

MODELING ECOHYDROLOGICAL CONTROLS ON ECOSYSTEM ENERGY BALANCE AND GHG EXCHANGE OF A TROPICAL BOG

Palanga Karaya Peat Swamp forest, Indonesia

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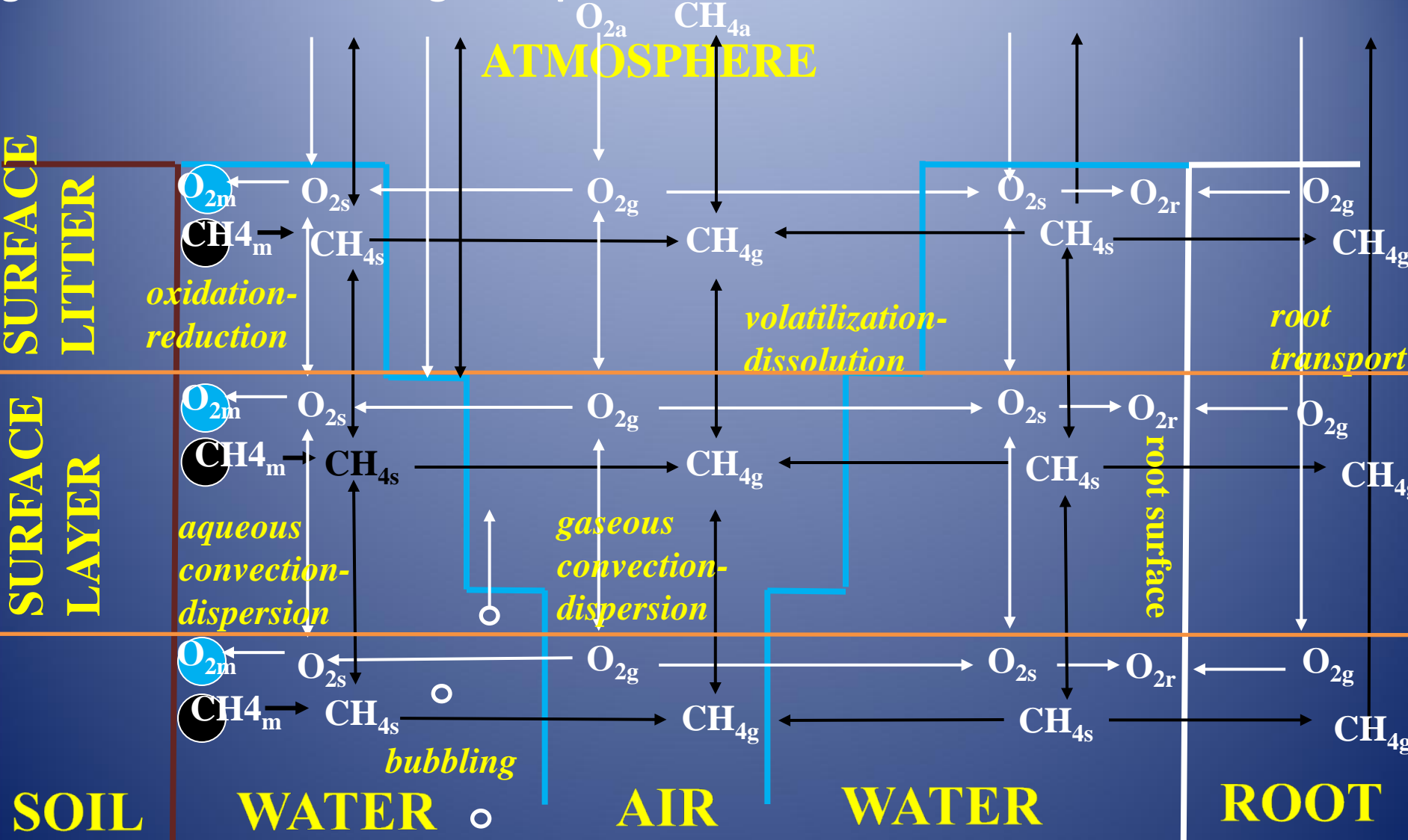
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Mezbahuddin, M., R.F Grant and T. Hirano. 2014. Modelling effects of seasonal variation in water table depth on net ecosystem CO₂ exchange of a tropical peatland. *Biogeosciences*. 11: 577-599. doi:10.5194/bg-11-577-2014.

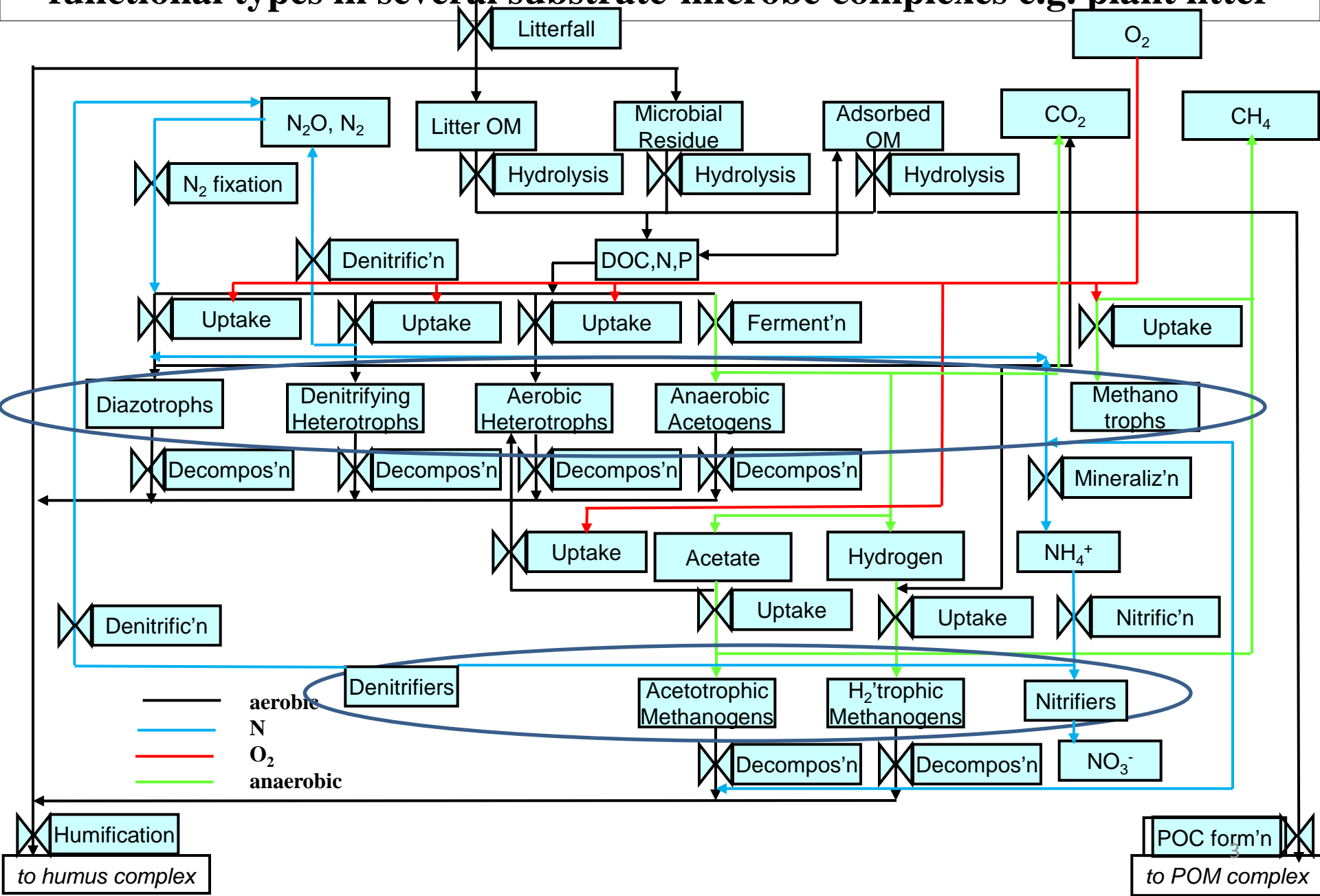
Mezbahuddin, M., R.F Grant and T. Hirano. 2015. How hydrology determines seasonal and interannual variations in water table depth, surface energy exchange and water stress in a tropical peatland: modelling vs. measurements. *Journal of Geophysical Research - Biogeosciences*. 120: 2132–2157.

Surface gas exchange is coupled with convective – dispersive transfers of gases and solutes through soil profile.



These transfers govern concentrations of reactants and products in oxidation-reduction reactions

These oxidation-reduction reactions are conducted by diverse microbial functional types in several substrate-microbe complexes e.g. plant litter



Microbial functional types in *ecosys*

- Represented as: OMC(M,N,K,L,NY,NX) where:

M = kinetic fraction

1 = labile,

2 = resistant

3 = storage

N = functional type:

heterotrophs
(K=0-4)

1 = obligate aerobe

2 = facultative anaerobe (denitrifier)

3 = fungi

4 = obligate anaerobe (fermenter)

5 = acetotrophic methanogen

6 = diazotrophic aerobe (N₂ fixer)

7 = diazotrophic anaerobe (N₂ fixer)

autotrophs
(K=5)

1 = NH₃ oxidizer (nitrifier)

2 = NO₂⁻ oxidizer (nitrifier)

3 = CH₄ oxidizer

5 = hydrogenotrophic methanogen

K = substrate

0 = coarse woody litter

1 = fine litter

2 = manure

3 = POC

4 = humus

5 = autotrophic

L = soil layer

NY = N – S position

NX = E – W position

The kinetics of these oxidation – reduction reactions are driven by energy yields from electron transfers using parameters taken from basic research e.g. heterotrophs ($K = 0,4$; $N = 1,7$):

This is done in 5 steps:

• 1. Respiration

$$- R_{h'k,n} = M_{k,n,a} \{R_{h'n} [Q_{k,c}]\} / \{(K_q + [Q_{k,c}])\} f_t$$

- $R_{h'k,n}$: oxidation of DOC by FT n in substrate k under nonlimiting O_2 ($g\ C\ m^{-2}\ h^{-1}$)
- $M_{k,n,a}$: biomass of active aerobes ($g\ C\ m^{-2}$)
- $R_{h'n}$: **specific oxidation by aerobes under nonlimiting DOC, O_2 , nutrients, θ and $25^\circ C$ ($0.10\ g\ C\ g\ C^{-1}\ h^{-1}$)**
- $[Q_{k,c}]$: aqueous concentration of DOC ($g\ C\ m^{-3}$)
- K_q : **M-M constant for uptake of $Q_{i,c}$ by heterotrophs ($12\ g\ C\ m^{-3}$)**
- f_t : Arrhenius function of soil temperature for growth-related processes

Heterotrophs (cont.)

• 2. O₂ constraint on respiration by aerobic heterotrophs

$$\begin{aligned}
 - R_{hk,n} &= R'_{hk,n} (U_{O_2k,n} / U'_{O_2k,n}) && \text{[O}_2\text{ constraint]} \\
 - U_{O_2k,n} &= U'_{O_2k,n} [O_{2mk,n}] / ([O_{2mk,n}] + K_{O_2}) && \text{[active O}_2\text{ uptake]} \\
 &= 4 \pi n_n M_{k,n,a} D_{sO_2} [r_m r_w / (r_w - r_m)] ([O_{2s}] - [O_{2mk,n}]) && \text{[spherical O}_2\text{ diffusion]}
 \end{aligned}$$

- $R_{hk,n}$: oxidation of DOC by aerobes under ambient O₂ (g C m⁻² h⁻¹)
- $U_{O_2k,n}$: O₂ reduction by aerobes under ambient O₂ (g m⁻² h⁻¹)
- $U'_{O_2k,n}$: O₂ reduction by aerobes under nonlimiting O₂ (g m⁻² h⁻¹)
 - = 2.67 * $R'_{hi,n}$
- $[O_{2mk,n}]$: O₂ concentration at aerobic microsites (g O₂ m⁻³)
- $[O_{2s}]$: aqueous O₂ concentration (g O₂ m⁻³)
- K_{O_2} : **M–M constant for O₂ reduction (0.064 g O₂ m⁻³)**
- n_n : number of aerobic microsites (m⁻²)
- D_{sO_2} : aqueous dispersivity–diffusivity of O₂ (m² h⁻¹)
- r_m : **radius of heterotrophic microsite (2.5 x 10⁻⁶ m)**
- r_w : thickness of water films (m)

Heterotrophs (cont.)

• 3. Energy from oxidation-reduction

$$- Y_n = -\Delta G_n / E_M$$

- $\Delta G'_n$: free energy change of oxidation (kJ g C⁻¹)
 - all aerobes 37.5
 - fermenters 4.50
 - acetotrophic methanogens 3.00
 - H₂trophic methanogens 11.00
- E_M : energy required to construct new M (25 kJ g C⁻¹)

Heterotrophs (cont.)

