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ORCHIDEE
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C_3 and C_4 photosynthesis models: An overview from the perspective of crop modelling

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- Based on Yin & Struik (2019)
- Analytical solution of the 3-equation system linking assimilation, stomatal conductance and intercellular CO_2 concentration

THE FARQUHAR, VON CAEMMERER AND BERRY (FvCB) MODEL

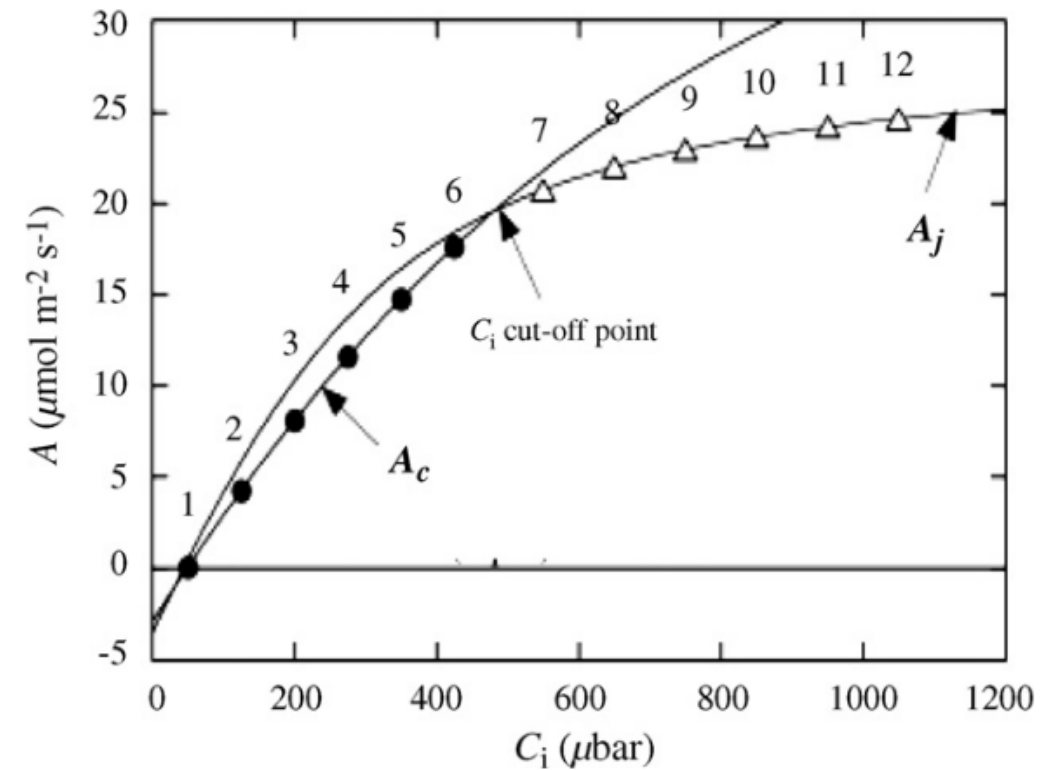
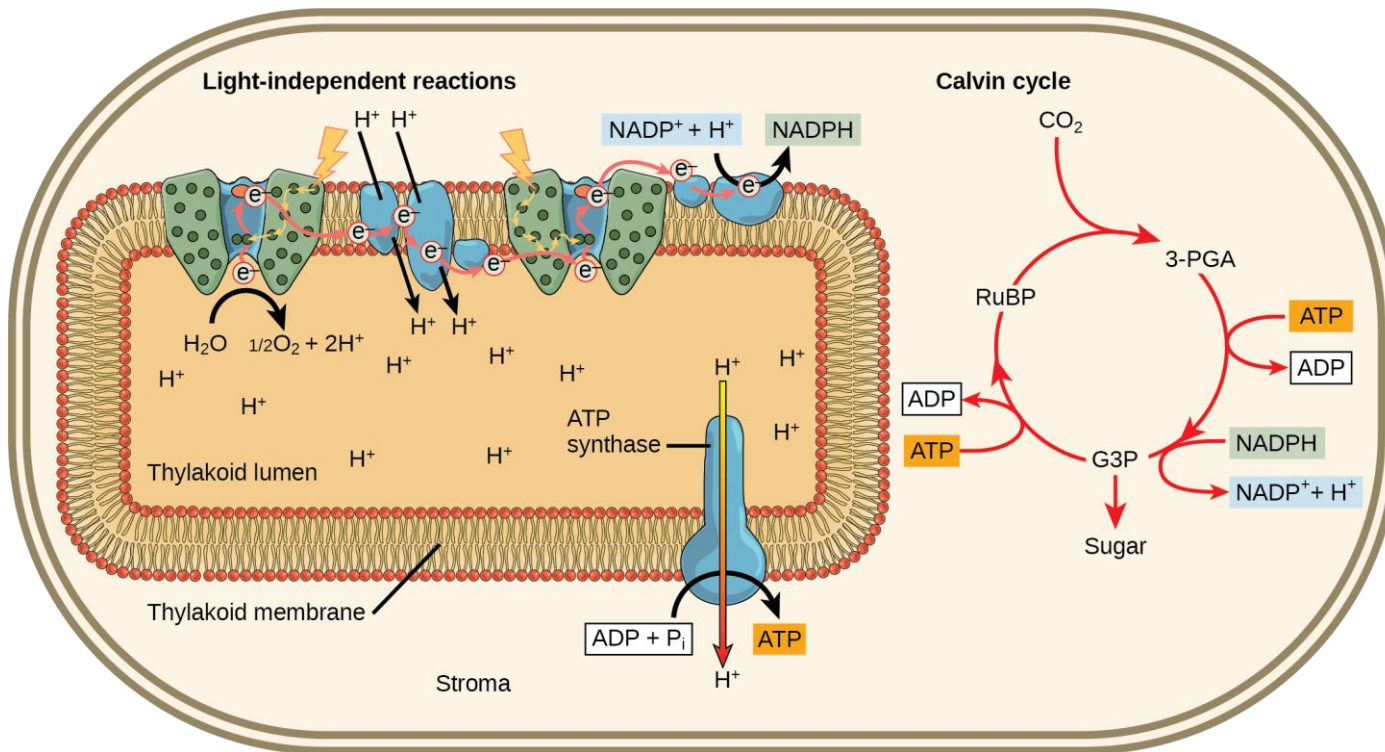


Fig. 1. An idealized curve for the response of net CO_2 assimilation rate (A) in C_3 plants to intercellular CO_2 partial pressure (C_i), in which 12 data points are shown. Points 1–6 locate within the range of the Rubisco-limited rate (A_c) whereas points 7–12 are within the range of electron transport-limited rate (A_j). The portions of each curve without data points are the extended parts as given by the A_c and A_j equation, respectively. The minimum of A_c and A_j gives the modelled CO_2 response curve as indicated by the 12 data points.

A S S I M I L A T I O N C 3

The FvCB model predicts A as the minimum of the Rubisco-limited rate of CO_2 assimilation (A_c) and the electron transport-limited rate of CO_2 assimilation (A_j):

$$A = \min(A_c, A_j) \quad (1)$$

An illustration of the two parts of limitations along the CO_2 -response curves is given in Fig. 1. Sharkey et al. [10] have drawn attention to a third limitation by triose phosphate utilization, which is not discussed here because it comes into play only occasionally at very high CO_2 levels.

The value of A_c is calculated as a function of the maximum carboxylation capacity of Rubisco ($V_{c\max}$) by:

$$A_c = \frac{(C_c - \Gamma_*)V_{c\max}}{C_c + K_{mC}(1 + O/K_{mO})} - R_d \quad (2)$$

where C_c is the CO_2 partial pressure at the carboxylating sites of Rubisco, K_{mC} and K_{mO} are Michaelis–Menten constants of Rubisco for CO_2 and O_2 , respectively, and Γ_* is the CO_2 compensation point in the absence of day respiration (R_d).

