

SMS 598: Calibration and Validation for Ocean Color Remote Sensing

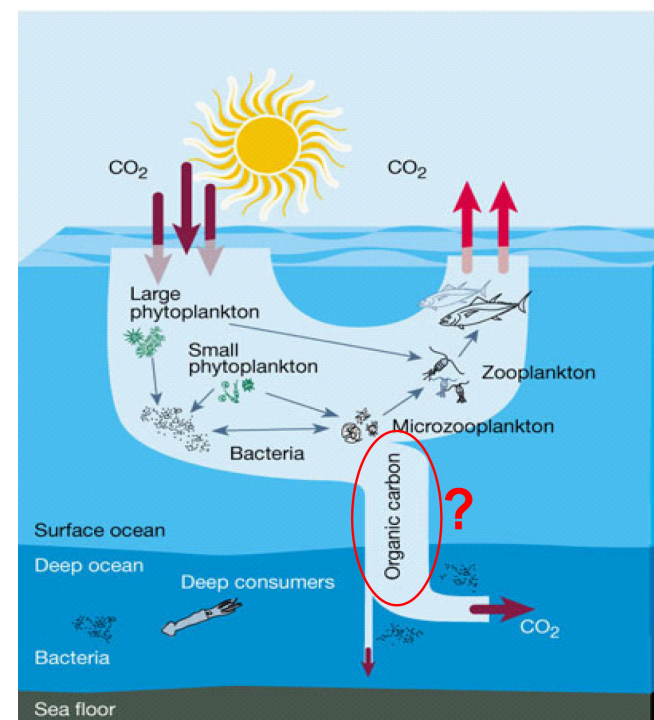
Lecture 17 Primary Productivity

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18 July 2013

Primary productivity =

light * phytoplankton * photosynthetic
mass coefficients



Primary productivity =

light (λ) * phytoplankton mass
chl? cell? carbon? or ?

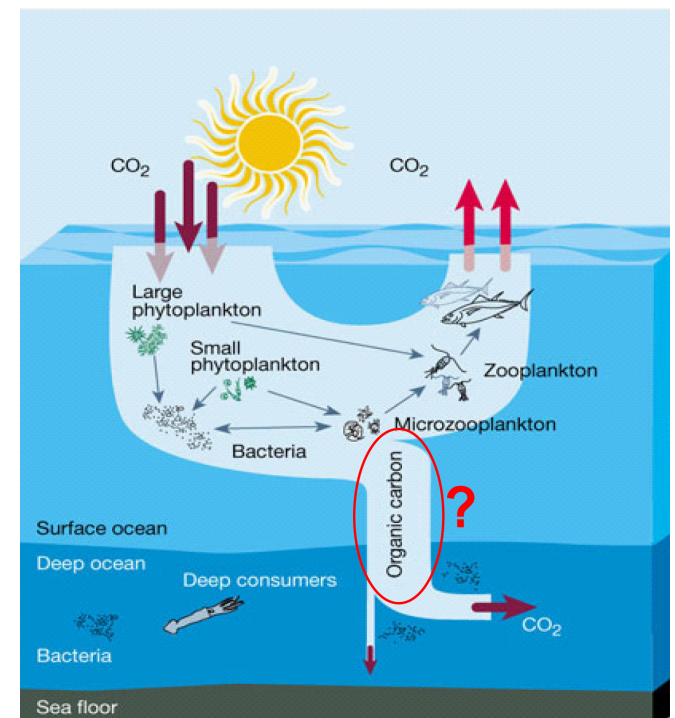
* photosynthetic coefficients
normalized to phytoplankton
and function of light, growth, etc.

What is photosynthesis ?

How many 'types' of productivity are in
aquatic systems; how are these different
types of productivities measured?

What parameters are in the productivity
models?

Against what data do we test these models?



Light: do we need surface or depth ?

Profile – typically one profile per location

Mooring – several depths,

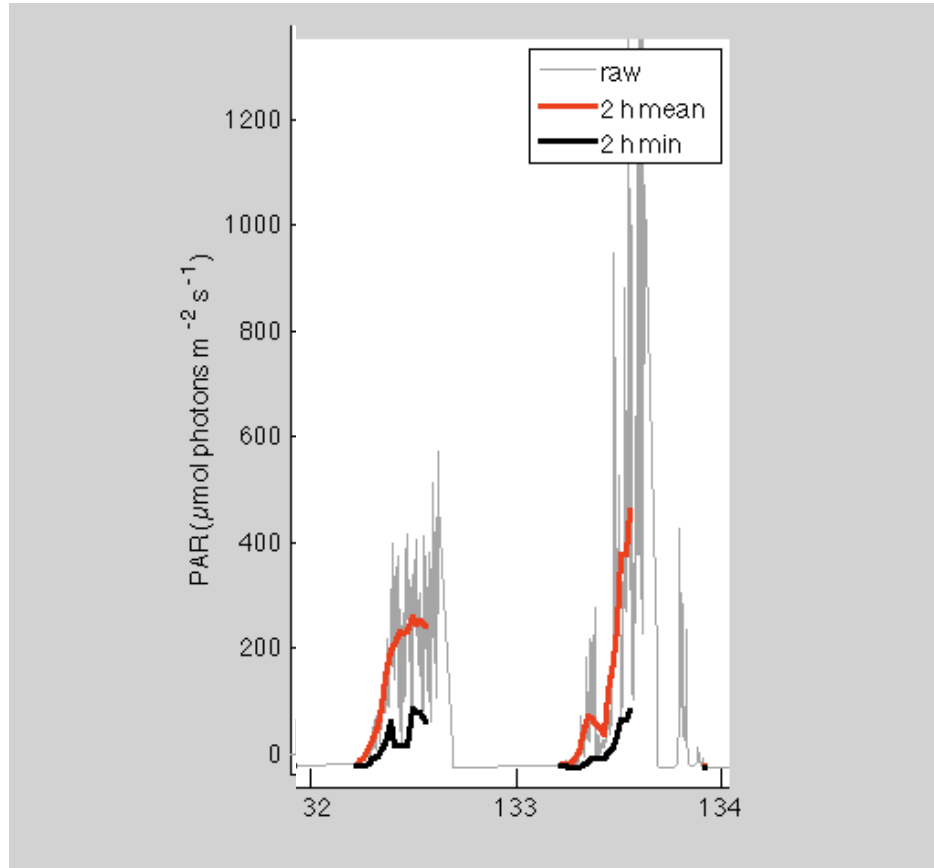
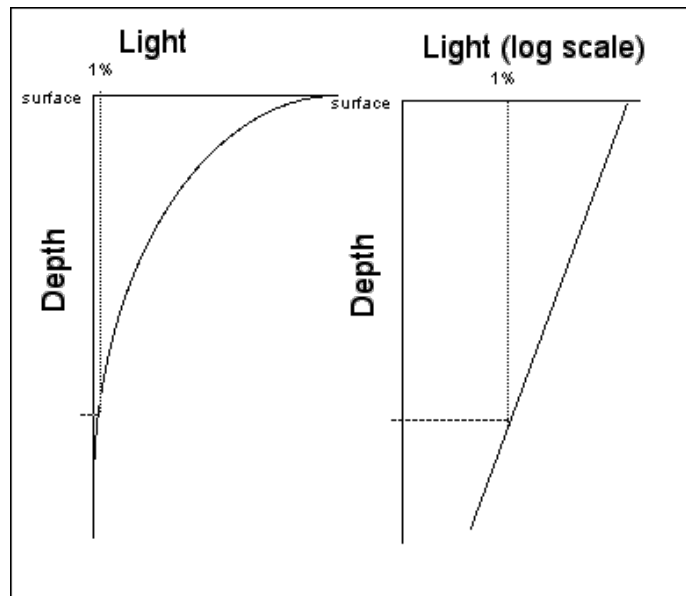
how is surface changing over time?

is K_d constant?

