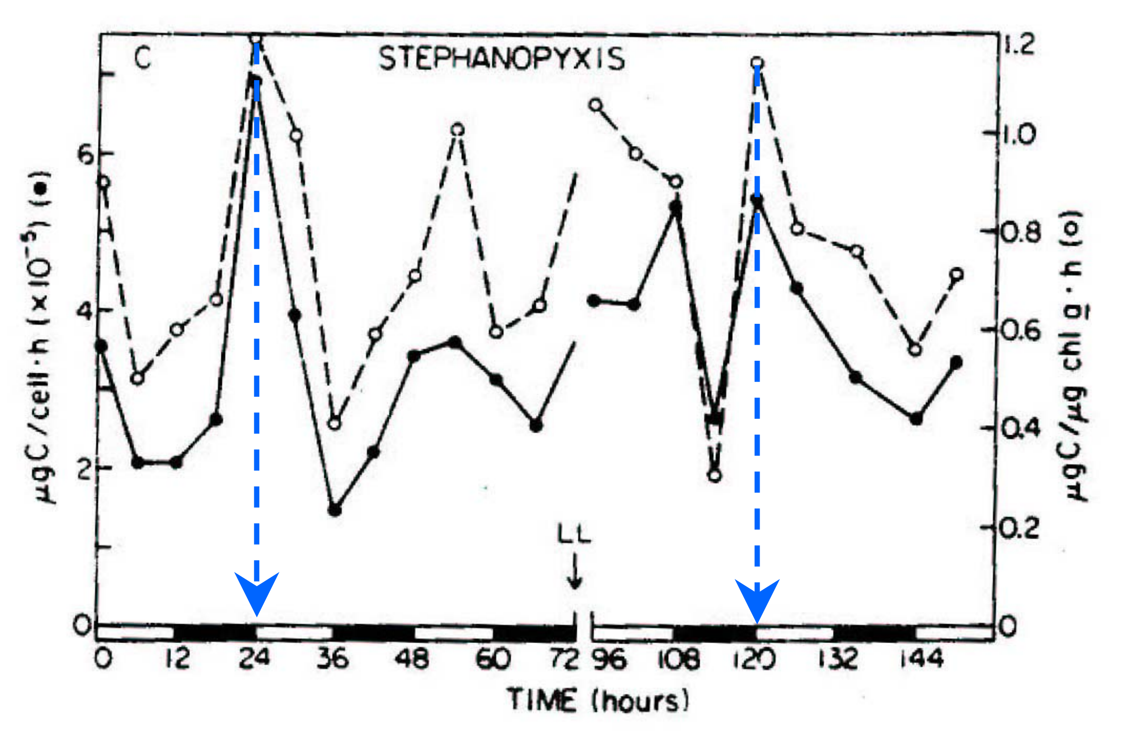
Diel variations in the photosynthetic parameters of *Prochlorococcus sp.*

Marcel Babin, Flavienne Bruyant
et al.

Starting point : a number of facts

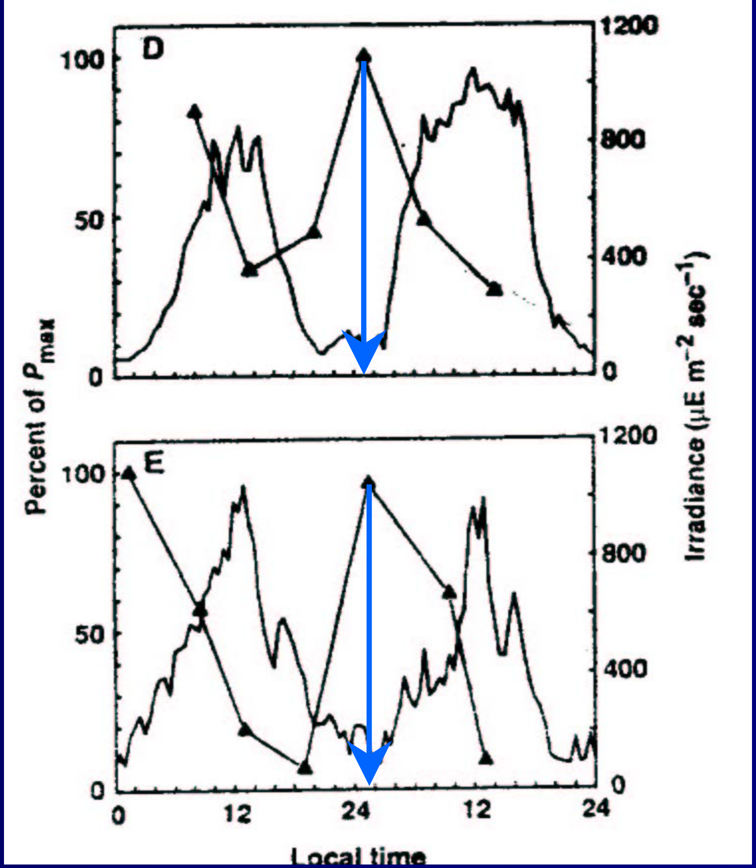
1. Diel variations in both α^B and P^B_{max} have been observed in numerous studies over the last 3 decades, and variation patterns have been observed.

Starting point : a number of facts



P^B_{max} peaks in the morning (Harding et al. 1981)

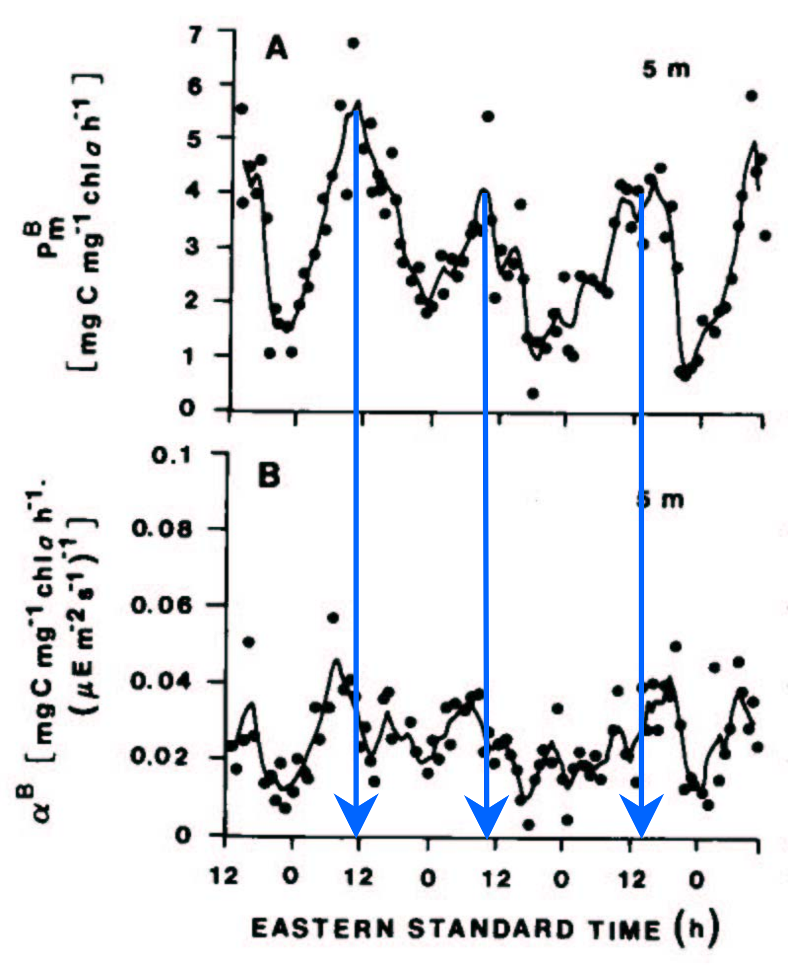
Starting point : a number of facts



P^B_{max} peaks in the middle of the night

(Rivkin & Putt 1987)

Starting point : a number of facts



P^B_{max} peaks in the middle of the day

(Vandevelde et al. 1989)

Starting point : a number of facts

2. α^B diel changes often parallel those of P^B_{max}, which suggests that photoacclimation is not or not only the cause

Starting point : a number of facts

3. Harding et al. (1981) observed that the diel changes in photosynthetic parameters are damped when approaching the stationary (non-dividing) phase in batch culture

⇒ The cell cycle may be a cause

Starting point : a number of facts

4. Putt and Prézelin (1988) found that batch cultures of non-dividing diatoms exhibit significant diel variations in $P^B{}_{max}$

⇒ Light may be a cause

Starting point : a number of facts

5. Rivkin and Putt (1987) noticed that P^B_{max} peaks by day when midday irradiance is low to moderate, and by night when midday irradiance is high

⇒ Both the cell cycle and light may be the causes

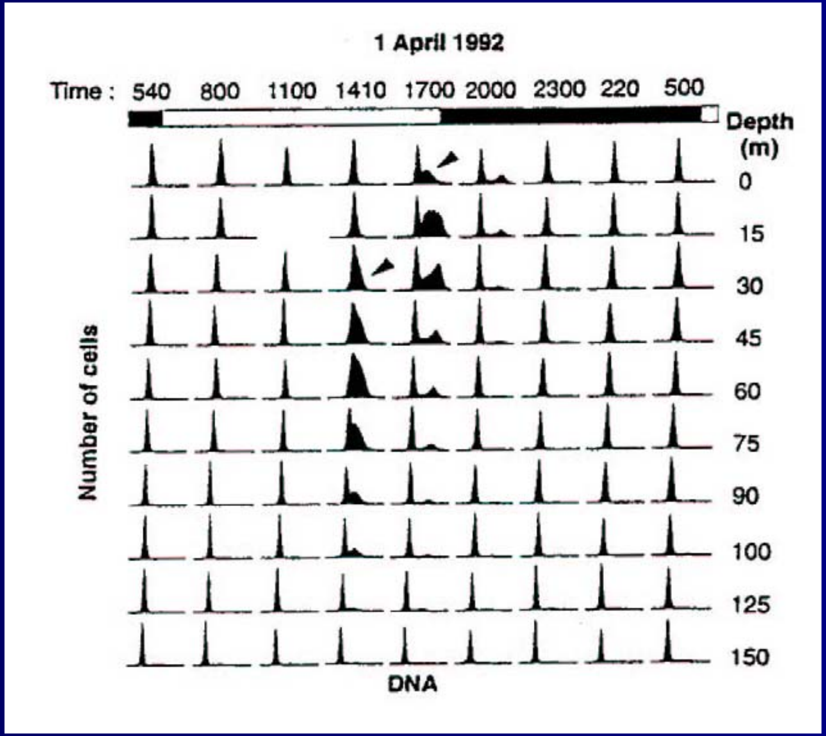
Question

What are the respective roles of light and the cell cycle in the diel variations of photosynthetic parameters ?

