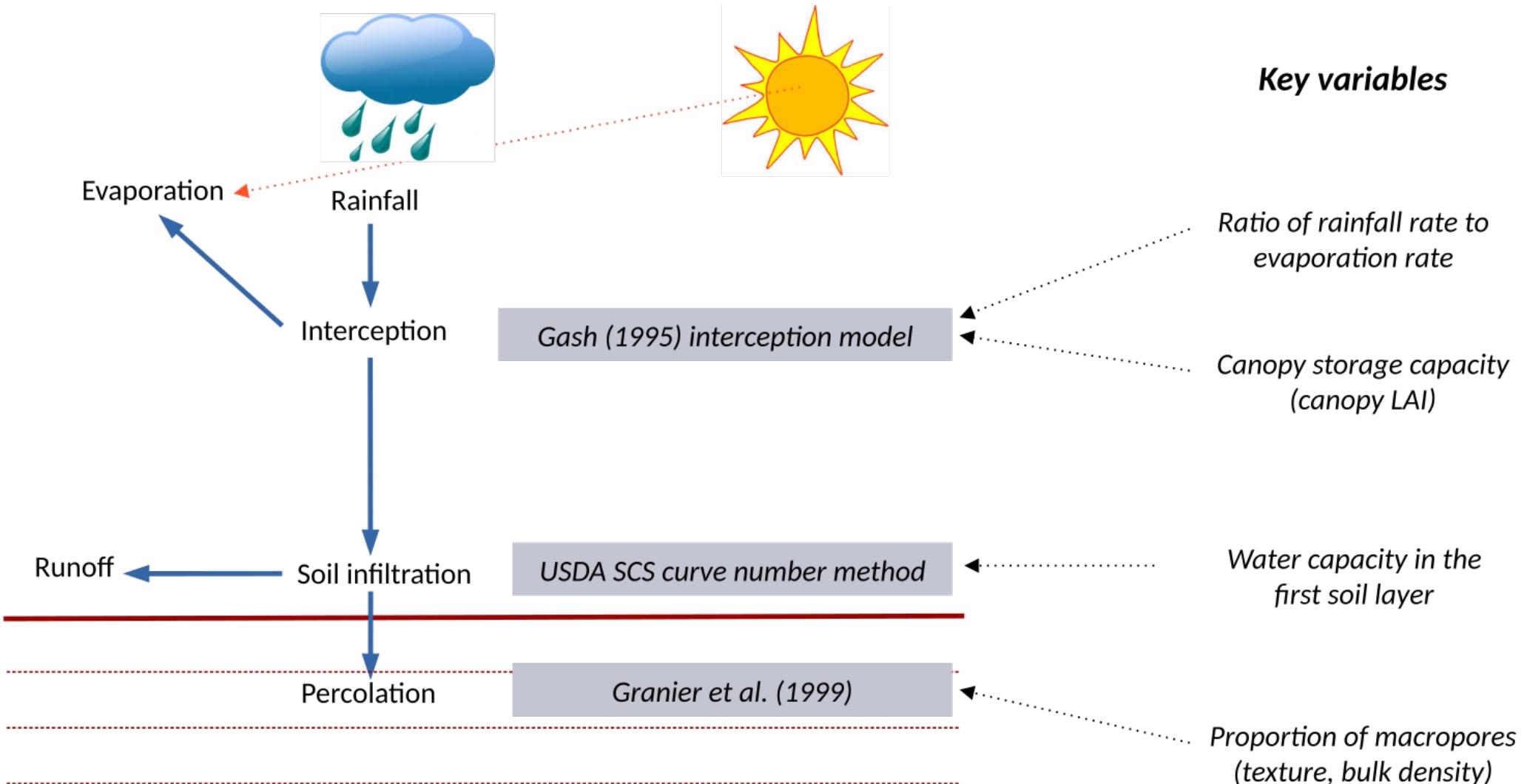
Component	Symbol	Description
Infiltration	<i>If</i>	Water entering the soil from above
Capillarity rise	<i>Cr</i>	Water entering the soil from below
Deep drainage	<i>Dd</i>	Water leaving the soil beyond root zone
Saturation excess	<i>Se</i>	Excess of water in the soil
Soil evaporation	<i>Es</i>	Evaporation from soil surface
Woody transpiration	<i>Tr_{woody}</i>	Woody plant transpiration
Herb transpiration	<i>Tr_{herb}</i>	Herbaceous plant transpiration

Variations in soil water content can be summarized as:

