

2.1 - 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

1. Preliminary concepts

Water potential

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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
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Gravity
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Matric
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But not all components are equally relevant in all contexts

1. Preliminary concepts

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)

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

1. Saxton model:

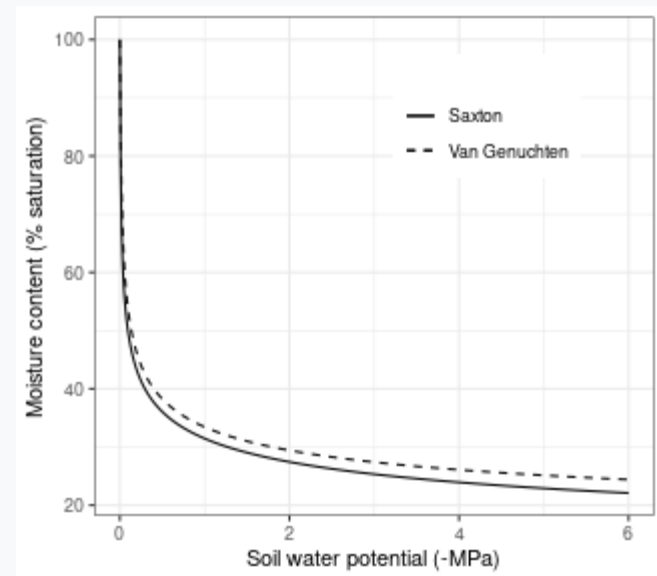
$$\theta(\Psi) = (\Psi/A)^{(1/B)}$$

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

2. 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.



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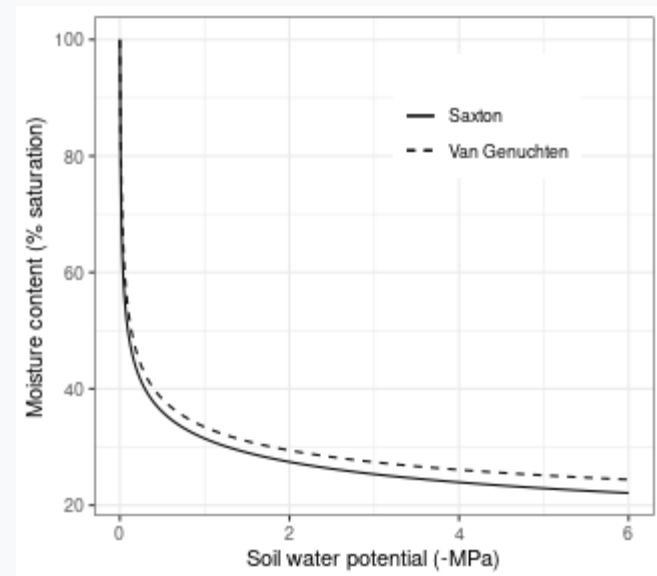
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1. Preliminary concepts

Water potential drop in plants

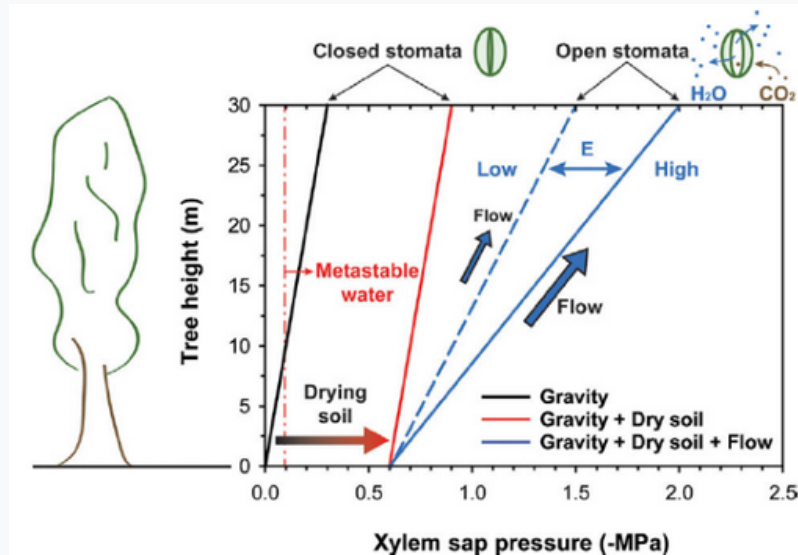
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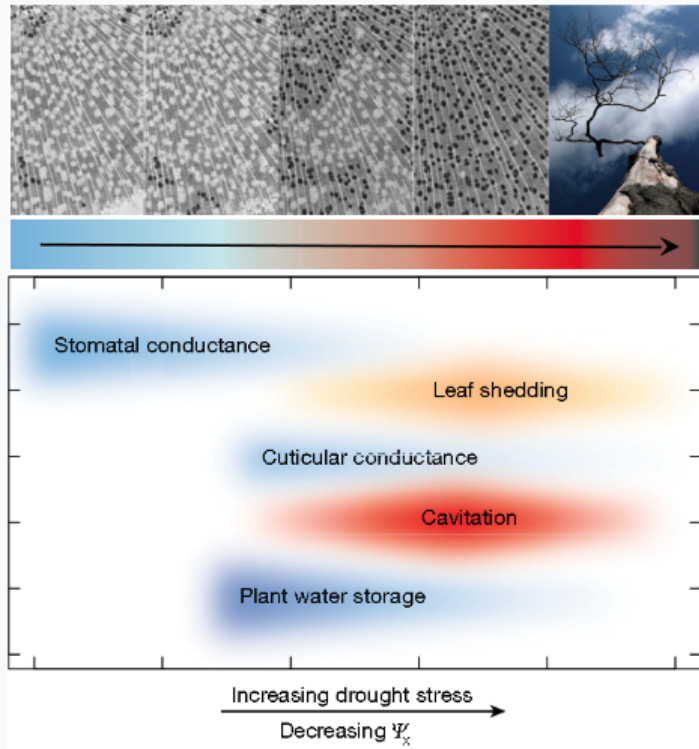
When stomata are open, a larger transpiration flow (E) implies (in steady state) a larger drop in water potential along the transpiration pathway:




