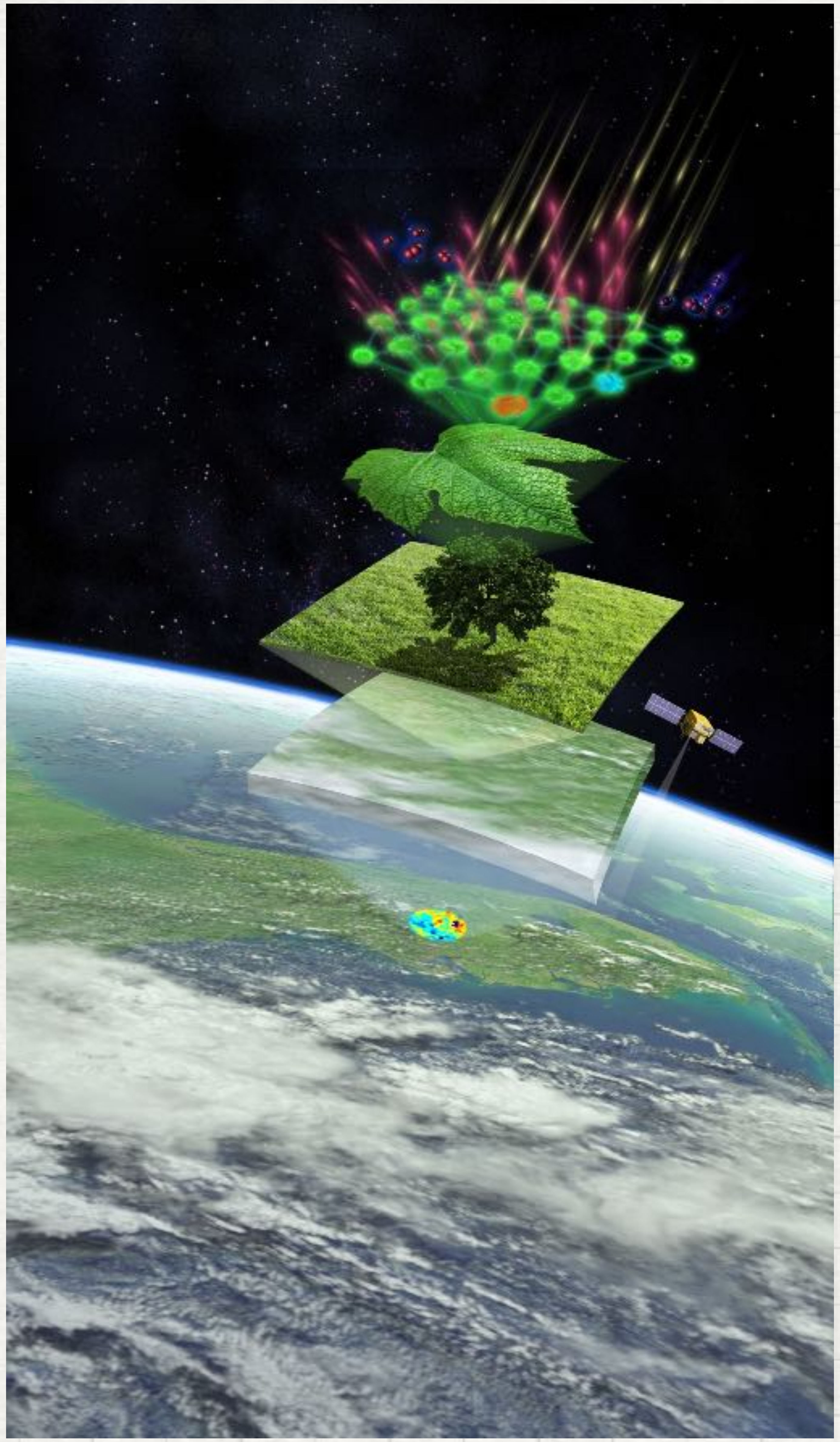
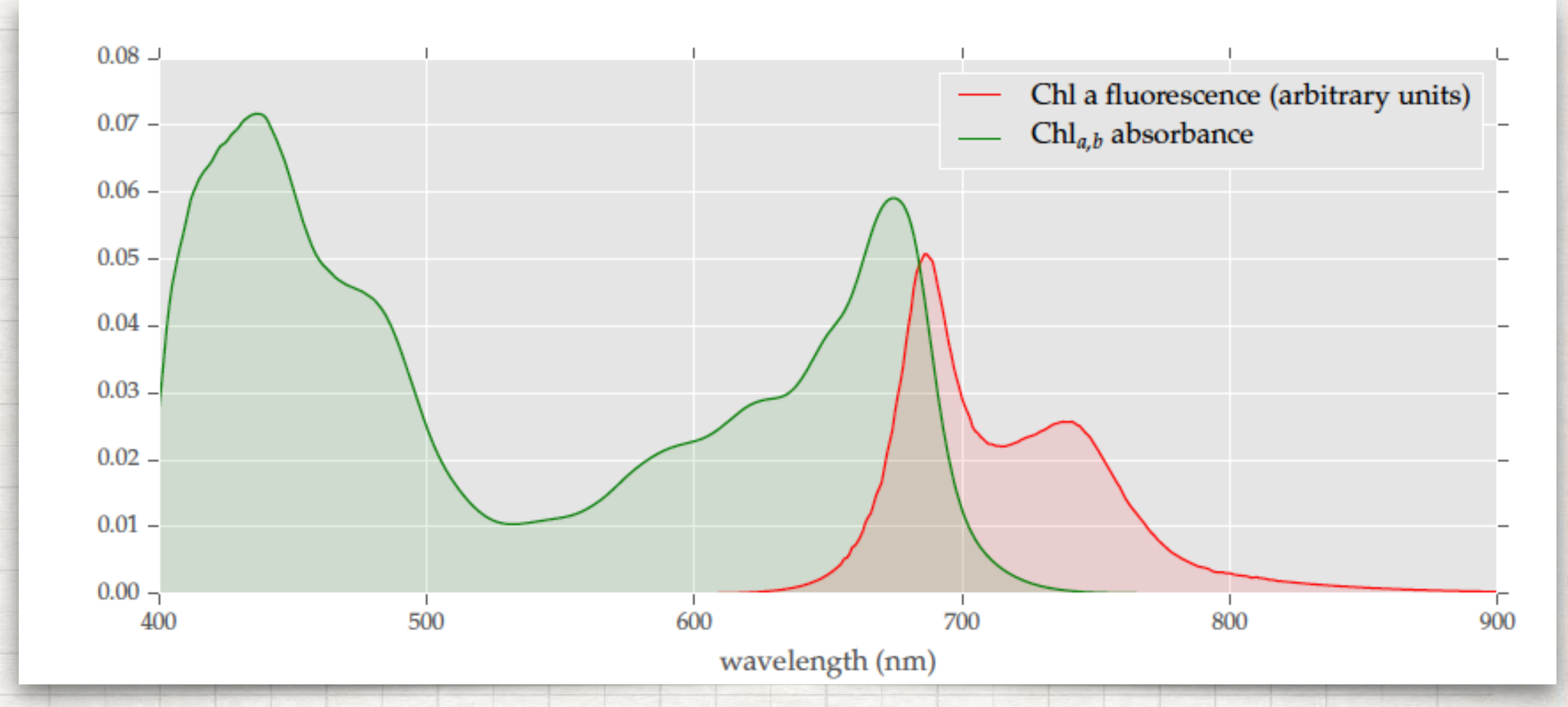


Canopy Structure, SIF and Photosynthetic Capacity

Joe Berry, Carnegie Inst. for Science



Separation of Reflected and Fluorescence Light

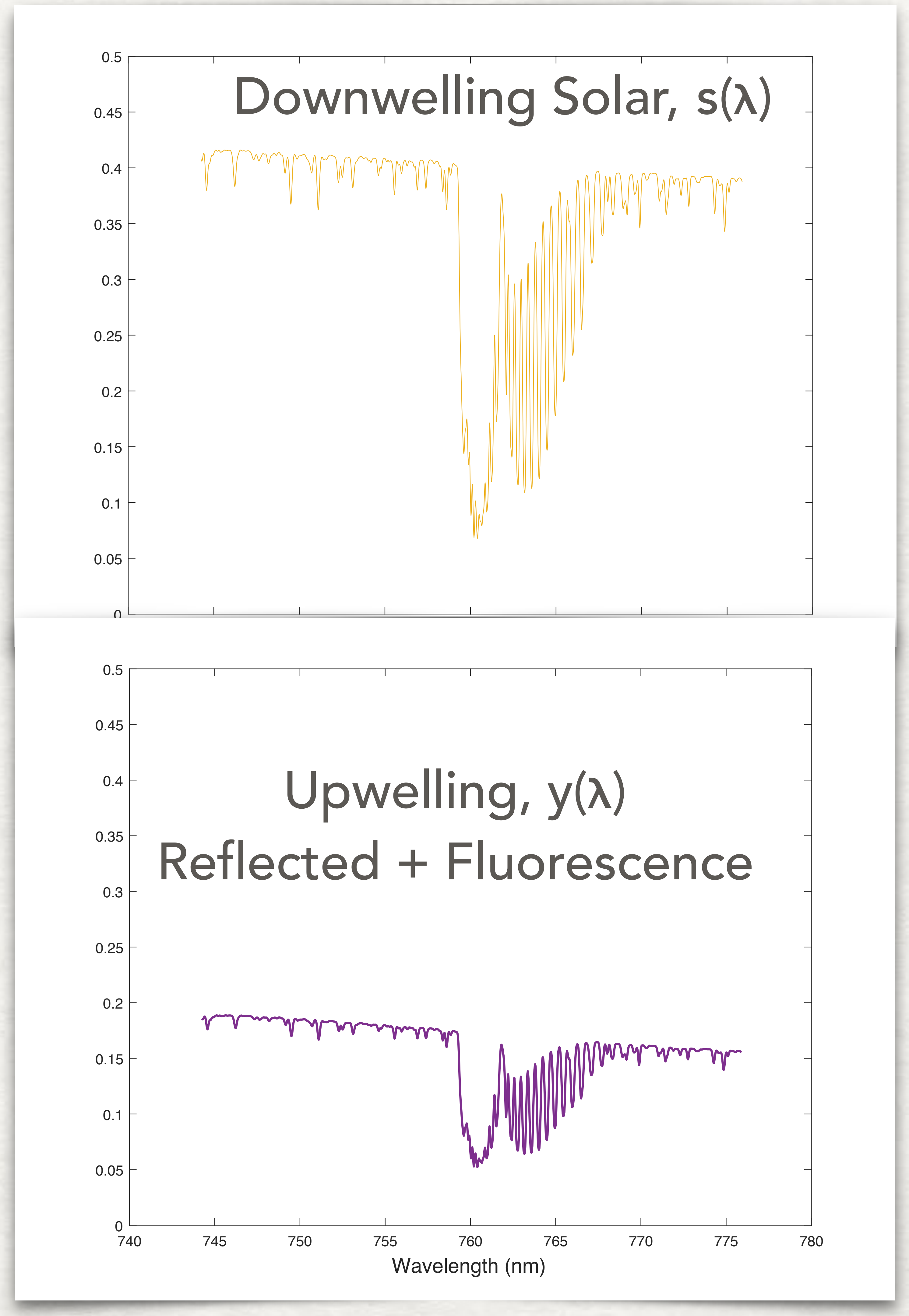
Forward Model

(a) Reflected light

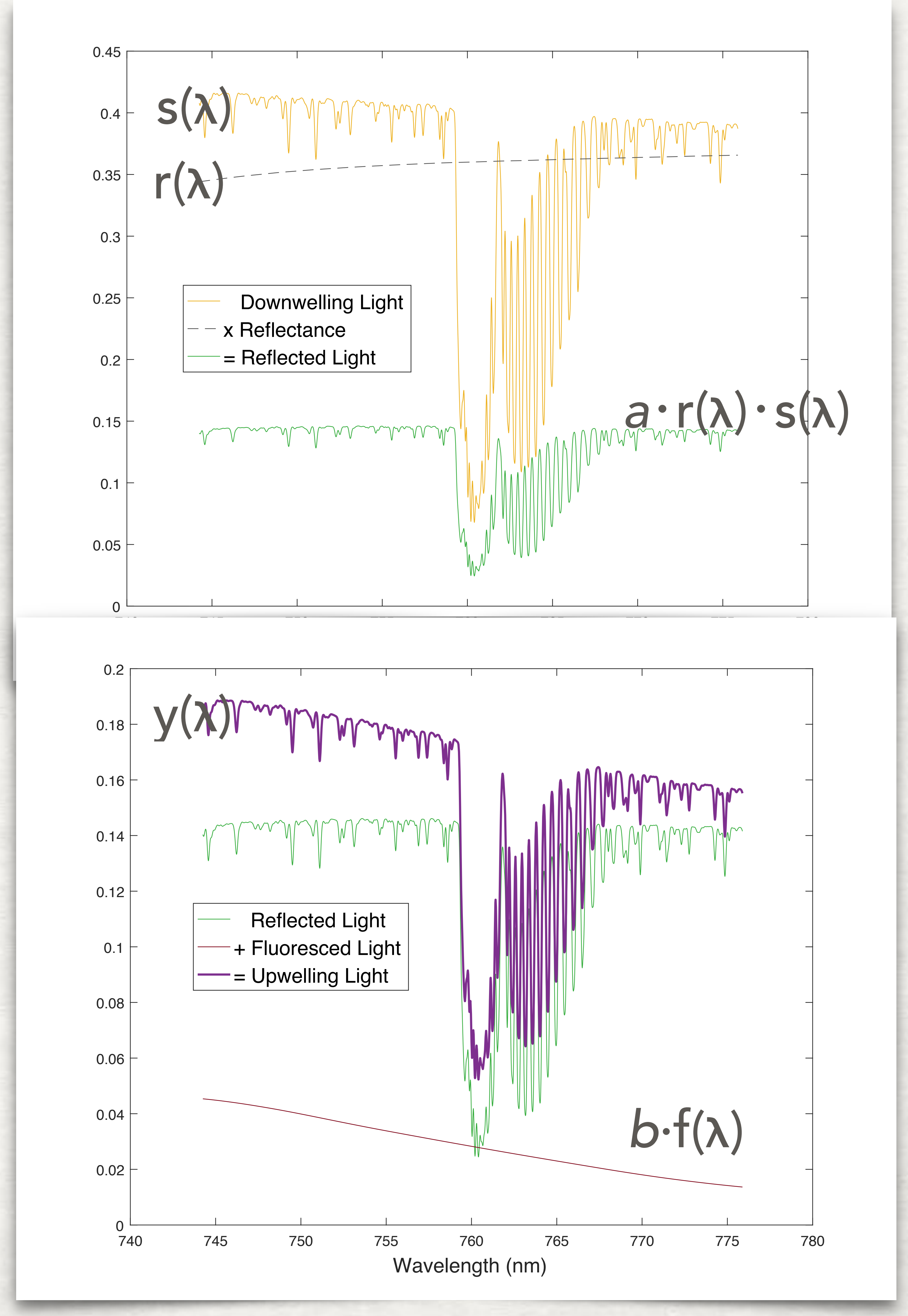
$$\mathrm{y}(\lambda) = a \cdot \mathrm{r}(\lambda) \cdot \mathrm{s}(\lambda) + b \cdot \mathrm{f}(\lambda)$$

(b) Fluorescence light

Measured

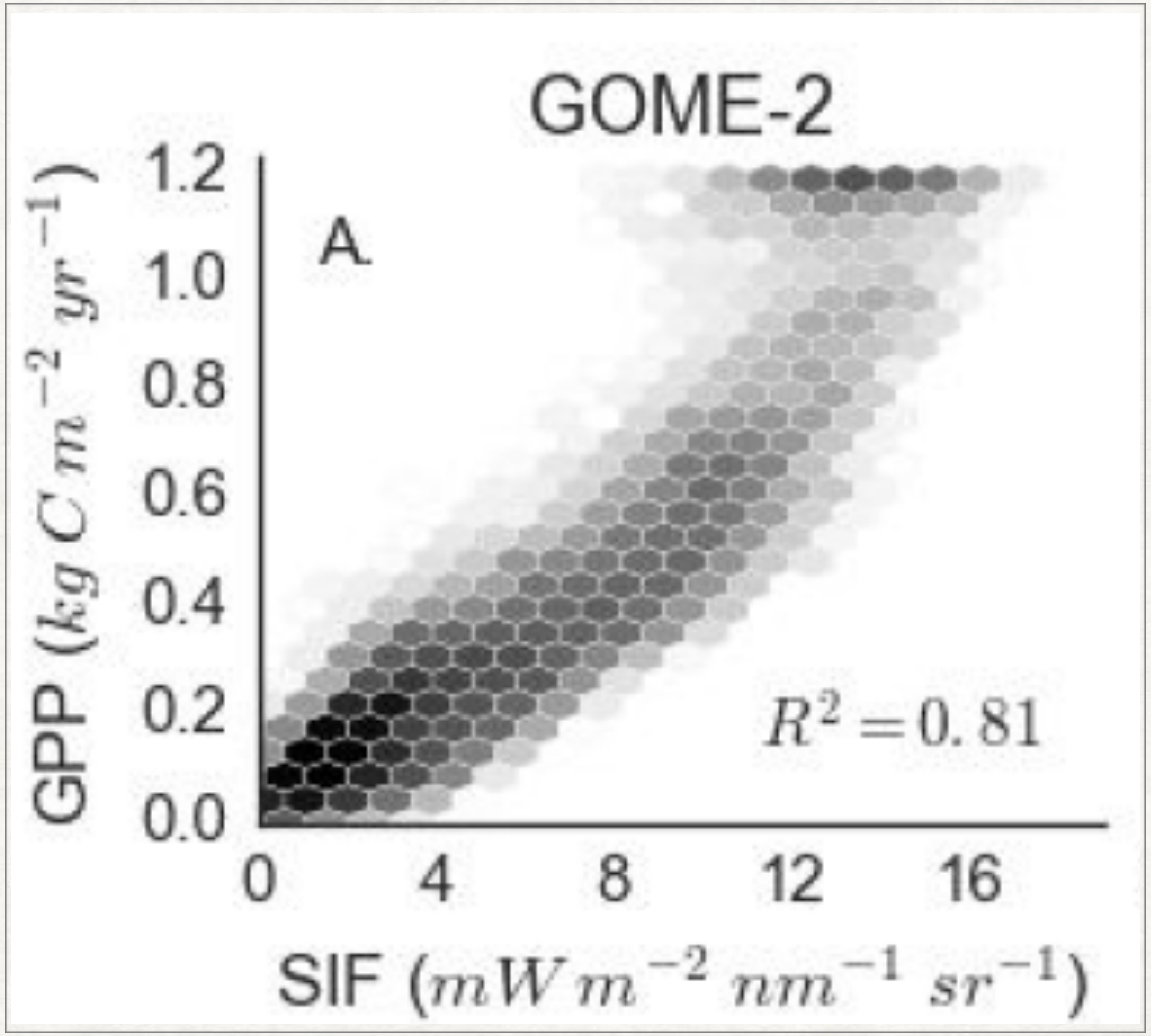


Components



SIF can be used to Estimate GPP

Monthly MPI-GPP at 0.5° *vs* SIF (GOME-2)



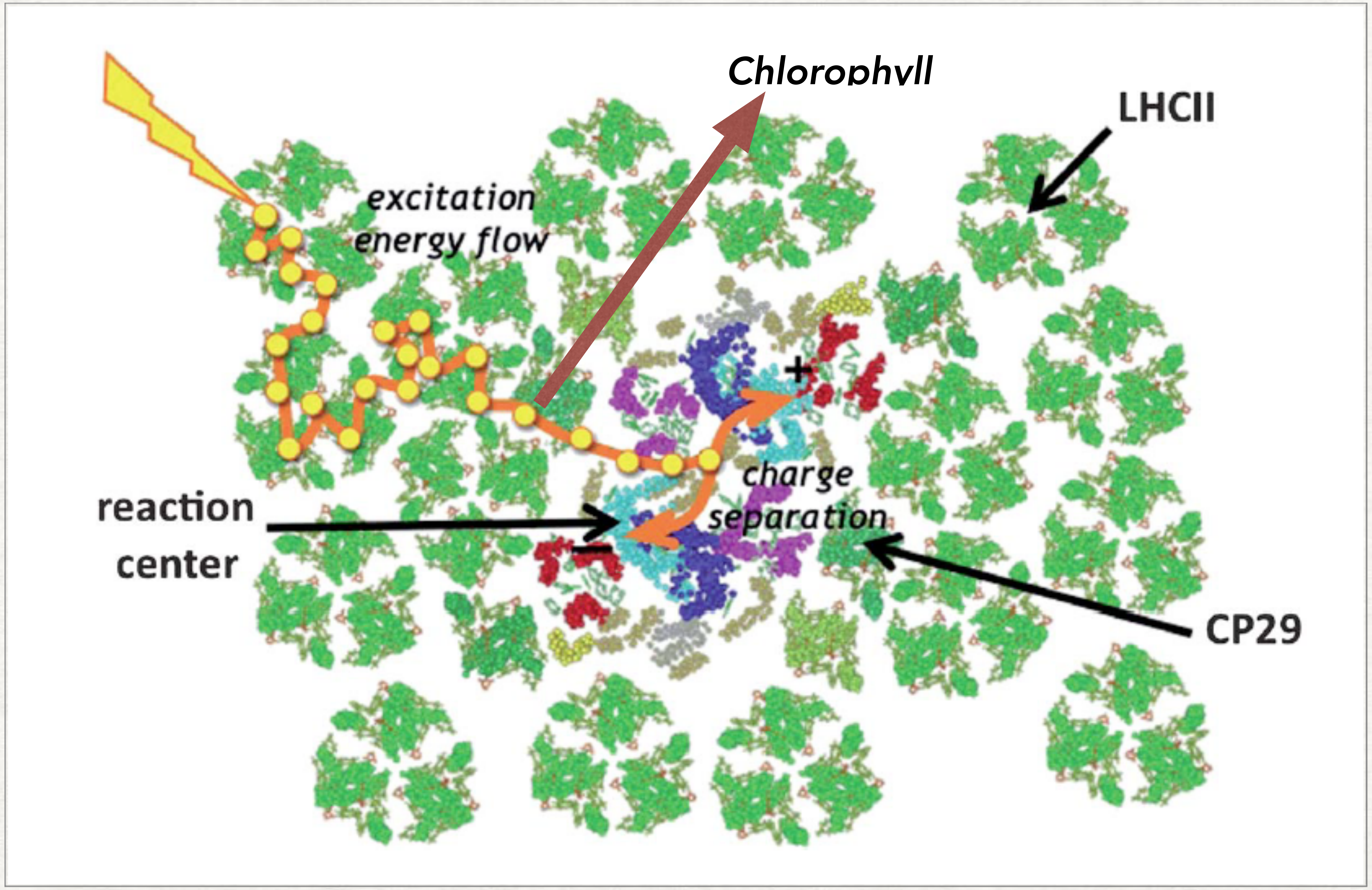
SIF:

- A new method based on resolving fine spectral details permits us to resolve the light emitted by chlorophyll.
- It seems to be a powerful proxy for photosynthesis.
- We want to know the basis of this:

  Is it fluorescence yield

  Or, is it biophysics?

