PHOTOSYNTHESIS

PREFACE

- The sun is the ultimate source of energy.
- The sun powers nearly all life forms.
- Photosynthesis converts solar energy into chemical energy.
- Photoautotrophs use solar energy to synthesize organic compounds from carbon dioxide and water.
 - They include plants, algae and some prokaryotes
 - They form the base of almost every food chain/web
- Fossil fuels represent stored solar energy from the past.

RECALL

- De Phototrophs: obtain energy from light
- Chemotrophs: obtain energy from chemicals
- □ Autotrophs: obtain carbon from CO2
- Heterotrophs: obtain carbon from organic sources

Photosynthesis

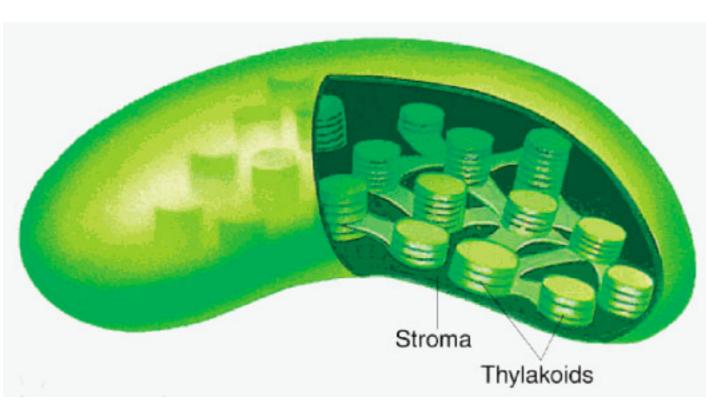
Main Idea: A series of enzymatic reactions use solar energy to produce large organic compounds from smaller inorganic compounds.

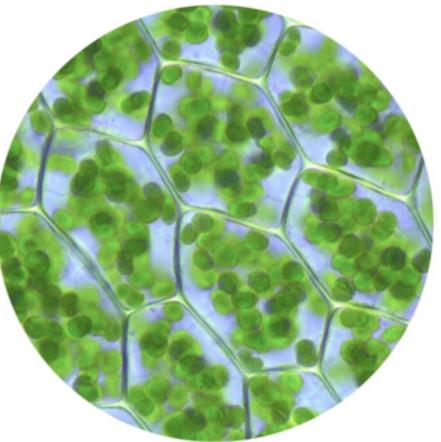


Tuesday, January 22, 2013

Solar Energy to Chemical Energy

- Photosynthesis likely evolved in prokaryotes which possessed infolded membranes with enzymes and other molecules that could harness solar energy to produce organic compounds
 - The site of photosynthesis in modern photoautotrophs is the chloroplasts
 - The endosymbiotic theory explains how chloroplasts may have evolved





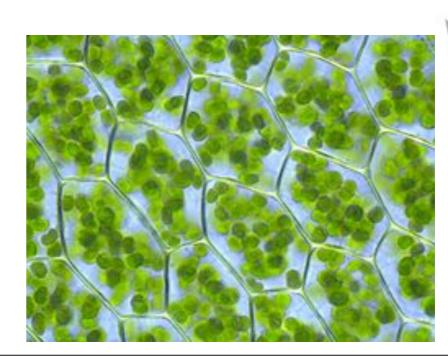
in a single leaf A typical mesophyll cell contains 30-40 chloroplasts

There are millions of chloroplasts in a single leaf

Chloroplasts

All green parts of a plant have chloroplasts

Mesophyll



Stomata



 CO_2

 \mathbf{O}_2

Vein

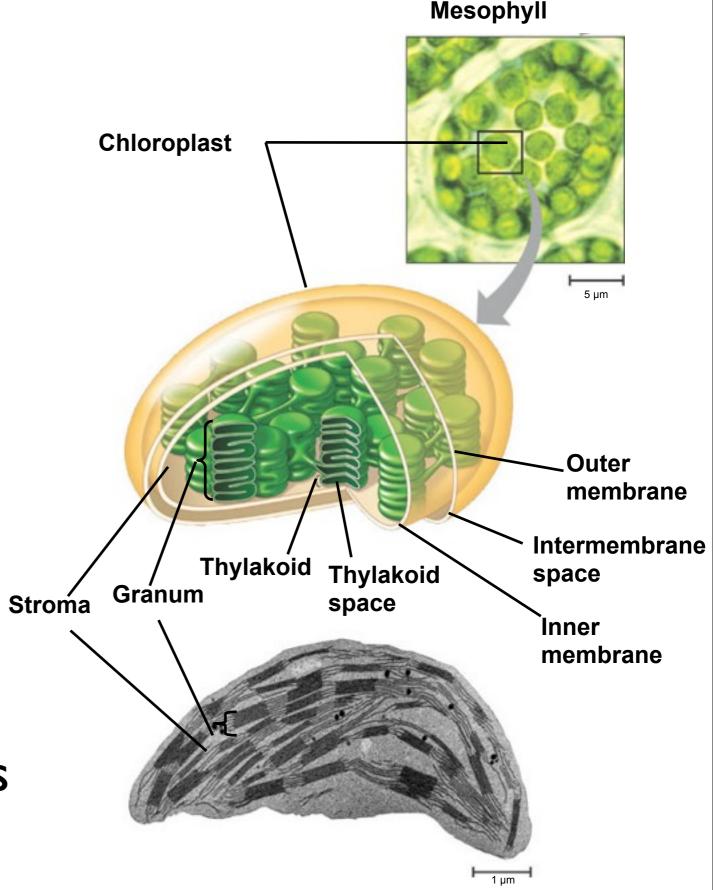
Chloroplasts

Double outer membrane

Chloroplasts filled with a dense fluid

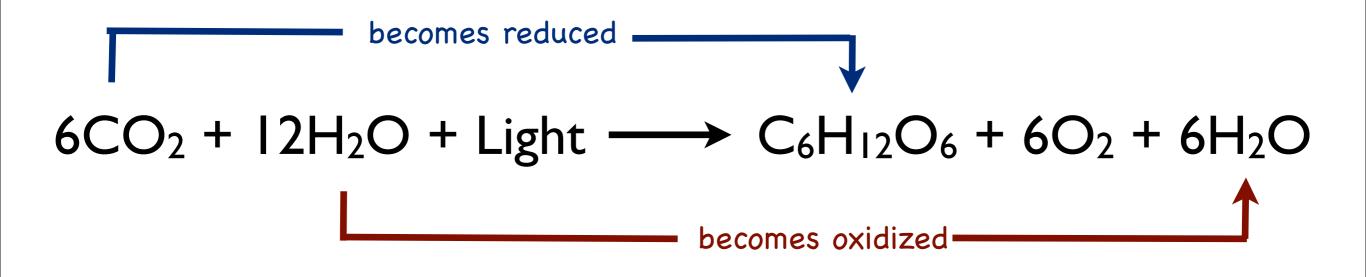
A third membrane system made of stacks called thylakoids

Green pigment chlorophyll found thylakoid membranes



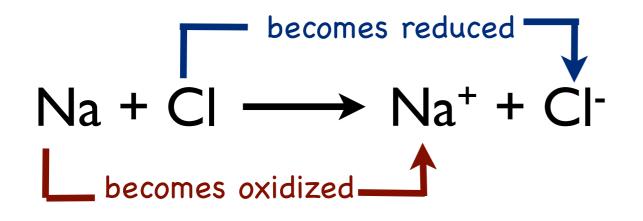
Photosynthesis is a "redox reaction"

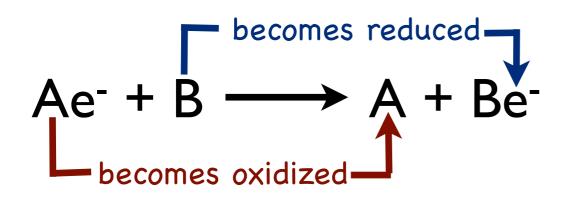
- Recall the following
 - Oxidation Reactions- removes electrons from a substance
 - catabolic / breaking down a substance / releases energy
 - Reduction Reactions- adds electrons to a substance
 - anabolic / building down a substance / requires energy



The principle of the "redox reaction"

- Oxidation Reactions- removes electrons from a substance
- Reduction Reactions- adds electrons to a substance





Ae⁻ the "electron donor" is the *reducing agent*

B the "electron acceptor" is the **oxidizing agent**

Redox Rxns Release Energy

- Energy is required to pull electrons away from an atom.
- The more electronegative the atom, the more energy is needed to pull away that/those electrons.
 - recall: electronegativity measures the pull that atom exerts on its electrons
- An electron(s) loses potential energy if moves from a less electronegative atom to a more electronegative atom.
 - Because a highly electronegative atom is more stable, it is going to require relatively more energy to pull it away, assume that the release of energy is roughly equal regardless of the atom, thus the amount of NET energy release will be less in the highly electronegative atom.

Redox Analogy

HIGH LOW Potential Energy Electronegativity

A ball rolling downhill loses potential energy A ball rolling downhill releases kinetic energy

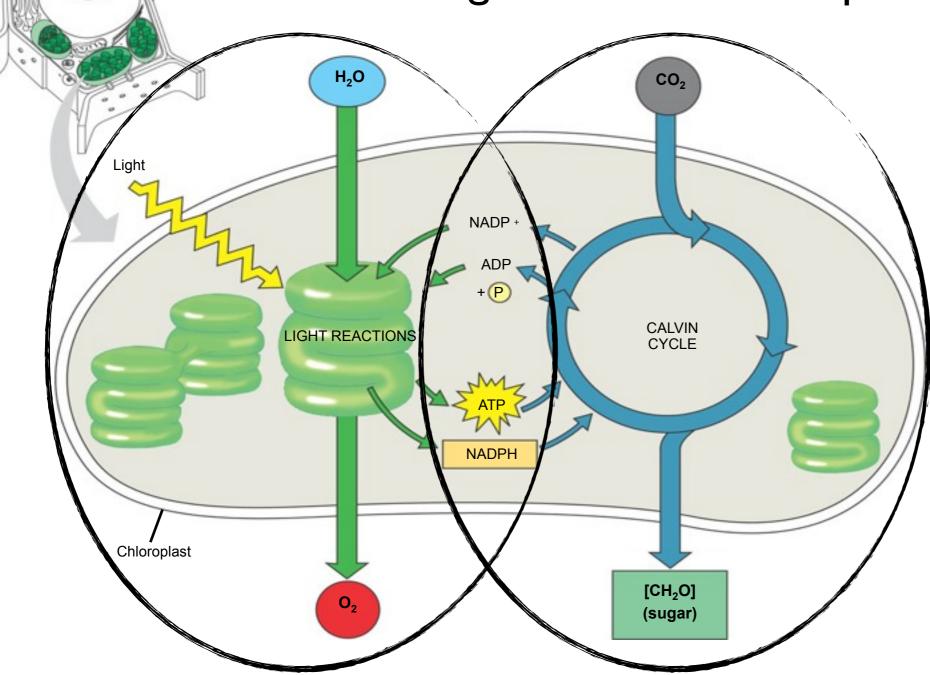
An electron moving from an an atom with lower electronegativity loses potential energy An electron moving from an an atom with lower electronegativity loses potential energy

LOW HIGH Potential Energy Electronegativity

Photosynthesis: Occurs in Two Stages

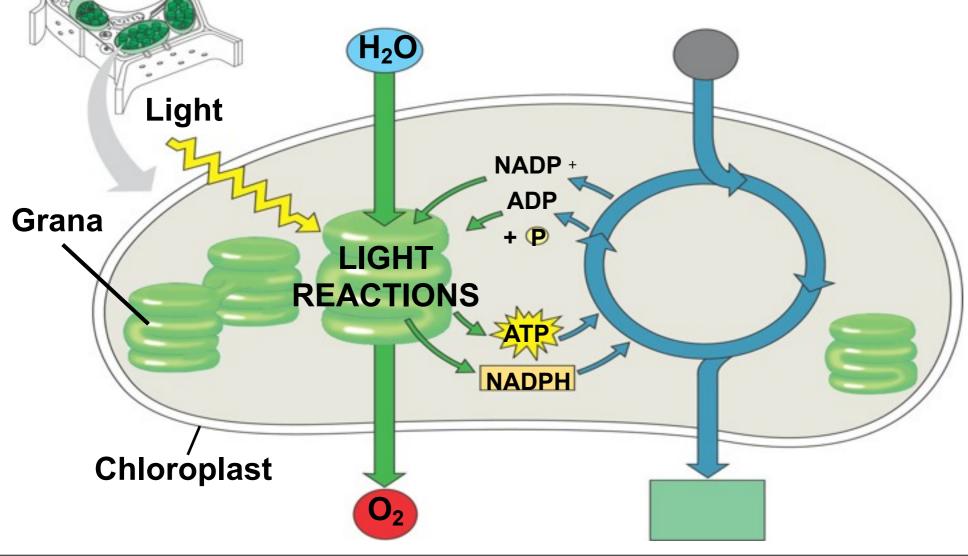


- The Light Reactions & The Calvin Cycle
 - Each stage consists of multiple steps



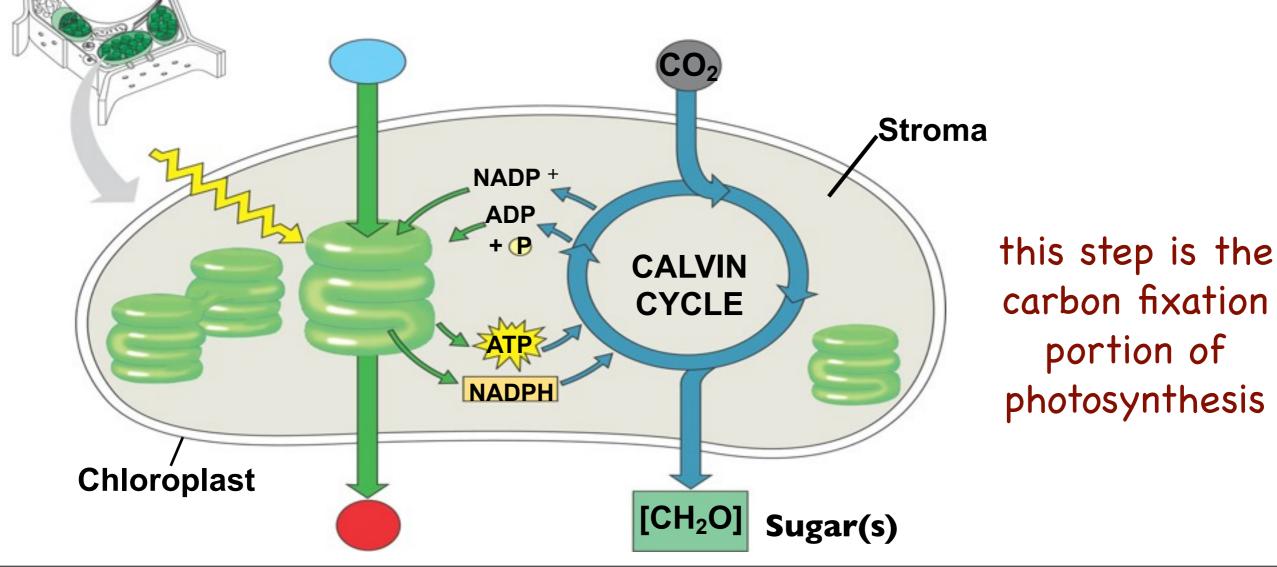
• Light Reactions

- occurs in the grana (thylakoid membranes)
 - converts solar to chemical energy (NADPH & ATP)
 - harvests electrons and hydrogens from water
 - generates ATP by photophosphorylation



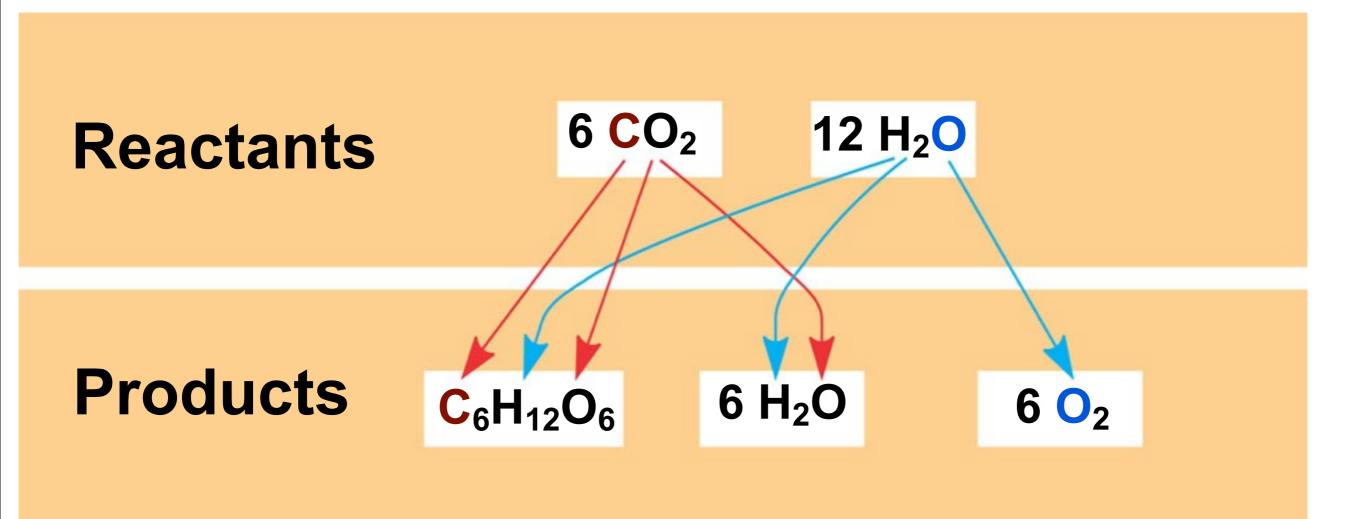
• <u>Calvin Cycle</u>

- occurs in the stroma
 - uses chemical energy (NADPH & ATP) to make sugar
 - builds sugars using carbon from CO₂
 - does not require light



Tuesday, January 22, 2013

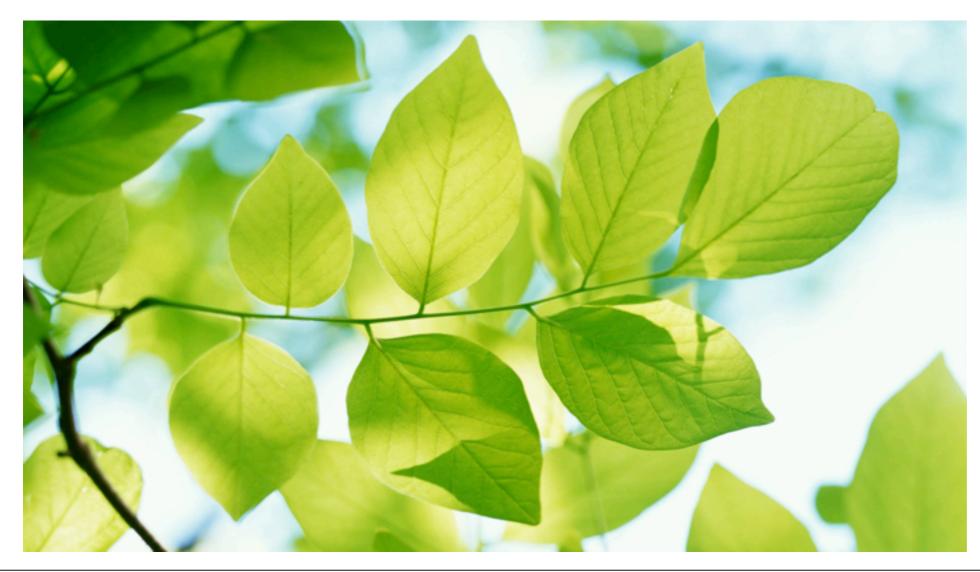
Splitting Water



Here is the significant point- Building a carbohydrate requires putting atoms together but the atoms need "glue" to hold them together...the electrons serve as the "glue" and they are harvested from water.

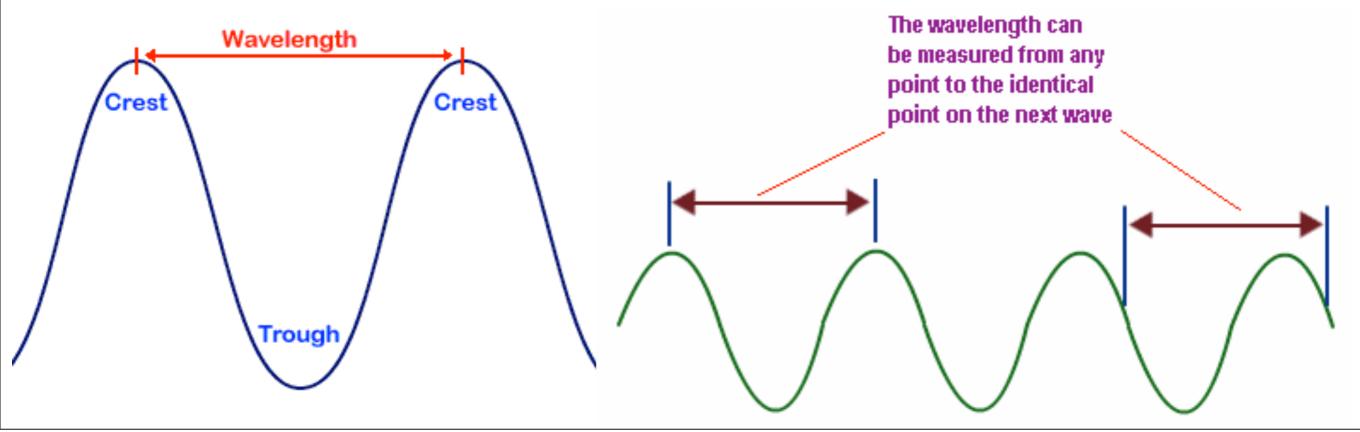
Photosynthesis

Main Idea: Comprehending photosynthesis requires knowledge of about the nature of light and pigments.