1. Preliminary concepts

Drought impacts on plants

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

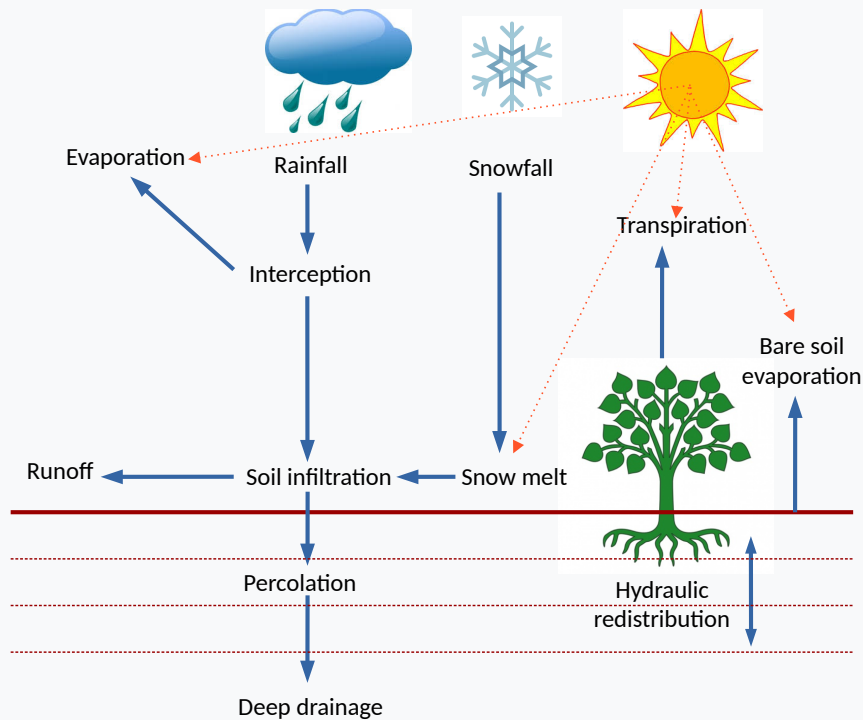


Process or variables affected	Reduction in tissue water potential ψ and turgor P
	0  -2/-12 MPa
Cell growth	-----
Growth respiration	-----
ABA release	-----
Stomatal conductance /transpiration	-----
Leaf energy budget	-----
Photosynthesis	-----
Xylem cavitation	-----
Root disconnection from soil	-----
Maintenance respiration	-----
NSC transport	-----
Leaf turgor loss	-----
Leaf shedding	-----
Plant mortality	-----

2. Forest water balance in medfate

Water balance components

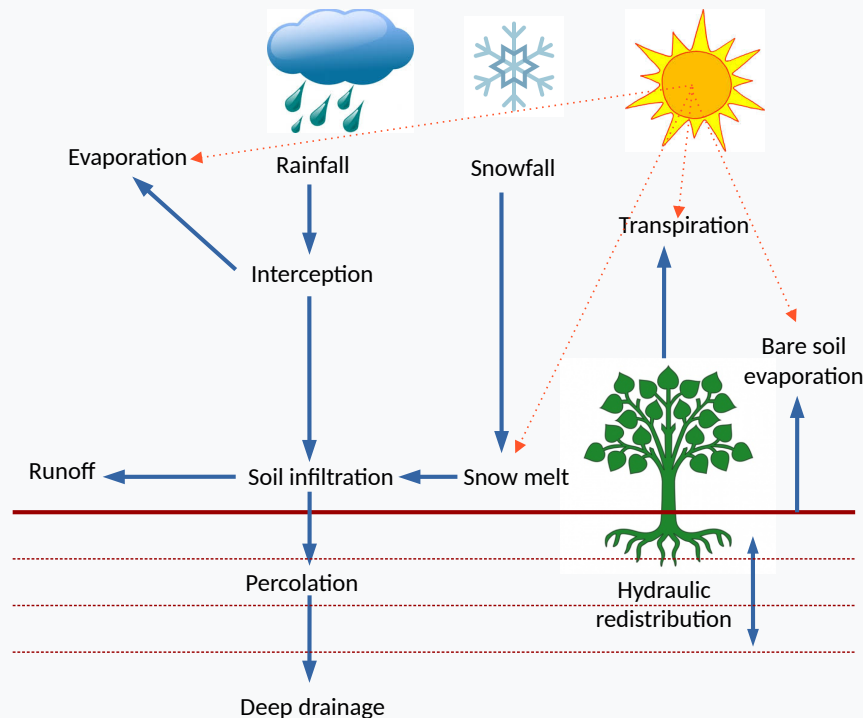
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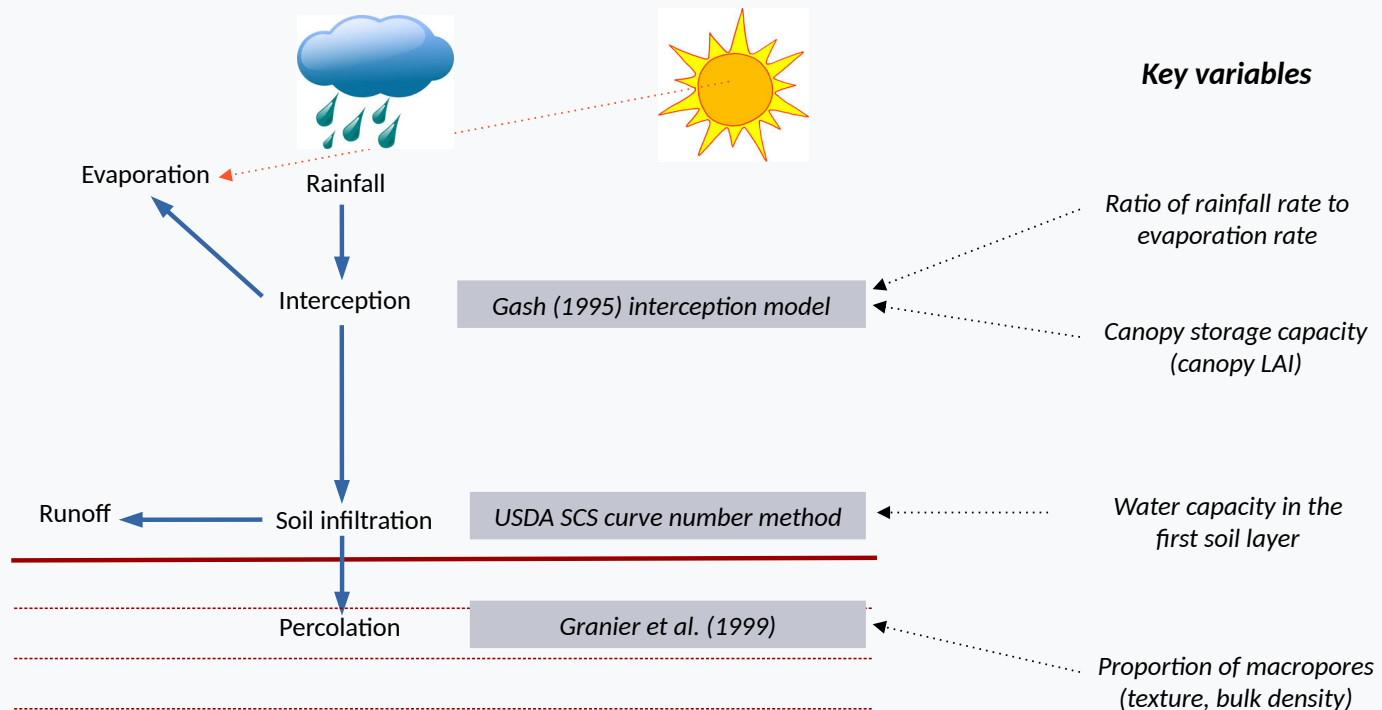
Variations in soil water content can be summarized as:

$$\Delta V_{soil} = Pr + Sm - In - Ru - Dd - Es - Ex$$

2. Forest water balance in medfate

Soil water inputs

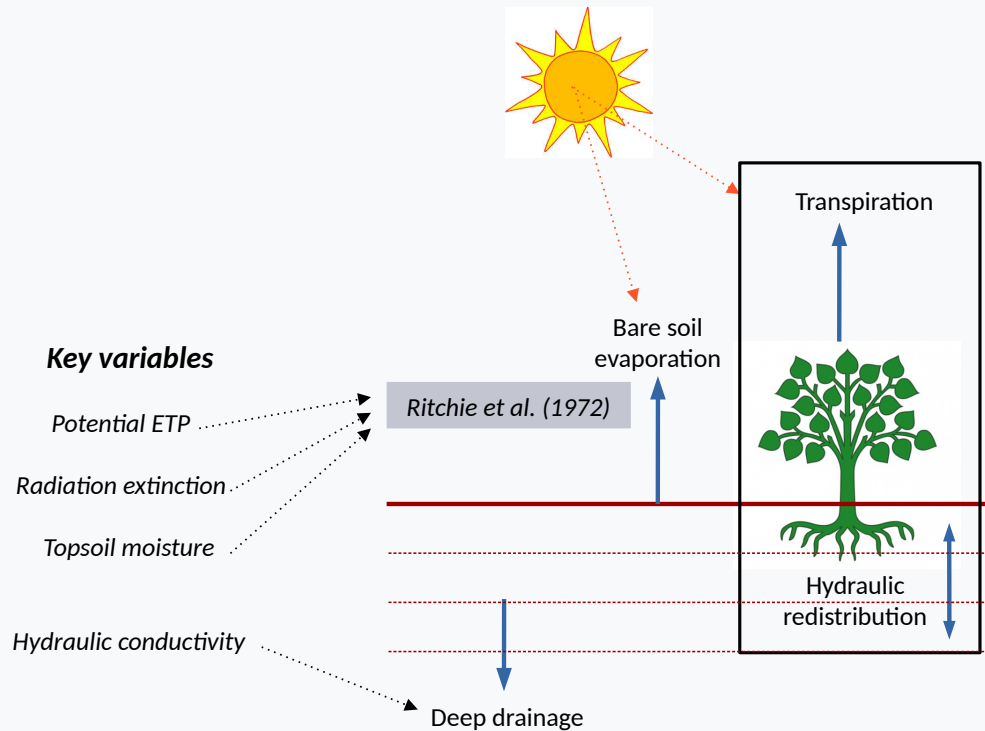
If rainfall occurs during a given day, three processes are simulated to update the water content in soil layers:



2. Forest water balance in medfate

Soil water outputs

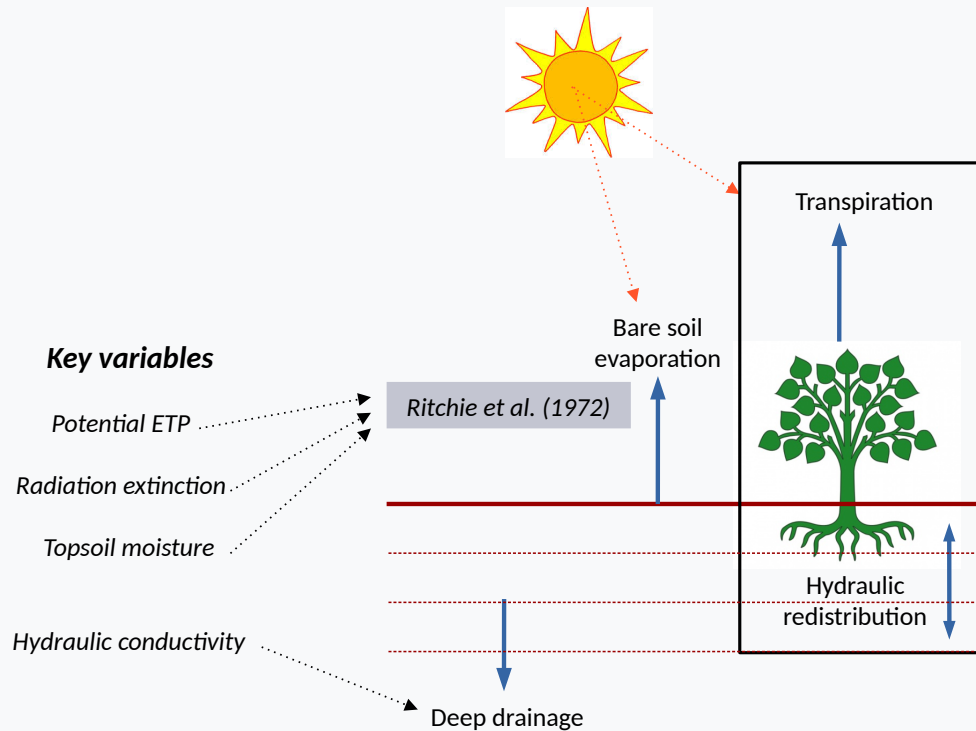
Regardless of precipitation, soil moisture can be modified due to the following processes:



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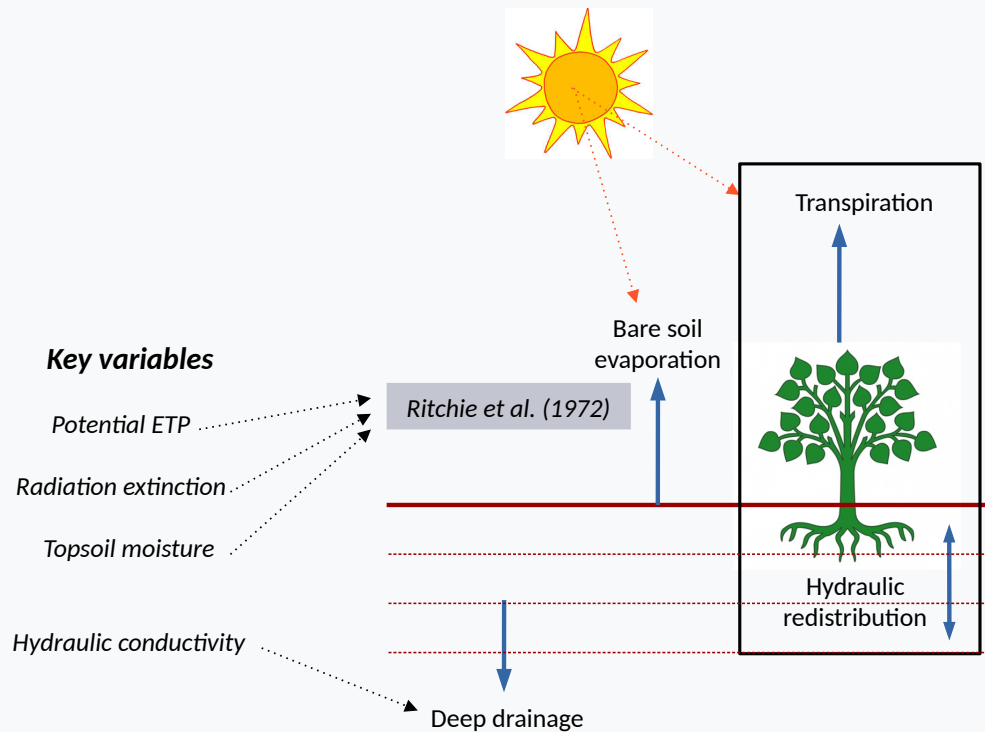


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Soil water outputs

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

Hydraulic redistribution is only simulated in the advanced water balance model.

3. Transpiration and photosynthesis under the basic model

Maximum transpiration

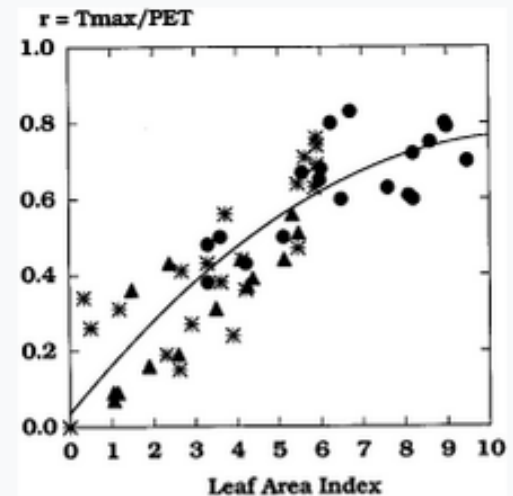
Maximum canopy transpiration

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:

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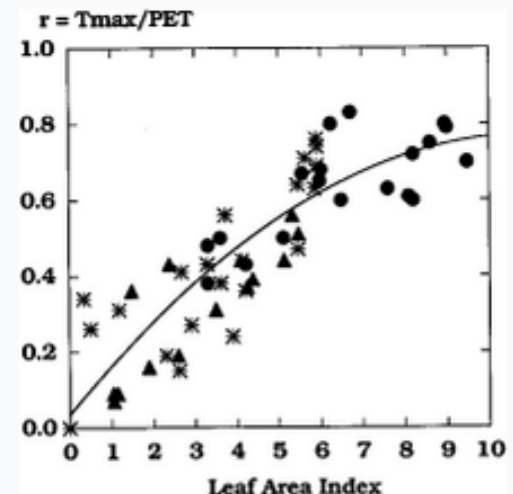
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Maximum plant transpiration

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

$$Tr_{\max,i} = Tr_{\max} \cdot \frac{f_i^{0.75}}{\sum_j f_j^{0.75}}$$

where f_i is the fraction of total absorbed short-wave radiation that is due to cohort i .