Satellite – surface only;

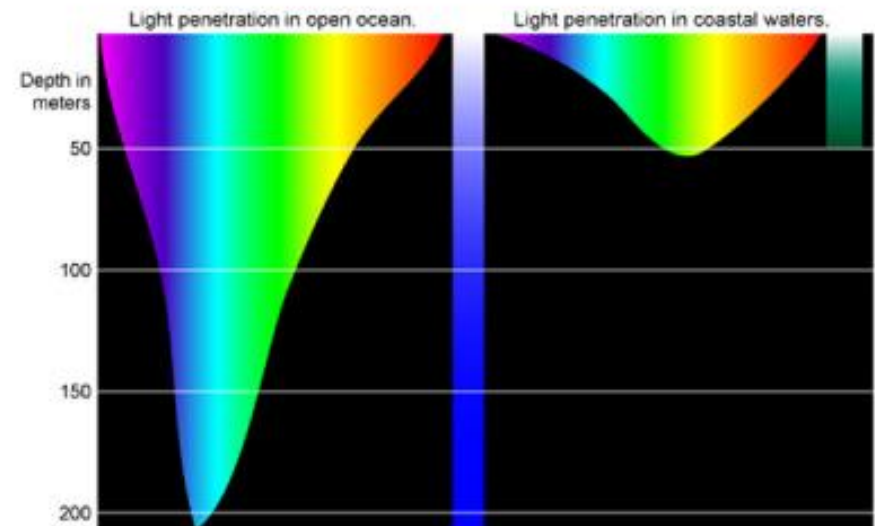
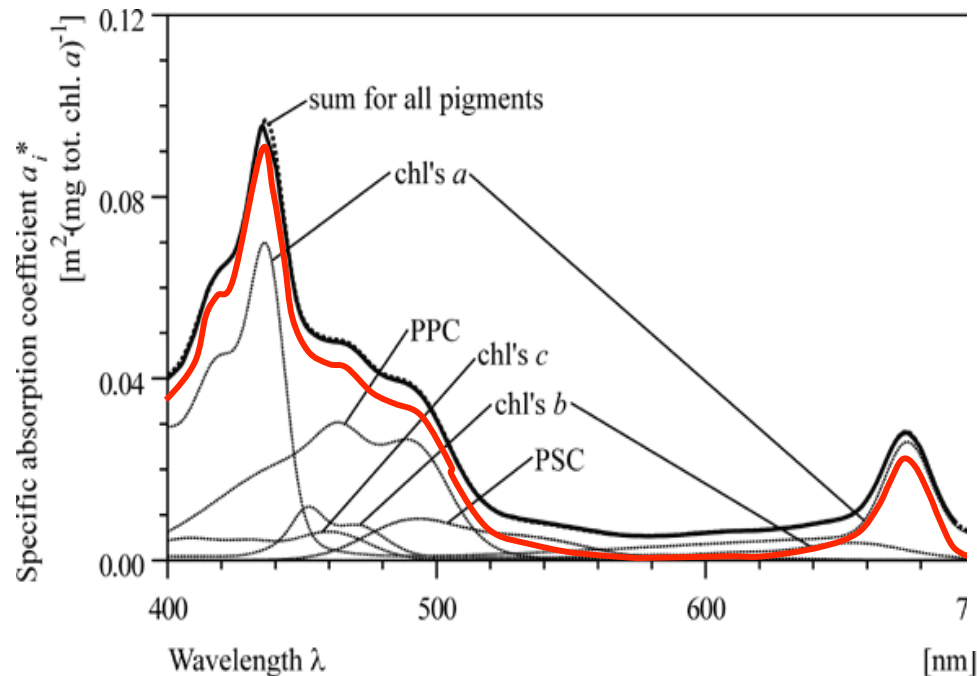
derive K_d – is it constant vs. z ? λ ?

Autonomous – moving in x, y, z plane



Light: do we need PAR or spectral?

Photon absorption for photosynthesis requires a **match between spectra of photosynthetic pigments ($a_{\text{phyt}}(\lambda)$) and spectra of underwater light field.**



Phytoplankton biomass: do we need chlorophyll, absorption coefficient, cell number, cell volume, phytoplankton carbon, other?

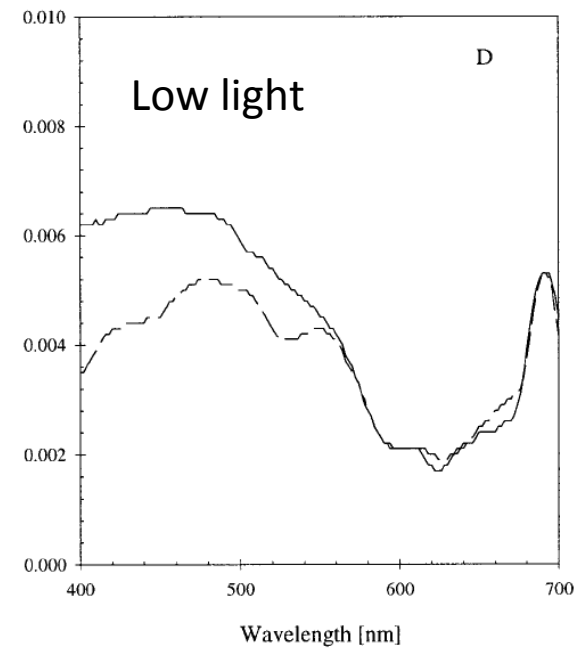
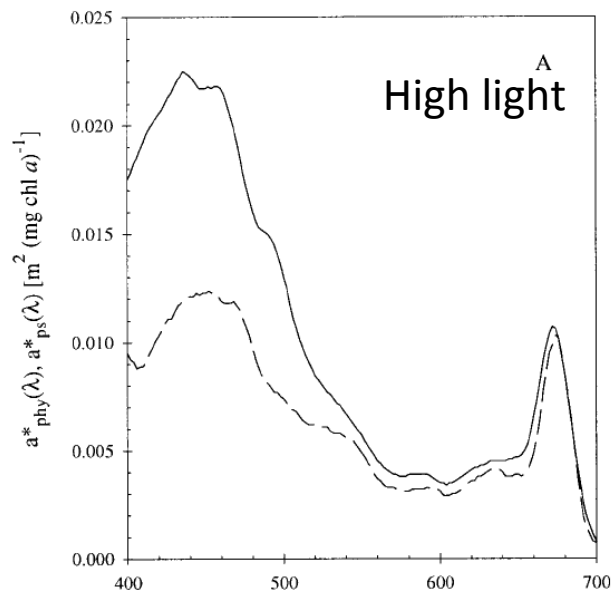
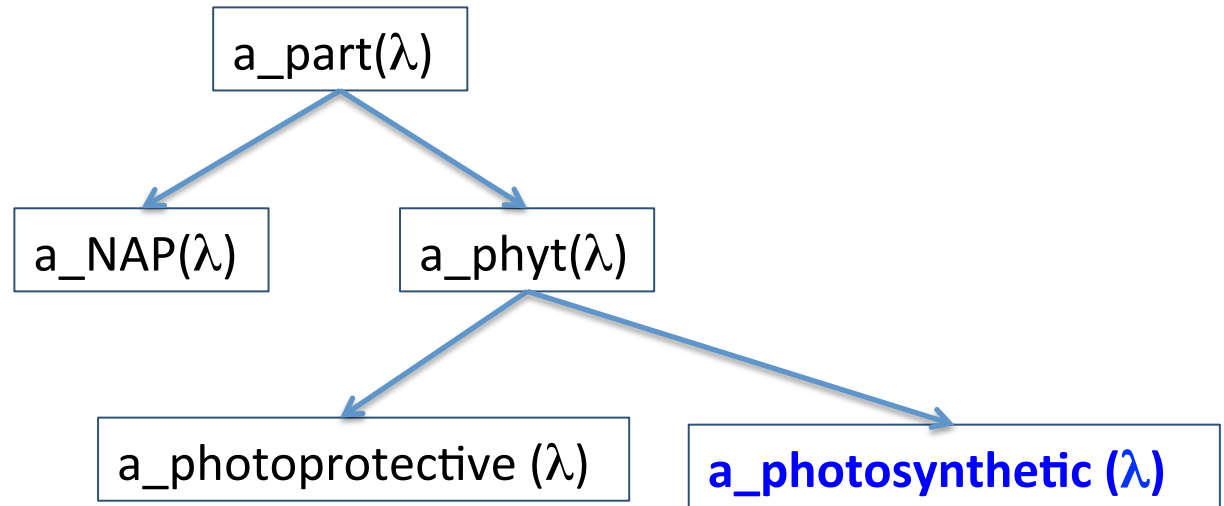
Note: Photosynthetic coefficients must be normalized to same units of phytoplankton biomass (biomass units cancel)

Primary productivity =

light (λ) * phytoplankton mass
chl? cell? carbon? or?

