

History of Photosynthetic Unit

- Early 20th Century, realized that Chlorophyll was a catalyst (wasn't destroyed during the reaction), and thought that it somehow absorbs light, produces O₂, and fixes CO₂
- 1932, Emerson and Arnold set up an experiment with a bunch of equipment to give very short, very bright flashes:
 - Allowed the dark time between flashes to vary
 - Long time between flashes (long dark period), O₂ evolution is independent of temperature
 - Short time interval, strongly temperature dependent (enzymes involved)
 - Took about 2500 chl molecules to produce O₂ (turns out it's between 1500-2500 on avg)
 - Determined 4 things VERY IMPORTANT:
 - Light and Dark reactions
 - High light, dark reactions (enzymes) are limited
 - Many chlorophyll molecules are required
- Von Warburg (1920s)
 1. CO₂ produces O₂, and it takes 4 electrons to carry out this reaction

Action Spectra

- So, we know chlorophyll is involved in photosynthesis, and it takes at least 4 electrons to produce O₂. This reaction has light and dark reactions, and involves a lot of chl molecules
- 1943, Emerson and Lewis asked what the other pigments (besides Chl a) were doing...
 - Shined other color lights on algae, discovered it's not as efficient
 - When they shined far-red light, very inefficient (red drop)
 - Shine blue AND red light, more efficient than either one by itself
 - Means there must be TWO independent light reactions (PSII, PSI)
 - PSI does NOT produce oxygen!
 - So, Von Warburg was technically correct in that it takes 4 electrons to produce O₂, but it takes 8 electrons to complete photosynthesis

Quantum Yields

- *Quantum Yield* is simply the efficiency with which a reaction proceeds...how fast does the reaction go as a function of the number of absorbed photons?
 - *Moles of photons absorbed per moles product*
 - NOT going to be equivalent for different products (for example, quantum yield of oxygen doesn't have to equal the quantum yield of CO₂ fixation)

- Von Warburg Experiment (he was a feared Nobel Laureate)
 - Used CO₂ starved Chlorella
 - Came up with quantum yield for O₂ of 0.25, meaning you need to absorb 4 electrons for each O₂ produced
 - Emerson in 1950s, said it was 0.10 to 0.125 (or about 8 electrons)

Effective Absorption Cross-Sections

- If you flash an algal culture with bright light, the oxygen produced increases in a Poisson Function, which can be described as:

$$Y/Y_{\max} = 1 - e^{-\sigma E}$$

Where Y is the yield (oxygen production), sigma is the slope, and E is the flash energy

- The “effective” cross section means it doesn’t have anything to do with the physical size
- Think of standing with arms outstretched—easier to hit me if I don’t turn sideways
- Quantum Yield of Photosynthesis is the relative ratio of the cross-section of PSII to the entire PSU
- So, if the ONLY reaction is absorption by PSII and PSI, maximum yield is 0.125

Measuring Photosynthesis

Several ways to measure photosynthesis:

Oxygen evolution – using either an electrode, or by using H₂O¹⁸. Add heavy water, measure how much appears in the “head space” over time. Extremely precise, but requires very expensive equipment. This measures “gross photosynthesis”

¹⁴C Method—most commonly used. Measures the acid-stable organic carbon that is assimilated over time. Einar Steeman-Nielsen came up with this in 1952.

- This is a true “tracer” method because add small quantity of radioisotope, which doesn’t perturb the system.
- Have to account for the “discrimination” of ^{14}C vs. ^{12}C though, because plants don’t like to use heavy isotopes.
- Problems: first, it’s radioactive.
Second, it measures something between net and gross productivity, because oxygen evolution can occur without carbon fixation.
Third, it’s done in a bottle

Photosynthetic Quotient (PQ) is the ratio of O_2 produced to CO_2 taken up. When cells are growing, they also use photosynthetic energy for other things besides carbon fixation, so oxygen yield is rarely the same as CO_2 assimilation. In general, phytoplankton growing on NH_4 have a $\text{PQ} = 1.2$, growing on NO_3 have a $\text{PQ} = 1.8$, because it takes extra energy (increased photosynthesis, so more oxygen produced per CO_2 assimilated) when using oxidized nitrogen substrates.

Photo-acoustics --When light is absorbed, produces heat. By putting a sample in a sealed, air-tight vessel and shining light on it, produces heat, causes expansion, which produces a pressure wave. If there’s a microphone inside, can acoustically measure the heat production.