Methods : Choice of a species for our experiment

Cell division within natural *Prochlorococcus sp.* populations is synchronous

Methods : Choice of a species for our experiment



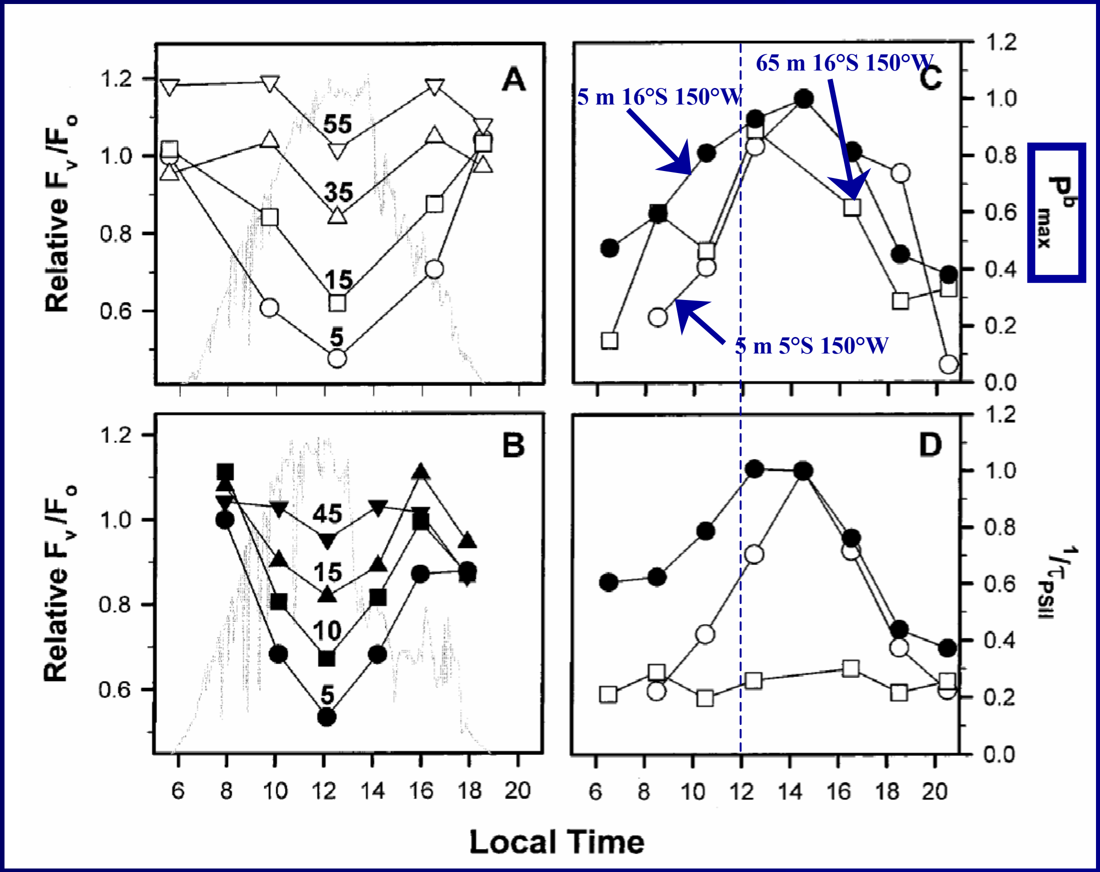
In the Equatorial Pacific, *Prochlorococcus* cells divides once a day around sunset

(Vaulot et al. 1995)

Methods : Choice of a species for our experiment

Prochlorococcus sp. does show diel changes in photosynthetic parameters in nature

Methods : Choice of a species for our experiment

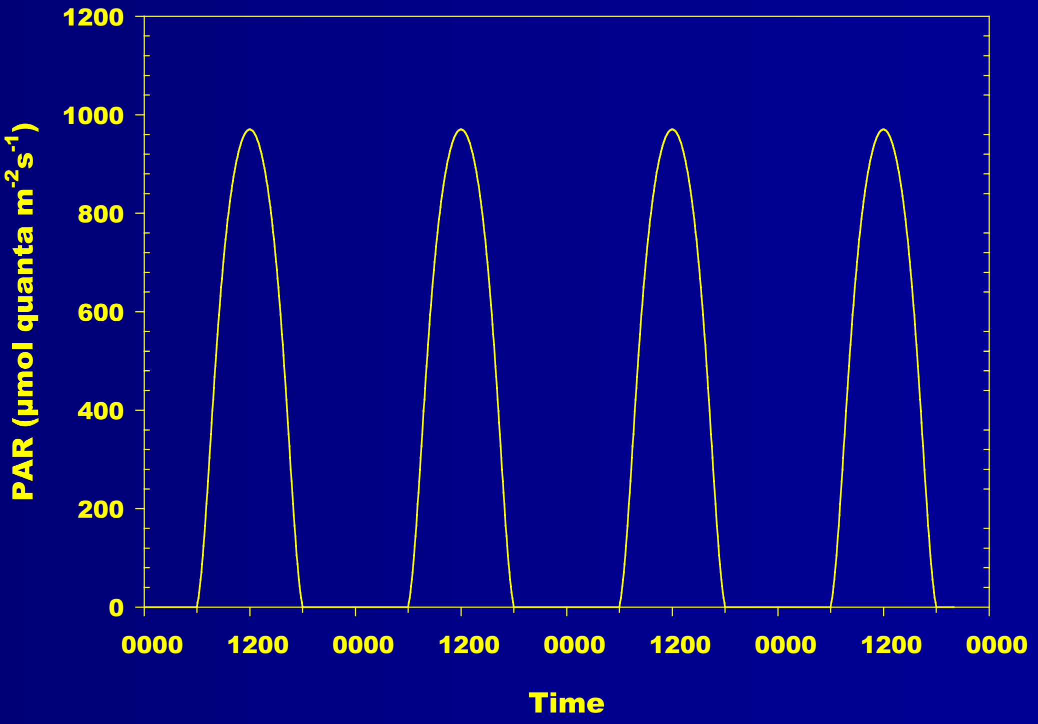


Subtropical Pacific

Behrenfeld et al. (1998)

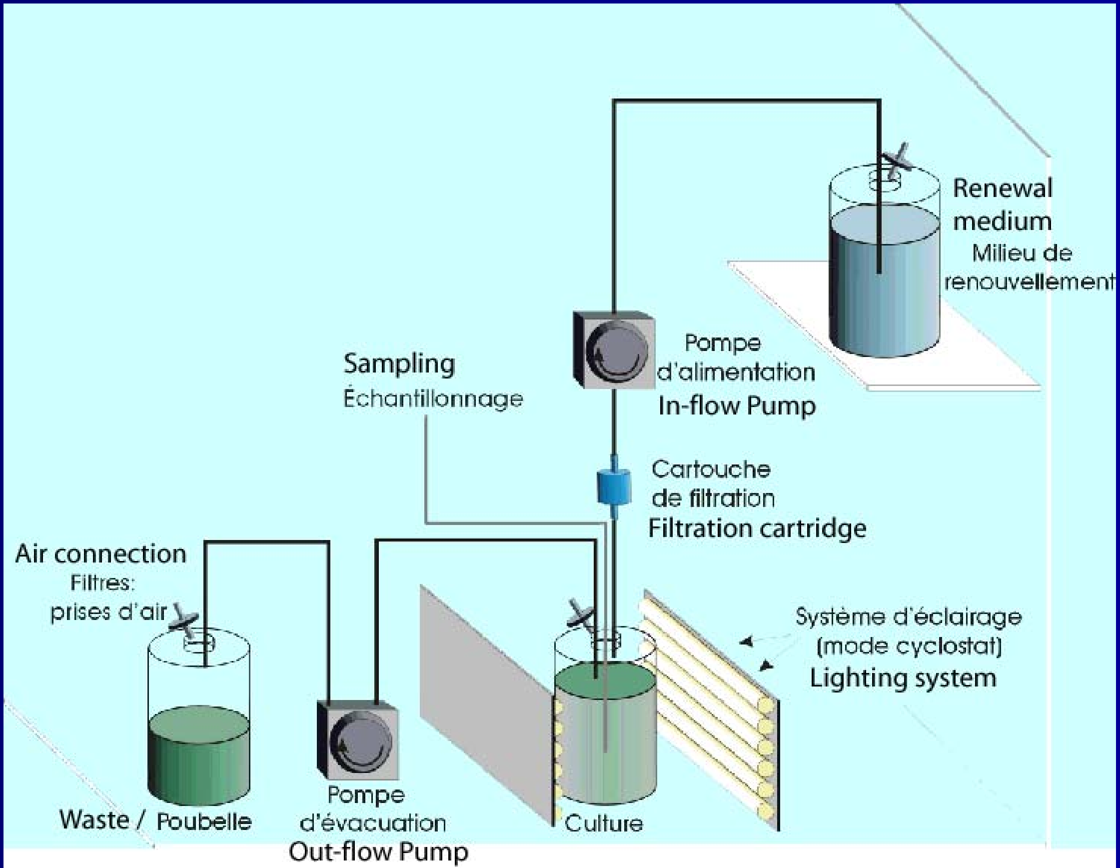
Methods : Experimental plan

- 12:12 light cycle
- Maximum PAR : 970 μmol photons m^{-2} s^{-1}
- 2 Turbidostat



Methods : Experimental setup

- 10 L
- Acclimated during 2 weeks
- Axenic
- Duplicate



Described in Bruyant et al. (2001)