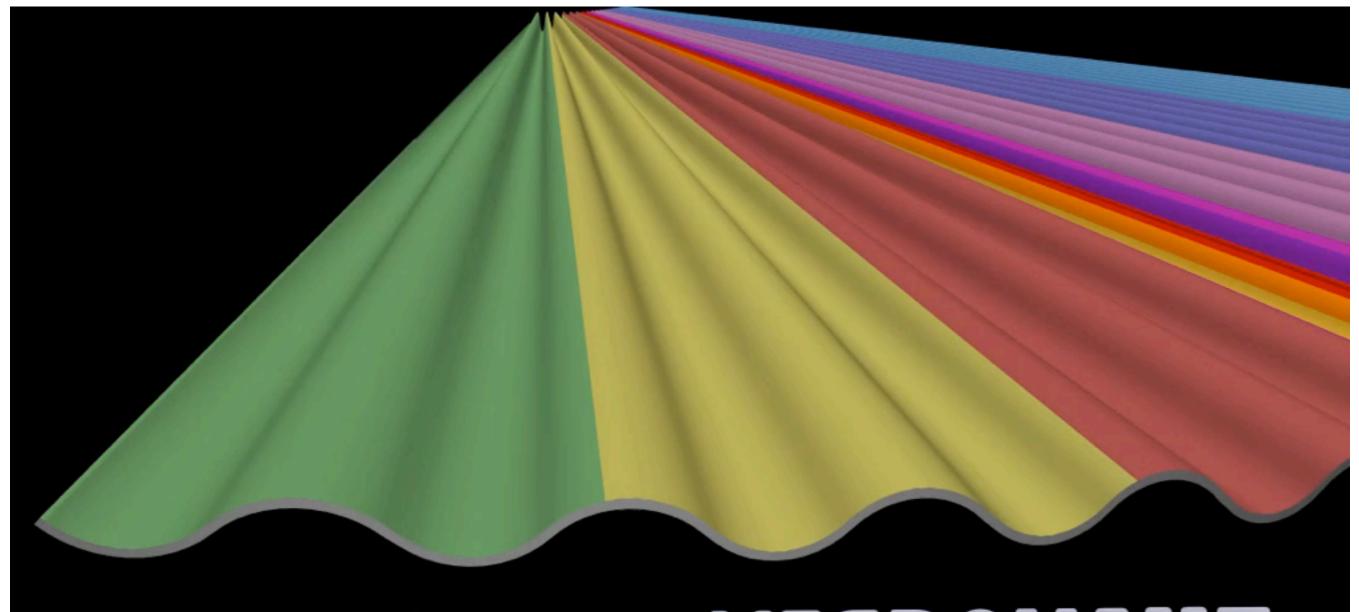
Nature of Sunlight

- Light is a type of energy called electromagnetic radiation.
 - Light travels as waves or particles.
 - Light waves are rhythmic disturbances in electric or magnetic fields.
 - The distance between the crests of these waves are called *wavelengths*, the amount of energy in this electromagnetic radiation is indirectly correlated with wavelength.



Nature of Sunlight

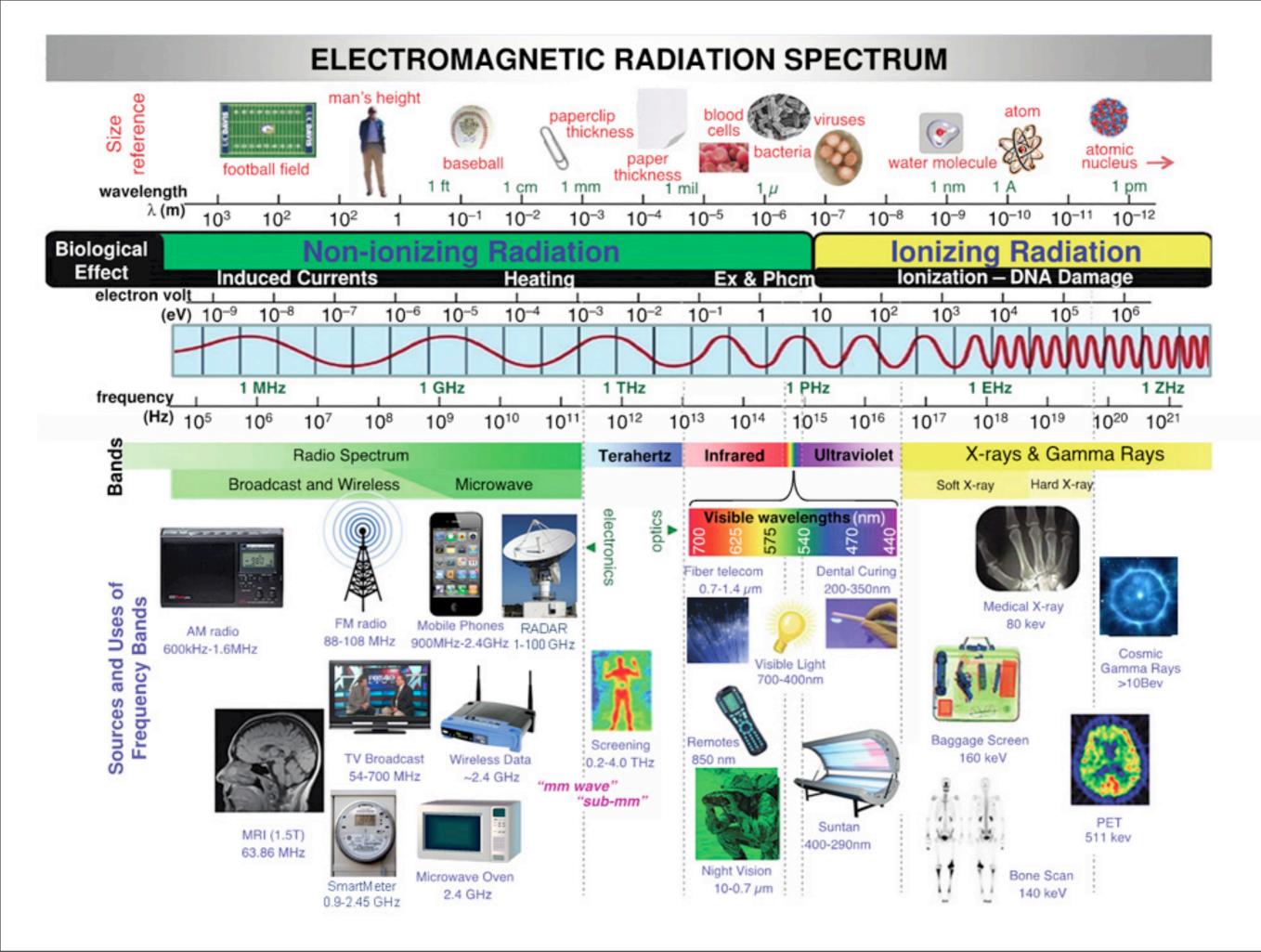
- The entire range of wavelengths of radiation is called *electromagnetic spectrum*.
 - Shorter wavelengths are the most energetic!





MICROWAVE

Tuesday, January 22, 2013

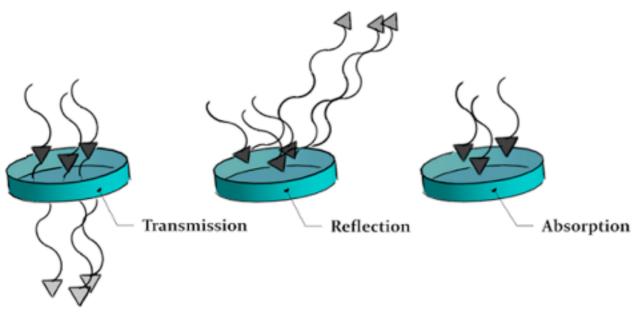


Nature of Sunlight

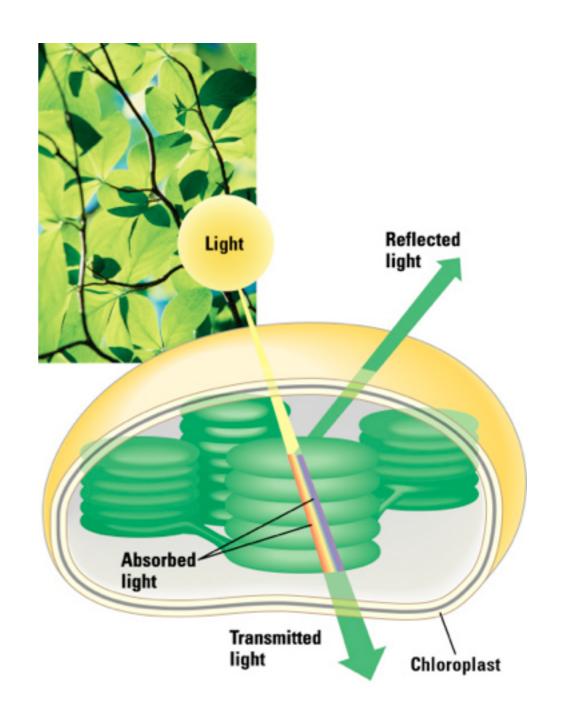
- Light also acts like a particles at times.
 - Light particles are called photons.
 - Each photon has a fixed amount of energy.
 - The amount of energy is inversely proportional to wavelength.
 - Violet light has almost 2X the energy of red light



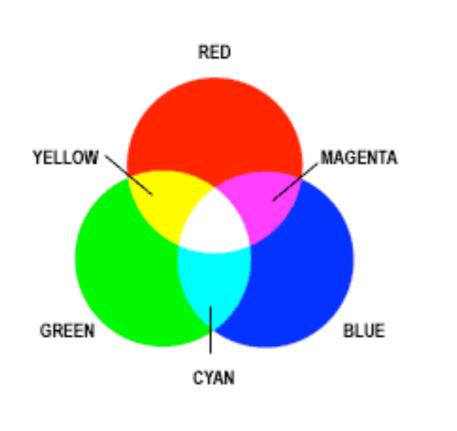
• When light hits matter it can be reflected, absorbed or transmitted.

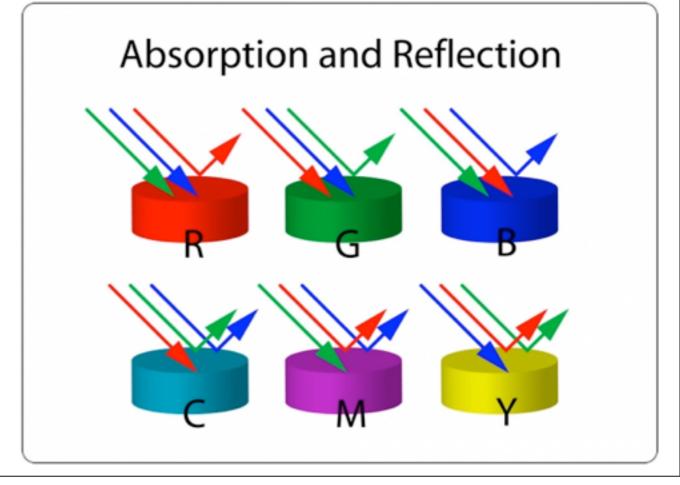


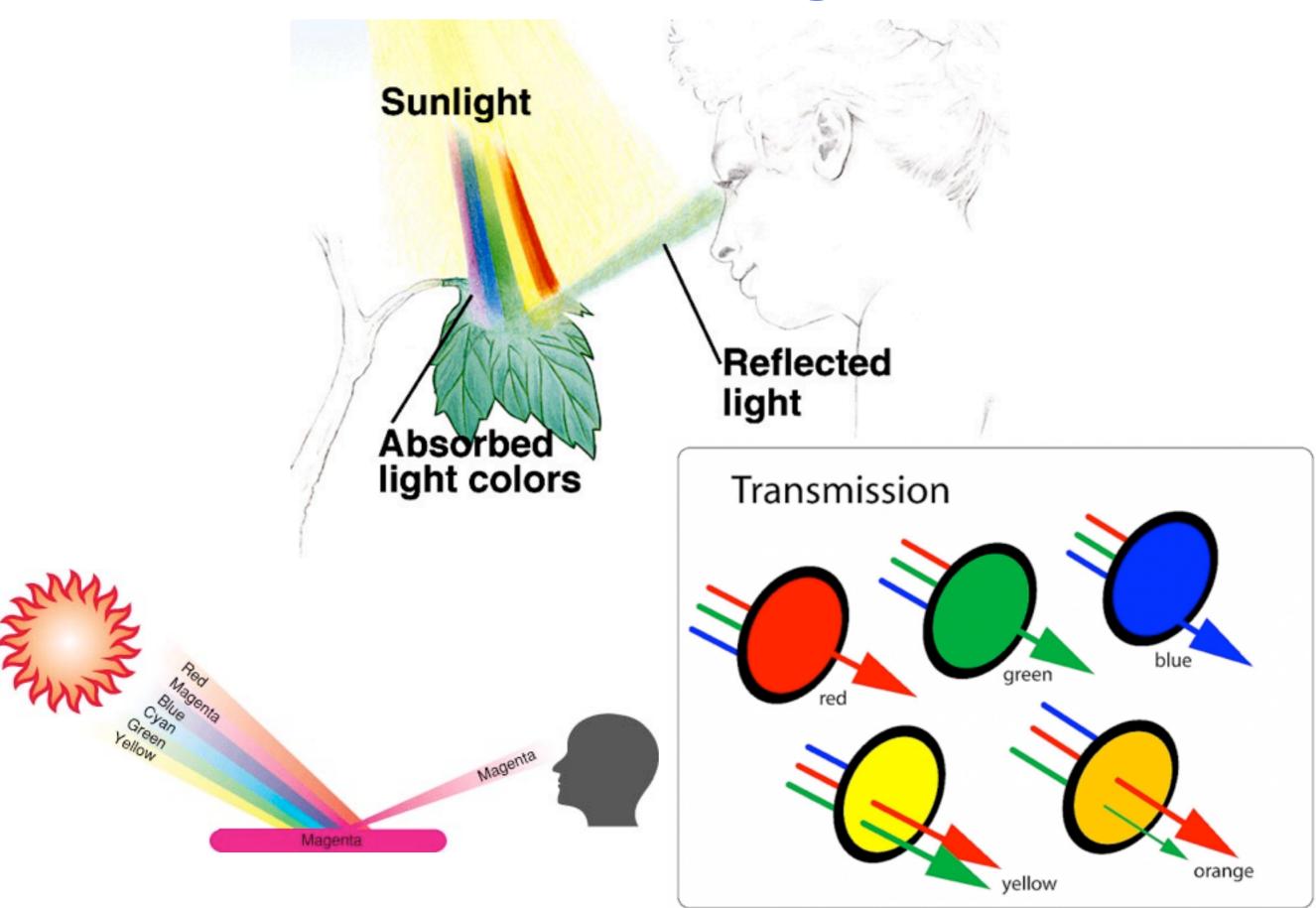
- Pigments are molecules that absorb light.
- Different pigments absorb different wavelengths of light.



- When white light strikes pigment the color we see, is the color that is reflected or transmitted.
 - White color / light = no pigments present in matter
 - Black color / no light = pigments absorb all wavelengths
 - Green color (etc) / green light = pigments absorb all wavelengths of light except green

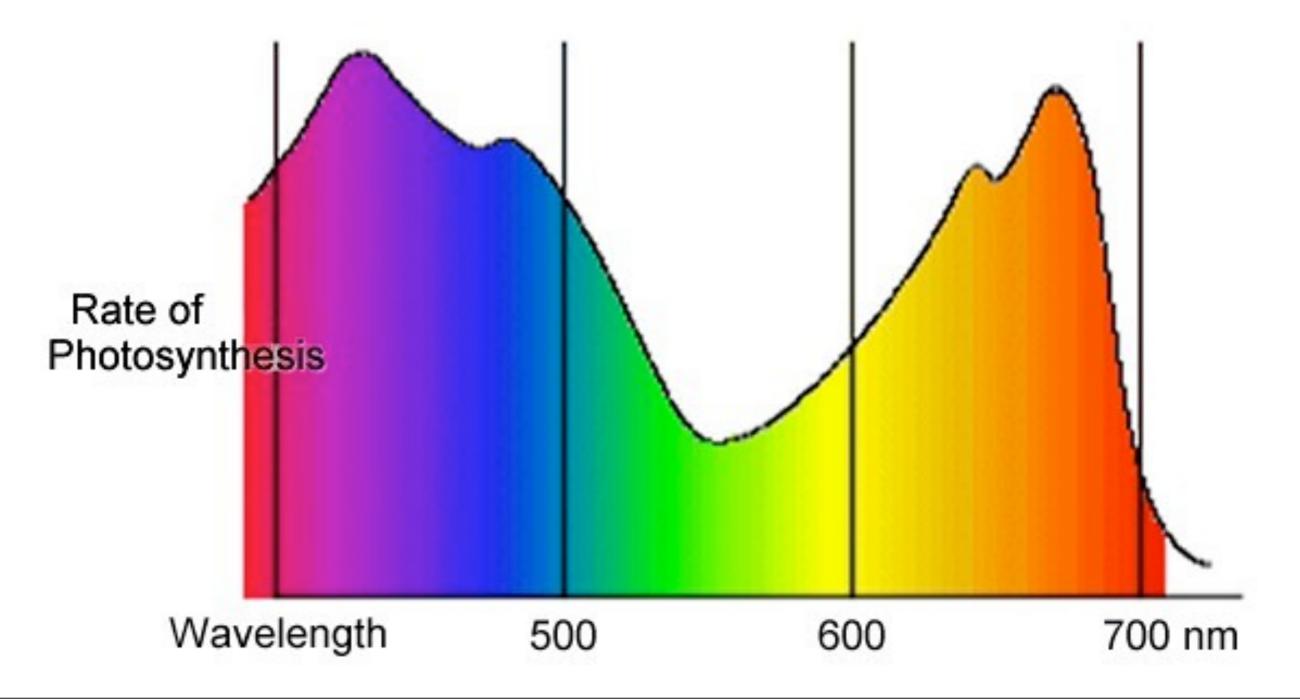






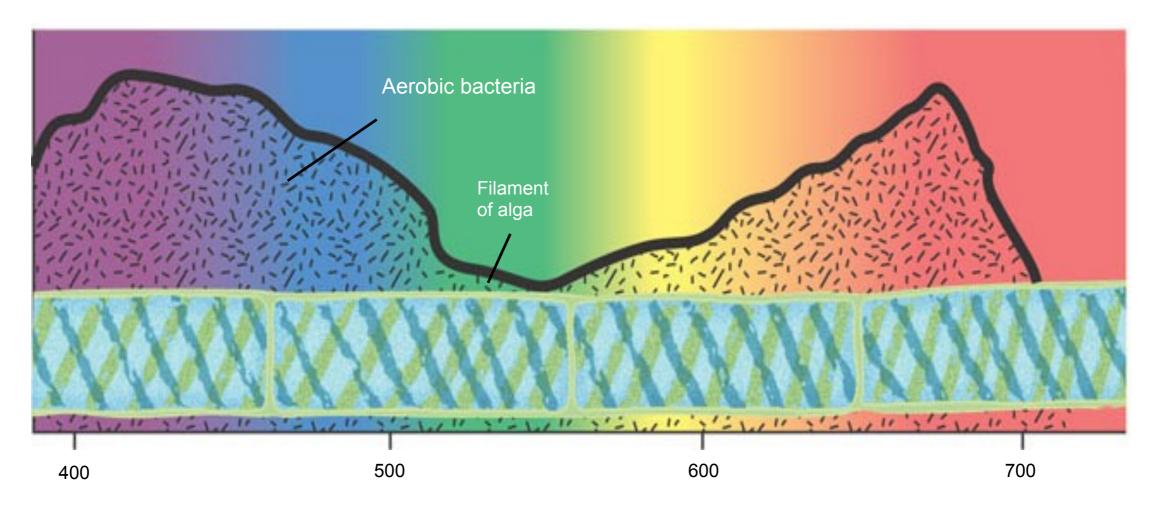
Action Spectrum

• The action spectrum profiles the relative effectiveness of each wavelength in driving photosynthesis.



Action Spectrum of Chlorophyll

• The first evidence emerged in the late 1800's

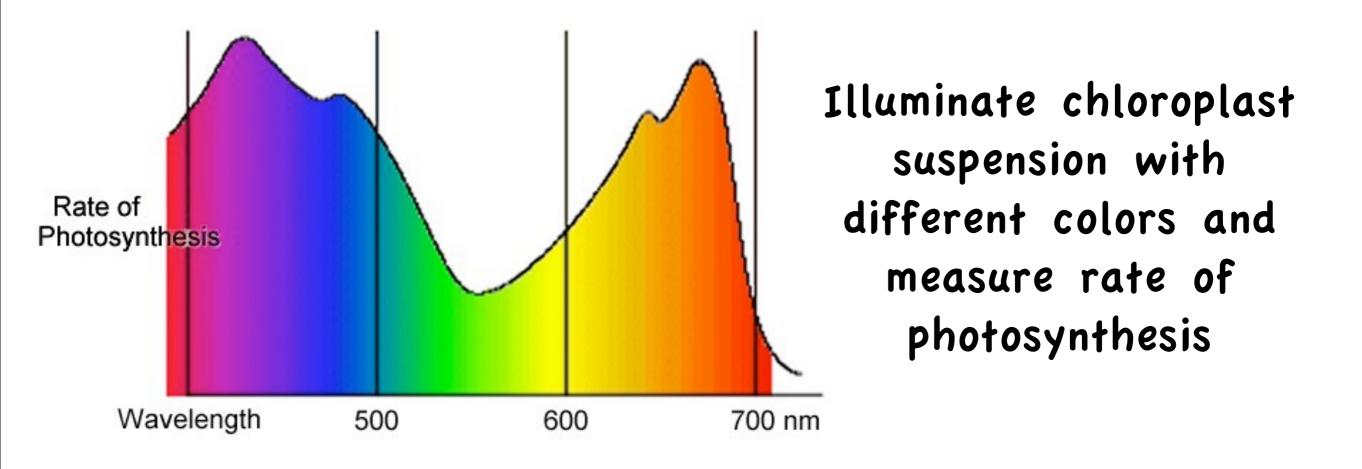


Engelmann's experiment. In 1883, Theodor W. Engelmann illuminated a filamentous alga with light that had been passed through a prism, exposing different segments of the alga to different wavelengths. He used aerobic bacteria, which concentrate near an oxygen source, to determine which segments of the alga were releasing the most O_2 and thus photosynthesizing most. Bacteria congregated in greatest numbers around the parts of the alga illuminated with violet-blue or red light.

Light in the violet-blue and red portions of the spectrum are most effective in driving photosynthesis.