In the calculation of A_j , the FvCB model assumes 100% non-cyclic e^- transport, thus excluding cyclic e^- transport around PSI (CET). There are two widely used forms of the equation for electron transport-limited rate of photosynthesis:

$$A_j = \frac{(C_c - \Gamma_*)J}{4C_c + 8\Gamma_*} - R_d \quad (3a)$$

$$A_j = \frac{(C_c - \Gamma_*)J}{4.5C_c + 10.5\Gamma_*} - R_d \quad (3b)$$

The relationship between e^- transport rate (J) in Eqs. (3a), (3b) and irradiance was first described as a rectangular hyperbola [11], using quantum yield of e^- transport under limiting light ($\alpha_{(LL)}$) and the maximum capacity of e^- transport (J_{\max}). Following Farquhar and Wong [12], most applications of the FvCB model, however,

describe J as a non-rectangular hyperbolic function of irradiance by:

$$J = \frac{\left(\alpha_{(LL)}I_{\text{abs}} + J_{\max} - \sqrt{(\alpha_{(LL)}I_{\text{abs}} + J_{\max})^2 - 4\theta J_{\max}\alpha_{(LL)}I_{\text{abs}}} \right)}{2\theta} \quad (4)$$

where θ is the convexity of the response curve of J to light absorbed by photosynthetic pigments (I_{abs}). Equations like Eq. (4) that describe the light response of e^- transport rate mimic well the photosynthetic down-regulation induced by high light levels via mechanisms such as non-photochemical quenching and chloroplast avoidance movement [13]. The theoretical maximum value for $\alpha_{(LL)}$ is 0.5 mol electron per mol photon absorbed [3] because one quantum must be absorbed by each of the two photosystems to move an electron from the level of H_2O to that of NADP^+ . However, in actual applications (e.g., [14–17]), $\alpha_{(LL)}$ has been empirically adjusted to a lower value to agree with a measured quantum efficiency for CO_2 uptake that is often lower than that expected from the theoretical maximum.

The temperature dependence of R_d and kinetic properties of Rubisco (involving three parameters $V_{c\max}$, K_{mC} and K_{mO}) in Eq. (2) is described by an Arrhenius function normalized with respect to their values at 25 °C:

$$\text{Parameter} = \text{Parameter}_{25} e^{(T-25)E/[298R(T+273)]} \quad (5)$$

where T is leaf temperature; E is the activation energy, defining the responsiveness of the relevant parameter to temperature; R is the universal gas constant. A modified Arrhenius function is used to describe the optimum response of other parameters (e.g., J_{\max}) to temperature as [17]:

$$\text{Parameter} = \text{Parameter}_{25} e^{(T-25)E/[298R(T+273)]} \times \frac{1 + e^{(298S-D)/(298R)}}{1 + e^{[(T+273)S-D]/[R(T+273)]}} \quad (6)$$

where S is an entropy term; E and D are the energies of activation and deactivation, defining the responsive shape of the sub- and supra-optimal ranges, respectively. June et al. [18] described an

A coupled modelling of leaf photosynthesis and stomatal conductance has been reported frequently in the literature (e.g., [16,46]). Few whole-plant modelling studies have considered g_m as a necessary term of the photosynthesis models [39]. Here we incorporate g_b (boundary-layer conductance), g_s and g_m into our modelling framework. First, on the basis of several existing models, we propose the following phenomenological sub-model for g_s :

$$g_s = g_0 + \frac{A + R_d}{C_i - C_{i*}} f_{vpd} \quad (15)$$

where g_0 is the residual stomatal conductance if the irradiance approaches zero, C_{i*} is the C_i -based CO_2 compensation point in the absence of R_d (by definition $C_{i*} = \Gamma_* - R_d/g_m$), and f_{vpd} is the function for the effect of leaf-to-air vapour pressure difference (VPD), which is not yet understood sufficiently and may be described empirically as:

$$f_{vpd} = \frac{1}{[1/(a_1 - b_1 VPD) - 1]} \quad (15a)$$

where a_1 and b_1 are empirical constants. Eq. (15) is consistent with the finding that stomata may sense C_i [47]. Furthermore, unlike the model of Leuning et al. [16], Eq. (15) uses $(A + R_d)$ instead of A to avoid a possible negative g_s below the light compensation point. Unlike the model of Dewar [48], Eq. (15) predicts a non-zero g_s if $C_i = C_{i*}$. It also differs from the model of Tuzet et al. [46] in that there is no need to calculate Γ —the CO_2 compensation point in the presence of R_d .

The following equations can be written, according to Fick's first law of diffusion for CO_2 transfer along the path from C_a to C_c :

$$C_i = C_a - A \left(\frac{1}{g_b} + \frac{1}{g_s} \right) \quad (16)$$

$$C_c = C_i - \frac{A}{g_m} \quad (17)$$

C O N D U C T A N C E S

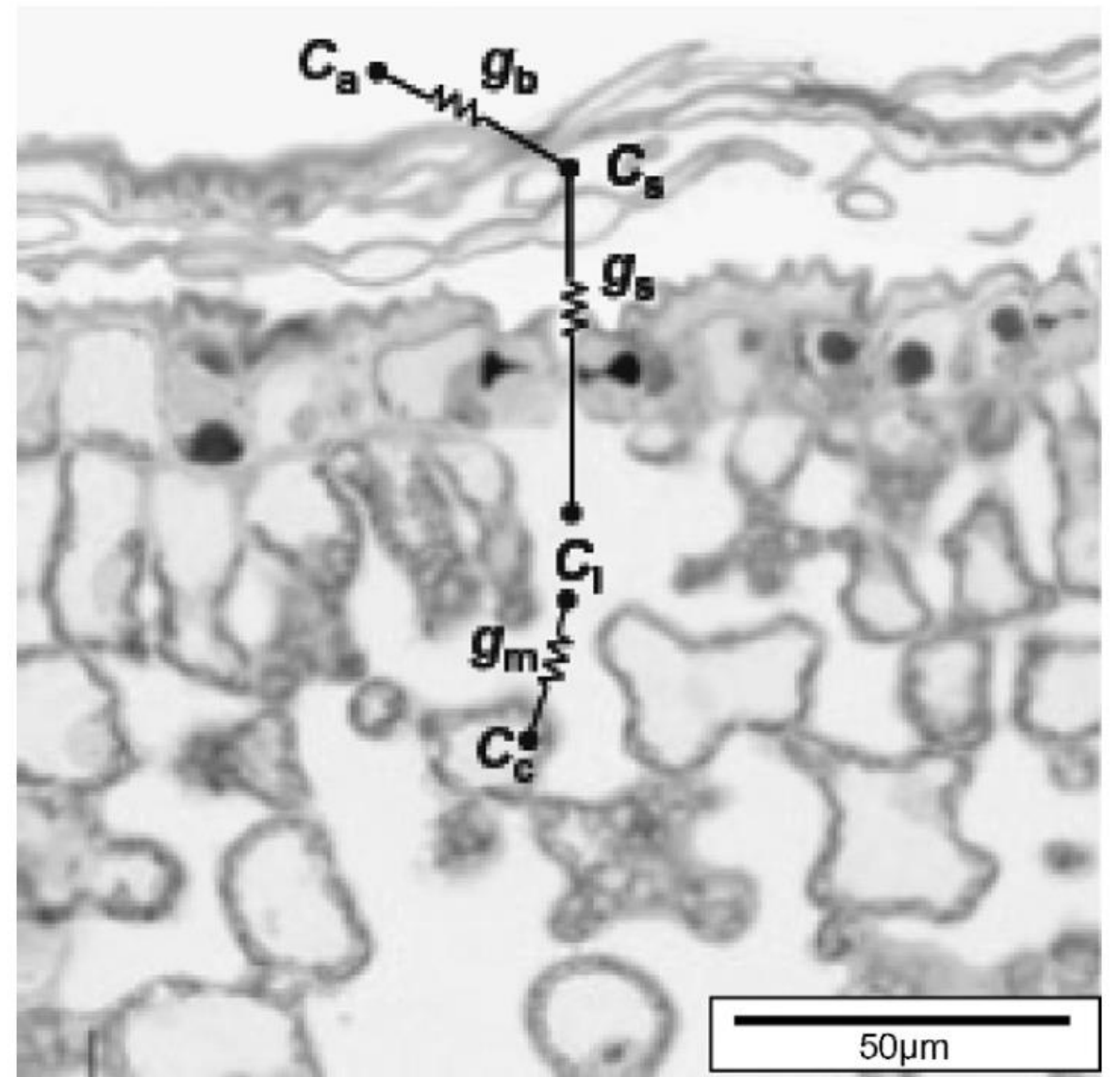


Fig. 4. Micrograph of the abaxial surface of a typical leaf, illustrating the pathway of CO_2 transfer from ambient air (C_a) through leaf surface (C_s) and intercellular air spaces (C_i) to the Rubisco carboxylation-sites in chloroplasts (C_c). Boundary-layer conductance (g_b), stomatal conductance (g_s), and mesophyll conductance (g_m) are indicated. Revised from Flexas et al. [39].