SIF Results from the Decay of an Excited Chlorophyll Molecule



The yield of fluorescence (τ_F), is related to the lifetime of the excited state (τ_P) and the intrinsic lifetime of chlrorphyll (τ_{Chl}).

$$\Phi_F = \frac{\tau_P}{\tau_{\mathrm{Chl}}} \approx 0.01$$

Fleming, G. R., Schlau-Cohen, G. S., Amarnath, K., & Zaks, J. (2012). Design principles of photosynthetic light-harvesting. Faraday Discussions, 155, 27. http://doi.org/10.1039/c1fd00078k

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The Fundamental Conservation Equation

$$\underbrace{\Phi_P + \Phi_N}_{\text{Dynamic}} + \underbrace{\overset{\text{Loss + PSI}}{\Phi_D} + \Phi_F}_{\text{Passive}} = 1$$

Yield of fluorescence ~ 0.01 to 0.05

Directly proportional to life time, τ of the excited state

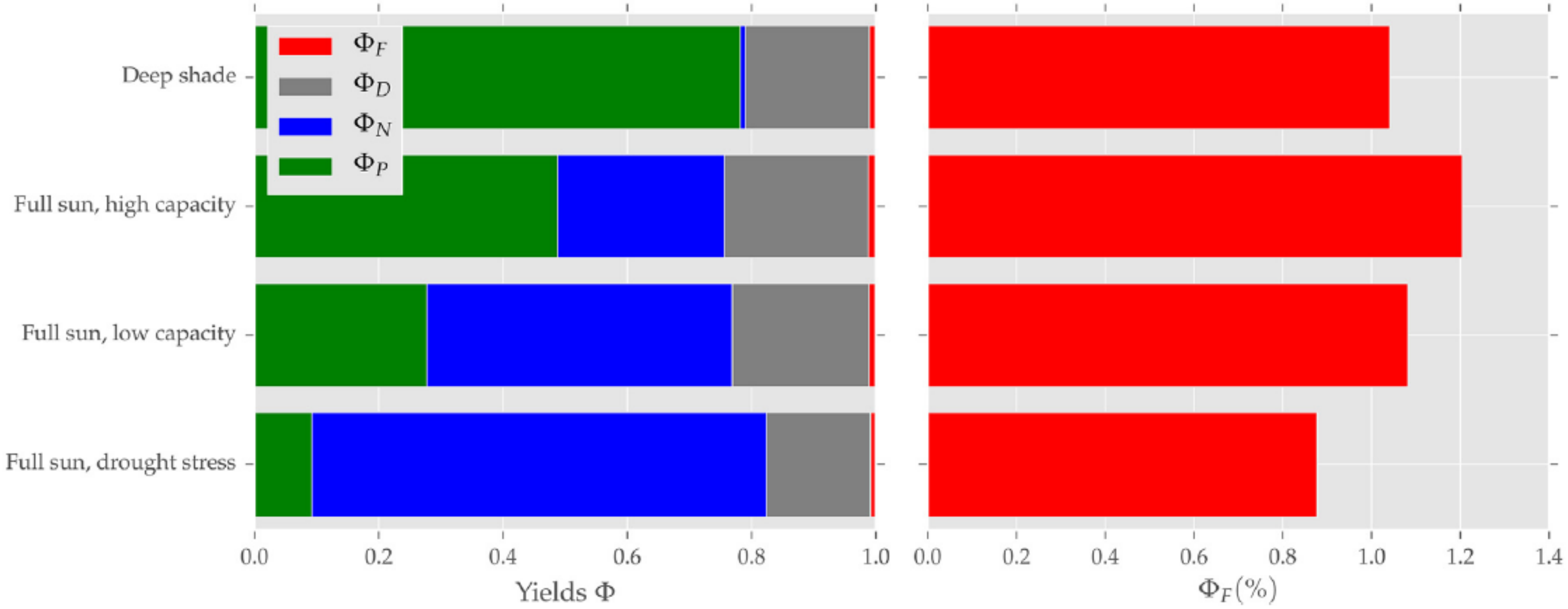


Fig. 2 Quantum yields (Φ) for the four pathways used by leaves to process photons depend on whether the leaf is shaded or exposed to full sun, whether the leaf has a high or low photosynthetic capacity, and whether drought stress is present. In the histogram, *green* denotes photosynthesis (PSII yield); *blue*, nonphotochemical quenching; *gray*, nonradiative decay; and *red*, fluorescence. The results shown here were obtained with a laboratory instrument called a PAM fluorometer. As the *right panel* shows, the fluorescence quantum yield changes less than the PSII yield but also noticeably with varying conditions, especially once nonphotochemical quenching becomes dominant.

Photoinhibition is a first order photochemical process

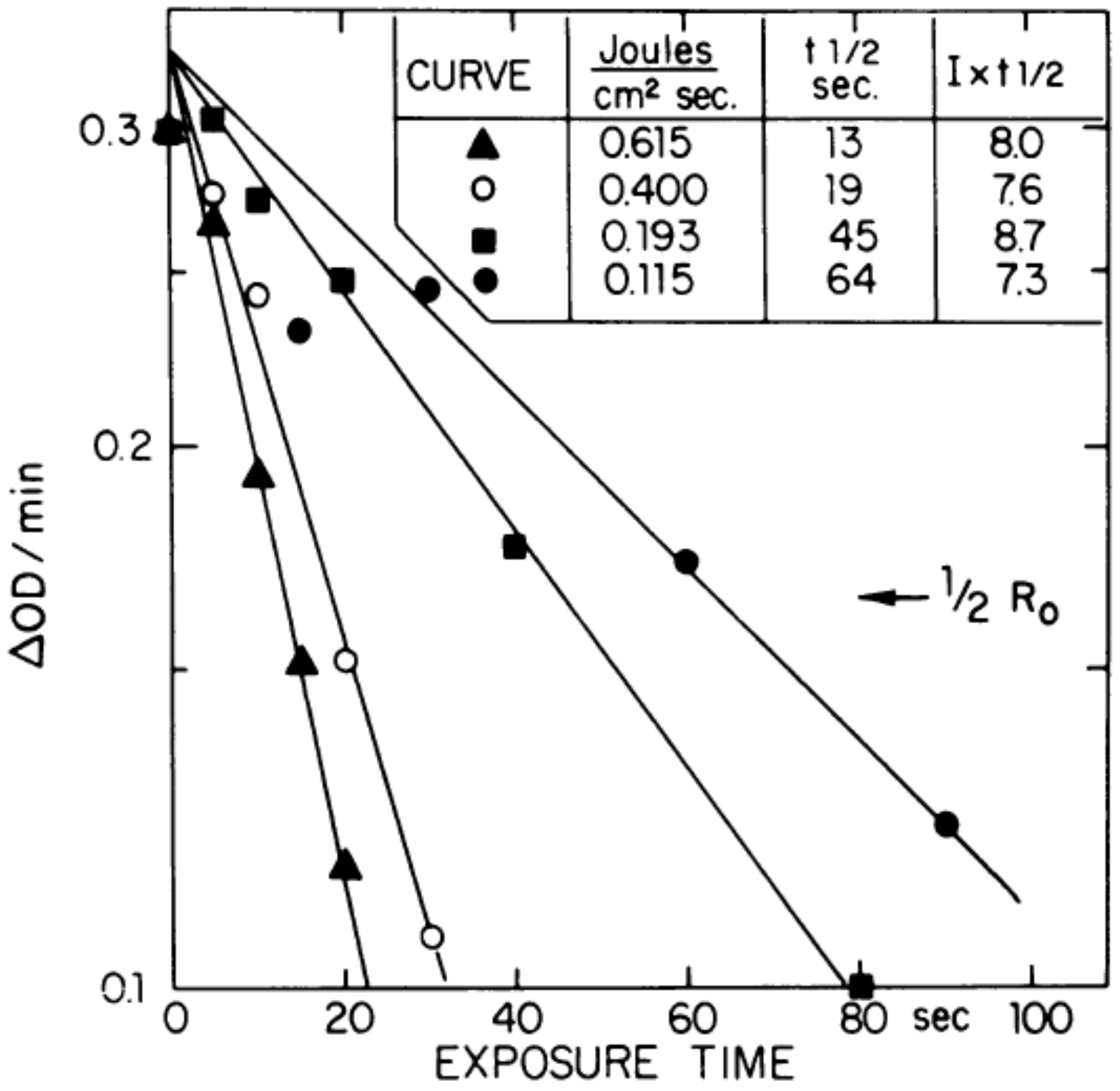
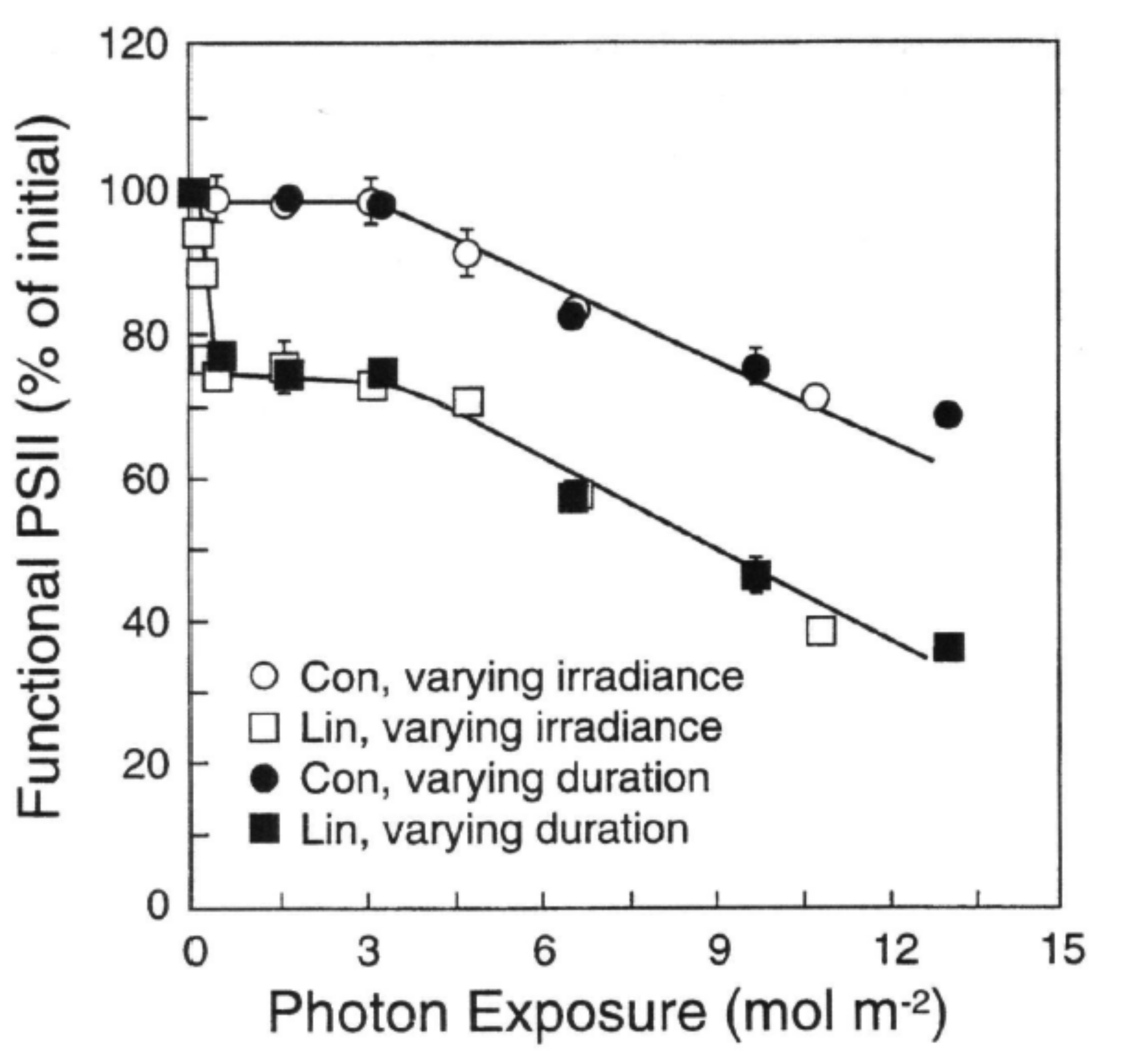


FIG. 2. Decay of dye reduction activity of chloroplasts during exposure to white light of various intensities. Dye reduction assayed as in Methods. Light from Xenon arc filtered through 4 layers of glass, 37 cm of water and wire screens. Intensity measured with calibrated thermopile.

Jones, L. W., & Kok, B. (1966). Photoinhibition of Chloroplast Reactions. I. Kinetics and Action Spectra. Plant Physiology, 41(6), 1037–1043. http://doi.org/10.1104/pp.41.6.1037

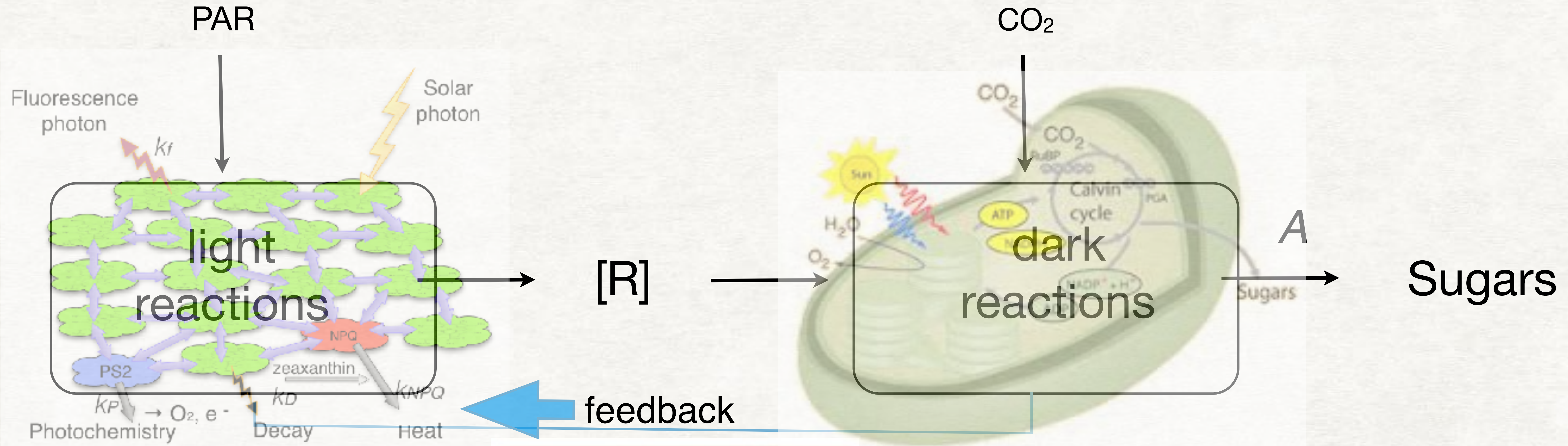
Anderson, J. M., Park, Y. I., & Chow, W. S. (1997). Photoinactivation and photoprotection of photosystem II in nature. Physiologia Plantarum, 100(2), 214–223. http://doi.org/10.1111/j.1399-3054.1997.tb04777.x



$$\Phi_i = \frac{K_i}{K_P + K_N + K_D + K_F + K_i}$$

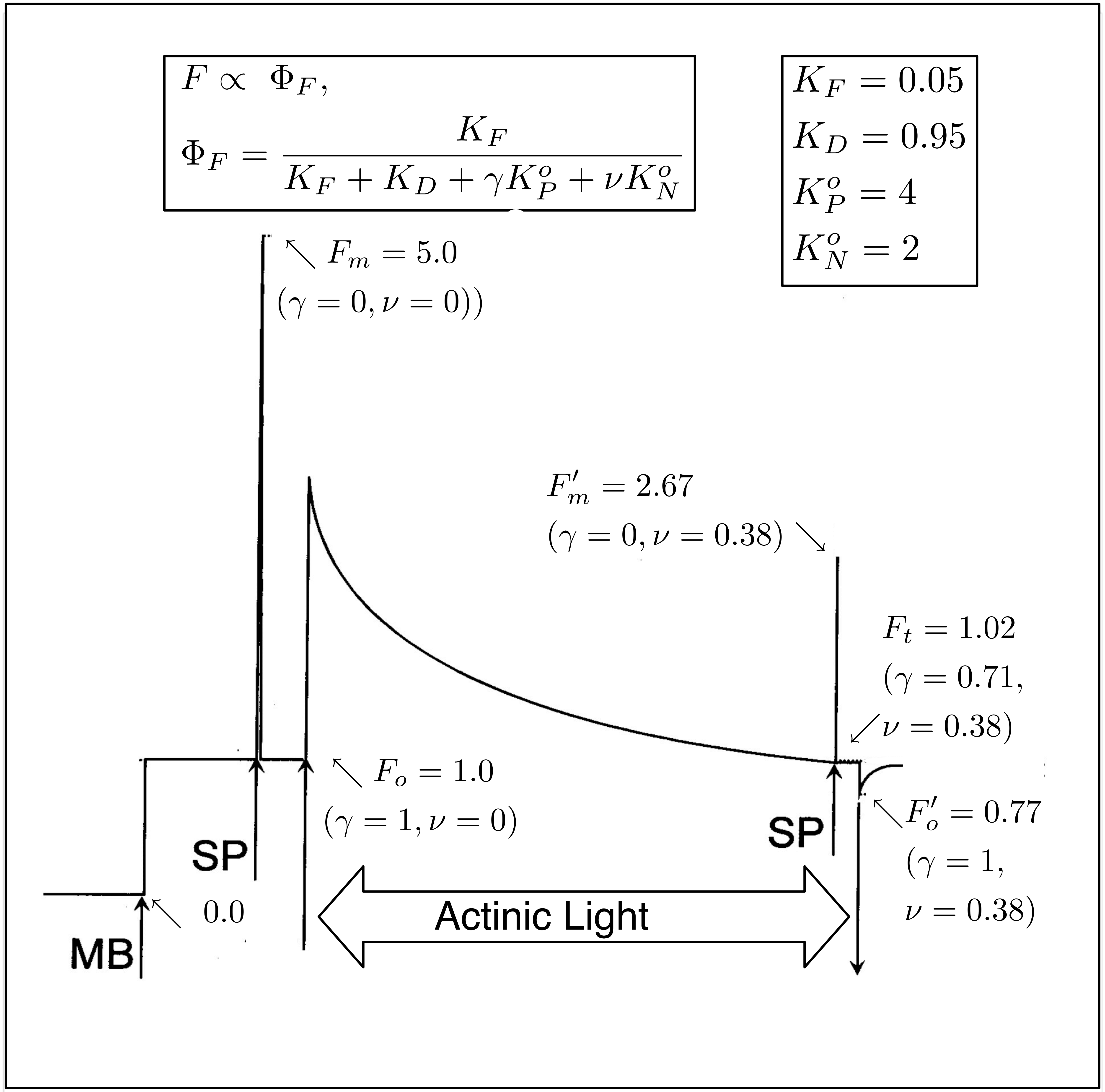
$$K_i \approx 1.5 \times 10^{-6}$$

Interactions between the light and dark reactions:



$$A \approx \min \begin{cases} \text{light reactions } (W_J) \\ \text{dark reactions } (W_C) \end{cases}$$

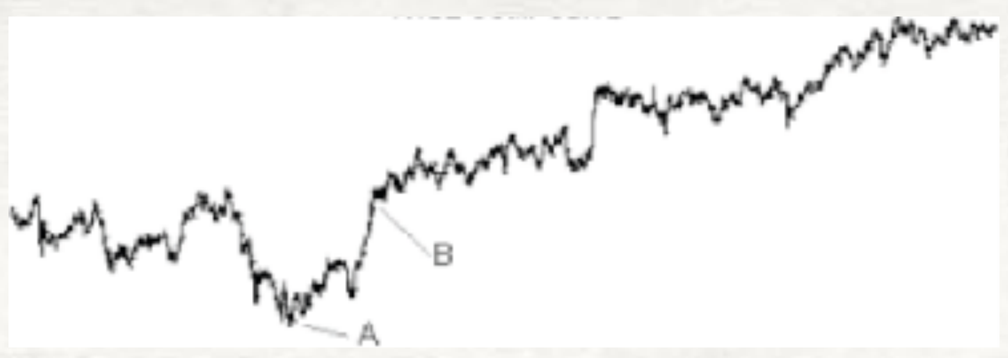
PAM Fluorometry - the key for understanding SIF



$$F \propto \Phi_F, \qquad \Phi_F = \frac{K_F}{K_F + K_D + \gamma K_P^o + \nu K_N^o}$$

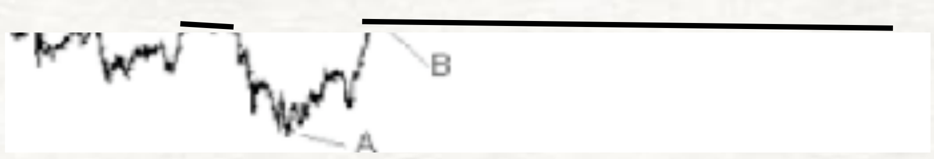
$K_F = 0.05$
$K_D = 0.95$
$K_P^o = 4$
$K_N^o = 2$

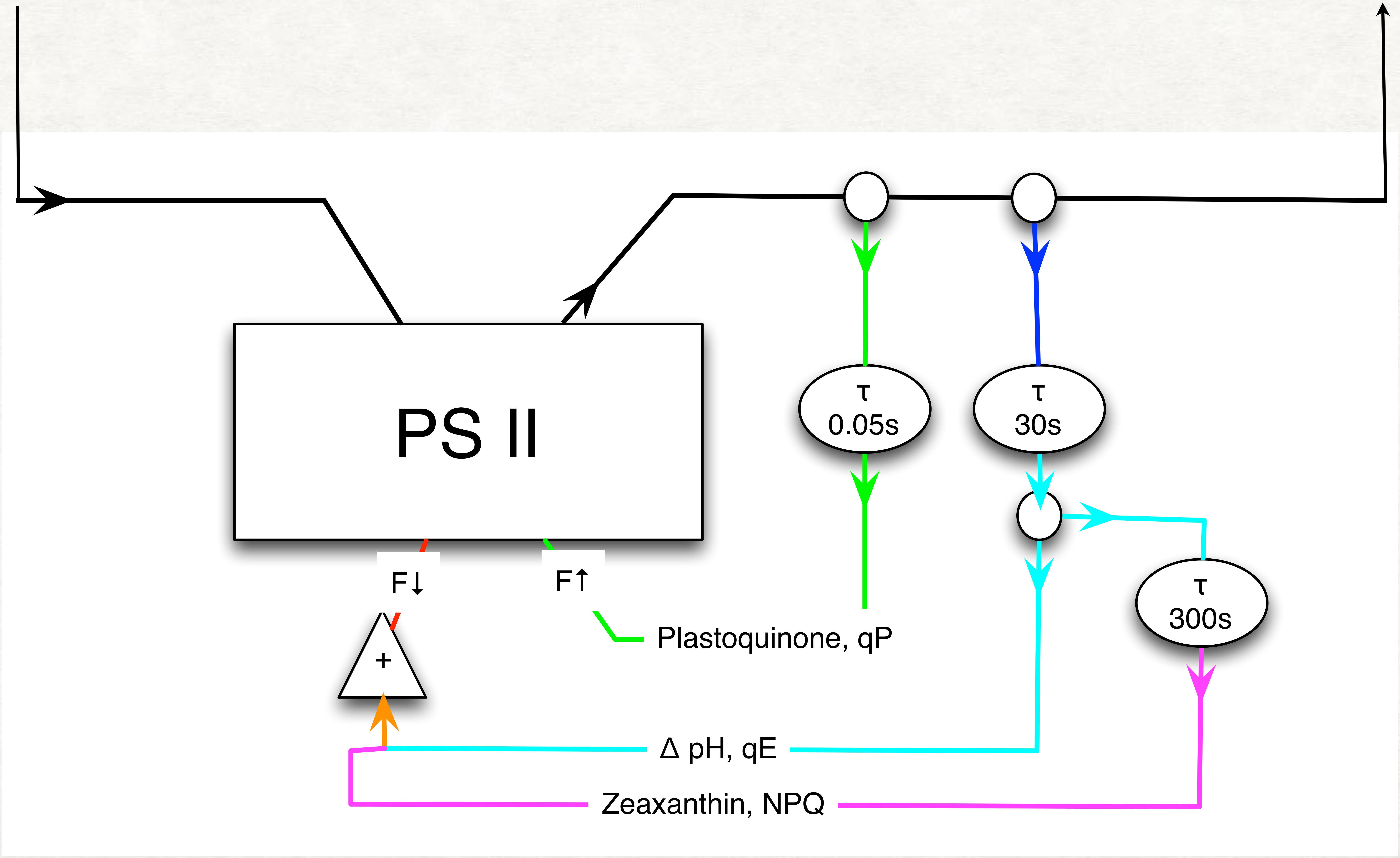
Input Light



Think of Photosystem 2 as a sophisticated IC.

