Forest water and energy balance (theory)

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Outline

1. Preliminary concepts: hydraulics and drought effects
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: hydraulics and drought effects

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:

$$\Psi = \Psi_{\Pi} + \Psi_{p} + \Psi_{g} + \Psi_{m}$$

Osmotic potential
(negative, living cells)

Pressure
(positive or negative)

Gravity
(negative)

Matric
(negative, soils)

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:

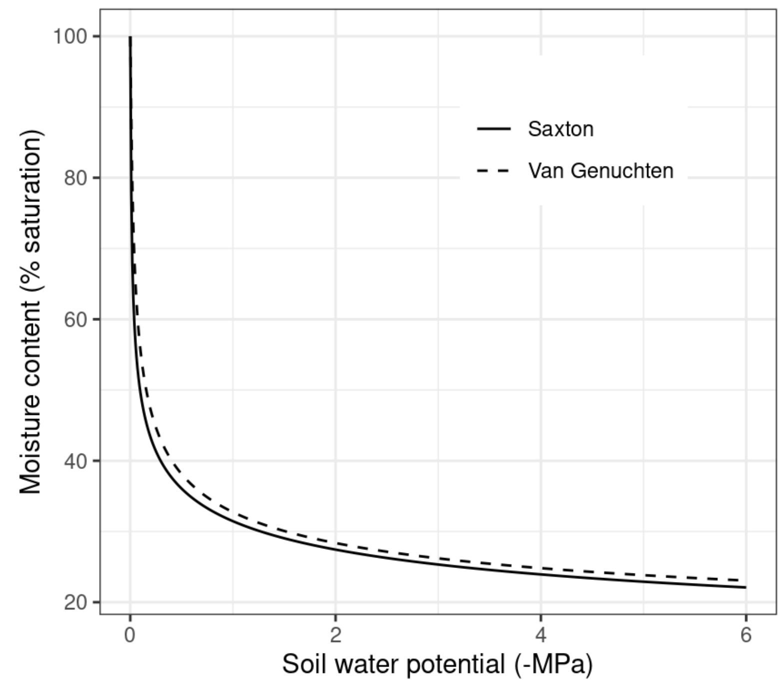
$$\theta(\Psi) = (\Psi/A)^{(1/B)}$$

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.

Plant pressure volume curves

The *pressure volume curve* of a plant tissue or organ is the relationship between relative water content (RWC, in $kg\ H_2O/kg\ \ H_2O$ at saturation) and the corresponding water potential (Ψ, in MPa).

The relationship between Ψ and RWC is formulating by separating Ψ into osmotic (solute) potential (Ψ_S) and the turgor pressure potential (Ψ_P):

$$\Psi = \Psi_S + \Psi_P$$

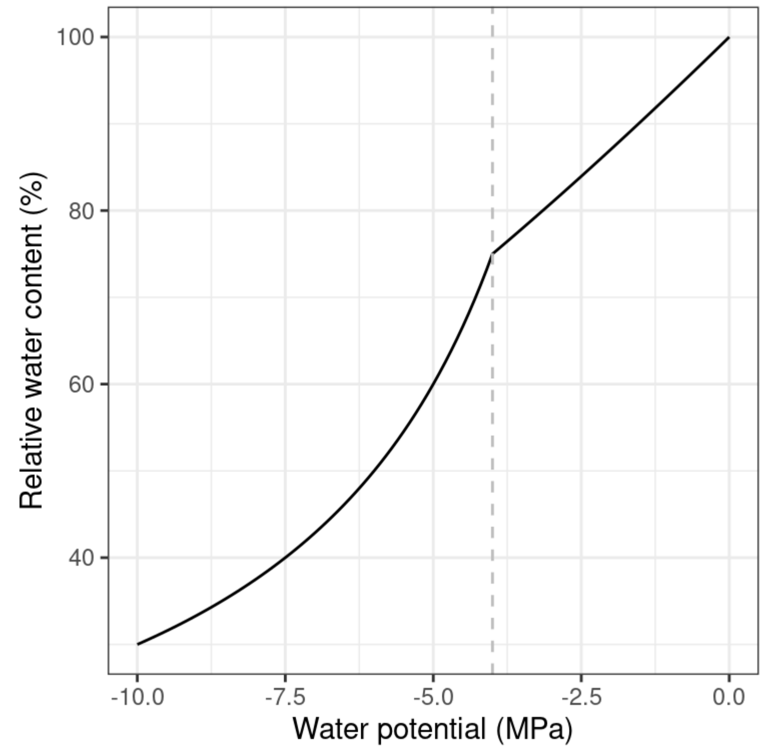
where

$$\Psi_P = -\pi_0 - \epsilon \cdot (1.0 - RWC)$$

and

$$\Psi_S = \frac{-\pi_0}{RWC}$$

where π_0 (MPa) is the osmotic potential at full turgor (i.e. when $RWC = 1$) and ϵ is the modulus of elasticity (i.e. the slope of the relationship).



When $\Psi \leq \Psi_{tlp}$, the water potential at turgor loss point, then $\Psi_P = 0$ and $\Psi = \Psi_S$. If $\Psi > \Psi_{tlp}$ then the two components are needed.