ASSIMILATION C4 PLANT SPECIES

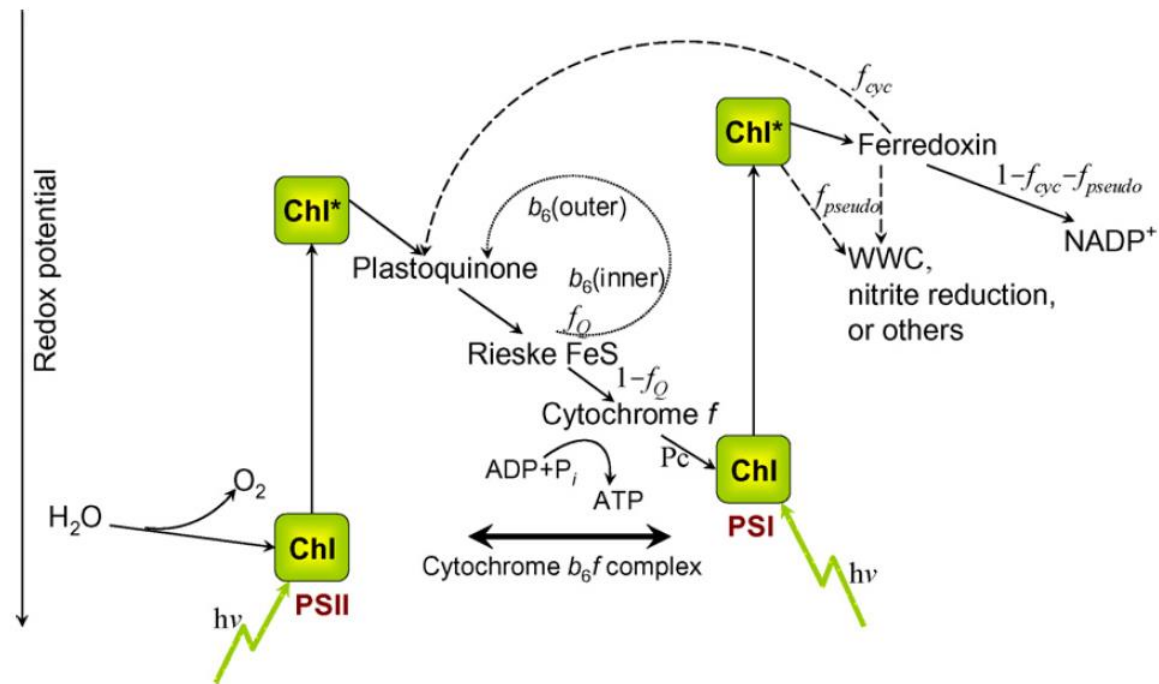


Fig. 3. The Z scheme for photosynthetic thylakoid reactions showing linear (solid arrows), cyclic and pseudocyclic (dashed arrows) electron transport routes. From reduced ferredoxin, a fraction, f_{cyc} , of the electrons follows the cyclic mode around PSI. Another fraction, f_{pseudo} , of the electrons that have passed PSI follows the pseudocyclic mode for supporting processes such as the water-water cycle (WWC, see [69]), or nitrite reduction, or other minor metabolic processes. The remaining fraction, $1 - f_{cyc} - f_{pseudo}$, is transferred to NADP⁺—the terminal acceptor of the linear electron transport for generating NADPH in support of CO₂ reduction or photorespiration. The efficiency of ATP synthesis along the chain depends on the operation of the Q-cycle. The scheme shows that a fraction, f_Q , of the electrons followed the Q-cycle (dotted arrow) through the concerted action of the Rieske FeS and b₆ of the cytochrome b₆f complex, and the remaining fraction, $1 - f_Q$, is transferred directly towards plastocyanin (Pc). Chl, chlorophyll; $h\nu$, photons absorbed either by PSI or by PSII. Redrawn from Yin et al. [70].

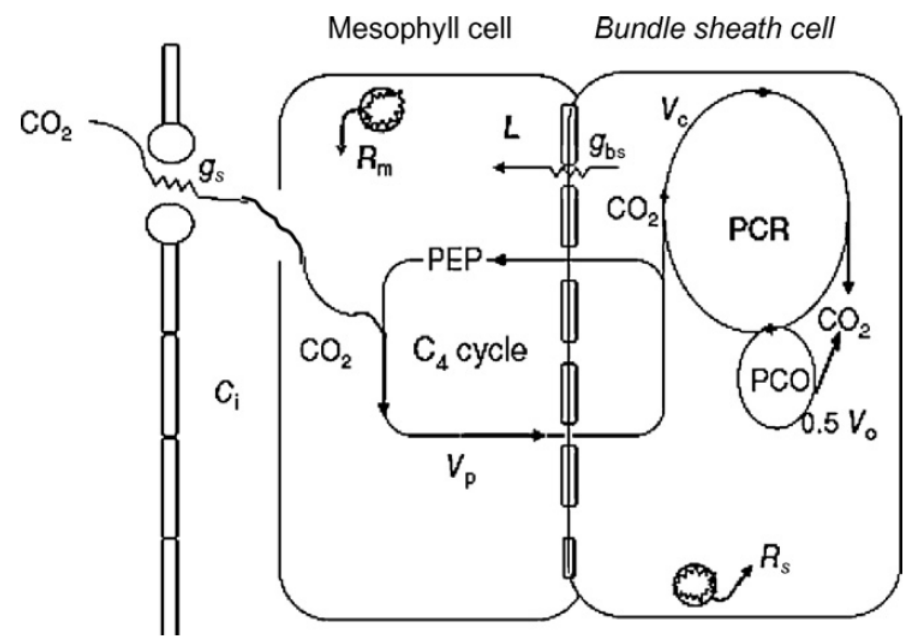


Fig. 5. Scheme of the C₄ photosynthesis model based on von Caemmerer and Furbank [9]. After passing the stomatal conductance (g_s) and entering the mesophyll cell, CO₂ is fixed by phosphoenolpyruvate (PEP) carboxylase at the rate of V_p . The formed C₄ acid crosses a bundle-sheath conductance (g_{bs}) and is decarboxylated at the same rate V_p . The released CO₂ either leaks back to the mesophyll cell (L) or can be fixed at the bundle-sheath cell by Rubisco at the rate V_c in the photosynthetic carbon reduction cycle (PCR – the normal C₃ cycle). Part of the CO₂ is again released by the photosynthetic carbon oxidation (PCO) cycle at half the rate of Rubisco oxygenation (V_o). CO₂ can also be released in the mesophyll and bundle sheath from mitochondrial respiration (R_m and R_s), which together make the total day respiration rate R_d .

STRESS FUNCTION FOR VEGETATION

$$u_s(1)=0$$

$$u_s(i>1) = n_{\text{root}}(i) \cdot F_w(i)$$

$$F_w(i) = \max(0, \min(1, (W_i - W_w) / (W_{\%} - W_w)))$$

n_{root} : mean root density in layer i

$$n_{\text{root}} = \int_{h_i} R(z) dz / \int_{h_{\text{tot}}} R(z) dz$$

$$R(z) = \exp(-c_j z)$$

c_j depends on the PFT

W_w = wilting point

W_f = field capacity

$$\text{AWC} = W_f - W_w$$

$W_{\%}$: moisture at which u_s becomes 1 (no stress)

$$W_{\%} = W_w + p_{\%} \text{AWC}$$

In *contantes_mtc.f90*:

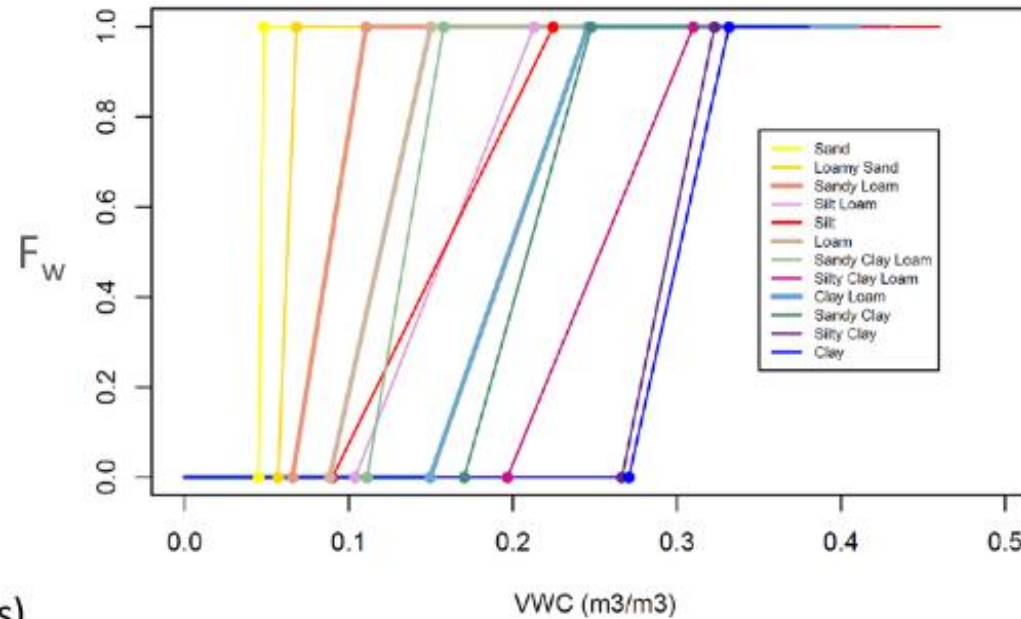
$$c_j = \text{humcste}$$

In *constantes_soil.f90*:

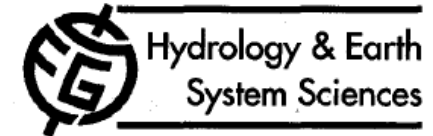
$$p_{\%} = \text{pcent} = (/ 0.8, 0.8, 0.8 /)$$

ORCHIDEE

@Ducharne



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Modelling root water uptake in a complex land surface scheme coupled to a GCM

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STRESS FUNCTION FOR VEGETATION

Table 8.4 Root distribution per vegetation type (in %) over the four layers. Vegetation indexes refer to Table 8.1.

Vegetation index	1	2	3	4	5	6	7	8	9	10	11	13	16	17	18	19
Layer 1	24	35	26	26	24	25	27	100	47	24	17	25	23	23	19	19
Layer 2	41	38	39	38	38	34	27	0	45	41	31	34	36	36	35	35
Layer 3	31	23	29	29	31	27	27	0	8	31	33	27	30	30	36	36
Layer 4	4	4	6	7	7	14	9	0	0	4	19	11	11	11	10	10

vapour deficit D_a and a minimum stomatal resistance $r_{s,\min}$, following ? given by

$$r_c = \frac{r_{s,\min}}{LAI} f_1(R_s) f_2(\bar{\theta}) f_3(D_a) \quad (8.9)$$

f_1 is a hyperbolic function of downward short-wave radiation only so that

$$\frac{1}{f_1(R_s)} = \min \left[1, \frac{bR_s + c}{a(bR_s + 1)} \right] \quad (8.10)$$

where $a = 0.81$, $b = 0.004 \text{ W}^{-1}\text{m}^2$ and $c = 0.05$.

Function f_2 is defined as

$$\frac{1}{f_2(\bar{\theta})} = \begin{cases} 0 & \bar{\theta} < \theta_{\text{pwp}} \\ \frac{\bar{\theta} - \theta_{\text{pwp}}}{\theta_{\text{cap}} - \theta_{\text{pwp}}} & \theta_{\text{pwp}} \leq \bar{\theta} \leq \theta_{\text{cap}} \\ 1 & \bar{\theta} > \theta_{\text{cap}} \end{cases} \quad (8.11)$$

where the soil moisture at permanent wilting point and at field capacity, θ_{pwp} and θ_{cap} , respectively, are defined in Table 8.9. $\bar{\theta}$ is a weighted average of the unfrozen soil water given by

$$\bar{\theta} = \sum_{k=1}^4 R_k \max[f_{\text{liq},k} \theta_k, \theta_{\text{pwp}}] \quad (8.12)$$

where R_k is the fraction of roots in layer k and the fraction of unfrozen soil water, $f_{\text{liq},k} = 1 - f_{\text{fr}}(T_k)$, is a parametrized function of the soil temperature of layer k , T_k , as specified in Subsection 8.5.2. Table 8.1 lists the coefficients a_r and b_r which are used to calculate the root fraction R_k according to ?:

$$R_k = 0.5[\exp(-a_r z_{k-1/2}) + \exp(-b_r z_{k-1/2}) - \exp(-a_r z_{k+1/2}) - \exp(-b_r z_{k+1/2})] \quad (8.13)$$

CTESSEL

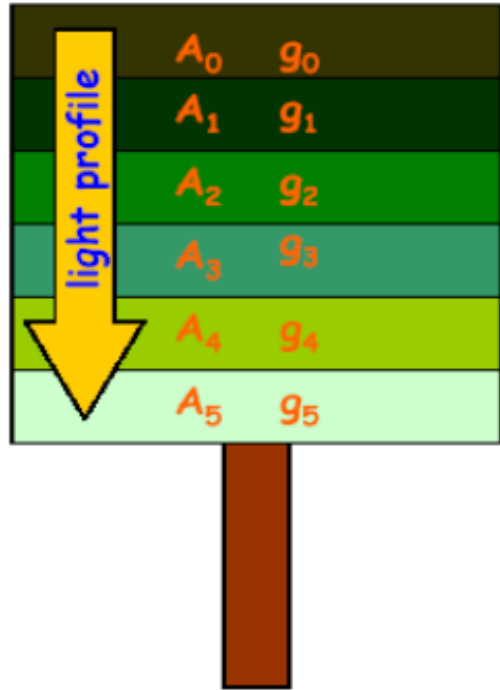
very similar

4-layer hydrology/root profile

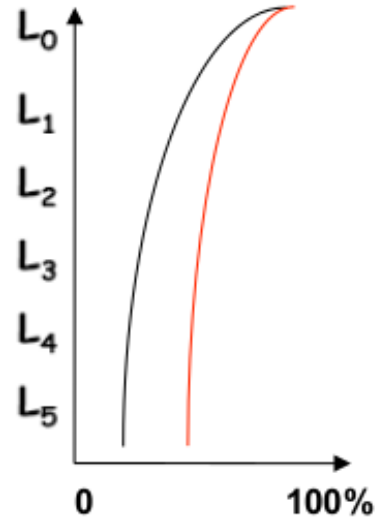
CTESSEL variable PF2 is used in the Farquhar module.

CANOPY DISCRETIZATION/SCALING

Canopy is discretized from top to bottom into several Leaf Area Index (LAI) levels.



Light & N profiles



For a given LAI level l :

Light is attenuated through the canopy following a Beer-Lambert law:

$$I(l) = I_0 \cdot e^{-k \cdot LAI(l)}$$

k extinction coefficient

$k = 0.5$ (Monsi and Saeki, 1953)

$V_{c/j}$ is scaled into the canopy due to reduction of **nitrogen** (Johnson and Thornley, 1984):

