Photosynthesis, Transpiration, and Surface Energy Balance

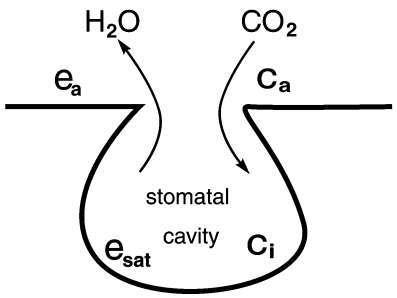
Please read

- Denning (1993, unpublished)
- Bonan Chapter on Photosynthesis

Photosynthesis

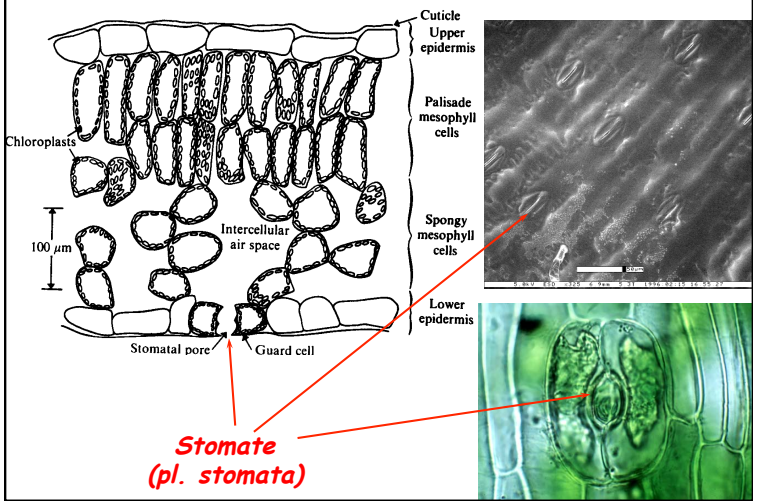
- Levels of control
  - Controls in individual leaves
  - Control by canopy processes
- Controlling factors
  - Direct controls: light, CO_2
  - Indirect controls: water, nutrients

Carbon and Water



- Plants eat CO_2 for a living
- They open their stomata to let CO_2 in
- Water gets out as an (unfortunate?) consequence
- For every CO_2 molecule fixed about 400 H_2O molecules are lost

Leaf Anatomy



Measuring Transpiration and Photosynthesis

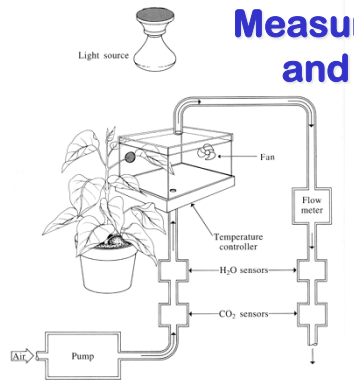


Figure 8.1
Experimental arrangement for the measurement of leaf transpiration and photosynthesis. The water vapor and CO_2 content of the gas entering a transparent chamber enclosing a leaf is compared with that leaving. If the water vapor concentration goes from 0.6 mol m^{-3} entering to 1.0 mol m^{-3} leaving for a gas flow rate of 10^{-5} m^3 s^{-1} (10 cm^3 s^{-1}), then J_w, for a leaf of area 10^{-3} m^2 (10 cm^2) would be (1.0 mol m^{-3} − 0.6 mol m^{-3})(10^{-5} m^3 s^{-1})/(10^{-3} m^2), or 0.004 mol $m^{-2}s^{-1}$. [See Field *et al.* (1989) and Leuning (1983) for refinements of measurement technique and analysis.]

- Control temperature, light level, humidity, and flow rates
- Measure changes in water vapor and CO2 concentration per unit time and leaf area

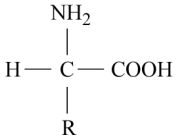
Nobel, 1991

Two major sets of reactions

- Light-harvesting reactions
  - Convert light into chemical energy (chlorophyll pigments inside the chloroplast)
  - Generate stored energy and "reductant"
- Carbon fixation ("dark") reactions
  - Uses chemical energy to convert CO_2 into sugars for later use by plant (or heterotrophs!)
  - Conversion of inorganic, oxidized carbon to organic, reduced carbon in an oxidizing environment requires energy and reductant
  - Primary fixation enzyme is called *Rubisco*