Output to carbon fixation





PS II

τ
0.05s

τ
30s

τ
300s

F↓

F↑

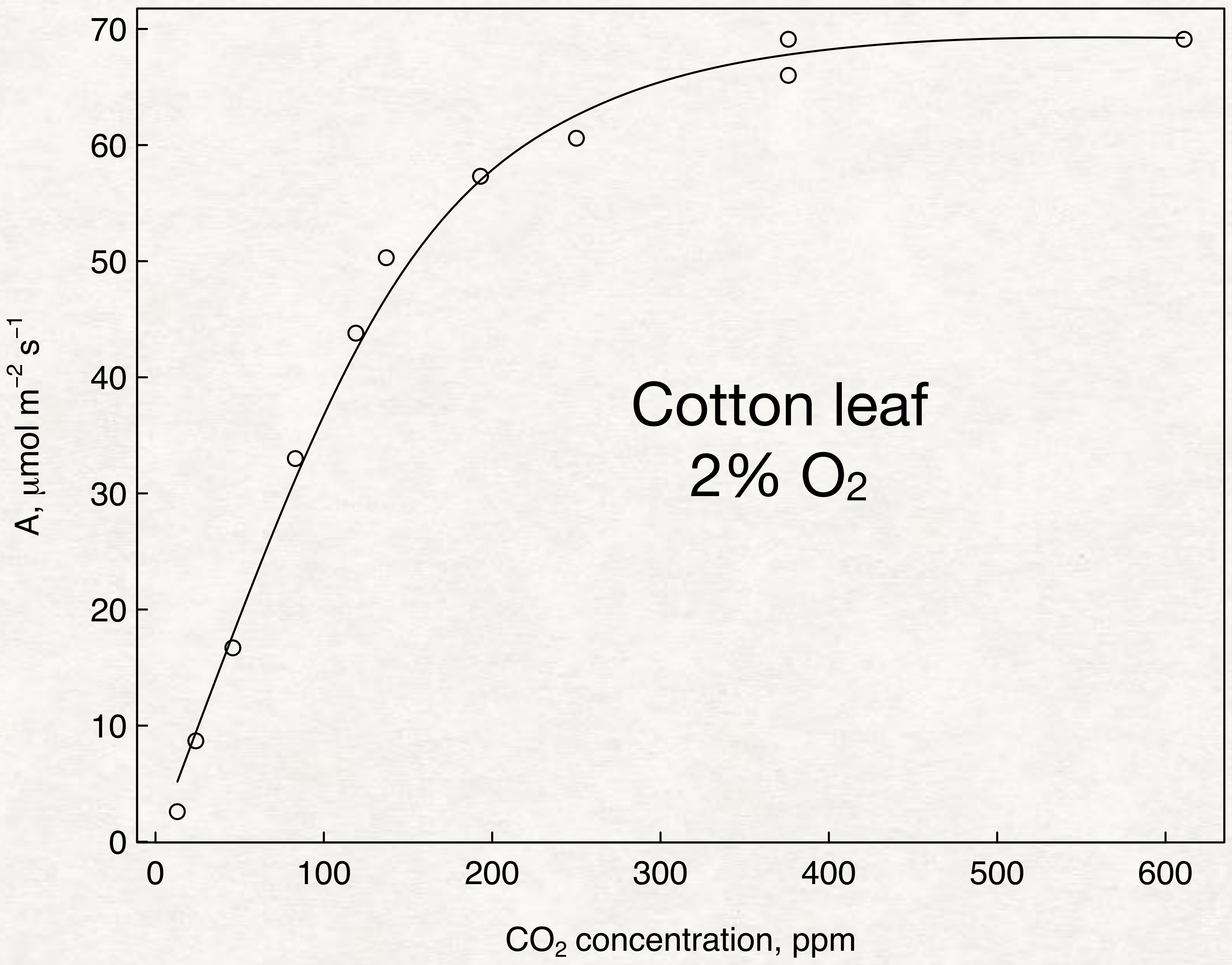
+

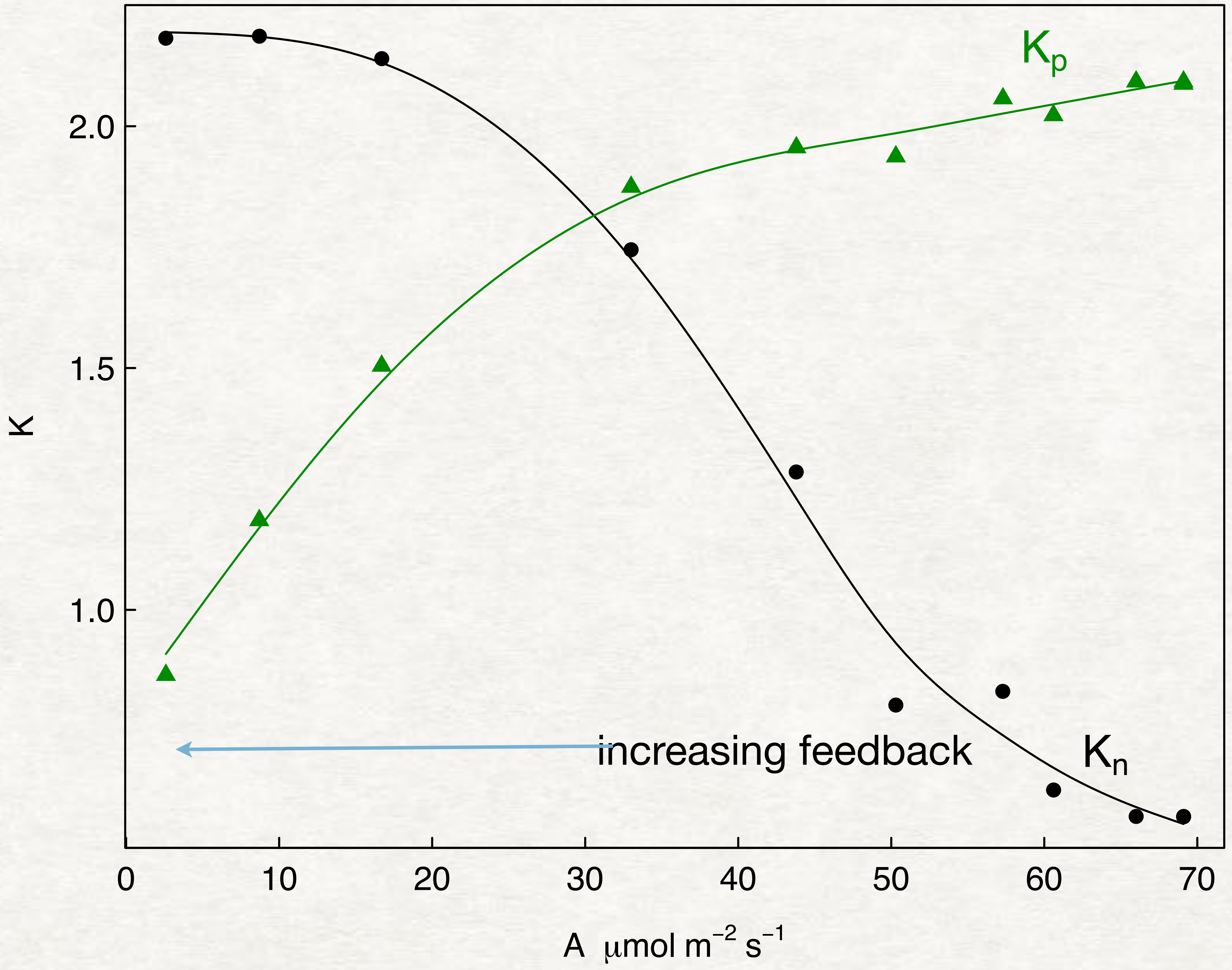
Plastoquinone, qP

Δ pH, qE

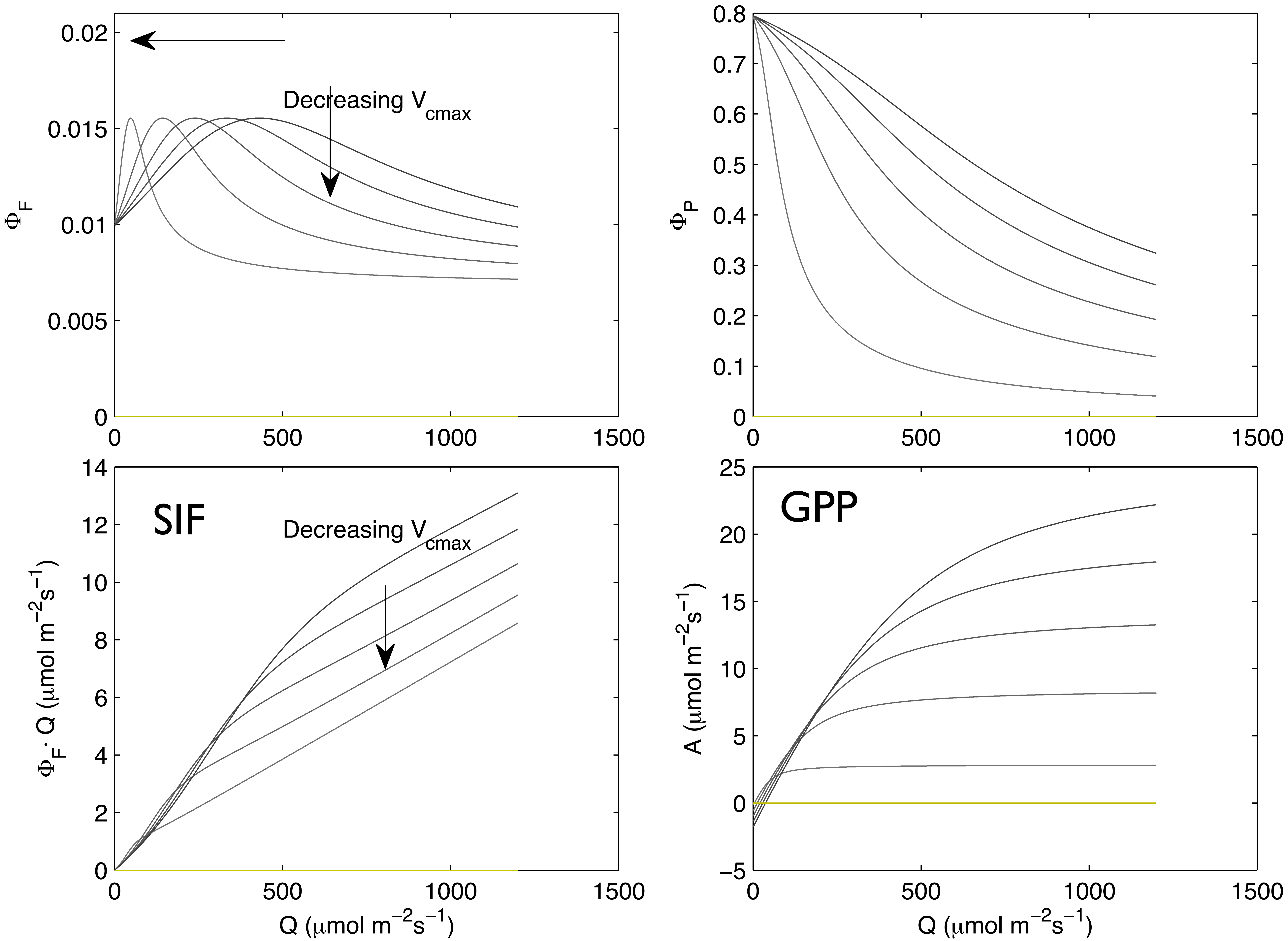
Zeaxanthin, NPQ

The Pattern of Feedback



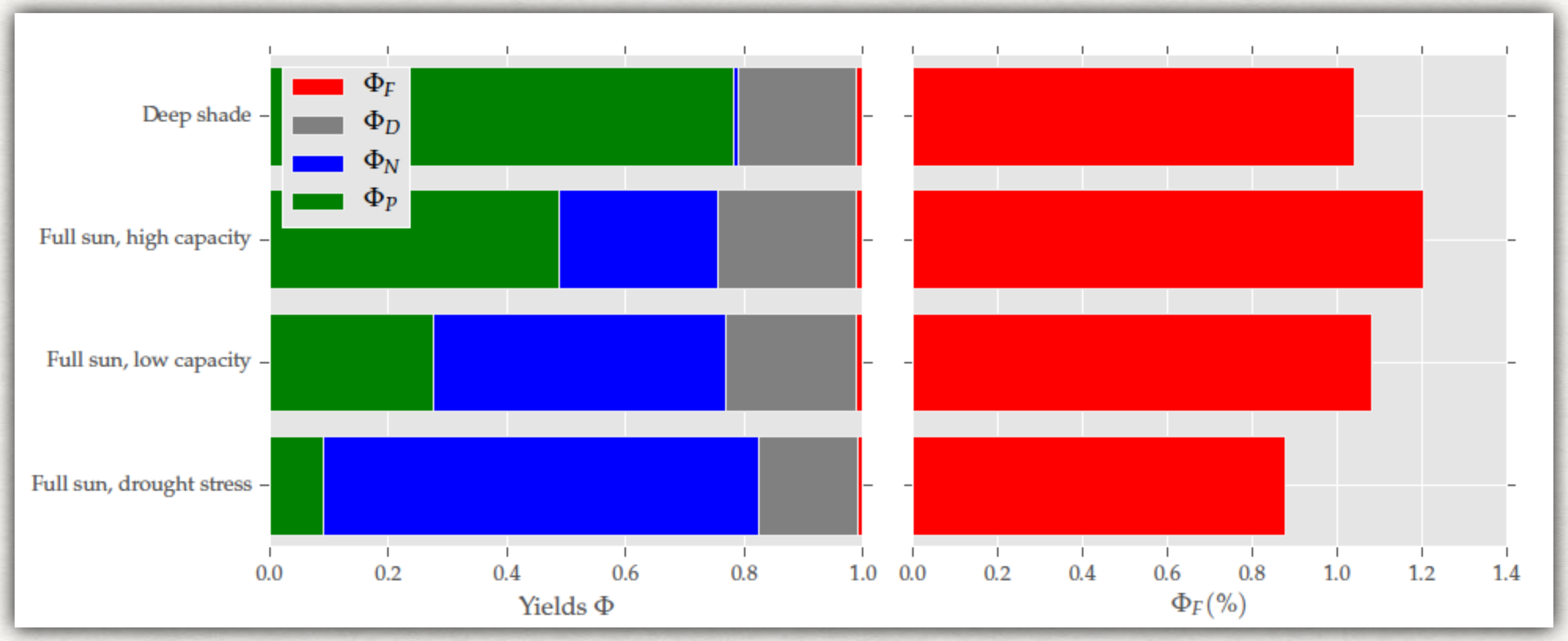


$$\Phi_P = \frac{K_P}{K_P + K_N + K_D + K_F}$$



Φ_F
0.02
0.015
0.01
0.005
0
Decreasing V_{cmax}
Φ_P
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
SIF
Decreasing V_{cmax}
$\Phi_F \cdot Q$ (μmol $m^{-2}s^{-1}$)
14
12
10
8
6
4
2
0
GPP
A (μmol $m^{-2}s^{-1}$)
25
20
15
10
5
0
−5
0
500
1000
1500
Q (μmol $m^{-2}s^{-1}$)

The Yield of SIF (Φ_F) is linked to Photochemistry (Φ_P) and Non-Photochemical Quenching (Φ_N)



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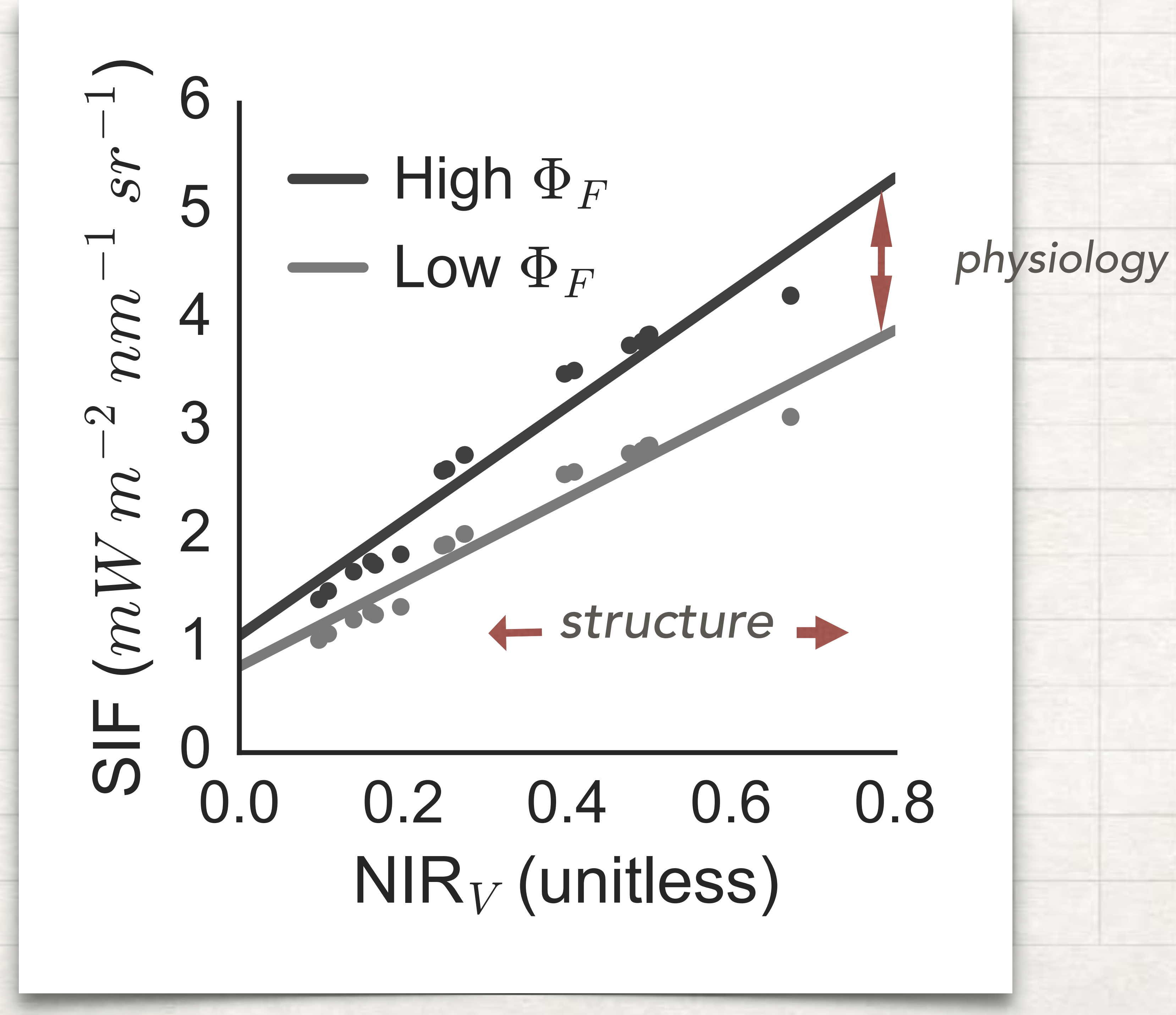
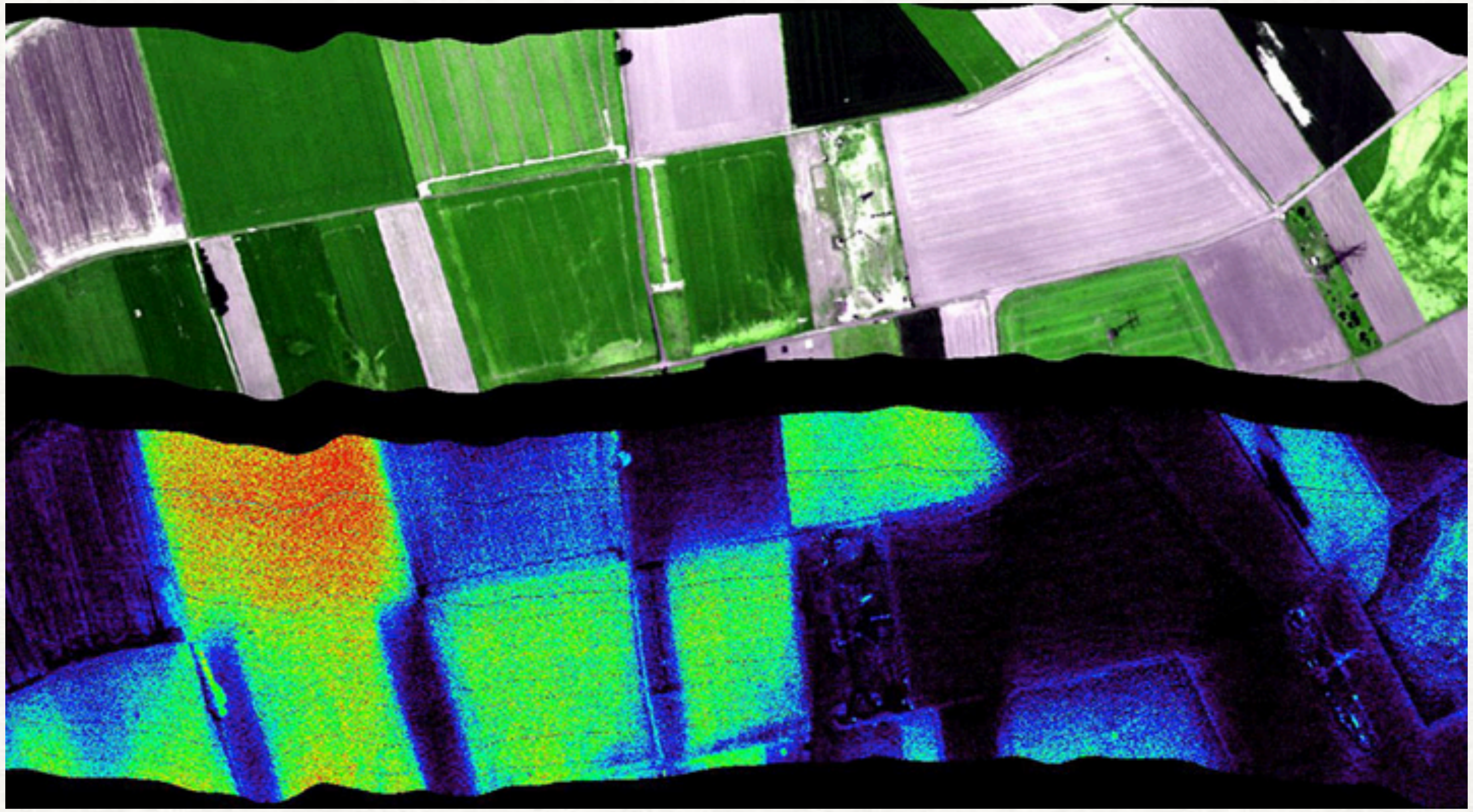
Summing up:

- We see that physiology works in the right direction, but it probably isn't sufficient to account for observed variation in SIF.
- Could it be the canopy structure?

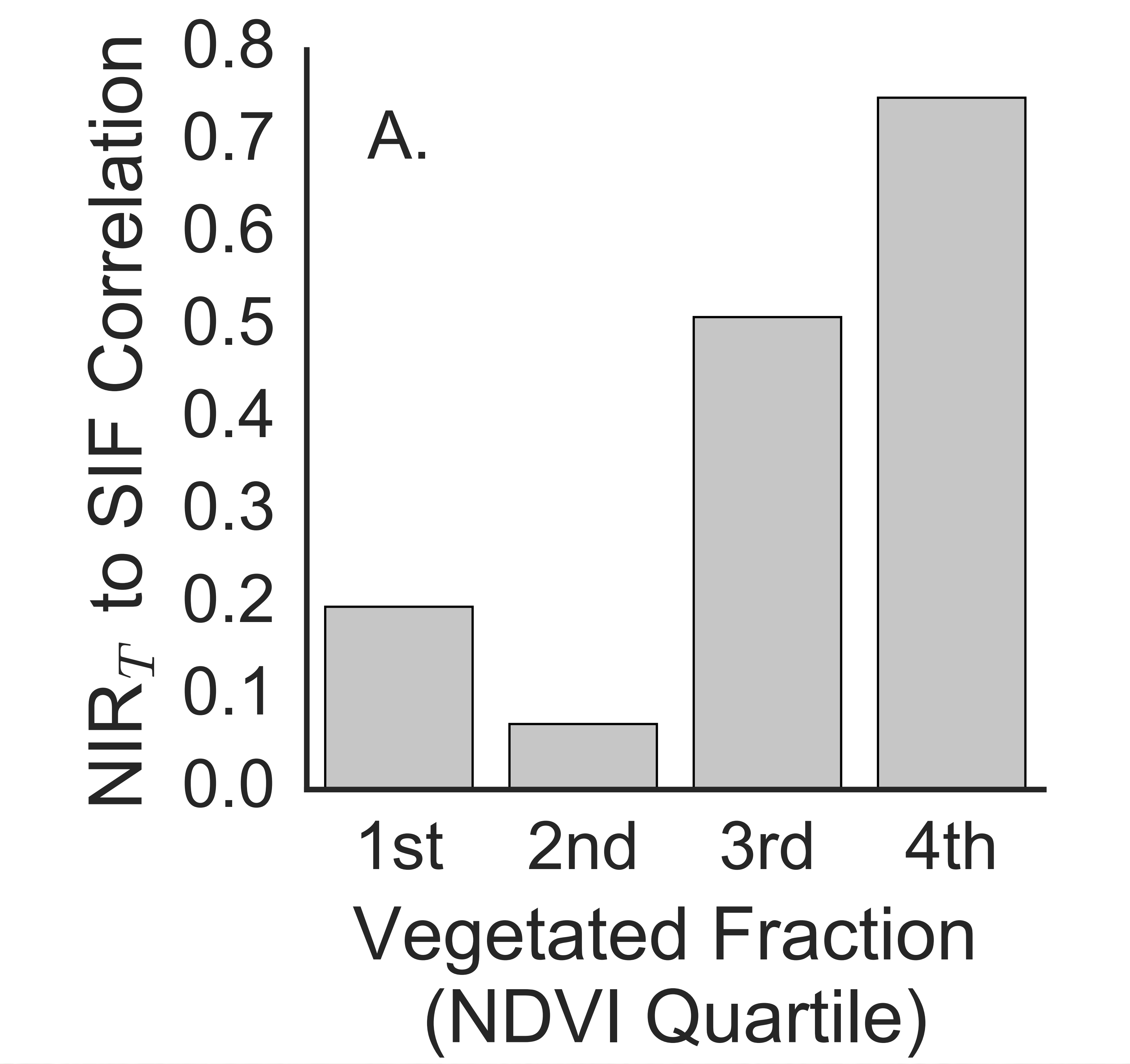


- SIF (bottom) is specific to vegetation, while reflectance (top) sees all surfaces of the scene.