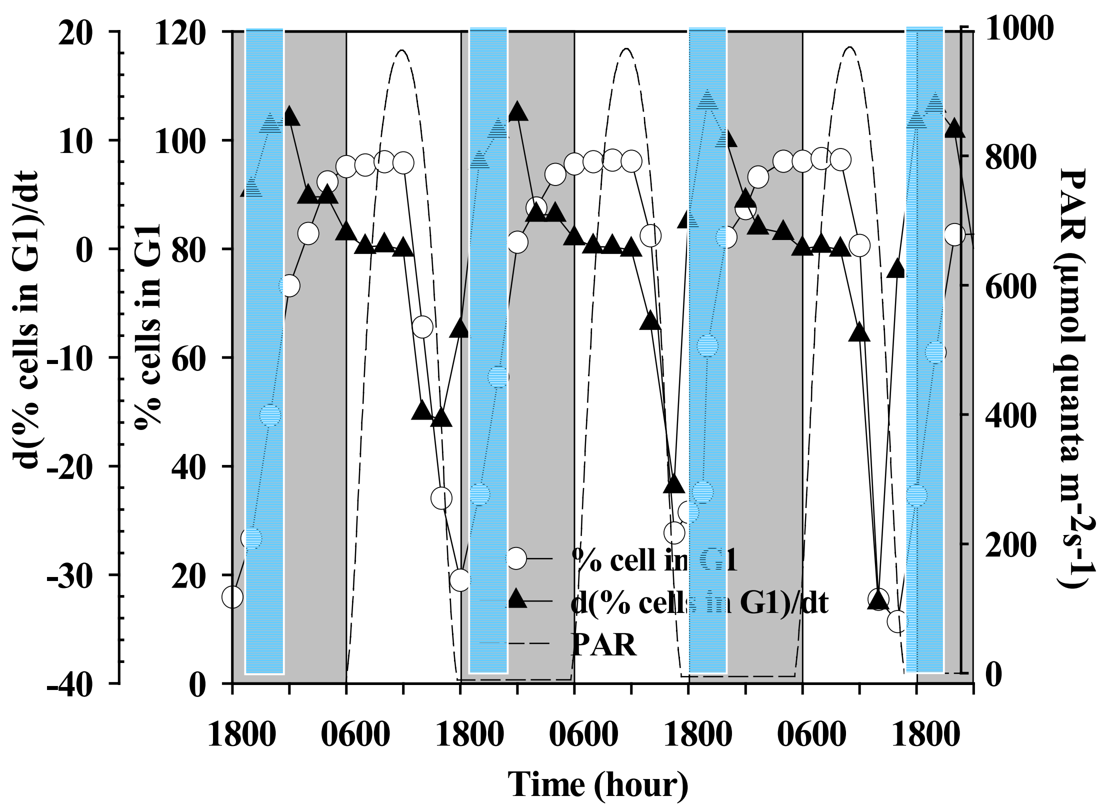
Methods : Measured variables

- F_o, F_m, σ_{PS2}
- α^B, P^B_{max}
- $a(\lambda)$
- Pigments
- Cell count (flow cytometry)
- RNA transcription (psbA, pcbA, rbcL)

Methods : Sampling strategy

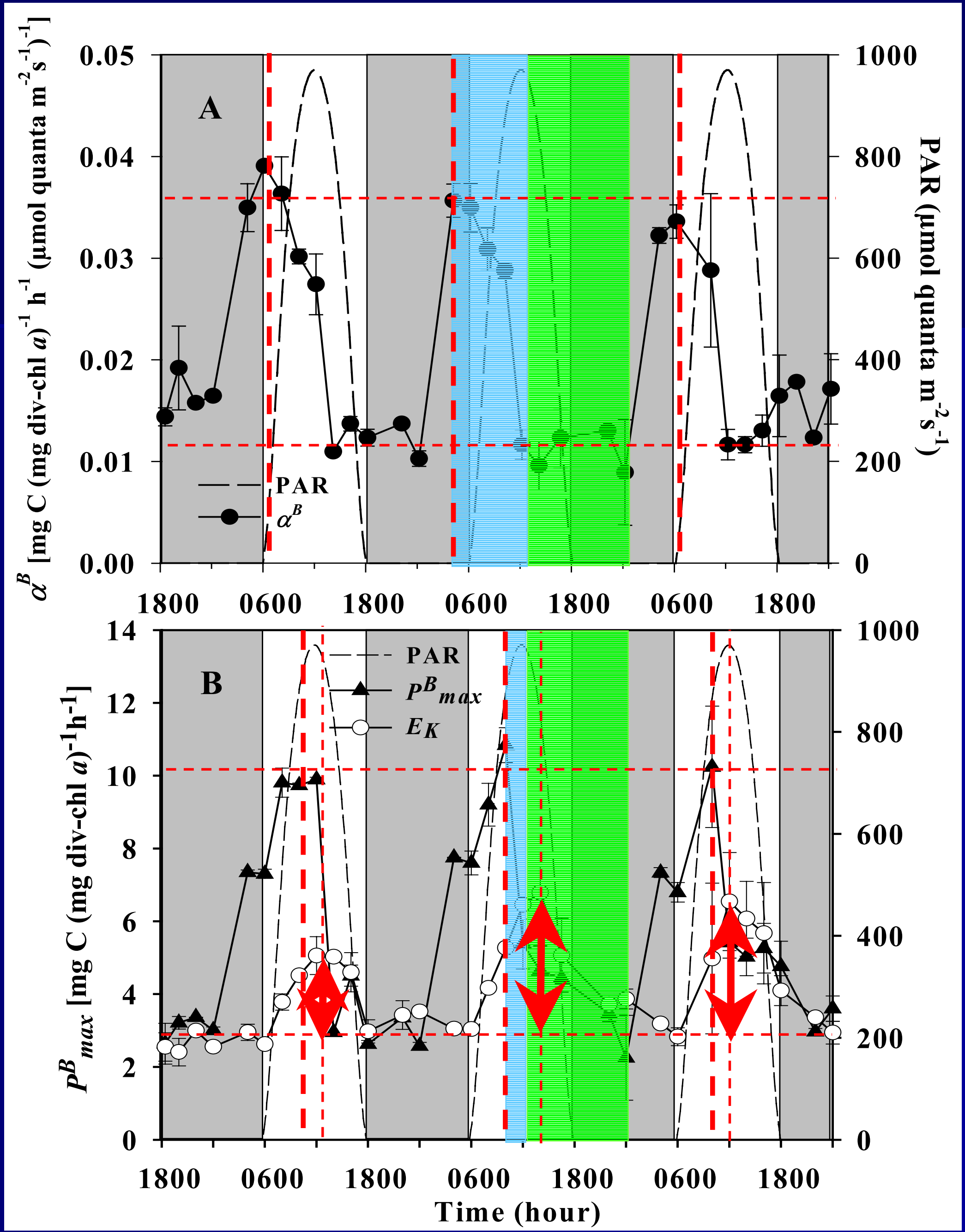
- **Turbidostat 1 :** sampling every 2nd hour for cell counts, pigments, absorption, PvsE, and variable fluorescence
- **Turbidostat 2 :** sampling every 4th hour for cell counts, variable fluorescence and RNA transcription
- Duration of the experiment : 4 days

Results



⇒ Cell division mostly occurs between 20:00 and 00:00

Results


A
B
0.05
0.04
0.03
0.02
0.01
0.00
1000
800
600
400
200
0
α^B [mg C (mg div-chl *a*)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$]
PAR (μmol quanta m^{-2} s^{-1})
PAR
α^B
1800
0600
1800
0600
1800
0600
1800
14
12
10
8
6
4
2
0
P^B_{max} [mg C (mg div-chl *a*)$^{-1}$h^{-1}]
PAR
P^B_{max}
E_K
Time (hour)

Results : α^B variations

Mean absorption coefficient [m^2 (mg chl)$^{-1}$]

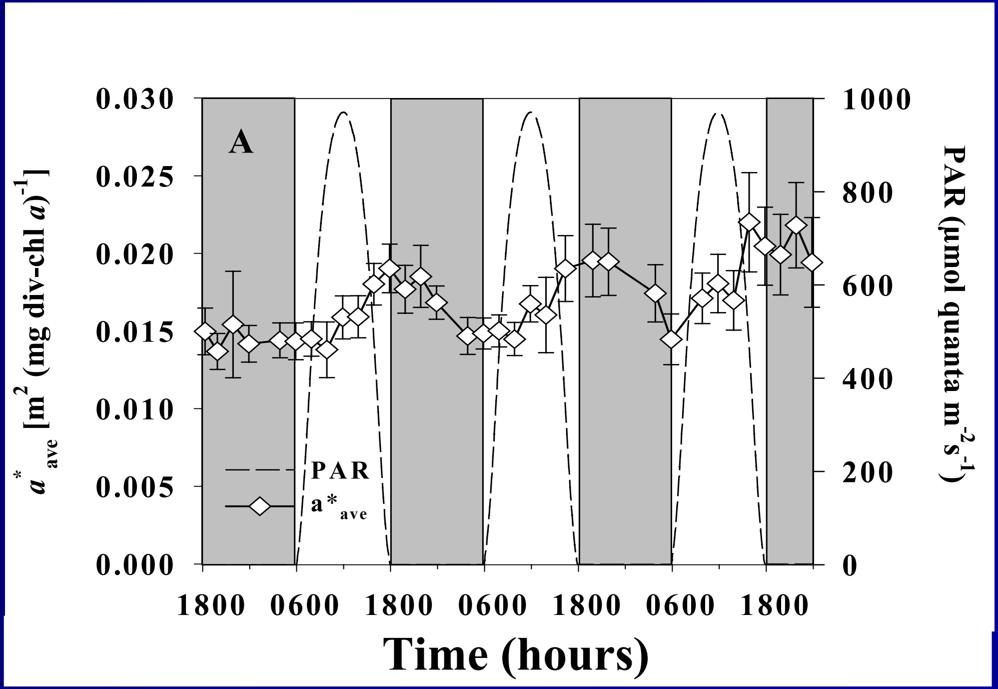
$$\alpha^B = \overline{a}^* \phi_{C\,max}$$

Maximum quantum yield of carbon fixation
[mol C (mol photons)$^{-1}$]

Is $\overline{a}^*$ a cause of α^B diel variations ?

Results : α^B variations

$$\alpha^B = \bar{a}^* \phi_{C\,max}$$



Is $\bar{a}^*$ a cause of α^B diel variations ?