Amino Acids, Proteins, and Enzymes

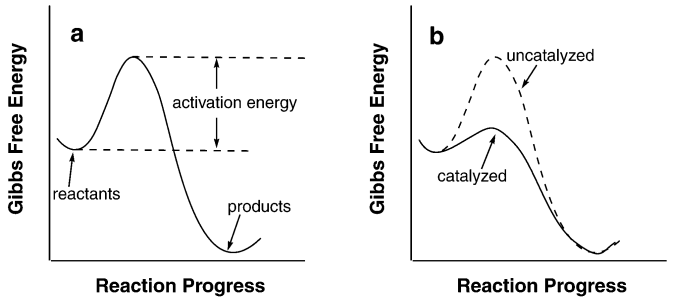
Structure of a generic amino acid



R *can be any functional group bonded to central C atom*

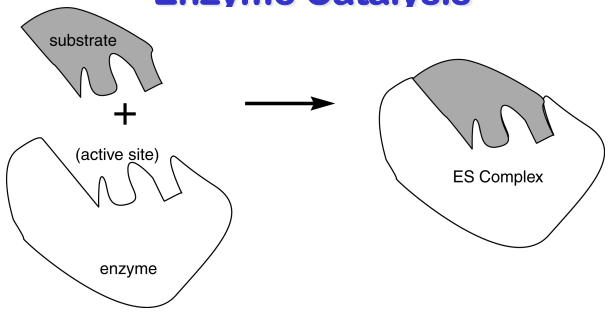
- All proteins are composed of amino acids, combined in long chains
- All amino acids contain nitrogen, which is therefore a key nutrient
- Some proteins act as *catalysts* for biochemical reactions (speed them up without being consumed)
- Catalytic proteins are called *enzymes*

Chemical Kinetics



- Chemical reaction proceeds towards lower free energy
- Reaction rate depends on activation energy to form an intermediate complex before products can be created
- Catalysts are chemicals which reduce the activation energy of a reaction, allowing it to run faster without consuming the catalyst

Enzyme Catalysis



- Enzymes have unique molecular structures that catalytic effects are specific to certain reagents
- Enzyme bonds to substrate molecule to form an enzyme-substrate (ES) complex
- ES complex then reacts with other reagent to form products, leaving enzyme free to bond with another substrate molecule

Michaelis-Menten Kinetics

Consider catalyzed reaction: $E + S \underset{k_2}{\overset{k_1}{\rightleftharpoons}} ES \xrightarrow{k_3} E + P$

Rate of product formation depends only on [ES] $V = k_3[ES]$

Amount of ES complex depends on

$$\frac{d}{dt}[ES] = k_1[E][S] - (k_2 + k_3)[ES]$$

production dissociation

At steady state, $[ES] = \frac{[E][S]}{(k_2 + k_3)/k_1} = \frac{[E][S]}{K_M}$ "Michaelis constant"

Michaelis-Menten Kinetics (cont' d)

Steady-state amount of ES $[ES] = \frac{[E][S]}{K_M}$

Define *total* amount of enzyme $E_T = E + ES$, then

$$[ES] = ([E_T] - [ES])[S]/K_M$$

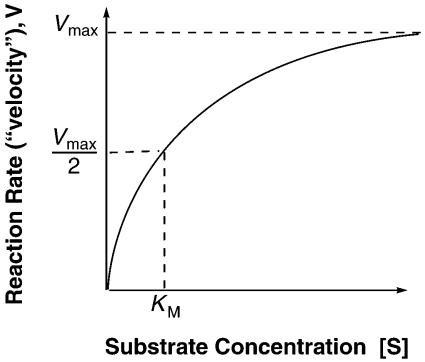
Solve for ES: $[ES] = [E_T]\frac{[S]}{[S] + K_M}$

Finally, rate of production of product is given by

$$V = k_3[E_T]\frac{[S]}{[S] + K_M} \qquad V = V_{max}\frac{[S]}{[S] + K_M}$$

Michaelis-Menten Kinetics (cont' d)