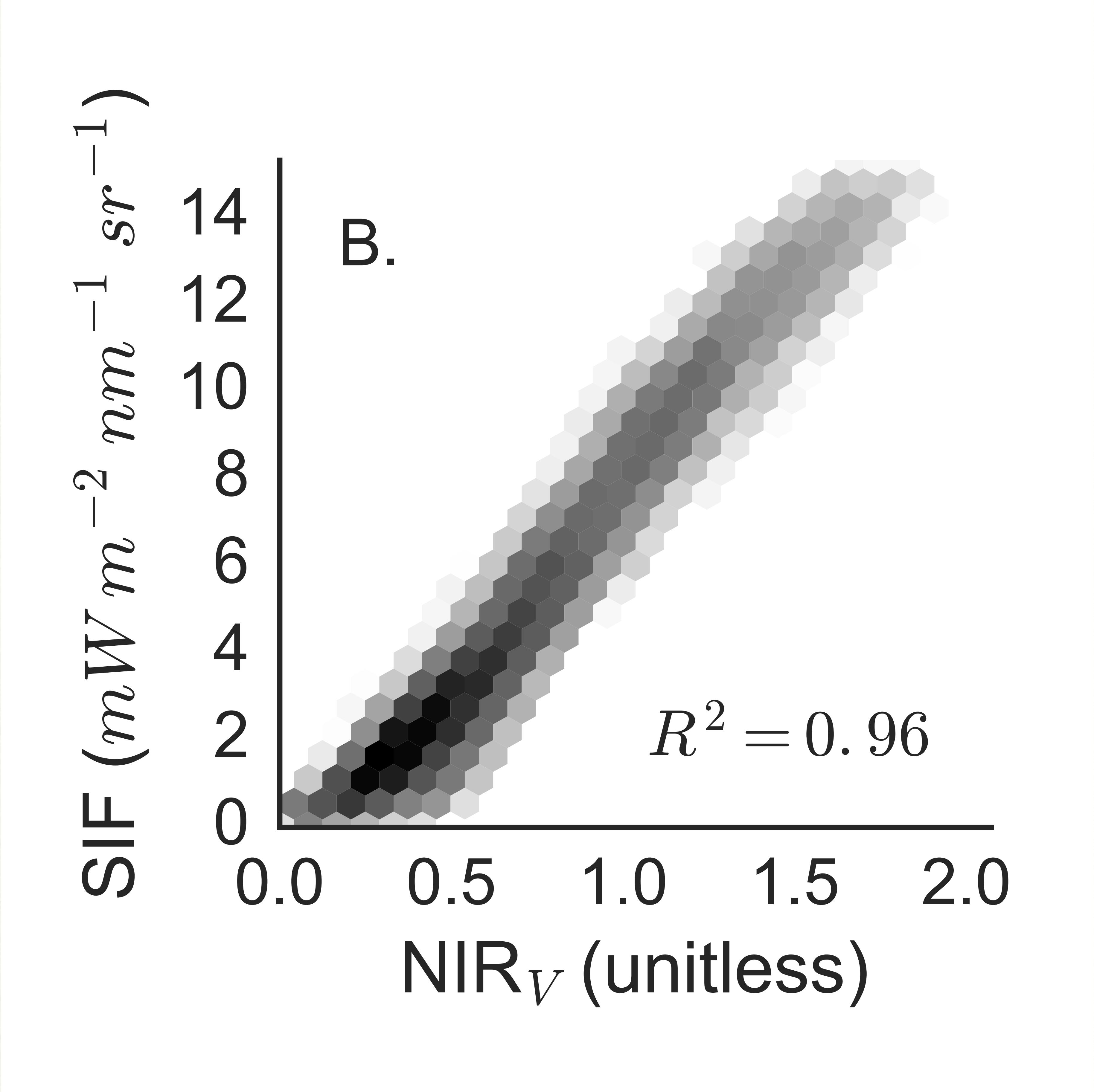


  - SIF seems to be proportional to the NIR reflectance of the canopy (excluding the soil).

NDVI x NIR Radiance = NIR_V (vegetation)?

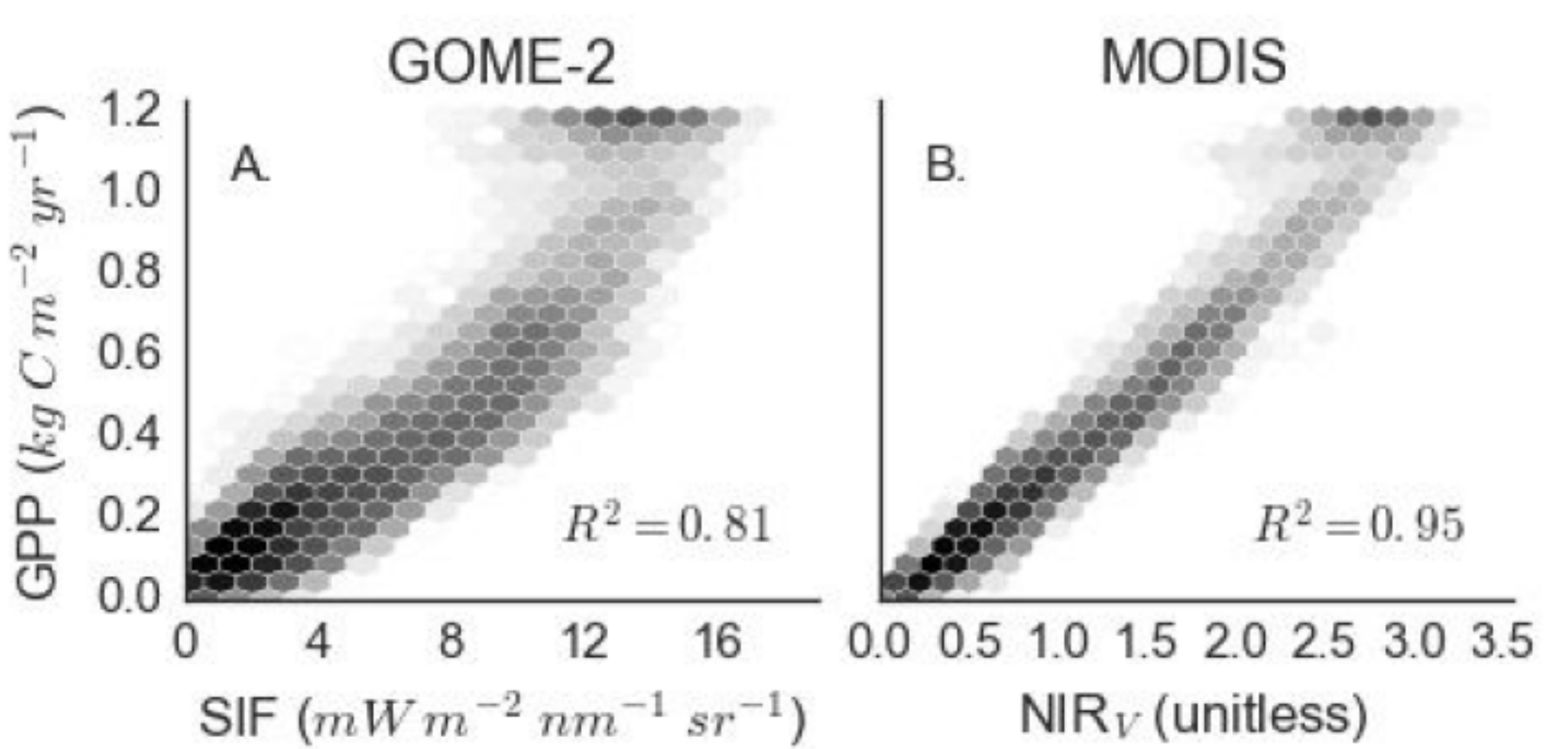


NIR_T * NDVI



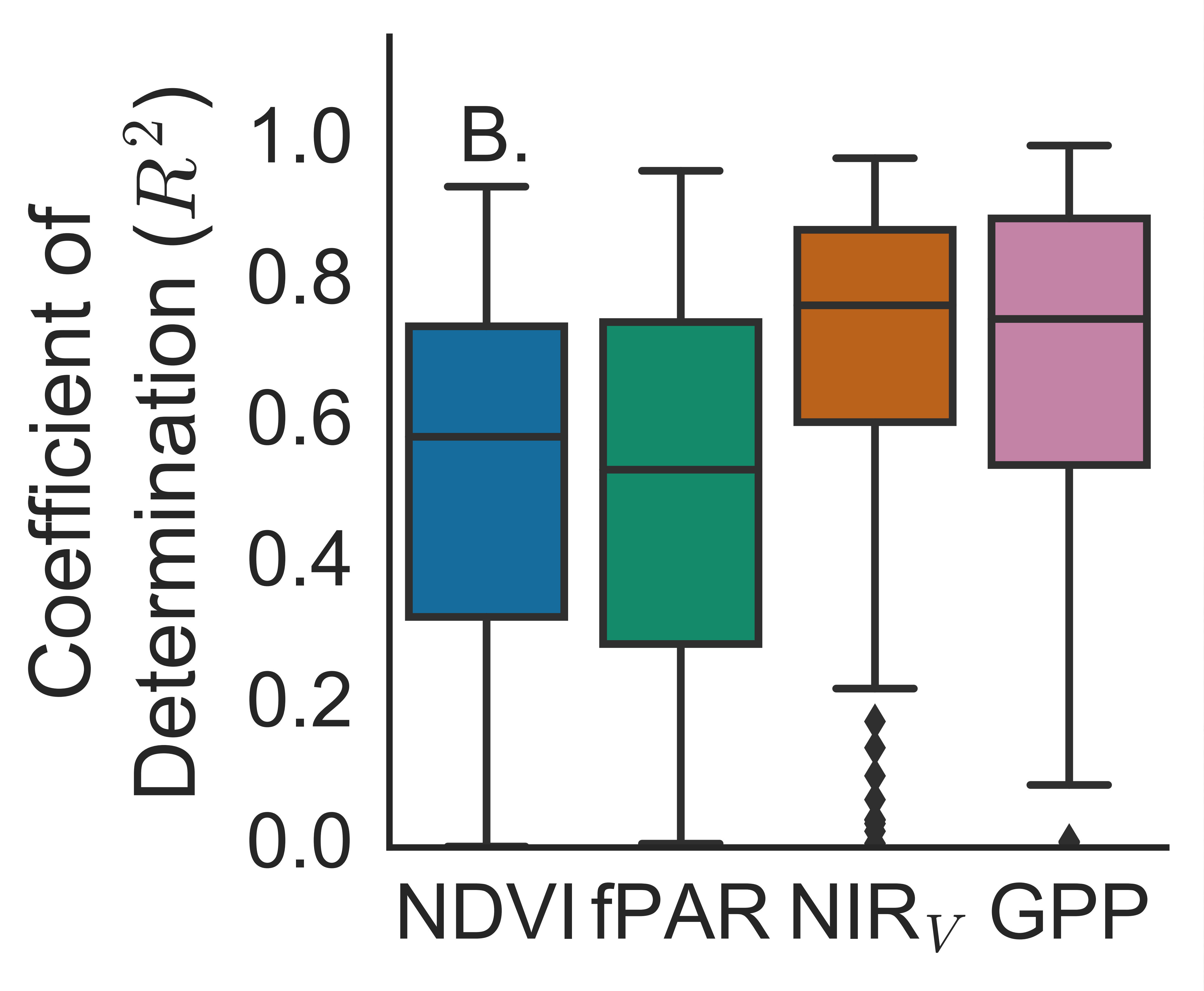
CAN WE USE NIR$_V$ TO ESTIMATE GPP?

Monthly MPI-GPP at 0.5° *vs* SIF (GOME-2) or NIR$_V$ (MODIS)



Badgley, G., Field, C. B., & Berry, J. A. (2017). Canopy near-infrared reflectance and terrestrial photosynthesis. Science Advances, 3(3), e1602244. http://doi.org/10.1126/sciadv.1602244

MODIS (0.5 km) used to evaluate NIR_V at 106 flux sites.



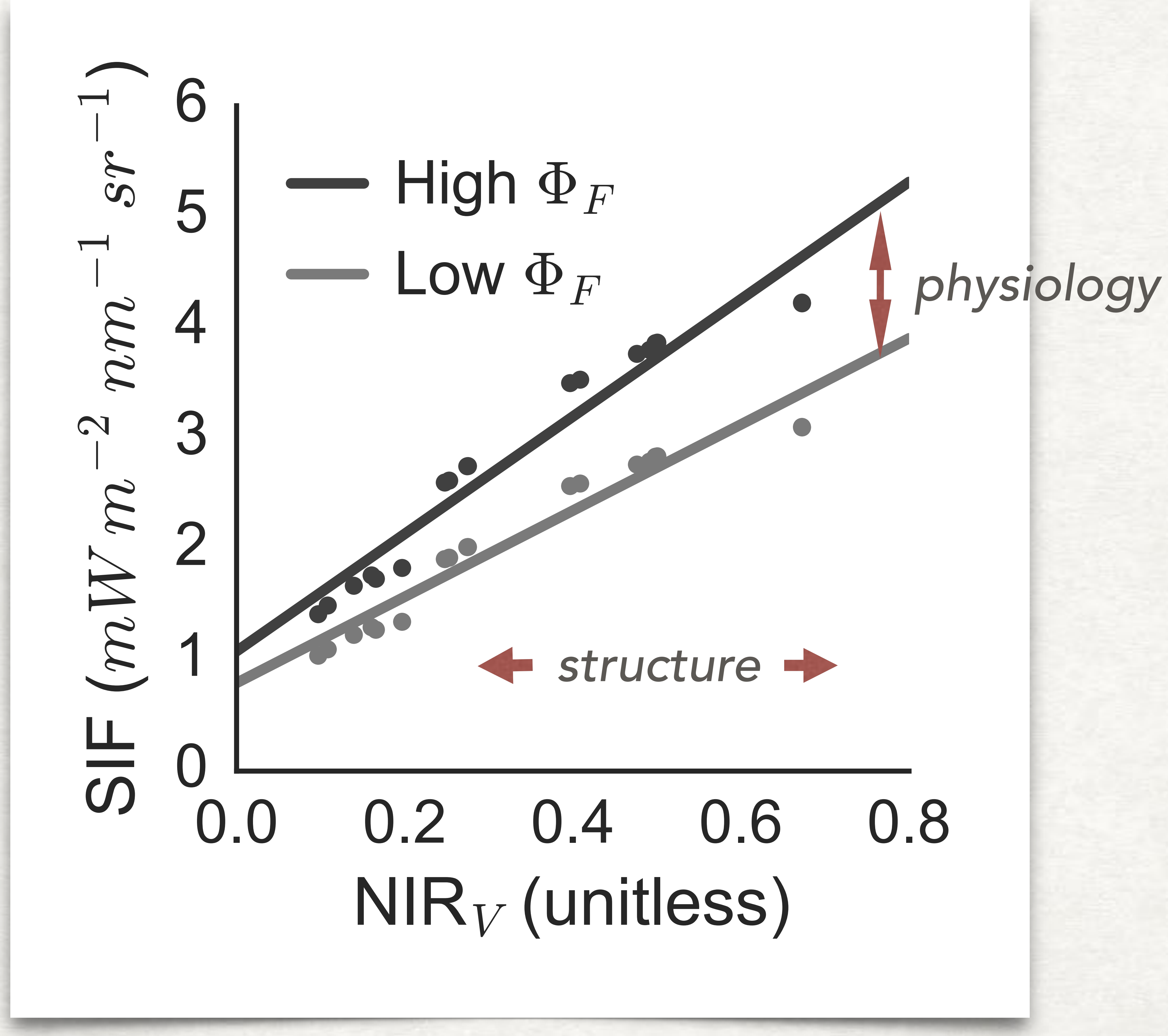
Values for the month of peak productivity

Land Cover Class	NIR_V (unitless)	fPAR (unitless)	GPP (gC m^{-2} d^{-1})
Deciduous Broadleaf	0.28	0.72	11.18
Cropland	0.27	0.62	12.57
Mixed Forest	0.22	0.68	9.35
Grassland	0.19	0.55	6.61
Wetland	0.19	0.58	6.41
Evergreen Broadleaf	0.17	0.70	7.87
Evergreen Needleleaf	0.17	0.67	7.85
Savanna	0.15	0.45	5.62
Woody Savanna	0.14	0.42	6.23
Open Shrubland	0.13	0.48	3.85
Closed Shrubland	0.10	0.46	5.30

$$J_{\mathrm{SIF}} = J_{\mathrm{PAR}}(f_{\mathrm{PAR}} \cdot \Phi_F \cdot \underset{\substack{\uparrow \\ \text{escape probability}}}{\Omega_C})$$

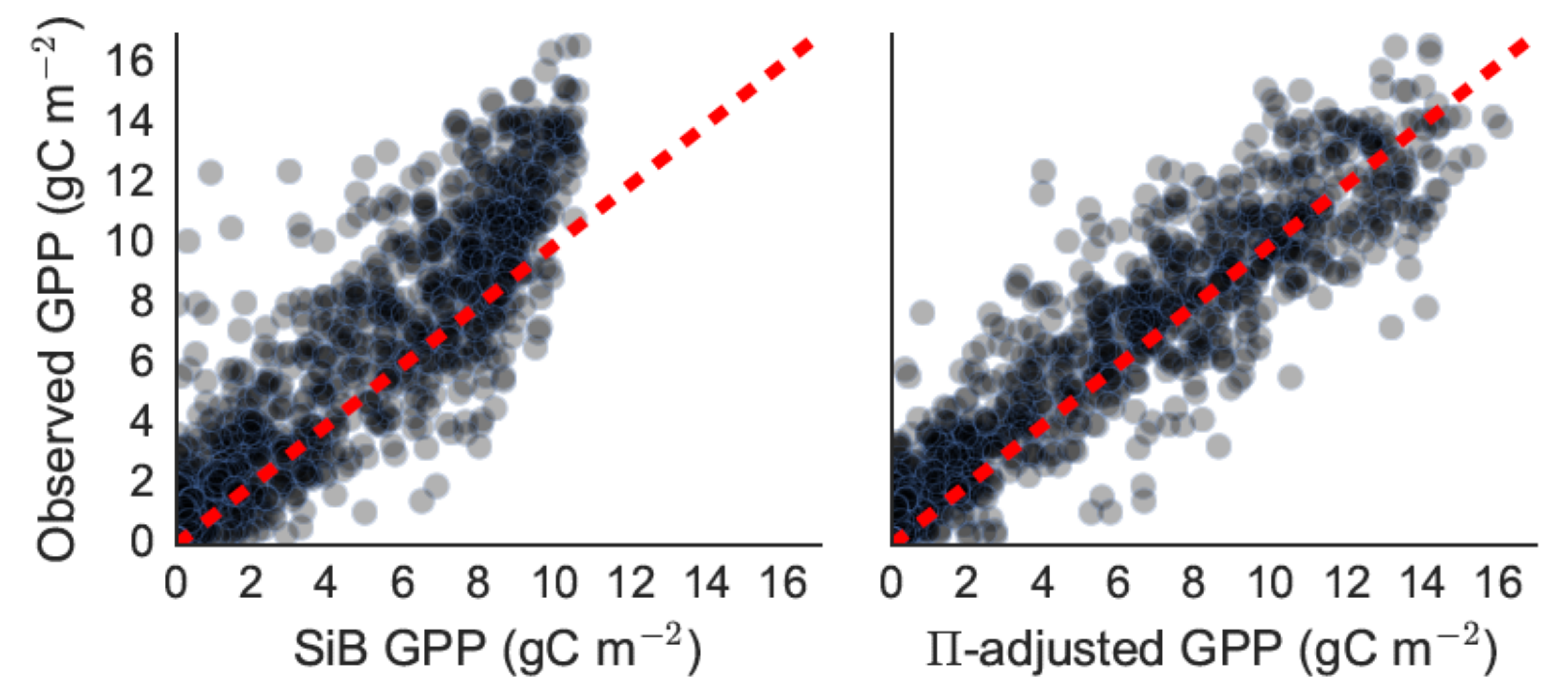
The correlation between SiF and GPP is based on:

- Physiological control of the yield of fluorescence (Φ_F)
- Structural properties of the canopy that effect leaf display