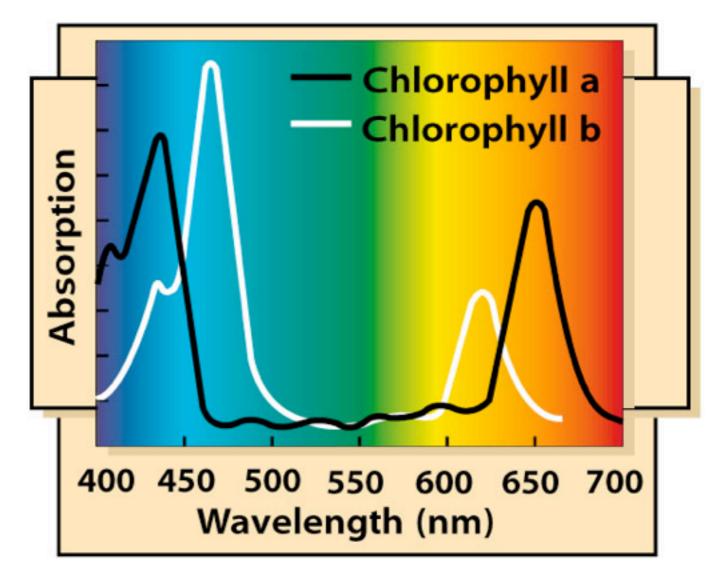
Action Spectrum

• Today's equipment has confirmed Engelmann's Conclusions.



You can measure rate of photosynthesis by examining CO2 uptake or O2 release

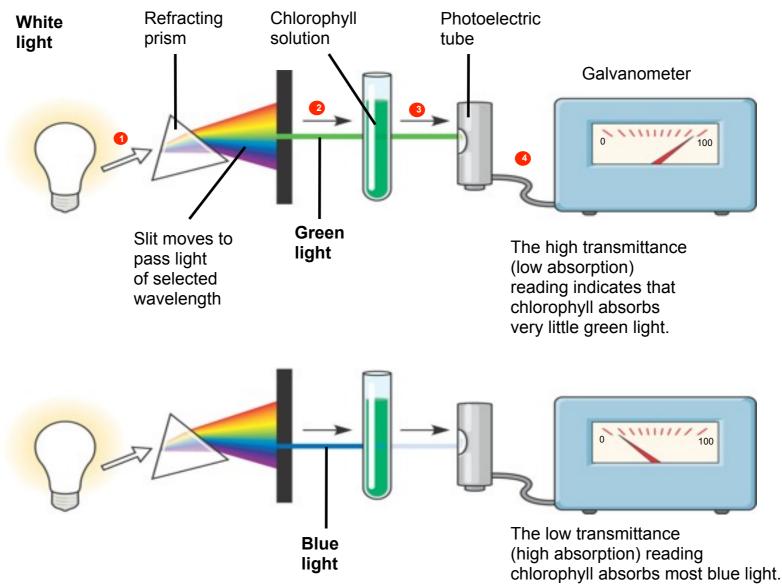
- An graph plotting a pigment's light absorption versus wavelength is called an *absorption spectrum*.
- The absorption spectrum of chlorophyll provides evidence to which wavelength(s) are driving photosynthesis.



How did we determine this absorption spectrum?

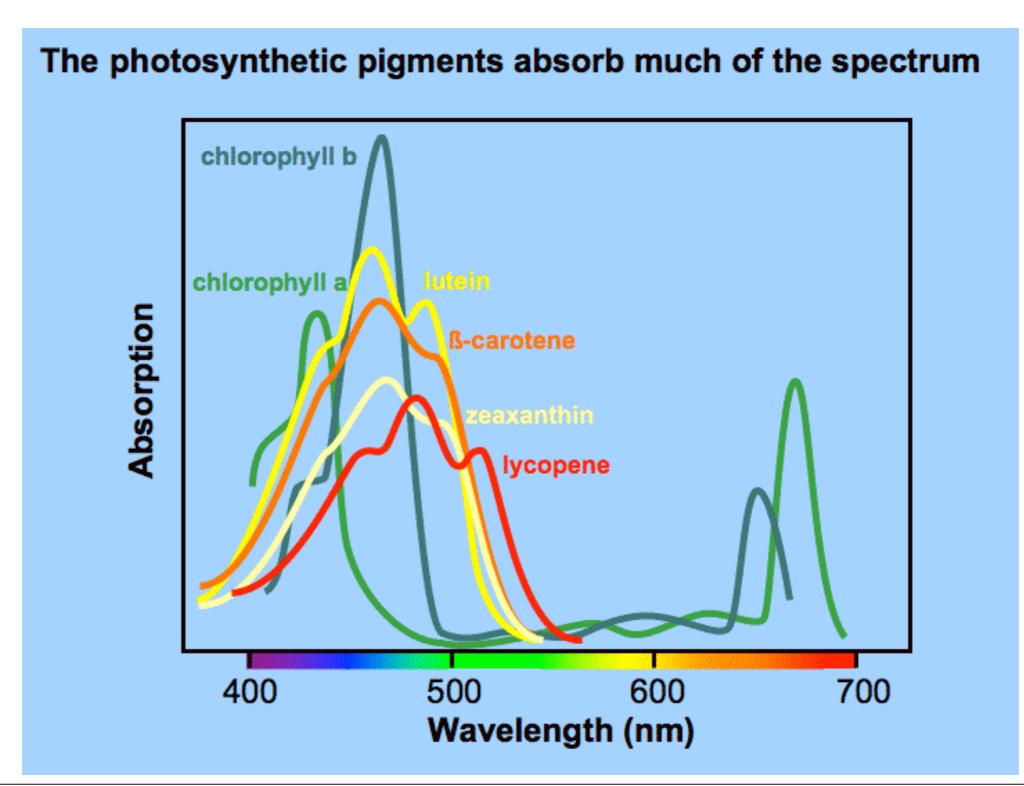
Absorption Spectrum of Chlorophyll

- Today we can determine absorption spectrums using spectrophotometers.
- A **spectrophotometer** measures the amounts of light of different wavelengths absorbed and transmitted by a pigment solution.



Absorption Spectrum

• Today, spectrophotometers can measure the absorption of certain wavelengths by individual pigments .

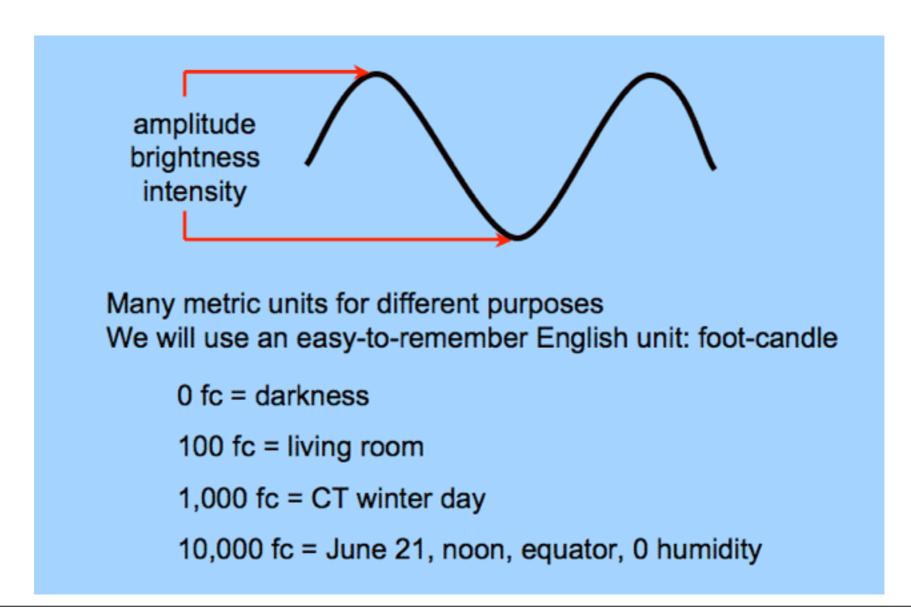


Absorption Spectrum

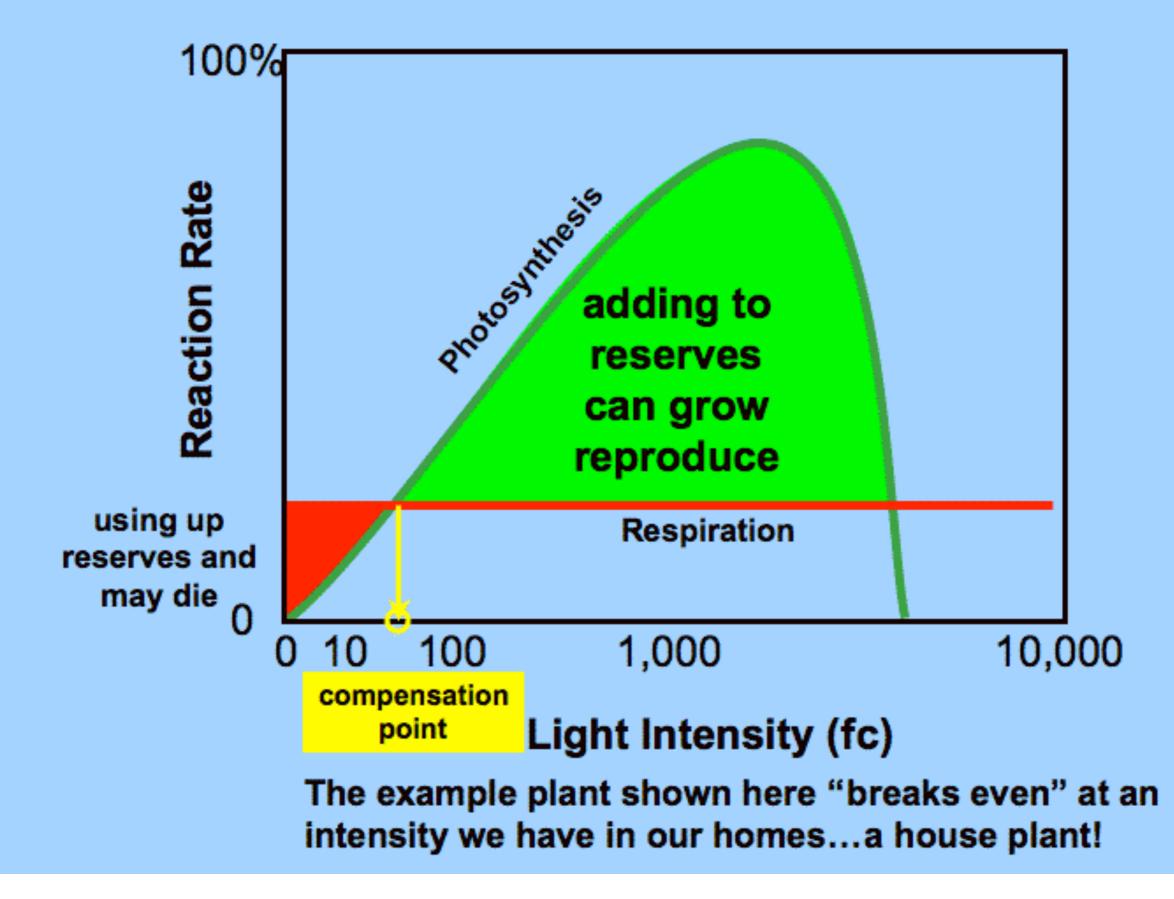
- Chlorophyll a and Chlorophyll b are the main pigments driving photosynthesis.
- Chlorophyll *a* reflects a blue-green color.
- Chlorophyll *b* reflects an olive green color.
- Carotenoids are accessory pigments that also drive photosynthesis.
- Carotenoids reflect yellow and orange colors.
- Interestingly carotenoid pigments are more important to plant for their photoprotective roles:
 - they dissipate excessive light energy that may do damage
 - they also act as antioxidants, binding harmful radicals

Light Intensities

- Light waves not only vary in wavelength but they can vary in amplitude as well.
- The amplitude is the height of each wave.
- Light with higher amplitudes are brighter or more intense



What intensities of light drive photosynthesis?

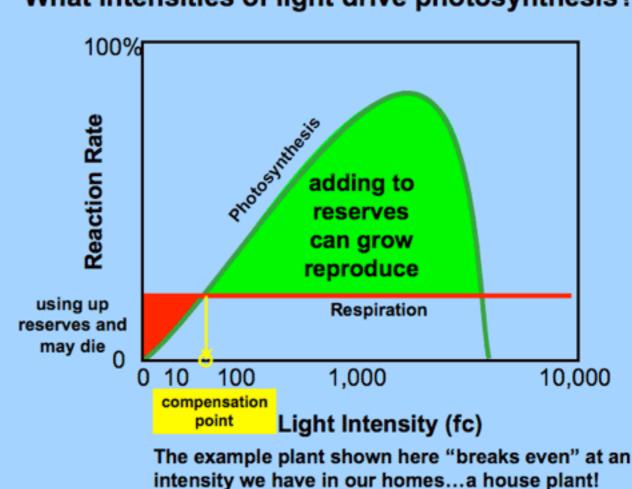


Light Intensity & Photosynthetic Rate

- The **compensation point** depicts the light intensity that produces more product (sugars) faster than they are being used up by cell respiration.
- Every plant has a different compensation point.
- Some plants can even be damaged or killed if light intensity is too great.
 What intensities of light drive photosynthesis?

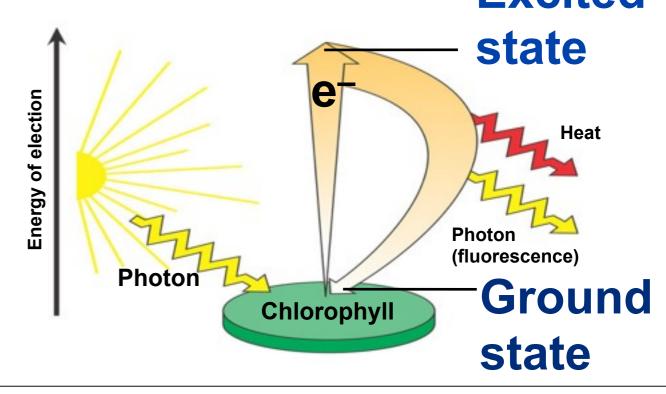
Can you suggest a plant that might have a low compensation point? High?

Low- houseplants, ferns High- crop plants, cacti

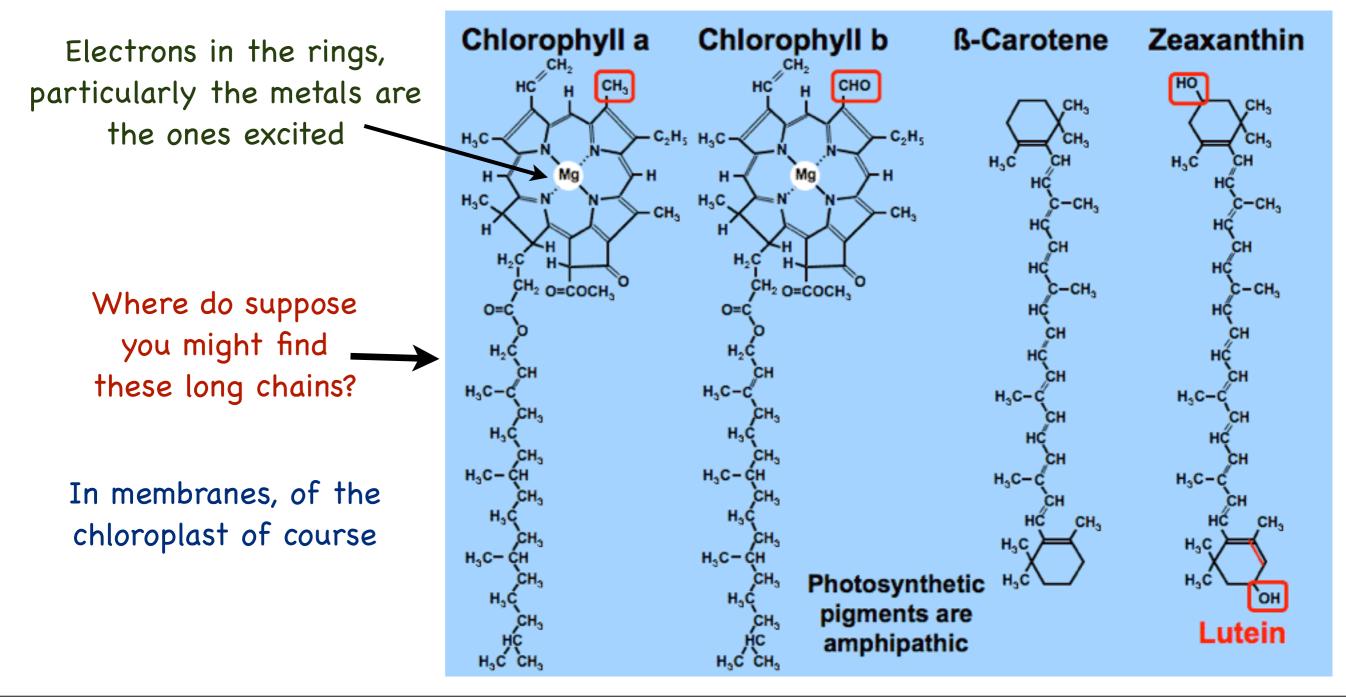


Exciting Chlorophyll by Light

- When a pigment absorbs a wavelength(s) of light that wavelength disappears but the energy can not!
- Remember light also acts as particles, when photons hit molecules they impact can send "electrons flying"
- Electrons in their normal energy level are said to be in their ground state. (they are stable)
- Photons can boost electrons to higher energy levels called their excited state. (they are unstable)
 Excited

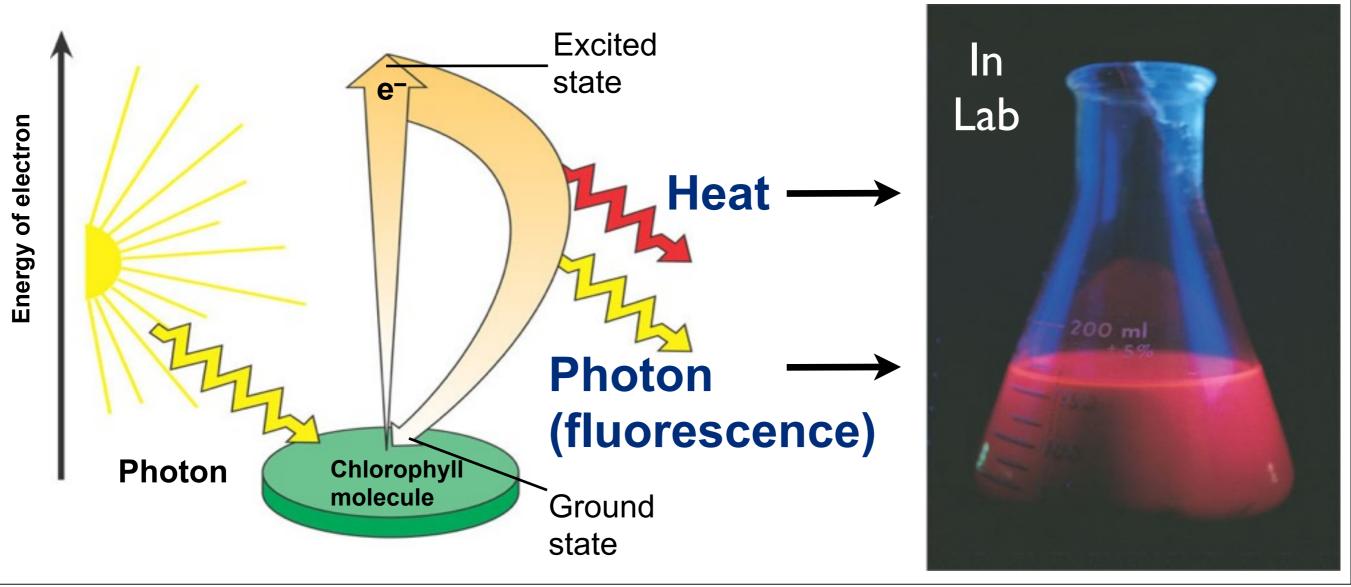


- Each photon carries a certain quantity of energy, this energy is equal to the difference between ground and excited states.
- The energy to boost electrons varies depending on the molecule which explains why some pigments absorb certain wavelengths and not others

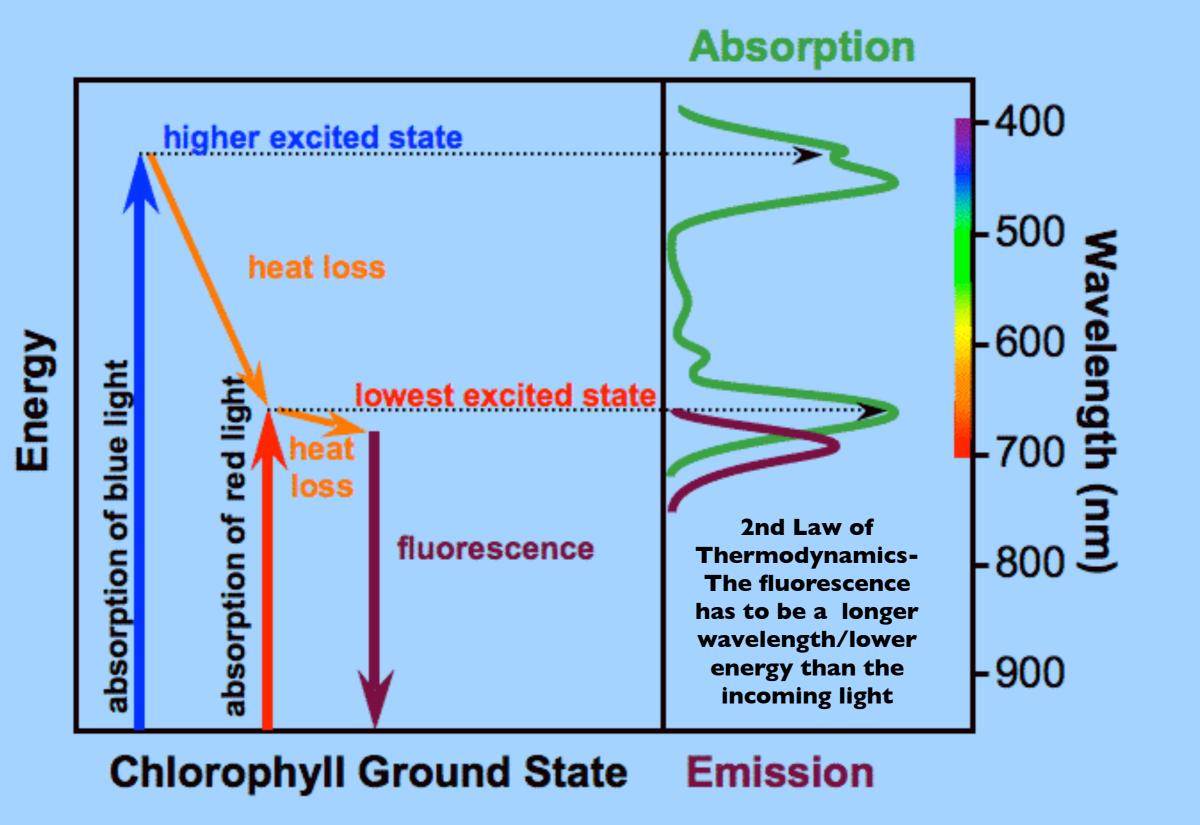


Exciting Chlorophyll by Light

- An electron can not stay in the unstable, excited state.
 - In a billionth of second it falls back to the ground state
 - releasing the excess energy as heat and sometimes light
- In isolation chlorophyll releases heat and light (fluorescence).