$$\Delta V_{soil} = (If + Cr) - (Dd + Se + Es + Tr_{herb} + Tr_{woody})$$

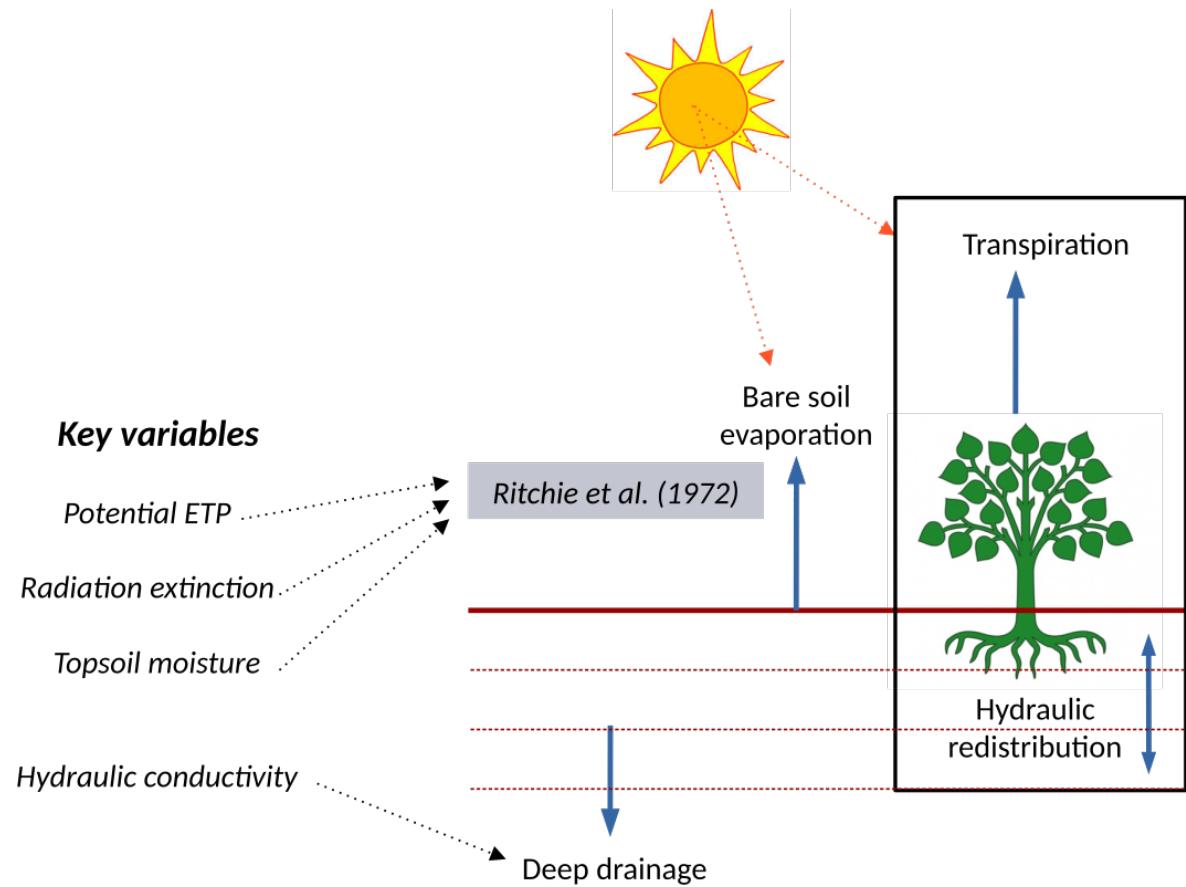
Soil water inputs

If rainfall occurs during a given day, three processes are simulated to update the water content in soil layers:



Soil water outputs

Regardless of precipitation, soil moisture can be modified due to the following processes:



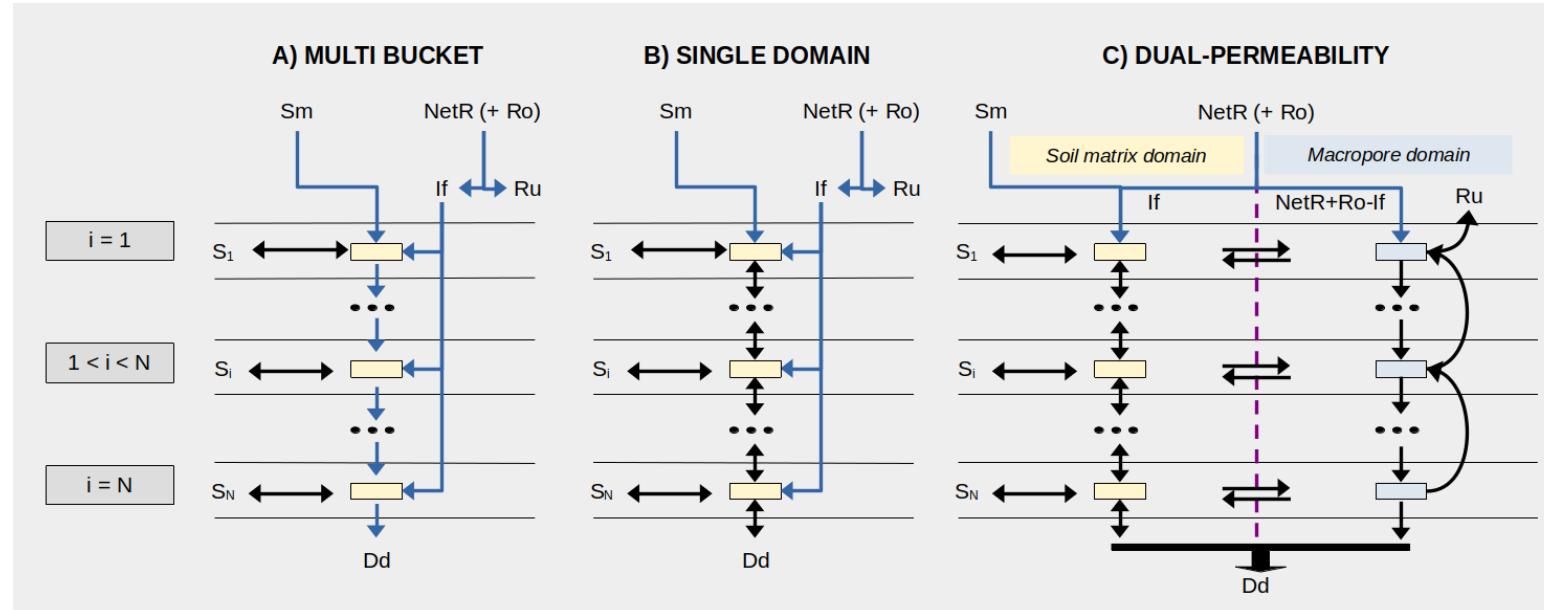
Important

Soil water uptake by plants, hydraulic redistribution and transpiration are modelled differently depending on the water balance model: **basic vs advanced**.

Flows in the soil

Three submodels are available to simulate water movement *into, out of and within* the soil:

- A. **Multi-bucket model:** Water inputs and drainage during a rainy day (and may be the next if over field capacity).
- B. **Single-domain model:** Vertical water movement any day following gravitational and matric potentials (Richards equation).
- C. **Dual permeability model:** Flows in the soil matrix following the previous model. Flows in the macropore domain following gravitational forces. Saturation excess possible.



Warning

The three sub-models differ greatly in computational demand.

3. Transpiration and photosynthesis under the basic model

Maximum transpiration

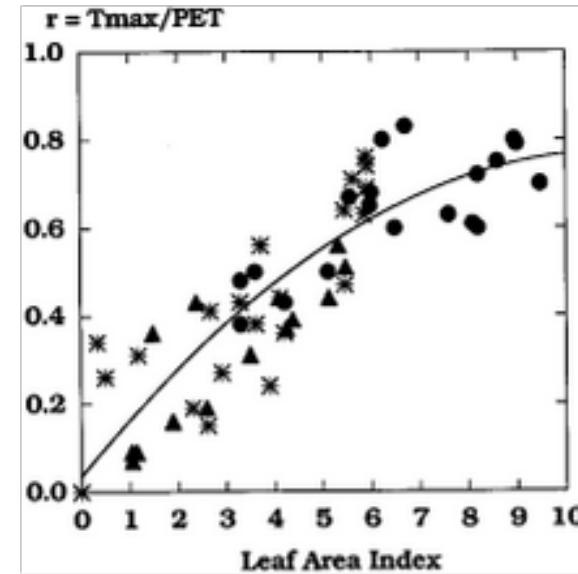
Maximum canopy transpiration

Maximum canopy transpiration Tr_{\max} depends on potential evapotranspiration, PET , and the amount of transpiring surface, i.e. the stand leaf area index, thanks to:

$$\frac{Tr_{\max}}{PET} = -0.006 \cdot (LAI_{stand}^{\phi})^2 + 0.134 \cdot LAI_{stand}^{\phi}$$

and therefore:

$$Tr_{\max} = PET \cdot (-0.006 \cdot (LAI_{stand}^{\phi})^2 + 0.134 \cdot LAI_{stand}^{\phi})$$



Granier et al. (1999). Ecol. Model., 116, 269-283.

Maximum canopy transpiration is divided among plant cohorts according to the amount of light absorbed by each one.

Note

Granier's equation is actually species-specific in medfate.

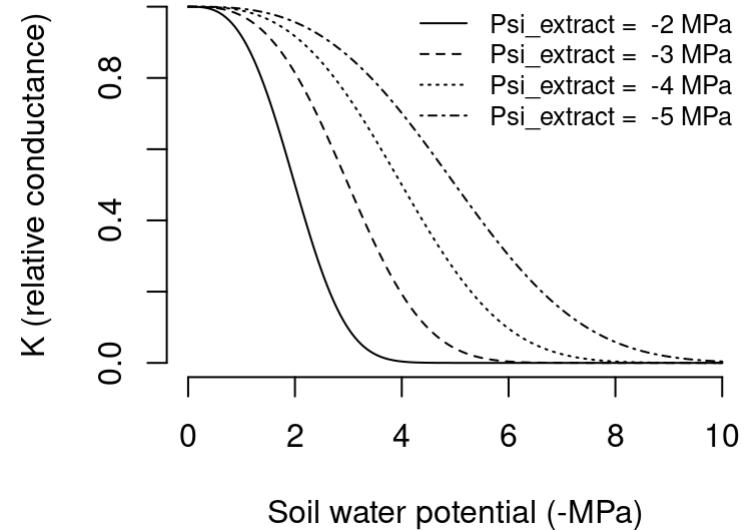
Actual plant transpiration

Actual plant transpiration depends on soil moisture and is calculated for each soil layer s separately.

A relative whole-plant water conductance, K is defined for any given soil layer s using:

$$K(\Psi_s) = \exp \left\{ \ln(0.5) \cdot \left[\frac{\Psi_s}{\Psi_{extract}} \right]^r \right\}$$

where $\Psi_{extract}$ is the water potential at which transpiration is 50% of maximum, and Ψ_s , the water potential in layer s .