Canopies are very diverse

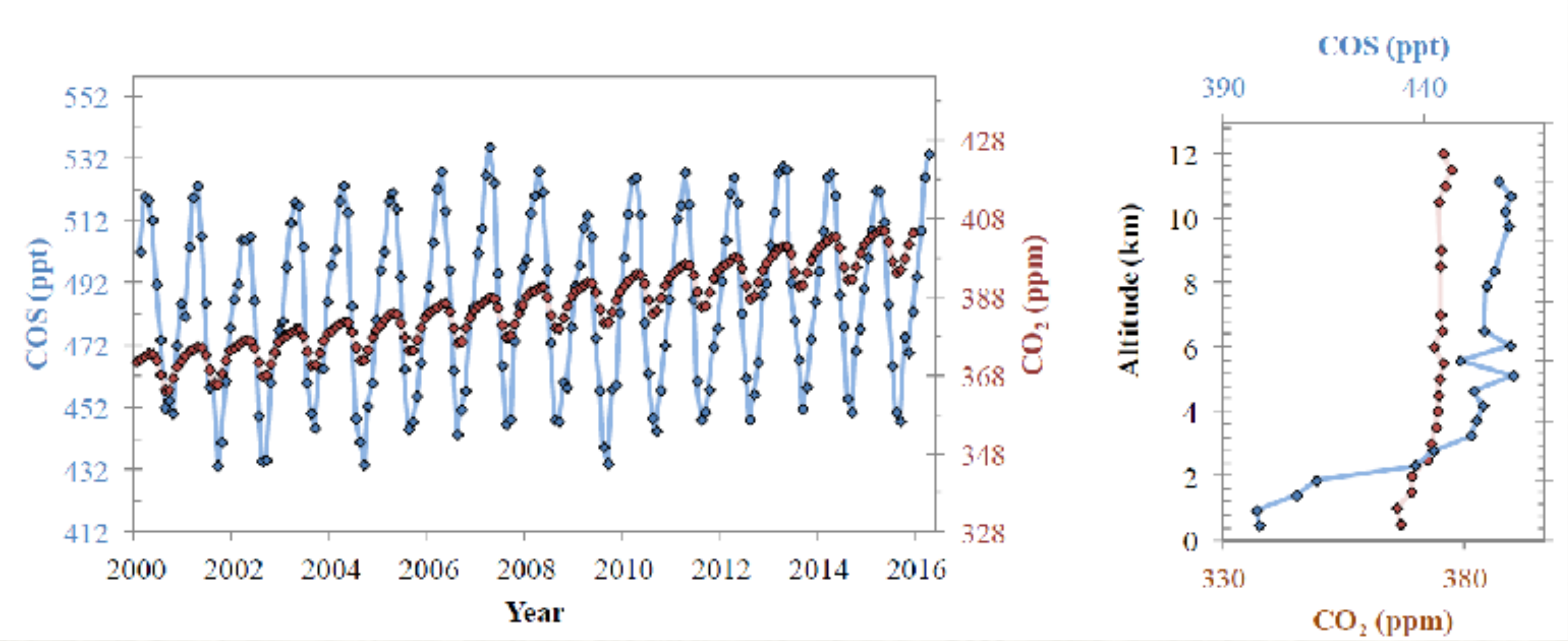
Scale π in SIB by SIF or NIR_V

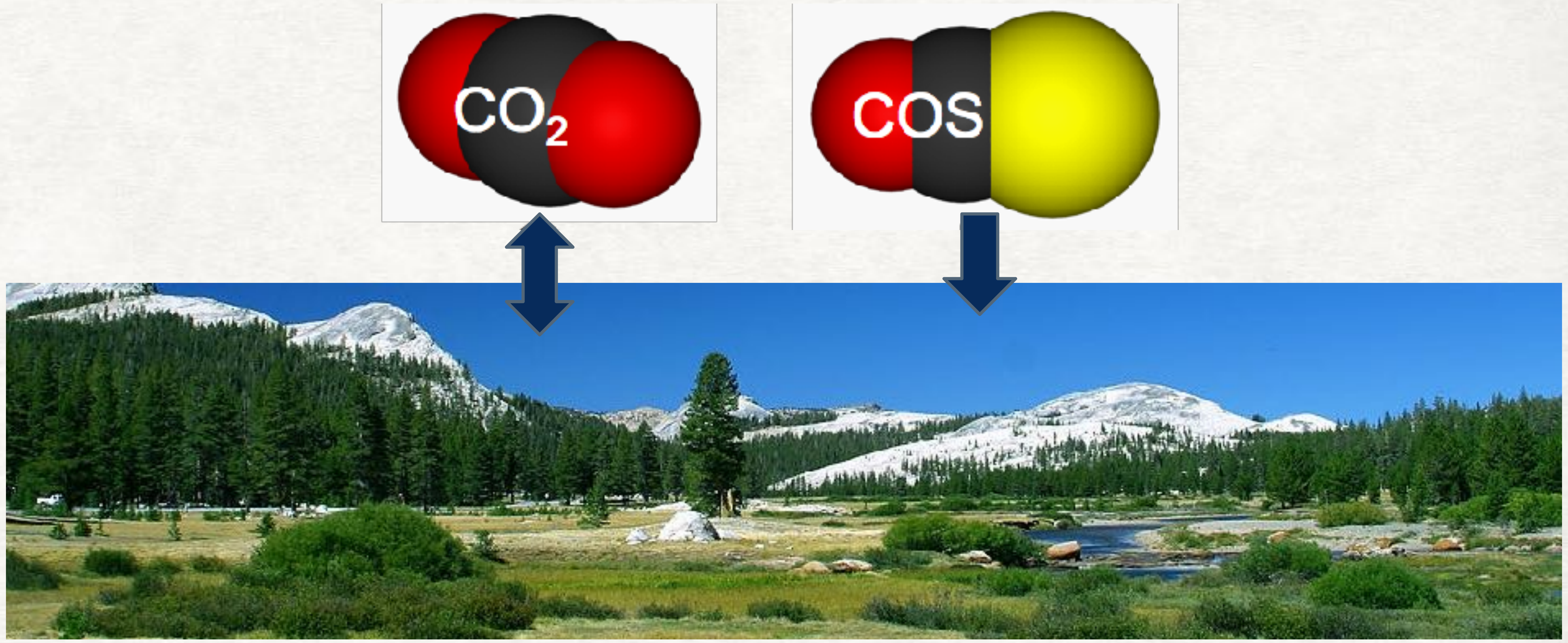


Summing up:

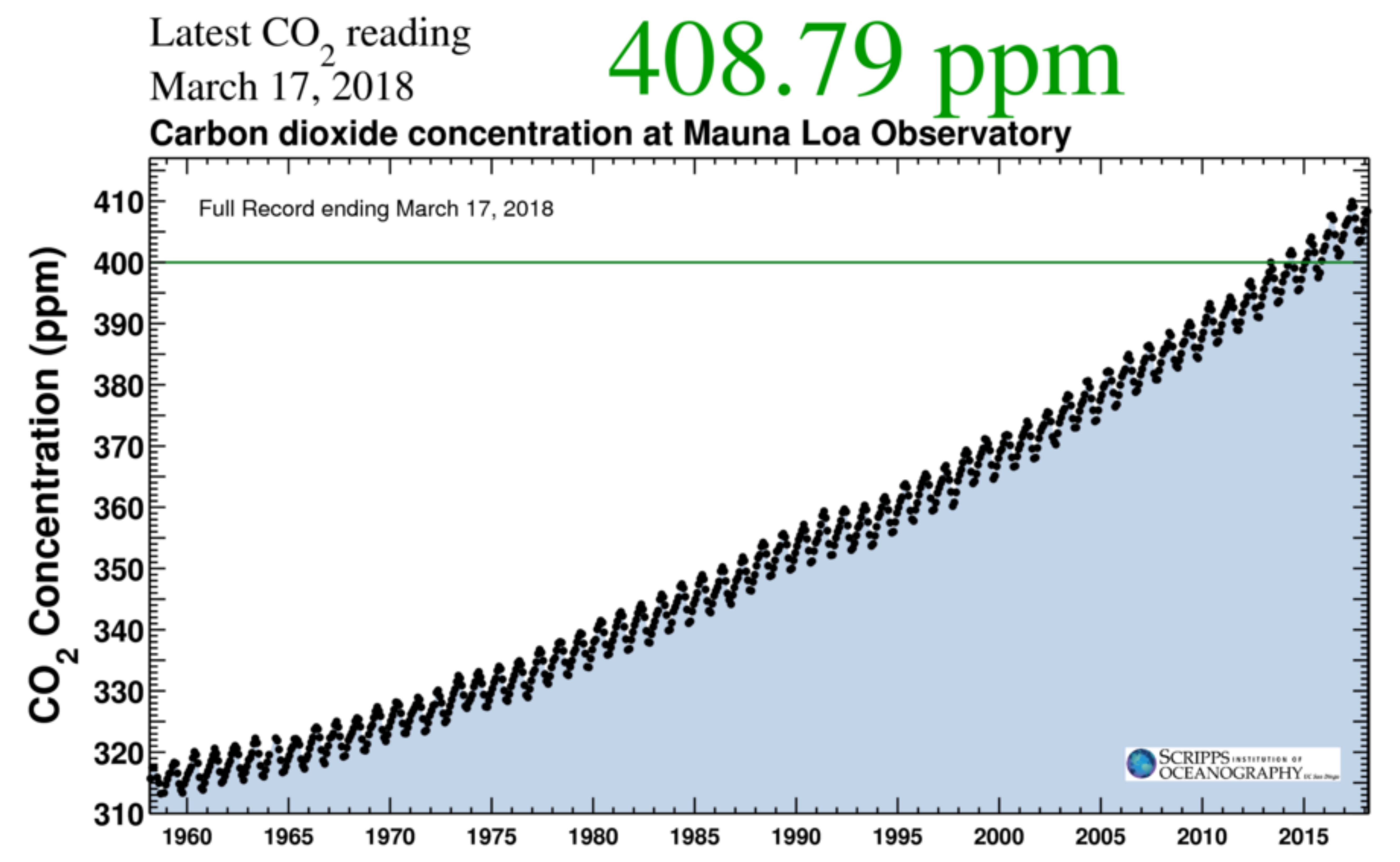
- Canopy structure seems to play a large role in SIF.
- This leaves us with the question of how does canopy structure have such a large control on the rate of photosynthesis.
- We are doing explicit 3-d modeling of leaf illumination in canopies of different structure and asking what would be the optimal distribution of photosynthetic capacity among the leaves.
- Preliminary results are promising - Sun leaves have more capacity and contribute more SIF.
- Leaf angle distribution is also important - using functions like “spherical” obscure important canopy properties.

COS - Another perspective on the Carbon Cycle



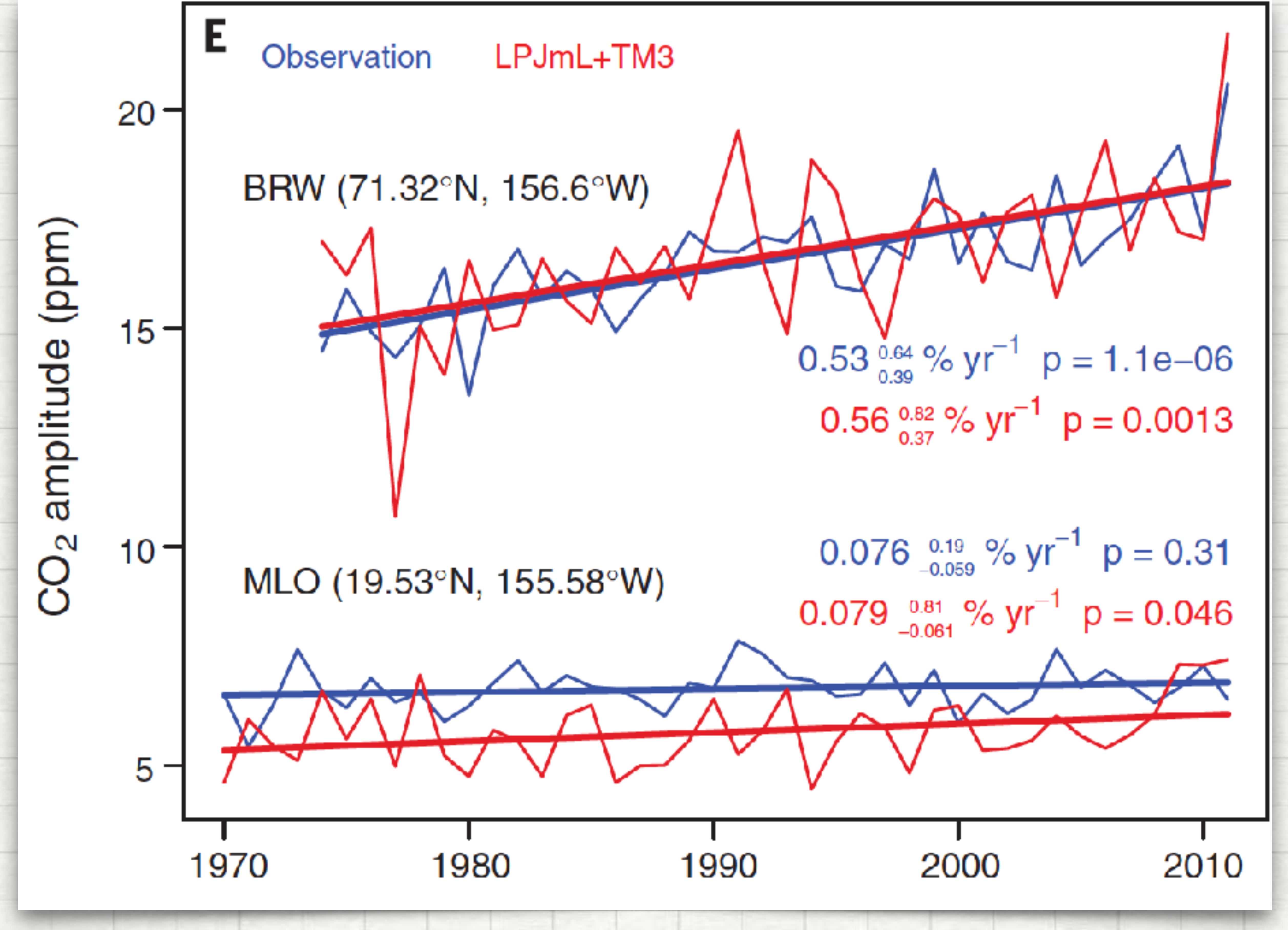


Enhanced Seasonal Exchange of CO_2 by Northern Ecosystems Since 1960



Graven, H. D., Keeling, R. F., Piper, S. C., Patra, P. K., Stephens, B. B., Wofsy, S. C., et al. (2013). Enhanced Seasonal Exchange of CO2 by Northern Ecosystems Since 1960. Science. http://doi.org/10.1126/science.1239207

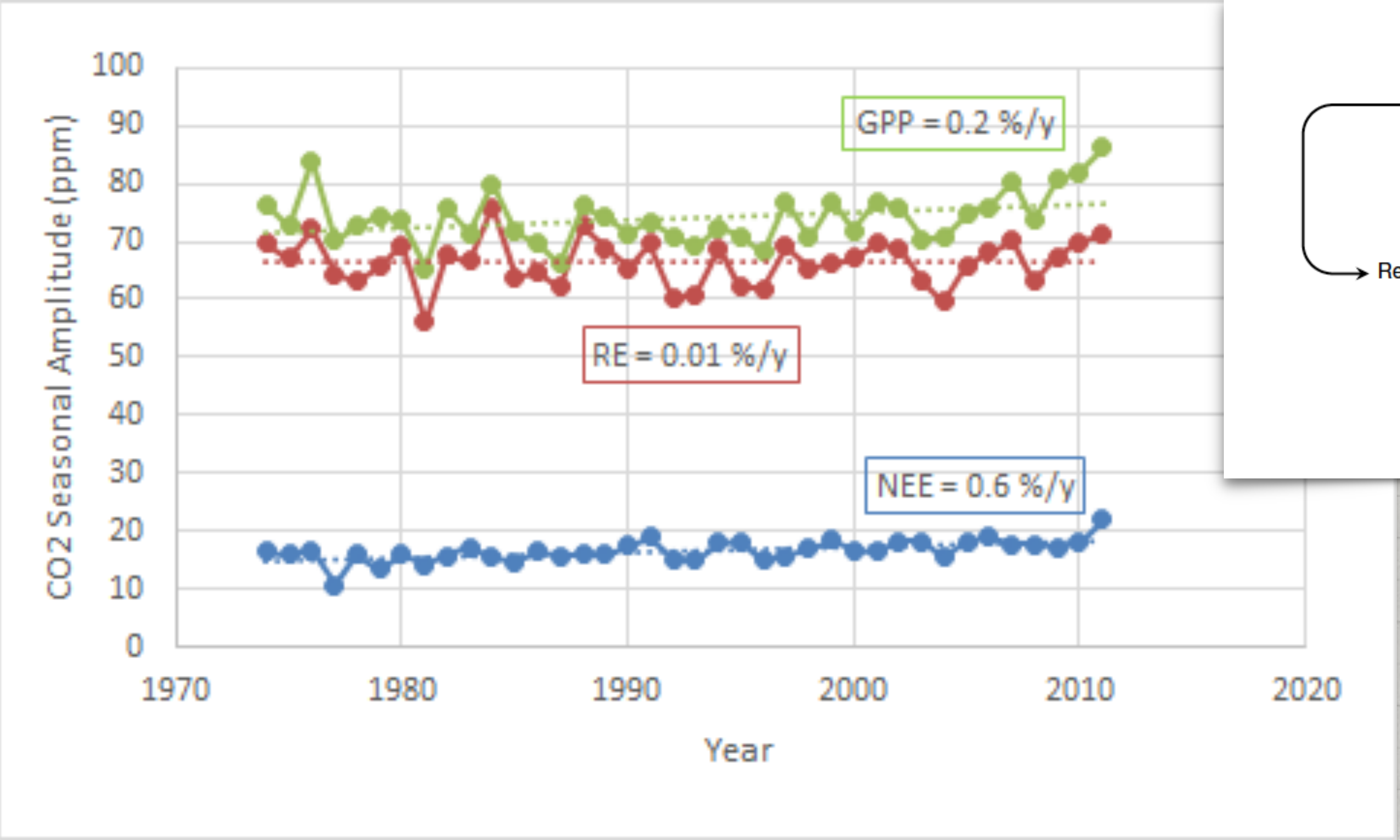
The peak to peak seasonal variation is increasing at Pt Barrow

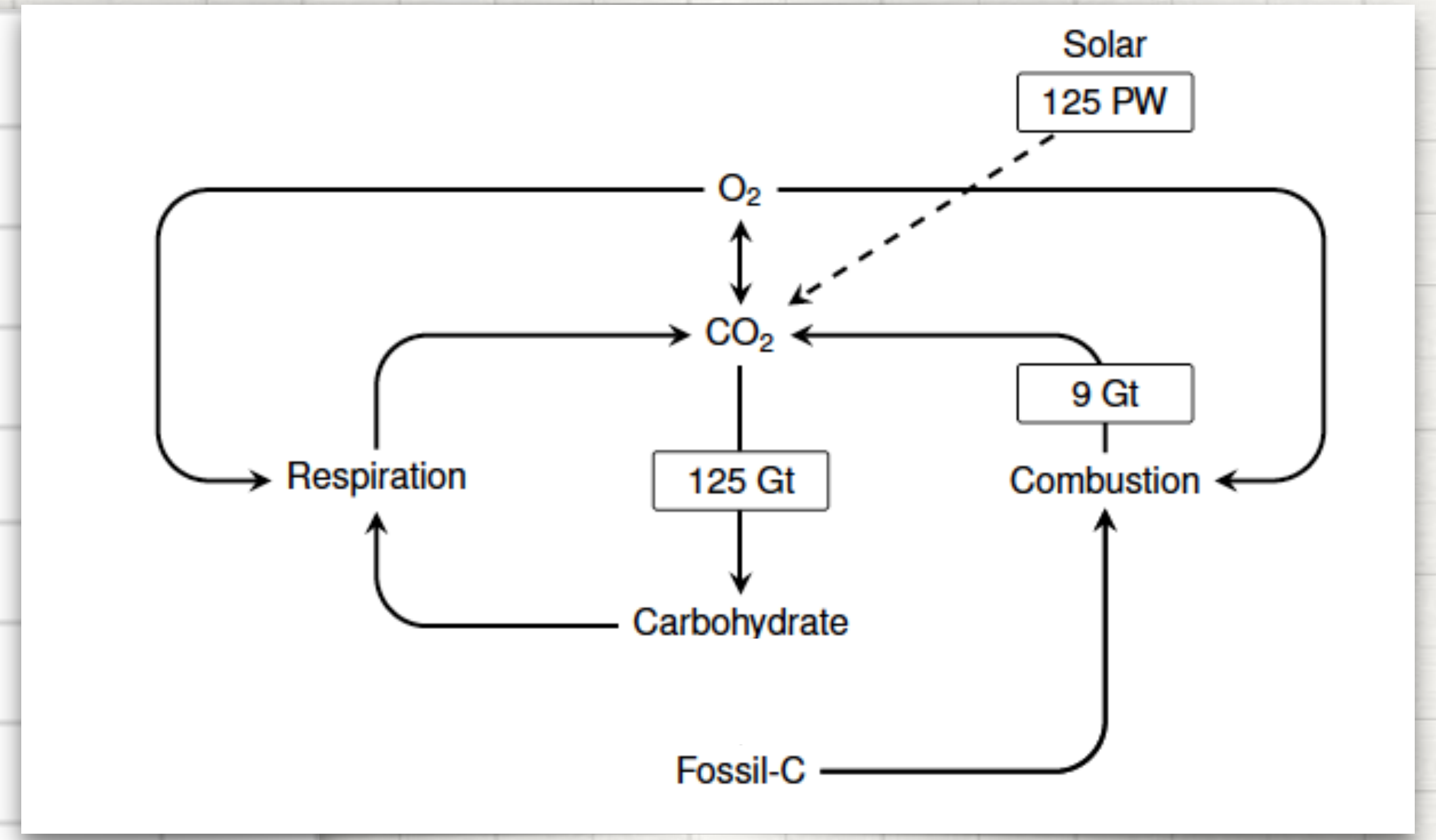


Graven, H. D., Keeling, R. F., Piper, S. C., Patra, P. K., Stephens, B. B., Wofsy, S. C., et al. (2013). Enhanced Seasonal Exchange of CO2 by Northern Ecosystems Since 1960. Science. http://doi.org/10.1126/science.1239207

Forkel, M., Carvalhais, N., Rödenbeck, C., Keeling, R., Heimann, M., Thonicke, K., et al. (2016). Enhanced seasonal CO2 exchange caused by amplified plant productivity in northern ecosystems. Science,, 351(6274), 696–699. http://doi.org/10.1126/science.aac4971

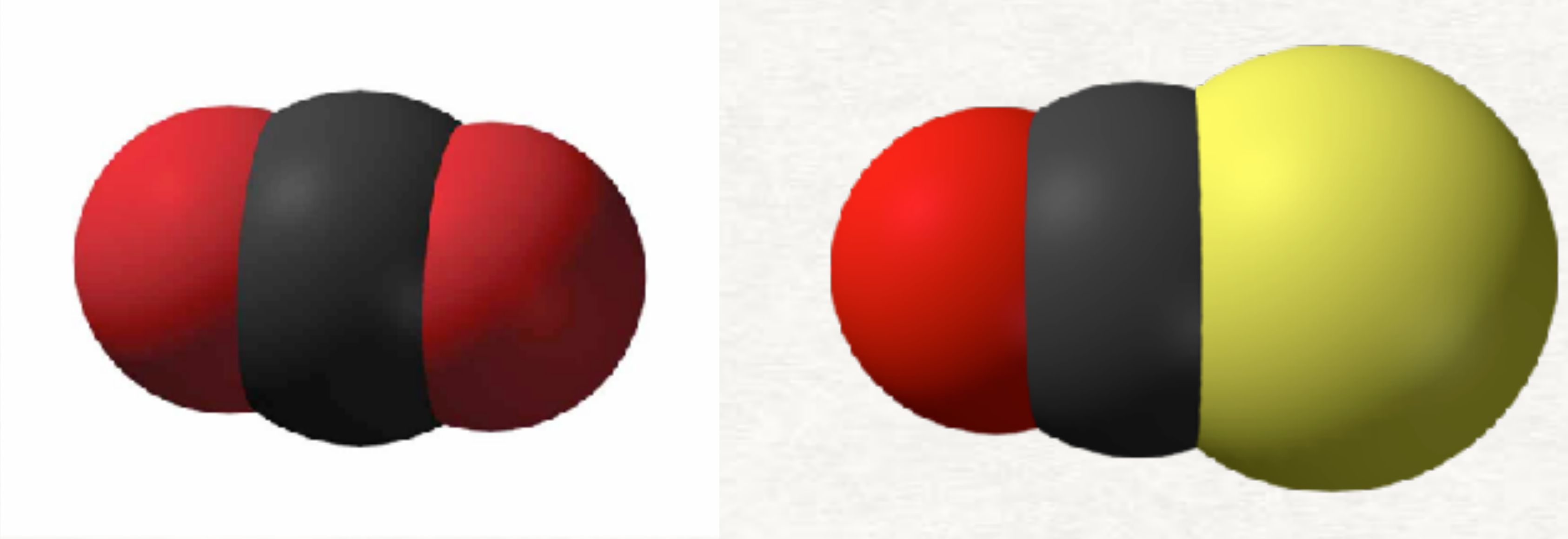
The observed response is the difference between photosynthesis and respiration.