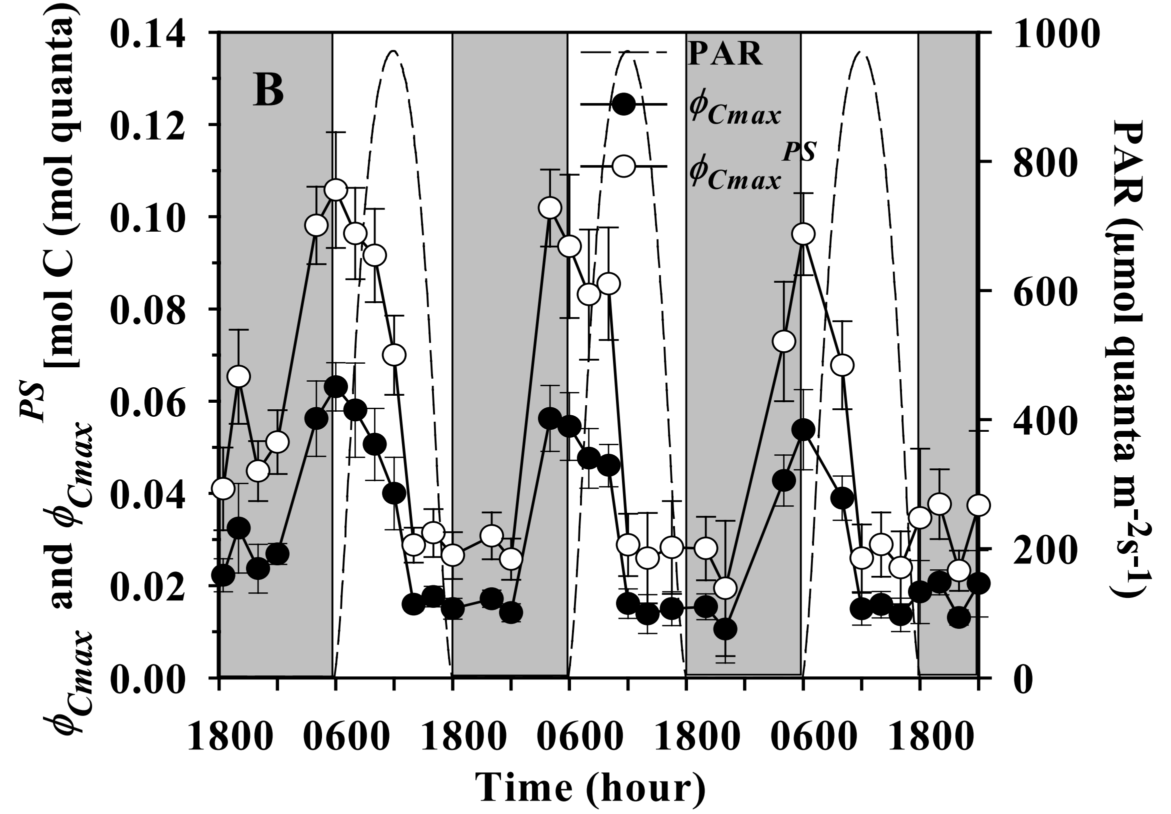
$\Rightarrow$ No!

Results : α^B variations

$$\alpha^B = \overline{a} * \phi_{C\,max}$$

Is $\phi_{C\,max}$ a cause of α^B diel variations ?

Results : α^B variations



Is $\phi_{C\,max}$ a cause of α^B diel variations ?

YES !

Results : α^B variations

of RC per chl (e- chl-1)

Effective absorption cross section (m^2 photon^{-1})

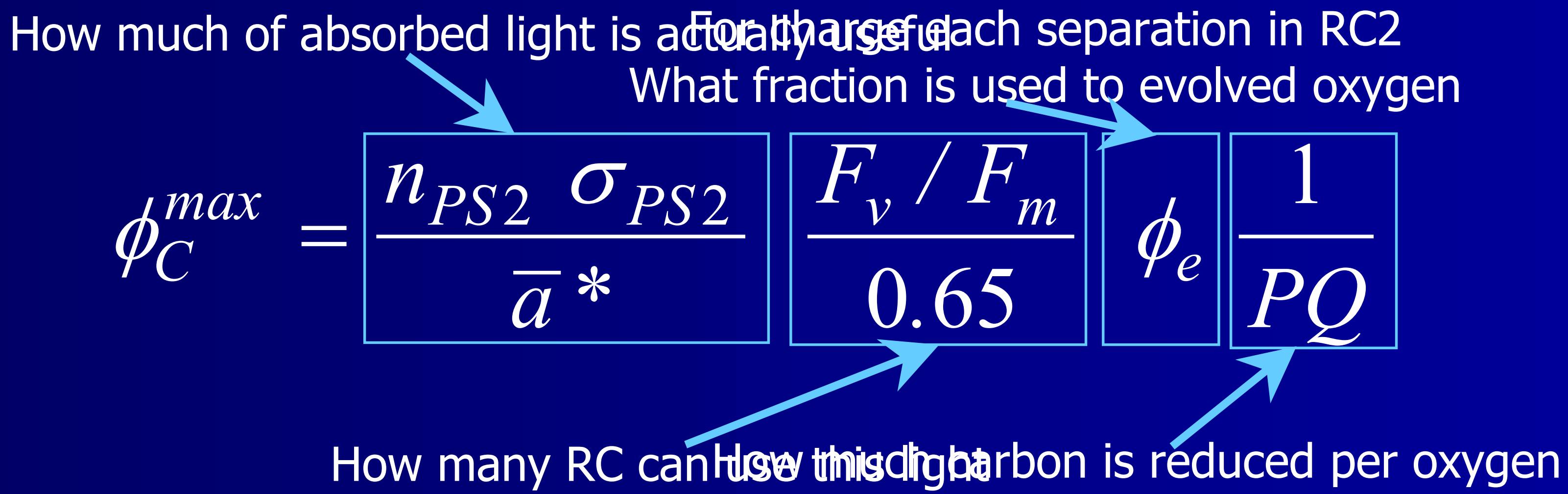
Yield of O_2 evolution per electron (O_2 per e^-)

$$\phi_C^{max} = \frac{n_{PS2}\ \sigma_{PS2}}{\overline{a}\,*} \boxed{\frac{F_v / F_m}{0.65}}\ \phi_e \frac{1}{PQ}$$

Fraction of functional RC2

Photosynthetic quotient (O_2 per C)

Results : α^B variations



How much of absorbed light is actually useful

For charge each separation in RC2

What fraction is used to evolved oxygen

$$\phi_C^{max} = \boxed{\frac{n_{PS2}\ \sigma_{PS2}}{\overline{a}^*}}\ \boxed{\frac{F_v / F_m}{0.65}}\ \boxed{\phi_e}\ \boxed{\frac{1}{PQ}}$$

How many RC can use this light

How much carbon is reduced per oxygen

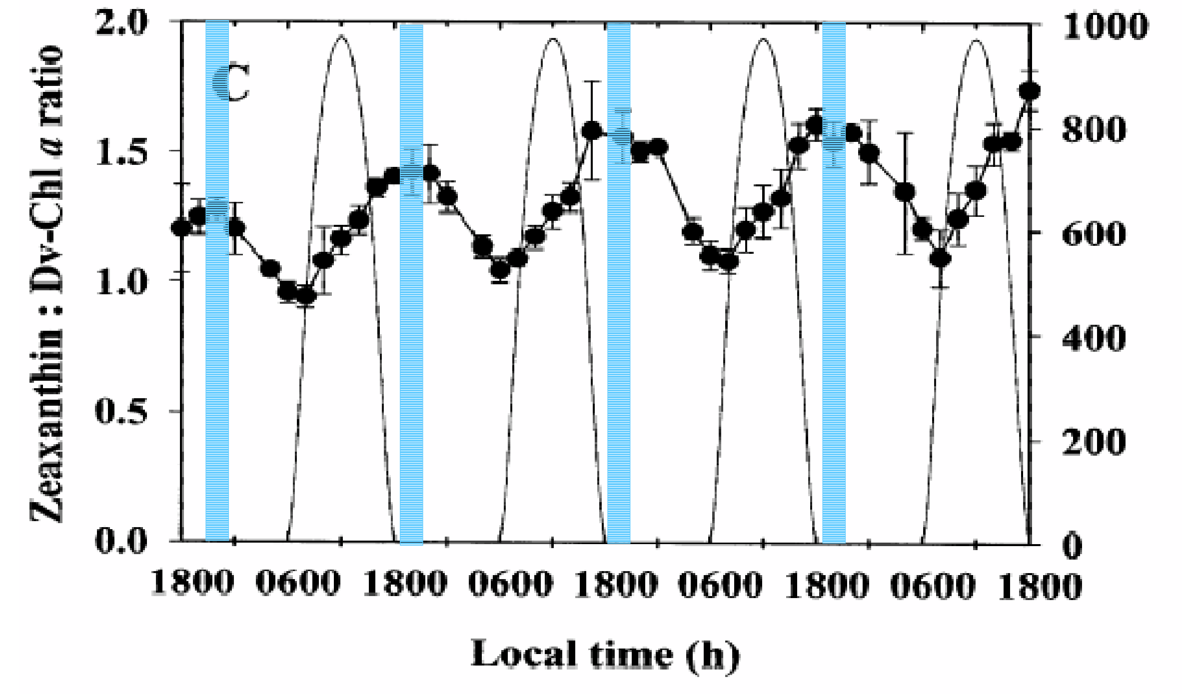
There are several energy leaks between light absorption and C fixation !

Results : α^B variations

$$\phi_C^{max} = \boxed{\frac{n_{PS2}\ \sigma_{PS2}}{\bar{a}^*}}\ \frac{F_v / F_m}{0.65}\ \phi_e\ \frac{1}{PQ}$$