• 4. Uptake of DOC by heterotrophs

$$- U_{k,n,c} = R_{mk,n} + R_{gk,n} (1 + Y_n)$$

- $U_{k,n,c}$: rate of DOC uptake by aerobes ($\text{g C m}^{-2} \text{h}^{-1}$)
- $R_{mk,f}$: maintenance respiration by aerobes ($\text{g C m}^{-2} \text{h}^{-1}$)
- $R_{gk,f}$: growth respiration = $R_{hk,n} - R_{mk,n}$ ($\text{g C m}^{-2} \text{h}^{-1}$)
- Y_n : biomass yield from aerobic oxidation ($\text{g M}_{k,n,c} \text{ g DOC}^{-1}$)

Heterotrophs (cont.)

- **5. Growth of heterotrophs**

- $\delta M_{k,n,c} / \delta t = U_{k,n,c} - R_{hk,n} - D_{k,n,c}$

- $D_{k,n,c}$: decomposition of aerobes ($\text{g C m}^{-2} \text{h}^{-1}$)

- partially recycled to $M_{k,n,3}$ depending on $[Q_{k,c}] / \{(\mathbf{K}_q + [Q_{k,c}])\}$

- The resulting value of $M_{k,n,c}$ drives the subsequent calculation of $R_{hk,n}$ in step 1

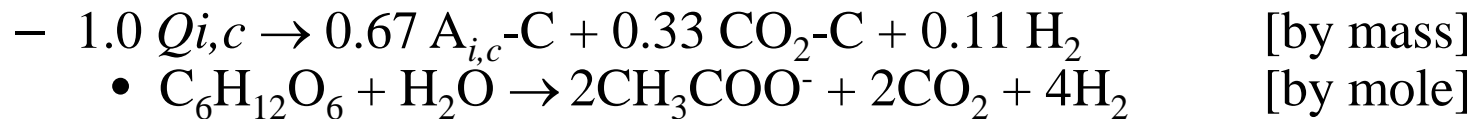
Anaerobic Fermenters

• Respiration by fermenters

$$- R_{i,f} = \{R'_f M_{i,f,a} [Q_{i,c}] / (K_f (1 + [O_{2s}] / K_i) + [Q_{i,c}])\} f_t$$

- $R_{i,f}$: oxidation of DOC by fermenters f in substrate i ($\text{g C m}^{-2} \text{h}^{-1}$)
- R'_f : **specific oxidation of DOC by fermenters at nonlimiting DOC, 25 °C and zero ψ_s ($0.1 \text{ g C g } M_{i,f,a}^{-1} \text{ h}^{-1}$)**
- $M_{i,f,a}$: biomass of active fermenters (g C m^{-2})
- $[Q_{i,c}]$: aqueous concentration of DOC (g C m^{-3})
- K_f : **M-M constant for uptake of DOC by fermenters (12 g C m^{-3})**
- $[O_{2s}]$: aqueous O_2 concentration ($\text{g } O_2 \text{ m}^{-3}$)
- K_i : **inhibition constant for O_2 on fermentation ($0.32 \text{ g } O_2 \text{ m}^{-3}$)**
- f_t : Arrhenius function of soil temperature for growth-related processes

• Oxidation-reduction by fermenters



Anaerobic Fermenters (cont.)

• Uptake of DOC by fermenters

- $U_{i,f,c} = R_{mi,f} + R_{gi,f} (1.0 + Y_f)$
 - $U_{i,f,c}$: rate of DOC uptake by fermenters ($\text{g C m}^{-2} \text{h}^{-1}$)
 - $R_{mi,f}$: maintenance respiration by fermenters ($\text{g C m}^{-2} \text{h}^{-1}$)
 - $R_{gi,f}$: growth respiration = $R_{i,f} - R_{mi,f}$ ($\text{g C m}^{-2} \text{h}^{-1}$)
 - Y_f : biomass yield from fermentation ($\text{g M}_{i,f,c} \text{g DOC}^{-1}$)

• Energy from oxidation-reduction

- $Y_f = -\Delta G_f / E_M$
- $\Delta G_f = \Delta G'_f + \{R T_s \ln([\text{H}_2]/[\text{H}_2'])^4\}$
 - ΔG_f : free energy change of fermentation at ambient $[\text{H}_2]$ ($\text{kJ g Q}_{i,c}^{-1}$)
 - E_M : energy required to construct new M (25 kJ g C^{-1})
 - $\Delta G'_f$: free energy change of fermentation when $[\text{H}_2] = [\text{H}_2']$ ($-4.43 \text{ kJ g Q}_{i,c}^{-1}$)
 - $[\text{H}_2']$: aqueous concentration of H_2 when $\Delta G_f = \Delta G'_f$ ($2.0 \times 10^{-4} \text{ g H m}^{-3}$)

• Growth of fermenters

- $\delta M_{i,f,c} / \delta t = U_{i,f,c} - R_{i,f} - D_{i,f,c}$
 - $D_{i,f,c}$: decomposition of fermenters ($\text{g C m}^{-2} \text{h}^{-1}$)
- The resulting value of $M_{i,f,c}$ drives the subsequent calculation of $R_{i,f}$

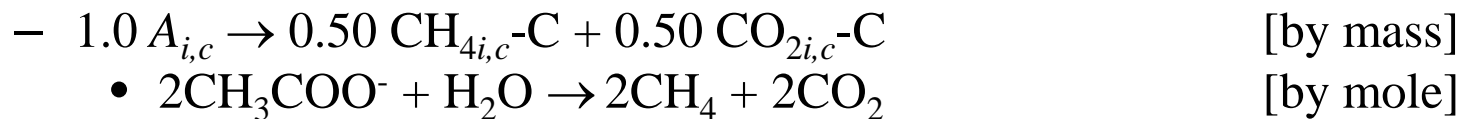
Acetotrophic Methanogens

• Respiration by acetotrophs

$$- R_{i,m} = \{R'_m M_{i,m,a} [A_{i,c}] / (K_m + [A_{i,c}])\} f_t$$

- $R_{i,m}$: oxidation of acetate by acetotrophs m in substrate i (g C m⁻² h⁻¹)
- R'_m : **specific oxidation of acetate by acetotrophs at saturating acetate, 25 °C and zero ψ_s (0.1 g C g $M_{i,m,a}^{-1}$ h⁻¹)**
- $M_{i,m,a}$: biomass of active fermenters (g C m⁻²)
- $[A_{i,c}]$: aqueous concentration of acetate (g C m⁻³)
- K_m : **M-M constant for uptake of acetate by acetotrophs (12 g C m⁻³)**
- f_t : Arrhenius function of soil temperature for growth-related processes

• Oxidation-reduction by acetotrophs



Acetotrophic Methanogens (cont.)

• Uptake of acetate by acetotrophic methanogens

$$- U_{i,m,c} = R_{mi,m} + R_{gi,m} (1.0 + Y_m)$$

- $U_{i,m,c}$: rate of acetate uptake by acetotrophs ($\text{g C m}^{-2} \text{ h}^{-1}$)
- $R_{mi,m}$: maintenance respiration by acetotrophs ($\text{g C m}^{-2} \text{ h}^{-1}$)
- $R_{gi,m}$: growth respiration = $R_{i,m} - R_{mi,m}$ ($\text{g C m}^{-2} \text{ h}^{-1}$)
- Y_m : biomass yield from acetate oxidation ($\text{g } M_{i,m,c} \text{ g } A_{i,c}^{-1}$)

• Energy from oxidation-reduction

$$- Y_m = -\Delta G'_m / E_M$$

- $\Delta G'_m$: free energy change of acetate oxidation ($-1.03 \text{ kJ g C}^{-1}$)
- E_M : energy required to construct new M (25 kJ g C^{-1})

• Growth of acetotrophs

$$- \delta M_{i,m,c} / \delta t = U_{i,m,c} - R_{i,m} - D_{i,m,c}$$

- $D_{i,m,c}$: decomposition of acetotrophs ($\text{g C m}^{-2} \text{ h}^{-1}$)

The resulting value of $M_{i,m,c}$ drives the subsequent calculation of $R_{i,m}$

Autotrophic Methanogens

- **Respiration by autotrophic methanogens**

$$R_h = \{R'_h M_{h,a} [H_2] / (K_h + [H_2]) [CO_2] / (K_c + [CO_2])\} f_t$$

- R_h : reduction of CO_2 by autotrophs h ($g\ C\ m^{-2}\ h^{-1}$)
- R'_h : **specific reduction of CO_2 by autotrophs at saturating $[H_2]$, $[CO_2]$, $25\ ^\circ C$ and zero ψ_s ($0.1\ g\ C\ g\ M_{h,a}^{-1}\ h^{-1}$)**
- $M_{h,a}$: biomass of active autotrophs ($g\ C\ m^{-2}$)
- $[H_2]$: aqueous concentration of H_2 ($g\ H\ m^{-3}$)
- $[CO_2]$: aqueous concentration of CO_2 ($g\ C\ m^{-3}$)
- K_h : **M-M constant for uptake of H_2 by autotrophs ($0.01\ g\ H\ m^{-3}$)**
- K_c : **M-M constant for uptake of CO_2 by autotrophs ($0.15\ g\ C\ m^{-3}$)**
- f_t : Arrhenius function of soil temperature for growth-related processes

- **Oxidation-reduction by autotrophs**



Autotrophic Methanogens(cont.)

• Uptake of CO₂ by autotrophic methanogens

- $U_{h,c} = R_{mh} + R_{gh} (1.0 + Y_h)$
 - $U_{h,c}$: rate of CO₂ uptake by autotrophs h (g C m⁻² h⁻¹)
 - R_{mh} : maintenance respiration by autotrophs (g C m⁻² h⁻¹)
 - R_{gh} : growth respiration = $R_h - R_{mh}$ (g C m⁻² h⁻¹)
 - Y_h : biomass yield from CO₂ reduction (g M_{*h,c*} g CO₂-C⁻¹)

• Energy from oxidation-reduction

- $Y_h = -\Delta G_h / E_M$
- $\Delta G_h = \Delta G'_h - \{R T_s \ln([H_2]/[H_2'])^4\}$
 - ΔG_h : free energy change of CO₂ reduction at ambient [H₂] (kJ g CO₂-C⁻¹)
 - E_M : energy required to construct new M (25 kJ g C⁻¹)
 - $\Delta G'_h$: free energy change of CO₂ reduction when [H₂] = [H₂'] (-0.27 kJ g CO₂-C⁻¹)
 - [H₂']: aqueous concentration of H₂ when $\Delta G_h = \Delta G'_h$ (2.0 x 10⁻⁴ g H m⁻³)

• Growth of autotrophs

- $\delta M_{h,c} / \delta t = U_{h,c} - R_h - D_{h,c}$
 - $D_{h,c}$: decomposition of autotrophs (g C m⁻² h⁻¹)
- The resulting value of $M_{h,c}$ drives the subsequent calculation of R_h

Aerobic Methanotrophs

• **Respiration by aerobic methanotrophs**

$$- R'_t = M_{t,a} \{R'_t [\text{CH}_4]\} / \{(K_t + [\text{CH}_4])\} f_t$$

- R'_t : CH_4 oxidation by methanotrophs t under nonlimiting O_2 ($\text{g C m}^{-2} \text{ h}^{-1}$)
- $M_{t,a}$: biomass of active methanotrophs (g C m^{-2})
- R'_t : **specific CH_4 oxidation under nonlimiting CH_4 , O_2 , nutrients, θ and 25°C ($0.33 \text{ g C g C}^{-1} \text{ h}^{-1}$)**
- $[\text{CH}_4]$: aqueous concentration of CH_4 (g C m^{-3})
- K_t : **M-M constant for uptake of CH_4 by methanotrophs ($0.0012 \text{ g C m}^{-3}$)**
- f_t : Arrhenius function of soil temperature for growth-related processes

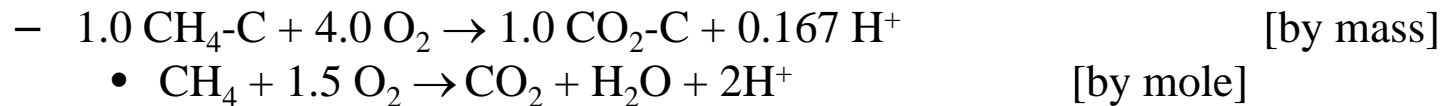
Aerobic Methanotrophs (cont.)

• **O₂ constraint on respiration by aerobic methanotrophs**

$$\begin{aligned}
 - R_t &= R'_t (U_{O_2t} / U'_{O_2t}) && \text{[O}_2 \text{ constraint]} \\
 - U_{O_2t} &= U'_{O_2t} [O_{2mt}] / ([O_{2mt}] + K_{O_2}) && \text{[active O}_2 \text{ uptake]} \\
 &= 4 \pi n_t M_{t,a} D_{sO_2} [r_m r_w / (r_w - r_m)] ([O_{2s}] - [O_{2mt}]) && \text{[radial O}_2 \text{ diffusion]}
 \end{aligned}$$

- R_t : CH₄ oxidation by methanotrophs t under ambient O₂ (g C m⁻² h⁻¹)
- U_{O_2t} : O₂ reduction by $M_{t,a}$ under ambient O₂ (g m⁻² h⁻¹)
- U'_{O_2t} : O₂ reduction by $M_{t,a}$ under nonlimiting O₂ (g m⁻² h⁻¹) = 2.67 R'_t
- $[O_{2mt}]$: O₂ concentration at methanotrophic microsites (g O₂ m⁻³)
- $[O_{2s}]$: aqueous O₂ concentration (g O₂ m⁻³)
- K_{O_2} : **M–M constant for O₂ reduction (0.064 g O₂ m⁻³)**
- n_t : number of methanotrophic microsites (m⁻²)
- D_{sO_2} : aqueous dispersivity–diffusivity of O₂ (m² h⁻¹)
- r_m : **radius of heterotrophic microsite (2.5 x 10⁻⁶ m)**
- r_w : thickness of water films (m)

• **Oxidation-reduction by methanotrophs**



Aerobic Methanotrophs(cont.)