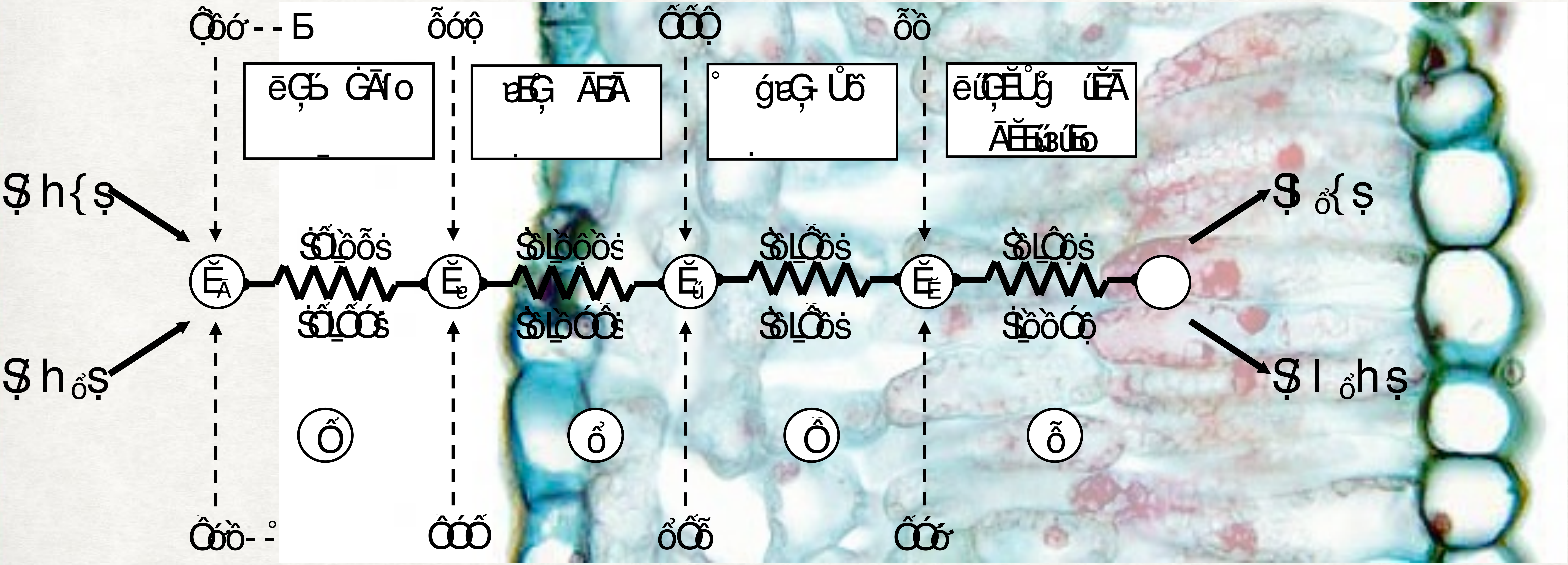
- Respiration and photosynthesis respond to different factors and must be modeled separately.
- We have two variables and one observation.

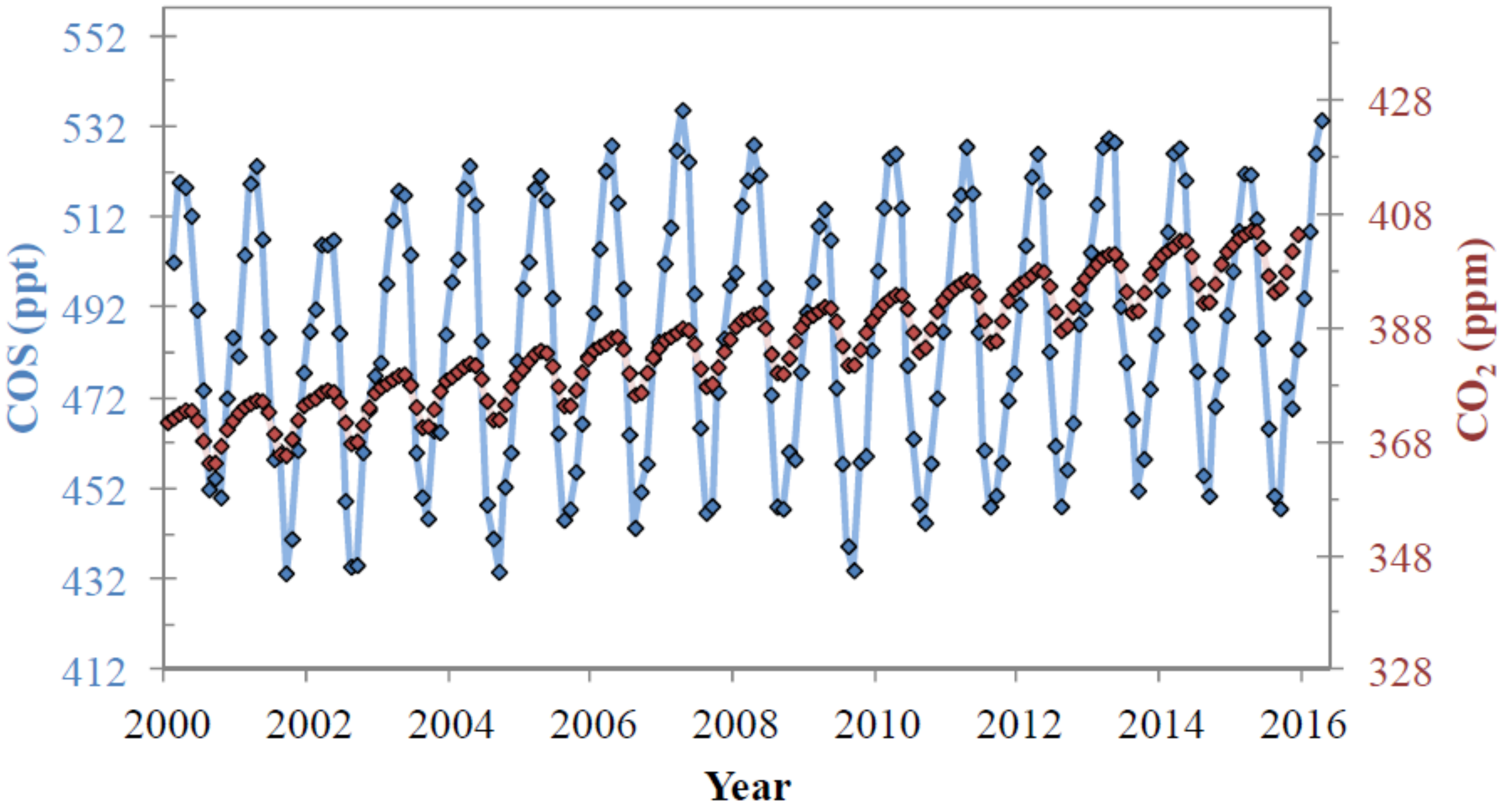
What do we know about COS?

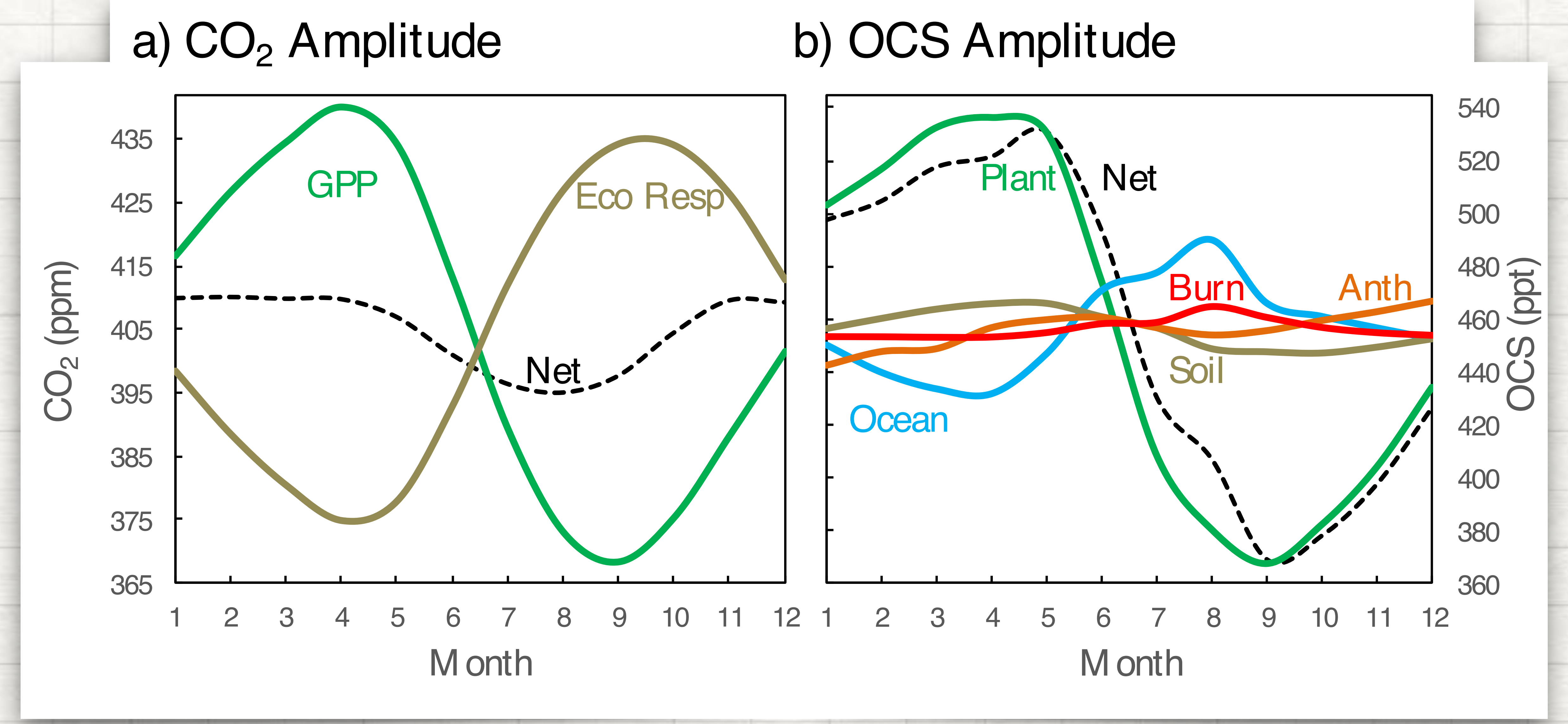


	CO_2	OCS or COS
atmospheric concentration	400 ppm	500 ppt
turnover time	~7 years	~2 years
net atmospheric change	5% per year	30% per year
key enzymes	Rubisco + respiration	Carbonic-anhydrase

Leaf Uptake OCS follows the same path as CO_2

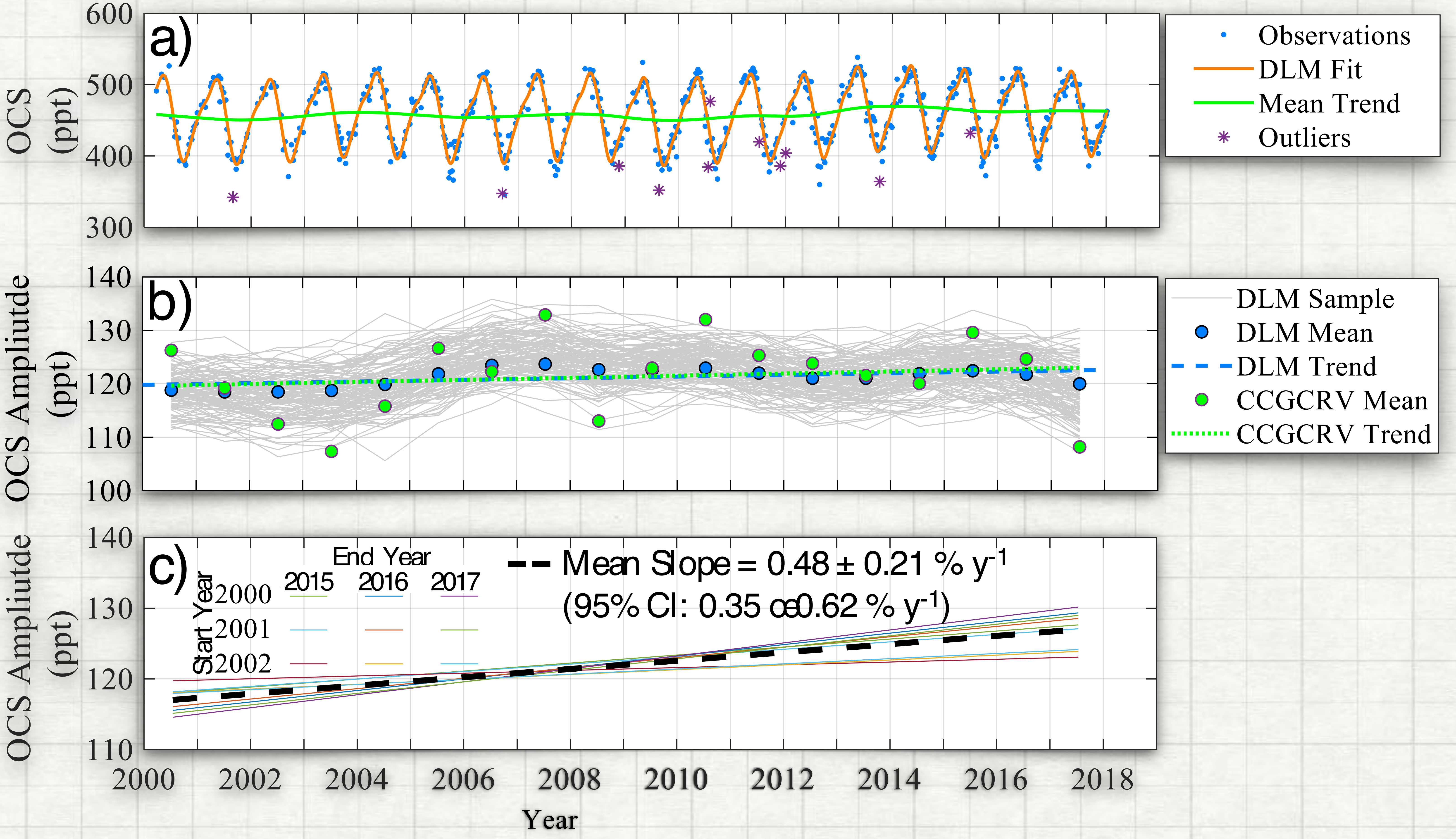


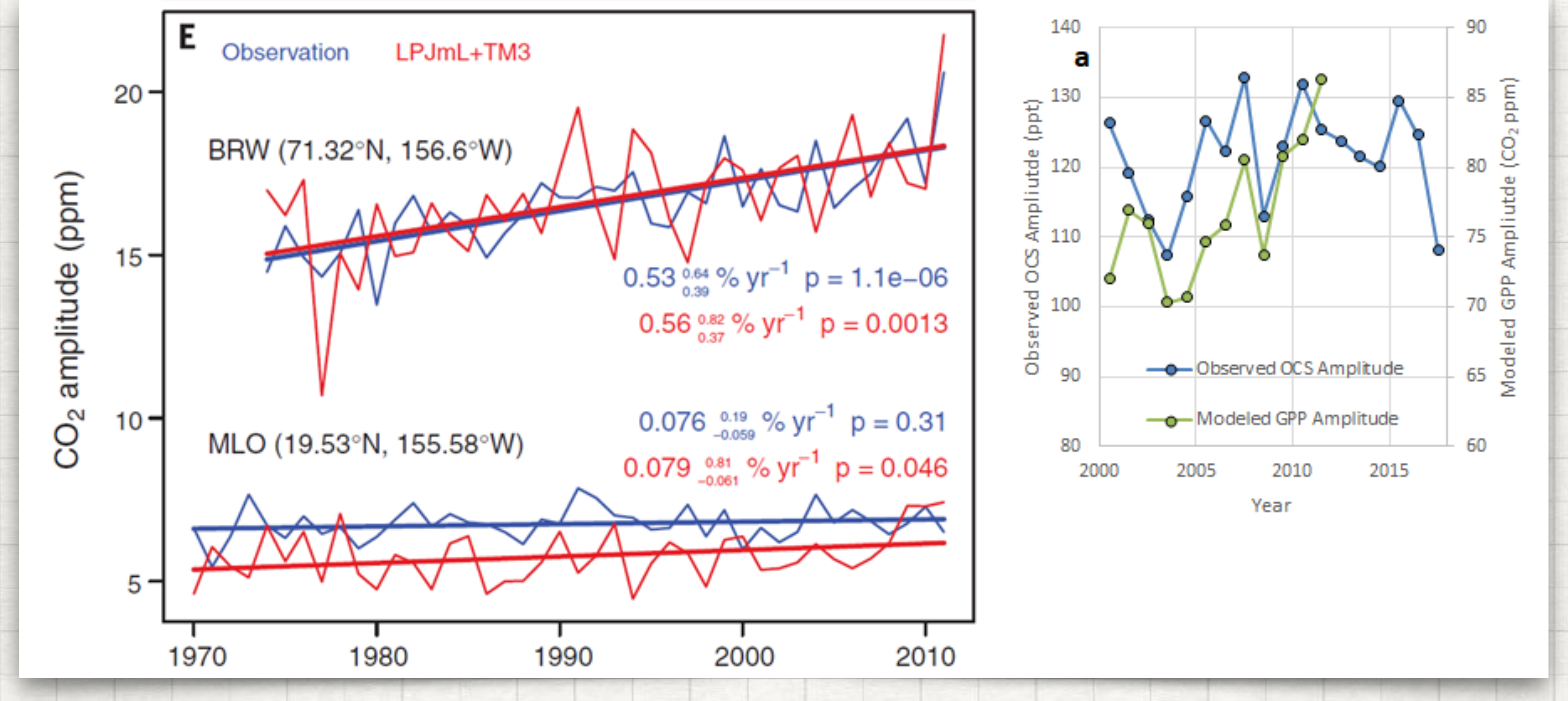

COS (ppt)
552
532
512
492
472
452
432
412
CO$_2$ (ppm)
428
408
388
368
348
328
2000
2002
2004
2006
2008
2010
2012
2014
2016
Year



Global 3-D atmospheric transport simulations extracted at Barrow. Budget components at the Barrow site were obtained from global gridded source and sink inventories which were simulated in 3-D atmospheric chemical transport models(Kuai et al. 2015, Forkel et al. 2016). The dominant regional budget components influencing the CO_2 amplitude at Barrow are gross primary production (green) and the offsetting ecosystem respiration source (brown) which result in a relatively small net signal (black) **(A)**. For OCS, the plant sink (green) is the dominant influence on the Barrow seasonality which results in a similar net sink (black) **(B)**. Other OCS sources and sinks were also accounted for including soil (brown), biomass burning (red), industry (orange), and ocean (blue) budget components. Detailed methods are in the supporting online materials.

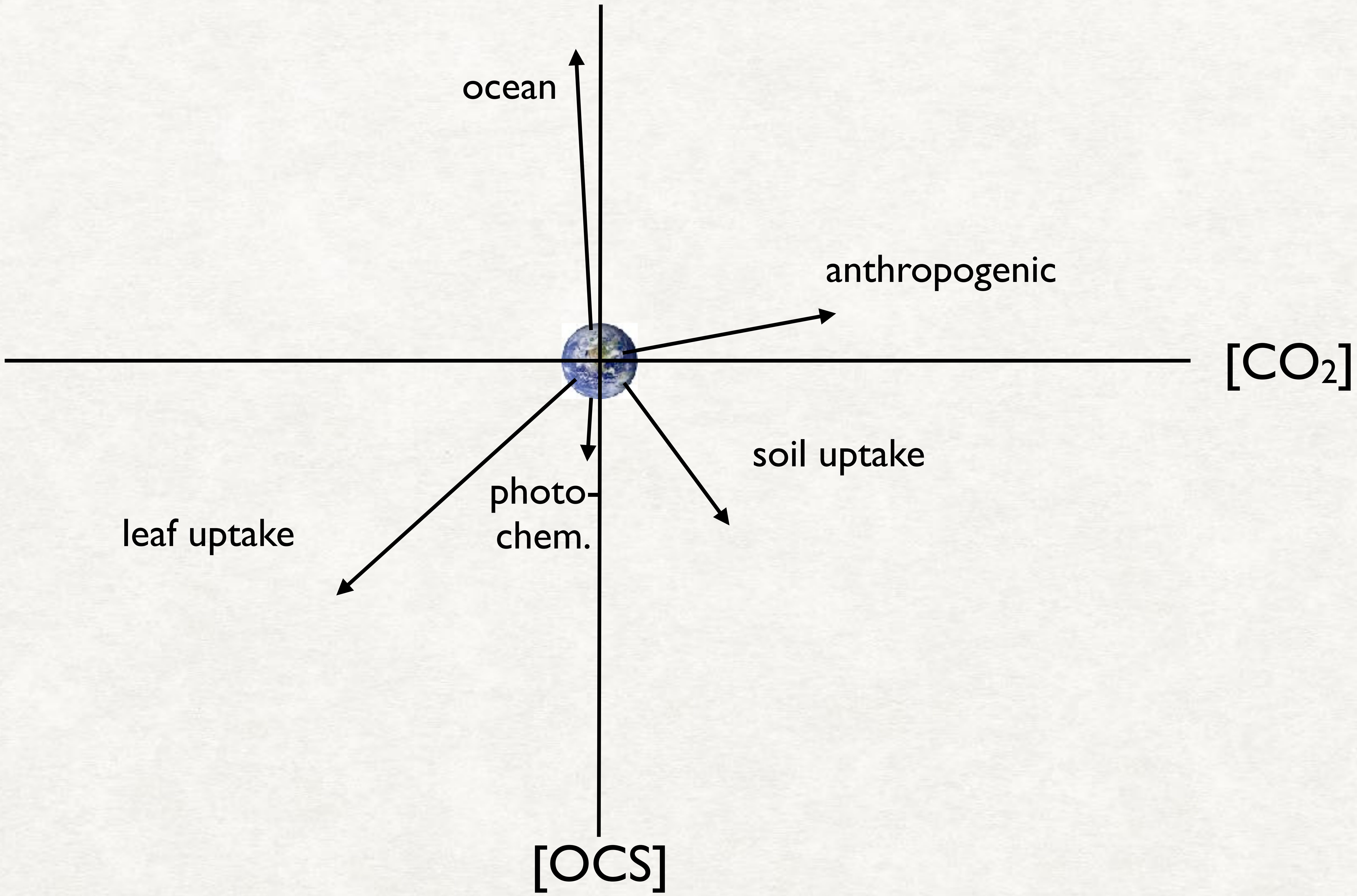
COS Seasonal Variation at Pt Barrow



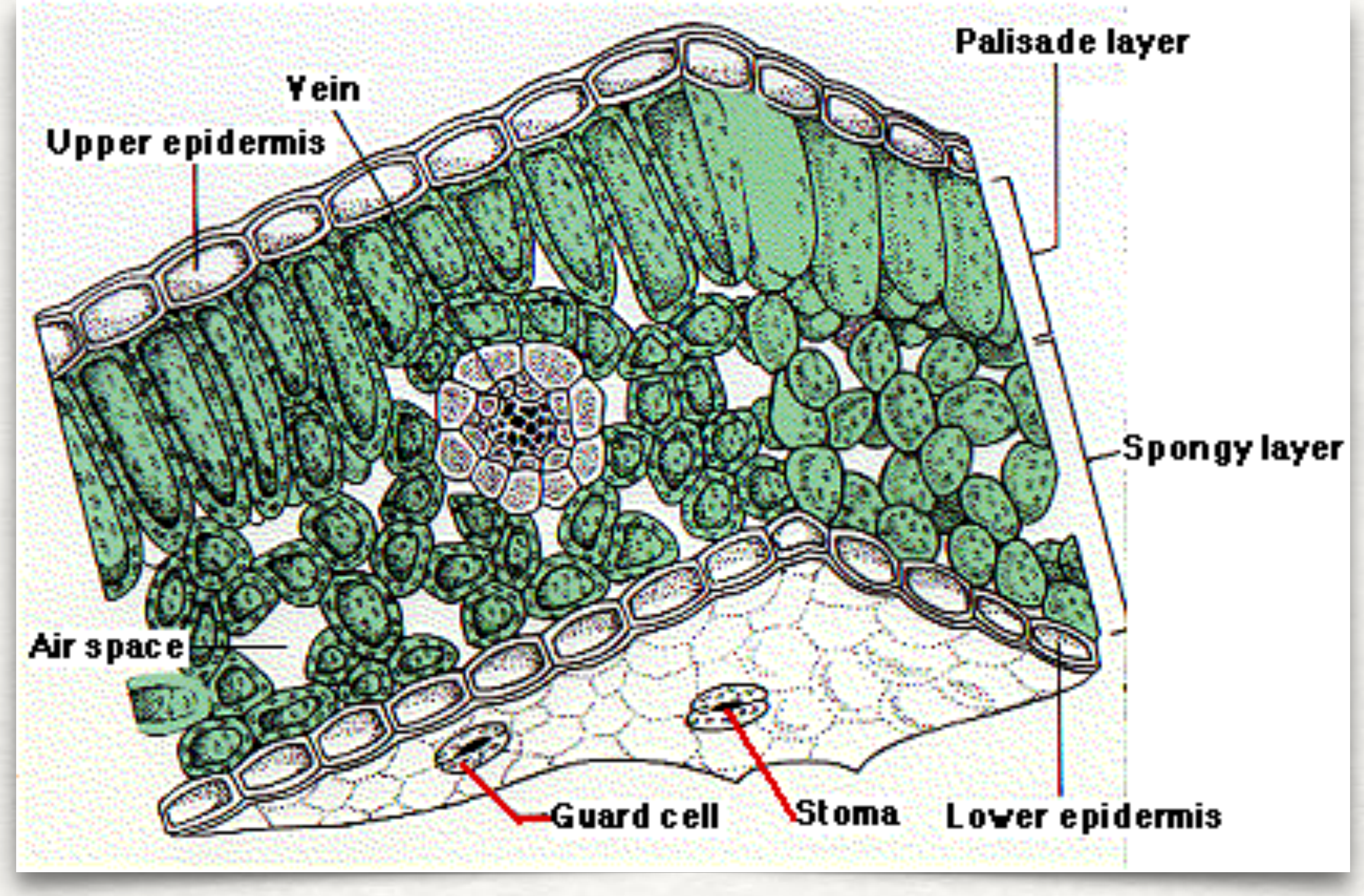


The measured COS seasonal variation (blue) matches the modeled GPP (green) fairly well.
Forkel et al., are probably getting photosynthesis about right.
It is increasing.