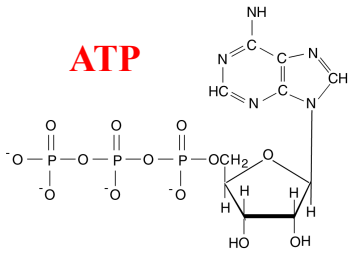
$$V = V_{max}\frac{[S]}{[S] + K_M}$$



- As substrate concentration increases, reaction speeds up
- When [S] >> K_m active sites are saturated, and V approaches V_{max}
- Recall V_{max} is proportional to E_T, the total amount of enzyme present

Energy and ATP

ATP



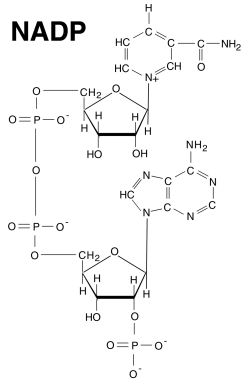
$$ADP + HPO_4^{2-} + H^+ \rightleftharpoons ATP + H_2O$$

Coupling ATP hydrolysis to another increases the equilibrium constant by 10^8

- Many biological reactions consume energy … "driven uphill" away from chemical equilibrium!
- This requires energy storage and later recovery
- ATP is the "currency" of energy in the biosphere
- Allows energy to be stored, transported, and recovered

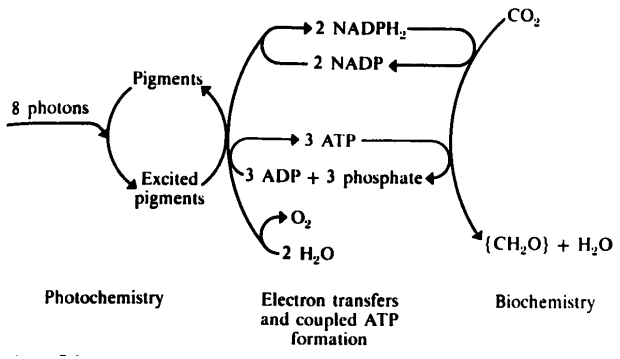
Oxidation and Reduction

NADP

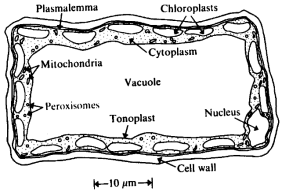


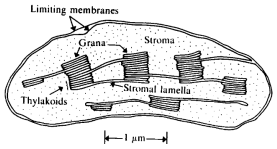
- Oxidation involves a "donor" species which loses an electron, becoming positively charged or "oxidized"
- Organic molecules are reduced … that is, they are electron donors
- Electrical batteries use pairs of redox reactions
- Photosynthesis uses $NADPH_2$ and NADP to provide reducing power required for formation of reduced carbon compounds from oxidized CO_2 in an oxidizing environment

Farquhar Photosynthesis Model



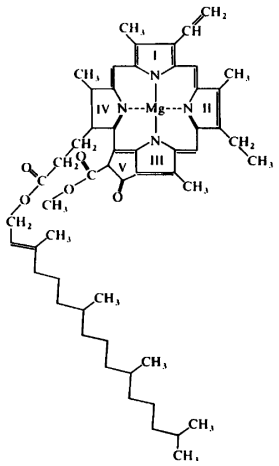
Anatomy and Physiology





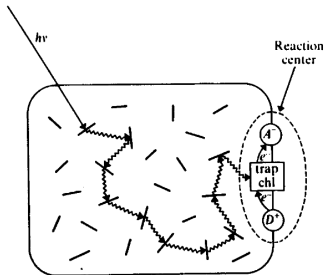
- Plant cells are mostly water-filled space
- Outer margins contain chloroplasts
- Chloroplasts contain chlorophyll, which is where the action is!

Chlorophyll Structure



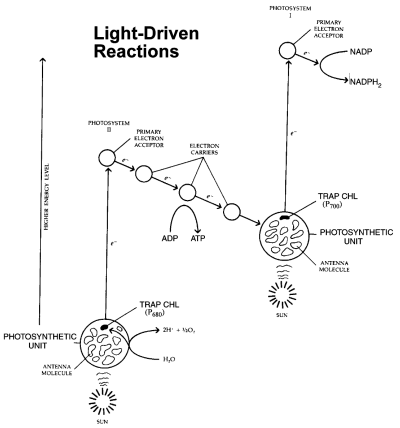
- Chlorophyll is a pigment
- "Head" and "tail" structure very closely related to hemoglobin
- Lots of N in head
- Head acts like an "antenna" to capture photons!
- Excited bonds in head transfer energy to adjacent molecules

