Theory of photosynthesis

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The traditional ecological perspective on photosynthesis:

- Light capture splits water, generating chemical energy and releasing oxygen
- Chemical energy drives fixation of carbon dioxide into a stable organic form
The emerging ecological perspective on photosynthesis:

- Absorbed light is partitioned between photochemistry, heat, and fluorescence
- Shift driven by advances in proximal and remote sensing over past decade
Why this matters for ecologists:

- At scales for ecological analysis, there are mitochondria as well as chloroplasts
- Mitochondrial respiration reverses the photosynthetic trace gas fluxes
Why this matters for Fluxcourse:

- We measure net fluxes of trace gases - then use theory to partition gross fluxes.
- The absorption of light and release of fluorescence are unique to photosynthesis.
Outline for today:

- Part 1: Environmental control of photosynthesis
  - Light: photons, photochemistry, and Cytochrome b6f
  - Carbon dioxide: diffusion, biochemistry, and Rubisco
  - Other resources and stressors

- Part 2: Quantitative expressions for photosynthesis
  - Top down: Monteith
  - Bottom up: Farquhar, von Caemmerer, and Berry
  - Connecting top down to bottom up: Johnson and Berry
The part of the solar spectrum that drives photosynthesis is called photosynthetically active radiation (PAR), which includes wavelengths in the 400-700 nm range.
Once photons are absorbed by chlorophyll, they have several potential fates

- For chlorophyll that is **isolated**:
  
  Energy in from absorption is either lost as heat or lost as fluorescence.

- For chlorophyll in a **leaf**:
  
  Energy in from absorption either drives photochemistry or it escapes as heat or as fluorescence.
Photochemistry occurs when excitation from antennae pigments is trapped by the photosynthetic reaction centers

- Excitons circulate between pigment molecules, and are funneled to the reaction centers of Photosystem I and II.
- Photosystem I and II are pigment-protein complexes that trap the energy from the Chl excited state in a stable chemical form.
Steady-state electron flow through Photosystems II and I is limited by an enzyme called the Cytochrome b₆f complex.

- Cyt b₆f has a dual role: it is both rate-limiting, and subject to feedback regulation.
The energy supply through the electron transport system is regulated to satisfy the energy demands of carbon metabolism.

- The pools of the energetic intermediates are small, and they turn over rapidly.
- The supply and demand for energy come into balance in the steady-state.
Photosynthesis is subject to regulation on both physiological and ecological timescales

- Regulation functions to manage energy flow in a way that is safe and efficient
Carbon dioxide diffuses from the atmosphere down a concentration gradient into the chloroplasts

- Transport is via turbulent diffusion in moving air, and molecular diffusion in still air
Diffusive transport is often conceptualized with analogies to electrical circuits:

- Ohm’s law: flux is proportional to product of driving gradient and conductance.
- NB, gradients are bidirectional & conductance is inverse of resistance (g = 1/r).
Net diffusive transport of CO$_2$ is coordinated with net CO$_2$ exchange of carbon metabolism

- Ultimately, the biochemical reactions can only go as fast as diffusion allows
Steady-state dynamics of carbon metabolism are limited by CO$_2$, O$_2$, and the enzyme Rubisco

- **PCR cycle**: photosynthetic carbon reduction cycle (Calvin cycle)
- **PCO cycle**: photosynthetic carbon oxidation cycle (photorespiration)
Relative abundance of CO$_2$ and O$_2$ at Rubisco determines PCR and PCO cycle activity

- $\Gamma$ (Gamma): the CO$_2$ compensation point, where PCR and PCO activity balance
Diffusive uptake of CO$_2$ coupled to loss of H$_2$O because both move through stomatal pores

- Stomatal conductance controls water loss through transpiration
Due to the high heat capacity of water, transpiration is a key control on leaf temperature

- Photosynthesis is controlled by the interaction of multiple resources and stressors
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The traditional ecological perspective on photosynthesis:

- Top down model was formulated by Monteith (1972)
- Bottom up model was formulated by Farquhar, von Caemmerer, and Berry (1980)
- Incomplete separation of environmental versus physiological controls
The Monteith model: $\text{GPP} = \text{APAR} \times \text{LUE}$

- $\text{GPP}$: gross primary production (photosynthesis)
- $\text{APAR}$: absorbed photosynthetically active radiation
- $\text{LUE}$: the light-use efficiency of photosynthesis
The Farquhar, von Caemmerer, Berry model: $A = \min \{A_j, A_c\}$

- $A_j$: potential light-limited rate of photosynthesis
- $A_c$: potential light-saturated rate of photosynthesis
FvCB: motivating observations

- Photosynthetic responses to light, temperature, and CO₂ are non-linear and interact with one another.
FvCB: key insight

- The steady-state fluxes are under the kinetic control of the rate-limiting step in electron transport or carbon metabolism, and the system switches efficiently as the environment varies.