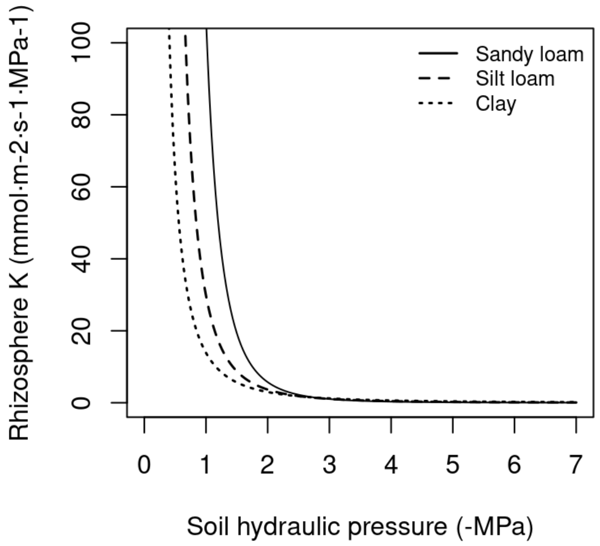
Hydraulic conductance and vulnerability curves

- **Hydraulic conductance** k measures how much flux exists along a pathway segment (e.g. soil, stem, leaves, $\ldots$) for a given difference in water potential.
- Hydraulic conductance decreases when **air replaces water** in any segment of the pathway.
- The **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:

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

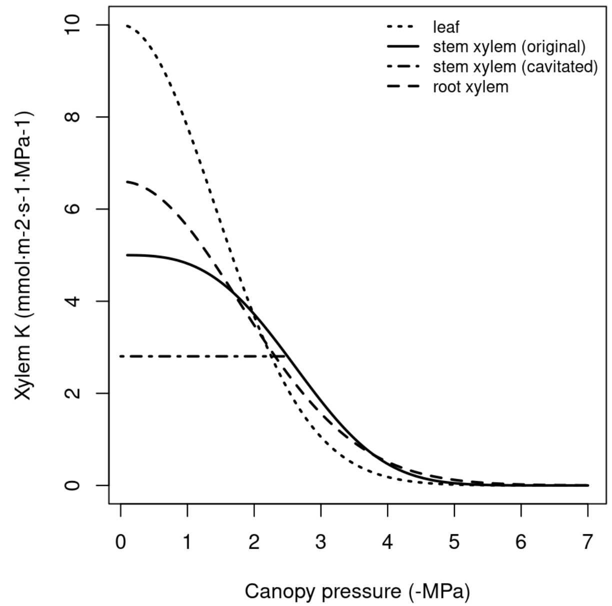


Xylem

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

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

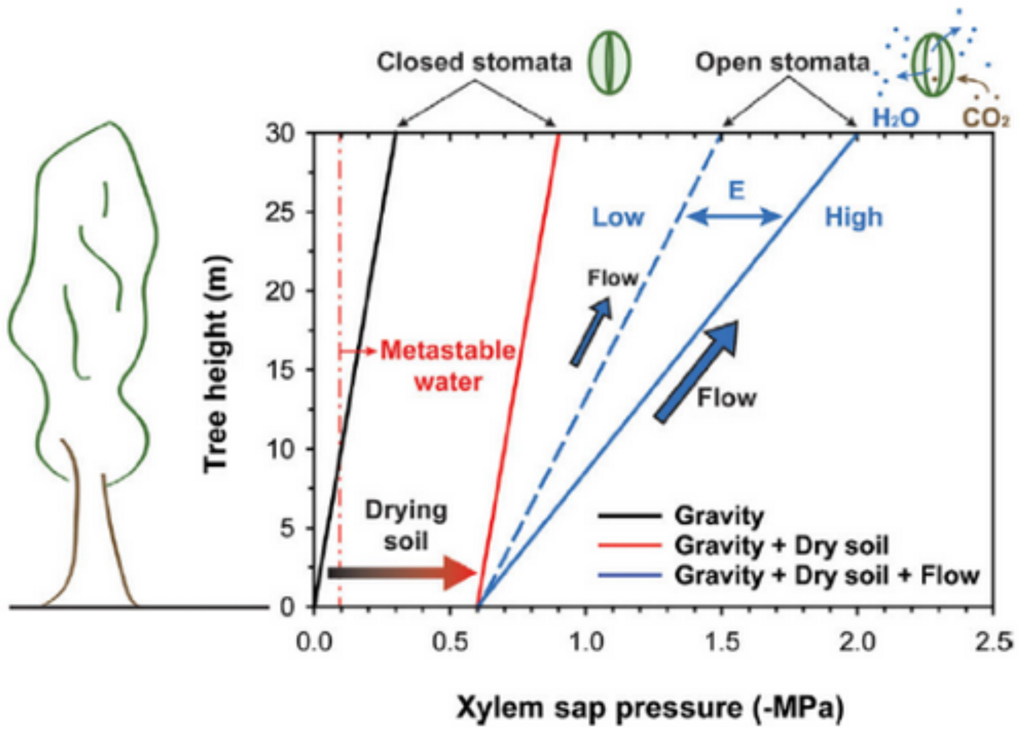
$$k(\Psi) = \frac{k_{max}}{1 + e^{(slope/25) \cdot (\Psi - \Psi_{50})}}$$



Water potential drop in plants

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

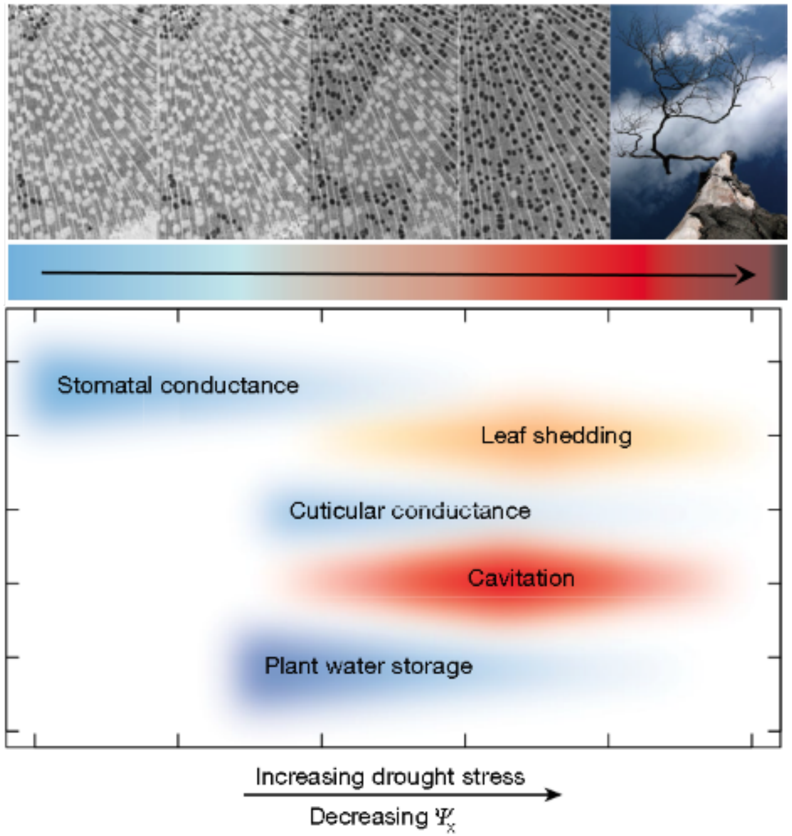
When stomata are **open**, a larger transpiration flow (E) implies a larger *drop in water potential* along the transpiration pathway due to the negative pressure (suction) that arises [1]:

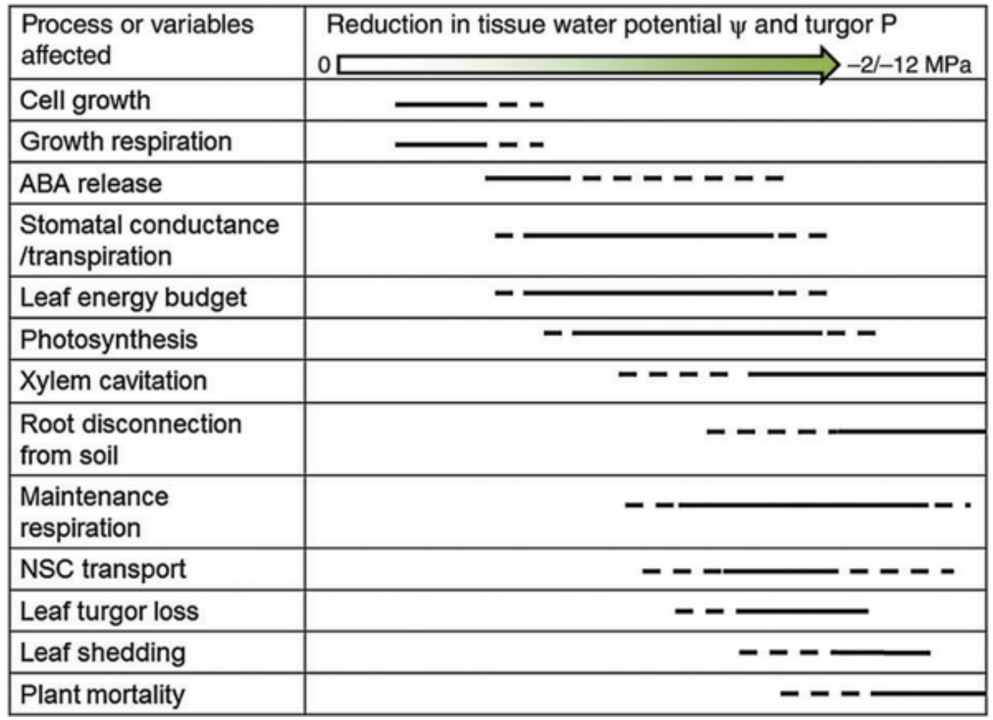


1. Granier et al. (1999), Ecol. Model., 116, 269-283

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].



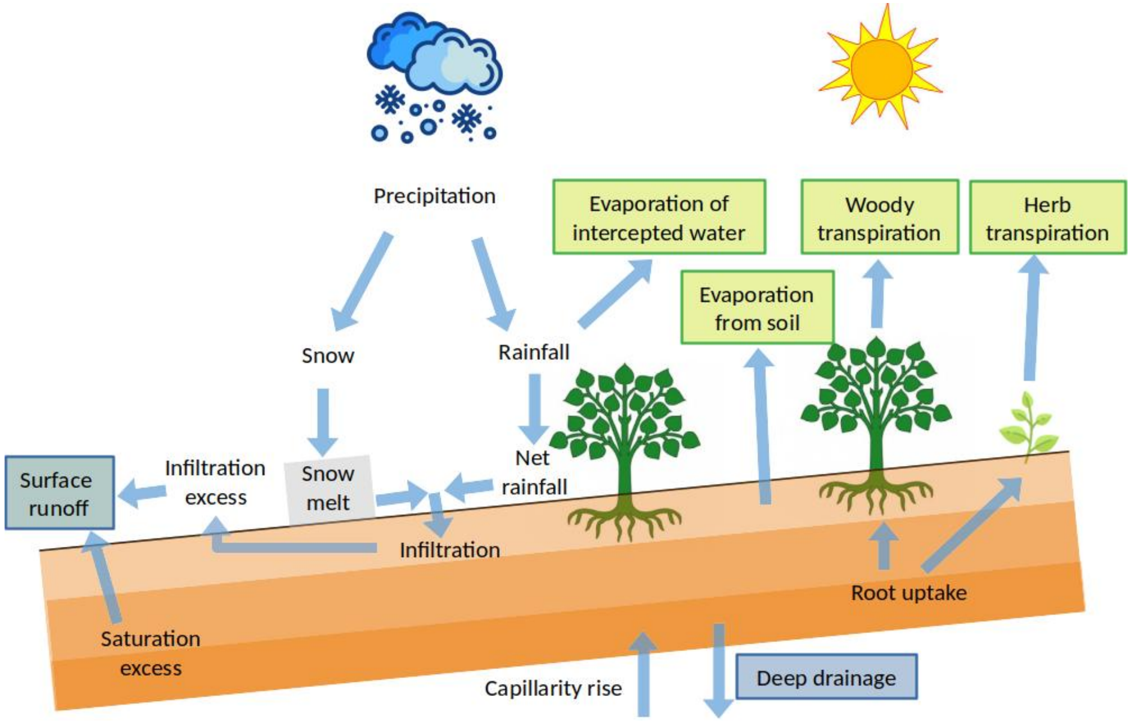


1. Choat et al. (2018) Nature, 558, 531-539.
2. Fatichi et al. (2016) Wiley Interdisciplinary Reviews: Water, 3, 327-368

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.