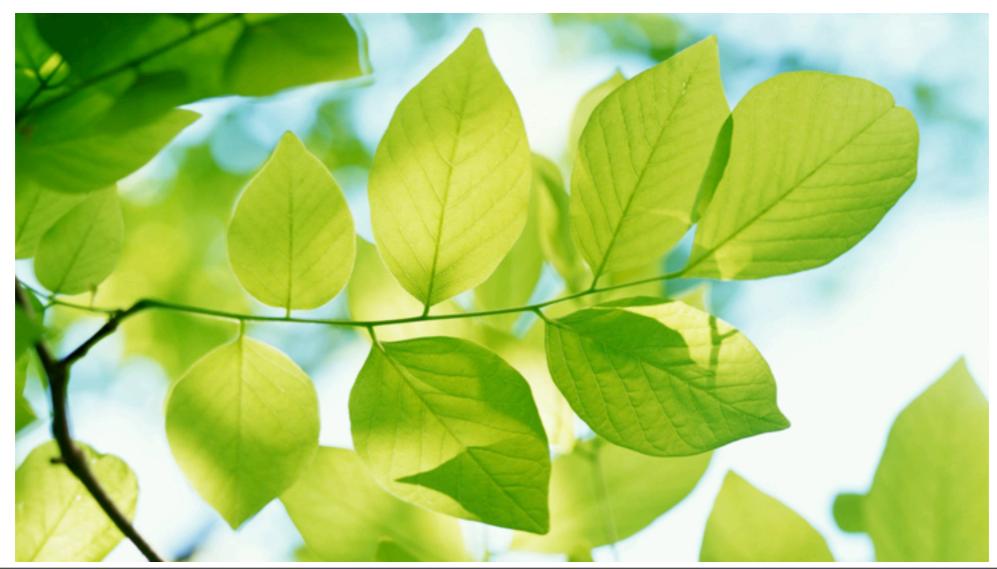


The absorption of light relates to electron excitation states



Photosynthesis

Main Idea: Light and an array of molecules found in the thylakoid membranes convert solar energy into chemical.



Tuesday, January 22, 2013

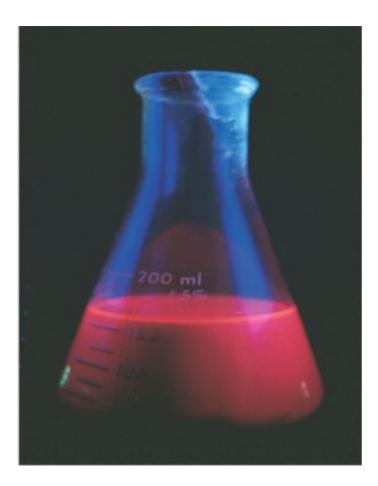
Light Reactions

- We know that light reactions convert solar energy into chemical energy
- We know that light reactions occur in the thylakoid membranes of the chloroplasts
- We know that the chemical reactions involve "redox" reactions
- We know that only certain wavelengths power photosynthesis
- We know that certain light intensities are also necessary
- We know that pigments absorb light
- We know that electrons are excited in pigment molecules when a photon of light strikes them

But we do not YET know...HOW

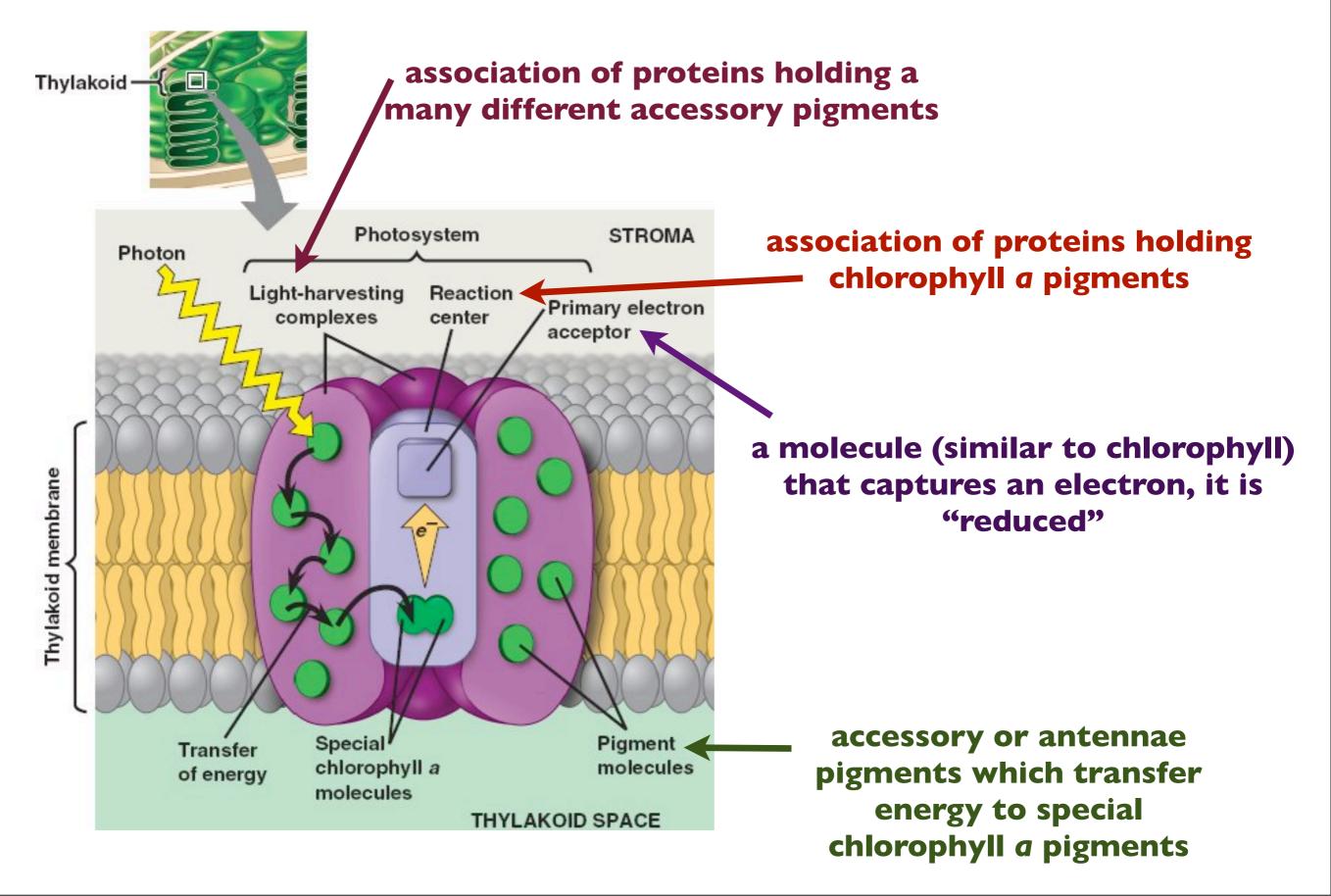
Photosystems

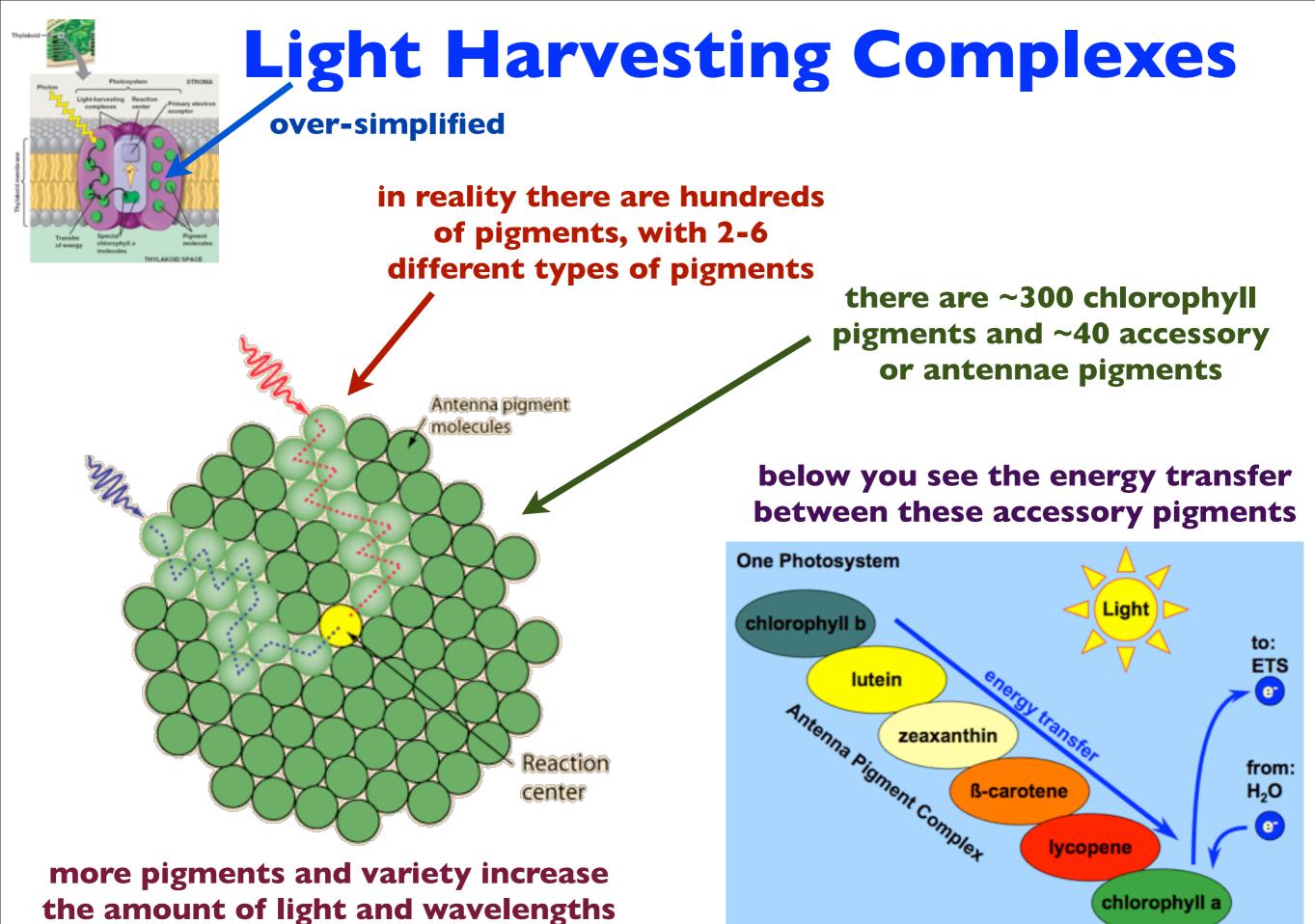
- Needless to say excited chlorophyll molecules act very differently in when they are intact in their chloroplasts compared to when we isolate them in a flask.
 - After all, leaves are not warm and fluorescent red in nature!



• To understand the mechanism of of the light reactions, the first of stages in photosynthesis we need to understand the structure of photosystems.

General Photosystem



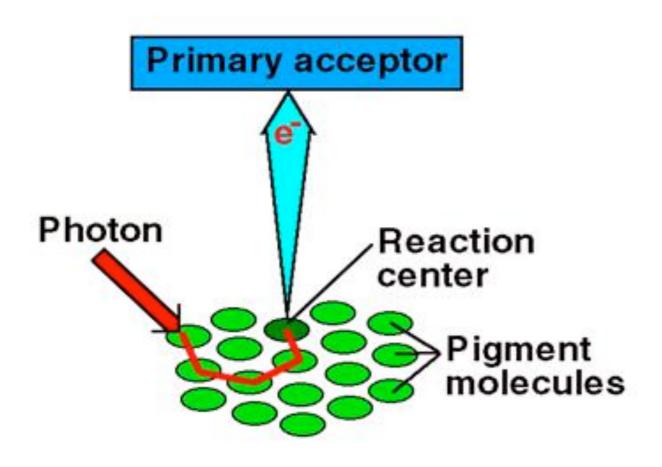


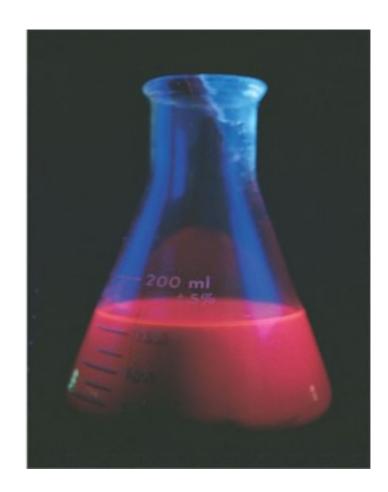
Reaction Center P680 or P700

that a plant can capture

Side Bar...

• Remember "leaves are not warm and fluorescent red in nature!"





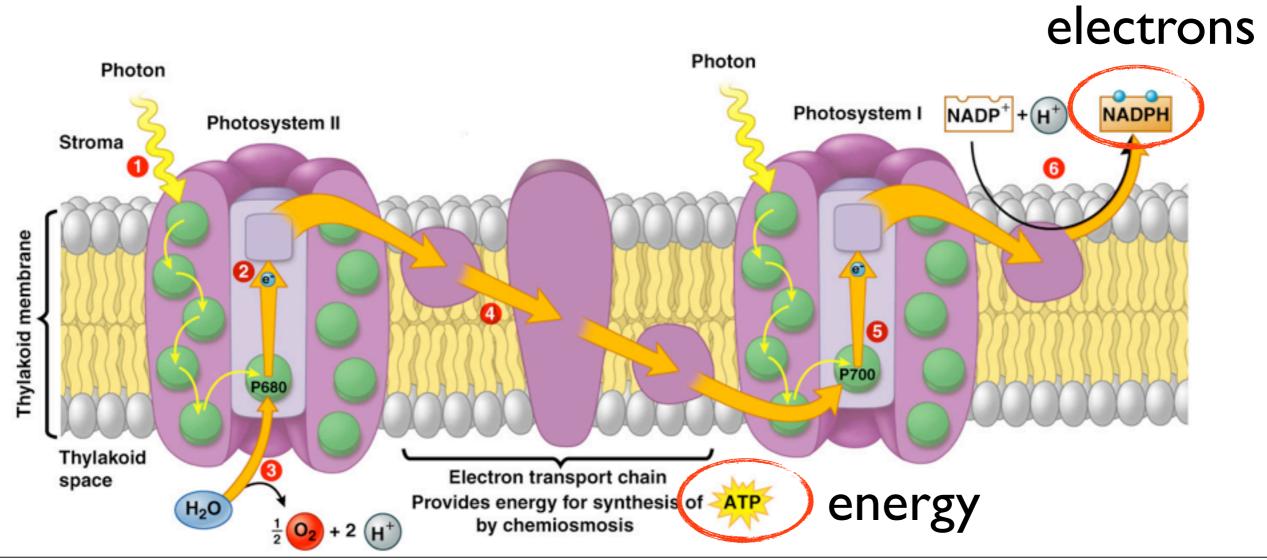
• When the pigment is excited in isolation the electrons fall back to the ground state, releasing energy as heat and light but in plants the primary acceptor does not allow the electron to fall back down and thus "keeps" that potential energy to do work we will see later.





Photosystem I and II

- To complete the light reactions plants require 2 different photosystems working together to harvest the <u>energy</u> and <u>electrons</u> needed to build sugar.
 - Photosystem I was the first one discovered but it turns out that it the second photosystem used in the light reactions.



E.T.C. Establishes a H⁺ ion Gradient

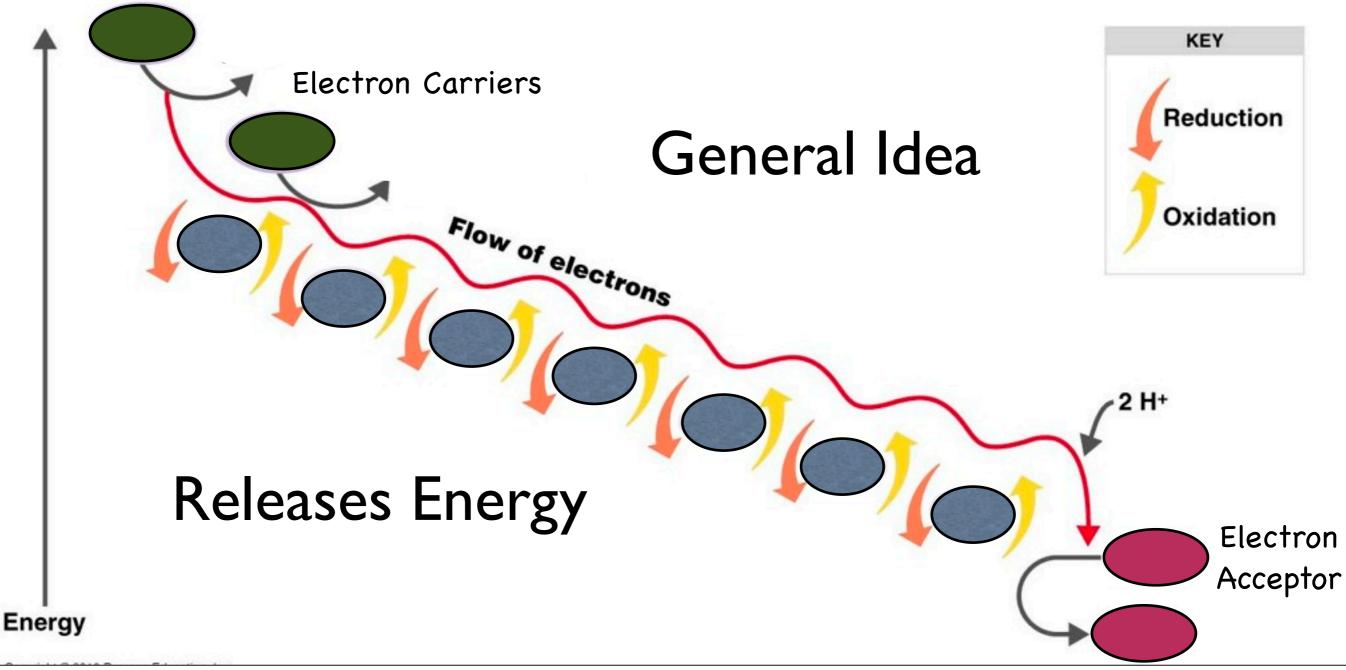
- The **electron transport chain** makes no ATP.
- The e⁻ transfer releases energy as the electron moves through the chain, this energy is used to pump H⁺ ions through a membrane.
 - This generates a electrochemical gradient with great potential energy

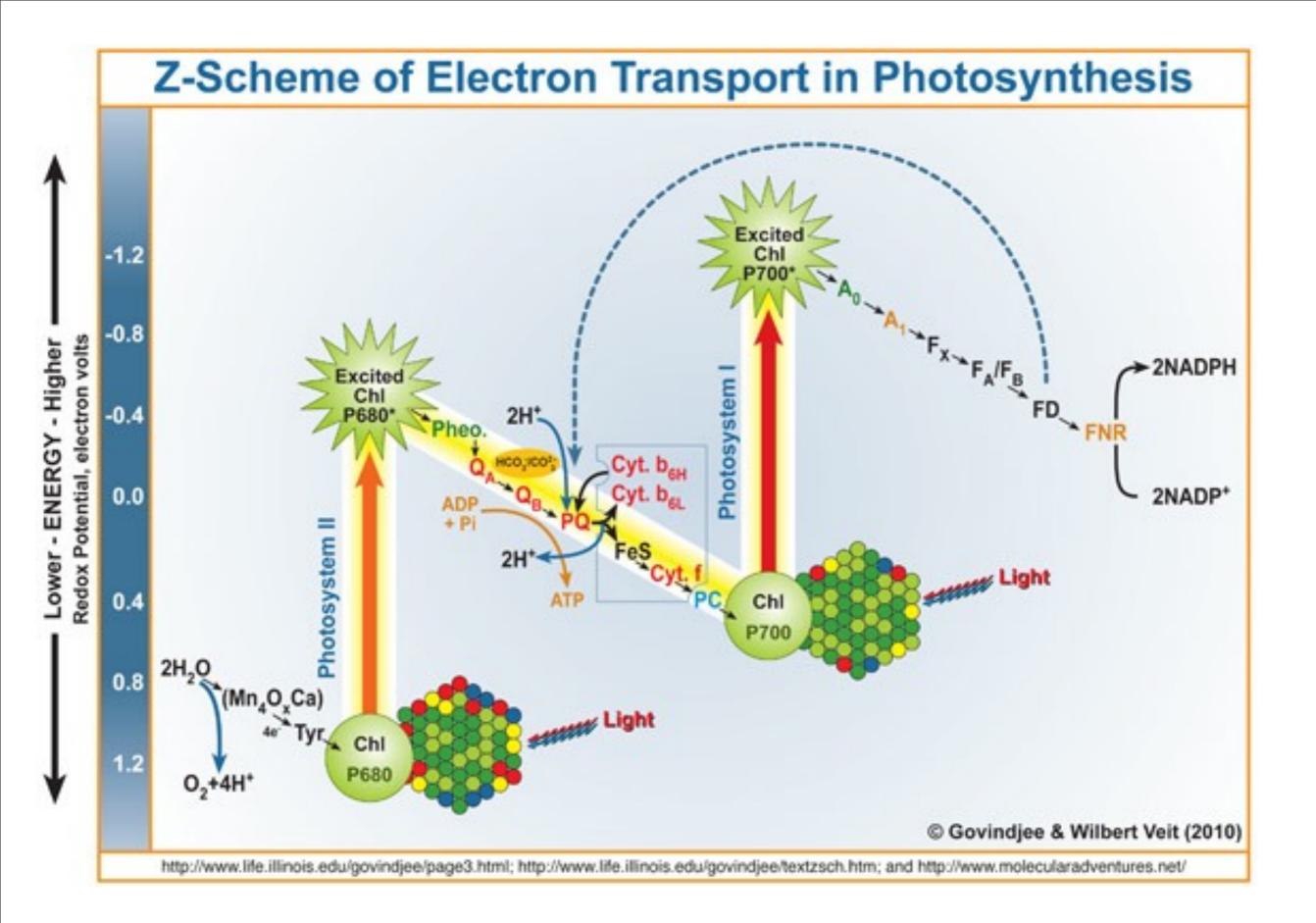
E.T.C. and Chemiosmosis

- Stored energy in the form a H⁺ ion gradient across a membrane is called the *proton motive force*, it is used to produce ATP (or drive other cellular work), which is called *chemiosmosis*.
- **Chemiosmosis** is an energy coupling mechanism that uses energy stored in in the form of H+ ion gradients across membranes to drive cellular work
 - Osmosis is the diffusion of water
 - Chemiosmosis is the diffusion of H⁺ ions
- Specifically an enzyme ATP synthase uses the energy to produce ATP from ADP