$$V_{c/j}(l) = V_{c/jlim} \cdot (1 - 0.7 \cdot (1 - e^{-k \cdot LAI(l)}))$$

Integration at the canopy level

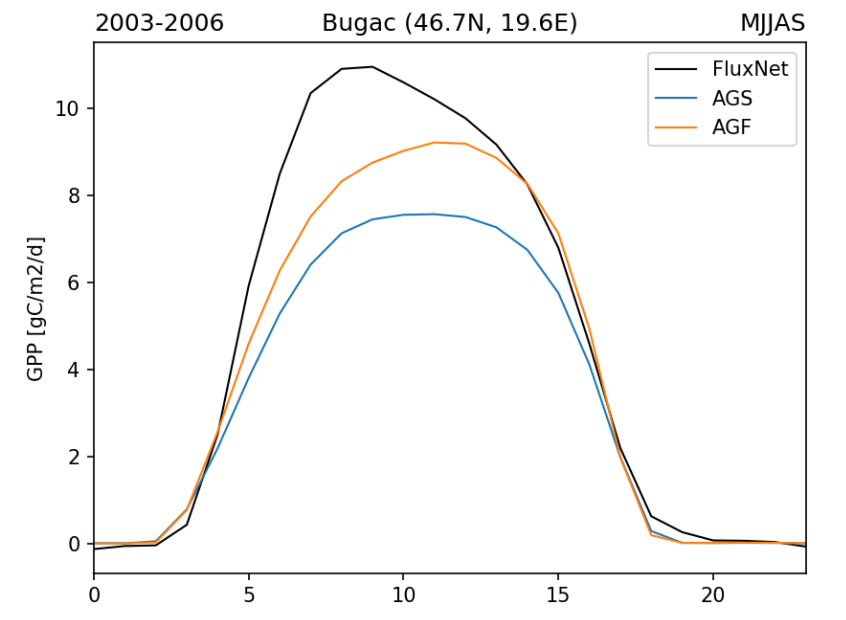
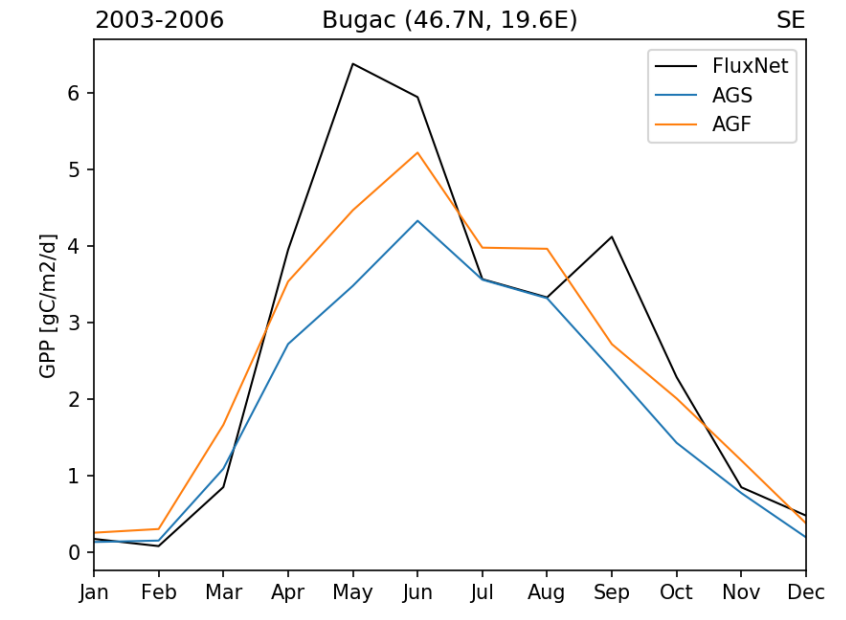
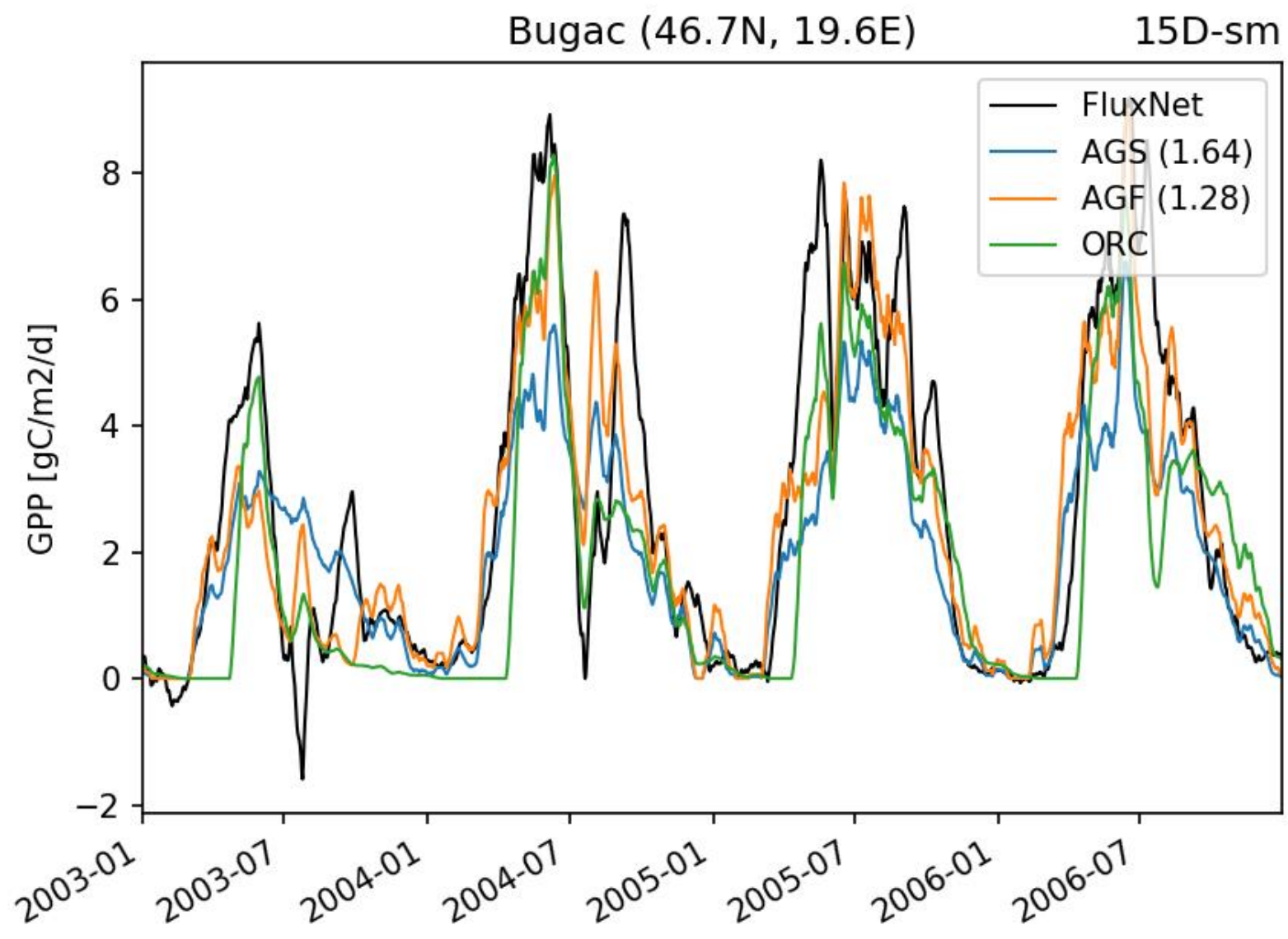
$$g_c = \int_0^{LAI} g_s(l) \cdot dl$$