• Uptake of CH₄ by methanotrophs

- $U_{t,c} = R_{mt} + R_{gt} (1 + Y_t)$
 - $U_{t,c}$: rate of CH₄ uptake by methanotrophs (g C m⁻² h⁻¹)
 - R_{mt} : maintenance respiration by methanotrophs (g C m⁻² h⁻¹)
 - R_{gt} : growth respiration = $R_{ht} - R_{mt}$ (g C m⁻² h⁻¹)
 - Y_t : biomass yield from CH₄ oxidation (g M_{t,c} g CH₄-C⁻¹)

• Energy from oxidation-reduction

- $Y_t = -\Delta G'_t / E_M Y_b$
 - $\Delta G'_t$: free energy change of CH₄ oxidation (37.5 kJ g C⁻¹)
 - E_M : energy required to construct new M (25 kJ g C⁻¹)
 - Y_b : biomass yield from CH₄ oxidation (0.45 g C g C⁻¹)

• Growth of methanotrophs

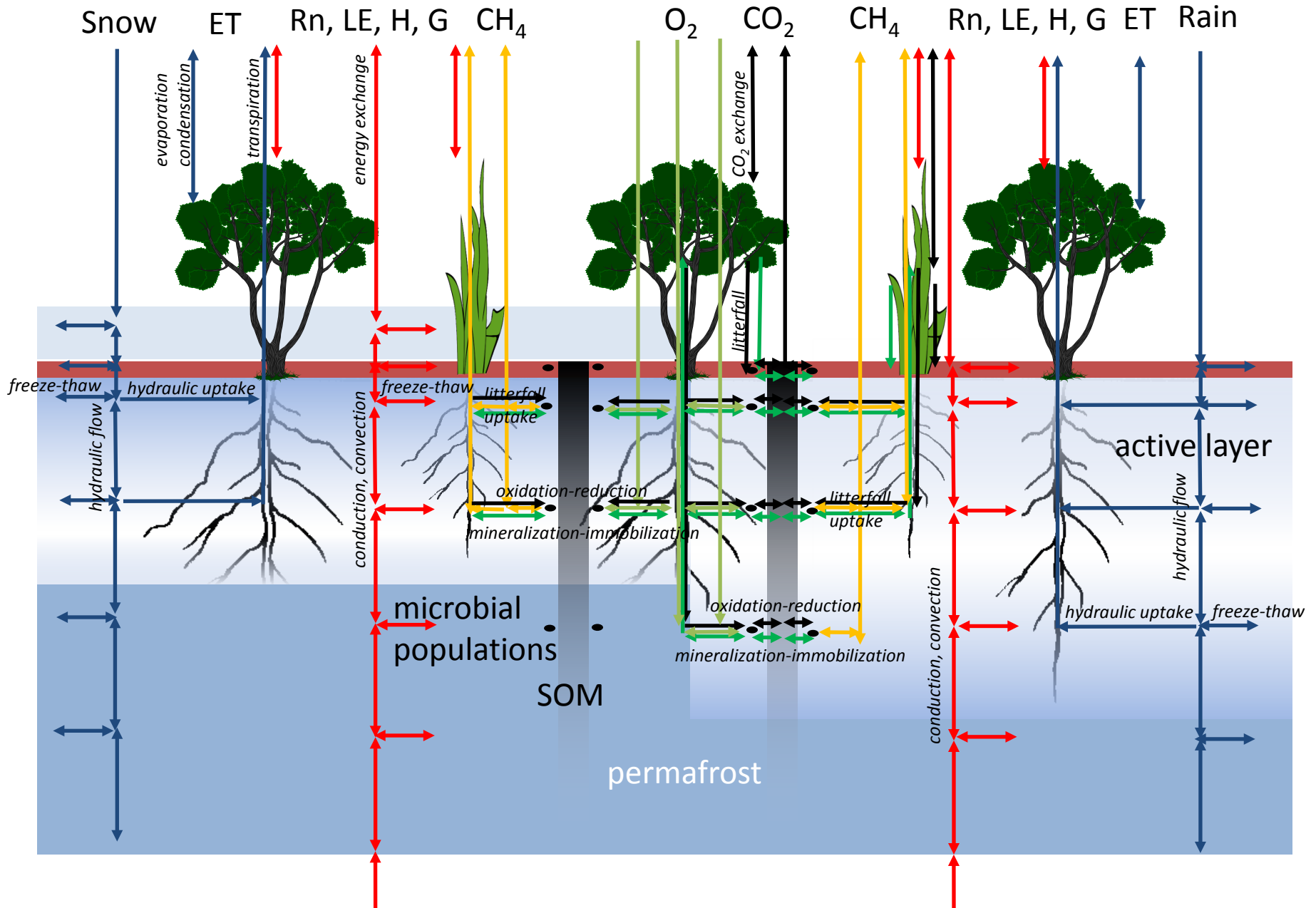
- $\delta M_{t,c} / \delta t = U_{t,c} - R_t - D_{t,c}$
 - $D_{t,c}$: decomposition of methanotrophs (g C m⁻² h⁻¹)
- The resulting value of $M_{t,c}$ drives the subsequent calculation of R_t

Transport of reactants and products of oxidation-reduction reactions

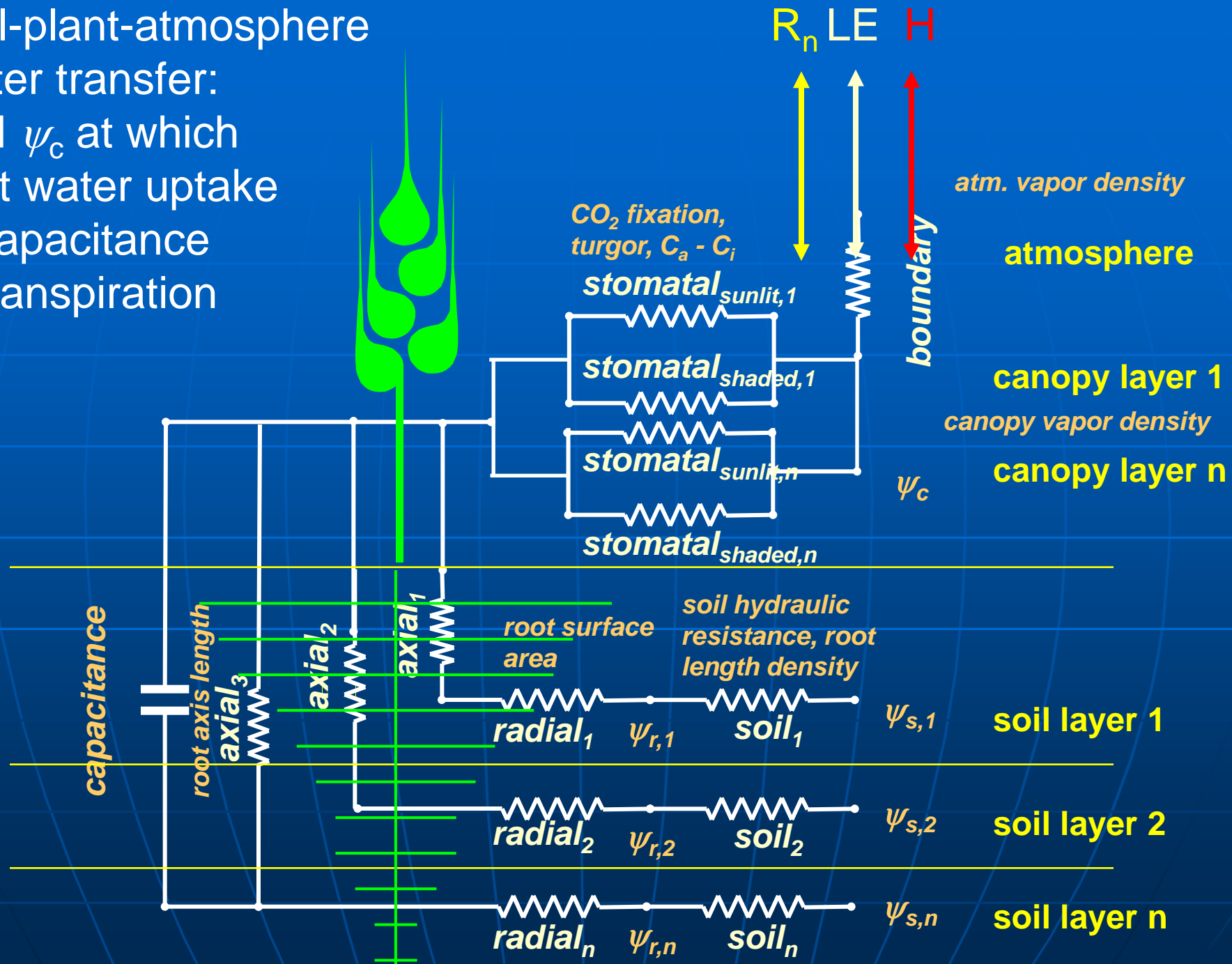
- All soluble reactants and products of oxidation-reduction reactions undergo convective-dispersive transport in aqueous phases of the soil
- All gaseous reactants and products of oxidation-reduction reactions undergo convective-dispersive transport in gaseous phases of the soil and roots

Winter

Summer



Soil-plant-atmosphere
 water transfer:
 find ψ_c at which
 root water uptake
 + capacitance
 = transpiration



Modeling protocols

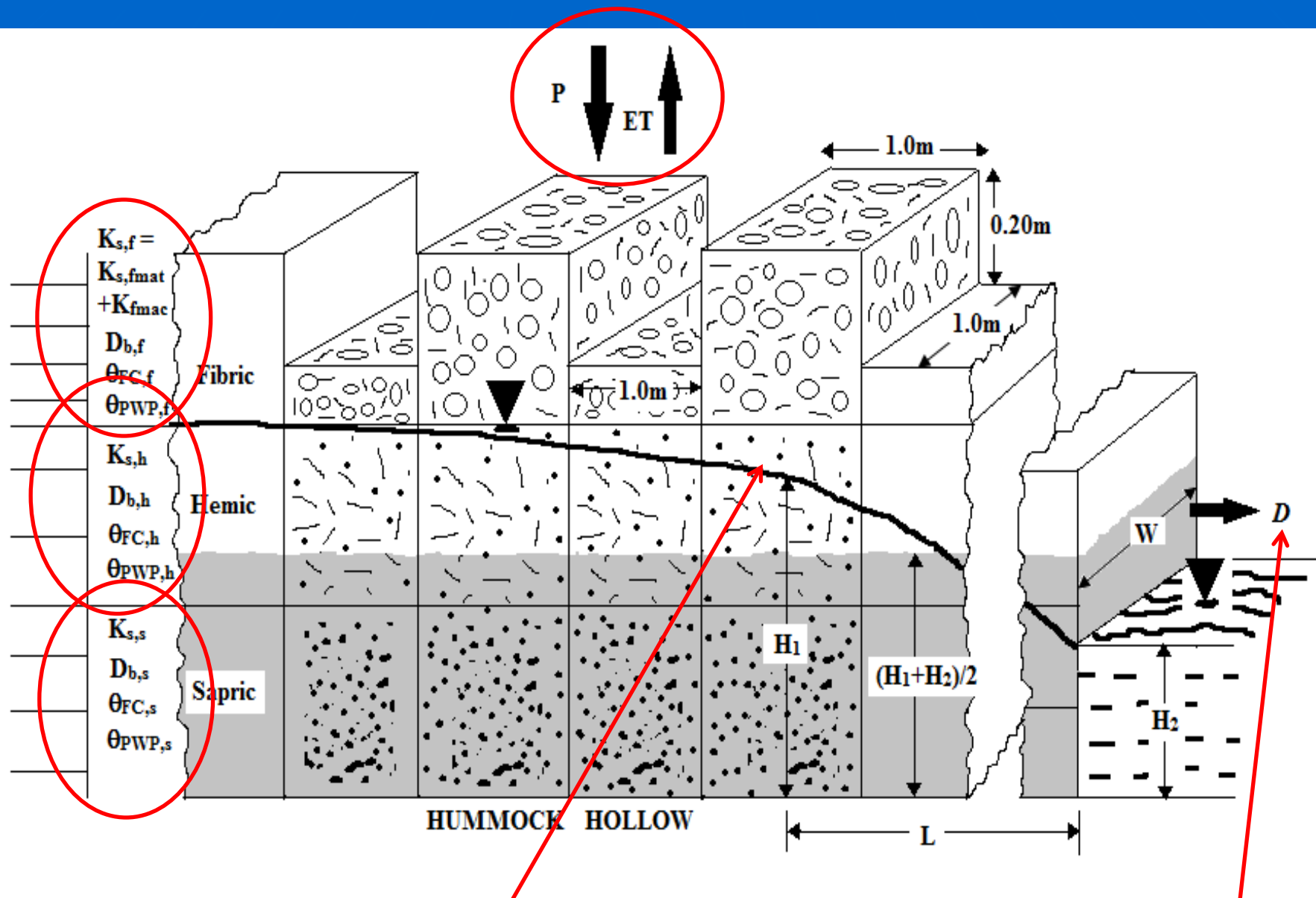
Representative soil physical properties of Palanga Karaya Peat Swamp forest, Indonesia used in *ecosys*