Electron Acceptors & Transport

Electron Carriers



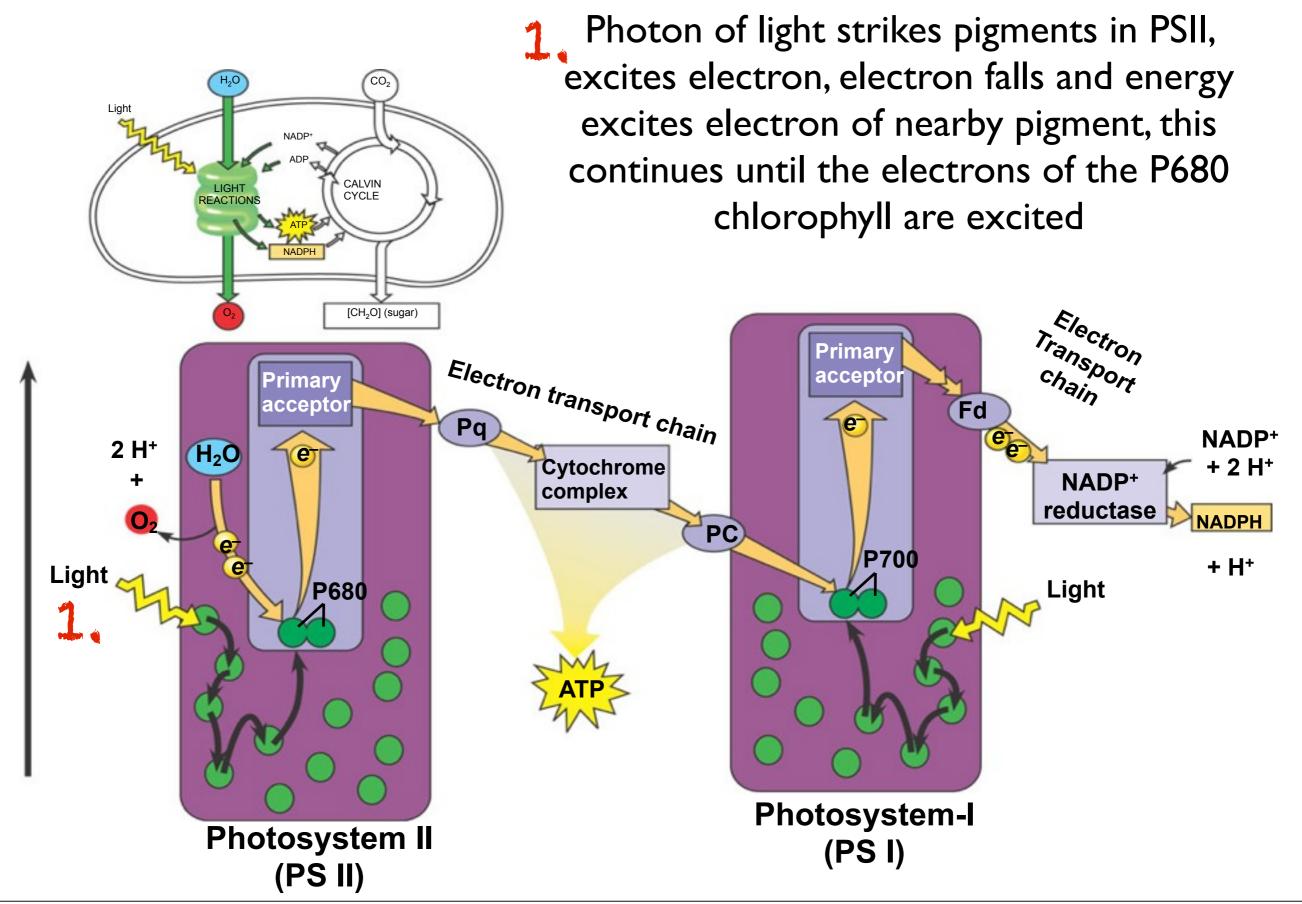


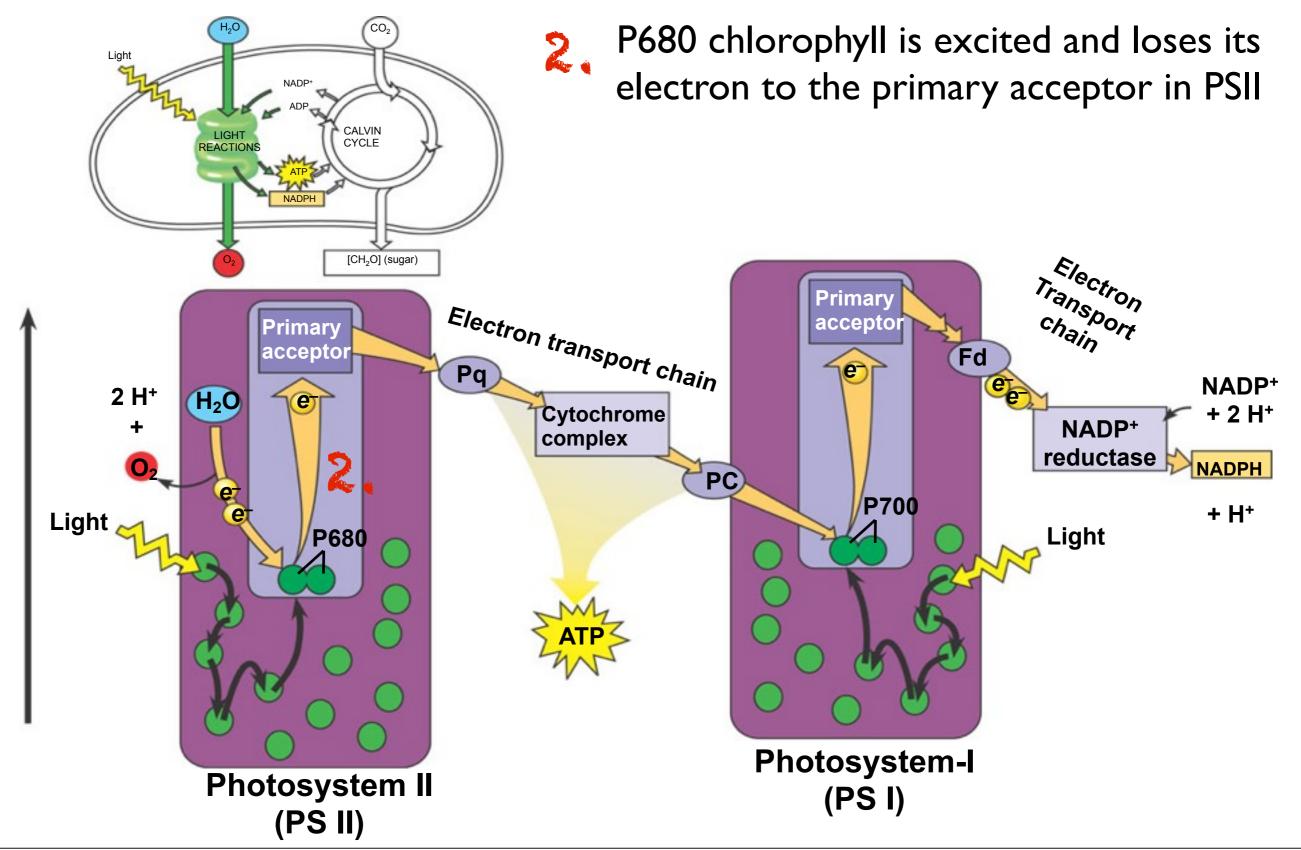
"The Big Picture Before We Continue"

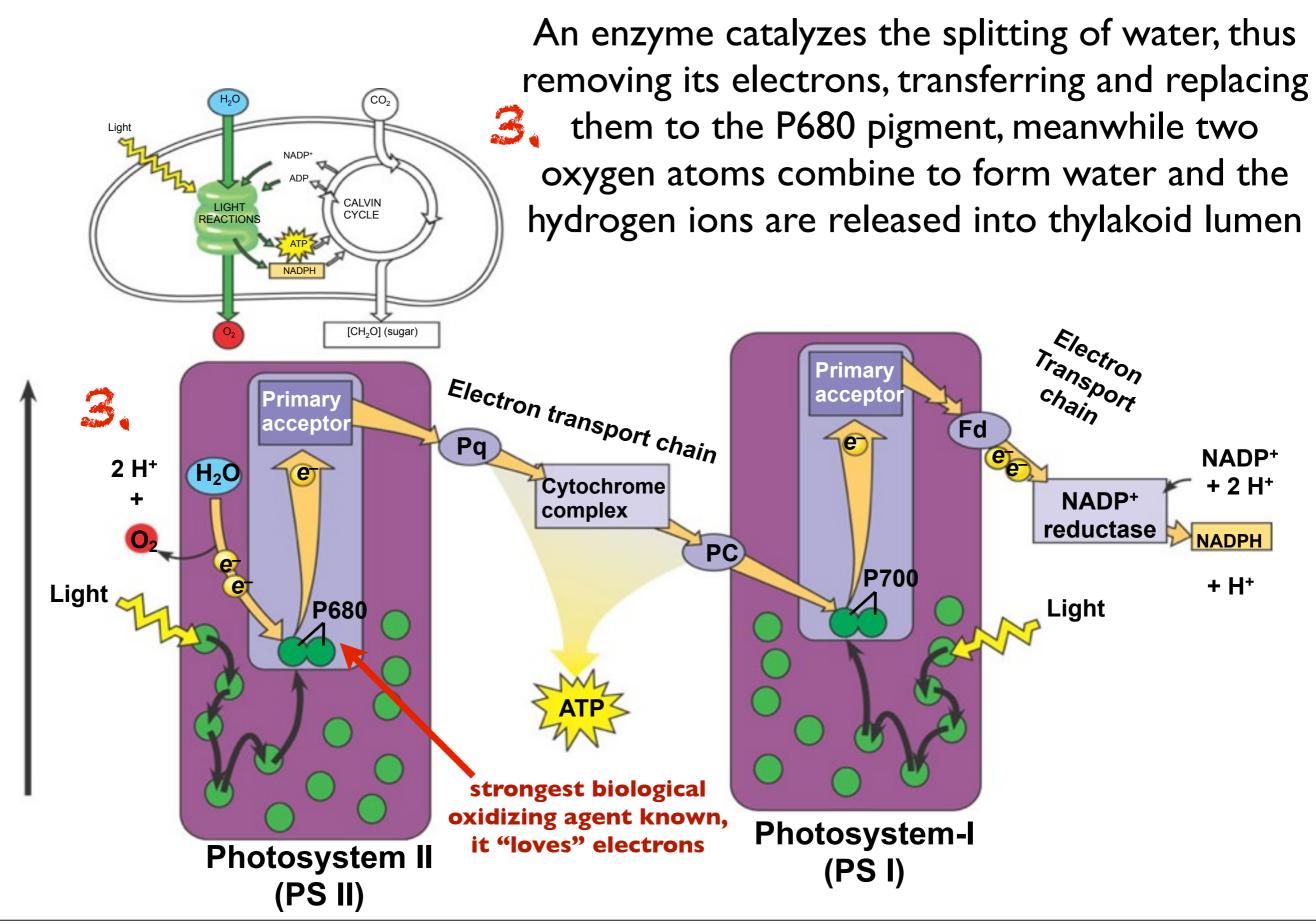
- Building sugar in stage 2 of photosynthesis (Calvin Cycle) requires:
 - building blocks,
 - electrons,

• energy

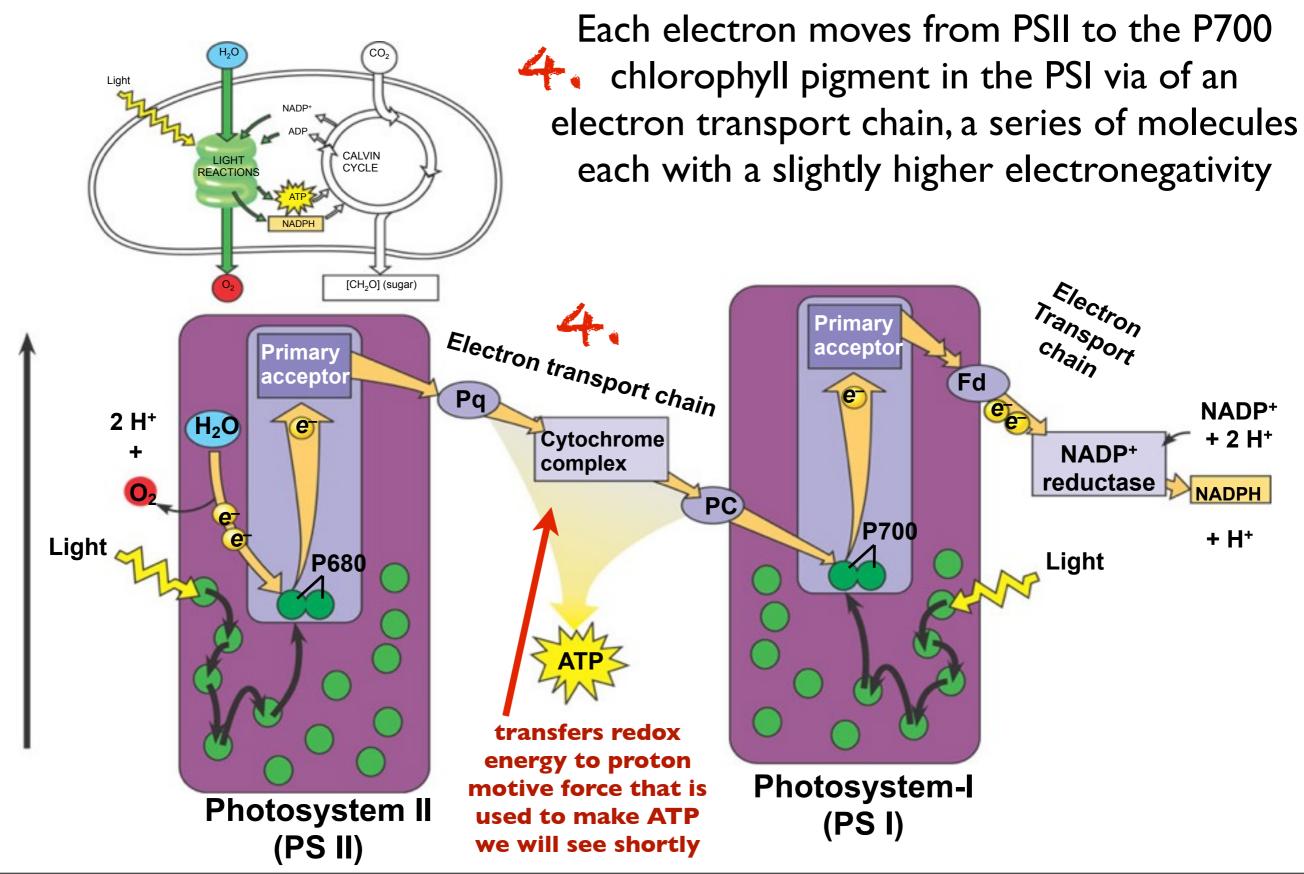
- The building blocks (carbon) simply come from atmosphere via carbon dioxide.
- But the electrons (carried by NADPH) have to come from the light reactions via water
- And the energy (ATP) has to also come from the light reactions