3. Transpiration and photosynthesis under the basic model

Actual plant transpiration

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

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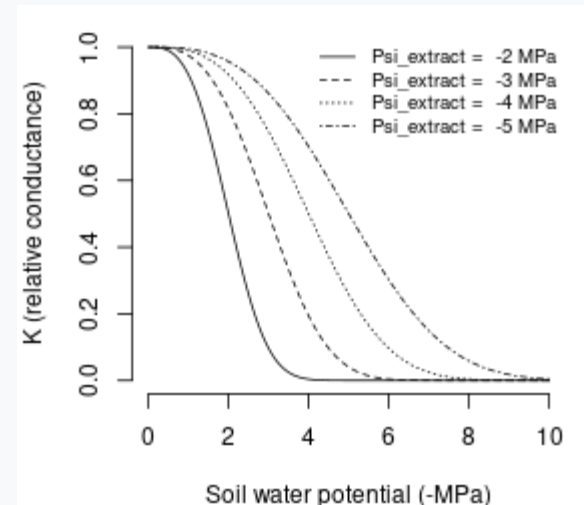
Actual plant transpiration

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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 .



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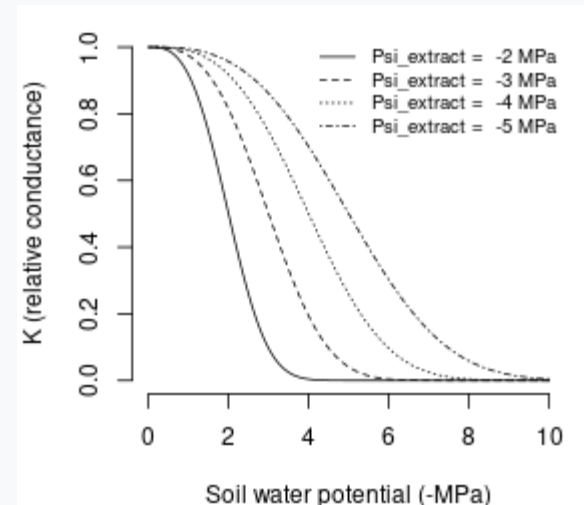
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The water extracted by a plant cohort from soil layer s and transpired, Tr_s , is the product:

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

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

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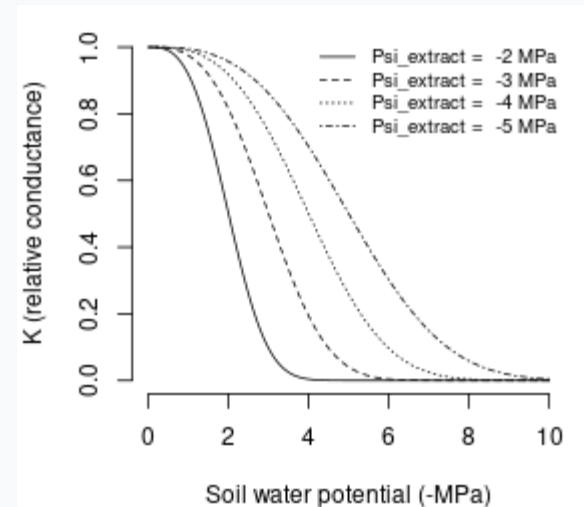
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The transpiration summed across soil layers is:

$$Tr = \sum Tr_s$$

3. Transpiration and photosynthesis under the basic model

Plant photosynthesis

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

$$A_g = Tr \cdot WUE_{\max} \cdot (L^{PAR})^{WUE_{decay}}$$

where WUE_{\max} is the maximum water use efficiency of the cohort under maximum light availability, L^{PAR} is the proportion of PAR available and WUE_{decay} is an exponent.

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The basic water balance model does not allow estimating a water potential drop from soil to the leaf. Despite its simplicity, a gross surrogate of 'plant' water potential, Ψ_{plant} , may be obtained using:

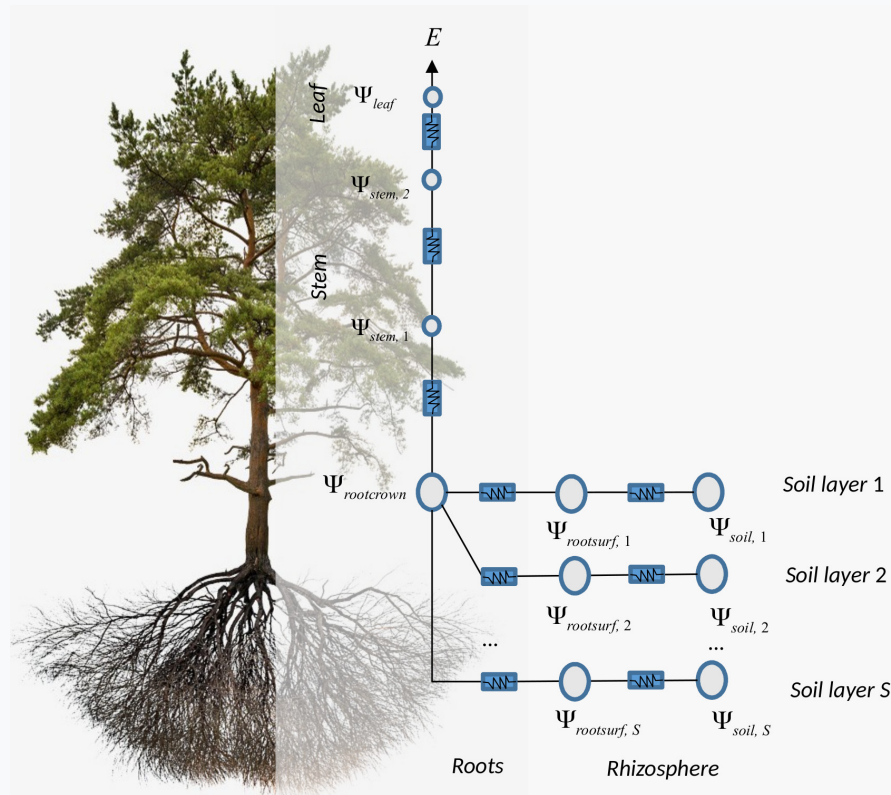
$$\Psi_{plant} = K^{-1} \left(\sum_s K(\Psi_s) \cdot FRP_s \right)$$