<i>Peat type</i>	D_{hum} (m)	D_{hol} (m)	BD_{dry} (Mg m ⁻³)	$\theta_{-0.002MPa}$ (m ³ m ⁻³)	$\theta_{-0.01MPa}$ (m ³ m ⁻³)	$\theta_{-1.5MPa}$ (m ³ m ⁻³)	K_s (mm h ⁻¹)
Fibric	0-0.2		0.149	0.410	0.287	0.211	25.00
Hemic	0.2-0.4	0-0.2	0.199	0.711	0.514	0.406	25.00
Sapric	0.4-4.0	0.2-3.8	0.251	0.749	0.512	0.286	25.00

Number of layers in fibric peat: 4, hemic: 2 and sapric: 10; total layers: 16

D_{hum} = Depth to the bottom of a layer in hummock grid cells; D_{hol} = Depth to the bottom of a layer in hollow grid cells; BD_{dry} = Dry bulk density; θ = volumetric soil water content; K_s = saturated hydraulic conductivity

(Ong and Yogeswaran, 1992; Kurnain et al. 2001)

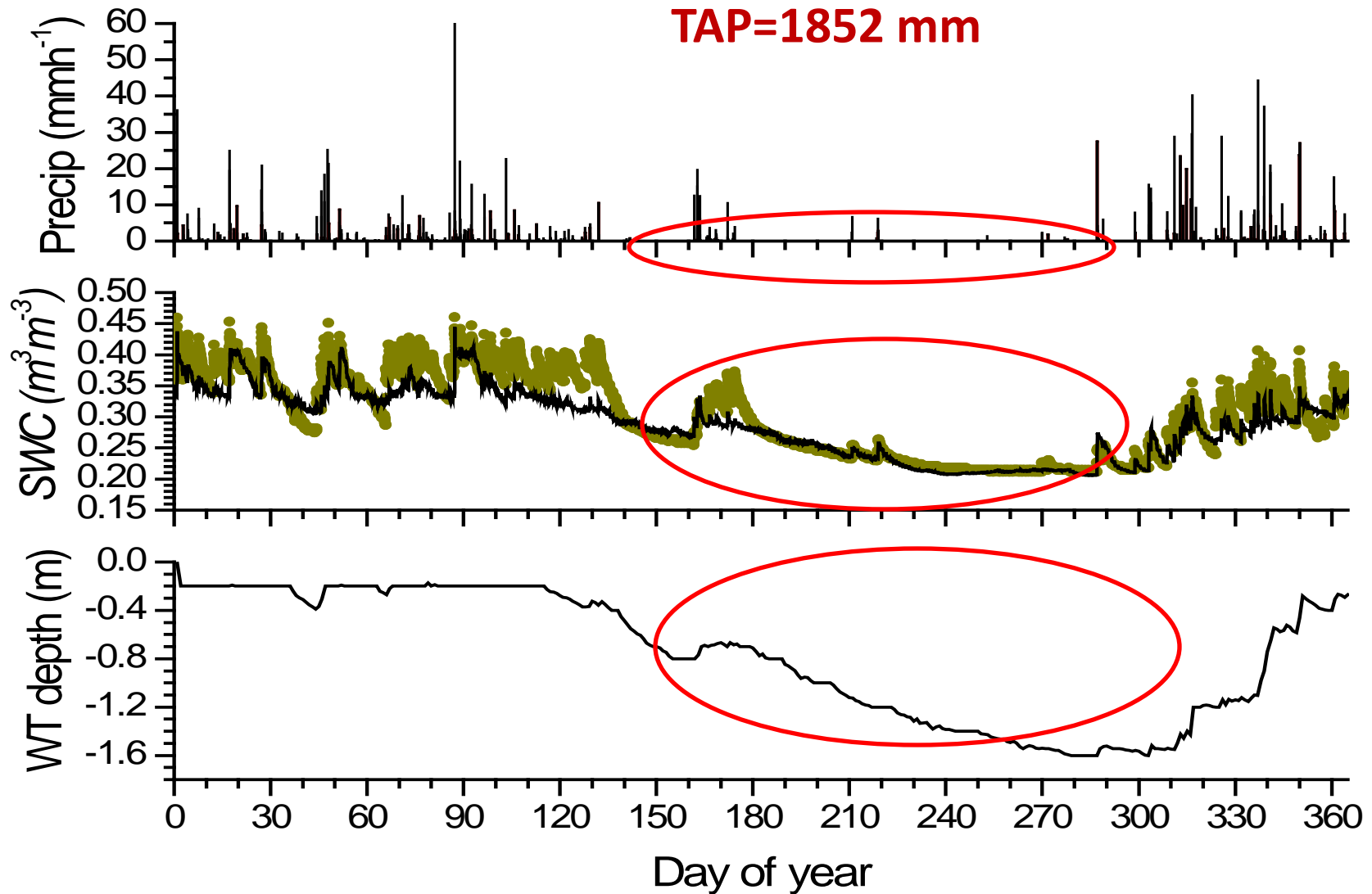


Elevation of water table H_1 relative to that of external water table H_2 is that at which discharge D equilibrates with $P - ET - \text{runoff}$

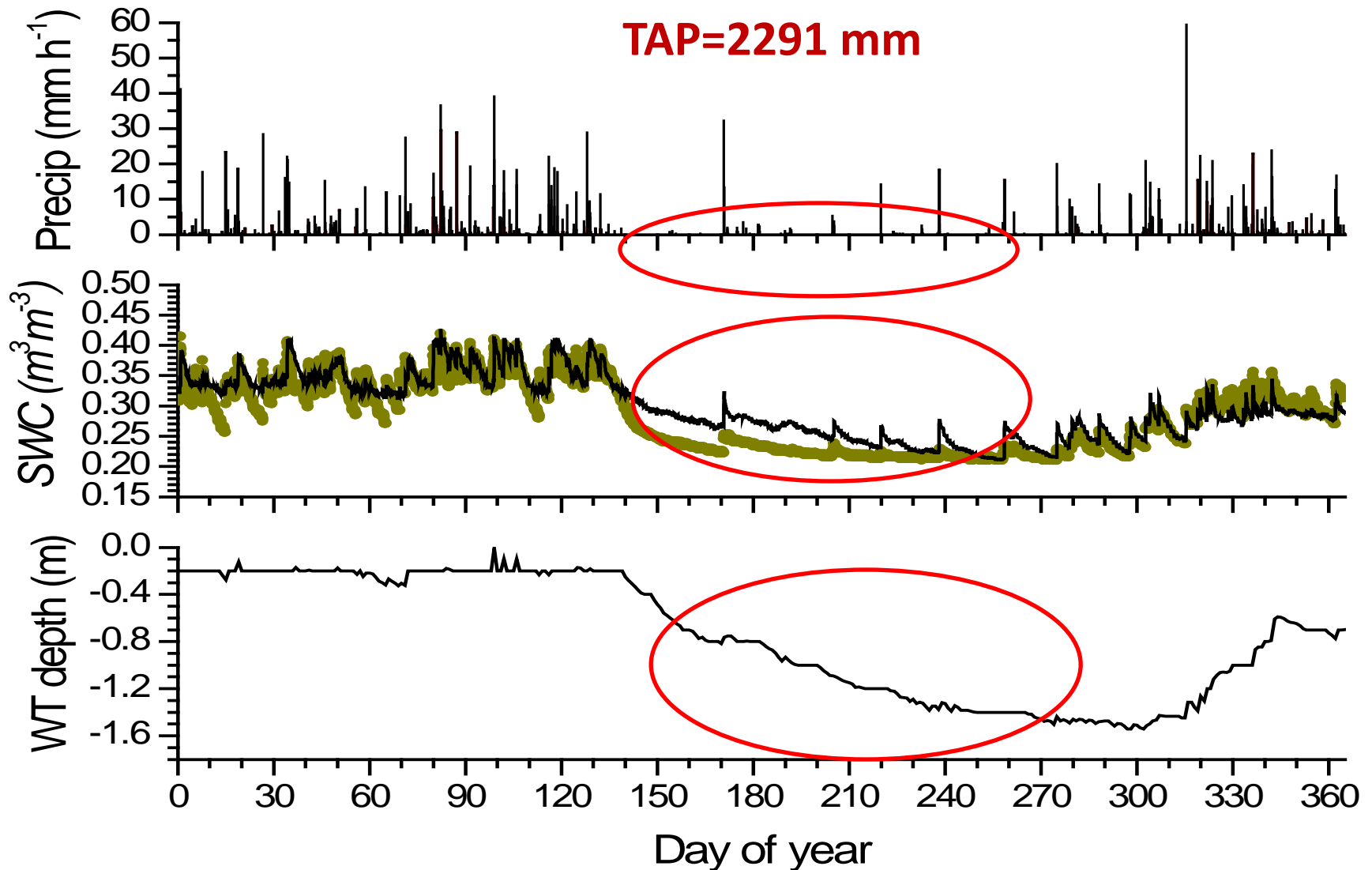
Modeling protocols contd.

- ❖ A 60-year spin up run using repeated weather cycles of 2002-2005 recorded at the **Palanga Karaya Peat Swamp forest**
- ❖ An under- and an over-storey evergreen vegetation were simulated by using plant physiological parameters described in **Grant et al. 2009** with the following species specific features
 - **Root porosity = 0.17** (Tanaka et al. 2011)
 - ♣ determines O₂ transport to the roots of the modeled plant species through aerenchyma
 - **Plant osmotic potential at full turgor = -1.13 MPa** (Naiola and Osaki 2000)
 - not particularly drought-resistant