The water extracted by a plant cohort from soil layer s and transpired, Tr_s , is the product:

$$Tr_s = Tr_{max} \cdot K(\Psi_s) \cdot FRP_s$$

where FRP_s is the proportion of plant fine roots in layer s .

Important

This transpiration model allows emulating stomatal closure in response to soil water deficit but do not allow modelling stomatal responses to other factors.

Plant photosynthesis

Gross photosynthesis for a plant cohort, A_g , is estimated as a function of transpiration, Tr , using:

$$A_g = Tr \cdot WUE_{\max} \cdot (L^{PAR})^{WUE_{PAR}} \cdot (1 - e^{WUE_{CO2} \cdot C_{air}}) \cdot VPD^{WUE_{VPD}}$$

where:

- WUE_{\max} is the maximum water use efficiency of the cohort under maximum light availability, $VPD = 1kPa$ and no CO2 limitations.
- L^{PAR} is the proportion of PAR available and WUE_{PAR} is an exponent.
- C_{air} is the carbon dioxide concentration in the air and WUE_{CO2} is a regulating coefficient.
- VPD is vapour pressure deficit and WUE_{VPD} is a regulating coefficient.

Note

Parameters regulating photosynthesis cannot be related to traits. The estimation of these parameters and those regulating transpiration is done via a [metamodelling exercise](#).

Plant water potential

The basic water balance model **does not** estimate the water potential drop from soil to the leaf.

Despite its simplicity, a gross surrogate of ‘plant’ water potential, Ψ_{plant} , may be obtained using:

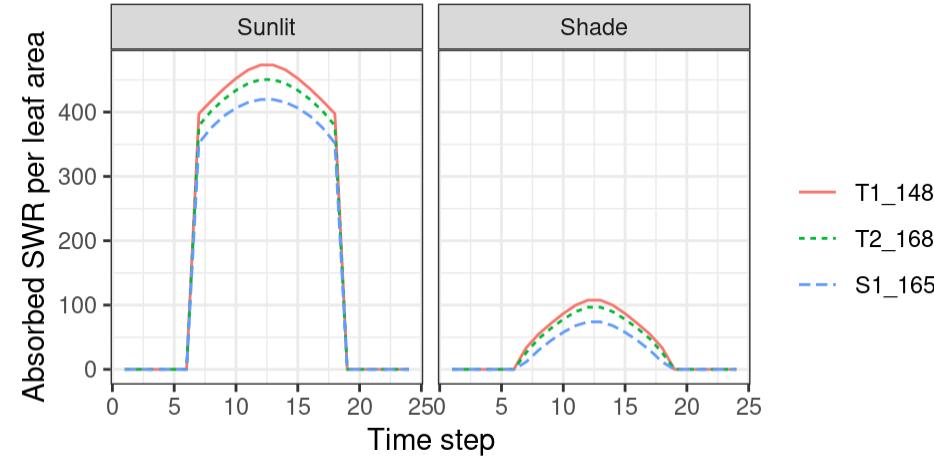
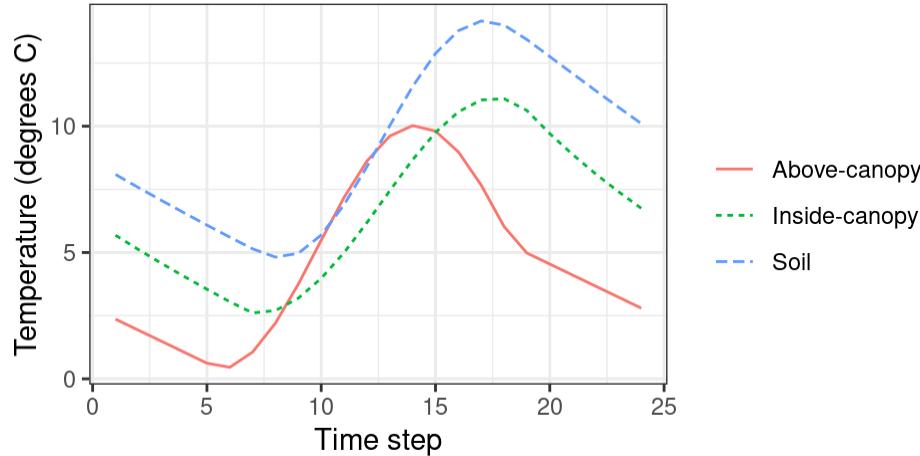
$$\Psi_{plant} = K^{-1} \left(\sum_s K(\Psi_s) \cdot FRP_s \right)$$

which can be intuitively understood as an *average of soil water potential* taking into account fine root distribution.

4. Transpiration and photosynthesis under the advanced model

Advanced features

- The advanced transpiration and photosynthesis model operates at **sub-daily** time steps.
- Temperature and radiation* inputs are temporally disaggregated.