The atmosphere [COS] integrates the impact of all exchanges



Modeling Photosynthesis



Solving for Stomatal Conductance (g).

The approach takes advantage of the observation that g is generally highly correlated with the rate of Photosynthesis (A_n), and that we have reasonably good models of Photosynthesis.

$$g = m \cdot A_n \frac{h_s}{c_s} + b$$

Where: h_s and c_s are the relative humidity and CO_2 concentrations at the leaf surface, respectively; m an b are regression coefficients, and:

$$A_n = f(\mathrm{PAR}, \mathrm{Temp}, \mathrm{CO_2}, \mathrm{Stress}, V_{max})$$

Solving for CO_2 Assimilation (A_n)

C_3: Farquhar *et al.*, assumed that photosynthesis could approach the capacity of the limiting step and that the identity of this limiting step could switch as environmental conditions change.

$$A_n \leq min \begin{cases} J_e \\ J_c \\ J_s \end{cases} - R_d$$

$$J_e \quad \text{(Light limited rate)} = \alpha_p \epsilon_m Q_p \frac{(p_i - \Gamma^*)}{(p_i + 2\Gamma^*)}$$

$$J_c \quad \text{(Carboxylase limited rate)} = \frac{V_m (p_i - \Gamma^*)}{p_i + K_{app}}$$

$$J_s \quad \text{(Regeneration limited rate)} \approx \frac{V_m}{2}$$

$$R_d \approx 0.015 V_m$$

A_n	Assimilation (mol m^{-2} s^{-1})
R_d	Mitochondrial respiration (mol m^{-2} s^{-1})
p_i	partial pressure of CO_2 (Pa)
Q_p	light flux (mol m^{-2} s^{-1})
Γ^*	CO_2 compensation point (Pa)
α_p	absorptance
ϵ_m	quantum yield (mol/mol)
V_m	Rubisco activity (mol m^{-2} s^{-1})
K_{app}	Rubisco apparent Km (Pa)

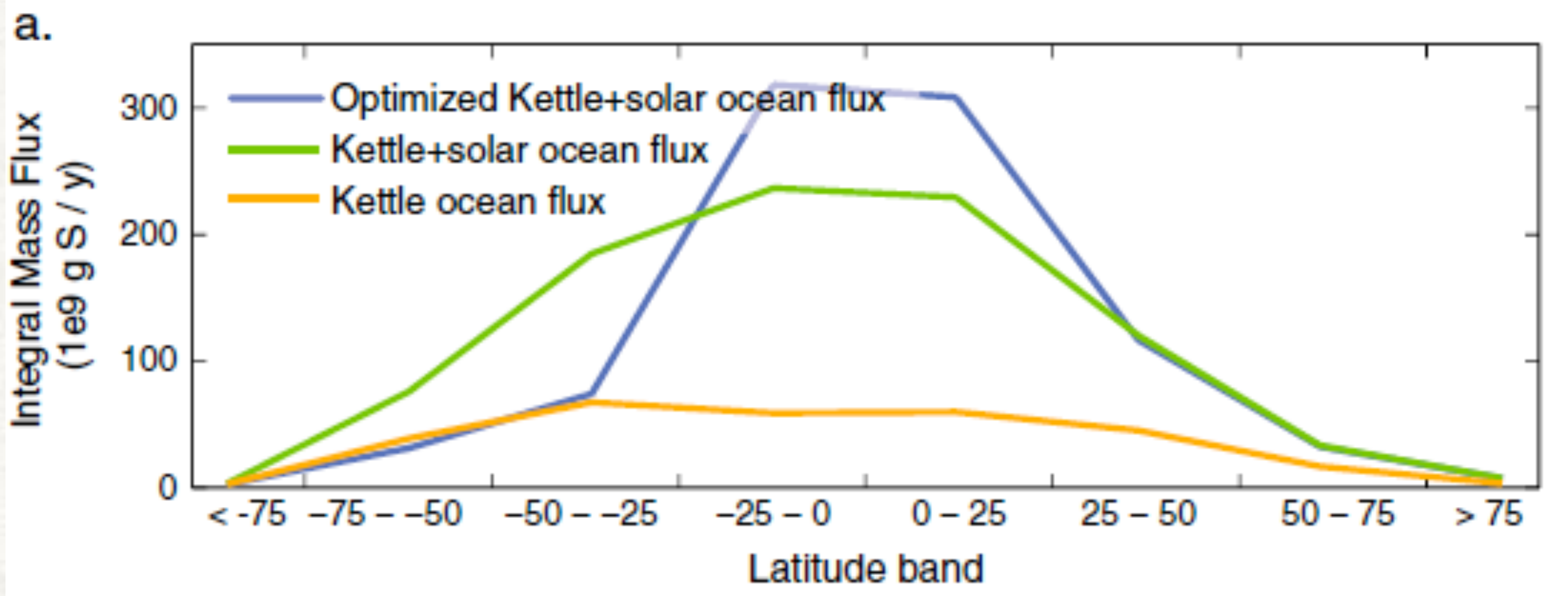
$$= K_m \left(1 + \frac{[O_2]}{K_i}\right)$$

$$\Gamma^* = \frac{[O_2]}{2\tau}$$

Rubisco specificity factor

A coupled model of the global cycles of carbonyl sulfide and CO_2: A possible new window on the carbon cycle

Joe Berry,[1] Adam Wolf,[2] J. Elliott Campbell,[3] Ian Baker,[4] Nicola Blake,[5] Don Blake,[5] A. Scott Denning,[4] S. Randy Kawa,[6] Stephen A. Montzka,[7] Ulrike Seibt,[8] Keren Stimler,[9] Dan Yakir,[9] and Zhengxin Zhu[6]



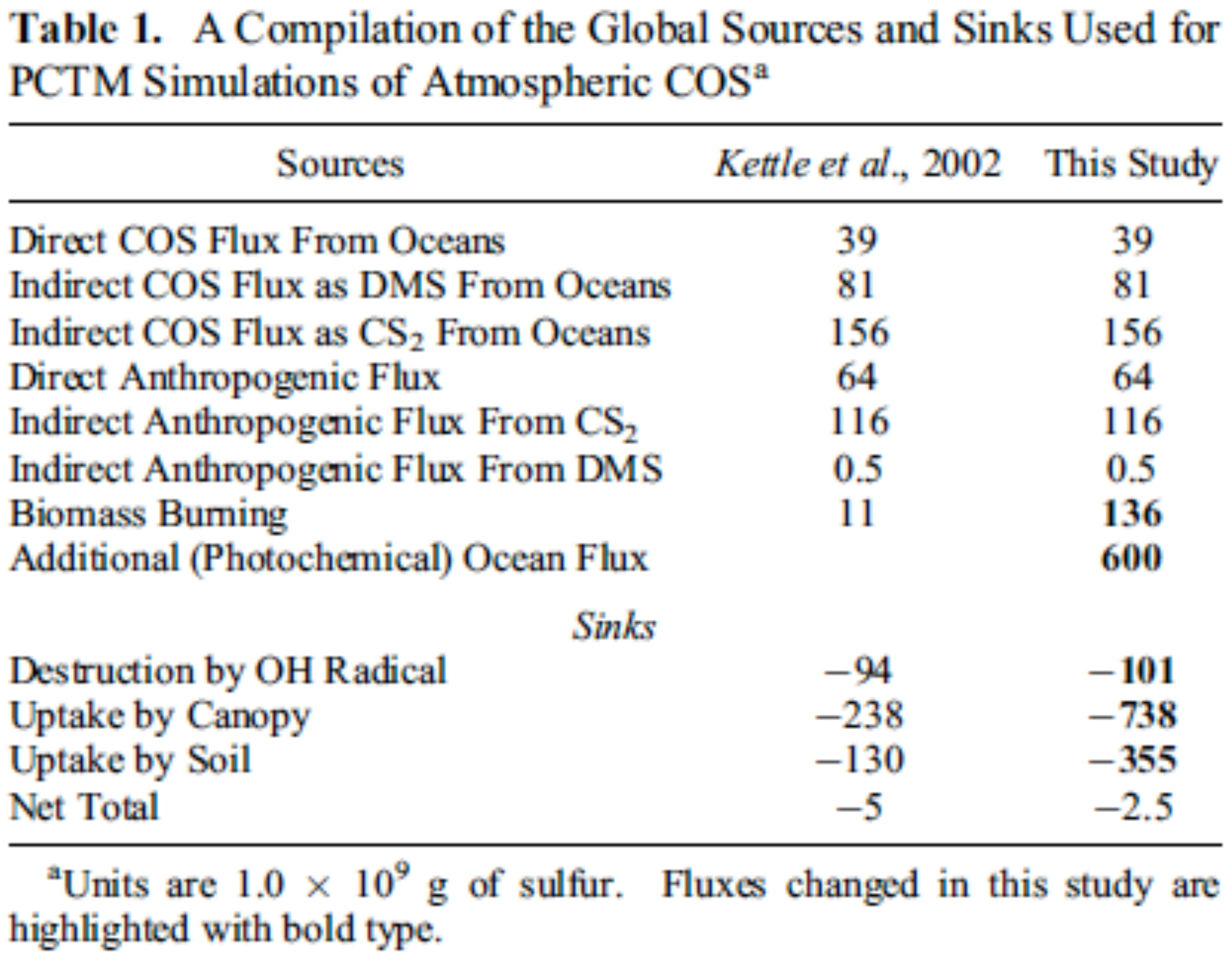
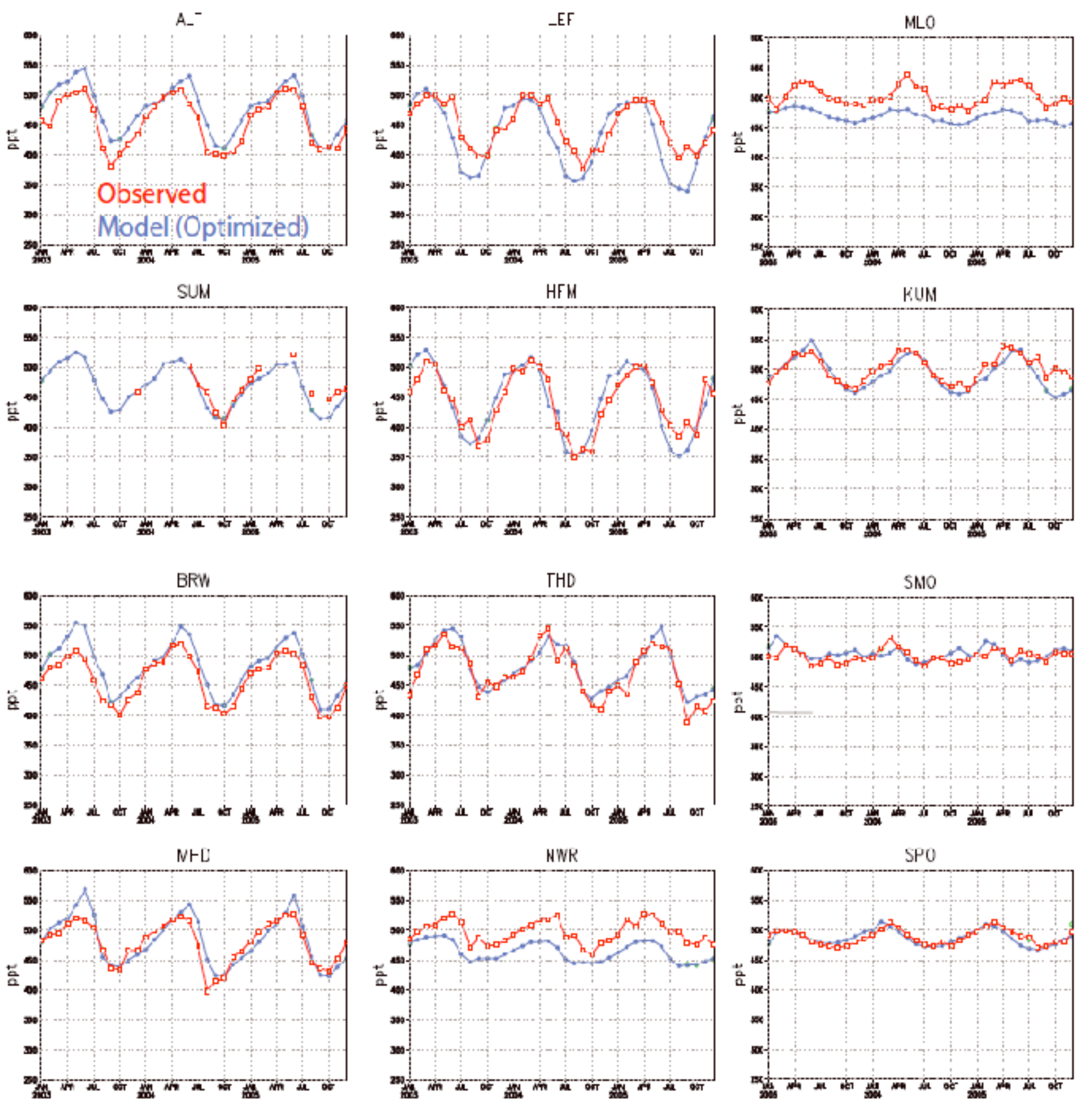


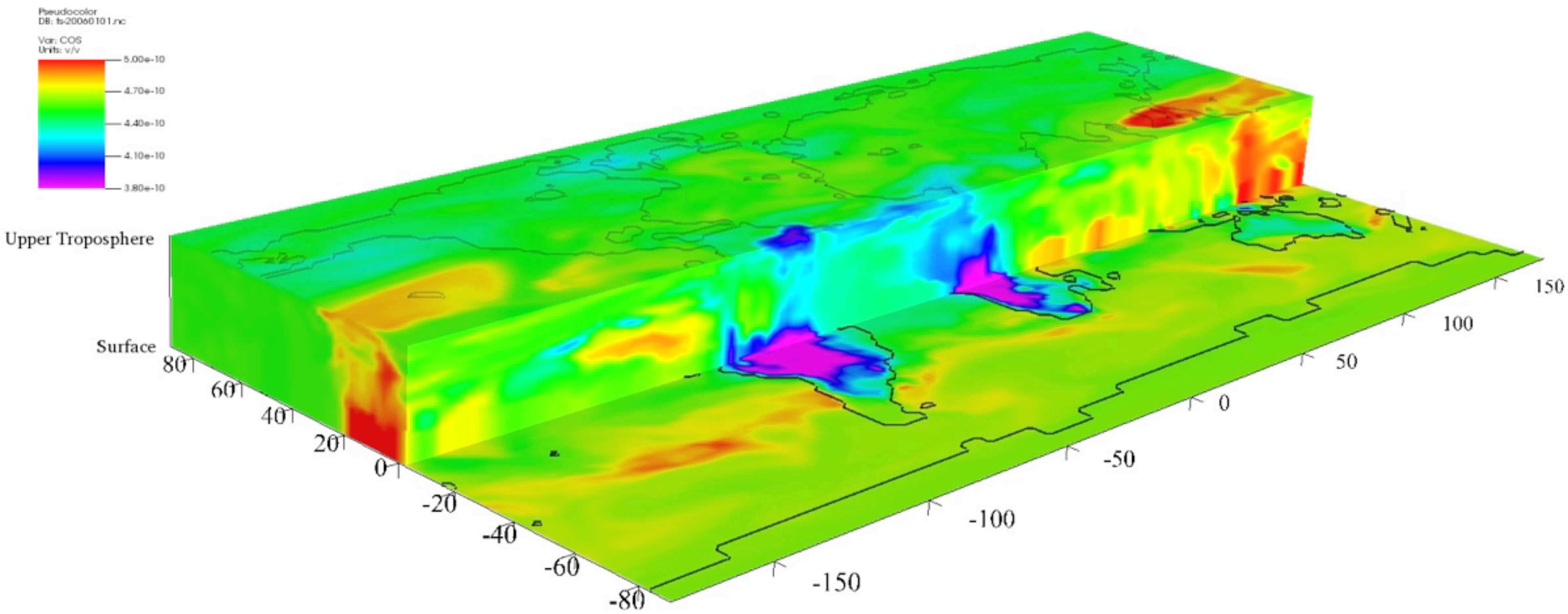
Table 1. A Compilation of the Global Sources and Sinks Used for PCTM Simulations of Atmospheric COS[a]

Sources	*Kettle et al.*, 2002	This Study
Direct COS Flux From Oceans	39	39
Indirect COS Flux as DMS From Oceans	81	81
Indirect COS Flux as CS_2 From Oceans	156	156
Direct Anthropogenic Flux	64	64
Indirect Anthropogenic Flux From CS_2	116	116
Indirect Anthropogenic Flux From DMS	0.5	0.5
Biomass Burning	11	**136**
Additional (Photochemical) Ocean Flux		**600**
Sinks		
Destruction by OH Radical	−94	**−101**
Uptake by Canopy	−238	**−738**
Uptake by Soil	−130	**−355**
Net Total	−5	−2.5

[a]Units are 1.0 × 10^9 g of sulfur. Fluxes changed in this study are highlighted with bold type.



[OCS] vertical slice at Equator



Jim Stinecipher and Elliott Campbell (unpublished)

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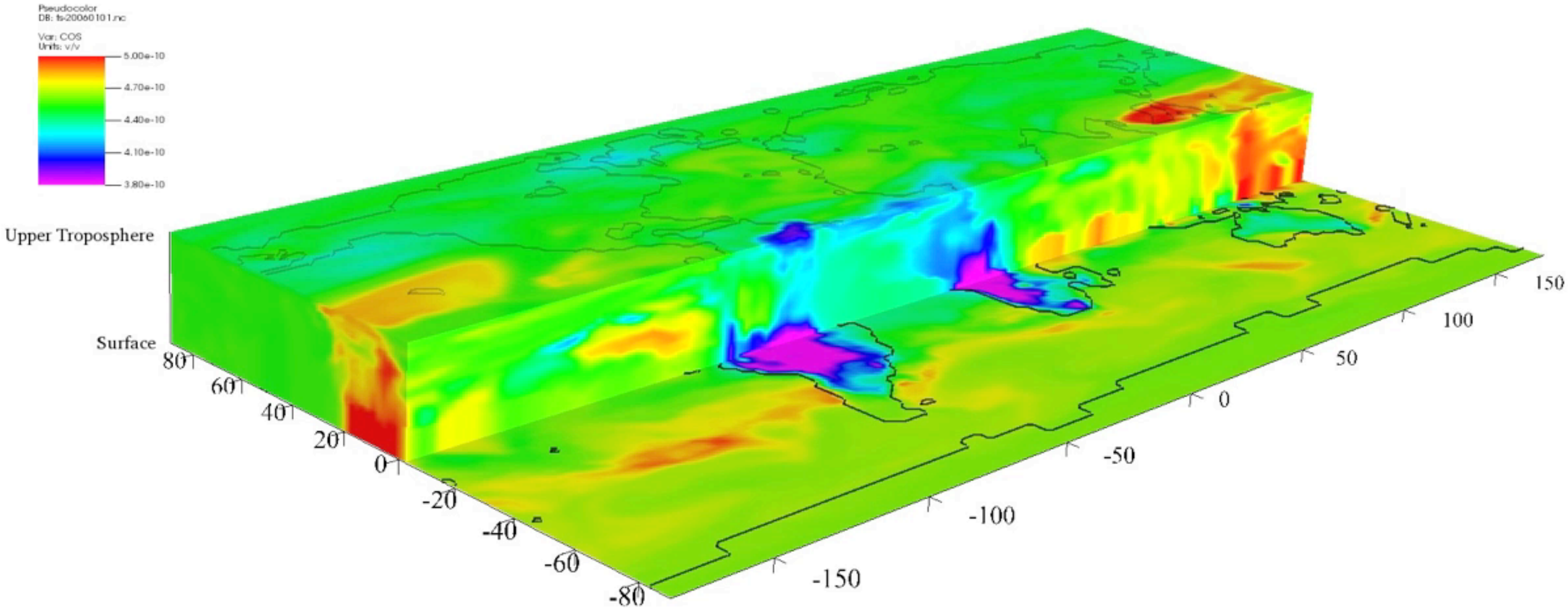
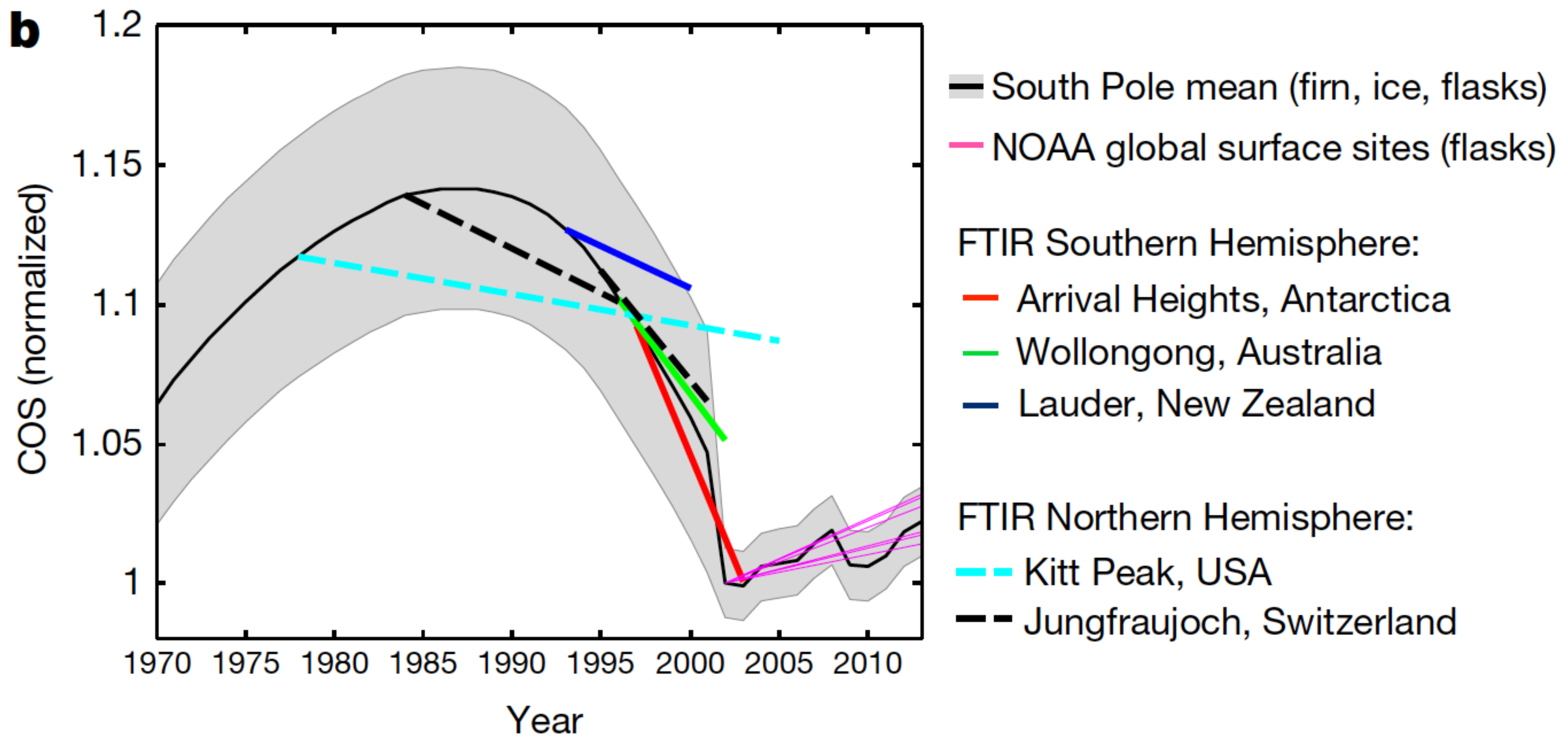
[OCS] vertical slice at Equator