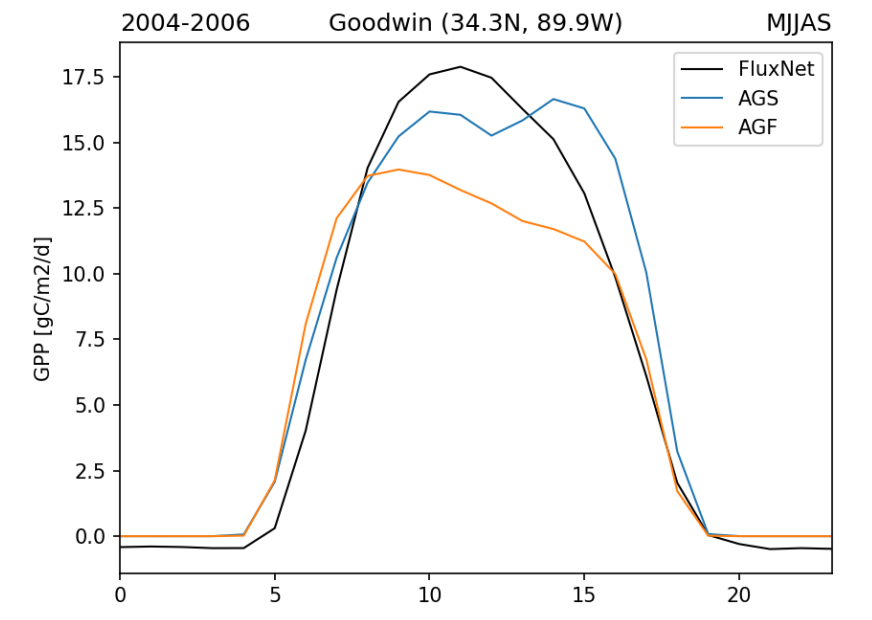
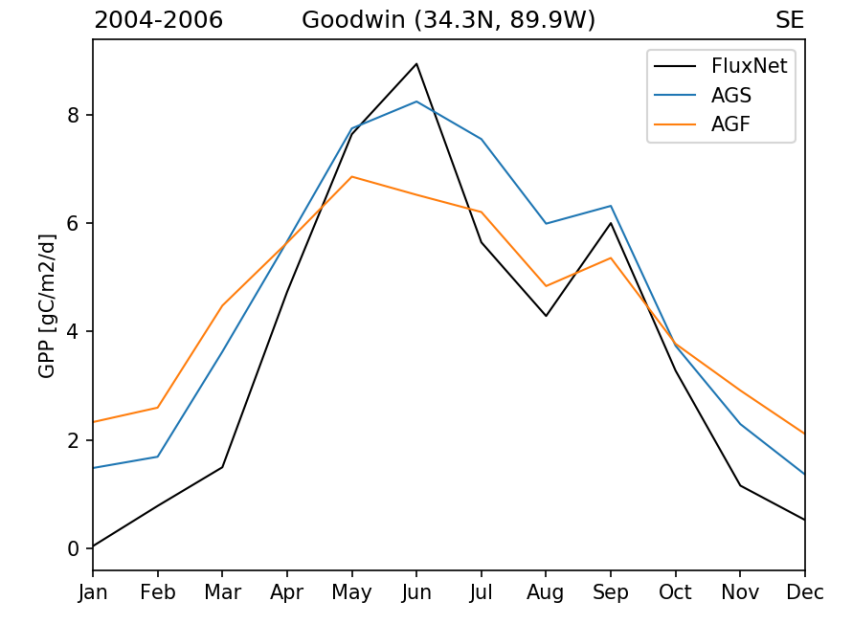
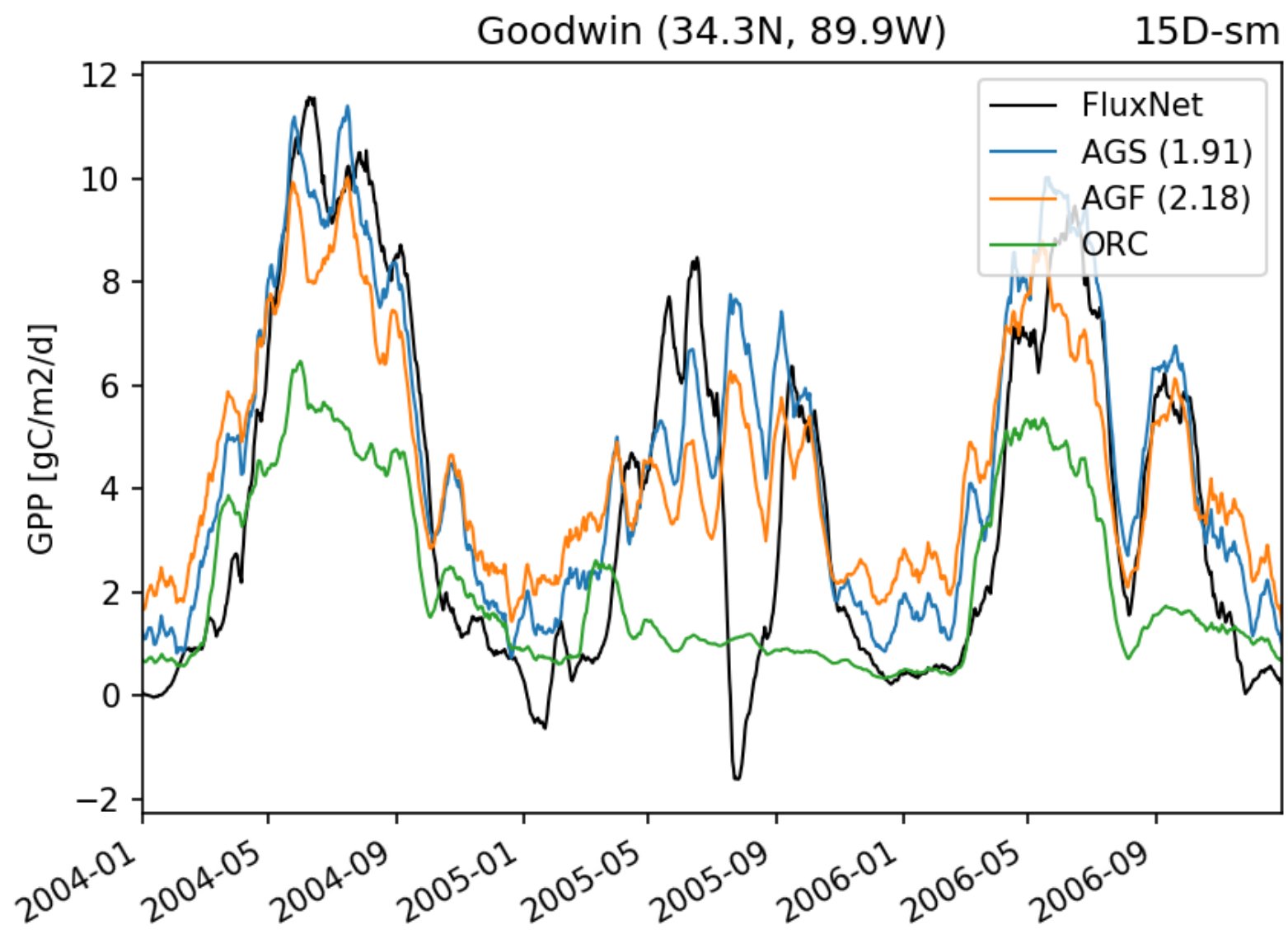
$$A_c = \int_0^{LAI} A(l) \cdot dl$$

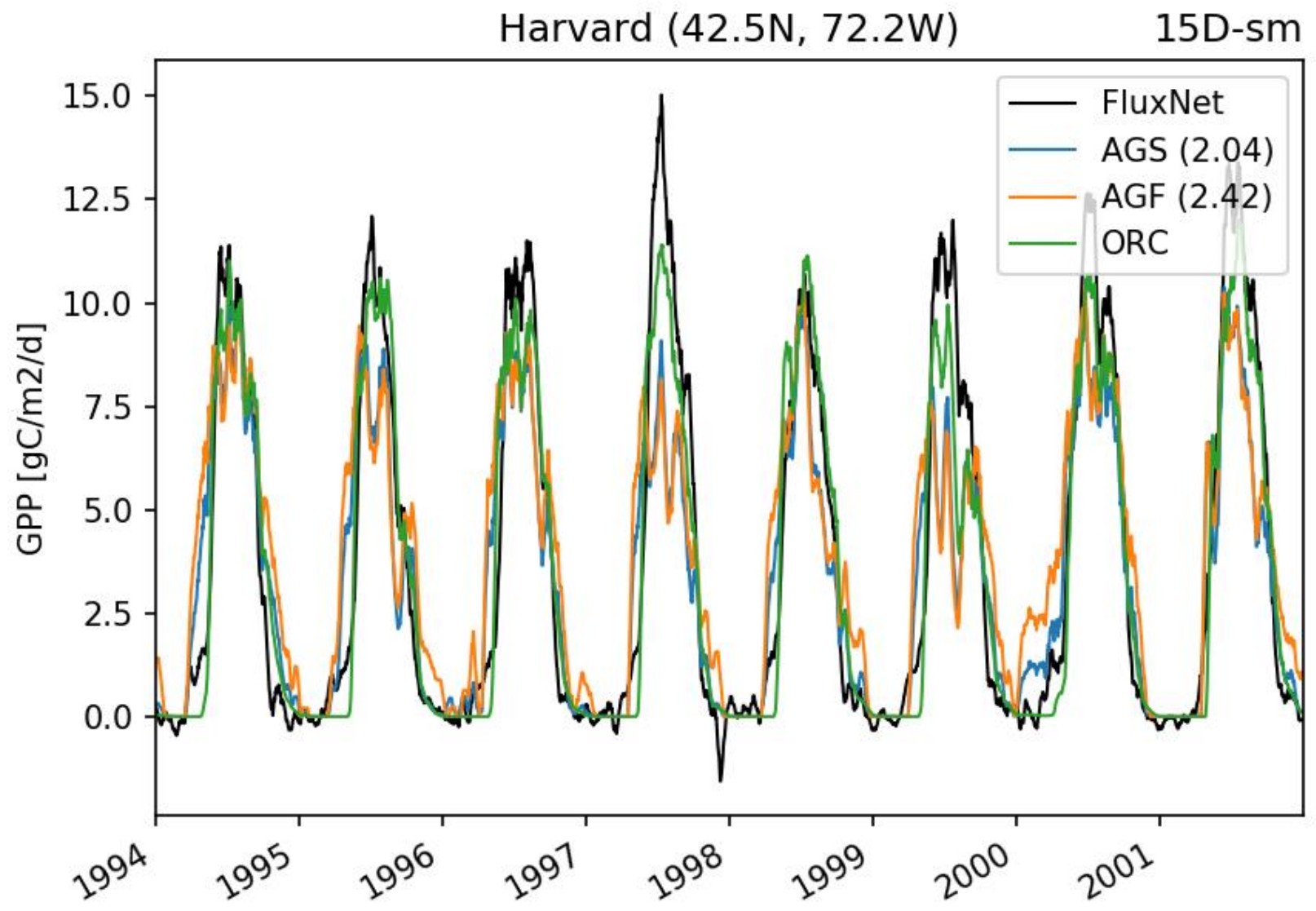
CTESSEL VARIABLES USED AS INPUT ARGUMENTS