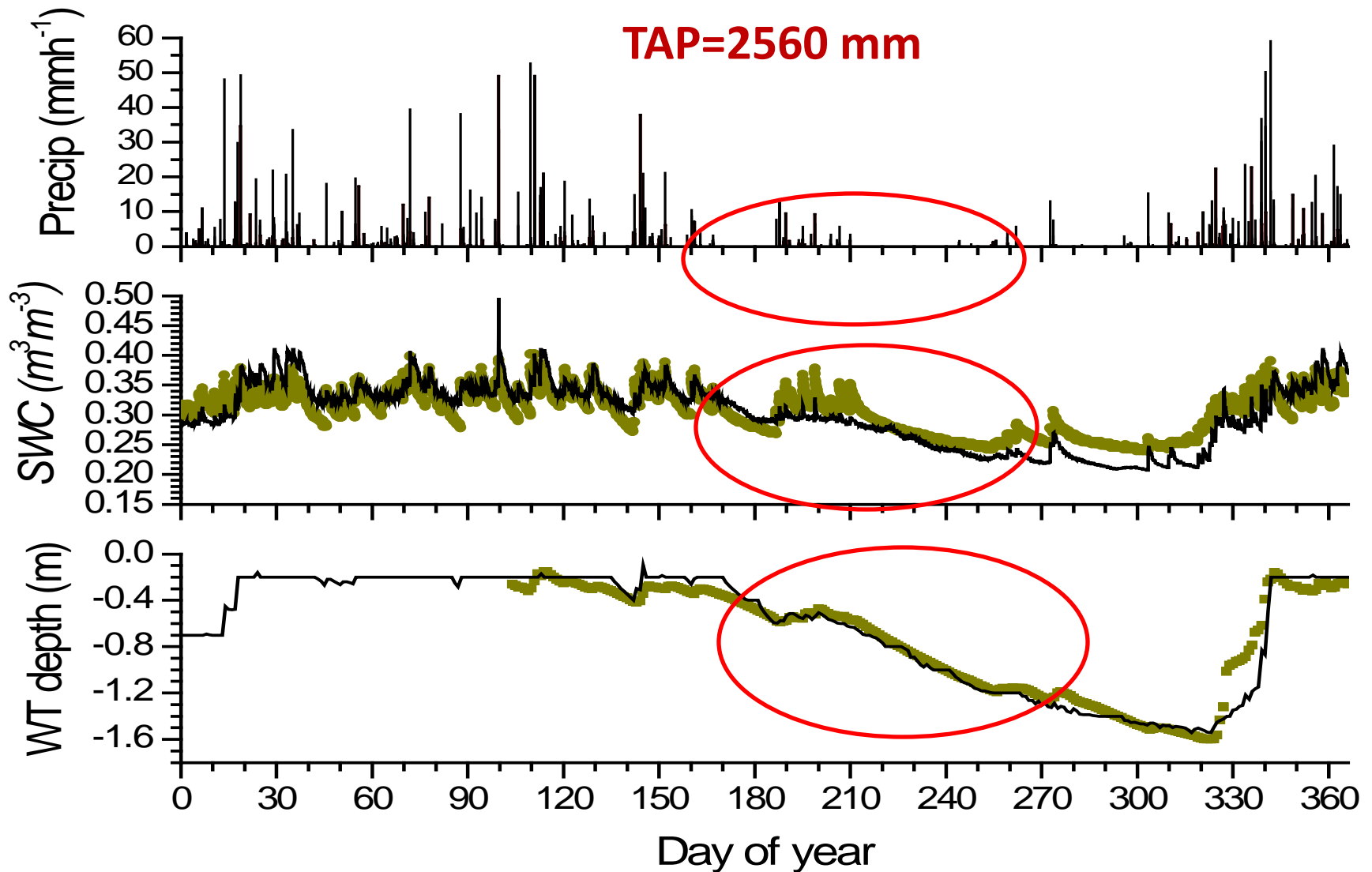
TAP=1852 mm



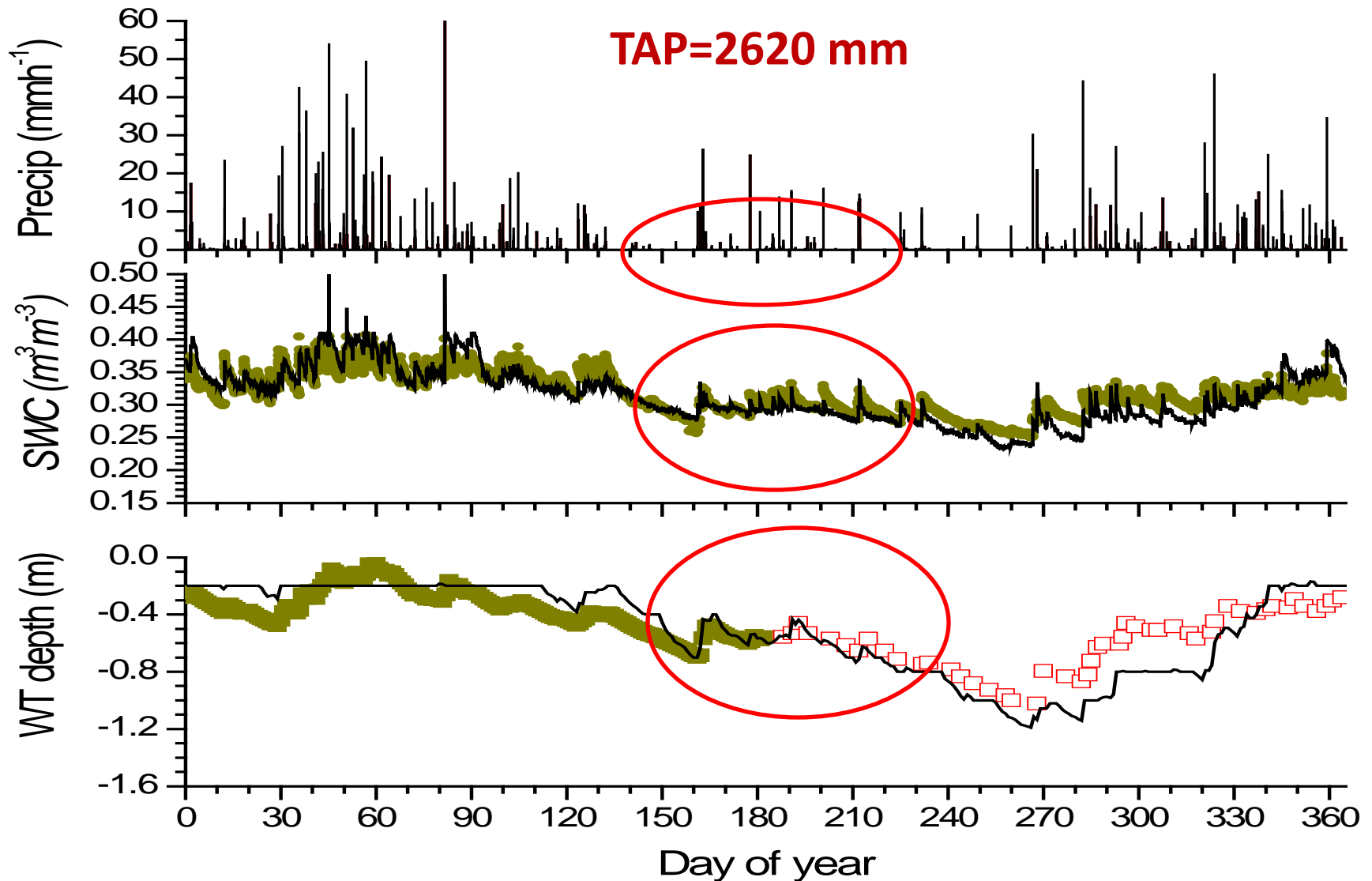
2002 was an El Nino year with a long dry season that caused soil drying and a low water table



The dry season in 2003 was less intense, with some soil rewetting and a slower decline in the water table

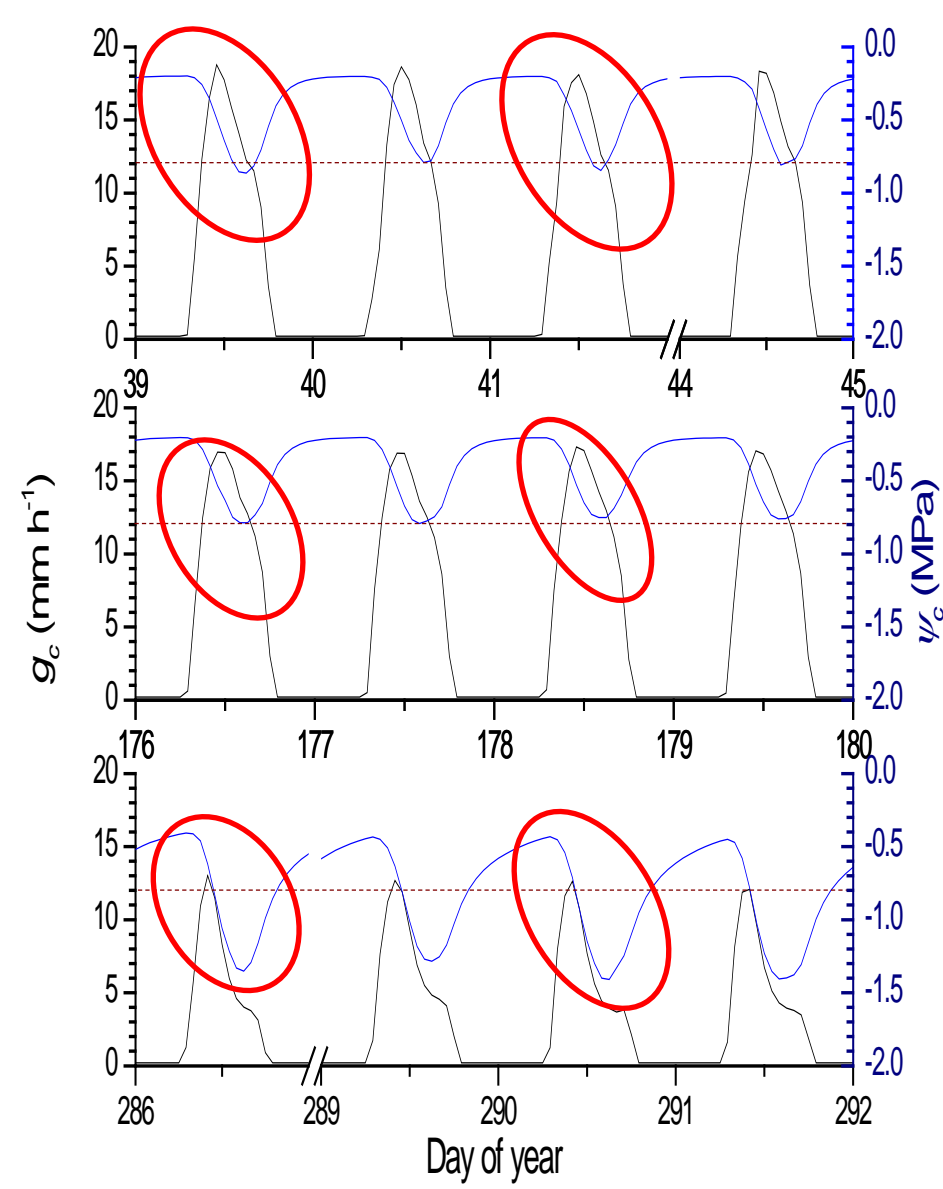
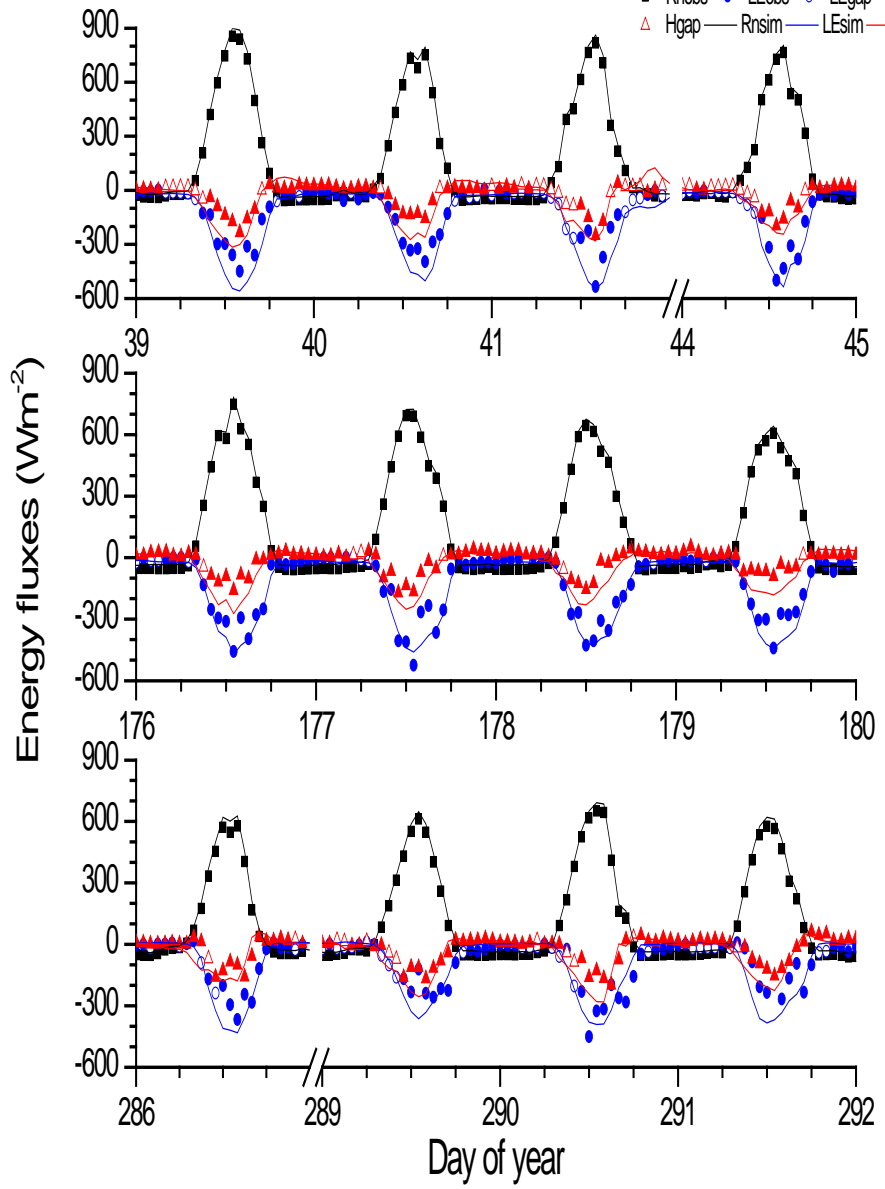


The dry season 2004 was even wetter, with less soil drying and a later decline in the water table



The dry season in 2005 was interrupted by several rainfall events, causing less soil drying and decline in the water table

