Primary Producer Carbon

Elemental Ecology
Week Three
General Photosynthesis Review

C₃ Photosynthesis

C₄ Photosynthesis

CAM Photosynthesis

Aquatic Photosynthesis
What are plants made of?

- **Hydrogen**: 6.3%
- **Nitrogen**: 1.3%
- **Carbon**: 44%
- **Oxygen**: 45%
2/3 of the CO$_2$ fixed via photosynthesis is fixed on land

Walker et al. 2020
The δ^{13}C of Atmospheric CO₂ Has Changed Over Time

How does this impact plant δ^{13}C values?

Hare et al. 2018
Photosynthesis

\[ 6 \text{CO}_2 + 6 \text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2 \]

**Light Reactions**
convert light energy into chemical energy (NADPH and ATP)
produce O\(_2\)

**Dark Reactions**
fix CO\(_2\)
produce carbohydrates
Photosynthesis Occurs in Chloroplasts
C$_3$ Photosynthesis

- **vein**
- **palisade mesophyll cells**
- **spongy mesophyll cells**
- **stomata**
The Calvin-Benson Cycle

~95% of all plant species use C₃ photosynthesis

Melvin Calvin and colleagues at UC Berkeley discovered the first organic product of carbon fixation using $^{14}$CO₂!

The initial product of CO₂ fixation is a molecule with three carbons.
**C₃ Photosynthesis**

**Carboxylation of RuBP is rate-limiting**

Rubisco has a high affinity for $^{12}\text{CO}_2$

- **CO₂ diffusion in air**
  - $\alpha = 1.0044$
  - $\varepsilon = 4.4\%$

- **CO₂ fixation by Rubisco**
  - $\alpha = 1.0270 – 1.0030$
  - $\varepsilon = 27.0 – 30.0\%$

O’Leary 1988
C$_3$ Photosynthesis

\[ \Delta ^{13}C = a - (b - a)(c_i / c_a) \]

- CO$_2$ diffusion in air
  \[ \varepsilon = 4.4\% \]

- CO$_2$ fixation by Rubisco
  \[ \varepsilon = 27.0\% \]

- Ratio of intracellular to atmospheric partial pressures of CO$_2$
C\textsubscript{3} Photosynthesis

\[ \delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{atm.}} - a - (b - a)(c_i / c_a) \]

- \( \delta^{13}\text{C}_{\text{atm.}} = -8.4\%o \)

- \( \delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{atm.}} - a - (b - a)(c_i / c_a) \)

- CO\textsubscript{2} diffusion in air \( \varepsilon = 4.4\%o \)

- CO\textsubscript{2} fixation by Rubisco \( \varepsilon = 27.0\%o \)
\[ \delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{atm.}} - a - (b - a)(c_i / c_a) \]

\[ \delta^{13}\text{C}_{\text{atm.}} = -8.4\% \]
\[ a = 4.4\% \]
\[ b = 27.0\% \]
\[ c_i / c_a = 0.7 \]

\[ \delta^{13}\text{C}_{\text{atm.}} = -8.4\% \]
\[ a = 4.4\% \]
\[ b = 27.0\% \]
\[ c_i / c_a = 0.9 \]
Impact of $c_i / c_a$ on $\Delta^{13}C$

$$\Delta^{13}C = a - (b - a)(c_i / c_a)$$

Ehleringer et al. 1980
C3 grasses
$\delta^{13}C = -26.7 \pm 2.3 \%\text{o}$

C4 grasses
$\delta^{13}C = -12.5 \pm 1.1 \%\text{o}$

-20 to -35\%o
-9 to -19\%o
Why is there so much variation in the $\delta^{13}C$ values of C$_3$ plants?

Acacia Plants from Australia

$\delta^{13}C$

Count

Fogel et al. unpublished data
Why is there so much variation in the $\delta^{13}C$ values of $C_3$ plants?

Factors that impact $\Delta$ and $\delta^{13}C$ in $C_3$ plants:

- CO$_2$ Source
- Salinity
- Precipitation
- Degree of Shading
- Level of Aridity
The sources and $\delta^{13}C$ values of CO$_2$ impact plant $\delta^{13}C$ values

Burning fossil fuels can decrease local atmospheric CO$_2$ $\delta^{13}C$ values

Salt Lake City, Utah

Pataki et al. 2007
The sources and δ\textsuperscript{13}C values of CO\textsubscript{2} impact plant δ\textsuperscript{13}C values

The canopy effect

Table 5 Estimates of leaf carbon discrimination (%), c\textsubscript{i} (μmol mol\textsuperscript{-1}) and c\textsubscript{i}/c\textsubscript{a} (μmol mol\textsuperscript{-1}) for a tropical rainforest during the dry and wet seasons. [CO\textsubscript{2}]\textsubscript{canopy} (μmol mol\textsuperscript{-1}) and δ\textsuperscript{13}C\textsubscript{canopy} [%o] are weighted by above-canopy photosynthetically active radiation PAR. δ\textsuperscript{13}C\textsubscript{leaf} is averaged for each canopy position.