Fig. 1. Simplified photosynthetic carbon reduction (PCR) and photorespiratory carbon oxidation (PCO) cycles, with cycle for regeneration of NADPH linked to light driven electron transport. For each carboxylation, $\phi$ oxygenations occur. Gly denotes glycine, $\text{Fd}^-$ denotes reduced ferredoxin (assumed equivalent to $1/2\text{NADPH}$), PGA denotes 3-phosphoglycerate, PGIA phosphoglycolate. At the compensation point $\phi = 2$. 

$\phi$ - stoichiometric proportion of oxygen consumed per carboxylation event.
FvCB: terminology

\[ A = \min\{A_j, A_c\} \]

\(A\), observed rate of net CO\(_2\) assimilation
\(\min\{}\), minimum of the terms in following brackets
\(A_j\), potential rate of net CO\(_2\) assimilation under light limitation
\(A_c\), potential rate of net CO\(_2\) assimilation under light saturation
FvCB: $A_c$ based on Michaelis-Menten kinetics

$$[E] + [S] \rightleftharpoons [ES] \rightarrow [E] + [P]$$

$$v_0 = \frac{k_3 \cdot E \cdot S}{(k_2 + k_3)/k_1 + S}$$

$E$, enzyme
$S$, substrate
$ES$, enzyme-substrate complex
$P$, product
$k_1$, rate constant for ES formation
$k_2$, rate constant for ES dissociation
$k_3$, rate constant for P formation
FvCB: $A_c$ accounts for competition between $\text{CO}_2$ and $\text{O}_2$

$$A_c = \frac{V_{\text{max}}(\text{RUBC}) \cdot C}{K_c \cdot (1 + O/K_o) + C} \cdot (1 - \Gamma_s/C) - R_d$$

$$\Gamma_s = \frac{1}{2} \cdot \frac{O}{S} = \frac{k_c}{K_c} \cdot \frac{K_o}{k_o}$$

$A_c$, Potential rate of net $\text{CO}_2$ assimilation under light saturation

$V_{\text{max}}(\text{RUBC})$, Maximum carboxylase activity of Rubisco

$k_c, k_o$, Catalytic constants of Rubisco for $\text{CO}_2$ and $\text{O}_2$

$K_c, K_o$, Michaelis constants of Rubisco for $\text{CO}_2$ and $\text{O}_2$

$S$, Specificity of Rubisco for $\text{CO}_2$ versus $\text{O}_2$

$\Gamma_s$, $\text{CO}_2$ compensation point in absence of $R_d$

$R_d$, Mitochondrial/dark respiration

$C, O$, Partial pressure of $\text{CO}_2$ and $\text{O}_2$ in the chloroplast
FvCB: simulations of the responses to CO$_2$ and O$_2$

**Fig. 4.** Quantum yield versus intercellular $p$(CO$_2$), C. The quantum yield is determined as the slope of the curve relating CO$_2$ assimilation rate, $A$, to absorbed irradiance, $I$, in the range 50-150 $\mu$mol photons m$^{-2}$ s$^{-1}$ at 25°C. The responses are plotted for two intercellular partial pressures of O$_2$, 10 and 210 mbar.