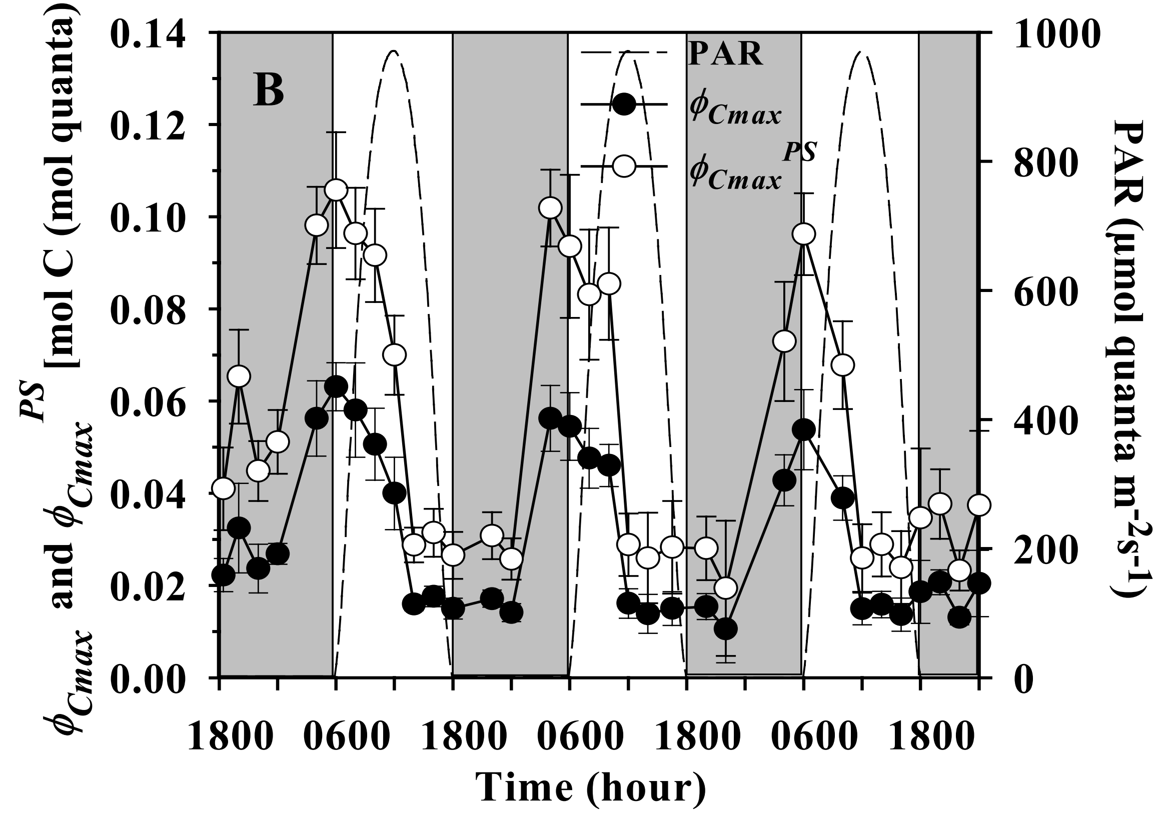
Does changes in this ratio occur due to zeaxanthin ?

Results : α^B variations



Claustre et al. (2002)

Results : α^B variations



Results : α^B variations

$$\phi_C^{max} = \boxed{\frac{n_{PS2}\ \sigma_{PS2}}{\bar{a}\,*}}\ \frac{F_v / F_m}{0.65}\ \phi_e\ \frac{1}{PQ}$$

Does changes in this ratio occur due to zeaxanthin ?

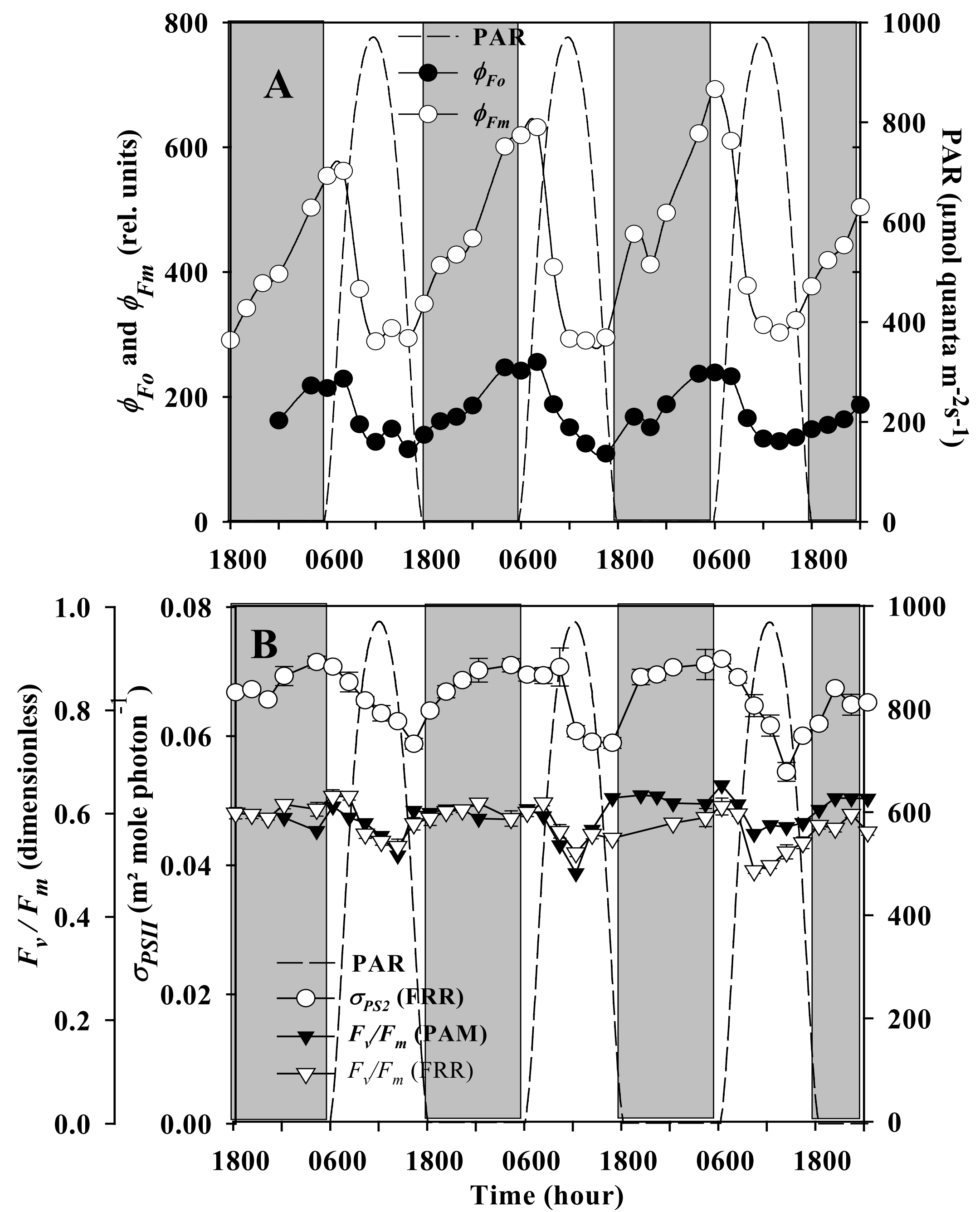
Not really !

Results : α^B variations

$$\phi_C^{max} = \boxed{\frac{n_{PS2}\ \sigma_{PS2}}{\bar{a}\,^*}}\ \frac{F_v / F_m}{0.65}\ \phi_e\ \frac{1}{PQ}$$

Does changes in this ratio occur due to changes in σ_{PS2} ?

Results


A
B
PAR
ϕ_{Fo}
ϕ_{Fm}
ϕ_{Fo} and ϕ_{Fm} (rel. units)
PAR (μmol quanta m^{-2}s^{-1})
0
200
400
600
800
1000
1800
0600
F_v / F_m (dimensionless)
σ_{PSII} (m² mole photon^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.02
0.04
0.06
0.08
σ_{PS2} (FRR)
F_v/F_m (PAM)
F_v/F_m (FRR)
Time (hour)

Results : α^B variations

$$\phi_C^{max} = \boxed{\frac{n_{PS2}\ \sigma_{PS2}}{\bar{a}^*}}\ \frac{F_v / F_m}{0.65}\ \phi_e\ \frac{1}{PQ}$$

Does changes in this ratio occur due to changes in σ_{PS2} ?

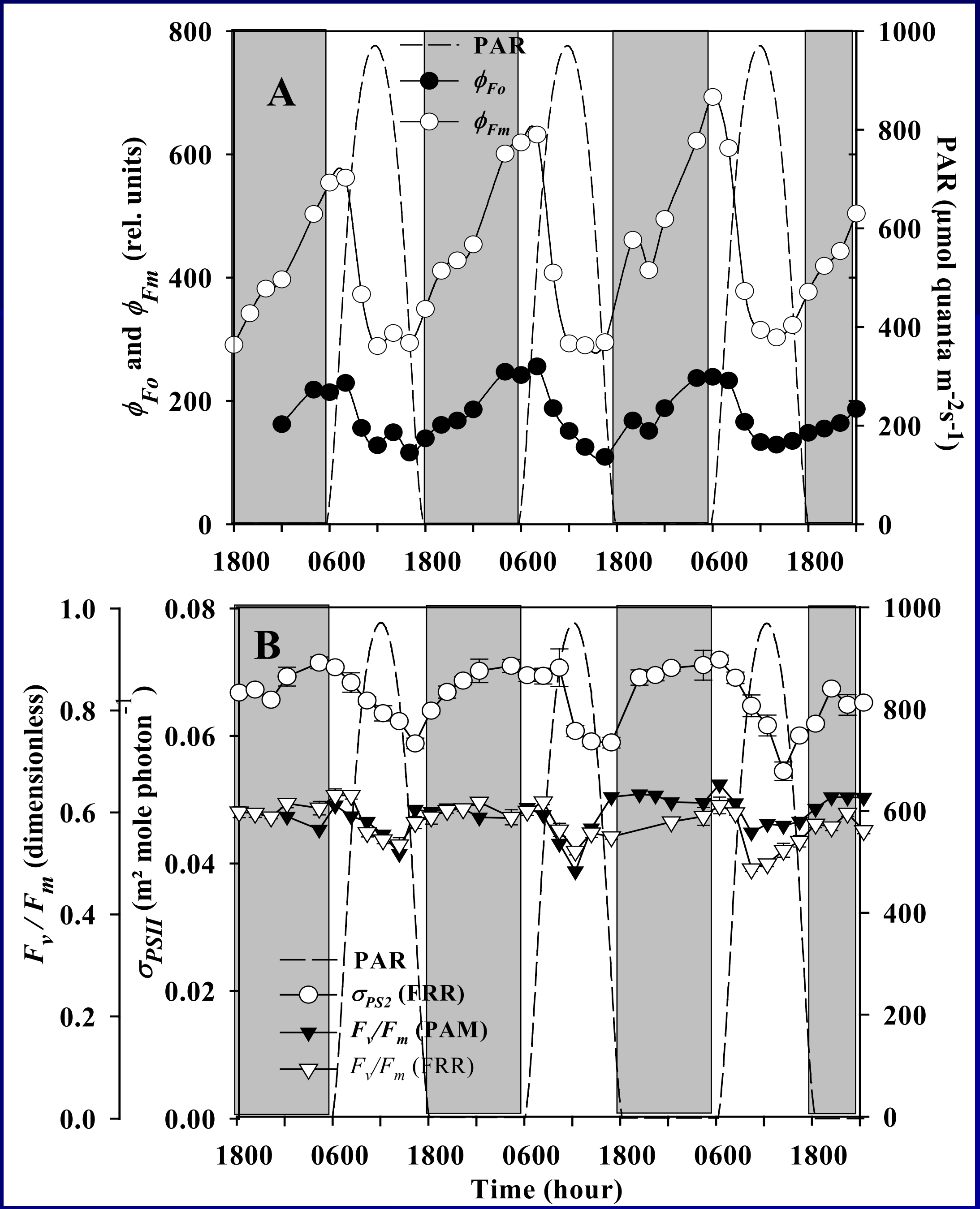
$\Rightarrow$ Unclear !

