Phytoplankton Photosynthesis

- RedOx Reactions
- Some more history
- Quantum Yields
- Photosynthetic Units
- Physical Structure
- The Z-Scheme
- The Calvin-Benson Cycle
- Measuring Photosynthesis
Every pigment has a characteristic Absorption Spectrum

- Optimal $\lambda$
A Brief History....

• Otto von Warburg, 1920’s

– Insisted that the quantum yield of oxygen evolution (the number of oxygen molecules evolved per photon, or quanta, absorbed) was about 0.25

**QUANTUM YIELD**: the amount of something produced for a given number of quanta (light photons) absorbed. A yield 0.25 means 4 photons are absorbed for every oxygen molecule produced (1 O₂ for 4 photons, or ¼)
REVIEW:

• Once a cell absorbs sunlight, there are only three possibilities:
  1) Fluorescence
  2) Heat
  3) Photosynthesis

So in our new terms, the QUANTUM YIELD of photosynthesis goes up as the quantum yield of fluorescence goes down (if energy is going to #3, then less energy goes to #1 and #2, and the yield has to decrease)
REVIEW 2:

• The QUANTUM YIELD is simply the yield of something (for example, oxygen production, fluorescence, & heat) for a given number of photons. You can calculate a quantum yield for anything that requires light.

• Since only 3 things can happen to absorbed photons (energy conversion, heat, or fluorescence) the quantum yields must account for 100% of the absorbed light.
Emerson and Arnold, 1932, described the PSU

In contrast to von Warburg, their data showed it takes at least 8 photons to produce oxygen
Emerson and Arnold, 1932, determined that the functional unit of photosynthesis could be called a Photosynthetic Unit, and was made up of about 2400 pigment molecules.

This is the same as our “funnel” that captures light and funnels it down to a bottleneck—if the funnel is blocked, have to produce heat or fluorescence.
New Terms:

- Emerson & Arnold said the PSU is made up of:
  - The Antenna (all the pigments that capture light)
  - Photosystem II (specialized chlorophyll molecule)
  - Photosystem I (specialized chlorophyll molecule)

...and demonstrated that they all work together as a single unit.

(How did they figure this out? They crystallized the proteins)
Emerson Red-Drop Effect

- 1952, Emerson determined that photosynthesis is maximal when blue AND red light is available
Photosynthetic Unit (PSU)

Based on these experiments, determined that:
- Oxygen is produced by plants using absorbed sunlight—von Warburg said it was a ratio of 1:4 (1 oxygen for 4 photons)
- It takes about 2400 pigment molecules working as a unit to do this
- Emerson and Arnold said it’s really a 1:8 ratio
- Emerson demonstrated that you get MORE oxygen when using two different wavelengths of light
Photosynthetic Unit (PSU)

• To explain these results, Emerson determined that the PSU is made up of 3 distinct units:
  – The ANTENNA (the ~2400 chlorophyll molecules that make up our funnel—in reality this is chlorophyll a plus other pigments
  – The REACTION CENTER where the electrons are funneled down into…this is called Photosystem II (PSII)
  – Another REACTION CENTER that responds to far-red light; this is called Photosystem I (PSI)
  – The whole complex works together to make up the PSU

Side note: oxygenic photosynthesis requires all of these pieces—anaerobic bacteria can still photosynthesize but don’t produce oxygen because they only have PSI
M&M Demonstration

- Two funnels, representing PSII and PSI
- M&M’s, representing photons
  - Doesn’t matter, for the most part, what color the M&M is as long as it makes it through the funnel
- Initially, the funnel is wide open, and it’s easy to get M&M’s through it (that’s equivalent to Fo), but it still takes some random amount of time.
- As the funnel fills up, more or more of the M&Ms spill over. This is heat and fluorescence (or Fm).
- So long as you are eating them or storing them faster than the funnel fills up, photosynthesis is in balance (not light-saturated)
- Relationship to a PE curve: initial slope (how many you eat) is mostly dependent on how fast the M&Ms come (the amount of light). Once you are saturated (eating as fast as you can), the maximum rate of M&Ms depends on how hungry you are and how fast you can eat or store them.
Growth on CO$_2$ and the Macronutrients N and P