* photosynthetic parameter
normalized to phytoplankton
and function of light, growth, etc.

if use absorption,
need $a_{PS}(\lambda)$



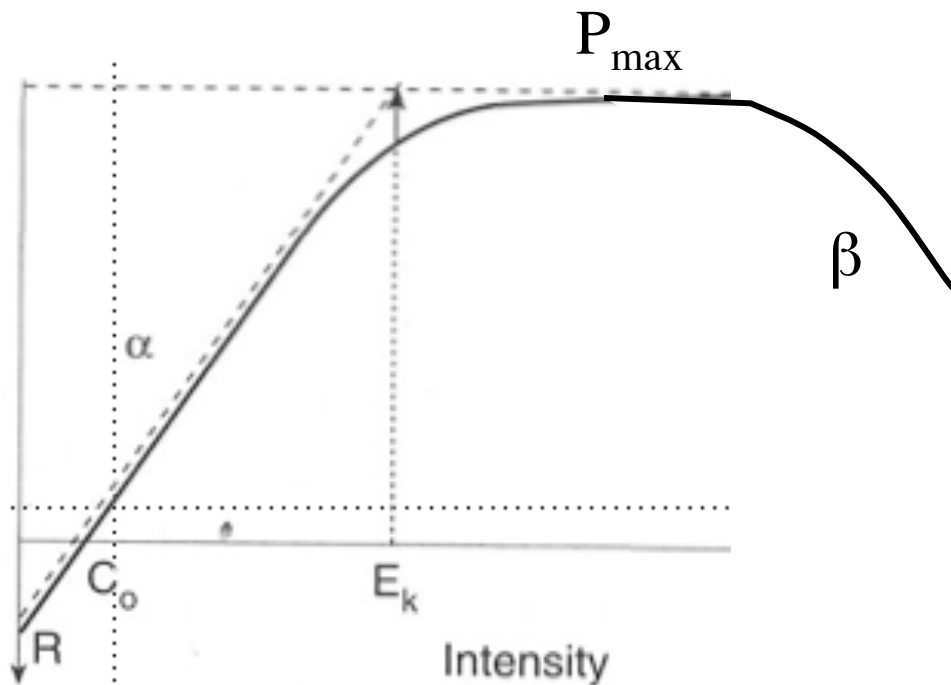
Amphidinium carterae grown at (A) 700 and (D) 5 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$

Photosynthetic coefficients

are normalized to phytoplankton biomass,
are a function of light, and

incorporate physiology (photo-adapatation, nutrient limitation, etc.)

$$P = P_{\max} (1 - e^{-(E/E_k)}) e^{-(E/E\beta)}$$



Note R = respiration

E (light)

P_{\max}^b (normalized
rate – usually Chl);
product is C or O_2

α (slope)

$$E_K = P_{\max} / \alpha$$

β (light inhibition)

$$E_{\beta} = P_{\max} / \beta$$

Units of photosynthetic parameters and photosynthesis vs. depth

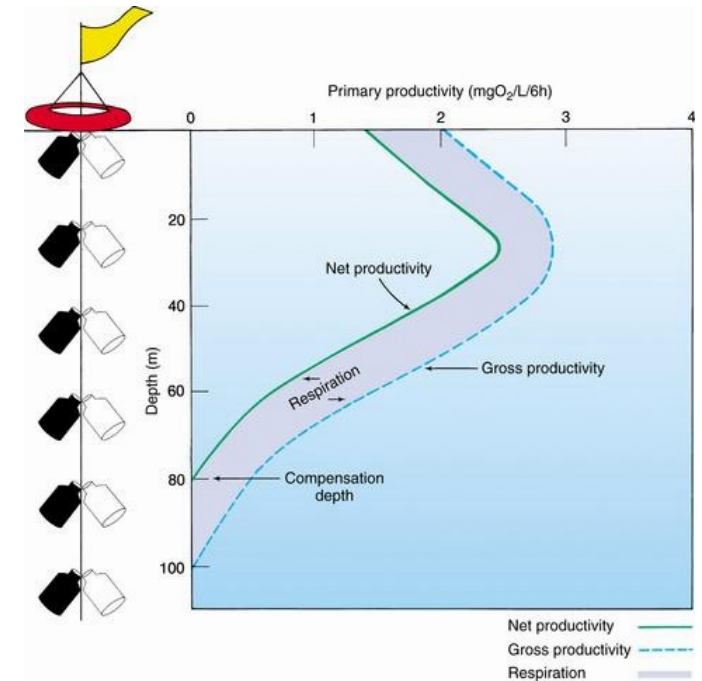
E = irradiance in photons (not energy)
units of $\mu\text{mole photon m}^{-2} \text{ s}^{-1}$

P_{max}^B = maximal, light-saturated photosynthetic rate
typically **normalized** to chlorophyll concentration
units of $\text{g C (g chl)}^{-1} \text{ s}^{-1}$

(normalization makes parameters 'portable')

Upper measured limit: P_{max}^B is $<25 \text{ g C/ g Chl/ h}$

α = slope of the P vs E curve
units of $\text{g C (g chl)}^{-1} \text{ s}^{-1} (\mu\text{mole photon m}^{-2} \text{ s}^{-1})^{-1}$ [ugly !]

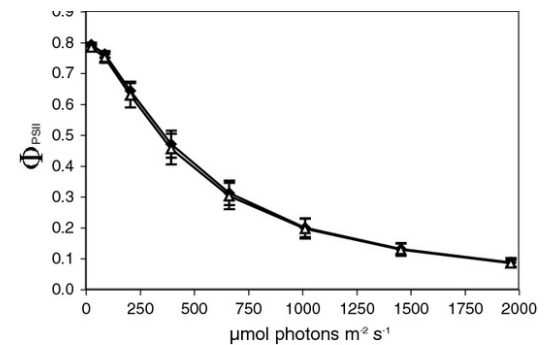
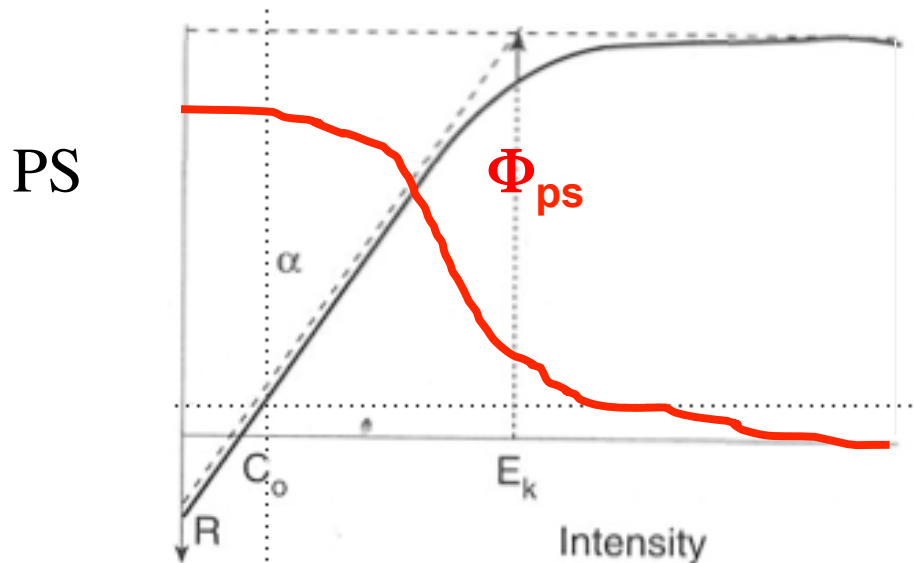