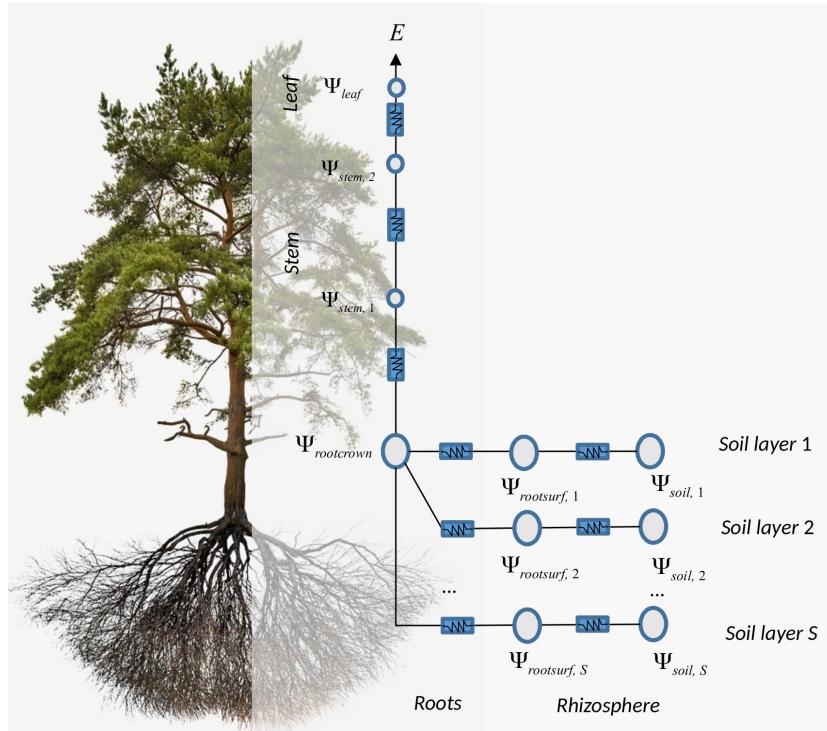


- The model is **explicit** with respect to many additional processes:

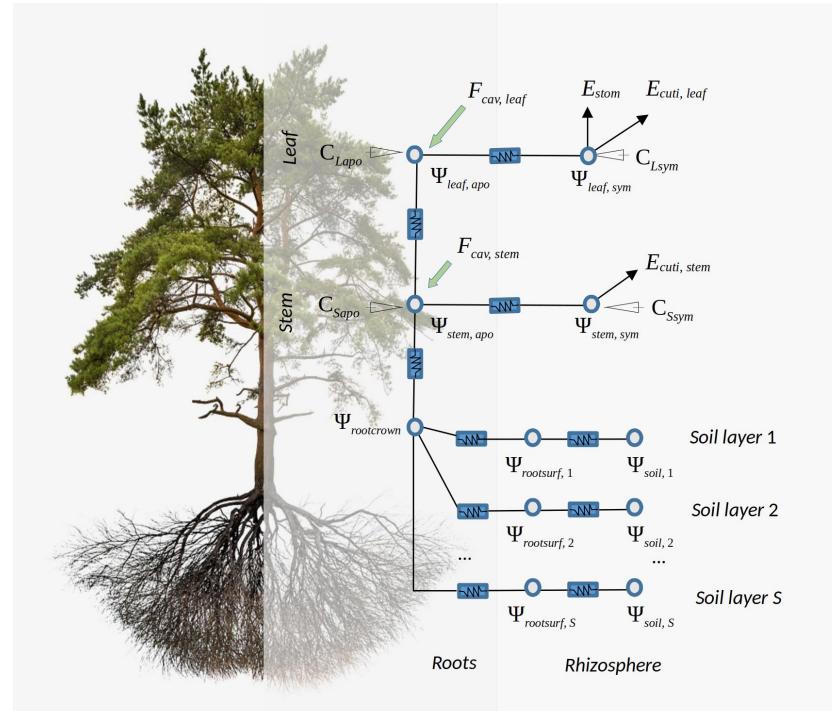
Process	Source
Soil & canopy energy balance	Best <i>et al.</i> (2011) <i>Geosci. Mod. Dev.</i> 4, 677-699
Canopy turbulence	Katul <i>et al.</i> (2004) <i>Bound. Lay. Met.</i> 113, 81-109
Sunlit/shade leaf photosynthesis	De pury & Farquhar (1997) <i>Plant, Cell & Env.</i> , 20, 537–557
Direct/diffuse short-wave extinction model	Anten & Bastiaans (2016) <i>Canopy photosynthesis: From basics to application</i>
Long-wave radiation model	Flerchinger <i>et al.</i> (2009) <i>Wan. J. Life Sci.</i> 57, 5-15
Plant hydraulics & stomatal regulation	[next slides]

Sperry and Sureau sub-models

Sperry



Sureau



- Steady-state plant hydraulics ¹.
- Optimality-based stomatal regulation ².

- Plant hydraulics of SurEau-ECOS ³, including plant water storage.
- Stomatal regulation based on a semi-empirical model.

1. Sperry et al. (1998) Plant, Cell & Environment, 21, 347–359.

2. Sperry et al. (2017) Plant, Cell & Environment, 40, 816–830.

3. Buffault et al. (2022) Geosci. Model Dev., 15, 5503–5526.

Sperry sub-model: Supply function

The supply function describes the **steady-state** rate of water flow, E , as a function of water potential drop.