Photochemical Reaction Center



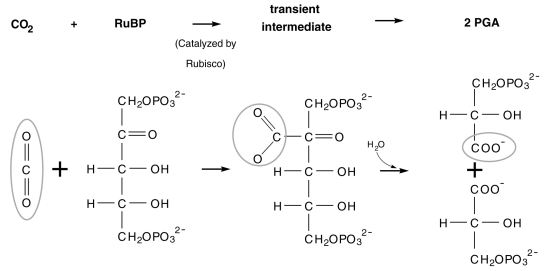
- Absorbed energy is passed among pigment molecules until it reaches a special molecule called "trap chlorophyll"
- Slightly lower energy level, energy can't get out
- Redox reactions reset trap, pass energy on as chemical potential

Photochemical Reactions



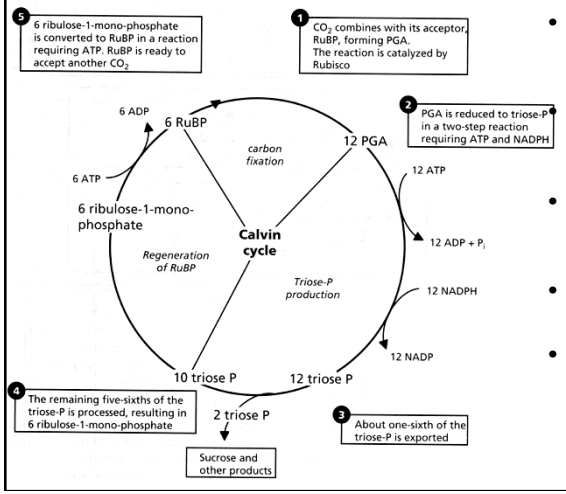
- Two primary "photosystems" use specific wavelengths (red)
- PS I drives formation of $NADPH_2$
- PS II splits water
- Redox half-cell used to drive ATP formation

Carbon Fixation



- 3-carbon compond PGA is formed from ribulose bis-phosphate
- Reaction catalyzed by RuBP Carboxylase
- Also goes "backward" to O_2 (oxygenase)
- ribulose bis-phosphate carboxylase oxygenase "RUBISCO"

Dark Reactions



- The "Calvin Cycle"
- Consumes ATP and $NADPH_2$
- Fixes CO_2 into organic intermediates
- Produces simple sugars
- Regenerates reagents

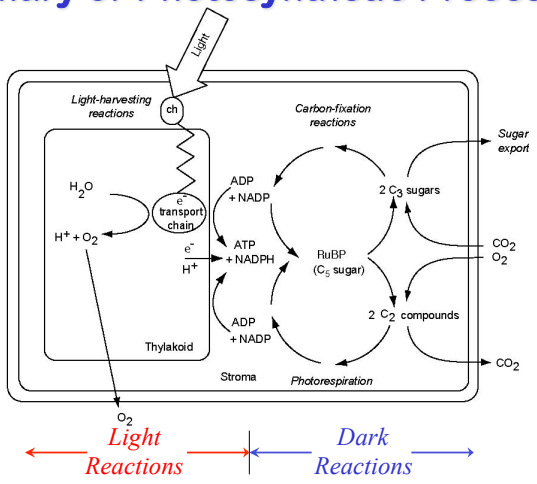
Photorespiration

- Rubisco molecule can work both ways ("carboxylase-oxygenase")
  - Catalyses formation of $\{CH_2O\}_n$ from CO_2 (assimilation)
  - Catalyses destruction of $\{CH_2O\}_n$ to form CO_2 (photorespiration)
- Unlike "dark" respiration, photorespiration provides no benefit at all to the plant … just a wasteful loss of energy
- Relative rates of carboxylation vs. oxygenation determined by competition between CO_2 and O_2 molecules for active sites on Rubisco enzyme
- Higher temperatures, increased O_2, and decreased CO_2 all favor photorespiration over assimilation