Alternative parameterization: $PS = E(\lambda) * a_{ps}(\lambda) * \Phi$

Photosynthetic quantum yield (Φ_{ps})

$$\Phi_{ps} = \frac{\text{moles product evolved}}{\text{moles photons absorbed}}$$

Φ is maximal at low irradiance,
and decreases as irradiance increases
(E_k term regulates decrease of Φ)



upper limits Φ for C is 0.10

What is photosynthesis?

(in text books, all terms shown times 6; reflects synthesis of simple sugar):

light

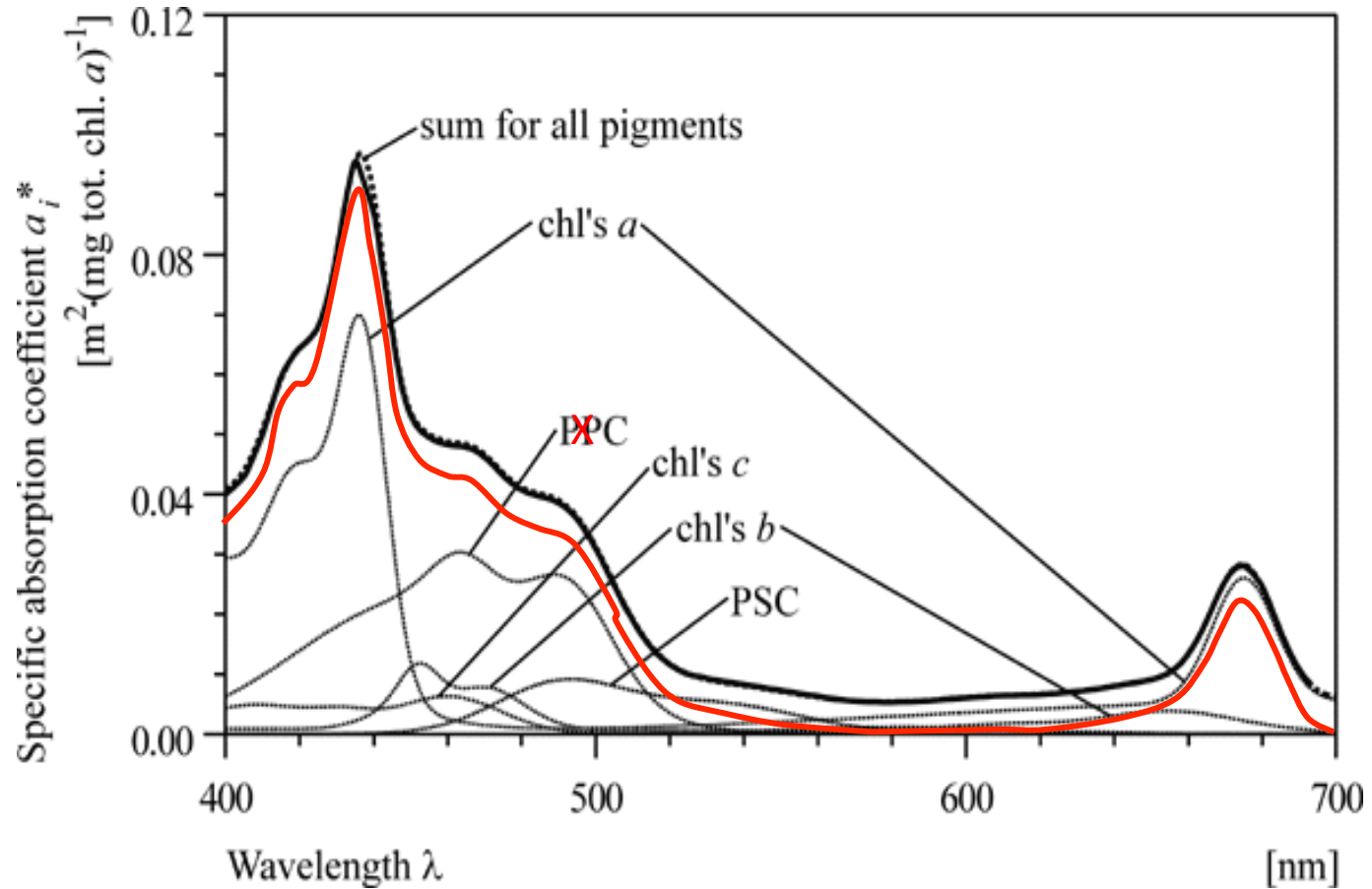


Respiration is reverse.

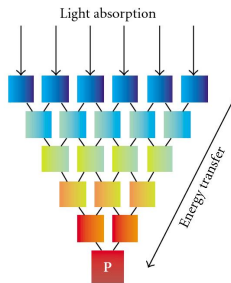
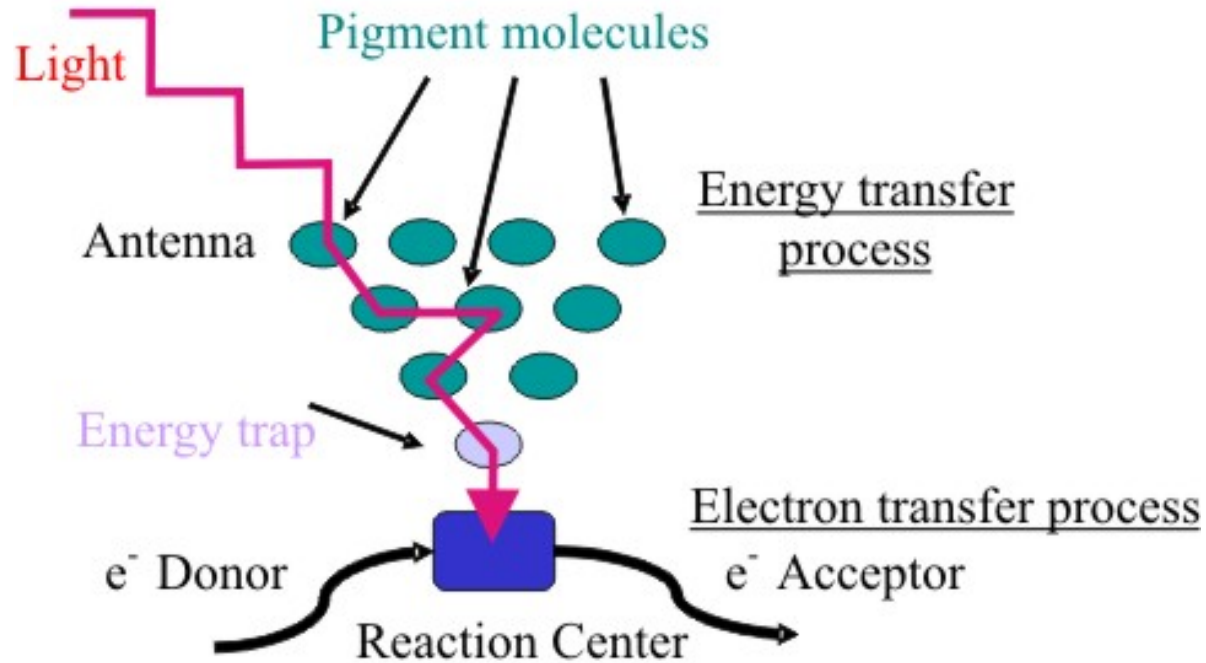
Photosynthesis – process and **products** (Should you expect stoichiometry between C and O₂ ?)