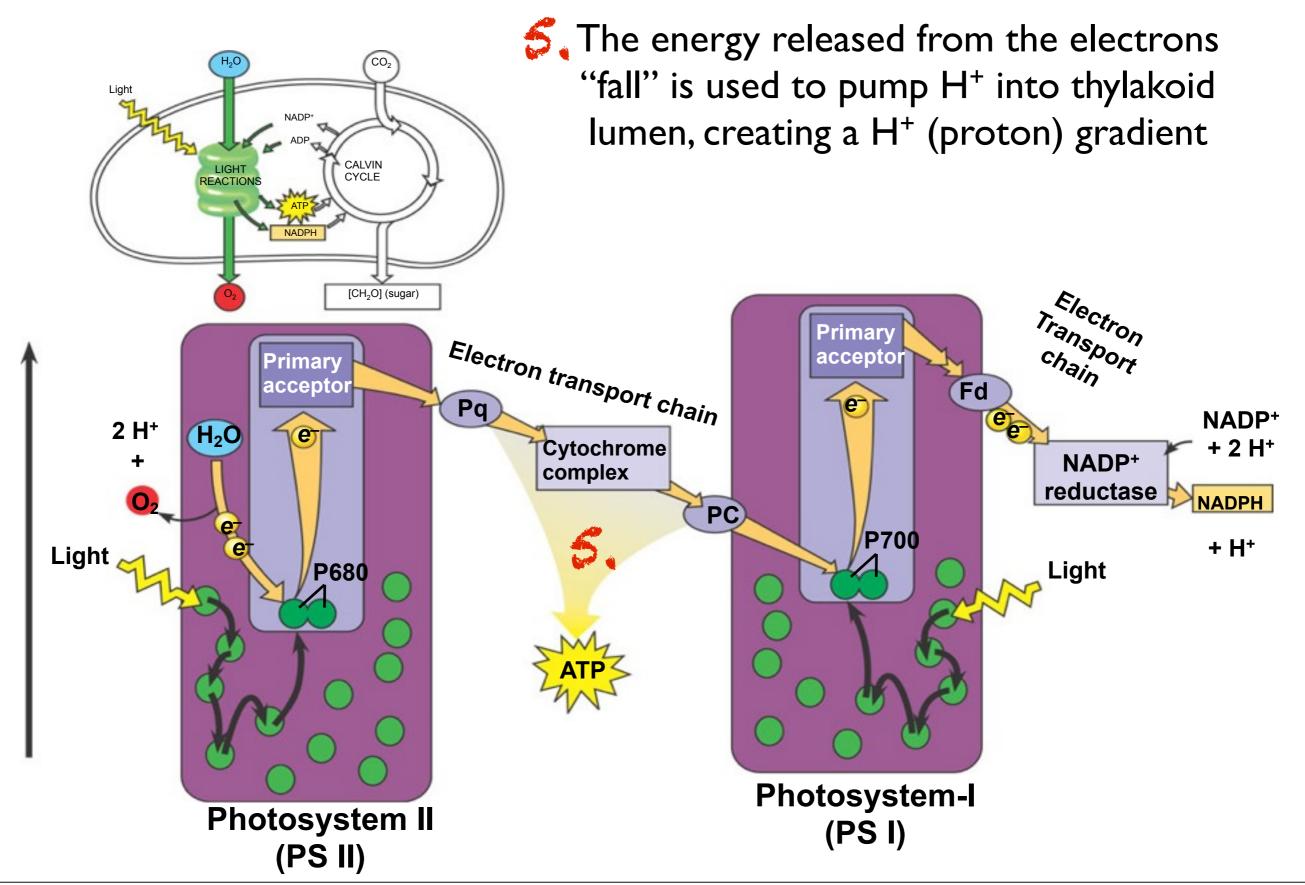


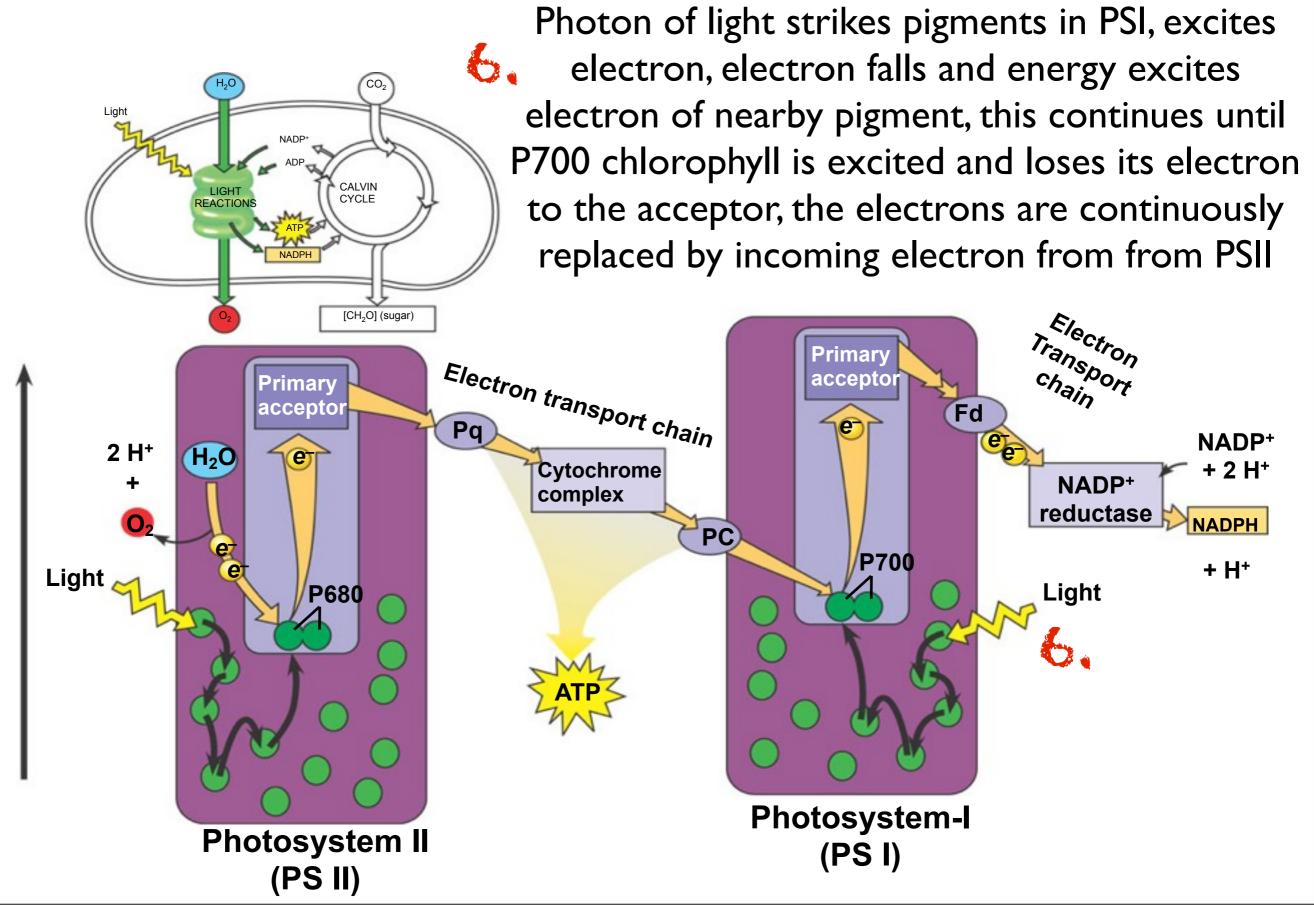


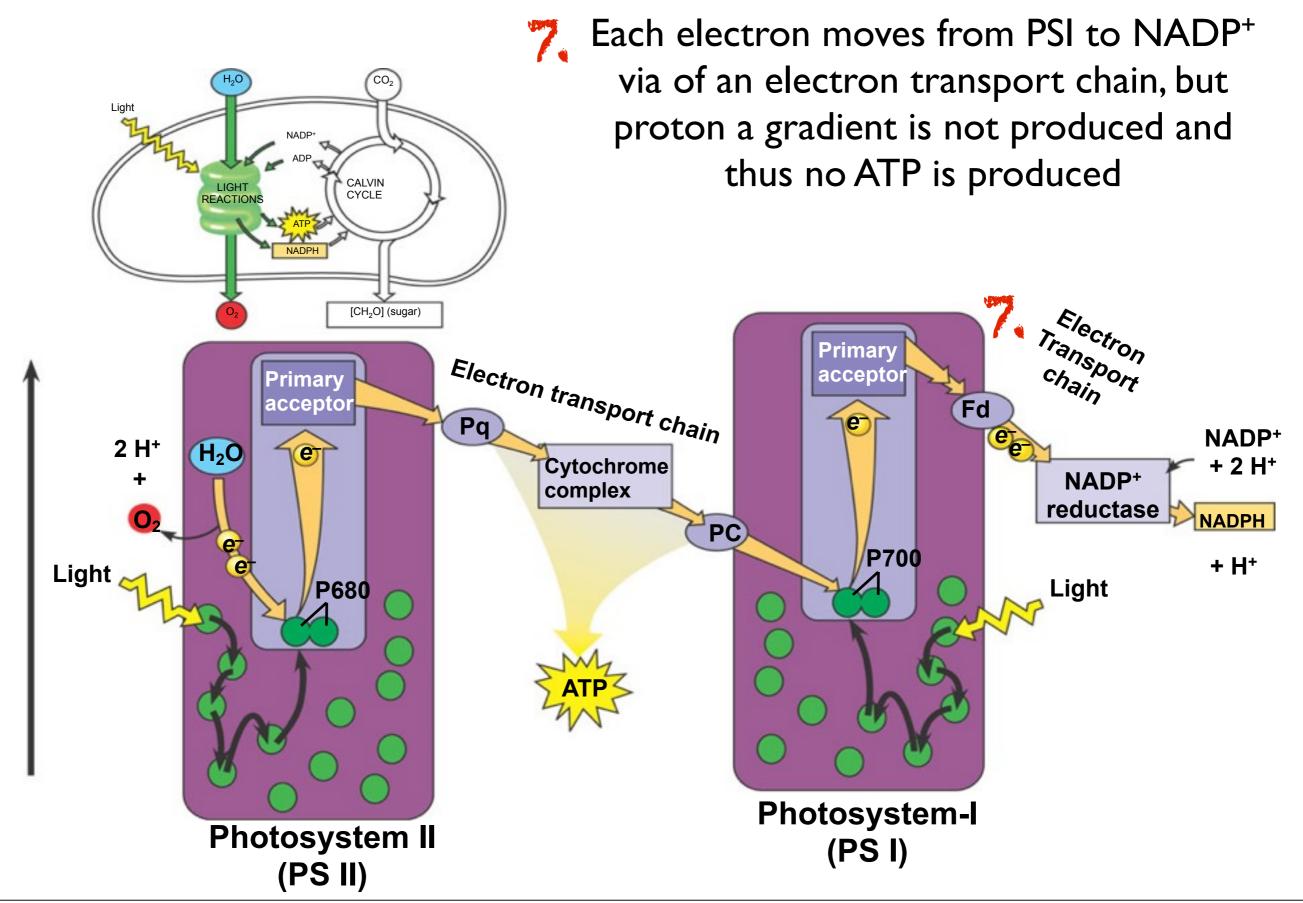
Tuesday, January 22, 2013

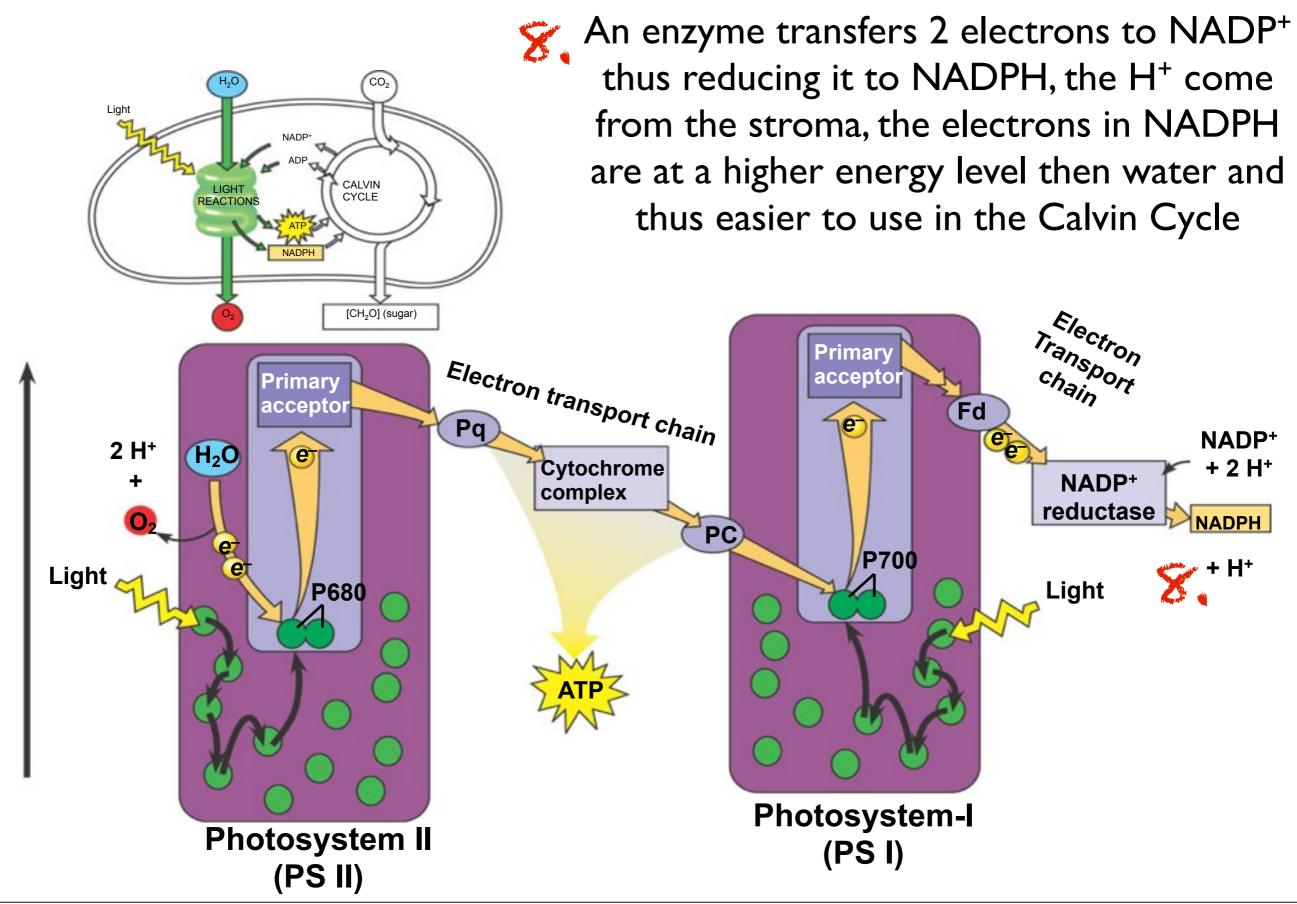


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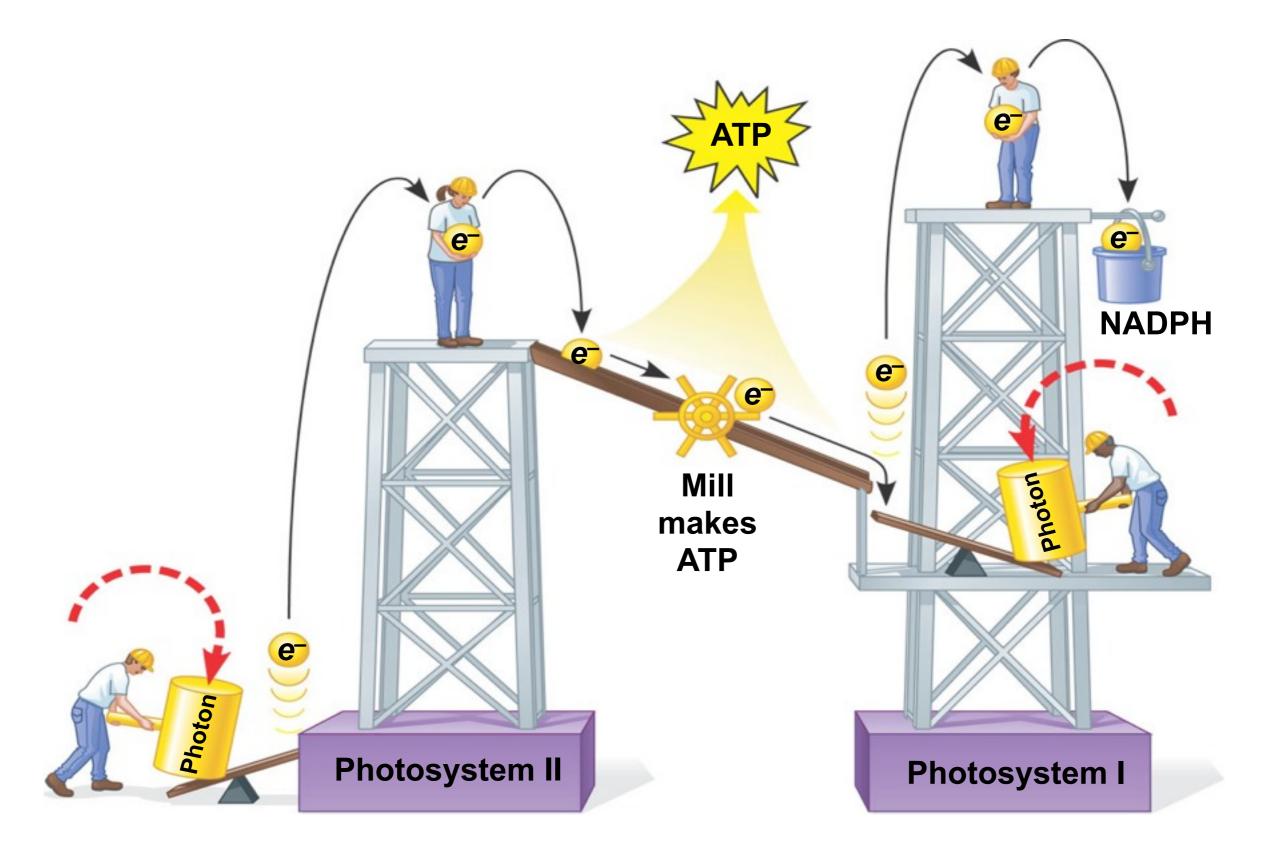






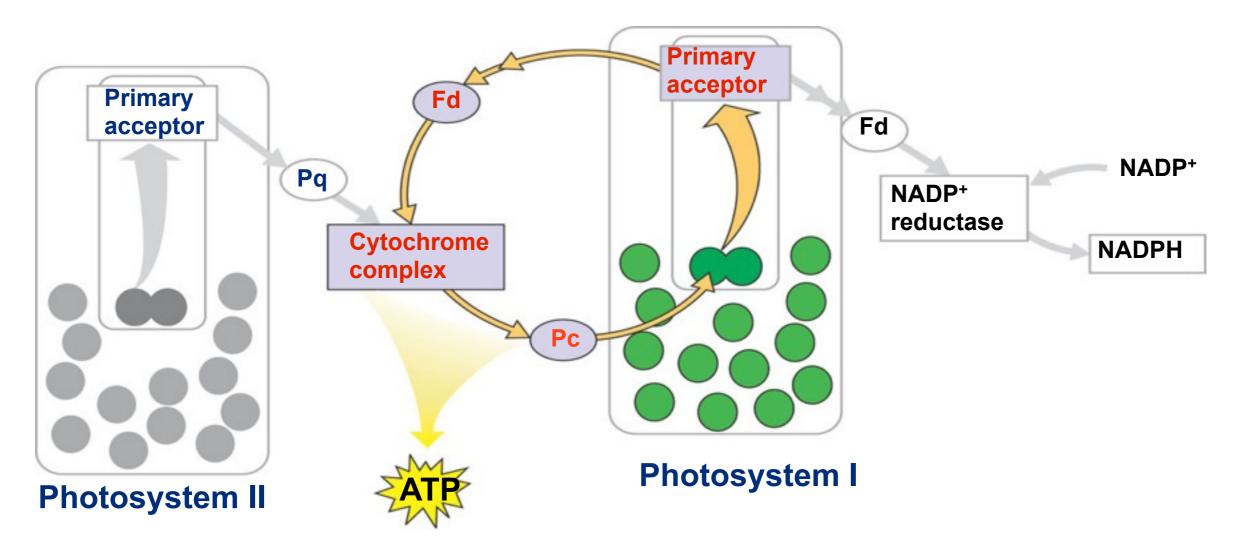


Light Reactions- Mechanical Analogy



Cyclic Electron Flow

 In some cases the electrons take an different route through the photosystems...the cyclic flow circuit



 Cyclic flow uses only photosystem 1 and generates additional ATP without any additional NADPH

Cyclic Electron Flow- Evolutionary Perspective

- Several groups of bacteria have photosystem I but no photosystem II for these bacteria cyclic flow is the sole means of generating their ATP
 - ex. purple sulfur bacteria
- Biologists hypothesize that cyclic flow may have been the precursor for modern photosynthesis
 - Today cyclic flow is found in photosynthetic organisms, even those that possess both photosystems.

*As it stands 1 ATP is made for every 1NADPH but more the Calvin Cycle requires 9 ATP and 6 NADPH,

We do know that cyclic flow is essential to C4 plants discussed later who adapted to very challenging conditions and

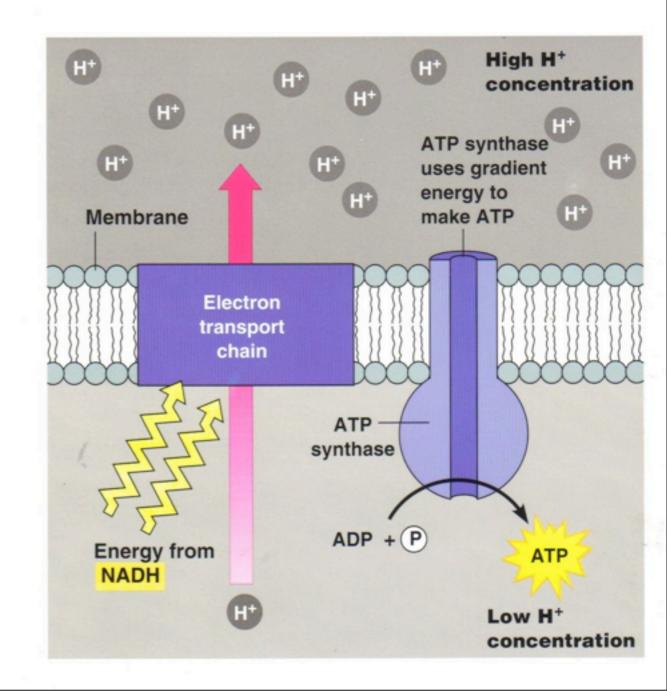
it may also play a photoprotective role.

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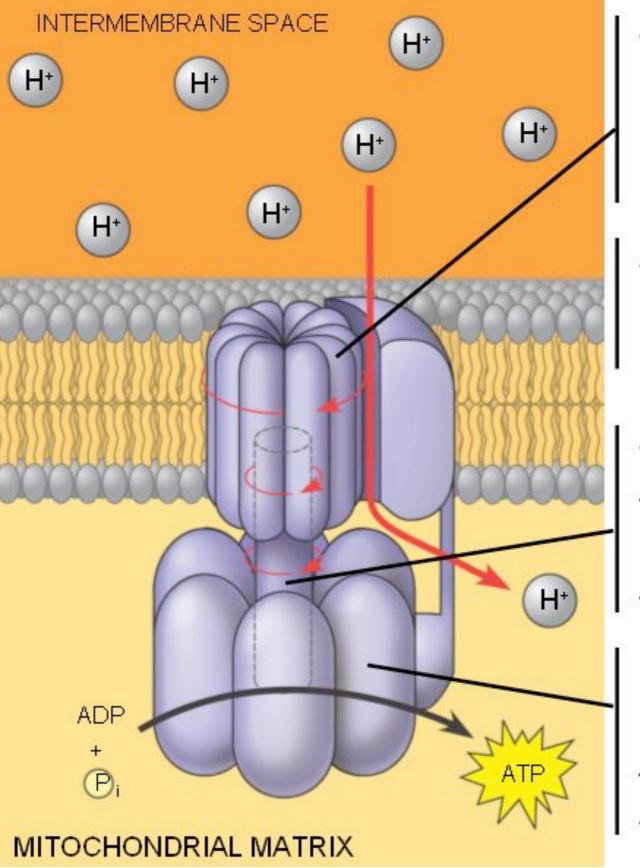
Chemiosmosis

- Chemiosmosis is an energy coupling mechanism that uses energy stored in the form of an H⁺ gradient across a membrane to drive cellular work
 - it employs an electron transport chain & ATP synthase
 - it can be found in prokaryotes & eukaryotes
 - it is used in photosynthesis & cell respiration

 (as well as other cellular processes)



ATP Synthase



A **rotor** within the membrane spins clockwise when H⁺ flows past it down the H⁺ gradient.

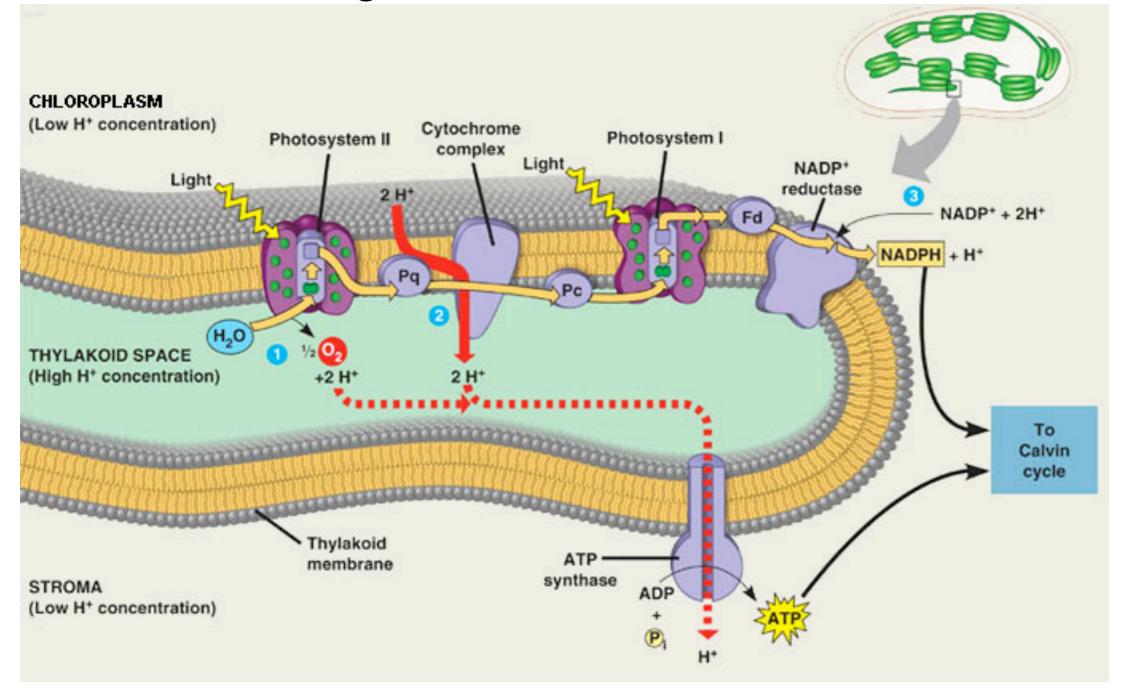
A **stator** anchored in the membrane holds the knob stationary.

A **rod** (or "stalk") extending into the knob also spins, activating catalytic sites in the knob.