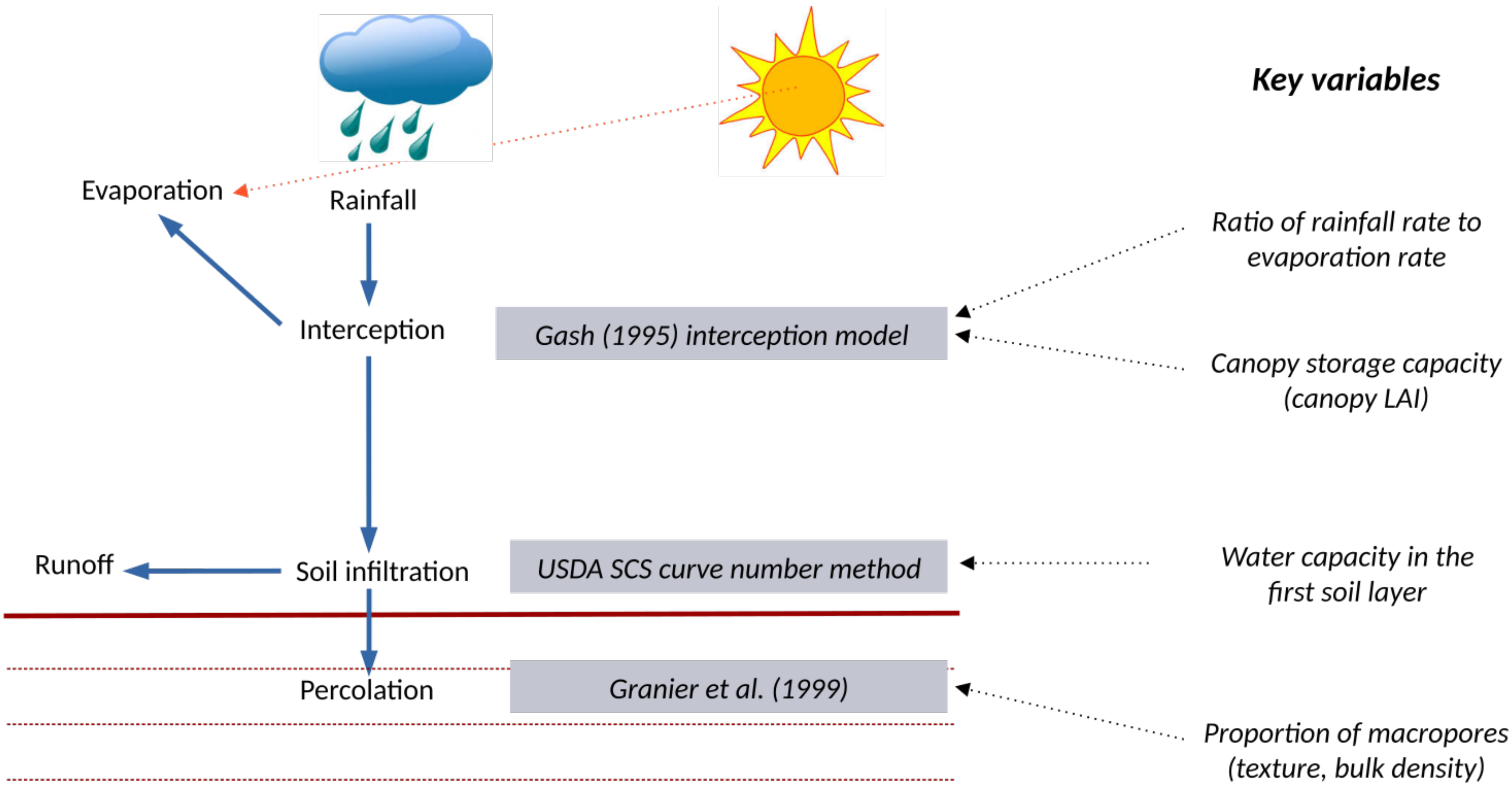
Component	Symbol	Description
Infiltration	If	Water entering the soil from above
Capillarity rise	Cr	Water entering the soil via capillarity from a lower saturated layer
Deep drainage	Dd	Water percolating beyond the root zone
Saturation excess	Se	Excess of water in the soil
Soil evaporation	Es	Evaporation from soil surface
Woody transpiration	Tr_{woody}	Woody plant transpiration
Herb transpiration	Tr_{herb}	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