Results : α^B variations

$$\phi_C^{max} = \frac{n_{PS2}\ \sigma_{PS2}}{\bar{a}\,*}\ \boxed{\frac{F_v / F_m}{0.65}}\ \phi_e\ \frac{1}{PQ}$$

Is this ratio responsible for ϕ_{Cmax} variations ?

Results


A
PAR
ϕ_{Fo}
ϕ_{Fm}
ϕ_{Fo} and ϕ_{Fm} (rel. units)
PAR (µmol quanta m^{-2}s^{-1})
0
200
400
600
800
1000
1800
0600
B
PAR
σ_{PS2} (FRR)
F_v/F_m (PAM)
F_v/F_m (FRR)
F_v / F_m (dimensionless)
σ_{PSII} (m² mole photon^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.02
0.04
0.06
0.08
Time (hour)

Results : α^B variations

$$\phi_C^{max} = \frac{n_{PS2}\ \sigma_{PS2}}{\overline{a}\,^*} \boxed{\frac{F_v / F_m}{0.65}} \phi_e \frac{1}{PQ}$$

Is this ratio responsible for ϕ_{Cmax} variations ?

$\Rightarrow$ Not much !

Results : α^B variations

$$\phi_C^{max} = \frac{n_{PS2}\ \sigma_{PS2}}{\overline{a}\,*}\ \frac{F_v / F_m}{0.65}\ \phi_e\ \frac{1}{PQ}$$

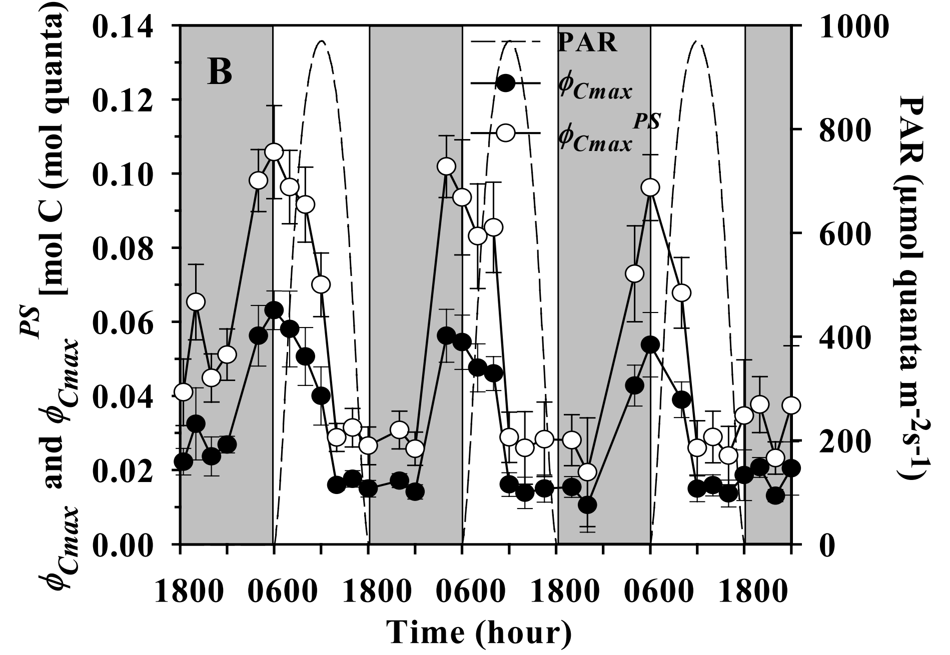
We made no measurement that allows us to assess the impact of this term

Results : α^B variations

$$\phi_C^{max} = \frac{n_{PS2}\ \sigma_{PS2}}{\overline{a}\,*} \ \frac{F_v / F_m}{0.65} \ \phi_e \ \frac{1}{PQ}$$

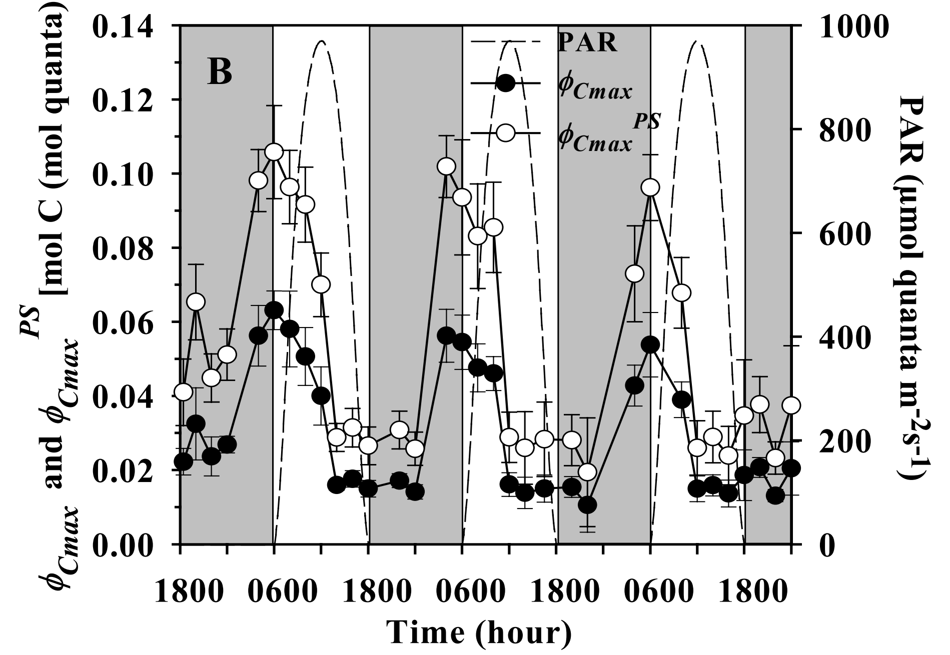
We expect this term to equal 1 for this experiment

Results : α^B variations



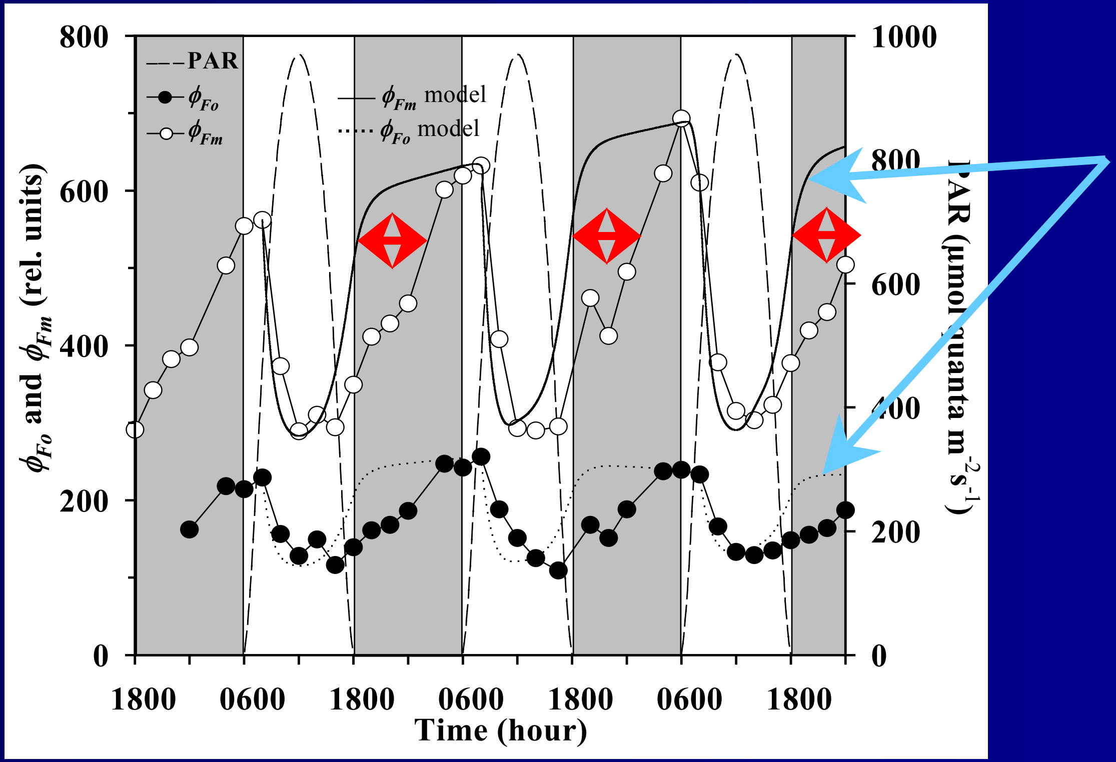
The early drop in α^B, ϕ_{Cmax}, F_o and F_m seems to be due to non-photochemical quenching (e.g. to light!) of unknown origin

Results : α^B variations



What about the recovery ?