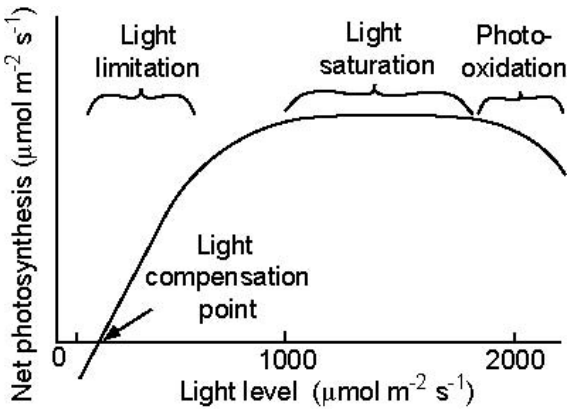
Rubisco can gain or lose carbon

- Carboxylase
  - Reacts with CO_2 to produce sugars
  - Leads to carbon gain
- Oxygenase
  - Reacts with O_2 to convert sugars to CO_2
  - Respires 20-40% of fixed carbon
  - Process known as photorespiration
  - Photoprotection mechanism

Summary of Photosynthetic Processes



Light Response of Photosynthesis



Photosynthetic Assimilation
(Farquhar-Berry-Collatz model)

$$A = \min(w_C, w_e, w_S) - R_D$$

$$w_C = V_m\left[\frac{c_i - \Gamma}{c_i + K_C(1 + O_2/K_O)}\right]$$

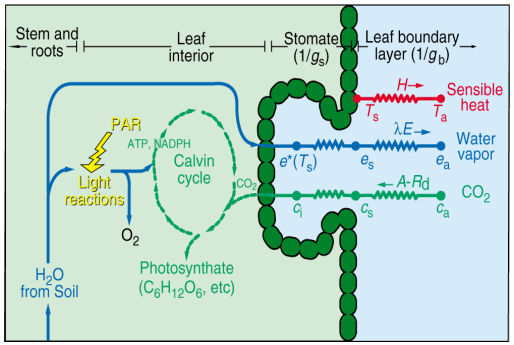
$$w_e = (\mathbf{F} \bullet \mathbf{n})\varepsilon(1 - \omega_v)\left[\frac{c_i - \Gamma}{c_i + 2\Gamma}\right]$$

$$w_s = V_m/2$$

$$R_d = 0.015 V_m$$

- Three limits:
  - Rubisco/CO_2
  - Light
  - "Sink" or starch
- Rubisco/CO_2 limited rate calculated by Michaelis-Menten catalysis
- Light limited rate: available PAR and stoichiometry of $NADPH_2$ and ATP consumption
- Sink limitation: related to V_m
- Dark respiration related to protein maintenance (V_m)

Leaf Physiology in SiB2

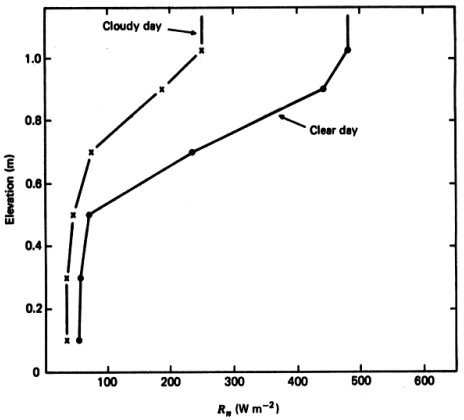


- Heat, water, and carbon fluxes are coupled by physiology
- Scaling to canopy and landscape fluxes based on resource allocation

Canopy Integration

- Farquhar photosynthesis model and Ball-Berry stomatal conductance calculation are derived for leaf-level fluxes
- How to integrate to entire canopy?
  - Could multiply fluxes (mol m^{-2} s^{-1}) at leaf level by total leaf-area index
  - That would assume all leaves have same properties and physical environment
  - What about shading inside canopy?
  - How does a plant respond to shading over time?

Canopy Attenuation of Radiation



- Radiation is absorbed and also scattered by individual leaves and stems
- Drops off steeply through canopy depth
- Penetration is deeper for diffuse than direct solar

Within-Canopy Radiative Transfer

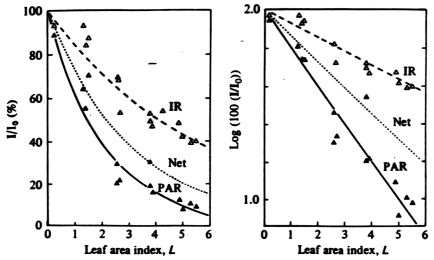


Fig. 2.18. Daily means of transmission of near-IR (- -△- -), PAR (——▲——) and net (.....) radiation in a wheat crop in early June (data from Szeicz 1974). In (*a*), irradiance in each waveband is expressed as a percentage of that incident on the top of the crop, and in (*b*) the data are transformed to logarithms.