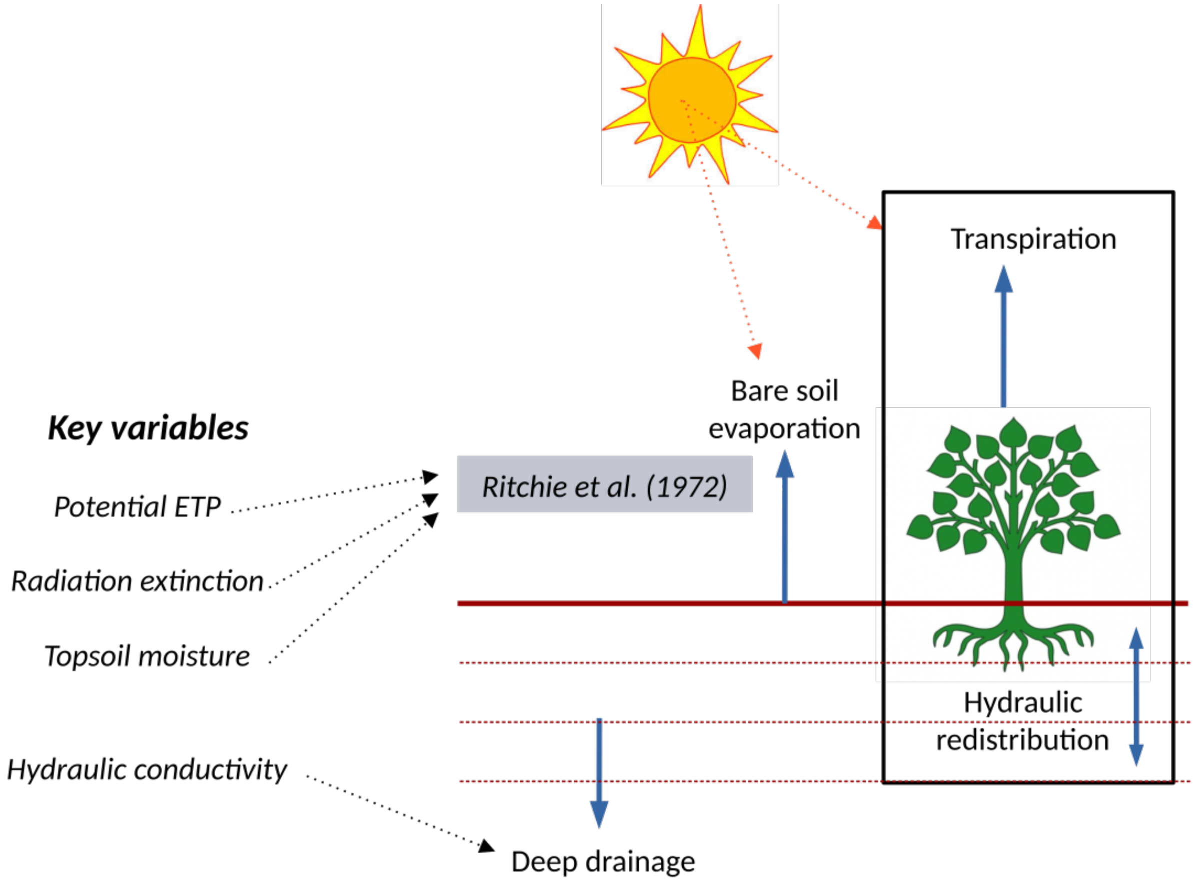
If rainfall occurs during a given day, three processes are simulated to update the water content in soil layers:



Sub-models involved in water inputs

Soil water outputs

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



Sub-models involved in water outputs

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

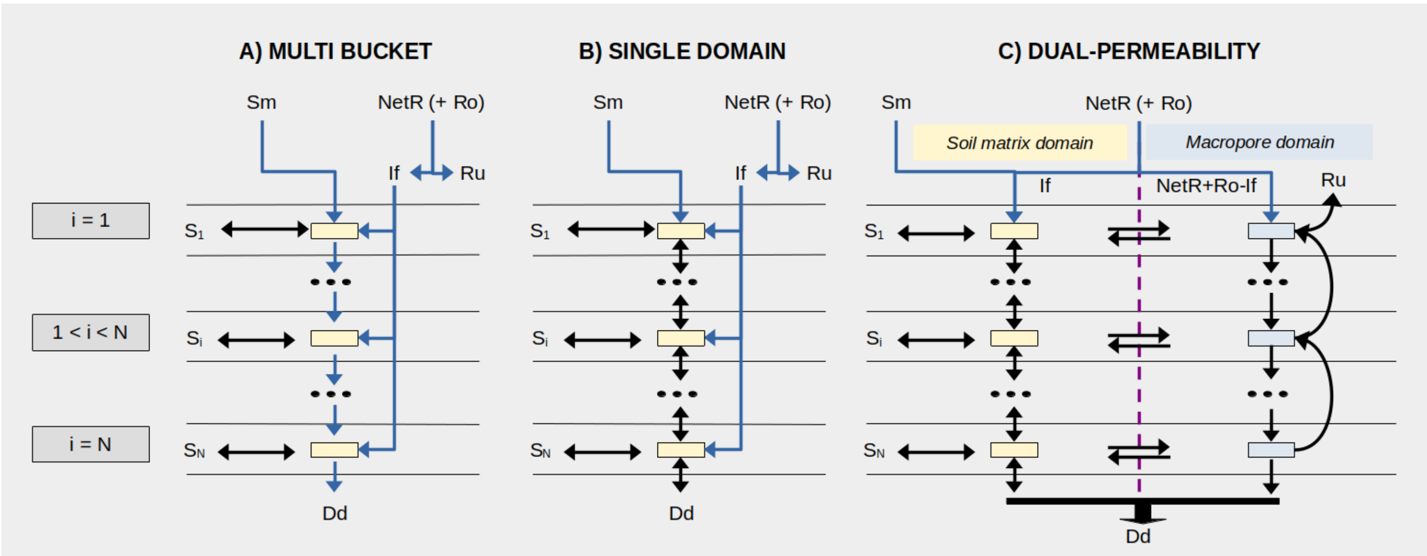
Soil water fluxes

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). Assumes an homogeneous porous media.

C. **Dual permeability model**: Flows in the soil matrix following the previous model. Flows in the macropore domain following gravitational forces. The two domains exchange water.



Sub-models of fluxes in the soil

> **Warning**
>
> The three sub-models differ greatly in computational demand (see Exercise 2b).