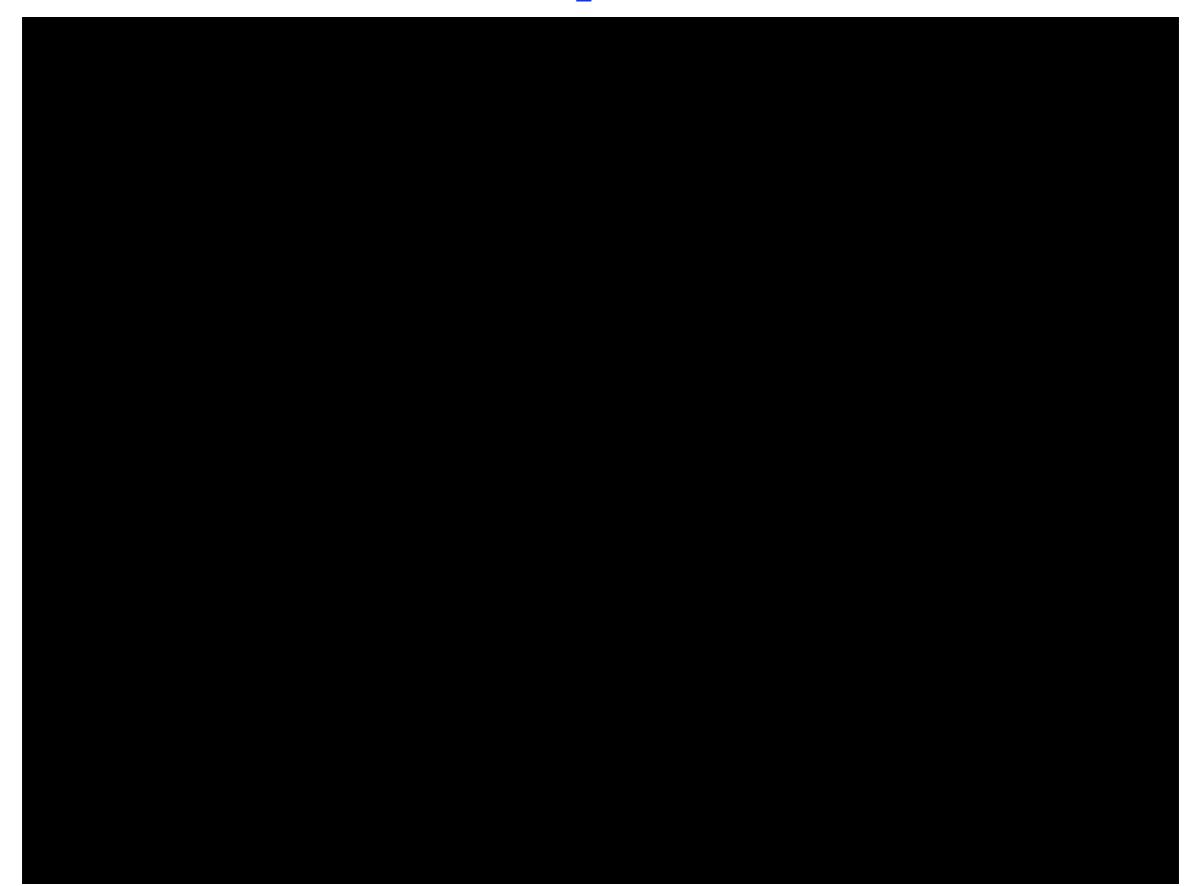
Three catalytic sites in the stationary **knob** join inorganic Phosphate to ADP to make ATP.

Photophosphorylation

- Chloroplasts are able harness solar energy (photo) to produce ATP (ADP + P = phosphorylation)
 - it does so through chemiosmosis



Photosynthesis



C₃ Photosynthesis

IV.

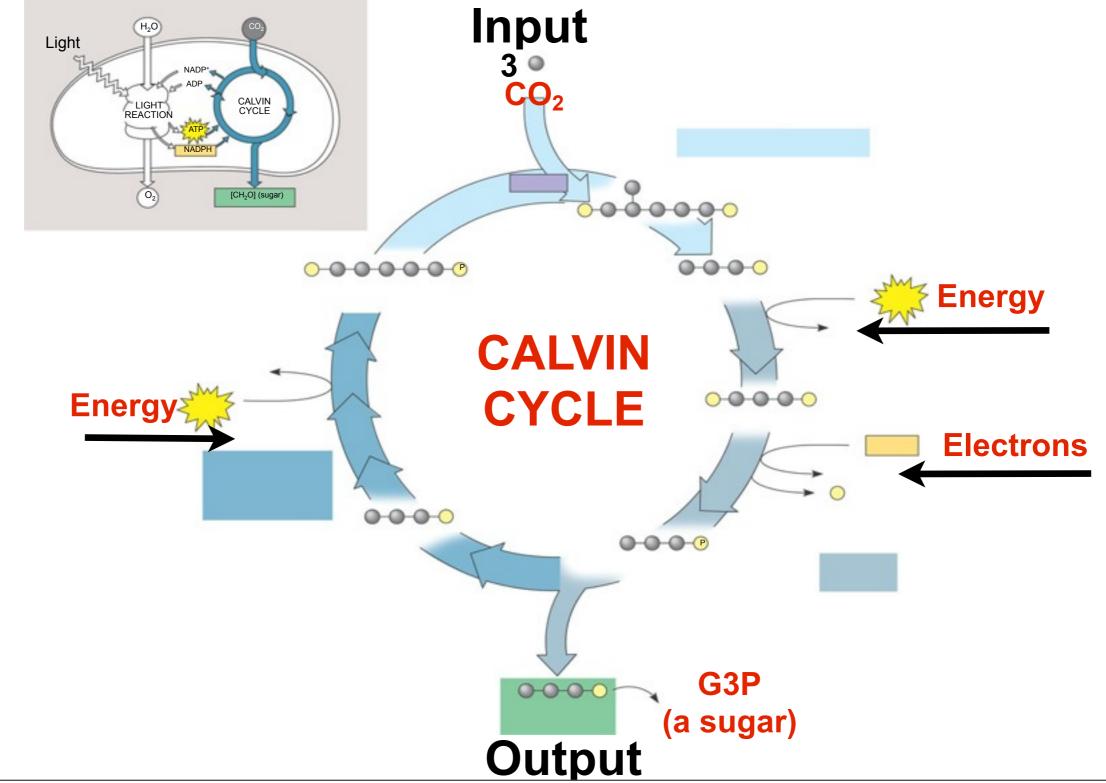
Main Idea: The Calvin Cycle builds sugars from carbon dioxide using energy from ATP and electrons from NADPH.



Tuesday, January 22, 2013

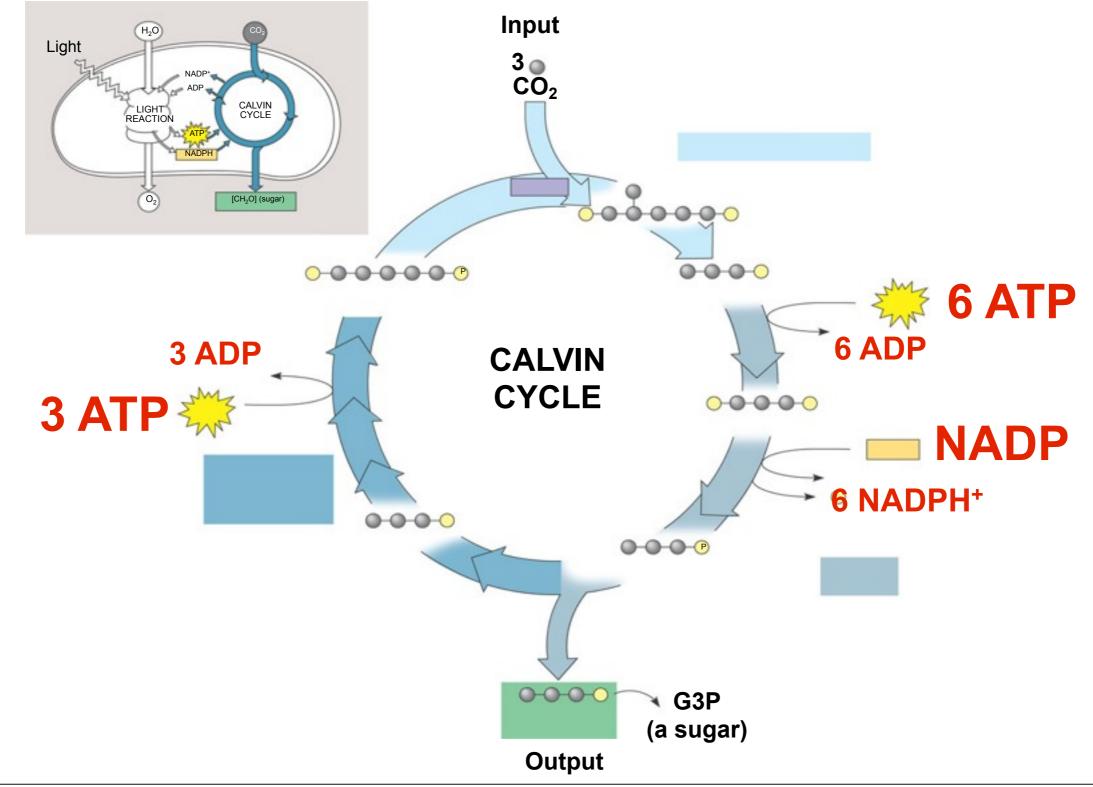
The Calvin Cycle (C3 photosynthesis)

• The Calvin Cycle is an anabolic, energy consuming pathway of reactions that produce sugar form carbon dioxide



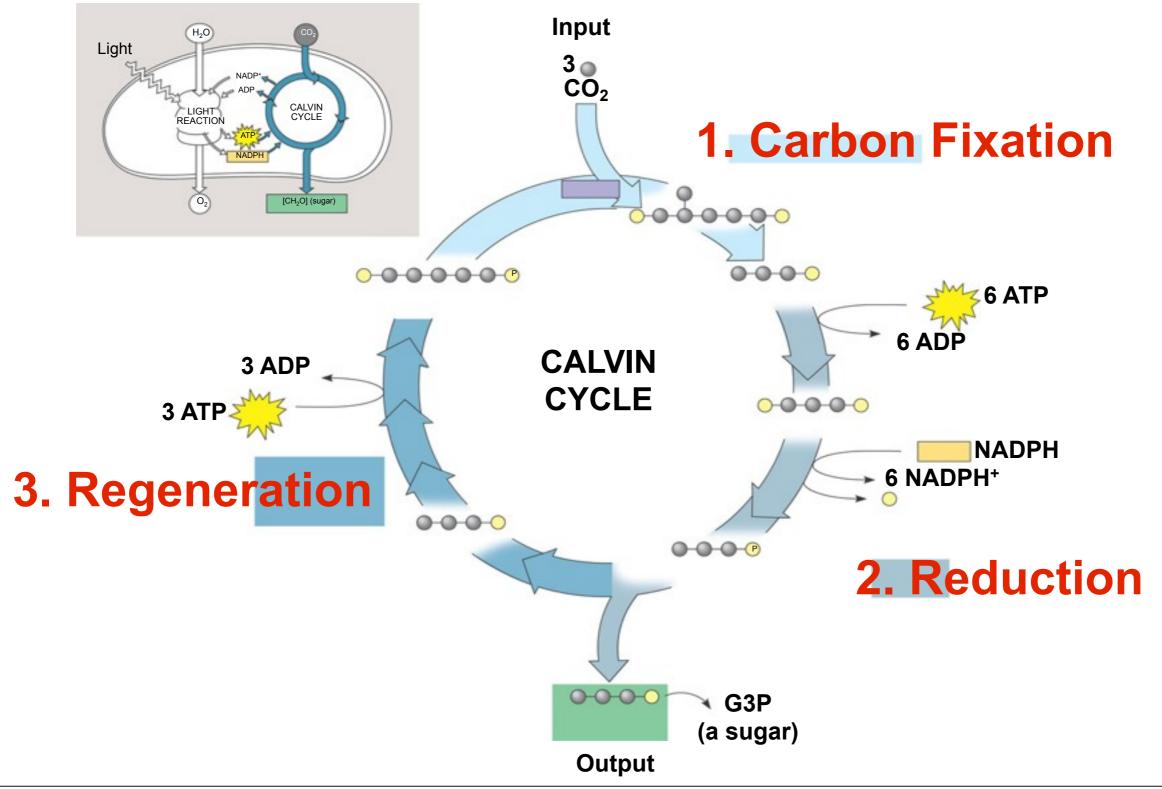
The Calvin Cycle (C₃ photosynthesis)

• The Calvin Cycle uses ATP and NADPH from the light reactions



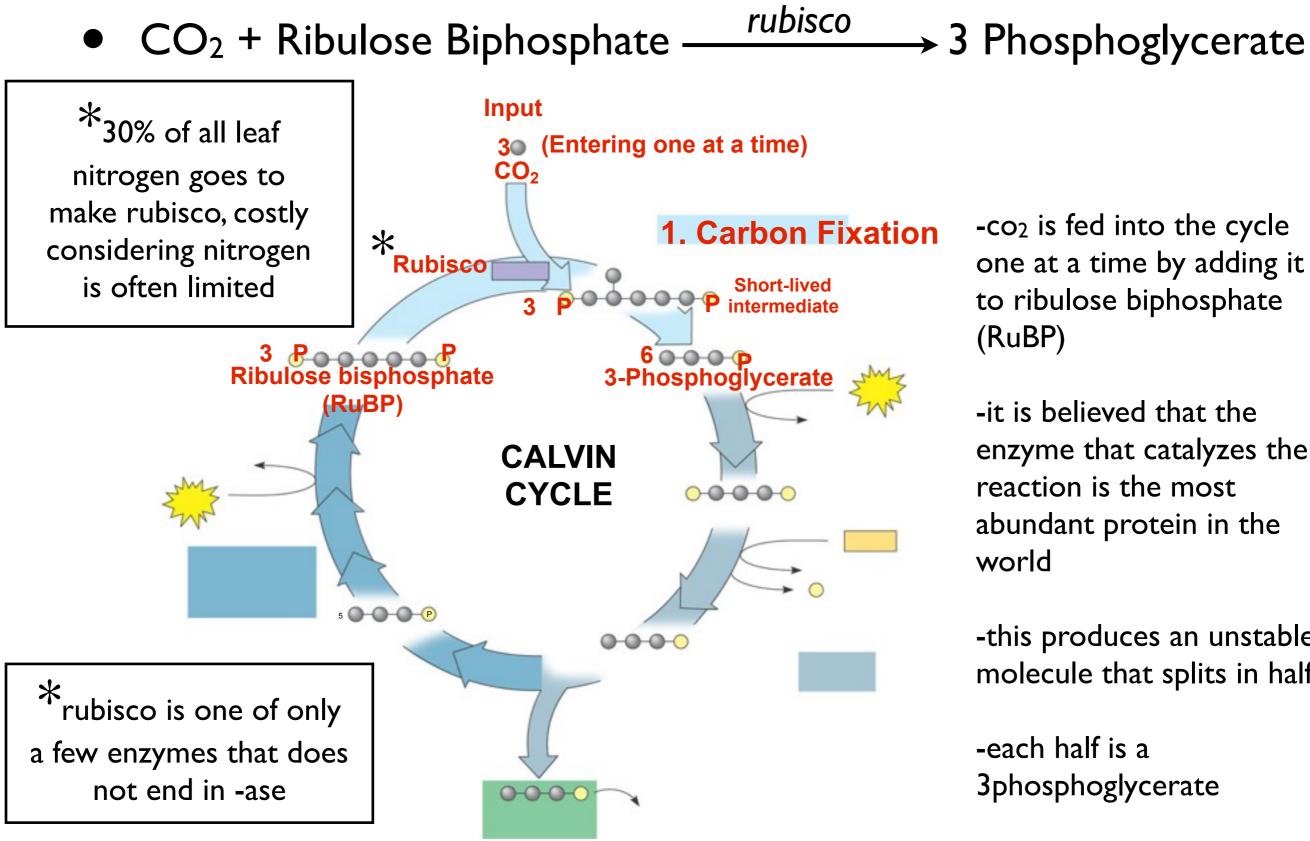
The Calvin Cycle (C3 photosynthesis)

• The Calvin Cycle can be divided into three phases.



The Calvin Cycle (C3 photosynthesis)

- Phase I: Carbon Fixation
 - CO₂ + Ribulose Biphosphate -



-co₂ is fed into the cycle one at a time by adding it to ribulose biphosphate (RuBP)

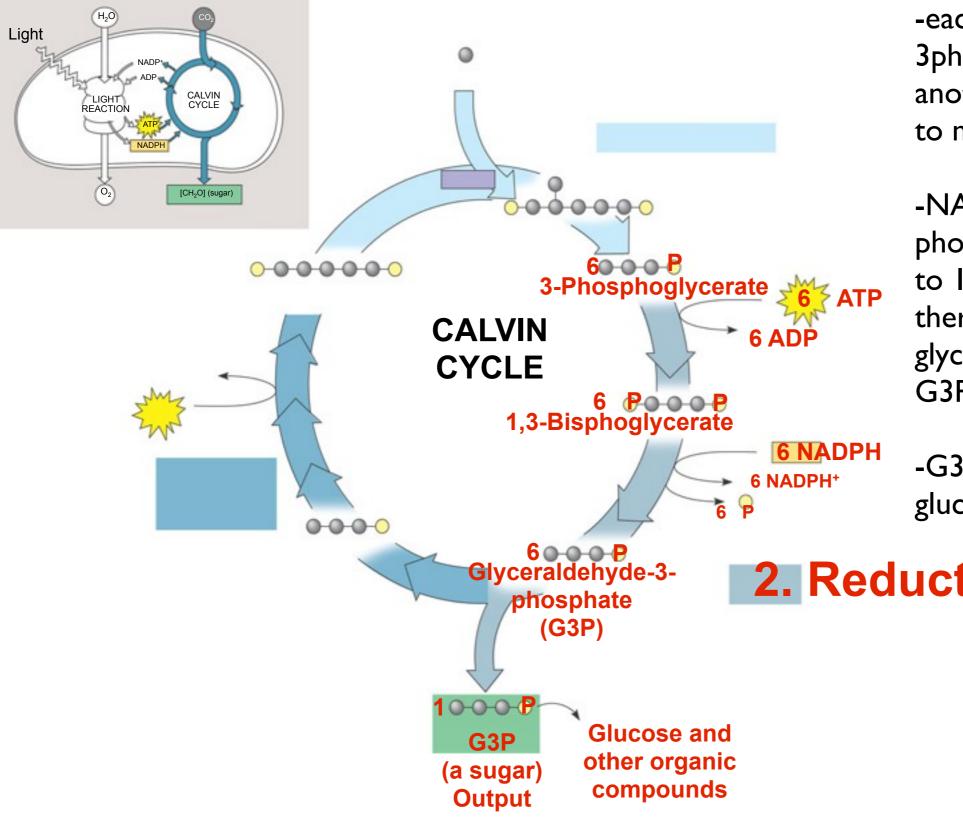
-it is believed that the enzyme that catalyzes the reaction is the most abundant protein in the world

-this produces an unstable molecule that splits in half

-each half is a 3phosphoglycerate

The Calvin Cycle (C₃ photosynthesis)

Phase 2: Reduction



-each molecule of 3phosphoglycerate receives another phosphate from ATP to make 1,3biphosphoglycerate

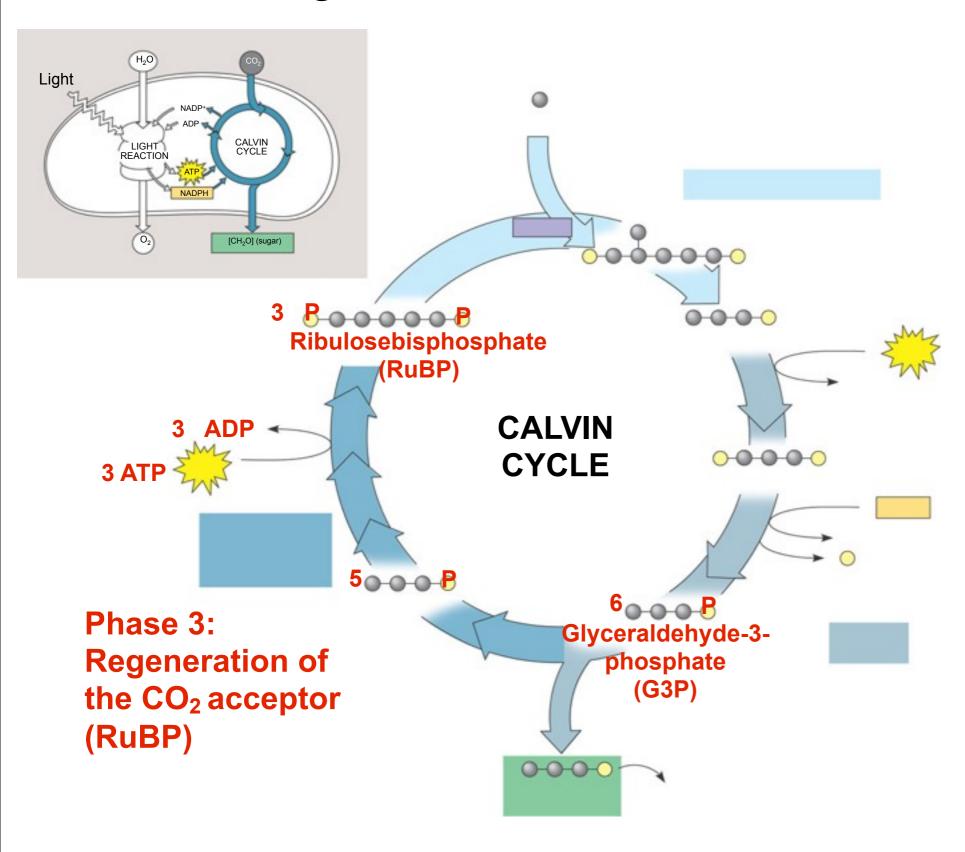
-NADPH then removes phosphates and adds electrons to 1,3biphosphoglycerate thereby reducing it to glyceraldehyde 3-phosphate or G₃P

-G3P is essentially a half of glucose

2. Reduction

The Calvin Cycle (C₃ photosynthesis)

