The flows of carbon are central to the cycles of life. Any story on the biosphere must include a thorough description and understanding of the carbon cycle.
Topics

- Background
  - Big Questions?
- Concepts
  - pools, fluxes, processes
  - Scales, Leaf, Ecosystem, Globe
- Carbon Stores and Fluxes
  - Stores: Vegetation and Soil C = f(x,y,z)
    - Soil Surveys
    - Biomass Inventories
  - Fluxes: NEP = f(x,y,t)
    - Global Fluxes

ESPM 2, The Biosphere
These are some general big questions. Can you think of others pertaining to the carbon cycle and your interests
Let’s start with carbon assimilation by leaves.

Leaves have many sizes and shapes, but their jobs are essentially the same: to be a vehicle for housing chloroplasts and chlorophyll, act as organs that intercept sunlight, while providing an architecture that facilitates the diffusion of CO2 to the site of carbon fixation, yet provide structures, like waxy cuticle and stomatal pores that prevent water to be lost to the atmosphere.
There are 3 major biochemical pathways for fixing CO2 by plants. The most abundant is the C3 pathway which uses the Calvin-Benson cycle (developed here at Berkeley, for which Melvin Calvin won a Nobel Prize, and Andrew Benson did not).

The C4 pathway is associated with many tropical grasses and is most efficient in warmer temperatures and during periods with low O2. It evolved about 10 Million years ago.

CAM pathway is associated with cactus and pineapple. It is an efficient path to conserve water as stomata remain closed during the day while the plant captures light energy, then dark reactions proceed at night when the transpiration demand is less.
An example of the stoichiometry of the photosynthetic carbon reduction (PCR) and the photosynthetic carbon oxidation (photorespiration cycles). In this case, it is scaled with an input of 3 CO2 molecules

The enzyme ribulose-1,5-bisphosphate carboxylase (Rubisco) catalyzes the reaction between gaseous carbon dioxide and ribulose-1,5-bisphosphate (RuBP).

Product of the reaction are two molecules of 3-phosphoglyceric acid for each CO2 molecule

\[ \text{C}_5\text{O}_3\text{H}_8(\text{PO}_4^{2-})_2 + \text{CO}_2 \rightarrow 2 \text{C}_3\text{O}_3\text{H}_4\text{PO}_4^{2-} \]

Chemical Energy (NADPH & ATP) is used to regenerate RUBP

We can observe the structure of Rubisco with X ray chrystallography. It has an affinity to either CO2 or O2.

The enzyme RuBisCO comprises 16 subunits: 8 small and 8 large units. The small units influence the stability and specificity of the large units, whereas the large units are the actual production sites. The interconnectivity affects catalysis, either in specificity or catalytic rate. (source: http://xray.bmc.uu.se/~michiel/research.php)

Plants invest large amounts of nitrogen in Rubisco; it comprises more than 50% of leaf protein in C₃ plants.
RUBISCO has an affinity for both CO$_2$ and O$_2$, with the later leading to photorespiration, a loss of CO$_2$. The rate of competitive oxygen fixation is a proportional to the oxygen concentration time the ratio of oxygenation (Vo) to carboxylation (Vc). At ambient conditions Vo/Vc is about 0.27 (2 times the CO2 compensation point divided by CO2; $\sim 2 \times 38/280$). In practice for each CO2 consumed by carboxylation 0.5 CO2 times Vo/Vc are lost by photorespiration; hence the amount of photorespiration decreases as CO2 concentrations increase.

Theta is the ratio of the oxygenation (Vo) to carboxylation (Vc) rates.
Critical Steps in C₃ Photosynthesis
Calvin-Benson Cycle

- **Light Reactions**
  - Chlorophyll, in chloroplasts, captures photons
  - Light energy is used to produce chemical energy in the forms of NADPH and ATP
  - Oxygen is produced

- **Dark Reactions**
  - A 3-C compound, PGA, is formed at the first Carboxylation step via the reaction between CO₂ and RUBP, a C₅ compound, and its subsequent cleaving (C₆ => 2 C₃)
  - The enzyme RUBISCO catalyzes the reaction between CO₂ and RUBP
  - RUBISCO has an affinity for both CO₂ and O₂, with the later leading to photorespiration, a loss of CO₂
  - Chemical Energy (NADPH & ATP) is used to regenerate RUBP
  - A carbohydrate, CH₂O, is formed

ESP 2 The Biosphere
C4 leaves have a unique anatomy, bundle sheaths
The enzyme PEP Carboxylase catalyzes a reaction between CO$_2$ and phosphoenolpyruvate (PEP) to form a C$_4$ compound, OAA.

The C$_4$ compound is transported into the specialized cells, the bundle sheaths, and is decarboxylated.

CO$_2$ is released into a low oxygen environment and photosynthesis is completed via the C$_3$ cycle.

Photorespiration is low; RUBISCO favors CO$_2$ in this environment because the ratio between CO$_2$:O$_2$ is high.
Critical Steps in C₄ Photosynthesis

- The enzyme PEP Carboxylase catalyzes a reaction between CO₂ and phosphoenolpyruvate (PEP) to form a C₄ compound
- The C₄ compound is transported into the specializes cells, the bundle sheaths, and is decarboxylated
- CO₂ is released into a low oxygen environment and photosynthesis is completed via the C₃ cycle
- Photorespiration is low; RUBISCO favors CO₂ in this environment because the ratio between CO₂:O₂ is high

ESPM 111 Ecosystem Ecology
Key Points $C_3$ vs $C_4$

- $C_3$ compound formed
- Uses enzyme called RuBP carboxylase/oxygenase in first dark fixation step
- Suffers from photorespiration
- Was one of the Earliest Pathways for Photosynthesis and has remained unchanged for ++100s Million years

- $C_4$ compound formed
- Uses enzyme called PeP Carboxylase in the first dark fixation step
- Bundle Sheath anatomy allows photosynthesis to occur in low $O_2$ environment and avoid photorespiration
- Evolved several times over last 10M years

ESPM 2, The Biosphere
Photosynthesis responds to changes in light and CO2 because it is a balance between Supply and Demand.