3. Transpiration and photosynthesis under the basic model

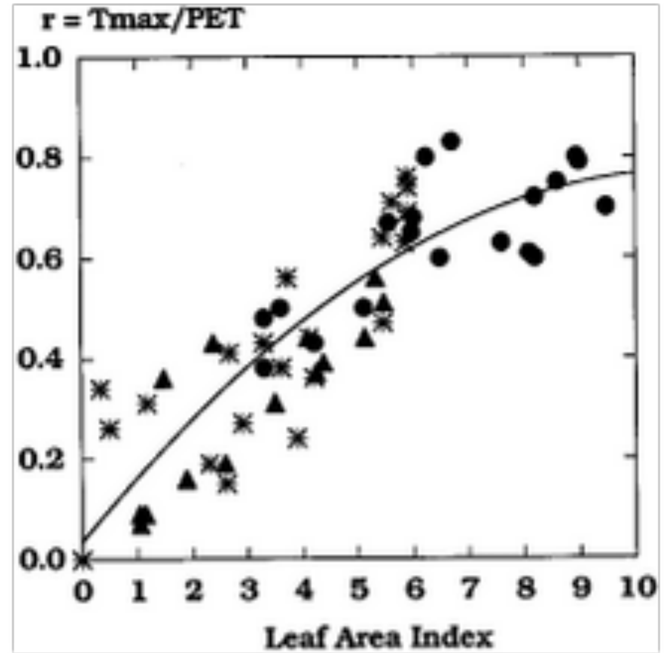
Maximum canopy transpiration

Maximum canopy transpiration $Tr_{\max}$ depends on potential evapotranspiration, PET, and the amount of transpirating surface, i.e. the stand leaf area index, thanks to an empirical relationship by Granier [1]:

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

and therefore:

$$Tr_{\max} = PET \cdot \left(-0.006 \cdot (LAI^{\phi}_{stand})^2 + 0.134 \cdot LAI^{\phi}_{stand}\right)$$



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**.

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

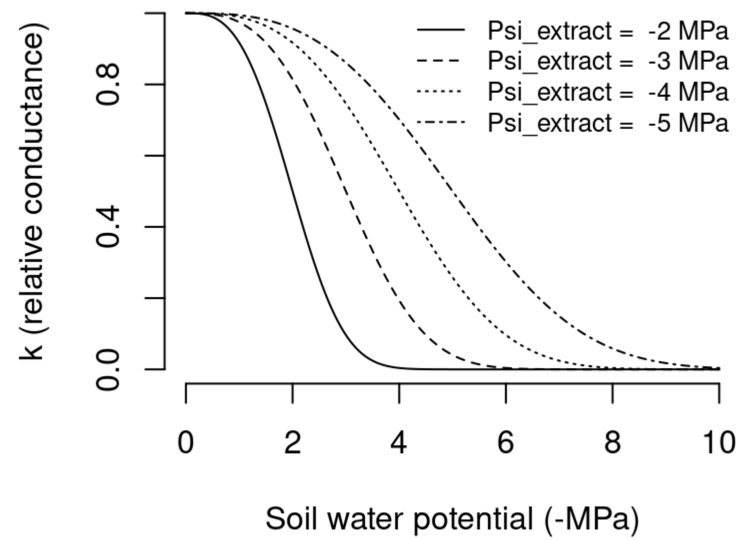
Actual plant transpiration

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

A *relative whole-plant water conductance*, k_{rel} is defined for any given soil layer s using:

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

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:

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

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 CO_2 limitations.
- L^{PAR} is the proportion of photosynthetically active radiation available and WUE_{PAR} is an exponent.
- C_{air} is the air CO_2 concentration 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:

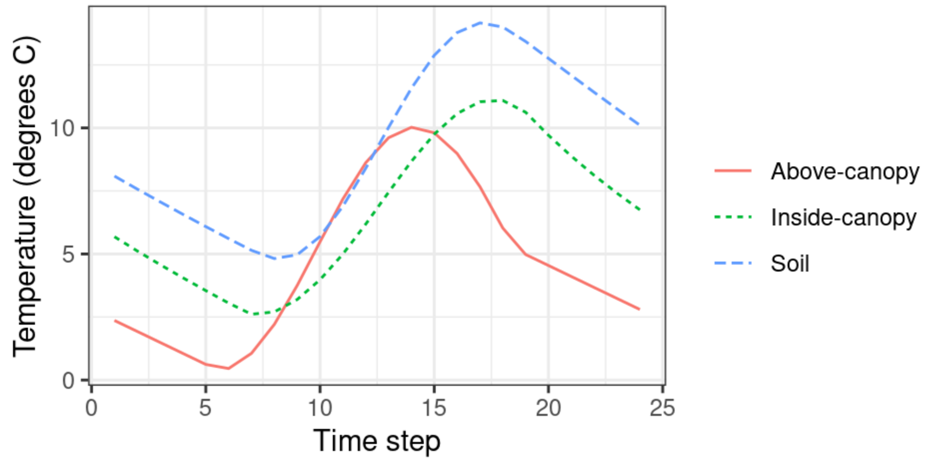
$$\Psi_{plant} = k_{rel}^{-1} \cdot \left(\sum_{s} k_{rel}(\Psi_s) \cdot FRP_s \right)$$

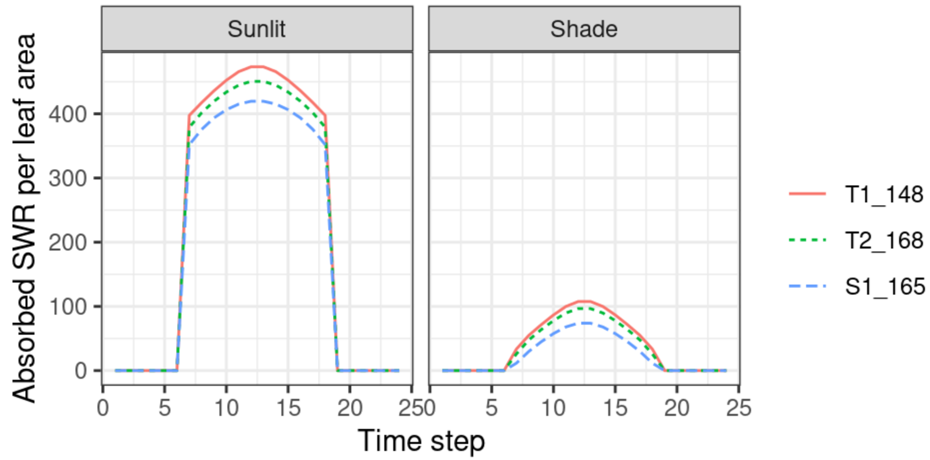
which can be intuitively understood as an *average of soil water potential* taking into account fine root distribution.