It is convenient (and often necessary) to consider the growth and decomposition of an “average” phytoplankter. Redfield showed strong relationships between elements that were consistent with the growth and decomposition of phytoplankton:

$$\begin{align*}
106 \text{ CO}_2 + 122 \text{ H}_2\text{O} + 16 \text{ HNO}_3 + \text{H}_3\text{PO}_4 & \rightarrow (\text{CH}_2\text{O})_{106} + (\text{NH}_3)_{16} + \text{H}_3\text{PO}_4 + 138 \text{ O}_2
\end{align*}$$

C:N:P ~ 106:16:1 - Termed the Redfield Ratios

This suggests that there is a cellular “currency” related to photosynthesis (growth) and that we can measure ANY ONE variable to get the other variables....
The Z-Scheme...
The Mn acts as a capacitor, storing up energy from 4 photons and using that to split water—but this only occurs at PSII
...embedded in a membrane.
Z-Scheme membranes

Stromal side of thylakoid membranes

Photon \( \rightarrow \) Chl* \( \rightarrow \) I \( \rightarrow \) PQ \( \rightarrow \) Cyt \( \rightarrow \) PC \( \rightarrow \) Chl* \( \rightarrow \) NADP+ \( + \) H+ \( \rightarrow \) NADPH \( + \) H+

\( \text{H}^+ \text{O}_2 \) \( \rightarrow \) Chl* \( \rightarrow \) PS 2 \( \rightarrow \) \( \frac{1}{2} \text{H}_2\text{O} \) \( \rightarrow \) PS 1 \( \rightarrow \) \( \text{NADP}^+ \)

Thylakoid becomes acidic
Non-Cyclic Photophosphorilation (Z-Scheme)
Cyclic Photophosphorylation

- Only PS I used
- NO O2 formed
- Produces ATP
Dark vs. Light Reactions

**Light Reactions**: Require light energy to run

**Dark Reactions**: technically don’t require light, but they stop very quickly in the dark
Z-Scheme Movie

You need to be on the internet.

GO BEAVERS!

https://www.youtube.com/watch?v=XsZlPeT3D10
Measuring Photosynthesis

If you understand the biochemical basis for photosynthesis (the Z-scheme, the relationship between heat, light, fluorescence, oxygen production, and carbon consumption), then there are a number of ways to estimate growth (photosynthesis)....
Measuring Photosynthesis

Some basic terms:

**Photosynthesis** is the conversion of inorganic carbon to organic carbon (by producing ATP and NADPH) through conversion of sunlight to chemical energy.

**Gross Primary Productivity** is the total energy (or carbon, or oxygen, etc) produced through photosynthesis in a given time. It has units of mass per unit area (or volume) per unit time, and is a rate.

**Net Primary Productivity** is the rate of accumulation of biomass (or carbon, or whatever currency you are tracking) after accounting for respiration.

**Primary Production** is the amount of material produced by Primary Productivity (amount versus rate), but they are often used interchangeably and for this class we will assume they are essentially the same.
Measuring Photosynthesis

- Change in biomass
- Change in H₂O, O₂
- Change in CO₂
- Production of Heat
- Production of Fluorescence
Measuring Productivity

• Oxygen bottles measure Gross and Net Production

• $^{14}$C measures something between gross and net production
# Photosynthesis Measurements

<table>
<thead>
<tr>
<th>Method</th>
<th>PROS</th>
<th>CONS</th>
</tr>
</thead>
<tbody>
<tr>
<td>14C</td>
<td>• Easy to use&lt;br&gt;• Tracer method&lt;br&gt;• Measures carbon&lt;br&gt;• Cheap&lt;br&gt;• Very Sensitive</td>
<td>• Requires a bottle&lt;br&gt;• Deck vs. In situ?&lt;br&gt;• Radioactive!&lt;br&gt;• Neither gross nor net productivity</td>
</tr>
<tr>
<td>Oxygen</td>
<td>• Measures GPP&lt;br&gt;• Not complicated&lt;br&gt;• Instantaneous&lt;br&gt;• No bottle</td>
<td>• Not easy to do&lt;br&gt;• Not very sensitive&lt;br&gt;• BIG assumptions&lt;br&gt;• Instrumentation</td>
</tr>
<tr>
<td>Fluorescence</td>
<td>• First principles</td>
<td></td>
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</tbody>
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# Photosynthesis Measurements