!	KIDIA	Begin point in arrays		
!	KFDIA	End point in arrays		
!	KLON	Length of arrays		
!	KVTYPE	VEGETATION TYPE CORRESPONDING TO TILE		
!	KSTEP	Time step index		
!	PTSTEP	Timestep		
!	PTM1	TEMPERATURE AT T-1	K	
!	PQM1	SPECIFIC HUMIDITY AT T-1	KG/KG	
!	PAPHM1	PRESSURE AT T-1	PA	→hPa
!	PLAI	LEAF AREA INDEX	M2/M2	
!	PSRFD	DOWNWARD SHORT WAVE RADIATION FLUX AT SURFACE	W/M2	
!	PF2	SOIL MOISTURE STRESS FUNCTION	-	
!	RCO2	atmospheric CO2 concentration	kgCO2 kgAir-1	→ppm

Note: Tair is taken as an approximation of Tleaf.







Next step is to optimize the parameters for the new AGF output as is done for the standard ORC.

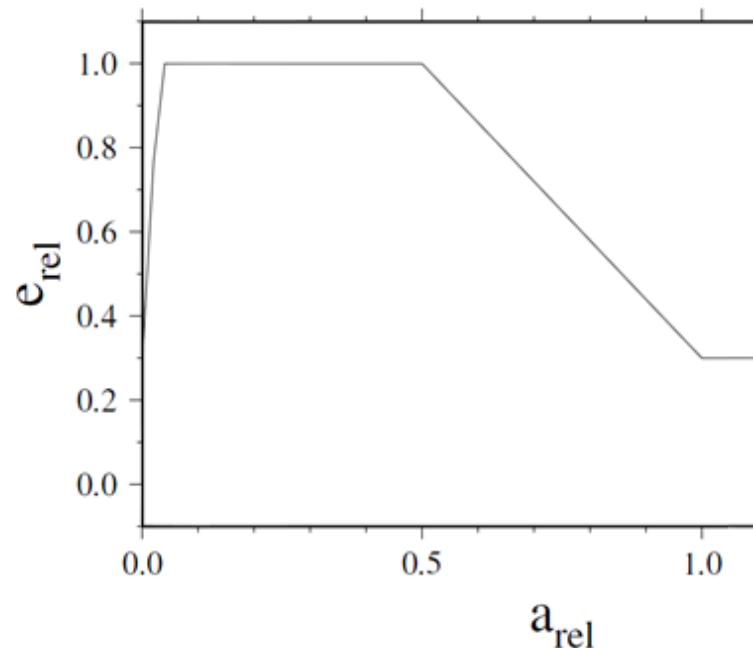
OUTLOOKS: PHOTOSYNTHETIC CAPACITY – LEAF AGE DEPENDENCE

V_{cmax_opt} maximum rate of carboxylation (carbon fixation)

V_{jmax_opt} maximum rate of RuBP regeneration

$V_{c/jmax_opt}$ are PFT-dependent constants.

$V_{c/jmax}$ is calculated based on $V_{c/jmax_opt}$ and leaf age efficiency (*Ishida et al., 1999*).

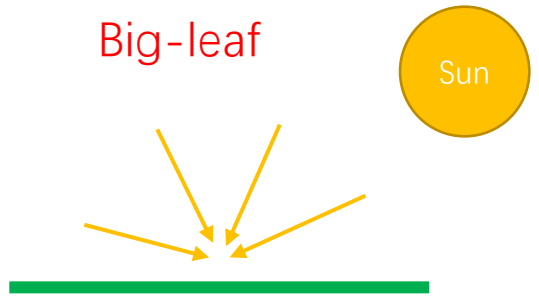


$$e_{rel} = \frac{V_{cmax}}{V_{cmax_opt}} = \frac{V_{jmax}}{V_{jmax_opt}}$$

Relative leaf efficiency e_{rel} as a function of relative leaf age a_{rel} ,
relative leaf age is defined as the leaf age a_i over critical leaf age A_{crit} .

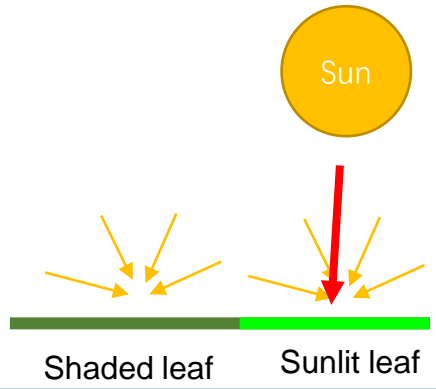
OUTLOOKS: DIFFERENT PARAMETERIZATIONS OF CANOPY LIGHT TRANSMISSION

Big-leaf

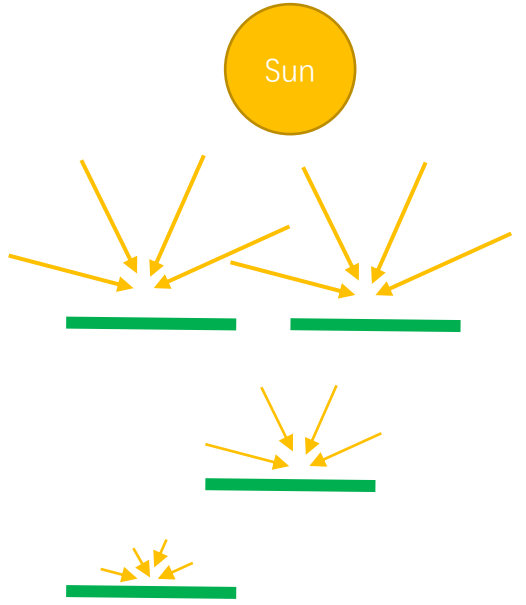


Two Big-leaf
(Dai et al. 2004)

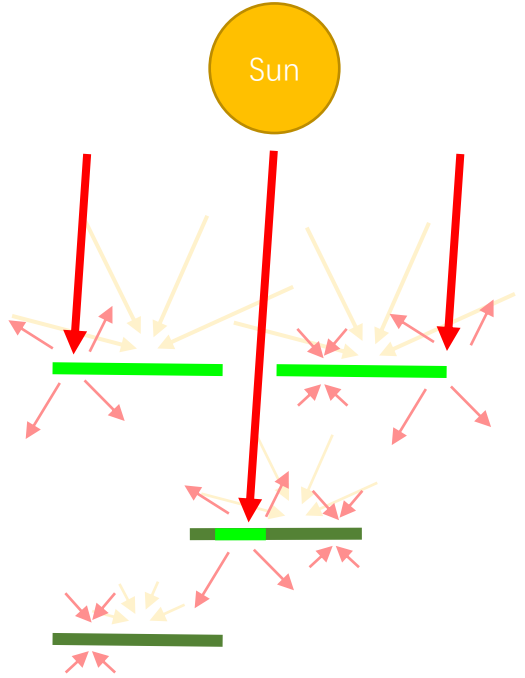
e.g. CLM4



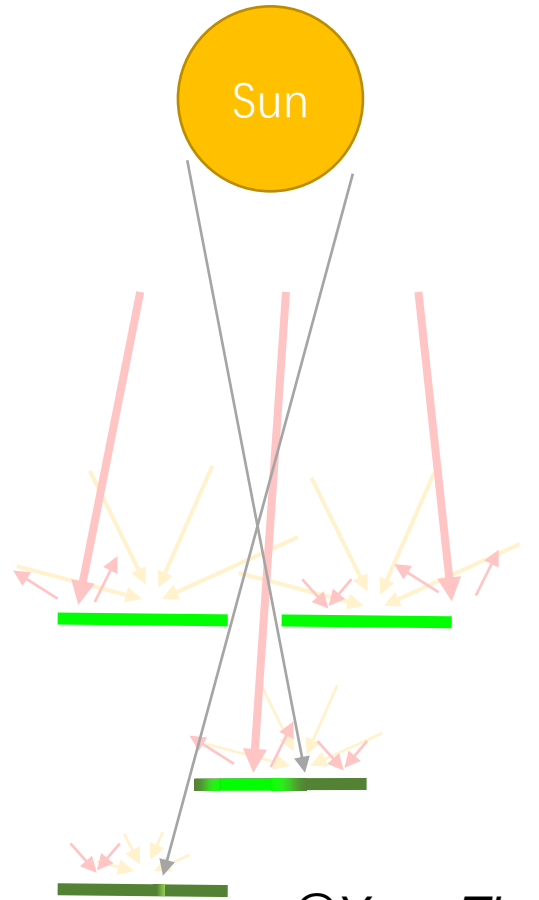
Multilayer, no direct light
e.g. current ORCHIDEE trunk