<table>
<thead>
<tr>
<th></th>
<th>2.00 m</th>
<th>Dry season 13.3 m</th>
<th>28.3 m</th>
<th>2.00 m</th>
<th>Wet season 18.2 m</th>
<th>31.6 m</th>
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<tbody>
<tr>
<td>[CO\textsubscript{2}]\textsubscript{canopy}</td>
<td></td>
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<tr>
<td>δ\textsuperscript{13}C\textsubscript{canopy}</td>
<td>-33.6</td>
<td>-33.2</td>
<td>-28.6</td>
<td>-34.2</td>
<td>-33.3</td>
<td>-29.9</td>
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<tr>
<td>δ\textsuperscript{13}C\textsubscript{leaf}</td>
<td>26.14</td>
<td>26.53</td>
<td>121.68</td>
<td>26.57</td>
<td>26.34</td>
<td>22.92</td>
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<tr>
<td>Δleaf</td>
<td></td>
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<td></td>
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<td></td>
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<tr>
<td>c\textsubscript{i}</td>
<td>324</td>
<td>316</td>
<td>249</td>
<td>339</td>
<td>323</td>
<td>271</td>
</tr>
<tr>
<td>c\textsubscript{i}/c\textsubscript{a}</td>
<td>0.88</td>
<td>0.90</td>
<td>0.70</td>
<td>0.90</td>
<td>0.89</td>
<td>0.75</td>
</tr>
</tbody>
</table>

Buchmann et al. 1997
Increasing salinity increases $\delta^{13}$C values

If a plant is water-stressed, it will close its stomata to prevent water loss, which decreases $c_i / c_a$ and thus, also decreases isotopic discrimination.

Guy et al. 1980
Increasing precipitation decreases $\delta^{13}\text{C}$ values.
Increasing light increases $\delta^{13}C$ values

Increasing light increases photosynthetic rate, which decreases isotopic discrimination.

Ehleringer et al. 1986
Increasing altitude increases $\delta^{13}C$ values

The atmospheric partial pressure of CO$_2$ decreases with increasing altitude.

Körner et al. 1988, Tieszen 1991
How does aridity influence $\delta^{13}$C values?
Kranz Anatomy and $C_4$ Photosynthesis

Cross section of corn leaf - Kranz architecture
The initial product of CO₂ fixation is a molecule with four carbons typically malate or aspartate is sent to the bundle sheath cell to be decarboxylated.
**C₄ photosynthesis evolved independently many times**

C₄ photosynthesis evolved independently in over 60 plant lineages within both Eudicots and Monocots

The evolution of C₄ photosynthesis depends on the co-occurrence of the necessary external (e.g., climatic conditions) and internal factors (e.g., genetic, structural, and biochemical conditions)

The oldest C₄ lineage (Chloridoideae) is ~30 million years old

Sage et al. 2011
C₄ photosynthesis evolved in a low [CO₂] atmosphere

WHY?

C₄ photosynthesis now accounts for almost 25% of terrestrial gross primary productivity despite only occurring in < 5% of plants!

Niklaus and Kelly 2018
Avoiding photorespiration with C\textsubscript{4} photosynthesis

Rubisco is both a \textit{carboxylase} (yay!) and an \textit{oxygenase} (boo!)

Photorespiration occurs when Rubisco fixes O\textsubscript{2} instead of CO\textsubscript{2}

Photorespiration is wasteful and energetically expensive

Photorespiration occurs more frequently as [CO\textsubscript{2}]/[O\textsubscript{2}] decreases
Avoiding photorespiration with C_4 photosynthesis

PEP carboxylase evolved in a low CO_2 / high O_2 atmosphere

PEP *carboxylase* fixes CO_2 and HCO_3^- (it never interacts with O_2)
C₄ photosynthesis evolved in a low [CO₂] atmosphere

Cerling et al. 1997
**C₄ Photosynthesis**

**Diffusion of CO₂ through the stomata is rate-limiting**

**PEP carboxylase is not as picky as Rubisco**

**CO₂ diffusion in air**

\[ \alpha = 1.0044 \]

\[ \varepsilon = 4.4\% \]

**CO₂ fixation by PEP carboxylase**

\[ \alpha = 0.9943 \]

\[ \varepsilon = -5.7\% \]

O’Leary 1988, Farquhar et al. 1989
\[ \Delta^{13}C = a - [b_{\text{PEP}} + b_{\text{RUB}}(\phi) - a](c_i / c_a) \]

- **CO\(_2\) diffusion in air**
  \( \varepsilon = 4.4\% \)

- **CO\(_2\) fixation by Rubisco**
  \( \varepsilon = 27.0\% \)

- **Effective discrimination by PEP carboxylase**
  \( \varepsilon = -5.7\% \)

- **Bundle sheath cell “leakiness”**
  \( \phi = 0.2–0.3 \)
C₄ Photosynthesis

\[ \delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{atm.}} - a - [b_{\text{PEP}} + b_{\text{RUB}}(\phi) - a](c_i / c_a) \]

- CO₂ diffusion in air
  \[ \varepsilon = 4.4\% \]

- Effective discrimination by PEP carboxylase
  \[ \varepsilon = -5.7\% \]

- Bundle sheath cell “leakiness”
  \[ \phi = 0.2–0.3 \]

- CO₂ fixation by Rubisco
  \[ \varepsilon = 27.0\% \]

- CO₂ diffusion in air
  \[ \varepsilon = -8.4\% \]
\[ \delta^{13}C_{\text{plant}} = \delta^{13}C_{\text{atm.}} - a - [b_{\text{PEP}} + b_{\text{RUB}}(\phi) - a](c_i / c_a) \]

\[ \delta^{13}C_{\text{atm.}} = -8.4\% \]
\[ a = 4.4\% \]
\[ b_{\text{PEP}} = -5.7\% \]
\[ b_{\text{RUB}} = 27.0\% \]
\[ \phi = 0.3 \]
\[ c_i / c_a = 0.4 \]
What leads to variation in $\delta^{13}C$ values in $C_4$ plants?

C$_4$ Grasses from Australia

Fogel et al. unpublished data
What leads to variation in $\delta^{13}C$ values in $C_4$ plants?
What leads to variation in $\delta^{13}C$ values in $C_4$ plants?

C$_4$ Grasses from Australia

$\delta^{13}C$

Bundle Sheath Cell “Leakiness”

Metabolic Subtype (e.g., NAD-ME, NADP-ME)