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<th>Method</th>
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| **18-Oxygen**| • VERY sensitive  
• GPP, NPP, R  
• Very Sensitive | • Requires a bottle  
• Very Expensive, hard to do |
| **Heat**     | • Really cool!  
• Non-invasive  
• First principles  
• Incredibly simple | • Lab only  
• VERY difficult!  
• Instrumentation  
• Space, Time-scale dependent |
| **Biomass**  | • Community NPP | • Not a rate! |
Now that we can measure photosynthesis, how do we turn that into equations that can be used in our model?
Photosynthesis versus Irradiance Curves (often abbreviated as PE, PI, PvsE, etc.)
Photosynthesis versus Irradiance Curves

- $P_{\text{max}}$
- $E_k$
- $\alpha$
- $\beta$
Photosynthesis versus Irradiance Curves

The rate of photosynthesis up to the $E_k$ point is controlled by the light reactions--after that, it slows down because the dark reactions are limiting.
Photosynthesis versus Irradiance Curves

Beta is caused by so much light that the cell starts to get damaged--can’t get rid of the energy as fluorescence or “work”, so heat builds up.
PE (or PI) Curves

<table>
<thead>
<tr>
<th>Functional form</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{l}{l_o}$</td>
<td>Linear response</td>
</tr>
<tr>
<td>$\frac{l}{l_o + l}$</td>
<td>Saturating response</td>
</tr>
<tr>
<td>$1 - \exp\left(-\frac{l}{l_o}\right)$</td>
<td>Saturating response</td>
</tr>
<tr>
<td>$\tanh\left(-\frac{l}{l_o}\right)$</td>
<td>Saturating response</td>
</tr>
<tr>
<td>$\frac{l}{l_o} \exp\left(1 - \frac{l}{l_o}\right)$</td>
<td>Saturating and photo-inhibiting response. Parameter $l_o$ determines irradiance at photosynthesis maximum.</td>
</tr>
</tbody>
</table>

There are many possible eqns. to describe the curve mathematically. Peter Franks gave several. We don’t really care which one is being used, so long as we know which one it is.
Photosynthesis versus Irradiance Curves

- Low
- Medium
- High

Adapted cells...
For a Photosynthesis versus Irradiance curve (PvsE), Ek is the special point where the cell goes from LIGHT LIMITATION to BIOCHEMISTRY LIMITATION... at first, as you increase the light, photosynthesis increases linearly (more light = more oxygen). At some point, you can’t push electrons through the Z-scheme any faster (the funnel is backing up) and the curve flattens out because the Calvin-Benson Cycle can’t go any faster...
Phytoplankton adapt to the light environment by changing the amount and type of pigment per cell, which changes the light reactions (the dark reactions are controlled primarily by cell size, nutrients, and temperature).
RED is low-light adapted
BLUE is high-light adapted

Under low light, it is advantageous to maximize light absorption (steep initial slope) but it’s a waste of energy to build up a big “back end” capacity so you saturate quickly

(upper panel—normalized to the amount of chlorophyll—red line has more chlorophyll; lower panel—how fast the cells are actually growing)
Summary

• There are many ways to measure photosynthesis, but in all cases we are simply tracking how fast the cell processes sunlight into organic material.

• For modeling purposes, it is convenient to describe the processes using P vs. E curves.

• Low-light adapted cells (plants) have more pigments, and sacrifice total capacity (dark reactions) for sensitivity to low light.

• High-light adapted cells have fewer pigments and more dark reaction components, so don’t do well at low light can handle more photons (high light) by not letting the “funnel” back up.

• Nutrient limitation primarily impacts the dark reactions—can’t use all the light energy, so you back up the funnel.