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

Hydraulic network

The analogy of a set of resistances in an electric circuit is often used to represent the resistance to water flow in an hydraulic network:



4. Transpiration and photosynthesis under the advanced model

Vulnerability curves

The concept of vulnerability curve can be used to specify the relationship between water potential, Ψ , and hydraulic conductance, k , in any portion along the flow path.

4. Transpiration and photosynthesis under the advanced model

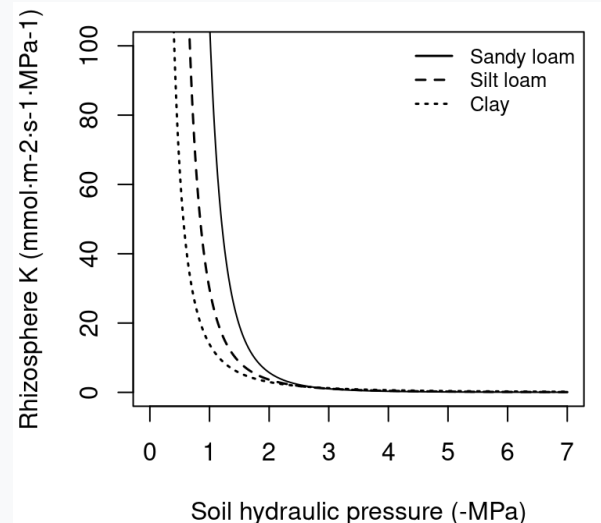
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Rhizosphere

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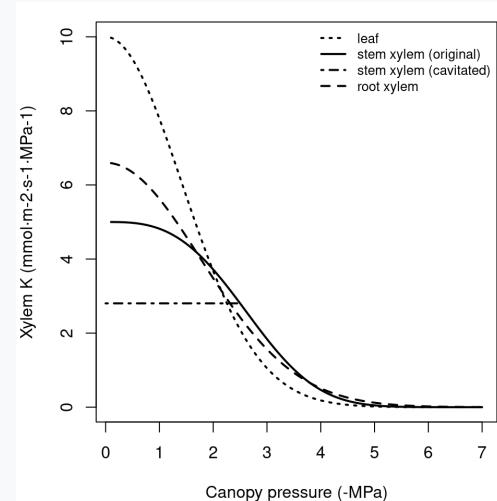
$$k(\Psi) = k_{max} \cdot v^{(n-1)/(2 \cdot n)} \cdot ((1 - v)^{(n-1)/n} - 1)^2$$



Xylem

Conductance is modelled using a two-parameter Weibull function:

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



4. Transpiration and photosynthesis under the advanced model

Hydraulic supply function

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

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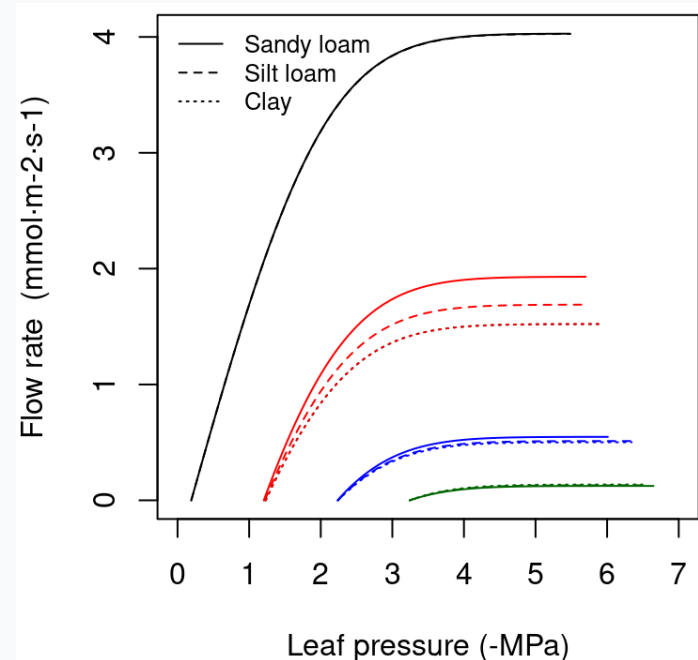
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The steady-state flow rate E_i through any element i is related to the flow-induced drop in water potential across that element, $\Delta\Psi_i = \Psi_{down} - \Psi_{up}$, by the integral of the vulnerability curve $k_i(\Psi)$:

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

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



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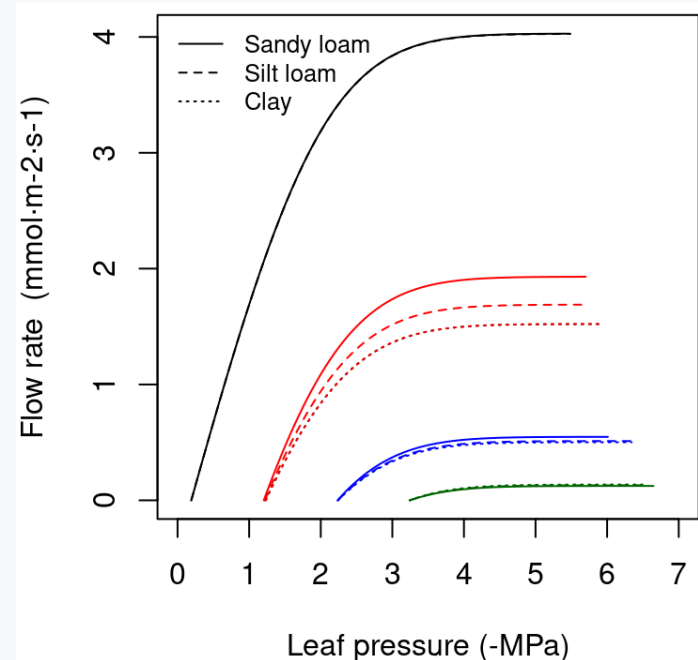
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The supply function can be integrated across the **whole hydraulic network**.

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

4. Transpiration and photosynthesis under the advanced model

Leaf energy balance, gas exchange and photosynthesis

If we know air temperature, wind conditions, radiative balance and water vapor pressure in which leaves are, we can translate the supply function into several functions:

- Leaf temperature: $T_{leaf}(\Psi_{leaf})$
- Leaf vapor pressure deficit (inside-outside difference): $VPD_{leaf}(\Psi_{leaf})$
- Leaf diffusive conductance: $g_w(\Psi_{leaf})$

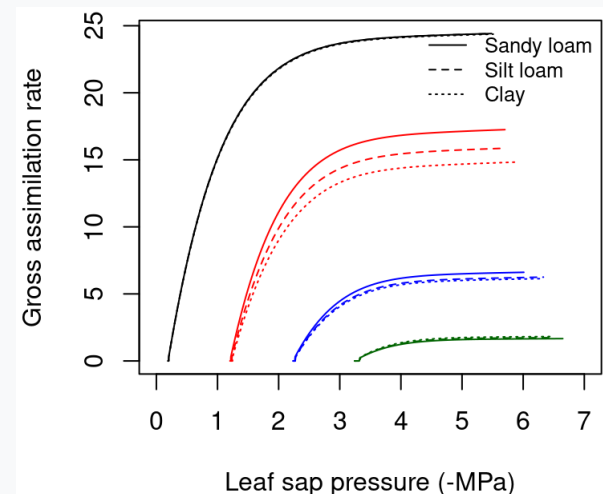
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If we know the absorbed PAR and $[CO_2]$ in the air, gross and net photosynthesis can be estimated using Farquhar's (1980) model as a function of Ψ_{leaf} , i.e. $A_g(\Psi_{leaf})$ and $A_n(\Psi_{leaf})$.



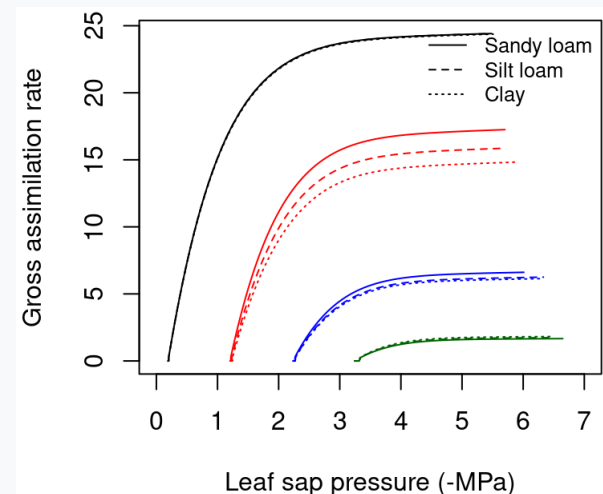
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Important parameters of Farquhar's model are the *maximum rate of Rubisco carboxylation*, V_{max} , and the *maximum rate of electron transfer*, J_{max} .

4. Transpiration and photosynthesis under the advanced model

Stomatal regulation

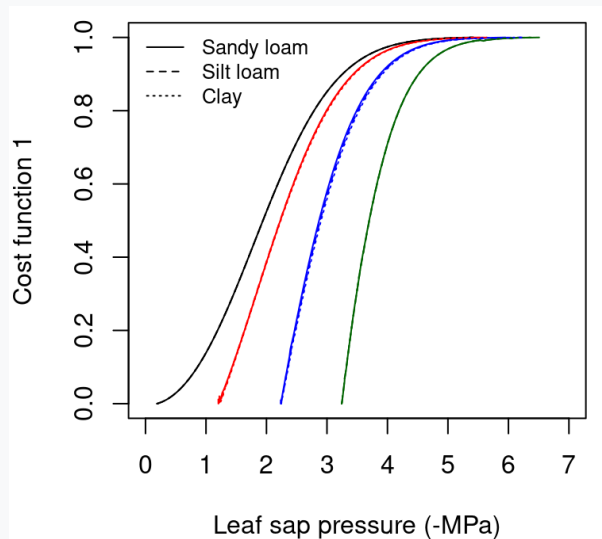
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The hydraulic supply function is used to derive a **cost function** $\theta(\Psi_{leaf})$ reflecting the increasing damage from cavitation.