1. **photon absorption** by Light Harvesting chlorophyll & accessory pigments
2. **exciton (energy) transfer** from LH pigments to reaction center
3. **PSII trans-membrane charge separation**: high energy electron is transferred from P680 across membrane to plastoquinone (electron acceptor)
4. **Electron is transported** to PSII; **ATP** is produced; electron transport from PSII replaces electrons lost by PSI (P700⁺)
5. **PSI trans-membrane charge separation**: high energy electron is transferred from P700 across membrane to pre-ferrodoxin (electron acceptor); **NADPH** is produced
6. **H₂O split (PSII)**
 - replace electrons lost by PS II (P680⁺) during charge separation;
 - produces **O₂ as waste product**;
 - produces H⁺; H⁺ gradient couples with electron transport from PSII to PSI (leading to **ATP** production)
7. **ATP & NADPH** used to reduce **CO₂, NO₃⁻** and drive biosynthesis, etc.

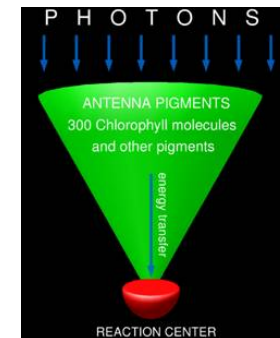
1. photon absorption by chlorophyll & LH accessory pigments



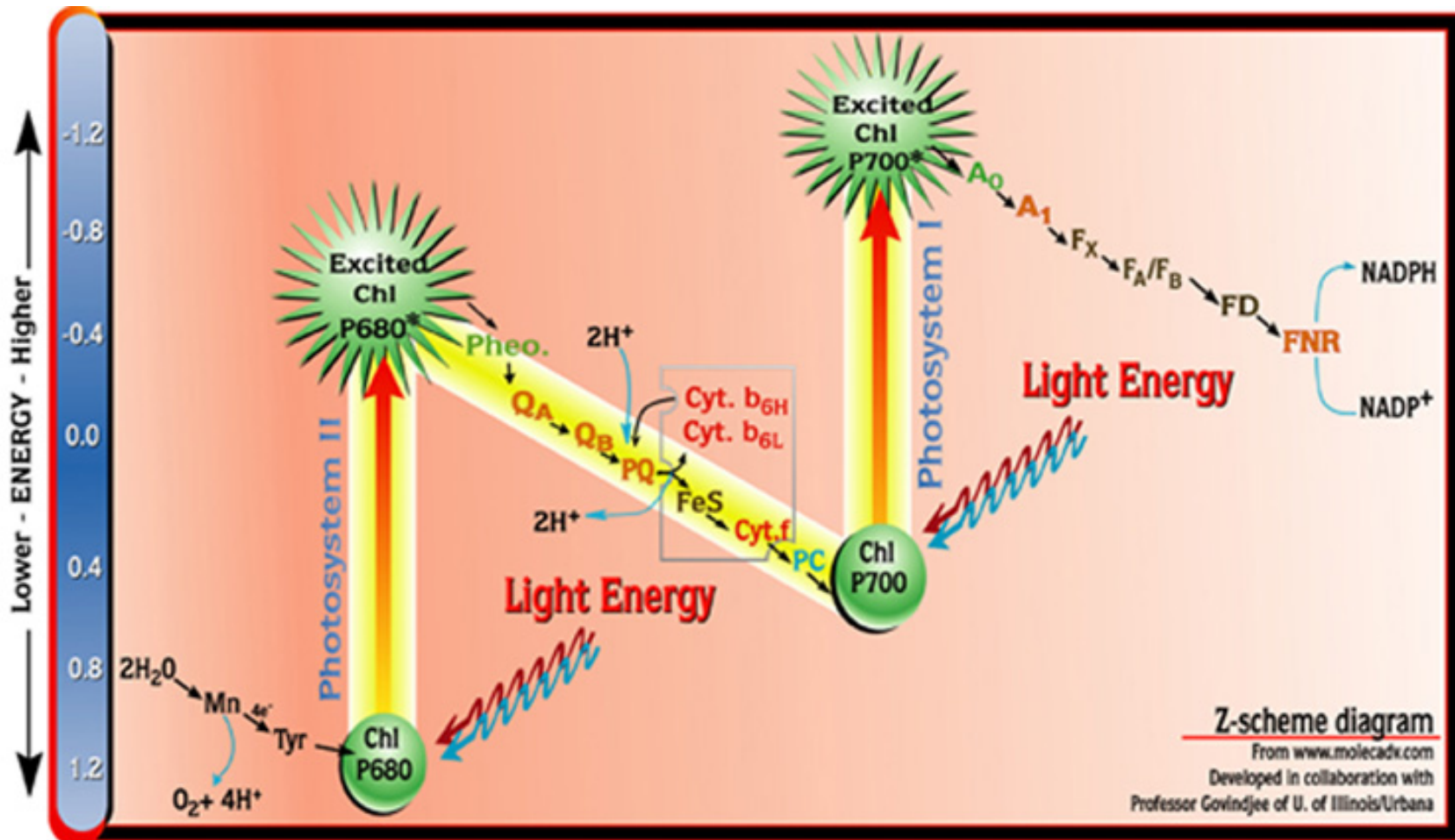
2. exciton (energy) transfer from excited pigment to reaction center