**Fig. 7.** CO$_2$ fluxes versus intercellular $p$(CO$_2$), C(bar). The solid lines at 25°C and 1000 $\mu$mol photons m$^{-2}$ s$^{-1}$ represent the situation in ambient (210 mbar) $p$(O$_2$), with $V_c$, $A$, and 0.5 $V_c$ denoting the rates of carboxylation, the net rate of assimilation of CO$_2$, and the rate of release of photorespired CO$_2$. The dashed line represents the rate of CO$_2$ assimilation in 10 mbar $p$(O$_2$).
FvCB: terminology

\[ A = \min\{A_j, A_c\} \]

\( A \), observed rate of net \( \text{CO}_2 \) assimilation
\( \min\{} \), minimum of the terms in following brackets
\( A_j \), potential rate of net \( \text{CO}_2 \) assimilation under light limitation
\( A_c \), potential rate of net \( \text{CO}_2 \) assimilation under light saturation
FvCB: $A_j$ also accounts for competition between $\text{CO}_2$ and $\text{O}_2$

$$A_j = \frac{J'_{P680}}{4 + 8 \cdot \frac{\Gamma_*}{C}} \cdot (1 - \frac{\Gamma_*}{C}) - R_d$$

$A_j$, Potential rate of net $\text{CO}_2$ assimilation under light limitation

$J'_{P680}$, Potential rate of linear electron transport

$\Gamma_*$, $\text{CO}_2$ compensation point in absence of $R_d$

$R_d$, Mitochondrial/dark respiration

$C$, Partial pressure of $\text{CO}_2$ in the chloroplast
FvCB: A_j expression for electron transport is empirical

\[ J'_{P680} = \begin{cases} 
  a = \frac{b + J_{max} - \sqrt{(b + J_{max})^2 - 4 \cdot \theta \cdot b \cdot J_{max}}}{2 \cdot \theta} \\
  b = Q \cdot \alpha_2 \cdot \Phi_{P2(max)} 
\end{cases} \]

- \( J'_{P680} \), Potential rate of linear electron transport
- \( J_{max} \), Observed maximum rate of linear electron transport
- \( \theta \), An empirical curvature parameter
- \( Q \), Photosynthetically active radiation (PAR) incident on the leaf
- \( \alpha_2 \), Fraction of incident PAR absorbed by Photosystem II
- \( \Phi_{P2(max)} \), Maximum photochemical yield of Photosystem II
FvCB: simulation of the light response

Fig. 10. Rate of assimilation of CO$_2$, $A$, versus absorbed irradiance, $I$, at three levels of carboxylase - 0, 3 and 1 g carboxylase/g chlorophyll. Rates of "dark respiration" are scaled accordingly.
FvCB: temperature-dependent parameters

<table>
<thead>
<tr>
<th>Saturating-type light dependence function:</th>
<th>Unsaturating-type light dependence function:</th>
</tr>
</thead>
<tbody>
<tr>
<td>$J_{max}$, Activation and deactivation</td>
<td>$V_{max} (RUBC)$, Activation and deactivation</td>
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<td>$V_{max} (RUBC)$, Activation only</td>
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</tr>
<tr>
<td>$1/S$, Activation only</td>
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</tr>
<tr>
<td>$R_d$, Activation only</td>
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</tr>
</tbody>
</table>
FvCB: temperature-dependence based on Arrhenius function

\[ k = k_{ref} \cdot \exp\left(\frac{E_a}{R} \cdot \left[\frac{1}{T_{ref}} - \frac{1}{T_{leaf}}\right]\right) \cdot \frac{\left[1 + \exp\left(\frac{T_{ref} \cdot \Delta S - H_d}{T_{ref} \cdot R}\right)\right]}{\left[1 + \exp\left(\frac{T_{leaf} \cdot \Delta S - H_d}{T_{leaf} \cdot R}\right)\right]} \]

- \( \Delta S \), Entropy factor (kJ mol\(^{-1}\) K\(^{-1}\))
- \( H_d \), Enthalpy of deactivation (kJ mol\(^{-1}\))
- \( R \), Universal gas constant (0.008314 kJ mol\(^{-1}\) K\(^{-1}\))
- \( T_{ref} \), Reference temperature (25°C = 298 K)
- \( T_{leaf} \), Leaf temperature (K)
FvCB: temperature-dependence based on $Q_{10}$ function

$$k = k_{ref} \cdot \frac{\exp\left(ln(Q_{10}) \cdot \frac{[T_{leaf} - T_{ref}]}{10}\right)}{1 + \exp(c \cdot [T_{leaf} - T_{limit}])}$$