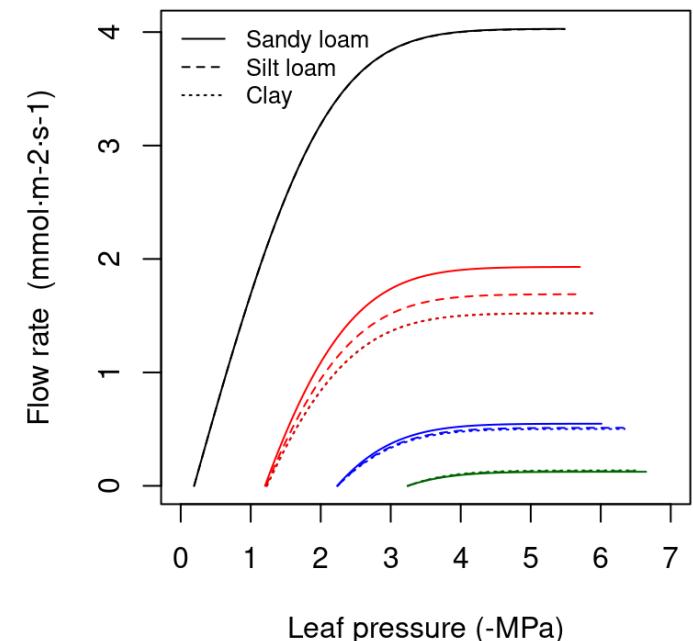
The steady-state flow rate E_i through any element i is related to the flow-induced drop in water potential across that element, $\Delta\Psi_i = \Psi_{down} - \Psi_{up}$, by the integral of the vulnerability curve $k_i(\Psi)$ ¹:

$$E_i = \int_{\Psi_{up}}^{\Psi_{down}} k_i(\Psi) d\Psi$$

where Ψ_{up} and Ψ_{down} are the upstream and downstream water potential values.

The supply function can be integrated across the **whole hydraulic network**.

$$E(\Psi_{leaf}) = \int_{\Psi_{soil}}^{\Psi_{leaf}} k(\Psi) d\Psi$$



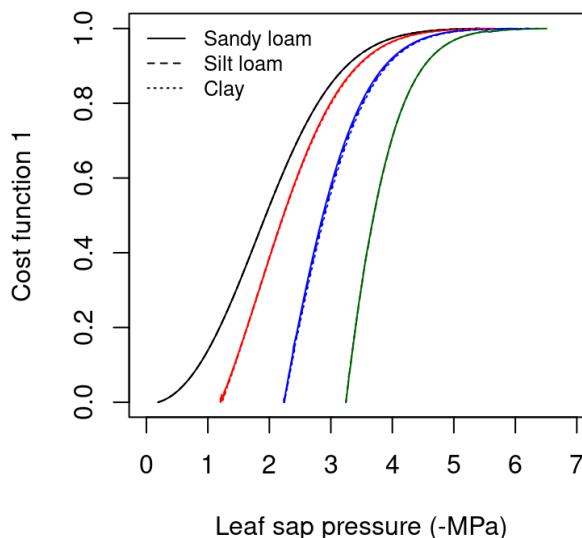
Sperry sub-model: Stomatal regulation

1. Cost function

The hydraulic supply function is used to derive a **cost function** $\theta(\Psi_{leaf})$, reflecting the increasing damage from cavitation.

$$\theta(\Psi_{leaf}) = \frac{k_{c,max} - k_c(\Psi_{leaf})}{k_{c,max} - k_{crit}}$$

where $k_c(\Psi_{leaf}) = dE/d\Psi(\Psi)$ is the slope of the (whole-plant) supply function.

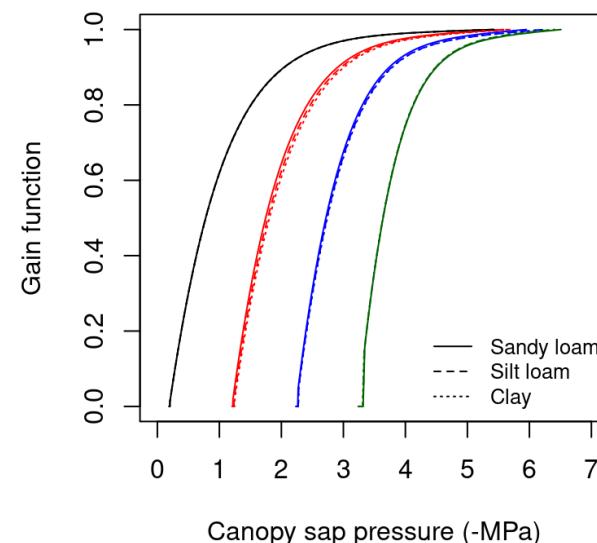


2. Gain function

The normalized photosynthetic **gain function** $\beta(\Psi_{leaf})$ reflects the increase in assimilation rate, with respect to the maximum.

$$\beta(\Psi_{leaf}) = \frac{A(\Psi_{leaf})}{A_{max}}$$

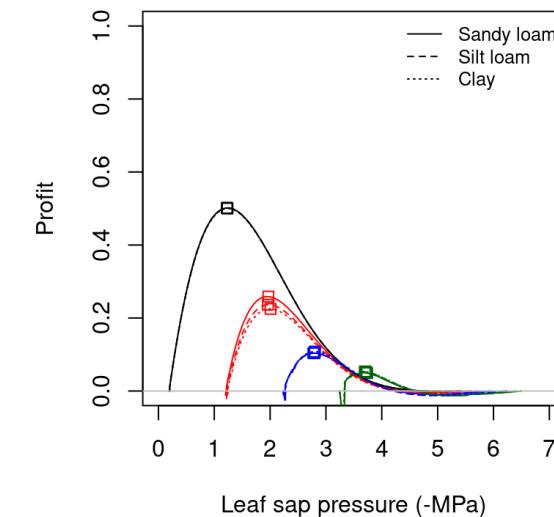
where A_{max} is the instantaneous maximum (gross) assimilation rate estimated over the full Ψ_{leaf} range.