Energy transferred
down gradient to
reaction center



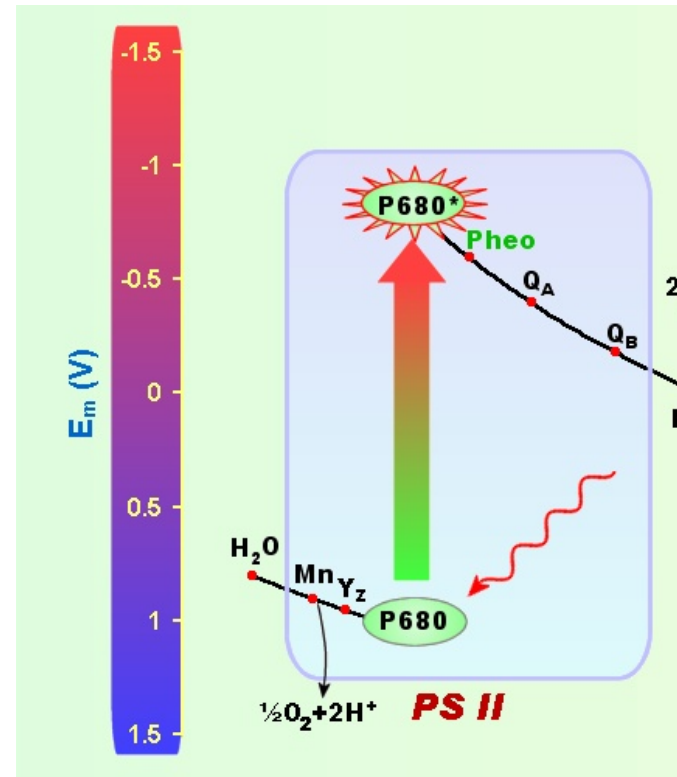
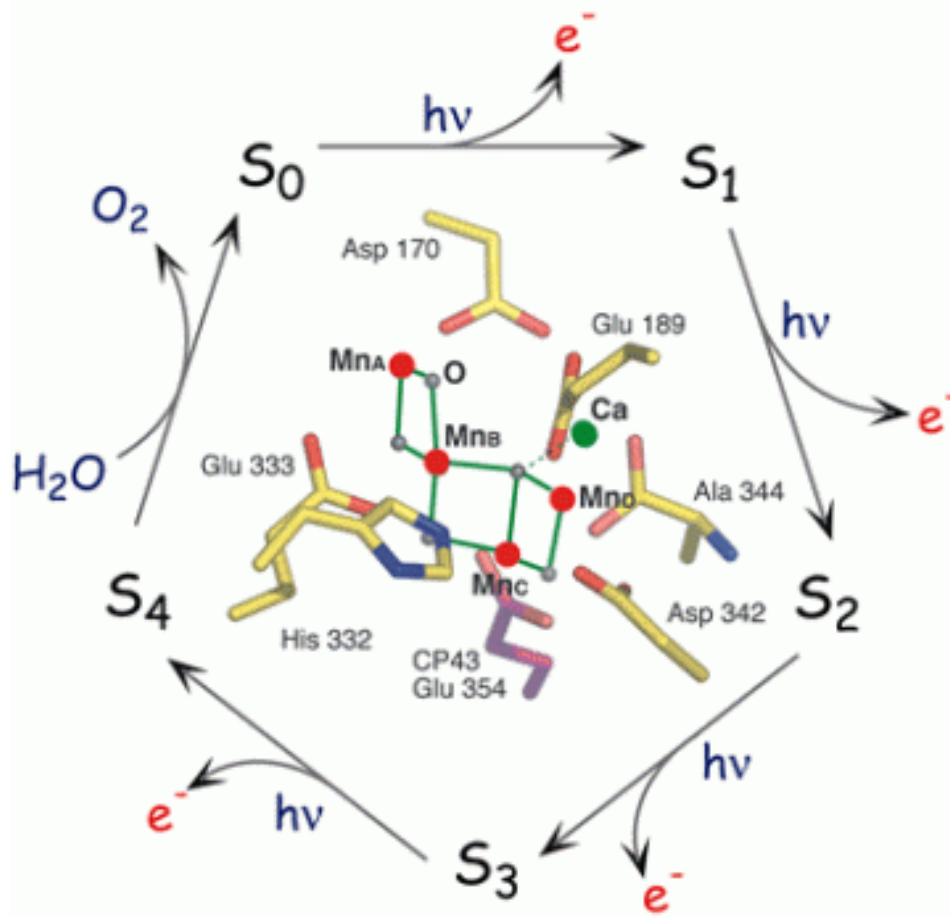
3. trans-membrane charge separation at PSII
4. electron transport from PSII to PS I (**ATP** is produced)
5. trans-membrane charge separation at PSI (**NADPH** is produced)



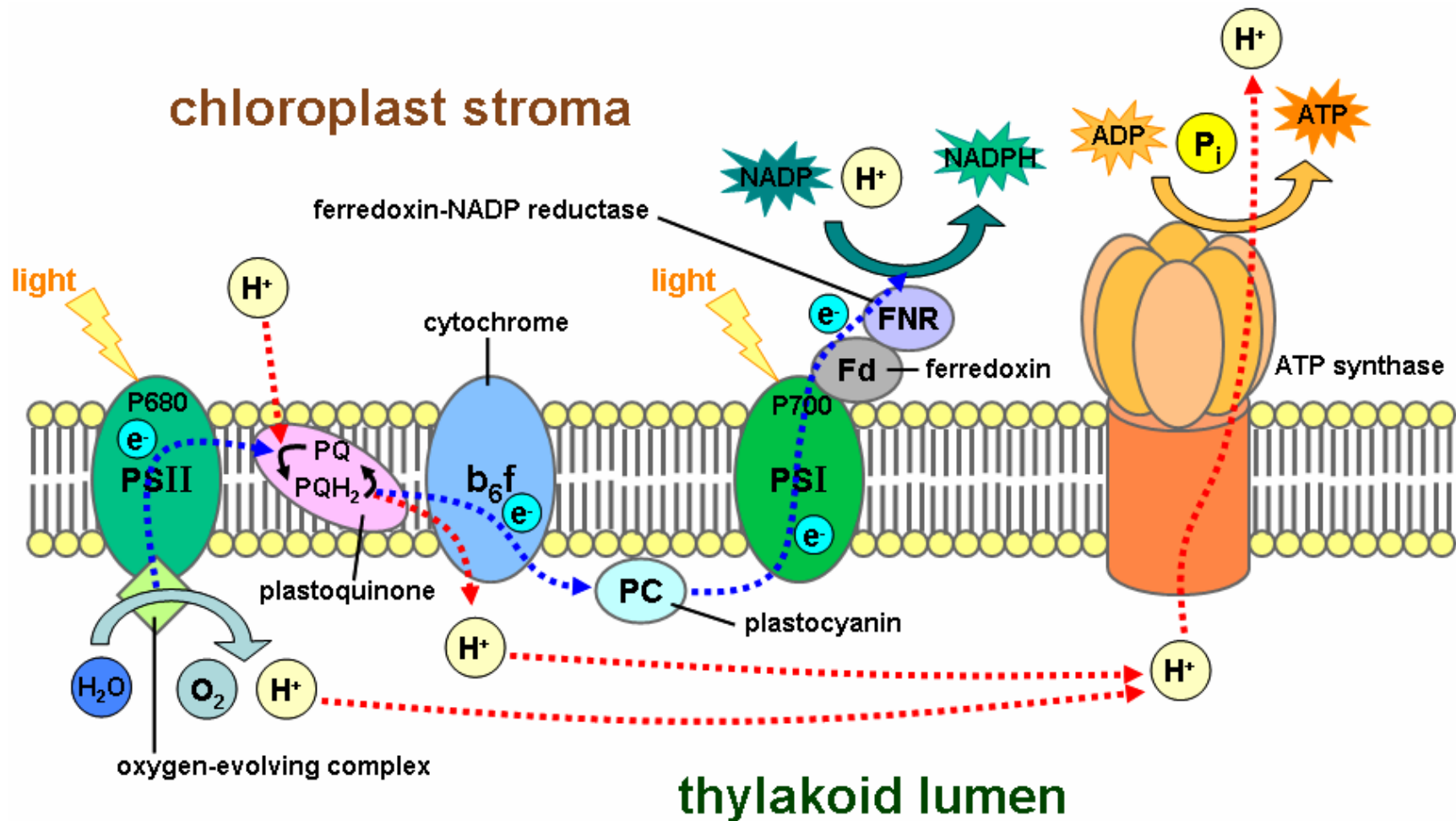
<http://www.life.illinois.edu/govindjee/ZSchemeG.html>

6. H₂O is split at PSII

- generate electrons to replace those lost by PS II (P680⁺) during charge separation;
- produces **O₂ as waste product**;
- H⁺ is produced; H⁺ gradient coupled with electron transport from PSII to PSI leads to **ATP** production

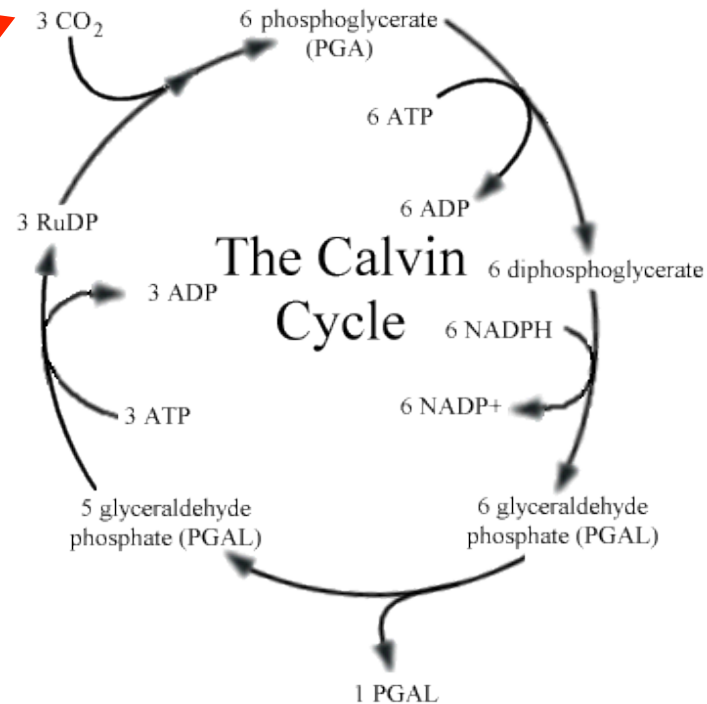


All these process happen on the thylakoid membrane,
but where's the carbon?