Multilayer, diffuse and direct light
ORCHIDEE_DF (this work)

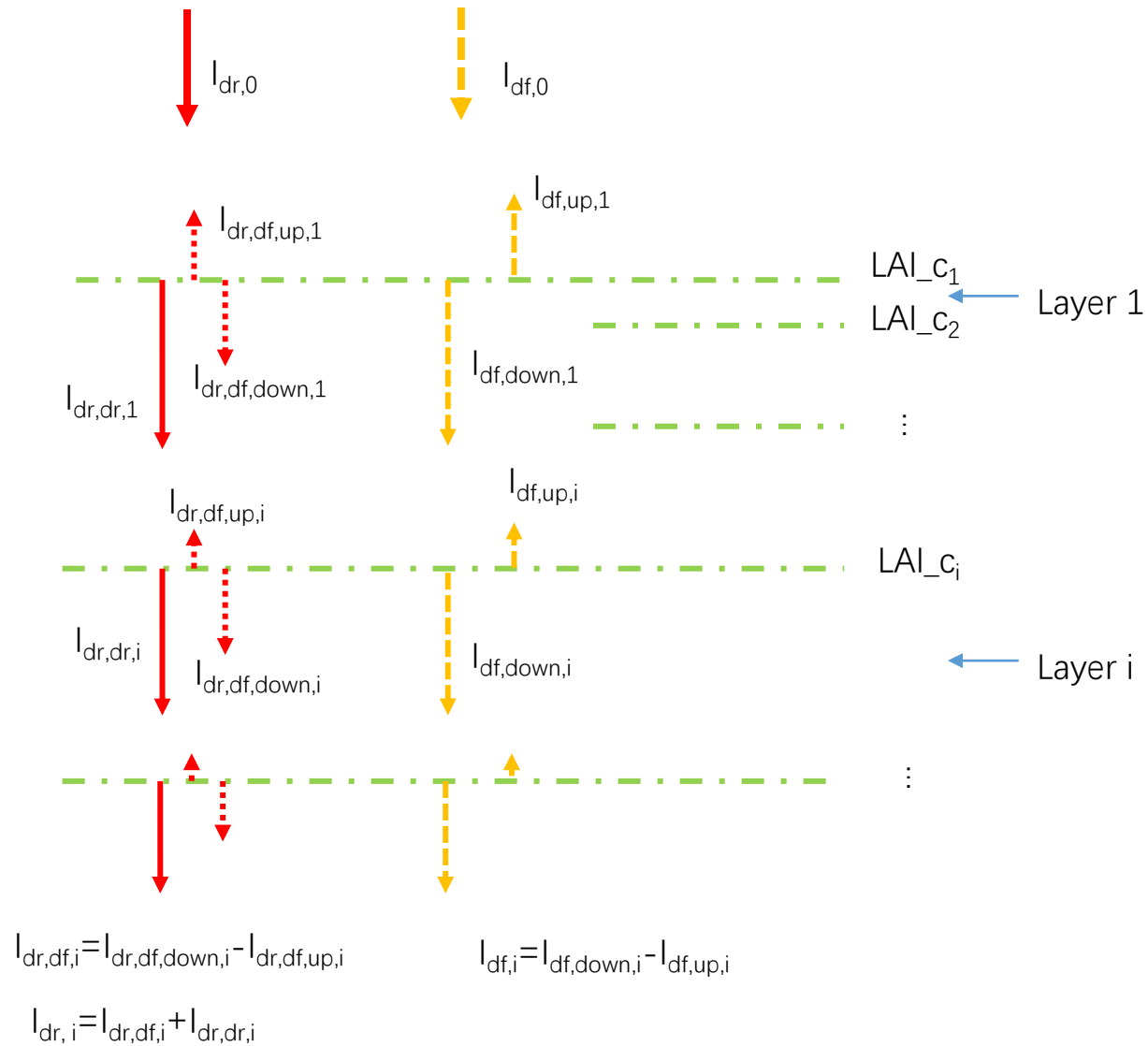


Complex model with penumbra
Future model?



@Yuan Zhang

OUTLOOKS: LIGHT TRANSMISSION IN ORCHIDEE_DF



For diffuse light $I_{df,i}$, a simple Beer-Lambert equation is used

$$I_{df,i} = (1 - \rho) I_{df,0} e^{-k_d LAI_{c_i}}$$

↑
Canopy scattering

For direct-source radiation $I_{dr,i}$, the total attenuation of PPFD is presented as:

$$I_{dr,i} = (1 - \rho) I_{dr,0} e^{-\sqrt{1 - \sigma} k_b LAI_{c_i}}$$

← leaf scattering

The transmission of direct light $I_{dr,dr,i}$ (direct components of direct-source radiation) is presented as:

$$I_{dr,dr,i} = I_{dr,0} e^{-k_b LAI_{c_i}}$$

The leaf-scattered light $I_{dr,df,i}$ is presented as:

$$I_{dr,df,i} = I_{dr,i} - I_{dr,dr,i}$$

OUTLOOKS: CONSTRAIN GPP WITH CARBONYL SULFIDE (COS)



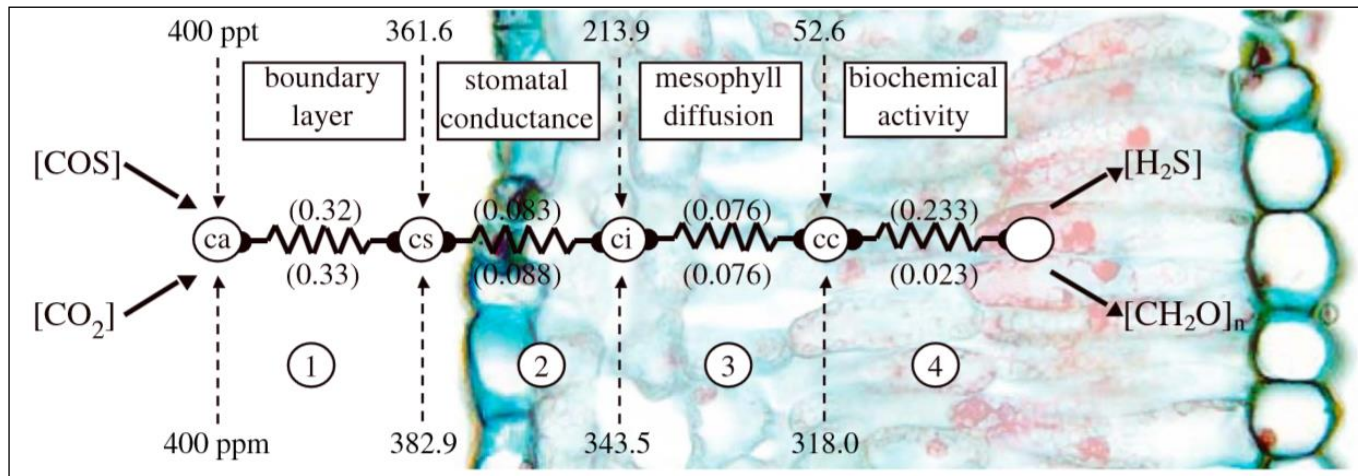
Leaf uptake of COS

$$F_{\text{cosbio}} = \text{GPP} \cdot [\text{COS}] / [\text{CO}_2] \cdot V_{\text{cos/co2}}$$

$V_{\text{cos/co2}}$ = Leaf Relative Uptake

No COS autotrophic respiration

Berry et al. (2013)



Maignan et al. (submitted)