3. Profit function

Stomatal regulation can be effectively estimated by determining the maximum of the *profit function*:

$$Profit(\Psi_{leaf}) = \beta(\Psi_{leaf}) - \theta(\Psi_{leaf})$$



The maximization is achieved when the slopes of the gain and cost functions are equal:

$$\frac{\delta\beta(\Psi_{leaf})}{\delta\Psi_{leaf}} = \frac{\delta\theta(\Psi_{leaf})}{\delta\Psi_{leaf}}$$

Sureau sub-model

SurEau's sub-model, leaf energy balance, stomatal and cuticular conductances, transpirational flows, photosynthesis and plant hydraulics are computed **iteratively** in small temporal sub-steps (e.g. 10 min).

Plant hydraulics

Water dynamics in SurEau-ECOS¹ are governed by **partial differential equations** of mass conservation:

$$C_i \cdot \frac{d\Psi_i}{dt} + \sum_j k_{ij} \cdot (\Psi_i - \Psi_j) - S = 0$$

where Ψ_i and Ψ_j are the water potential of compartments i and j , respectively, C_i is the **capacitance** associated to the compartment i and S is an outflow component (e.g. stomatal transpiration, cuticular transpiration or cavitation flux).

Stomatal regulation

Stomatal conductance takes into account the dependence of stomata on light and temperature², as well as leaf water status:

$$g_{sw} = g_{sw,light,temp} \cdot \lambda(\Psi_{leaf,sym})$$

where $g_{sw,light,temp}$ is the stomatal conductance value without water stress, and λ is a regulation factor that represents stomatal closure according to leaf water potential, using a sigmoid function.

Cuticular conductance

Cuticular conductances are not only species-specific but also change with leaf temperature, according to changes in permeability of lipids in the epidermis.

1. Ruffault et al. (2022) Geosci. Mod. Dev., 15, 5593-5626

2. Baldocchi D. (1994) Tree Phys., 14, 1069-1079

5. Plant drought stress and cavitation

Daily drought stress

Daily drought stress, DDS , is defined using ϕ , the phenological status, and the *one-complement* of relative whole-plant conductance:

Basic model

Since K is defined as a relative whole-plant conductance:

$$DDS = \phi \cdot (1 - K(\Psi_{plant}))$$

Advanced model

Since the derivative of the supply function, i.e. $dE/d\Psi_{leaf}$, is the *absolute* whole-plant conductance:

$$DDS = \phi \cdot \left[1 - \frac{dE/d\Psi_{leaf}}{k_{max,plant}} \right]$$

Cavitation

If cavitation has occurred in previous steps then the capacity of the plant to transport water is impaired via the estimation of percent loss conductance (PLC).

Basic model

Estimation of PLC:

$$PLC_{stem} = 1 - \exp \left\{ \ln(0.5) \cdot \left[\frac{\Psi_{plant}}{\Psi_{critic}} \right]^r \right\}$$

Effect on plant transpiration:

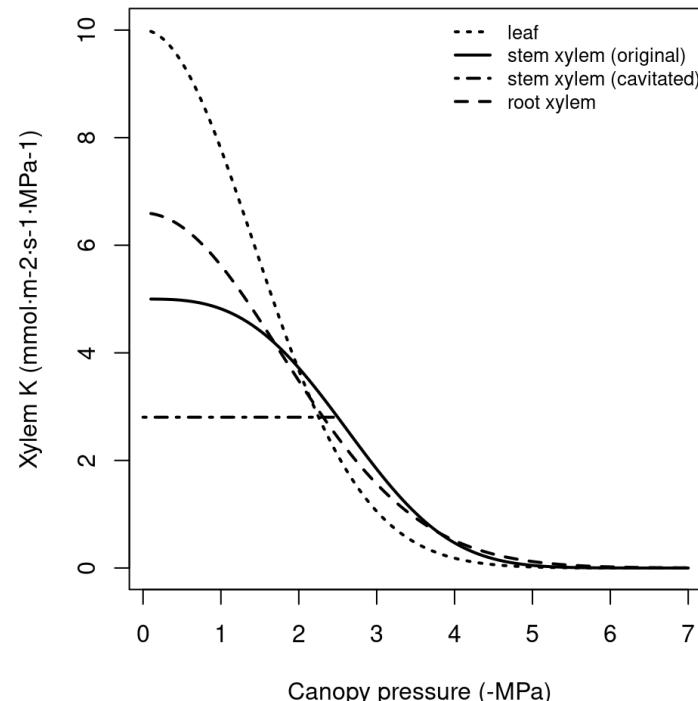
$$K_s^{PLC} = \min\{K_s, 1.0 - PLC_{stem}\}$$