Using this method, determine that photosynthesis is about 35% efficient (e.g. can use 35% of the energy absorbed for photochemistry). Fluorescence is about 2-5%, rest is heat production (of that 35% used for photosynthesis, it’s >90% efficient, meaning additional energy is rarely lost to heat)

Fluorescence -- Big advantage, because it’s passive, non-destructive, and can be measured without using a bottle. Also instantaneous. Can measure it as long as you want to. Finally, the only things that fluoresce are things with chlorophyll, so it’s very specific to primary production.

- Big disadvantage—we have to assume a known relationship between the quantum yield of fluorescence and photosynthesis

- Pump-and-Probe method
- PAM method
- FRRF

Back to ¹⁴C method

Can either do the classic light-dark bottle technique:

- use floating array (this is the best method)
- use an in situ incubator (not so good)
- both of these methods have problems....long time period, no mixing, constant (spectrally incorrect?) light, temperature, etc.
- need to normalize to biomass—typically use chl, even though we know this changes dramatically due to a number of factors
- **assimilation index:** mg C per mg Chl per time

P vs. E curves:

-this tells much more about the **physiology** of the phytoplankton, but can be much more difficult to interpret.

PAR: Photosynthetically Available Radiation

PUR: Photosynthetically Utilizable Radiation

PSR: Photosynthetically Stored Radiation

Anatomy of a PvsE curve:

Alpha—the light limited slope of a PvsE curve. This is controlled by the relative ability to absorb energy, and is the light-limited portion of the curve (controlled by how fast photons can be processed)

Pmax—the maximum assimilation rate—this is really determined by how much RUBISCO, how fast you can grow, etc.

Ek—the inflection point between light limited and RUBISCO limited growth. Mathematically, it's the point half way between zero and Pmax.

Beta—the light inhibited slope of the curve (photodamage)

To solve a P vs. E curve, we need to know:

- the spectral characteristics of the light source (color, intensity)

- the absorption characteristics of the algae
- the rate of photosynthesis at each light level

Given those two things, we can determine exactly the potential photosynthesis at all light colors and levels, by solving the curve fit.

Problems with PvsE:

- We know physiology changes...non-photochemical quenching, number of functional PSUs, quantum yields, etc. These will all result in changes in the P vs. E curve.
- We can measure photosynthesis in the laboratory, but it's difficult to exactly match the light (color, intensity, etc) in the natural environment
- We need to pick a method of measuring photosynthesis, and can bias the P vs E curve depending on what we measure (oxygen, carbon uptake, fluorescence, etc.)
- We need to account for respiration, but we often ignore it when estimating a P vs. E curve

Factors Affecting Photosynthesis

Physiological

Respiration. Typically, we assume it's about 10% of gross photosynthesis, but this is variable and not really known very well.

-Compensation Depth...depth in the water column at which respiration exactly equals photosynthesis.

$$D_c = (\log_e(I_0) - \log_e(I_c)) / k$$

-Critical Depth...(Sverdrup, 1953) The depth to which phytoplankton can be mixed and still survive...not the same as the compensation depth!

$$\text{Mean Light} = I_0/kZ(1-e^{-kZ}) \quad (Z=\text{euphotic depth})$$

$$Z_{cr}=I_0/kI_c(1-e^{-kZ_{cr}}) \quad (I_c \text{ is compensation light intensity})$$

Can assume $kZ_{cr} \gg 0$, $Z_{cr}=I_0/kI_c$

Note: in both of the above depths, we're measuring **community respiration**, not just the respiration of phytoplankton. In other words, the compensation depth is where the **community** (phytoplankton plus everything else) consumes all of the oxygen produced by photosynthesis.

Temperature. In general, biological organisms increase their metabolism proportionally to changes in temperature.

-Cold temperatures (sea ice, for example) slow the metabolism down in cells...causes electron transport to slow down. This makes light "seem" brighter to the phytoplankton, because they can't process it as quickly

- Eppley (1972) determined empirically that phytoplankton growth (regardless of species) always falls below a particular level (the Eppley Temperature Curve). Although not based in physiology, this curve allows us to estimate maximum possible growth rates of phytoplankton at **any** temperature.

- Q10 values: Since metabolism increases with increasing temperature, it's possible to give a number to the difference in metabolism (or growth rate, etc.) for a temperature interval. When calculated for a 10 degree C difference, we get the "Q10" value.

Nutrients. Can affect phytoplankton in a variety of ways (see additional notes).