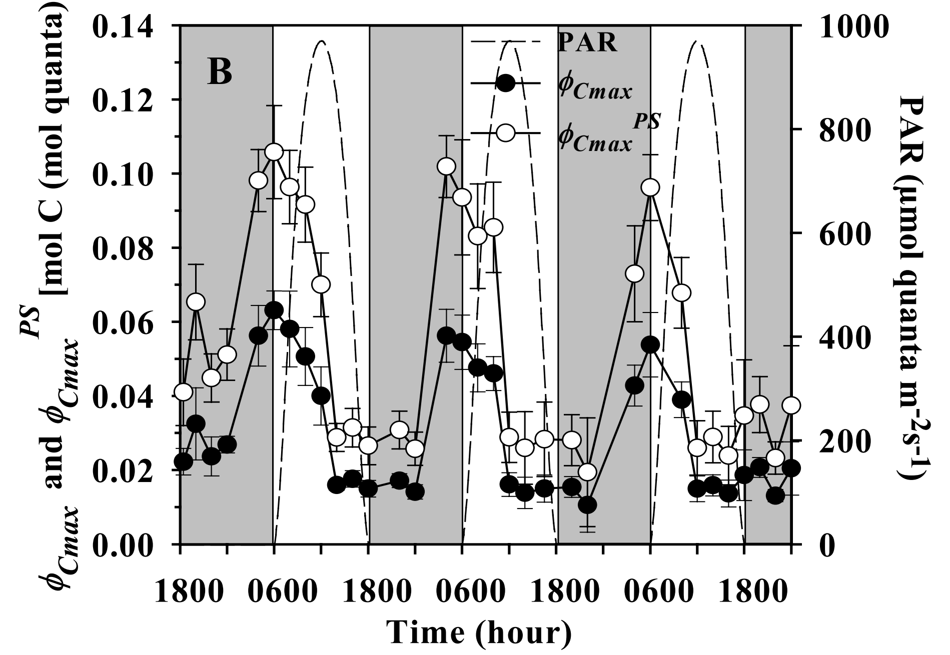
Results



Model modified from Neale (1987) with :

- K_r determined in the dark, around noon
- K_q determined from model fitting on the morning data

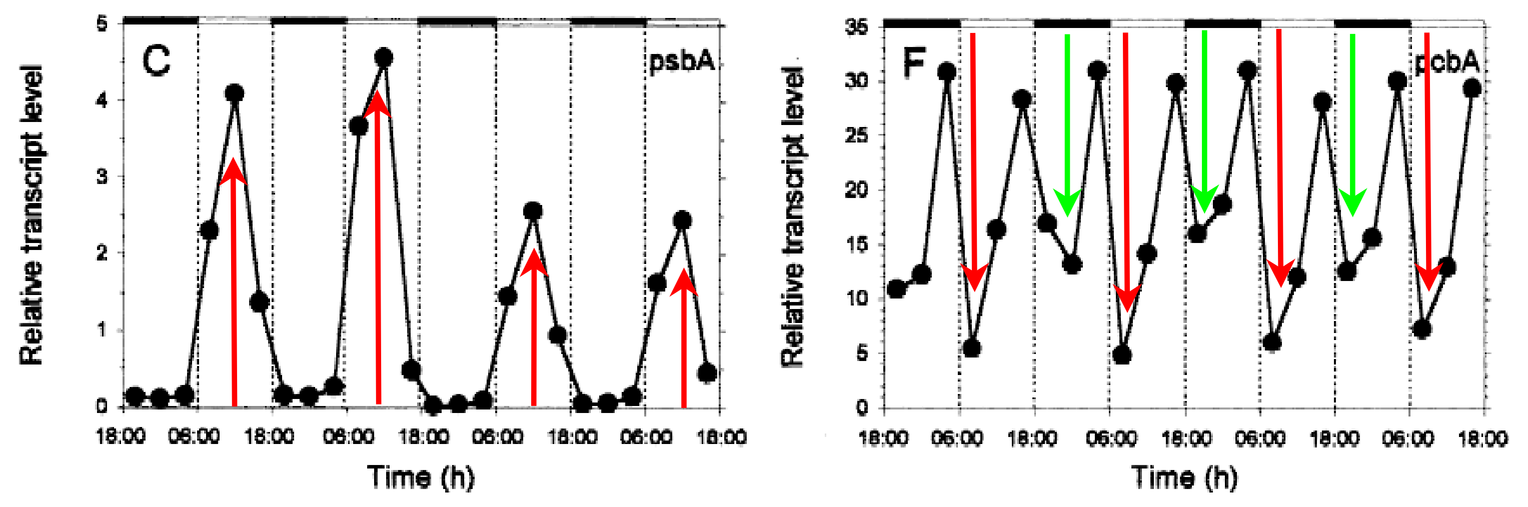
Results : α^B variations



Cell division is responsible for slow recovery ?

Results : α^B variations

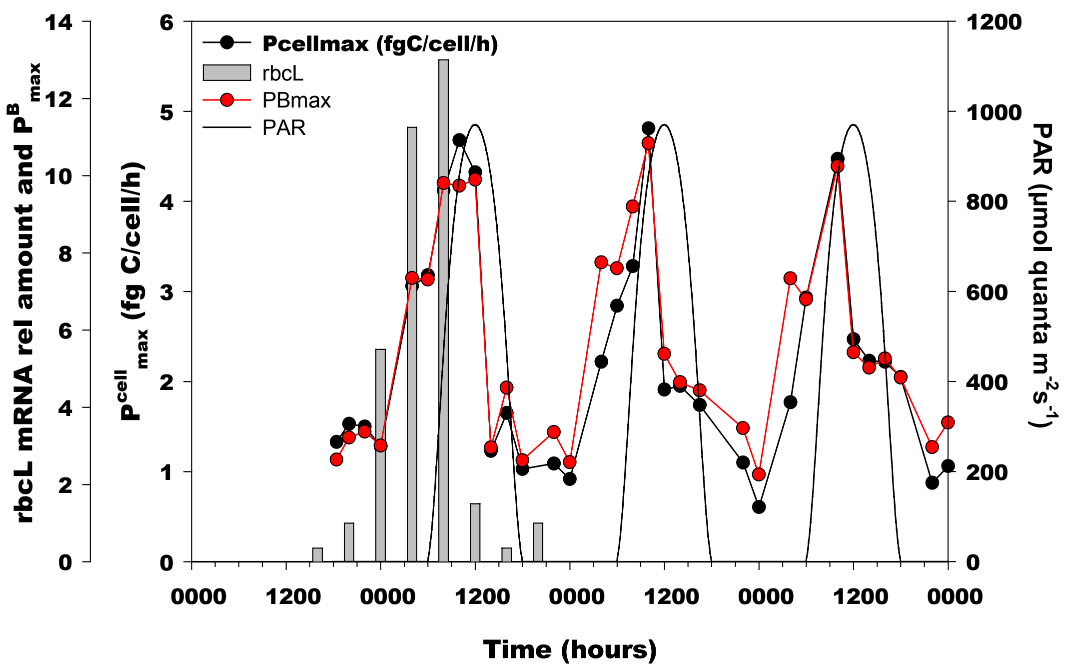
Interesting observations (Garczarek et al. 2001) :



Reaction centre protein (D1)