Advanced model

Estimation of PLC:

$$PLC_{stem} = 1 - \frac{k_{stem}(\Psi_{stem})}{k_{max,stem}}$$

Effect on the stem vulnerability curve:



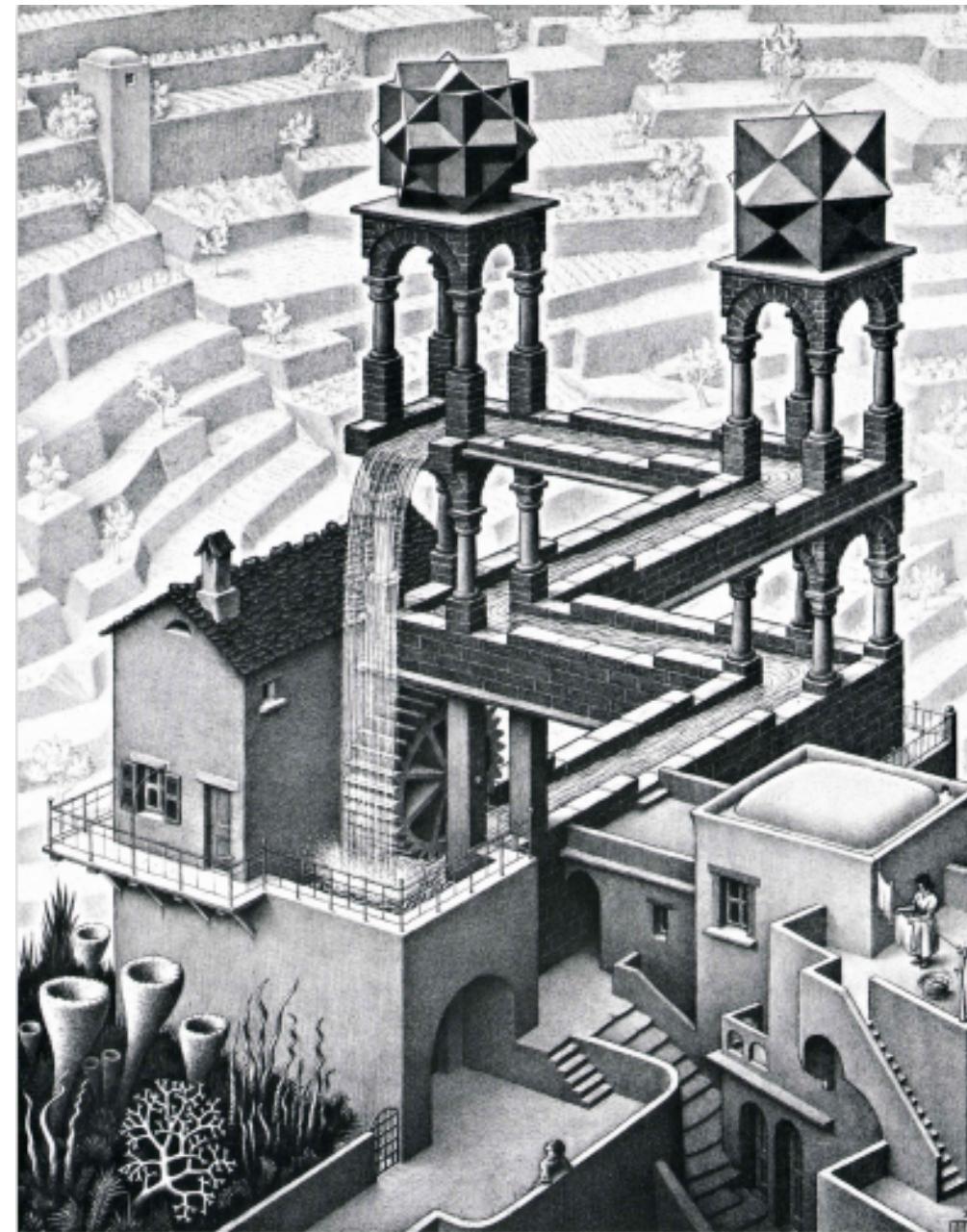
6. Basic vs. advanced models: a summary of differences

Process representation

Group	Process	Basic	Advanced
Forest hydrology	Rainfall interception	*	*
	Infiltration/percolation	*	*
	Soil gravitational and matric flows	[*]	[*]
	Bare soil evaporation	*	*
	Snow dynamics	*	*
	Transpiration through stomata	[*]	*
	Cuticular transpiration	[*]	
Radiation balance	Hydraulic redistribution	[*]	*
	Radiation extinction	*	*
	Diffuse/direct separation		*
	Longwave/shortwave separation		*
Plant physiology	Photosynthesis	[*]	*
	Stomatal regulation		*
	Plant hydraulics		*
	Stem cavitation	*	*
Energy balance	Leaf energy balance		*
	Canopy energy balance		*
	Soil energy balance		*

Basic vs. advanced: State variables

Group	State variable	Basic	Advanced
Soil	Soil moisture gradients	*	*
	Soil temperature gradients		*
Canopy	Canopy temperature gradients		*
	Canopy moisture gradients		*
	Canopy CO_2 gradients		*
Plant	Leaf phenology status	*	*
	Plant water status	*	*
	Plant water content		*
	Water potential gradients		*
	Stem cavitation level	*	*



M.C. Escher - Waterfall, 1961