$k$, Parameter value at leaf temperature of interest
$k_{ref}$, Parameter value at reference temperature ($25^\circ C = 298$ K)
$T_{ref}$, Reference temperature ($25^\circ C = 298$ K)
$T_{leaf}$, Leaf temperature ($^\circ C$ or K)
$Q_{10}$, Upward scaling parameter quantifying change per $10^\circ C$
$T_{limit}$, Limiting temperature above which to scale downward ($^\circ C$ or K)
c, Downward scaling parameter applied above $T_{limit}$
FvCB: simulations of photosynthetic temperature-dependence

Fig. 6. CO₂ compensation point, F (μbar) versus temperature, at two absorbed irradiances (100 and 1,000 μmol photons m⁻² s⁻¹) and an intercellular p(O₂) of 210 mbar

Fig. 8. Effect of intercellular p(CO₂), C(μbar), on the temperature response of net CO₂ assimilation rate. The absorbed irradiance is 700 μmol photons m⁻² s⁻¹ and the p(O₂) is 210 mbar

Fig. 9. Effect of absorbed irradiance, I, on the temperature dependence of net CO₂ assimilation rate. The effect of removal of "dark respiration," Rₐ, is shown as the dotted line and the effect of removal of electron transport limitations (potential electron transport, J → ∞) is shown as the dotted line. The simultaneous removal of both Rₐ=0, J → ∞ is shown as (· · · · ·)
The emerging ecological perspective on photosynthesis:

- How exactly is absorbed light used to drive the fixation of carbon dioxide?
- Johnson and Berry (2021) separate the environmental vs. physiological controls
JB: mechanistic expression for the potential rate of electron flow

\[
J'_{P700} = \frac{V_{max\ (CB6F)} \cdot Q}{\alpha_1 \cdot \Phi_{P1\ (max)}} + Q
\]

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
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<tbody>
<tr>
<td>(J'_{P700})</td>
<td>Potential rate of electron transport through Photosystem I</td>
</tr>
<tr>
<td>(Q)</td>
<td>Photosynthetically active radiation incident on leaf</td>
</tr>
<tr>
<td>(\alpha_1)</td>
<td>Absorption cross-section of Photosystem I</td>
</tr>
<tr>
<td>(\Phi_{P1\ (max)})</td>
<td>Maximum photochemical yield of Photosystem I</td>
</tr>
<tr>
<td>(V_{max\ (CB6F)})</td>
<td>Maximum activity of Cytochrome b\textsubscript{6}f complex</td>
</tr>
</tbody>
</table>
Light-limited (Cyt b6f-limited) state:

\[ A_j = \frac{J'_{P680}}{4 + 8 \cdot \Gamma_*/C} \cdot (1 - \Gamma_*/C) - R_d \]

Light-saturated (Rubisco-limited) state:

\[ A_c = \frac{V_{max} (RUBC) \cdot C}{K_c \cdot (1 + O/K_o) + C} \cdot (1 - \Gamma_*/C) - R_d \]

Actual state:

\[ A = \min \{ A_j, A_c \} \]

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<tr>
<td>( A_j )</td>
<td>Potential rate of net carbon dioxide assimilation under Cyt b6f limitation</td>
</tr>
<tr>
<td>( A_c )</td>
<td>Potential rate of net carbon dioxide assimilation under Rubisco limitation</td>
</tr>
<tr>
<td>( C, O )</td>
<td>Partial pressures of carbon dioxide and oxygen in the chloroplast</td>
</tr>
<tr>
<td>( J'_{P680} )</td>
<td>Potential rate of linear electron transport</td>
</tr>
<tr>
<td>( K_c, K_o )</td>
<td>Michaelis-Menten constants of Rubisco for carbon dioxide and oxygen</td>
</tr>
<tr>
<td>( R_d )</td>
<td>Rate of dark respiration (mitochondrial respiration)</td>
</tr>
<tr>
<td>( V_{max} (RUBC) )</td>
<td>Maximum carboxylase activity of Rubisco</td>
</tr>
<tr>
<td>( \Gamma_* )</td>
<td>Carbon dioxide compensation point in the absence of dark respiration</td>
</tr>
</tbody>
</table>
JB: new tool for understanding and simulating photosynthesis

- Diagnostic applications: interpret experimental measurements of leaves & canopies
- Prognostic applications: simulate leaf-level photosynthesis in land surface models
References

- Slides 2-5: diagrams made with biorender.com
Questions?

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