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.



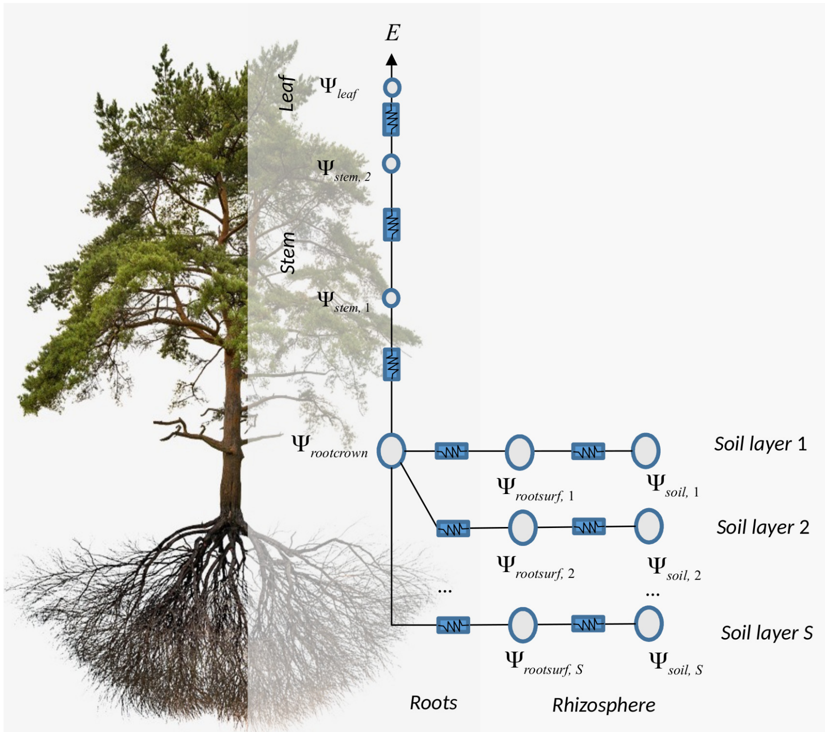


- The model is **explicit** with respect to many additional processes:

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

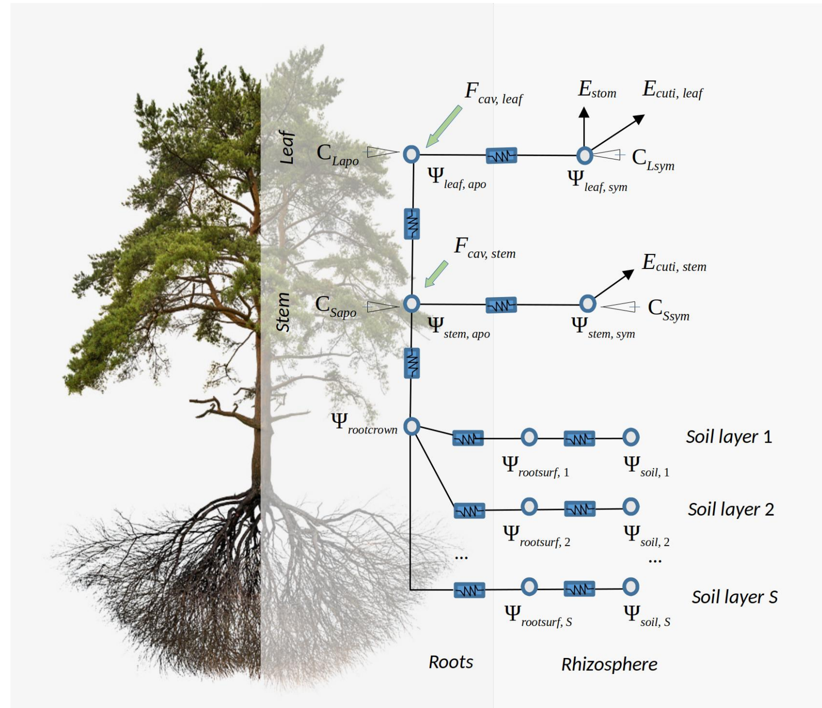
Sperry and Sureau sub-models

Sperry



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

Sureau



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

Sperry sub-model: Supply function

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

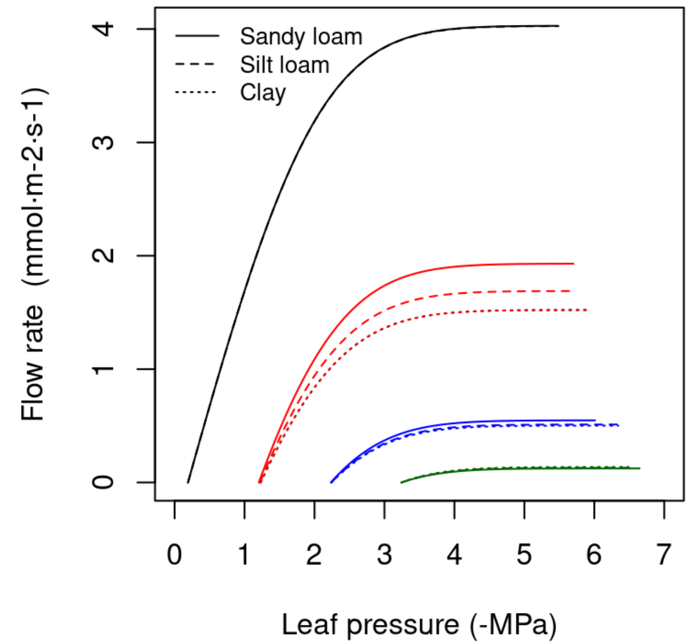
The steady-state flow rate E_i through any element i is related to the flow-induced drop in water potential across that element, $\Delta\Psi_i = \Psi_{down} - \Psi_{up}$, by the integral of the vulnerability curve $k_i(\Psi)$ [1]:

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

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**.