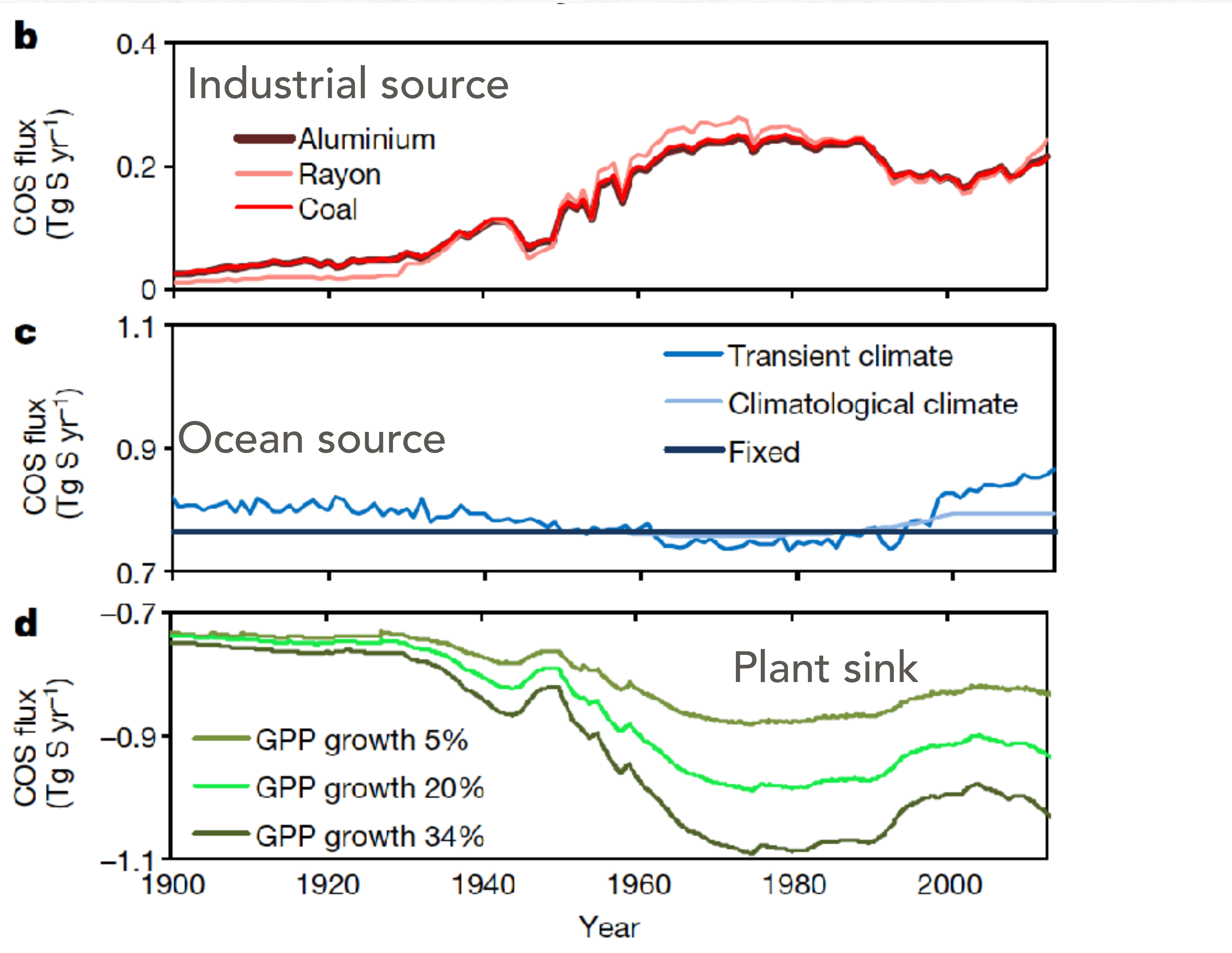
Jim Stinecipher and Elliott Campbell (unpublished)

A history of [COS] can be obtained from Antarctic ice

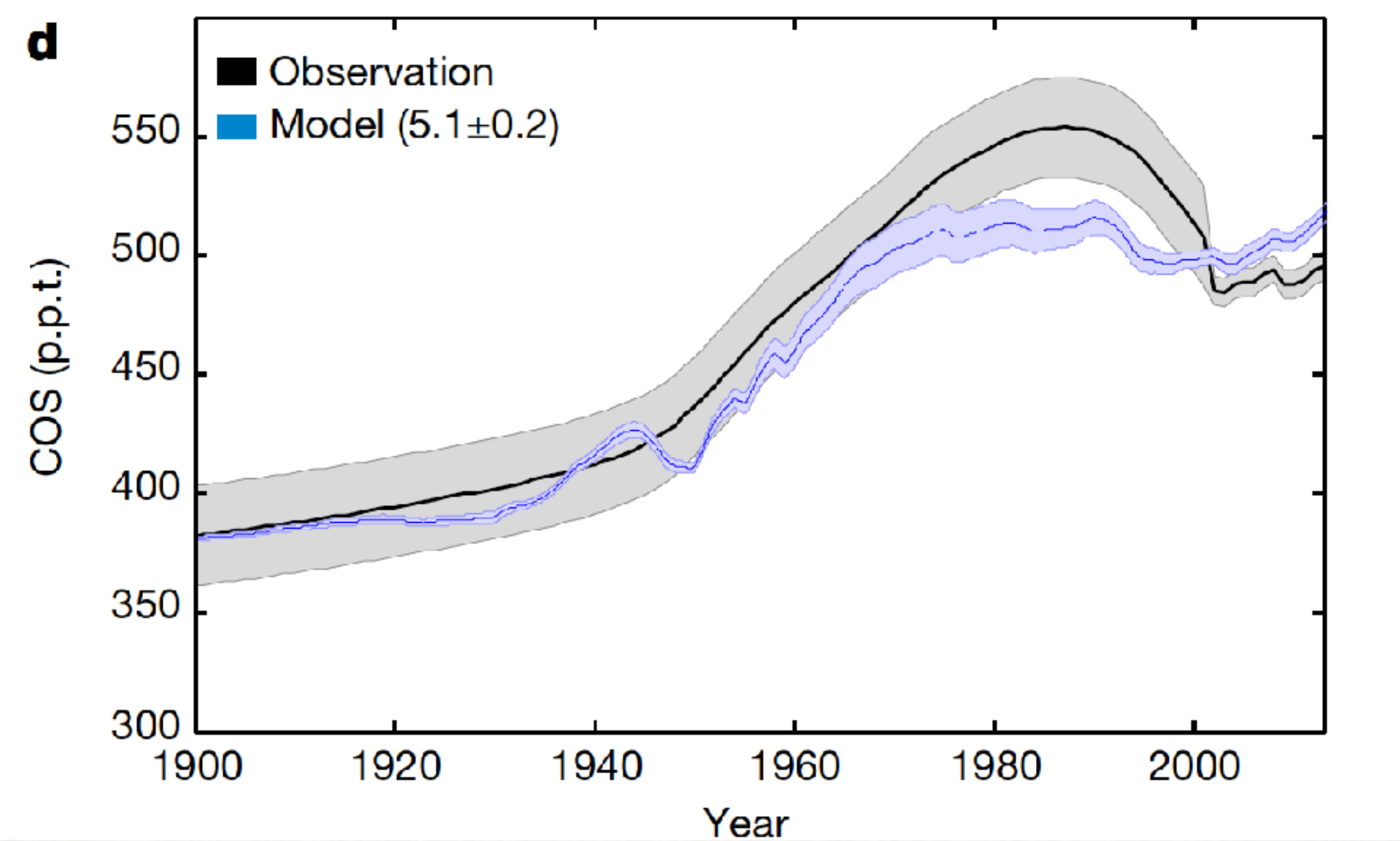


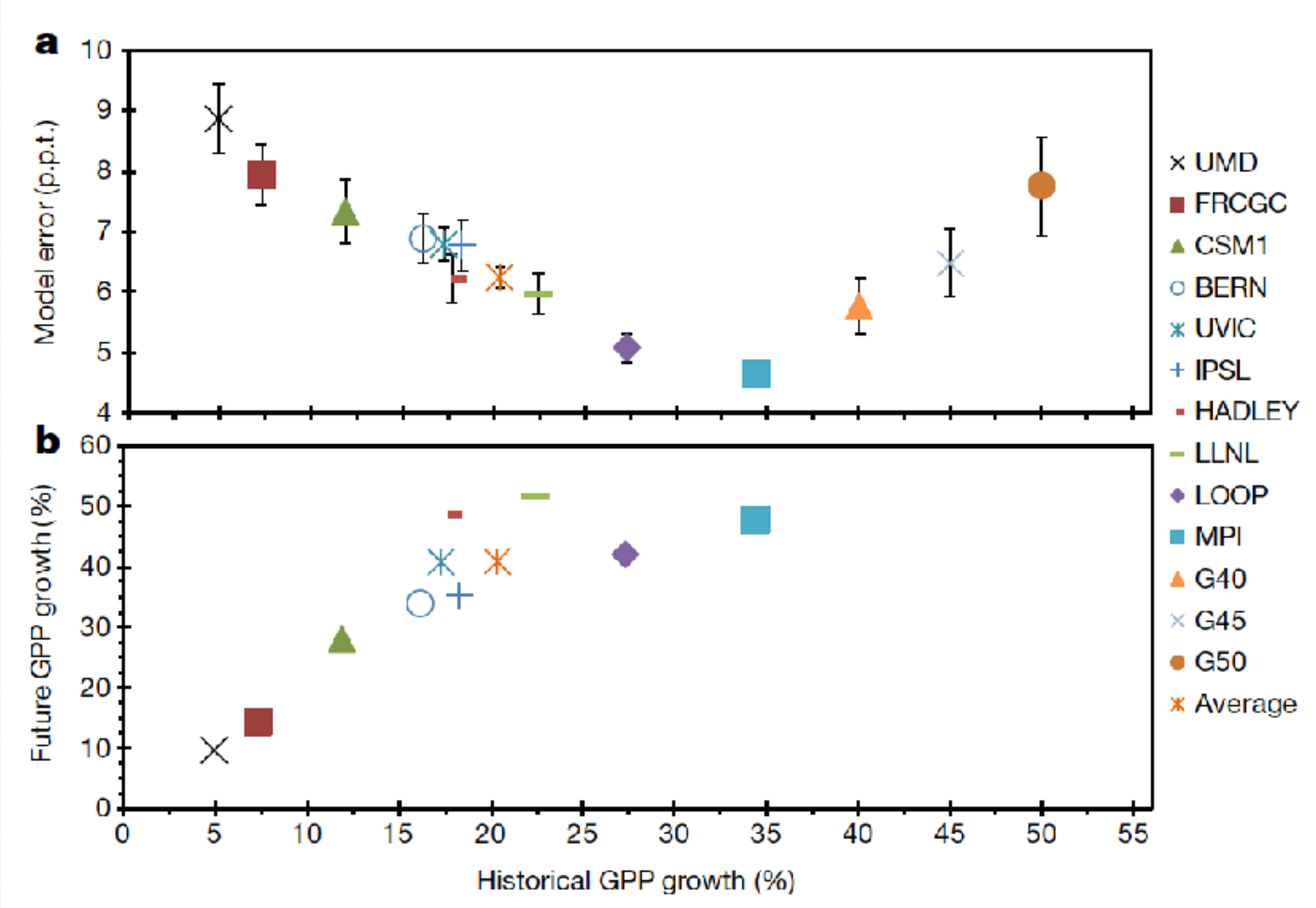
Can this tell us something about past photosynthesis?

Fluxes that contribute to the changing global [COS]

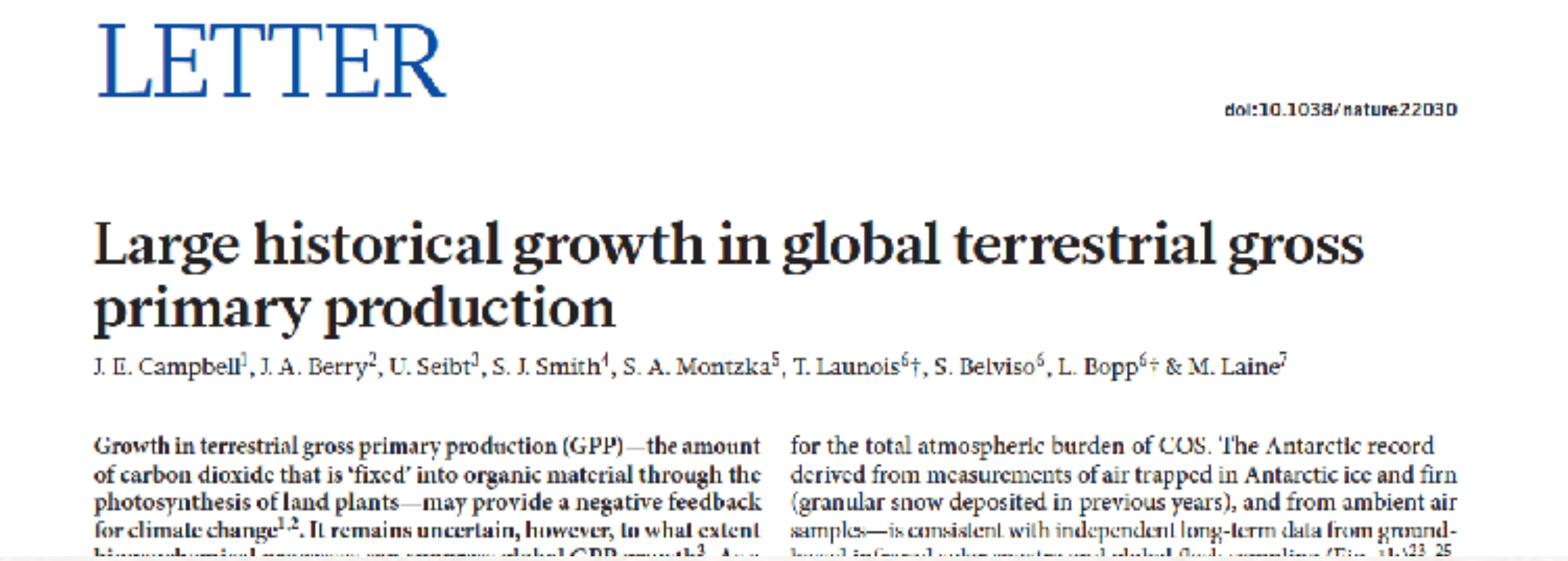


Find the GPP to minimize the error in COS growth





Models that predict moderate stimulation of photosynthesis by CO_2 best predict the observed COS growth



LETTER

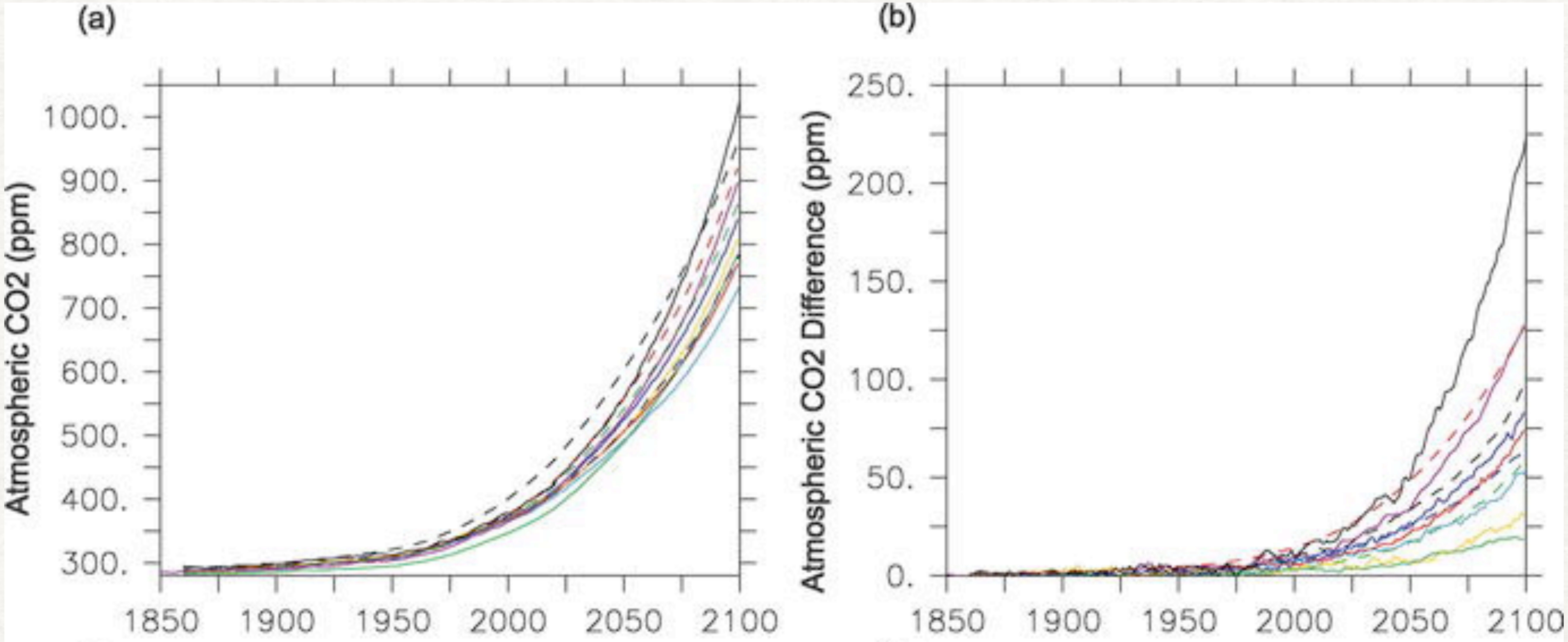
doi:10.1038/nature22030

Large historical growth in global terrestrial gross primary production

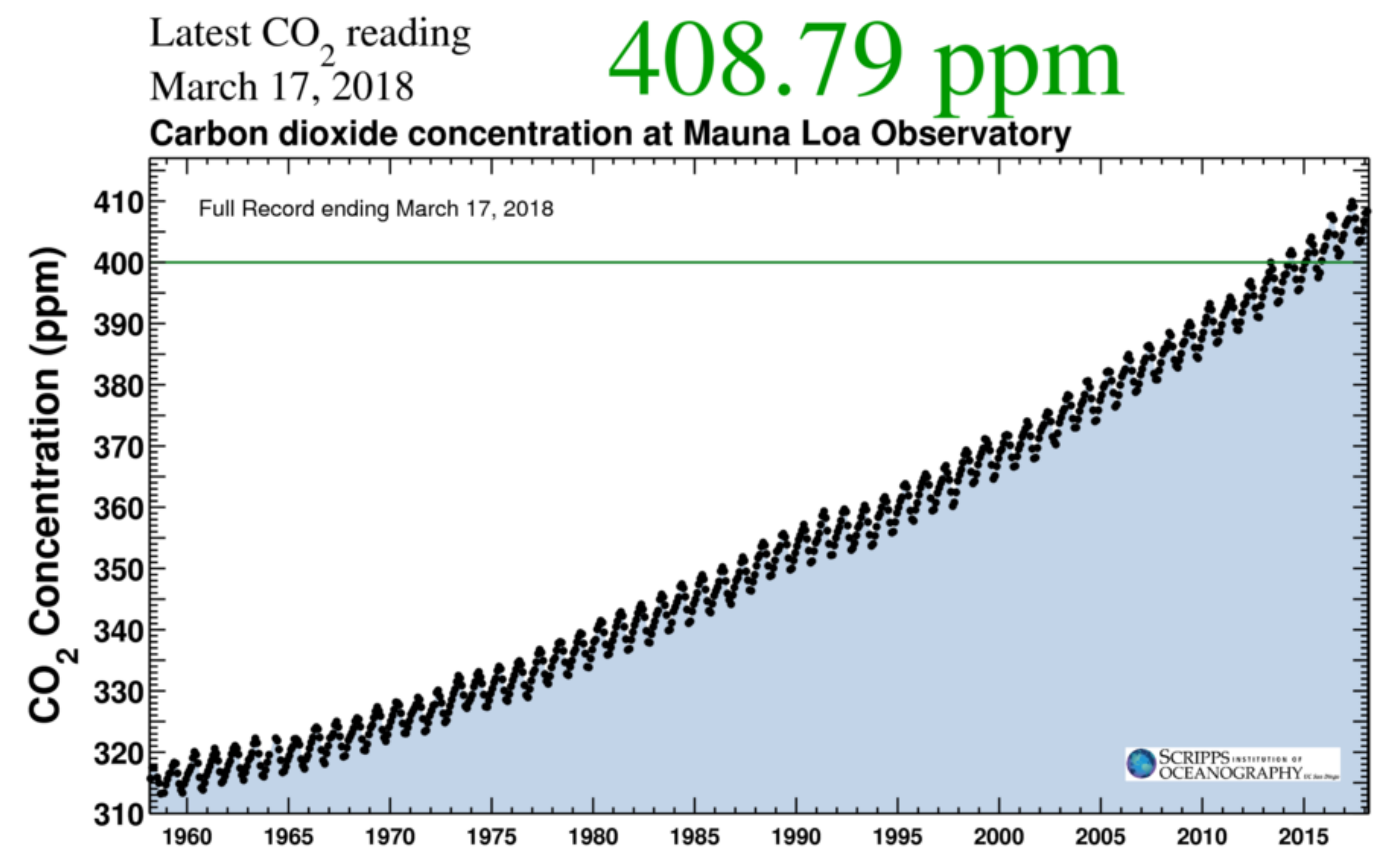
J. E. Campbell[1], J. A. Berry[2], U. Seibt[3], S. J. Smith[4], S. A. Montzka[5], T. Launois[6]†, S. Belviso[6], L. Bopp[6]† & M. Laine[7]

Growth in terrestrial gross primary production (GPP)—the amount of carbon dioxide that is 'fixed' into organic material through the photosynthesis of land plants—may provide a negative feedback for climate change[1,2]. It remains uncertain, however, to what extent

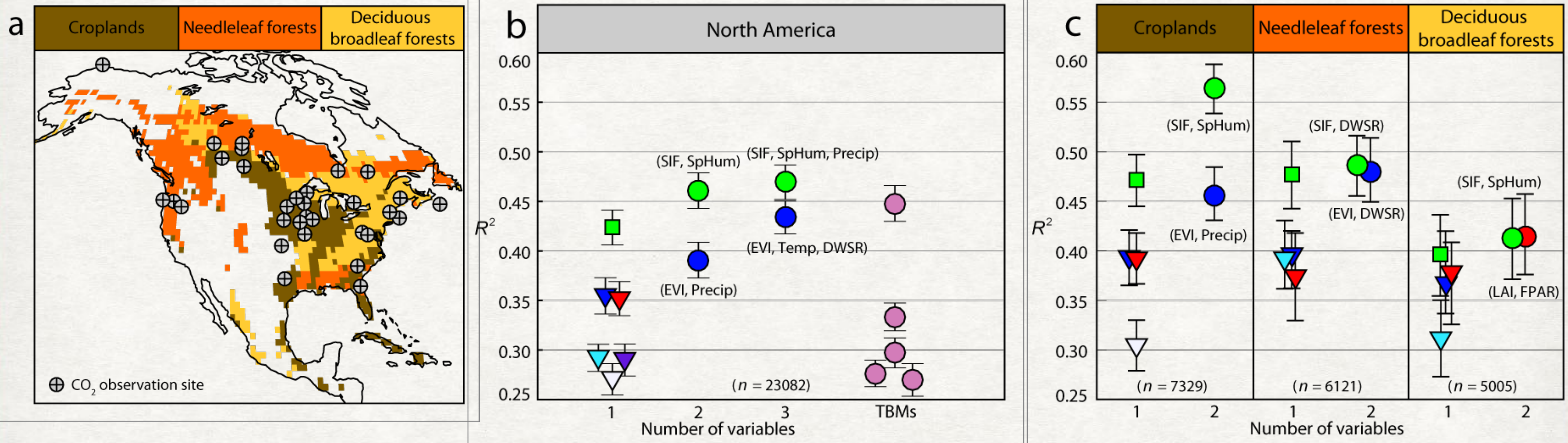
for the total atmospheric burden of COS. The Antarctic record derived from measurements of air trapped in Antarctic ice and firn (granular snow deposited in previous years), and from ambient air samples—is consistent with independent long-term data from ground-



Ok, We have a feedback mechanism. Is it adequate to control raising [CO_2]?



SIF alone explains more variation in regional CO$_2$ inversions than most TBMs (terrestrial biosphere models)



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