- Attenuation is greater for visible (photosynthetically active radiation, PAR) than for near IR
- Attenuation is nearly log-linear with cumulative leaf-area index

Canopy Integration

(Sellers et al, 1992)

$$\frac{I(L)}{I_0} = e^{-kL}$$

L = "cumulative LAI" (vertical coordinate)

$$k = \frac{G(\mu)}{\mu}$$

$G(\mu)$ = projected LAI normal to beam

$$A_{canopy} = A_{sun-leaf} \int_0^{L_T} e^{-kL} dL$$

$$= A_{sun-leaf} \left[\frac{-\left(e^{-kL_T} - 1\right)}{k} \right]$$

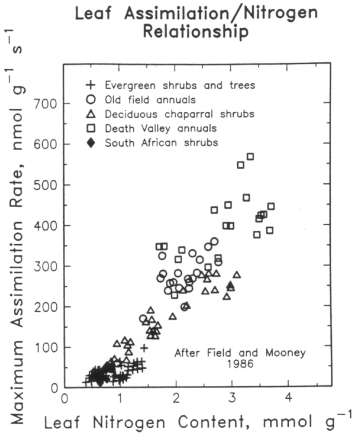
$$= A_{sun-leaf} \Pi$$

$$\Pi \equiv \frac{1 - e^{-kL_T}}{k} = \frac{FPAR}{k}$$

- How to efficiently integrate leaf-level equations across all leaf angles and light levels?
- Assume light levels drop off inside canopy according to Beer's Law
- Maximum photosynthesis rate (V_{max}) depends on Rubisco, an enzyme used to catalyze C fixation
- Rubisco is mostly nitrogen (most abundant protein on Earth)
- Assume plant allocates scarce N where it will yield the most C gain (following time-mean light!)

Canopy scaling factor Π ~ FPAR … get by remote sensing

Economics of Carbon and Nitrogen

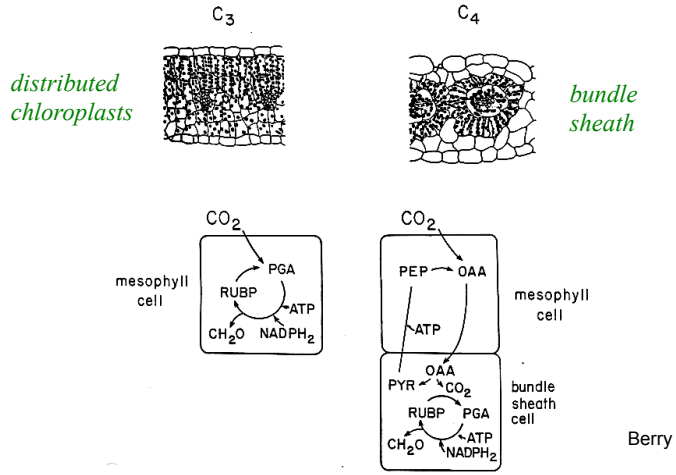


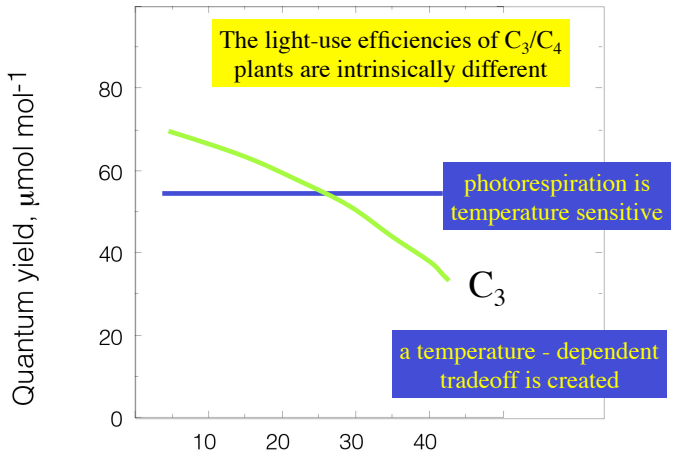
- Plants are not dumb
- Most plants are N-limited … more N makes them grow new tissue (leaves)
- Given scarce N, they invest it where it will return the highest yield in C gained
- Top ("sun") leaves are N-rich, green and juicy and healthy