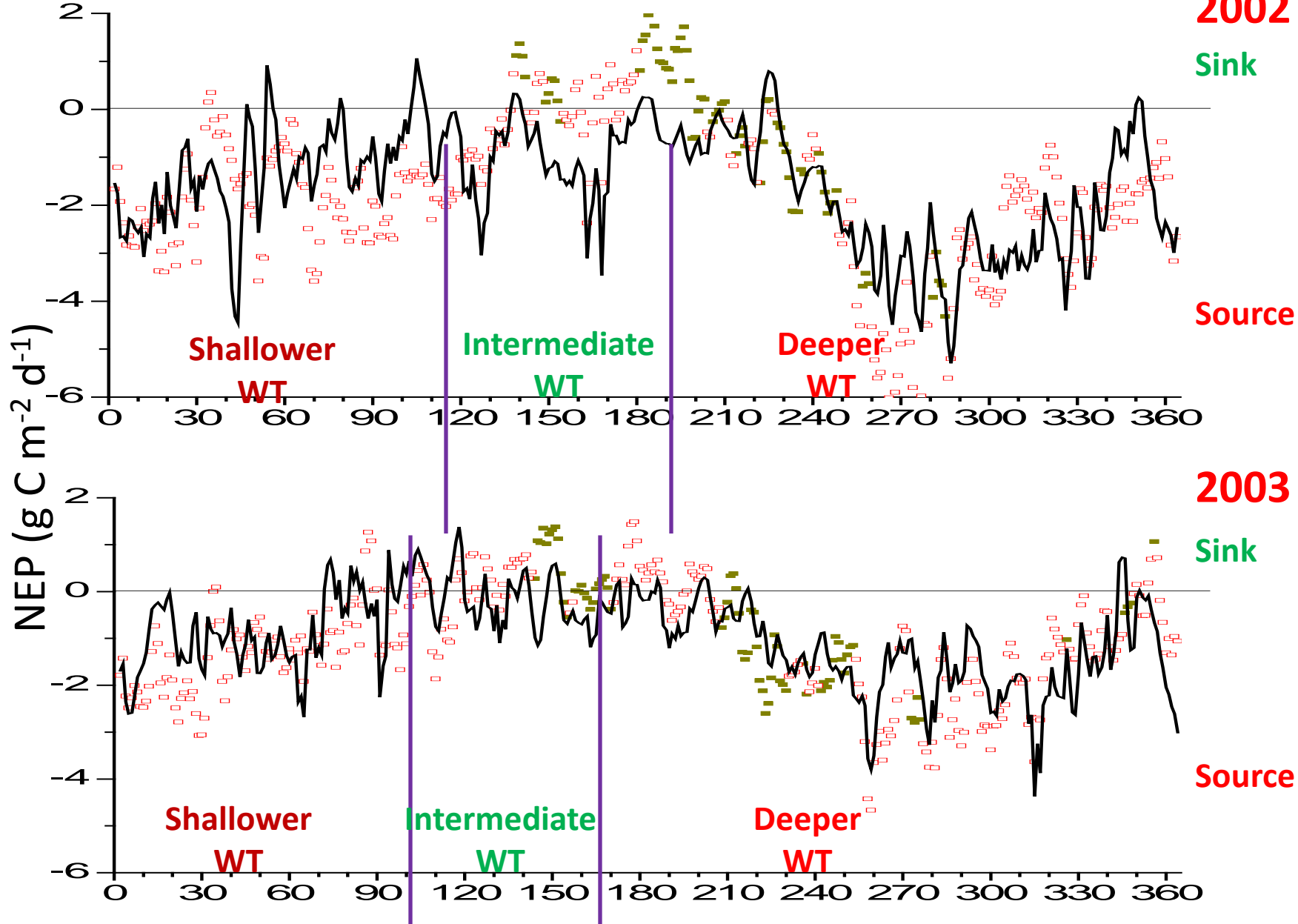
■ Rnobs ● LEobs ○ LEgap ▲ Hobs
 △ Hgap — Rnsim — LESim — Hsim



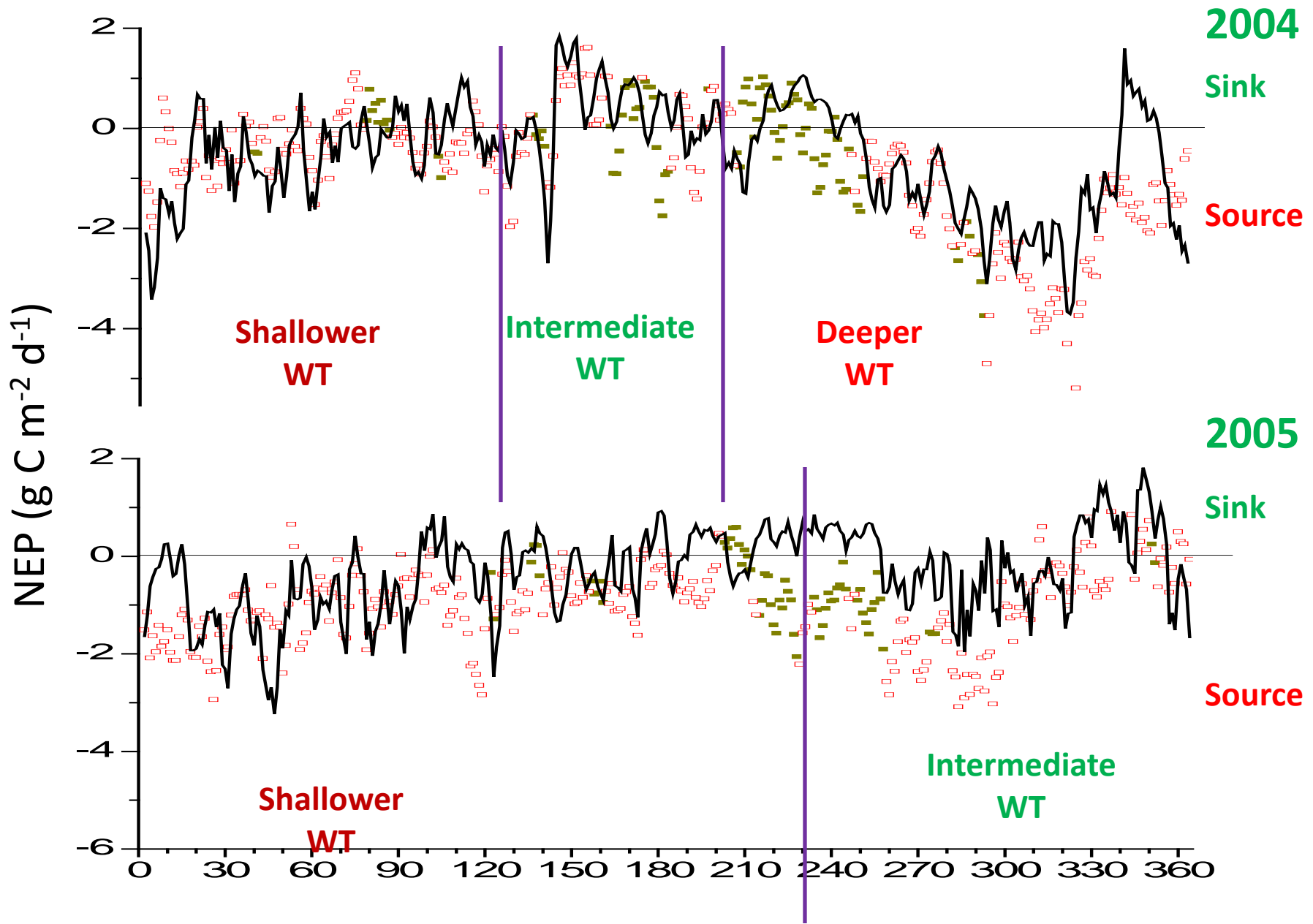
Seasonal changes in energy fluxes were caused by changes in canopy water potentials and conductances

Summary

- ❖ The three hydroperiods proposed in our hypotheses enabled us to model:
 - ❖ Slightly lower water status caused by flooding stress during the rainy seasons, likely caused by slower nutrient uptake.
 - ❖ Optimum water status during the early dry seasons.
 - ❖ Lower water status during the later dry seasons caused by water stress due to inadequate recharge of near surface peat layers through capillary rise.
- ❖ The duration of these hydroperiods varies from year to year.
- ❖ These durations will likely affect peatland productivity.



The peatland is a small C source during the rainy season, near C neutral during the early dry season, and a large C source during the late dry season



The seasonality of these C sources and sinks became less pronounced with less intense dry seasons

2004 (zoom in)

+ influxes
- effluxes

Ecosystem CO₂ fluxes (μmol m⁻² s⁻¹)