- **Physical limitation: delivery of CO₂ to leaf**
  - Diffusion through Leaf Boundary Layer
  - Diffusion through Stomatal Pores
  - Potential Gradient between free Atmosphere and substomatal Cavity
- **Biochemical limitation: carboxylation rate**
  - Light limitation
  - Enzyme limitation

ESPM 2, The Biosphere
Under ample light, the carboxylation rate is limited by CO2 and follows the RuBP-saturate rate of Michaelis-Menton enzyme kinetics.

Under ample CO2, the carboxylation rate is limited by light, which provides the electrons to ATP and NADPH to regenerate RuBP.
The response curve between photosynthesis and CO2 experiences several key states and a non-linear, saturating response.
The response curve between photosynthesis and light also experience a non-linear response and key states: 

- Photosynthesis is limited by light at low light levels.
- Photosynthesis saturates with respect to light at high levels.
- Zero Net Photosynthesis occurs at Non-Zero light levels due to Dark Respiration, denoted at the light compensation point.
- Net Carbon exchange at zero light is negative and represents Dark Respiration.
- The initial slope of the Photosynthesis-Light response is the Light Use Efficiency.

Data of Xu and Baldocchi 

ESP2, The Biosphere
Explains why C4 grasses advanced during the ice age.

- C₃ leaves exposed to low O₂ behave like C₄ plants at low CO₂ because photorespiration is inhibited.

- C₄ leaves had a physiological advantage during the Ice Age when CO₂ was about 180 ppm because they don't photorespire like C₃ plants.
Temperature Response of C$_3$ and C$_4$ Leaves

![Graph showing temperature response of C$_3$ and C$_4$ leaves.]

**Figure 10.** Response of photosynthesis to leaf temperature in the winter active C$_3$ desert ephemeral *Camissonia claviformis* and the summer active C$_4$ desert ephemeral *Amaranthus palmeri*. Data are redrawn from Mooney et al. (1976a) and Ehleringer (1983).

Photosynthesis of C$_4$ Plants is better adapted to High temperatures

Pearcy and Ehleringer, 1984 PCE

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Key Points

- Know how photosynthesis varies with light, temperature, CO2 and photosynthetic pathway
This lecture will cover material spanning ideas on how leaves assimilate carbon and how we produce integrated information at the ecosystem scale and how this integrates to over year and across the globe.
Classic carbon balance of an ecosystem. Know sources and sinks of carbon
Key terms to understand regarding gross and net carbon fluxes and their sources and sinks

Terms

- Gross Primary Productivity, GPP
- Net Primary Productivity, NPP
- Autotrophic Respiration, $R_{\text{auto}}$
- Net Ecosystem Productivity, NEP
- Heterotrophic Respiration, $R_{\text{hetero}}$
- Net Biome Productivity, NBP
What the terms mean. Know the difference between autotrophic respiration (respiration by self-feeders, like plants) and heterotrophic respiration (respiration by microbes, fungi, animals)
Visual graphic of the flows of carbon in and out of the biosphere. The thickness of the arrows gives you relative sense of the magnitudes of the in and out fluxes.
C Fluxes Across the World

ESP M 2, The Biosphere
Ecosystem Respiration ($F_R$) Scales with Ecosystem Photosynthesis ($F_A$), But with an Offset and Parallel Line is associate with Disturbed Sites

Baldocchi, Austral J Botany, 2008  ESPM 2, The Biosphere
The Ratio between Autotrophic Respiration (R) and Photosynthesis (P) is Constant: Regardless of Plant Size, Treatment etc

Emerging and Useful Ecological Rules

Gifford, 1994, Australian J Plant Physiol

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GPP and Climate Drivers

Climate explains 70% of variation in GPP

Luyssaert et al. 2007, GCB

ESPM 2, The Biosphere
NPP and Rain

Lieth

\[ Y = 3000 \left(1 - e^{-0.001664x}\right) \]

Dry Matter Production vs Precipitation

ESPM 2, The Biosphere
Climate explains 5% of variation in NEP

Luyssaert et al. 2007, GCB

ESPM 2, The Biosphere
C Cycling, Below Ground

Law and Ryan, 2005, Biogeochemistry

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De-Convolving Soil Respiration

Kuzyakov, 2006

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Soil Respiration and Temperature, Adequate Soil Moisture

- Respiration increases exponentially with temperature and respiration rates tend to double with every 10°C increase in temperature.
Temperature drives soil respiration, but so do other factors like leaf area, metabolic activity.
Soil dryness reduces soil respiration
Soil respiration scales strongly with C inputs, eg NPP. Most productive systems have the greatest soil respiration.
Key Points

• Know the flows and Fluxes of Carbon dioxide in and out of an ecosystem. What are the different terms and are they associated with leaves, stems, roots, soil, microbes?
• Know how the net and gross carbon fluxes vary with environmental variables