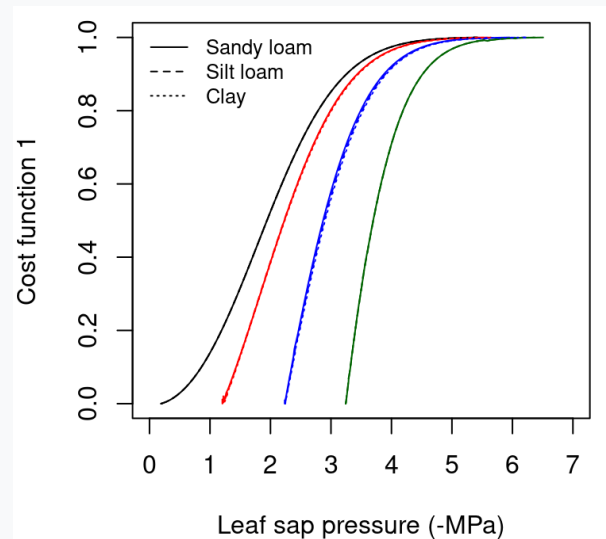


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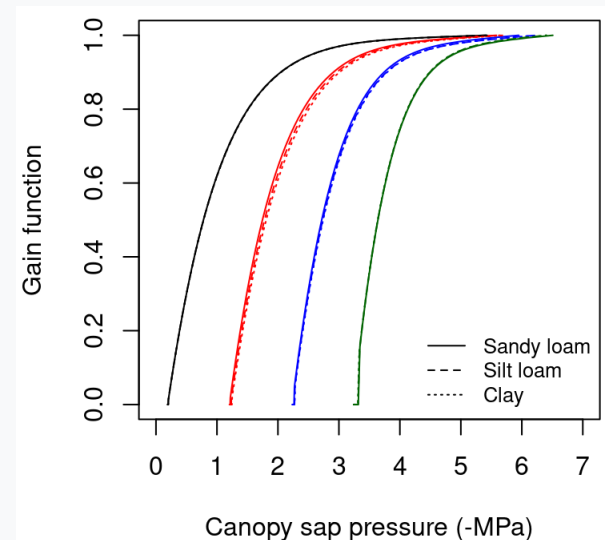
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The normalized photosynthetic **gain function** $\beta(\Psi_{leaf})$ reflects the increase in assimilation rate, with respect to the maximum.



4. Transpiration and photosynthesis under the advanced model

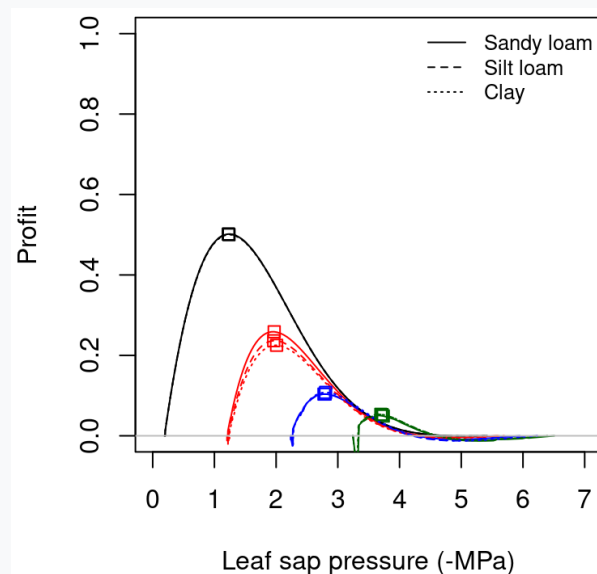
Stomatal regulation

Sperry et al (2017) suggested that 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:

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



4. Transpiration and photosynthesis under the advanced model

From leaf to the canopy

Calculating transpiration and photosynthesis following the Sperry model requires:

1. Building the supply function for each plant cohort
2. Dividing the canopy into vertical layers and determine the direct and diffuse radiation at subdaily time steps
3. Differentiating between sunlit and shade leaves (De Pury & Farquhar, 1997)
4. Determining absorbed SWR and PAR in sunlit/shade leaves at subdaily time steps
5. Determining photosynthesis functions and stomatal regulation for sunlit and shade leaves at subdaily time steps.

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Once stomatal conductance is decided for sunlit and shade leaves, one obtains an average flow and the water potentials along the transpiration pathway are determined.

Hydraulic redistribution is an emergent output of the model when soil layers have different degree of moisture and stomata are closed (mainly at night).

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 the relative whole-plant conductance:

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

Advanced model

Since $dE/d\Psi_{leaf}$ is the *absolute* whole-plant conductance:

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

5. Plant drought stress and cavitation

Cavitation

If cavitation has occurred in previous steps then the capacity of the plant to transport water is impaired.

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:

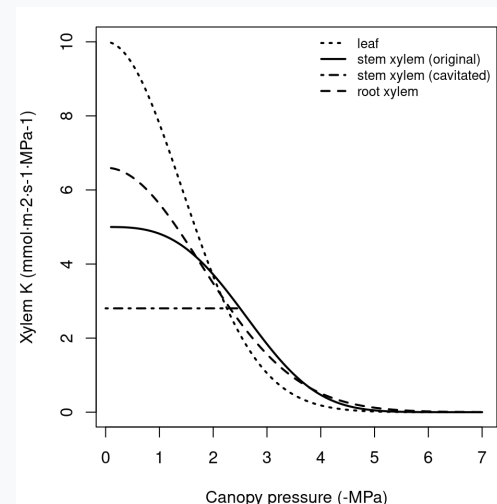
$$K_s^{PLC} = \min\{K_s, 1.0 - PLC_{stem}\}$$

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

Comparison of processes

Group	Process	Basic	Advanced
Forest hydrology	Rainfall interception	*	*
	Infiltration/percolation	*	*
	Bare soil evaporation	*	*
	Snow dynamics	*	*
	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		*

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

Comparison of 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	*	*
	Water potential gradients		*
	Stem cavitation level	*	*

M.C. Escher - Waterfall, 1961