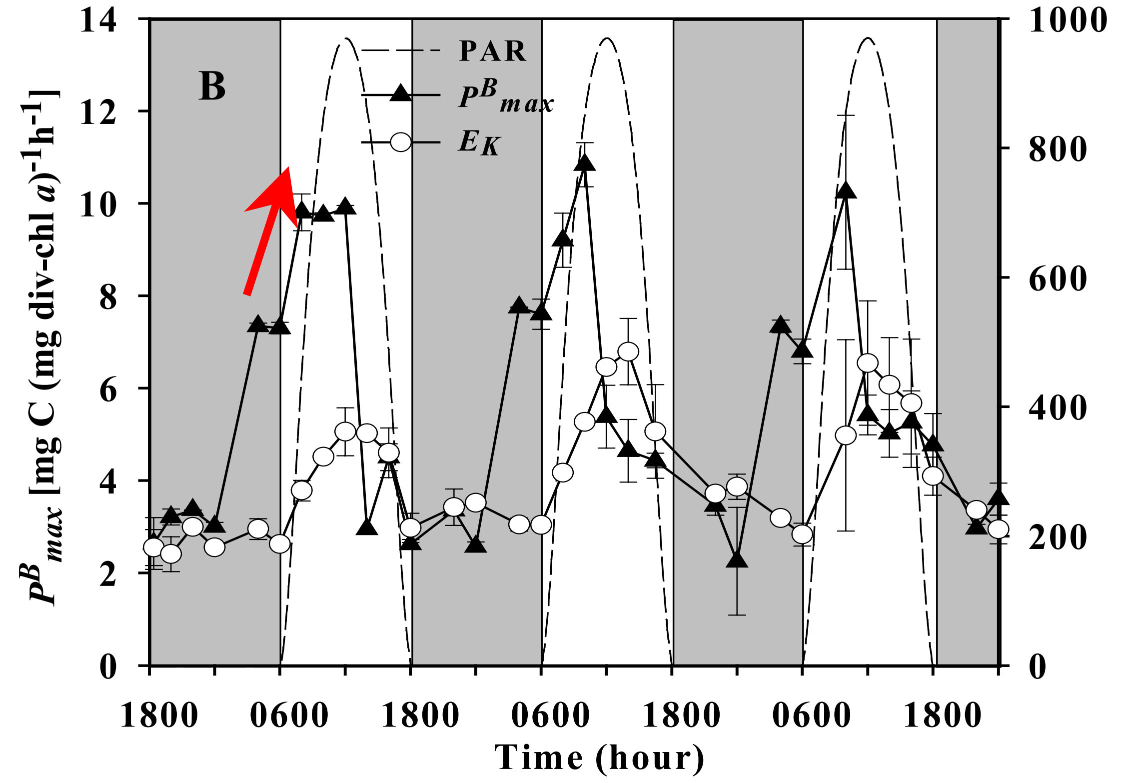
Major light-harvesting complex of PS2

Results : P^B_{max} variations



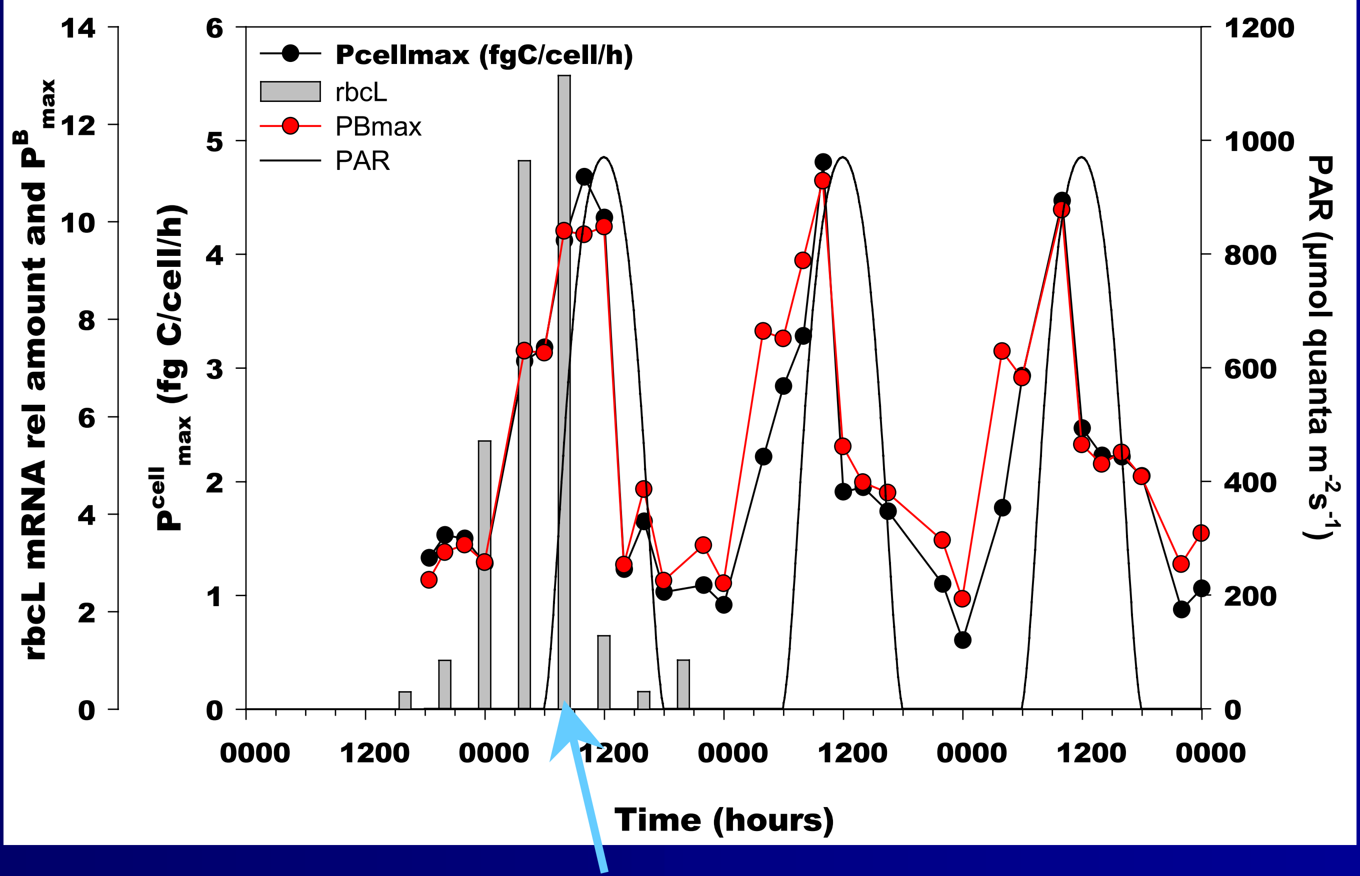
P^{cell}_{max} show mostly the same variation pattern as P^B_{max}, so P^B_{max} variations are not due to changes in chl per cell

Results : P^B_{max} variations



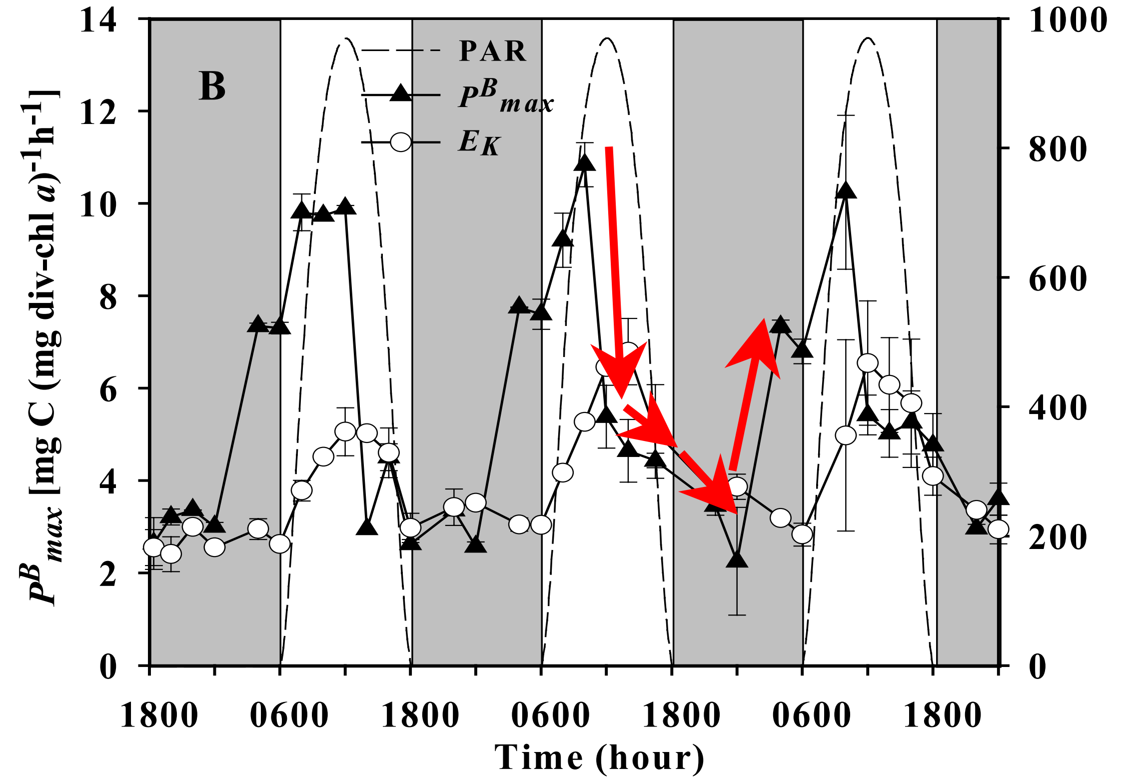
Light-dependent activation of Rubisco and/or synthesis of Rubisco ?

Results : P^B_{max} variations



Transcription for the large subunit of Rubisco

Results : $P^B{}_{max}$ variations

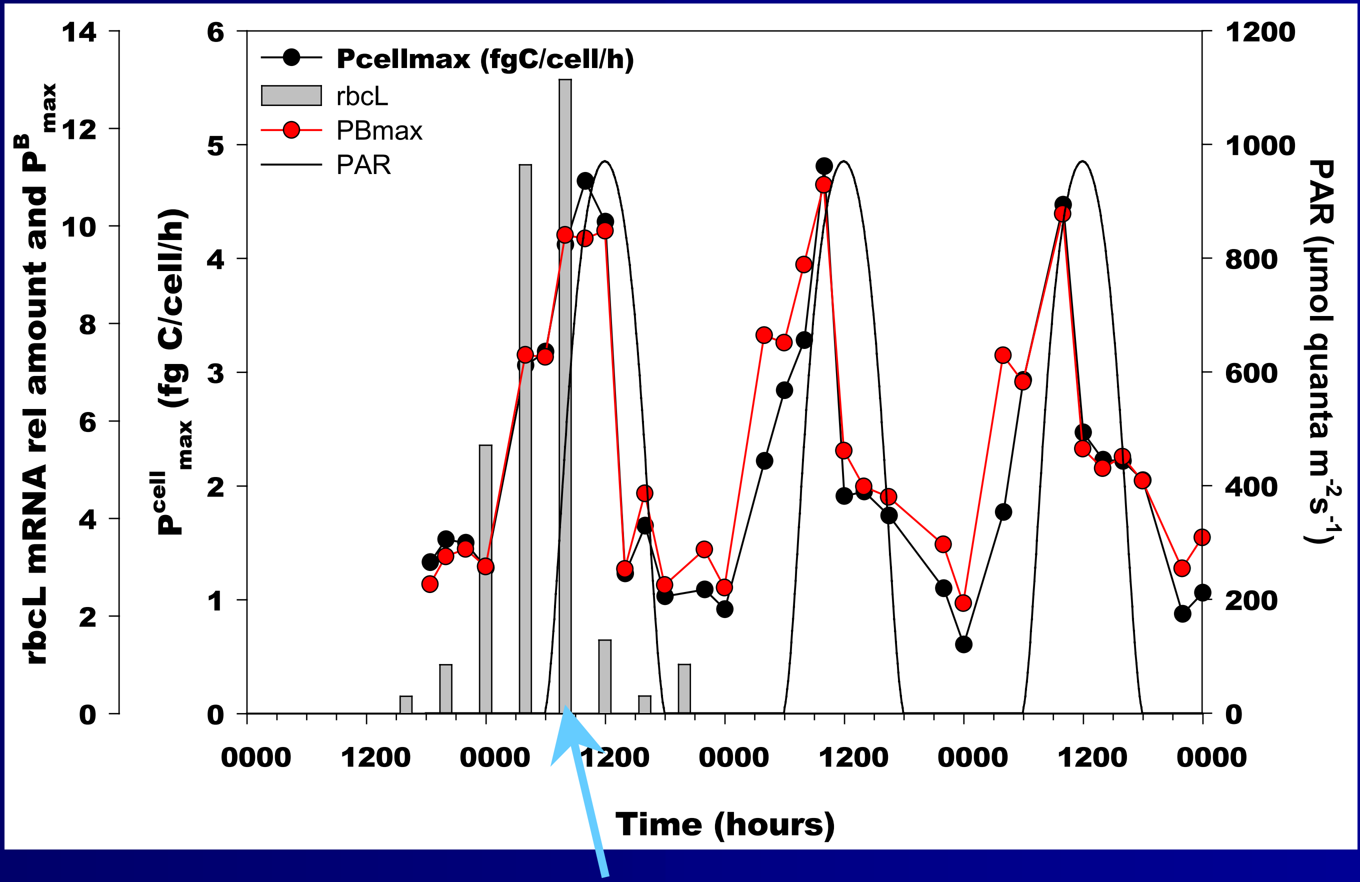


Alternative sinks for NADPH and ATP ? Photorespiration ?

Light-dependent activation of Rubisco ?

Synthesis of Rubisco ?

Results : P^B_{max} variations



Transcription for the large subunit of Rubisco

Conclusion

Our initial question :

What are the respective roles of light and the cell cycle in the diel variations of photosynthetic parameters ?

Conclusion

More specifically :

What caused diel variations in α^B during this experiment ?

$\Rightarrow$ Probably, light ! Energy dissipation related to non-photochemical quenching

$\Rightarrow$ May be, cell division : it may induce delay in recovery from quenching, and then contribute through protein synthesis after cell division

Conclusion

More specifically :

What caused diel variations in P^B_{max} during this experiment ?

⇒ Unclear : Rubisco synthesis and light dependent increase/decrease in activity ?

⇒ Unclear : alternative sinks for the products of light reactions ?

⇒ May be, cell division : it may also induce a decrease in Rubisco per cell, followed by an increase through sustained protein synthesis after cell division

Conclusion

A hypothesis :

Rivkin and Putt (1987) noticed that P^B_{max} peaks by day when midday irradiance is low to moderate, and by night when midday irradiance is high :

It may be that the light effect dominates under high irradiance, which would lead to maxima in photosynthetic parameters during the night (more or less as during this experiment),

and that a possible cell division effect dominates under low to moderate irradiance, which would lead to maxima by day (as often reported).

What may be the impact on primary production ?