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



1. Sperry et al. (1998) Plant, Cell & Environment, 21, 347–350

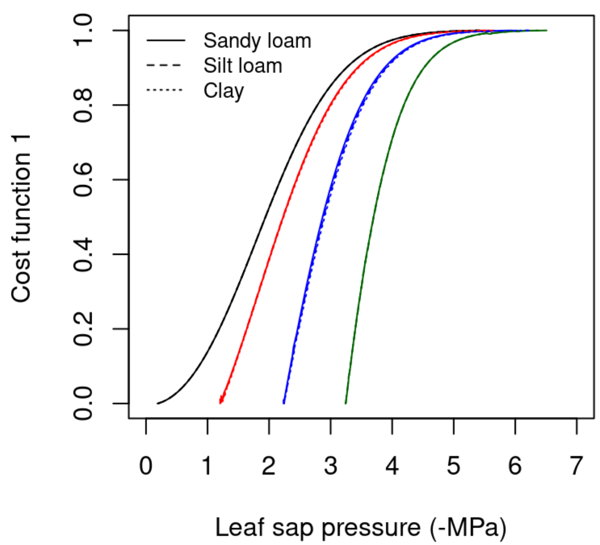
Sperry sub-model: Stomatal regulation

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.

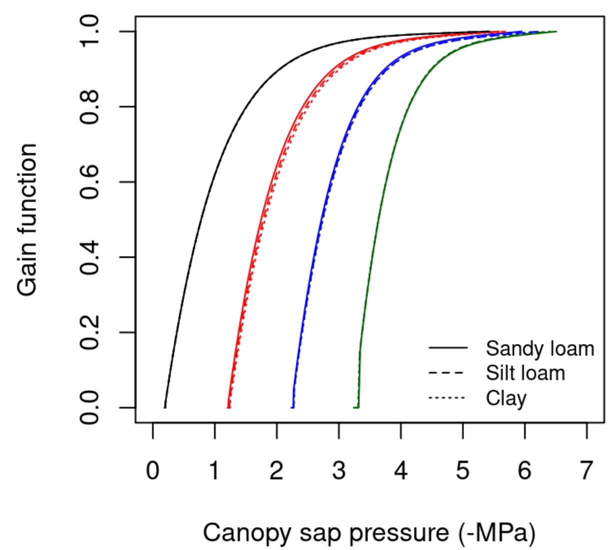


2. Gain function

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

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

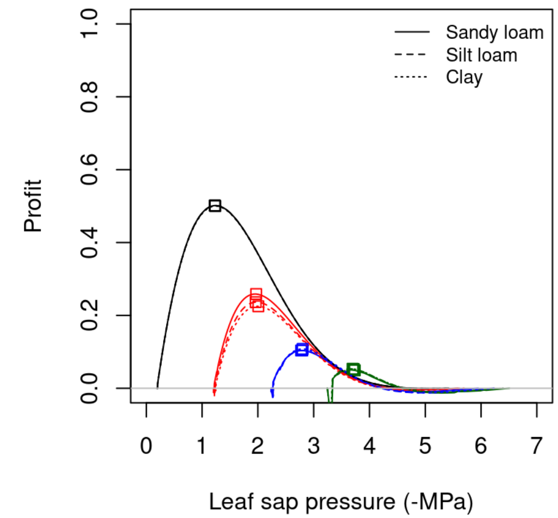
where A_{max} is the instantaneous maximum (gross) assimilation rate estimated over the full Ψ_{leaf} range.



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-ECOS [1] are governed by **partial differential equations** of mass conservation:

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

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 temperature [2], 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_{rel} is already defined as a relative whole-plant conductance:

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

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:

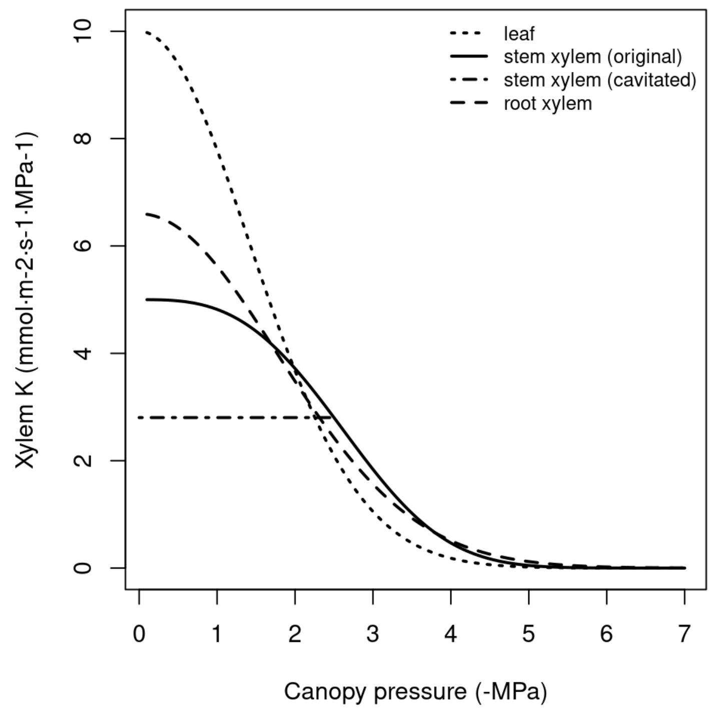
$$k_{rel}^{PLC}(\Psi_s) = \min\{k_{rel}(\Psi_s), 1.0 - PLC_{stem}\}$$

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		[*]
	Hydraulic redistribution	[*]	*
Radiation balance	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