7. **ATP & NADPH** used to reduce CO_2 , NO_3^- , SO_4^{2-} and provide energy for **biosynthesis of proteins, lipids, nucleic acids, etc., etc.**

Here's the carbon



http://highered.mcgraw-hill.com/sites/007352543x/student_view0/chapter7/how_the_calvin_cycle_works.html

Summary of “Light” reactions of PS:

absorption of **8 photons** produces **2 ATP, 2 NADPH, 1 O₂**

PS quantum yield: mol O₂ produced/mol photon absorbed;
Φ max ~ 0.125 at low light; Φ lower at higher light

Summary of “Dark” reactions:

use products of photosynthesis (ATP and NADPH):

1. Reduce CO₂ to **-[CH₂O]-** (fixed C increases ‘biomass’, used at night in respiration, excreted as DOC)
2. Directly use as energy source in biosynthesis;
lipids, proteins, complex carbohydrates require more energy – ATP, NADPH.
3. Reduce **NO₃⁻, SO₄⁻²**, etc.

absorption of **10 photons** to reduce CO₂ (**3 ATP, 2 NADPH**)

PS quantum yield: mol C produced/mol photon absorbed;
Φ max ~ 0.10; Φ lower at higher light;
lower if other uses for ATP and NADPH

Photosynthetic quotient: O₂ evolved to C fixed is >1; 1.5 & higher.
Leads to some uncertainty in mass balance calculations.

There is more than one type of carbon productivity

1. **GOP:** gross photosynthesis as oxygen evolution
2. **NPP:** net primary productivity, rate of phytoplankton fixation of carbon minus phytoplankton respiration (24 h)
3. **NCP:** NPP minus local heterotrophic consumption: (grazing by protozoa and zooplankton; microbial respiration)
4. **EP:** export production, need to boundary conditions – sinking of organics, zooplankton vertical transport, DOC subduction, resource harvesting {aside: in 2005, humans consumed 25% terrestrial PP}
5. **SP:** sequestration production, what gets through the twilight zone

NB: **Time period** for integrating makes a difference:
NPP and NCP will be different if PP is integrated per hour vs. per day vs. per year. Or, at different seasons.

There is more than one type of carbon productivity

1. **GOP:** gross photosynthesis as oxygen evolution. Bottle ^{18}O , *in situ*: triple O
2. **NPP:** net primary productivity, rate of phytoplankton fixation of carbon minus phytoplankton respiration (24 h). Bottle ^{14}C ; *in situ*: diel changes in biomass
3. **NCP:** NPP minus local heterotrophic consumption: (grazing by protozoa and zooplankton; microbial respiration). *In situ*: mass balance O_2 , Ar/O, NO_3
4. **EP:** export production, need to boundary conditions – sinking of organics, zooplankton vertical transport, DOC subduction, resource harvesting. *In situ*: mass budgets, traps, cameras, etc.
5. **SP:** sequestration production, what gets through the twilight zone

NB: **Time period** for integrating makes a difference:
NPP and NCP will be different if PP is integrated per hour vs. per day vs. per year. Or, at different seasons.

An evaluation of ocean color model estimates of marine primary productivity in coastal and pelagic regions across the globe

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Abstract. Nearly half of the earth's photosynthetically fixed carbon derives from the oceans. To determine global and region specific rates, we rely on models that estimate marine net primary productivity (NPP) thus it is essential that these models are evaluated to determine their accuracy. Here we assessed the skill of 21 ocean color models by comparing their estimates of depth-integrated NPP to 1156 in situ ¹⁴C measurements encompassing ten marine regions including the Sargasso Sea, pelagic North Atlantic, coastal Northeast

Atlantic, Black Sea, Mediterranean Sea, Arabian Sea, subtropical North Pacific, Ross Sea, West Antarctic Peninsula, and the Antarctic Polar Frontal Zone. Average model skill, as determined by root-mean square difference calculations, was lowest in the Black and Mediterranean Seas, highest in the pelagic North Atlantic and the Antarctic Polar Frontal Zone, and intermediate in the other six regions. The maximum fraction of model skill that may be attributable to uncertainties in both the input variables and in situ NPP measurements was nearly 72%. On average, the simplest depth/wavelength integrated models performed no worse than the more complex depth/wavelength resolved models. Ocean color models were not highly challenged in extreme conditions of



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Table 2. Contributed satellite-based ocean color primary productivity models. Specific details for each model are described in Appendix A of the Supplement.

Model #	Contributer	Type	Input variables used:				Reference
			Chl- <i>a</i>	SST	PAR	MLD	
1	Saba	DI, WI	x				Eppley et al. (1985)
2	Saba	DI, WI	x	x	x	x	Howard and Yoder (1997)
3	Saba	DI, WI	x	x	x		Carr (2002)
4	Dowell	DI, WI	x	x	x	x	Dowell, unpublished data
5	Scardi	DI, WI	x	x	x	x	Scardi (2001)
6	Ciotti	DI, WI	x	x	x		Morel and Maritorena (2001)
7	Kameda; Ishizaka	DI, WI	x	x	x		Kameda and Ishizaka (2005)
8	Westberry; Behrenfeld	DI, WI	x	x	x		Behrenfeld and Falkowski (1997)
9	Westberry; Behrenfeld	DI, WI	x	x	x		Behrenfeld and Falkowski (1997); Eppley (1972)
10	Tang	DI, WI	x	x	x		Tang et al. (2008); Behrenfeld and Falkowski (1997)
11	Tang	DI, WI	x	x	x		Tang et al. (2008)
12	Armstrong	DR, WI	x	x	x		Armstrong (2006)
13	Armstrong	DR, WI	x	x	x		Armstrong (2006); Eppley (1972)
14	Asanuma	DR, WI	x	x	x		Asanuma et al. (2006)
15	Marra; O'Reilly; Hyde	DR, WI	x	x	x		Marra et al. (2003)
16	Antoine; Morel	DR, WR	x	x	x	x	Antoine and Morel (1996)
17	Uitz	DR, WR	x		x	x	Uitz et al. (2008)
18	Mélin; Hoepffner	DR, WR	x		x		Mélin and Hoepffner (2011)
19	Smyth	DR, WR	x	x	x		Smyth et al. (2005)
20	Waters	DR, WR	x	x	x	x	Ondrusek et al. (2001)
21	Waters	DR, WR	x		x	x	Ondrusek et al. (2001)

DI = Depth-integrated, DR = Depth-resolved, WI = Wavelength-integrated, WR = Wavelength-resolved.

Table 1. Description of each region and study from which NPP measurements were recorded.