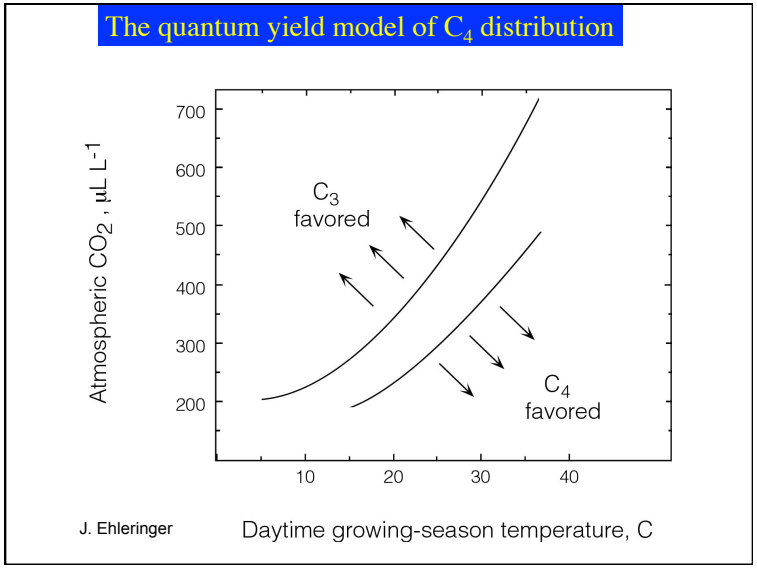
C_3 and C_4 Photosynthesis

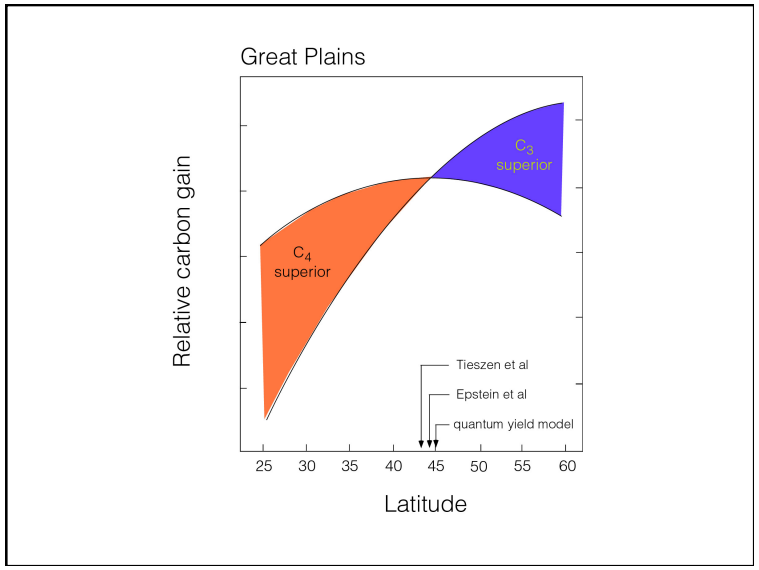
- Most plants produce sugars by the pathway outlined above, in which the first organic compounds have three carbon atoms (C_3)
- Some tropical and subtropical plants have evolved a separate mechanism in which the first products have four carbon atoms (C_4)
- C_4 photosynthesis is a mechanism to overcome photorespiration (high O_2/CO_2 ratio, high T)
- Involves active transport of dissolved CO_2 to specialized "bundle-sheath" cells to overwhelm O_2 at Rubisco active sites
- Uses energy to do this … only "pays off" when photorespiration is a big problem
- Evolved only ~ 10 My BP, when CO_2 levels dropped

C_3 and C_4 Physiology & Biochemistry








Great Plains
Relative carbon gain
C4 superior
C3 superior
Tieszen et al
Epstein et al
quantum yield model
25 30 35 40 45 50 55 60
Latitude