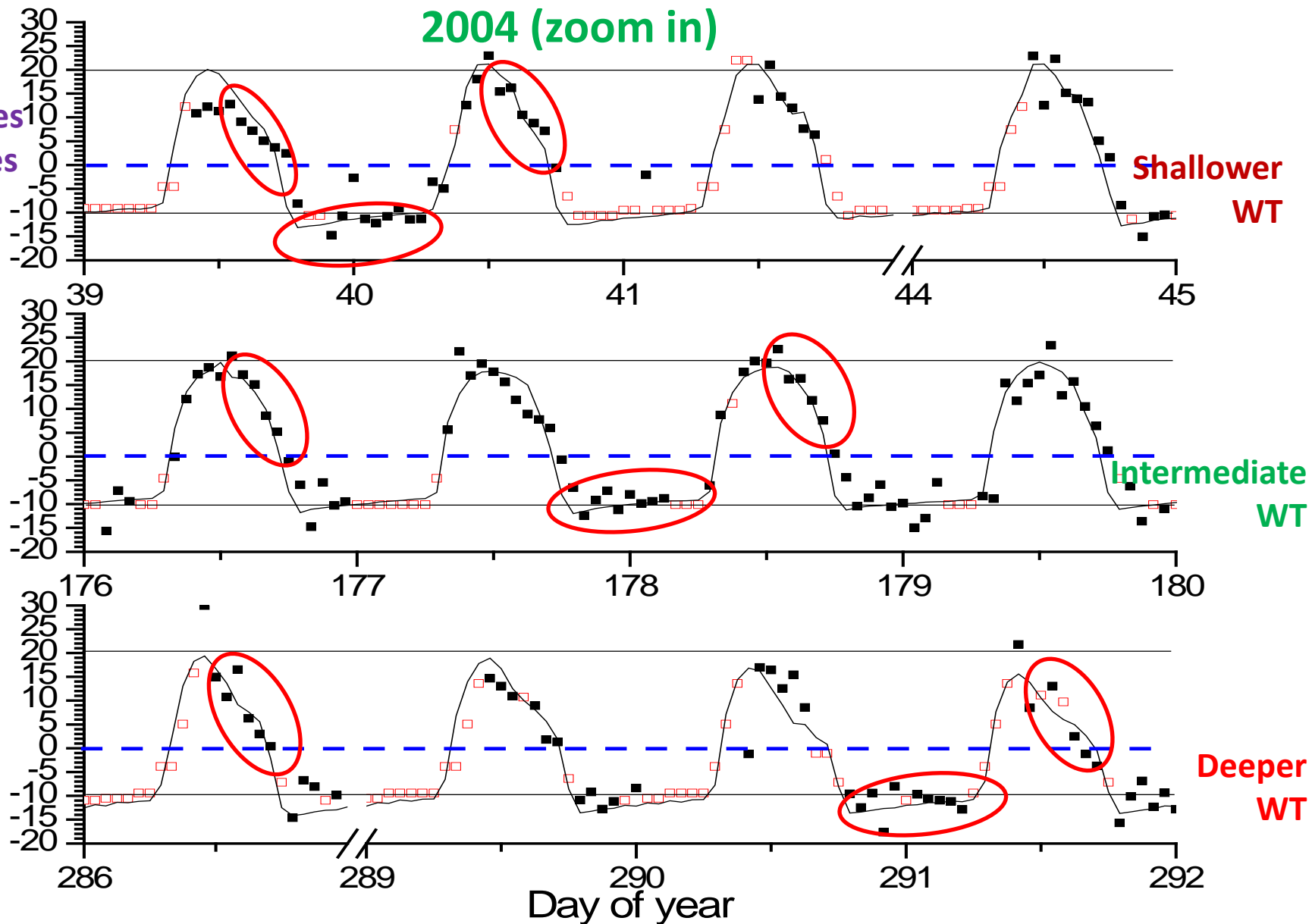
Shallower
WT

Intermediate
WT

Deeper
WT

Day of year

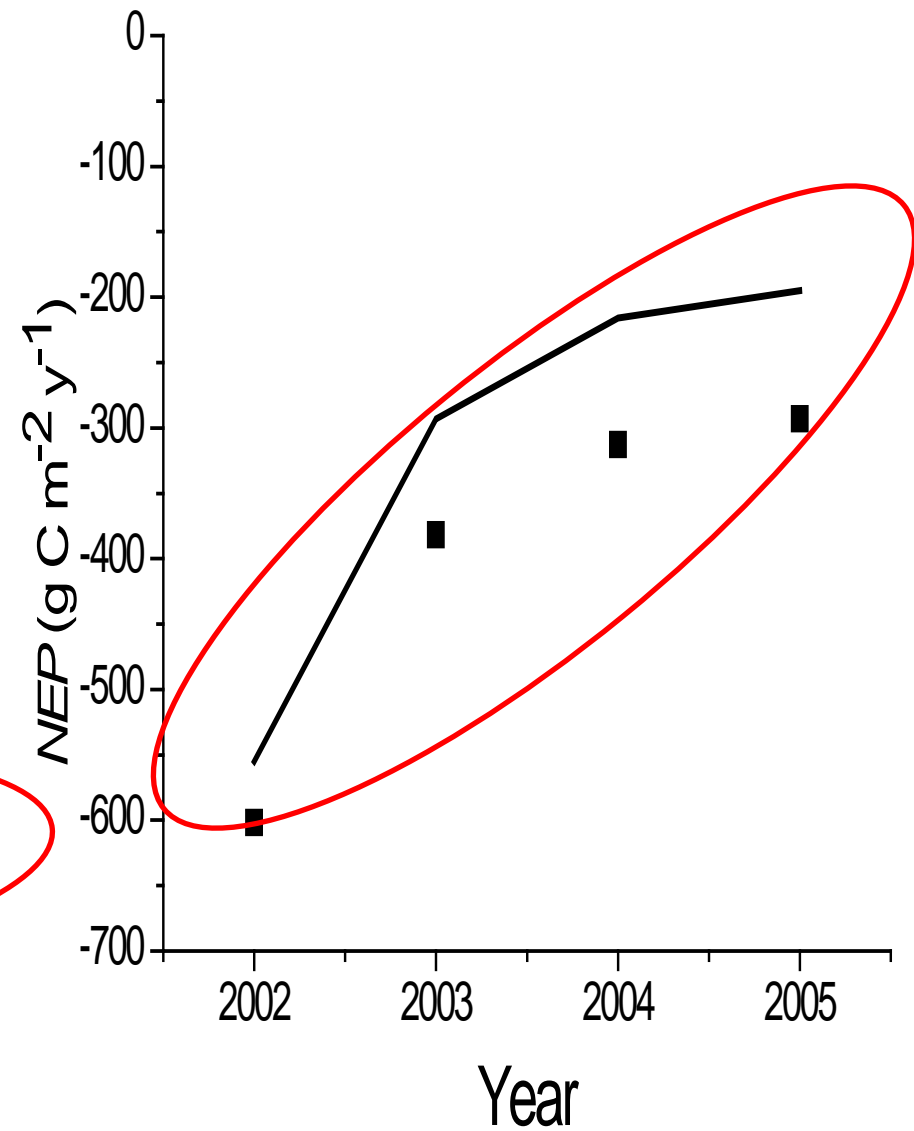
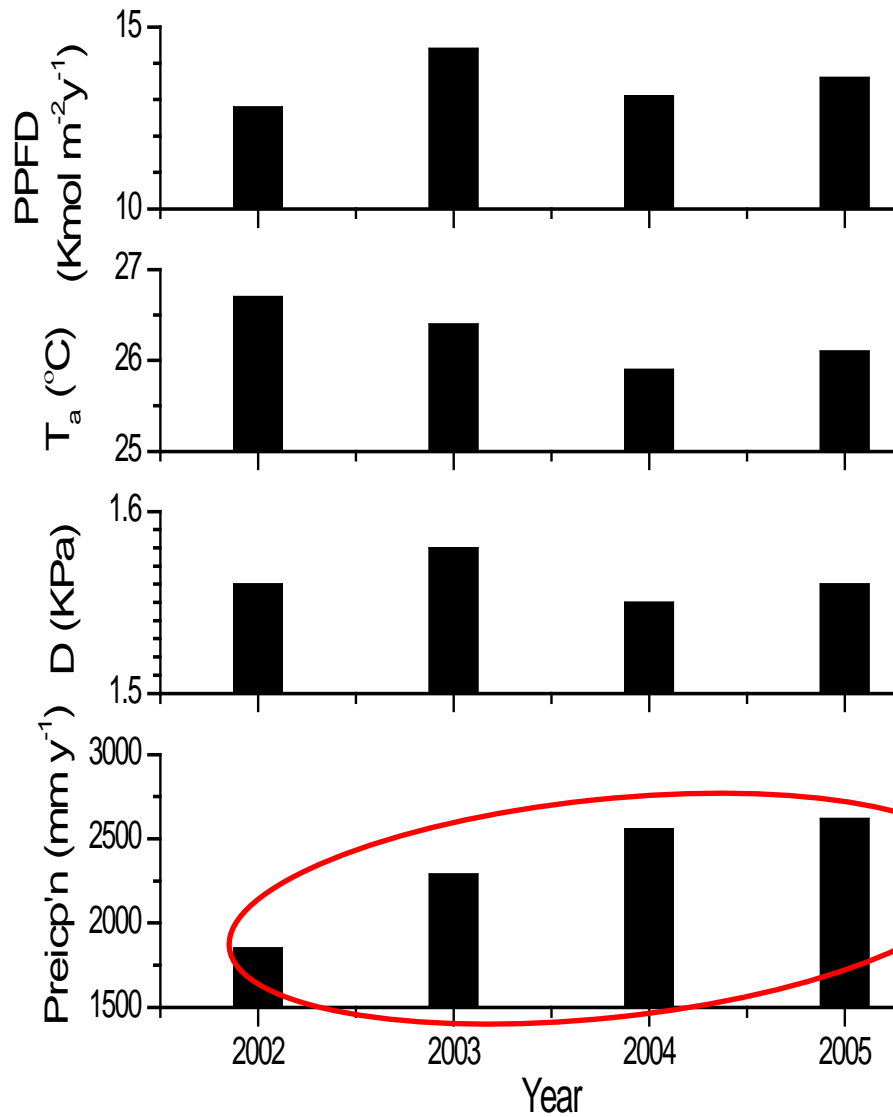
Dry season C sources were caused by earlier midafternoon declines in CO₂ uptake and by increases in CO₂ emissions during nights



The model explained ~ 80% of variation in measured CO₂ fluxes with slopes close to one during each year, in spite of varying precipitation

Year	Precip'n (mmy ⁻¹)	<i>n</i>	<i>a</i> [‡]	<i>b</i> [‡]	<i>R</i> ^{2‡}	<i>RMSD</i> [†]	<i>RMSE</i>
2002	1852	3007	0.57	0.98	0.77	5.7	5.5
2003	2291	2595	0.56	1.00	0.82	5.0	5.9
2004	2560	3299	0.88	1.00	0.83	5.0	5.8
2005	2620	3164	1.50	1.05	0.81	5.2	5.6

RMSE (root mean square for errors due to measurements) are calculated from EC data using the equation of Richardson et al. 2006



C losses declined as the intensity and duration of the dry seasons decreased from 2002 to 2005

Summary: Effects of hydrology on NEP

❖ During the first hydroperiod:

❖ Shallow WT: $NEP \downarrow = GPP \downarrow - RE \downarrow$

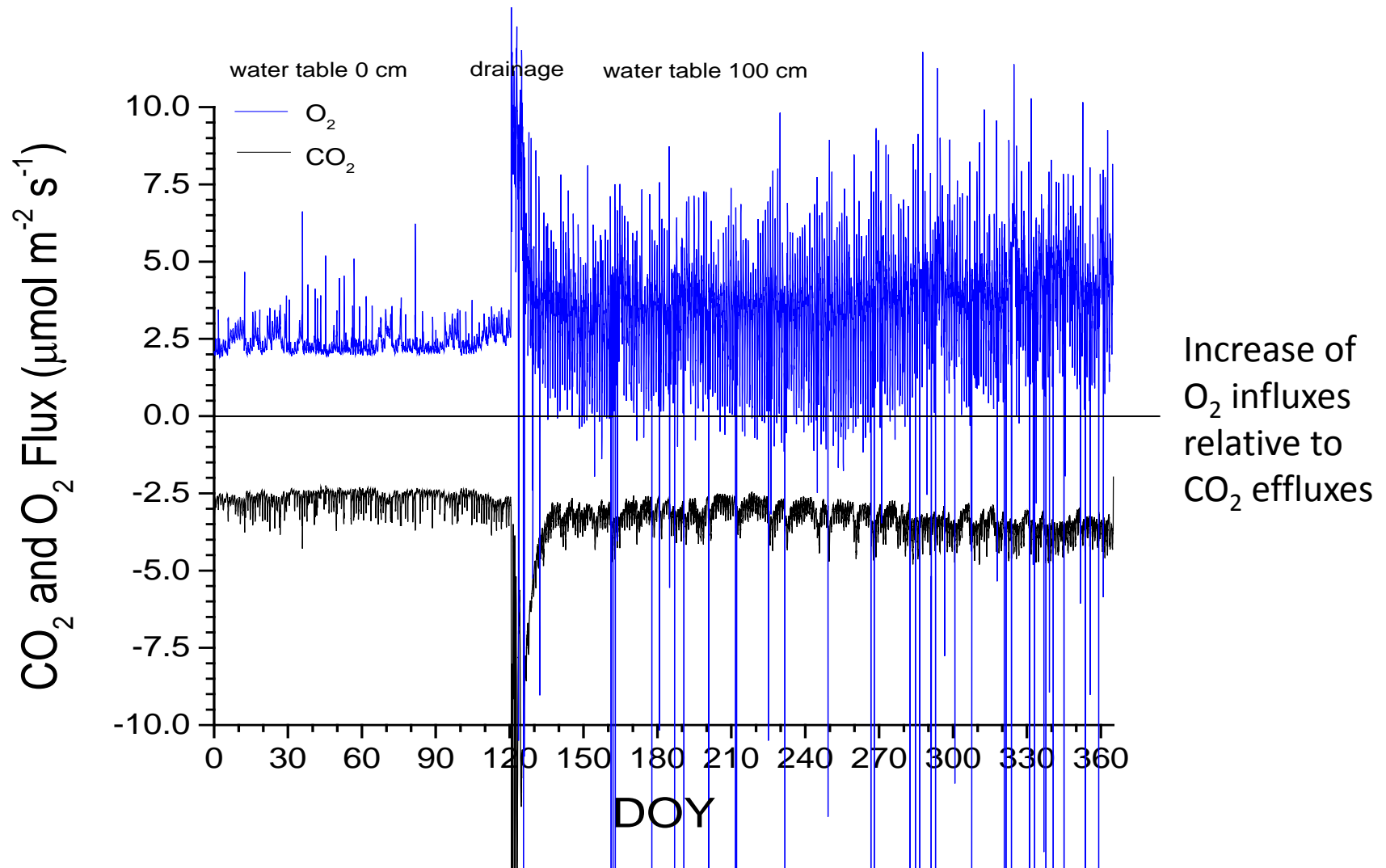
❖ During the second hydroperiod:

❖ Intermediate WT: $NEP \uparrow = GPP \uparrow - RE$

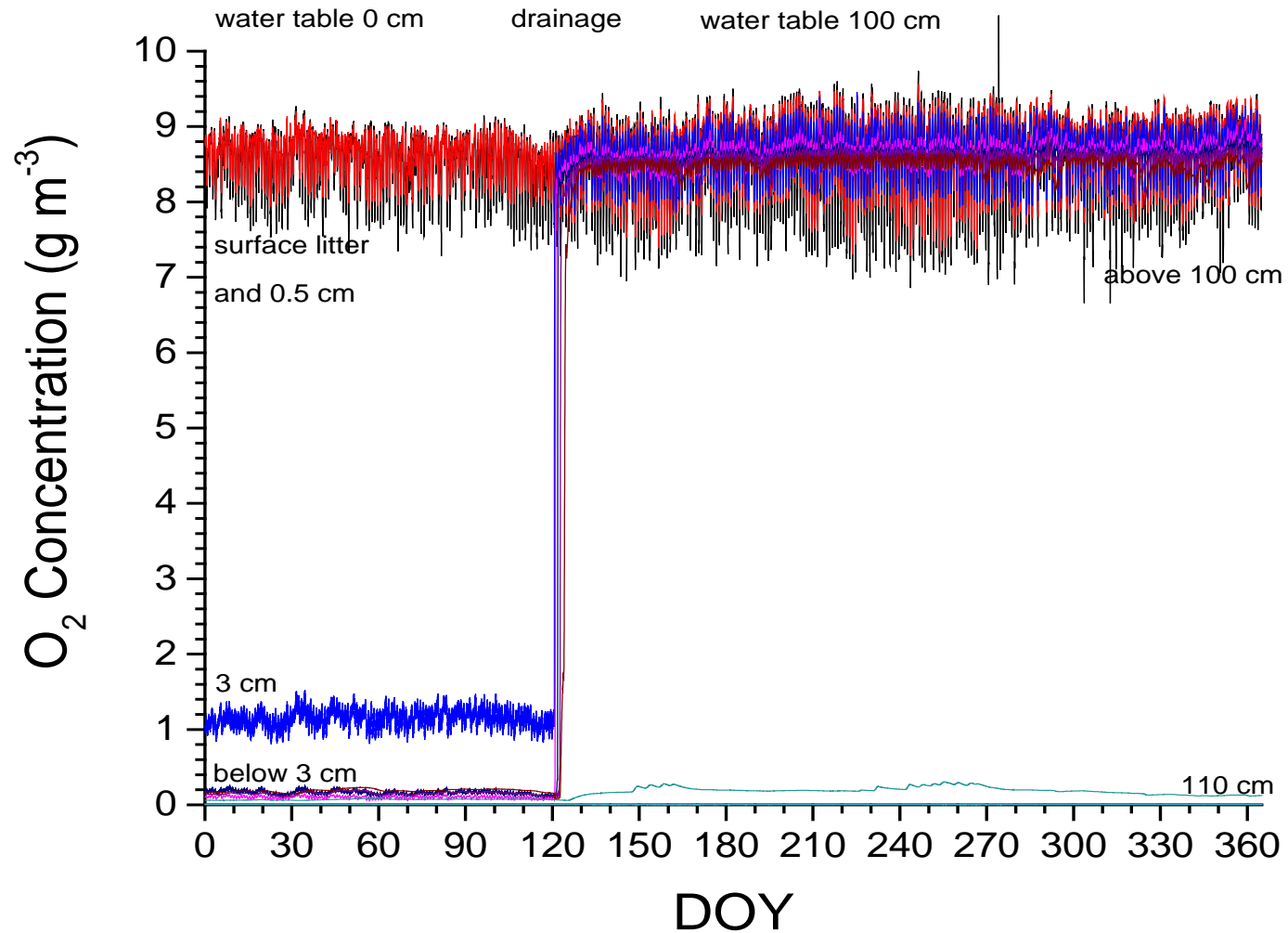
❖ During the third hydroperiod:

❖ Deeper WT: $NEP \downarrow = GPP \downarrow - RE \uparrow$

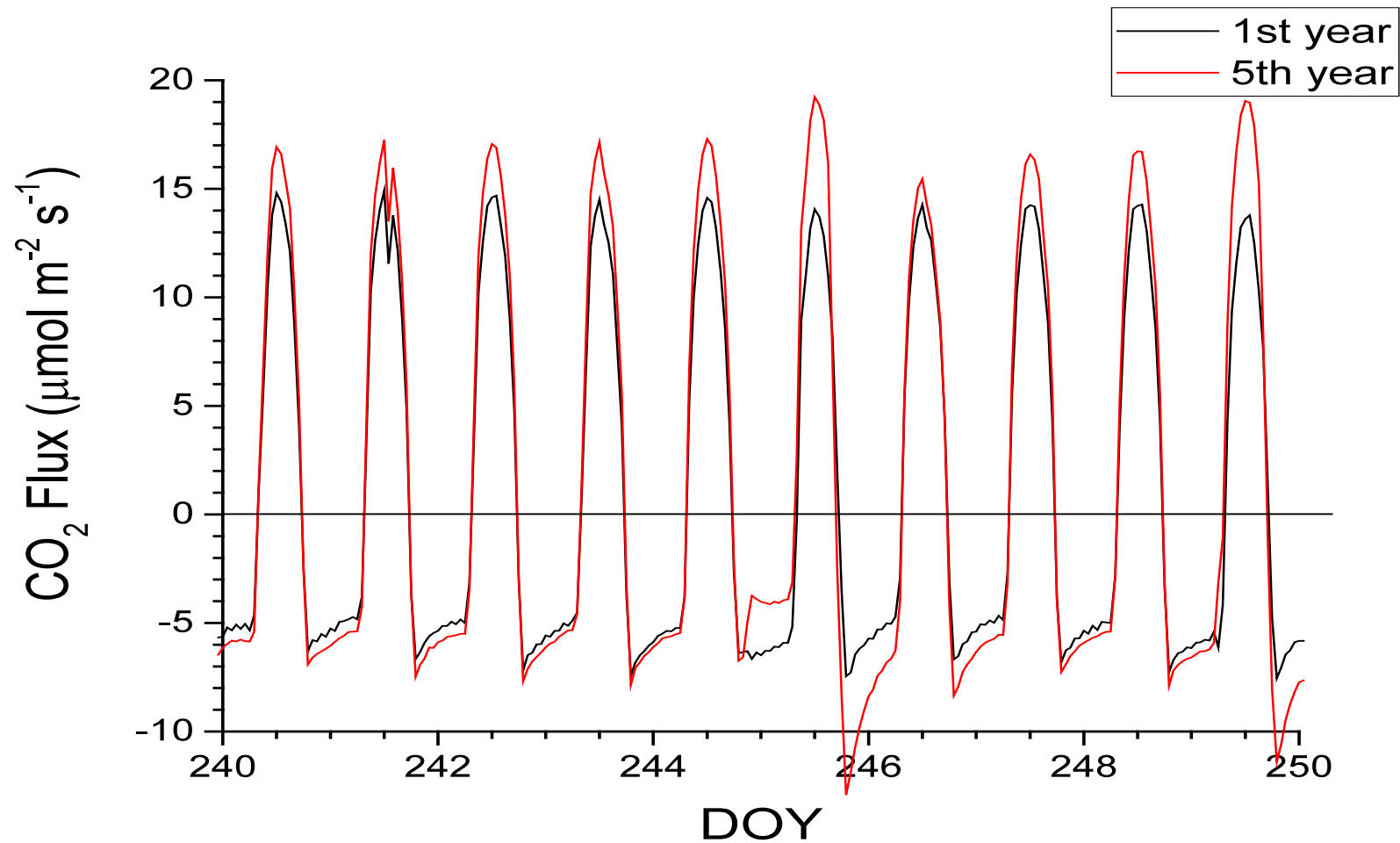
How does drainage affect gas exchange in peatland?



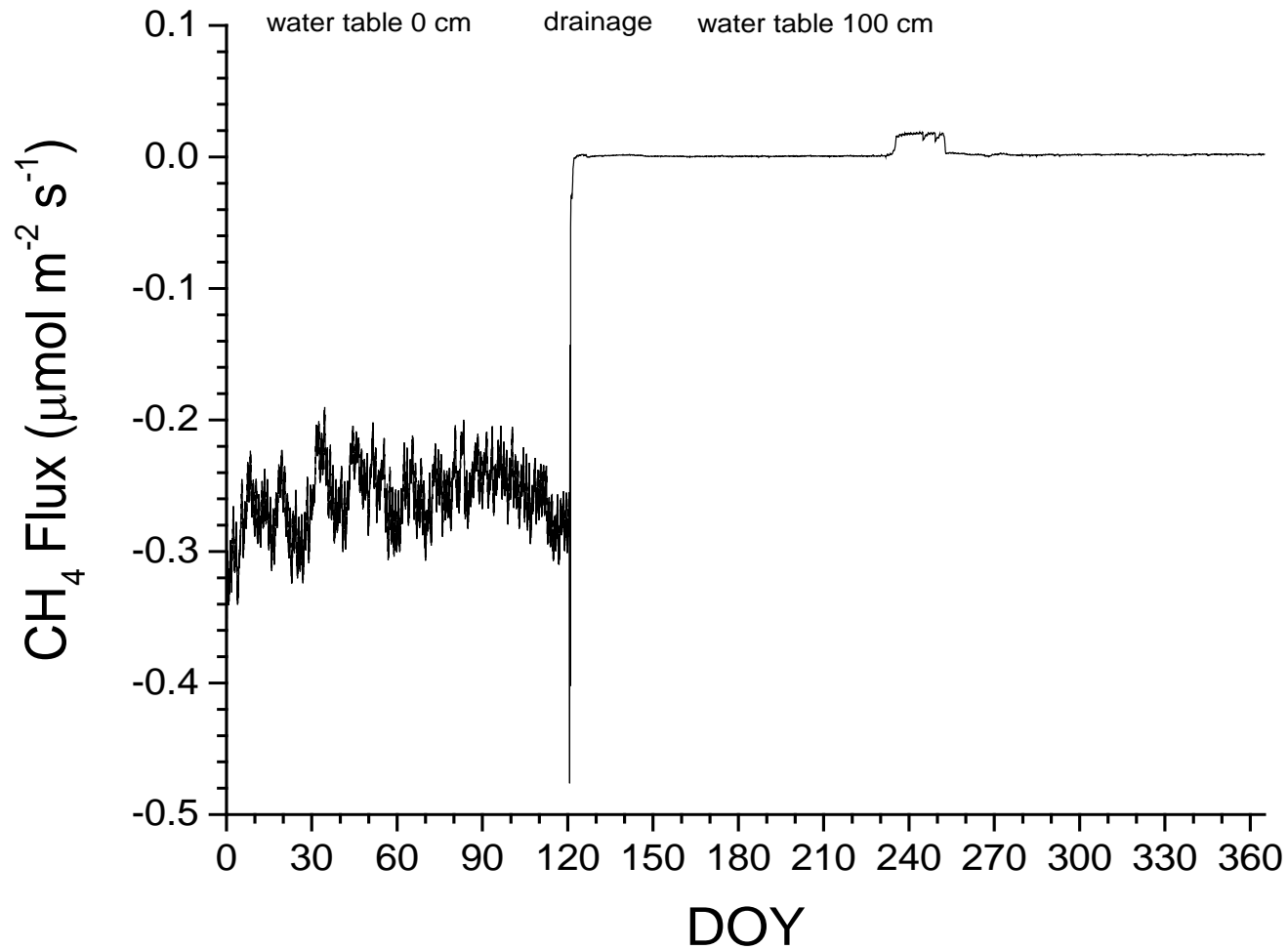
Drainage caused reoxygenation of the soil above the drainage depth



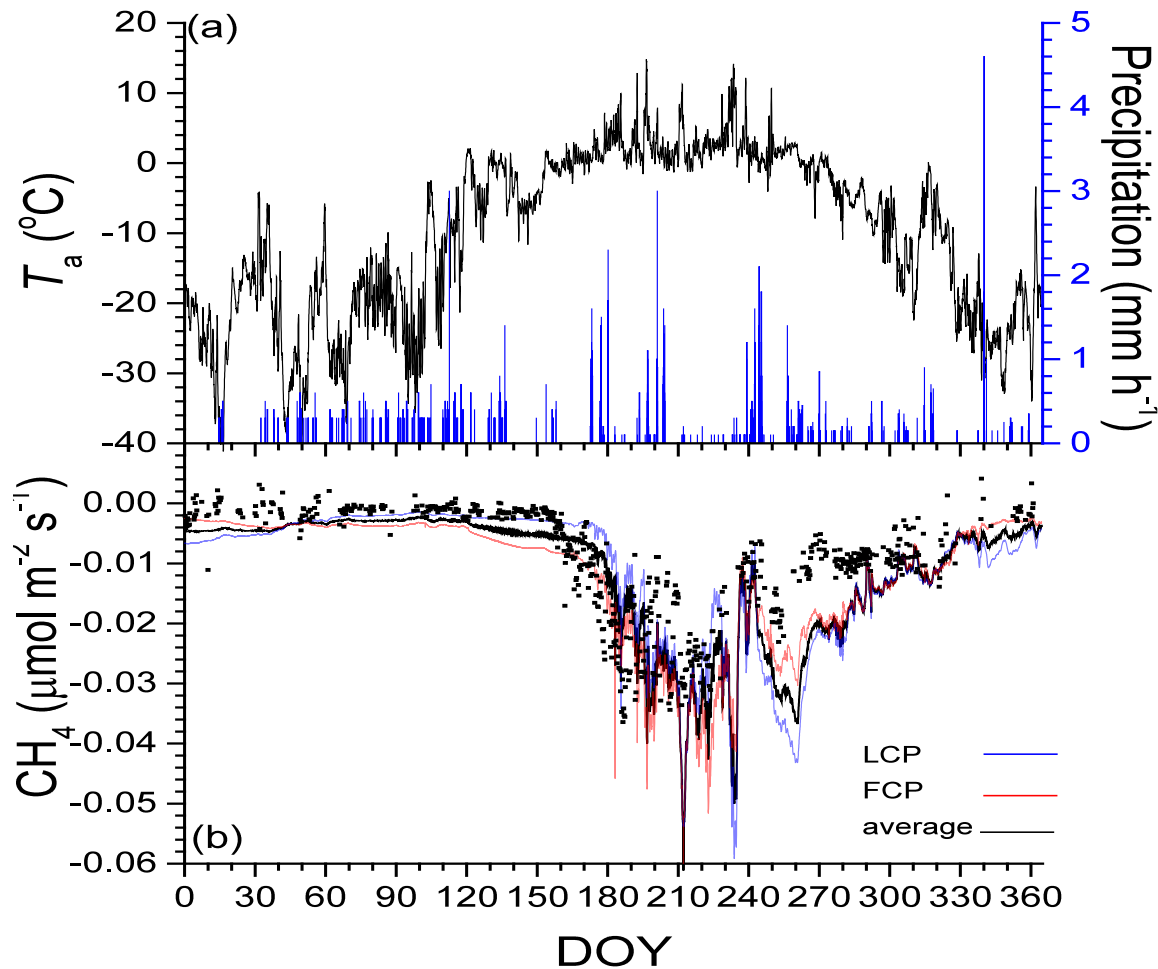
Both influxes and effluxes of CO₂ rose gradually during the years following drainage



Reoxygenation suppressed fermentation, methanogenesis, hastened methanotrophy



Model test of CH₄ emissions from polygonal tundra near Barrow, Alaska



(a) Air temperature (T_a) and precipitation, and (b) CH₄ flux measured during 2014 (symbols) and modelled during 2084 (2014) of the baseline run (line). In (b) positive values represent influxes, and negative values effluxes. Measured fluxes from Zona et al. (2015).

For application of *ecosys* in a polygonal tundra landscape, see:

Grant, R. F., Mekonnen, Z. A., Riley, W. J., Wainwright, H. M., Graham, D. & Torn, M. S. (2017). Mathematical modelling of arctic polygonal tundra with *ecosys*: 1. Microtopography determines how active layer depths respond to changes in temperature and precipitation. *Journal of Geophysical Research: Biogeosciences*, 122, 3161–3173.

<https://doi.org/10.1002/2017JG004035>

Grant, R. F., Mekonnen, Z. A., Riley, W. J., Arora, B. & Torn, M. S. (2017). Mathematical modelling of arctic polygonal tundra with *ecosys*: 2. Microtopography determines how CO₂ and CH₄ exchange responds to changes in temperature and precipitation. *Journal of Geophysical Research: Biogeosciences*, 122, 3174– 3187. <https://doi.org/10.1002/2017JG004037>