General region	Program	Ecosystem type	<i>N</i>	Sampling time range	Spatial coverage	NPP method (incubation, tracer, incubation time)
Northwest Atlantic Ocean: Sargasso Sea	BATS ⁴	Subtropical – Gyre	197	Dec 1988 to Dec 2003	Single station	in situ, ¹⁴ C, 12–16 h
Northeast Atlantic Ocean	NABE	Temperate – Convergence Zone	12	Apr 1989 to May 1989	Multiple stations	in situ, ¹⁴ C, 24 h
Northeast Atlantic Ocean	NEA (OMEX I, II), SeaMARC	Temperate – Convergence Zone	52	Jul 1993 to Jul 1999	Multiple stations	on deck, ¹⁴ C, 24 h
Black Sea	NATO SfP ODBMS	Temperate Anoxic Basin	43	Jan 1992 to Apr 1999	Multiple stations	on deck, ¹⁴ C, 24 h
Mediterranean Sea	DYFAMED, FRONTS, HIVERN, PROSOPE, VARIMED, ZSN-GN	Temperate Basin	86	Feb 1990 to Sep 2007	Multiple stations	on deck, ¹⁴ C, 24 h
Arabian Sea	Arabian Sea (Process Study)	Tropical – Monsoonal	42	Jan 1995 to Dec 1995	Multiple stations	in situ, ¹⁴ C, 24 h
North Pacific Ocean	HOT	Subtropical – Gyre	139	Jul 1989 to Dec 2005	Single station	in situ, ¹⁴ C, 12–16 h
Southern Ocean	Ross Sea (AESOPS, CORSACS)	Polar – Polynya	133	Oct 1996 to Dec 2006	Multiple stations	on deck, ¹⁴ C, 24 h
Southern Ocean	WAP (LTER-PAL)	Polar – Continental Shelf	440	Jan 1998 to Jan 2005	Multiple stations	on deck, ¹⁴ C, 24 h
Southern Ocean	APFZ (AESOPS)	Polar – Convergence Zone	12	Dec 1997	Multiple stations	on deck, ¹⁴ C, 24 h

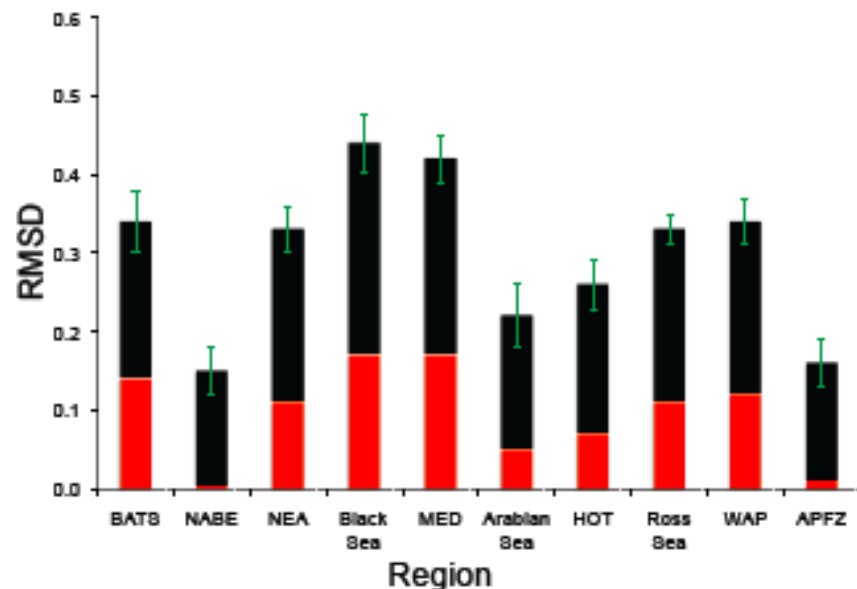
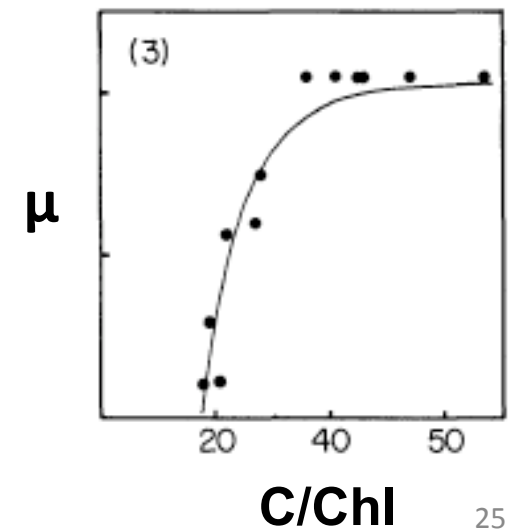
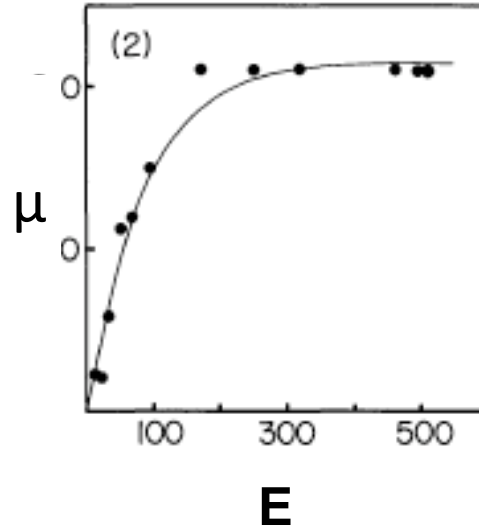
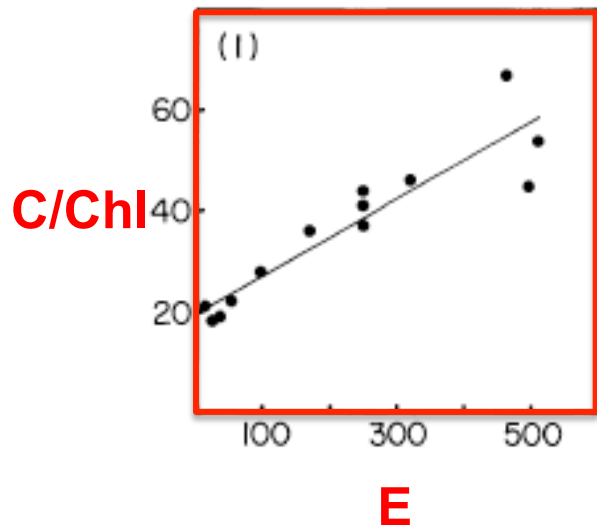


Fig. 2. Average RMSD for all 21 models at each region. Lower values of RMSD are equivalent to higher model skill. Green error bars are $2\times$ standard error. Red bars represent the maximum reduction in RMSD (increase in model skill) when the uncertainty in both the input variables and in situ NPP measurements are considered.

Table 3. Uncertainties in each input variable at each region based on differences between satellite, modeled, and in situ data sources. Ocean color models were provided with 81 perturbations of input data for each NPP measurement based on these region-specific uncertainties.

Region	Chl- <i>a</i> \pm	SST \pm	PAR \pm	MLD \pm
BATS	35%	1 °C	20%	40%
NABE	50%	1 °C	20%	40%
NEA	50%	1 °C	20%	20%
Black Sea	50%	1 °C	20%	40%
Med. Sea	65%	1 °C	20%	40%
Arabian Sea	50%	1 °C	20%	40%
HOT	35%	1 °C	20%	40%
Ross Sea	65%	1 °C	20%	60%
WAP	65%	1 °C	20%	60%
APFZ	65%	1 °C	20%	40%

Ocean color model performance was highly limited by the accuracy of input variables. Roughly half of the model-data misfit could be attributed to uncertainty in the four input variables, with the largest contributor being uncertainties in Chl-*a*. Moreover, another 22% of misfit could be attributed to uncertainties in the NPP measurements. These results suggest that ocean color models are capable of accurately estimating NPP if errors in measurements of input data and NPP are considered. Therefore, studies that use ocean color models to estimate NPP should note the degree of error in their estimates based on both the input data they use and the region where NPP is being estimated.



Figures from Geider, 1987, *New Phytologist*, 106: 1-34