• Phase 3: Regeneration



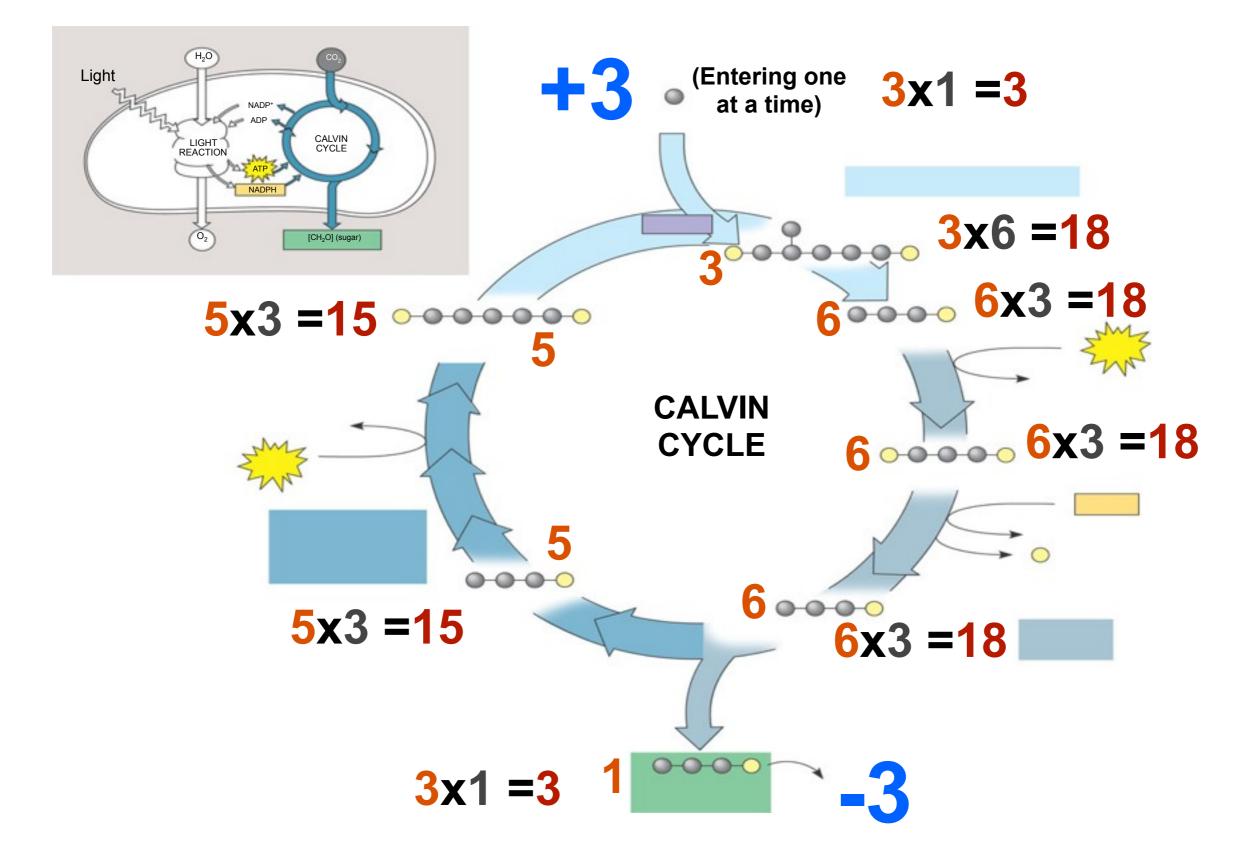
-in a complex series of reactions the G3P is rearranged back into RuBP

-to accomplish these reactions 3 more ATP are required

-regenerating RuBP enables the cycle to continue to fix carbon dioxide and thus make more sugar

The Calvin Cycle (C₃ photosynthesis)

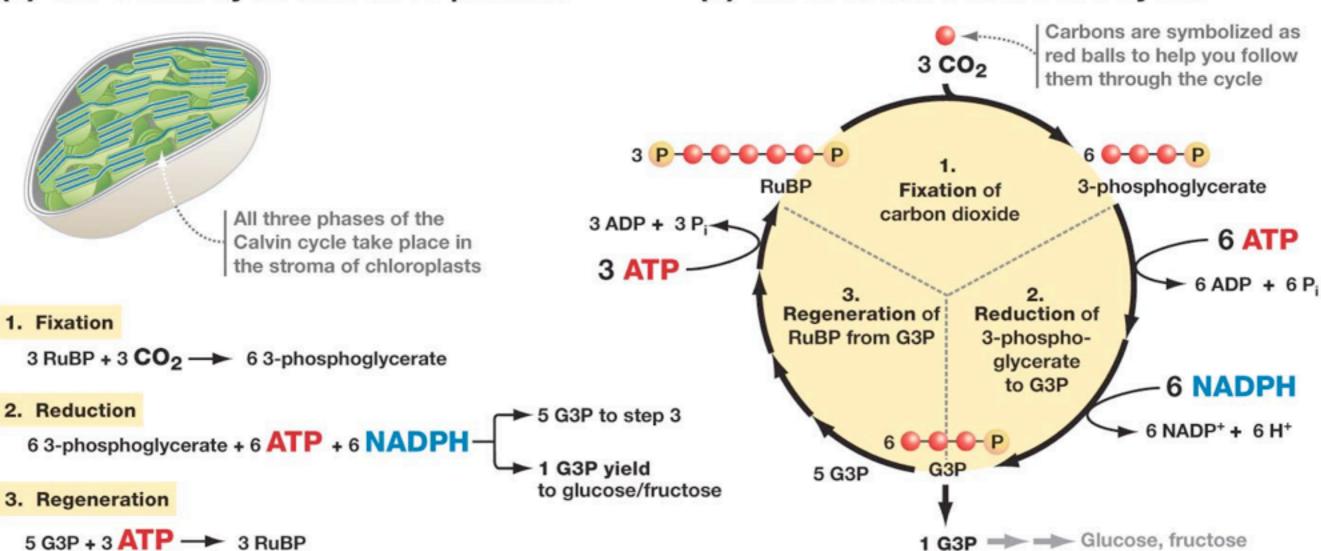
• Do some accounting work! (Track the number of carbon atoms)



The Calvin Cycle (C₃ photosynthesis)

NOW put it all together!

(a) The Calvin cycle has three phases.

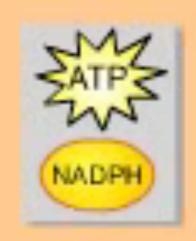


(b) The reaction occurs in a cycle.

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1. Fixation





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Maximum Photosynthetic Production

- There are two in which plants can increase there photosynthetic output or production.
 - Increase the rate of CO₂ into the leaf (could be accomplished by opening more and more stomata).
 - Increase the rate of carbon fixation (could be accomplished by using nitrogen and other nutrients to build more enzymes).

Why do you suppose that actual plant production is much lower than its theoretical maximum?
Because life is all about trade-offs, open too many stomates plant dehydrates, build too many enzymes plant depletes its nitrogen stores which are usually limited to begin with

Photosynthesis

V.

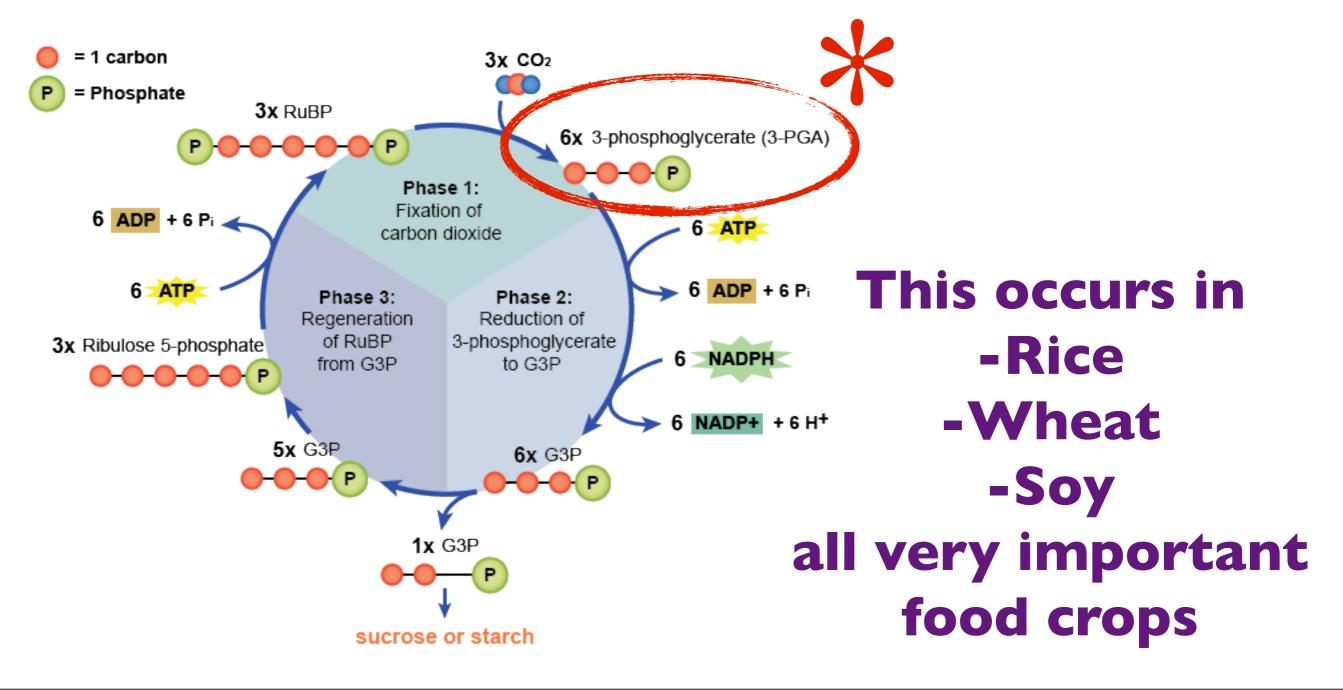
Main Idea: Metabolic adaptations have evolved that help plants conserve water in dehydrating environments while still producing a sufficient amount of sugar to sustain themselves.



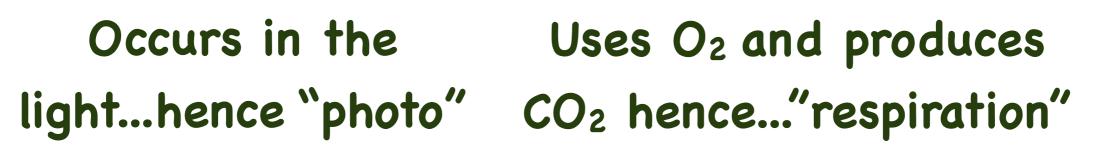
The Challenge of Terrestrial Life

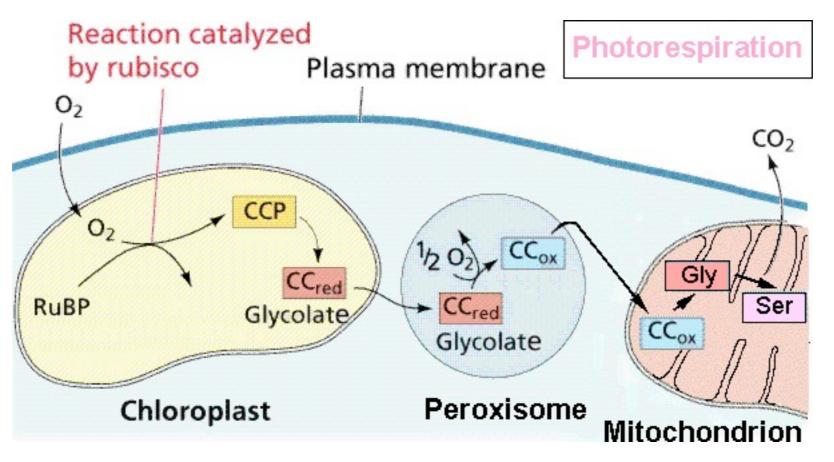
- Ever since plants moved on land they have struggled to obtain and conserve sufficient amounts of water to sustain themselves.
- Interestingly the water problem for plants is really an energy problem.
 - Carbon dioxide is required to build sugars and sugars of course lead to the production of cellular fuel (ATP).
 - CO₂ enters the leaf through stomata, and it is the stomata that allow most water loss through the plant.
 - Should plants close stomata in hot, dry climates to conserve water they risk a low photosynthetic output, if they keep stomata open in hot, dry climates they risk dehydration.
- Plants have the precarious task of balancing sugar production with water loss

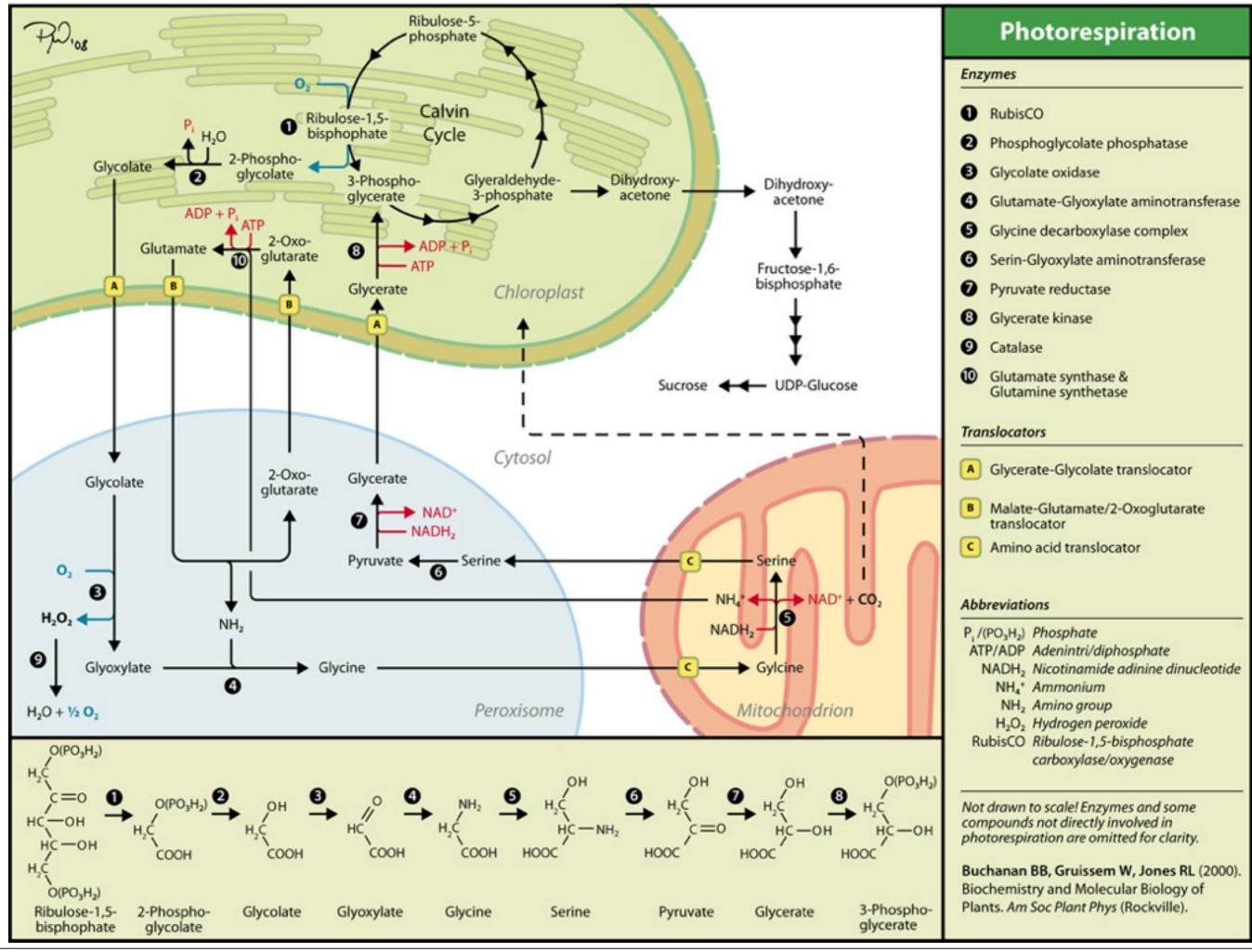
- RECALL, the Calvin Cycle
- We call this C3 photosynthesis because the first product of the Calvin Cycle is a 3 carbon compound (PGA).



- ...the aberrant use of O_2 by chloroplasts.
- ...an interference with carbon fixation as a result of O₂ outcompeting CO₂ for the binding site of rubisco.



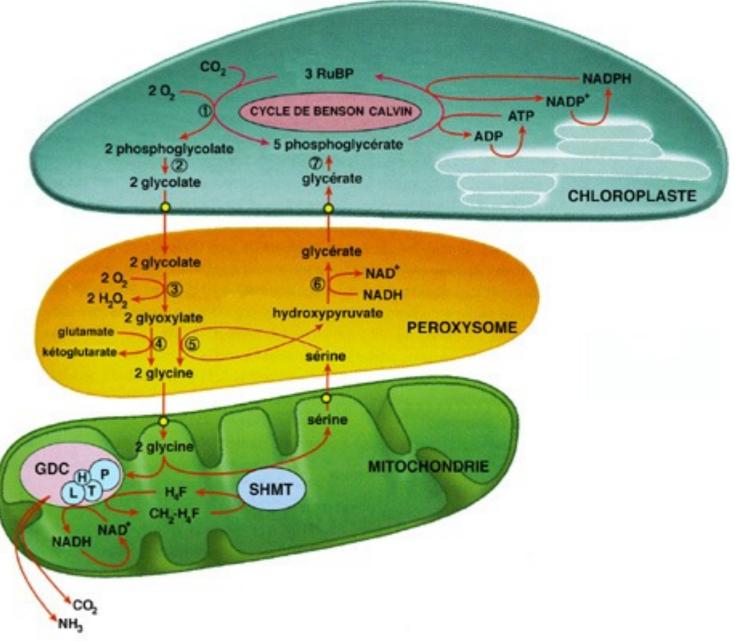




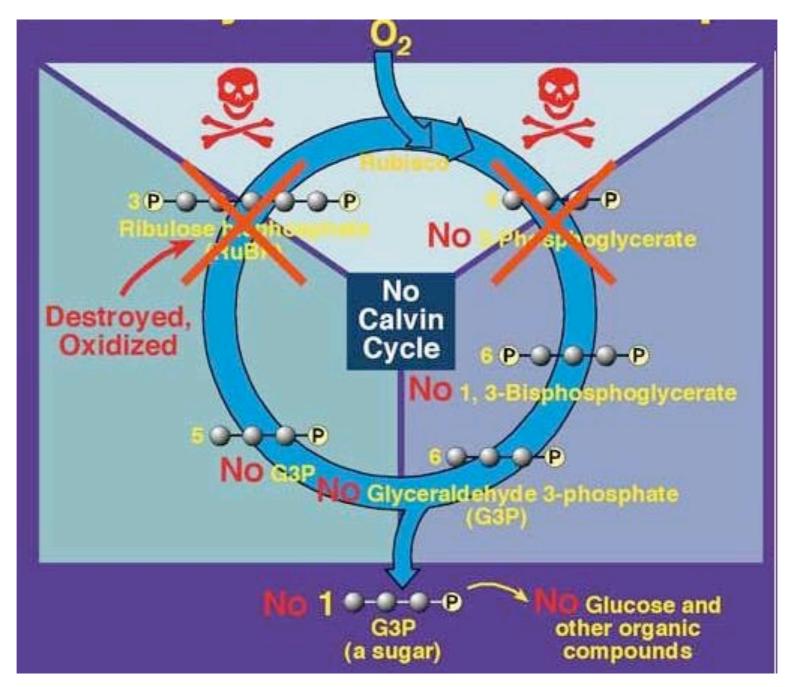
Tuesday, January 22, 2013

- ...occurs in hot, dry, windy conditions when plants close stomata.
- ...as plants close stomata to conserve H₂O the [O₂] increases and while the [CO₂] decreases and O₂ outcompetes CO₂ for the binding site of rubisco.

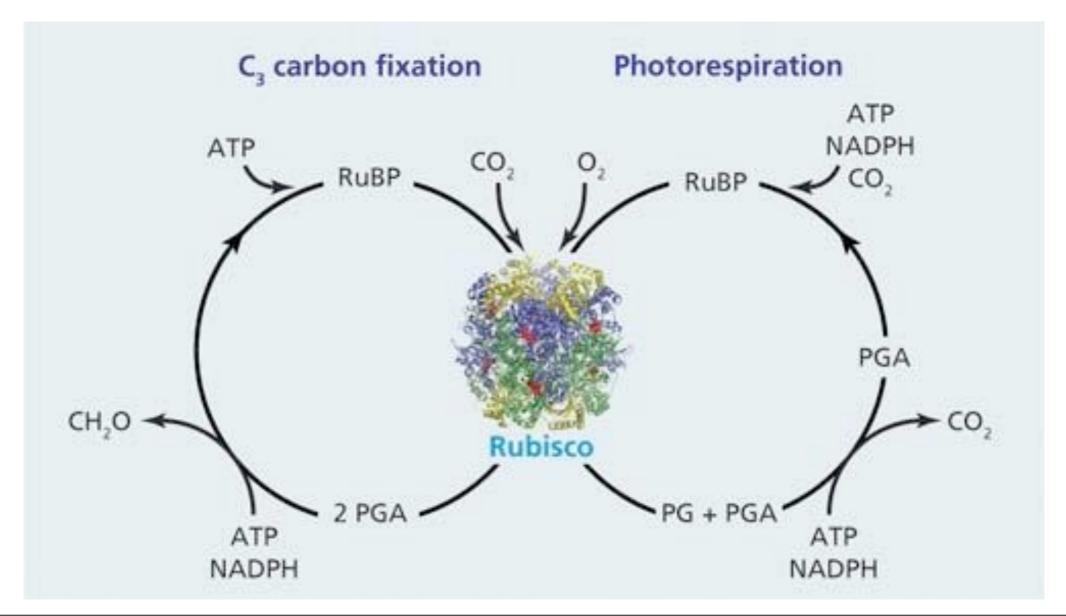
this not only drains away CO₂ and decreases the sugar production but also consumes ATP



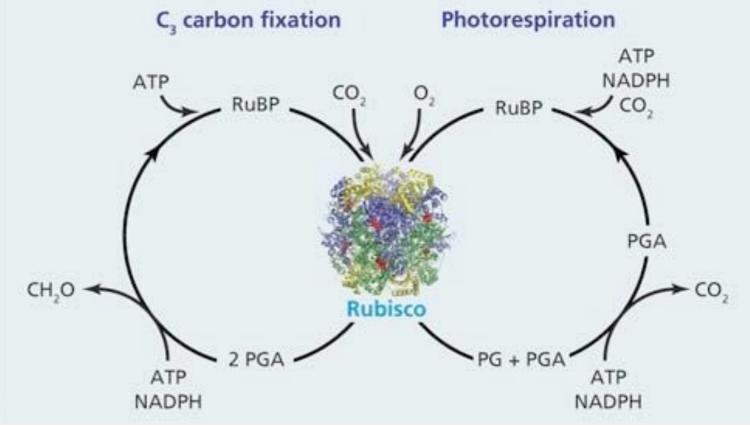
- ...is wasteful.
- ...ultimately it decreases photosynthetic output and when the plant is a crop plant this equates to a lower crop yield (less food).



- ...is likely evolutionary, metabolic relic.
- ...when photosynthesis first evolved rubisco's binding site would NOT have needed to be CO₂ specific because the concentration of O₂ at that time was so very small.



What phenotype would be highly beneficial for C₃ plants today? If you could "order up" a mutation what would it do?



One that would effect the rubisco binding site, one that would change the binding site to bind solely CO_2

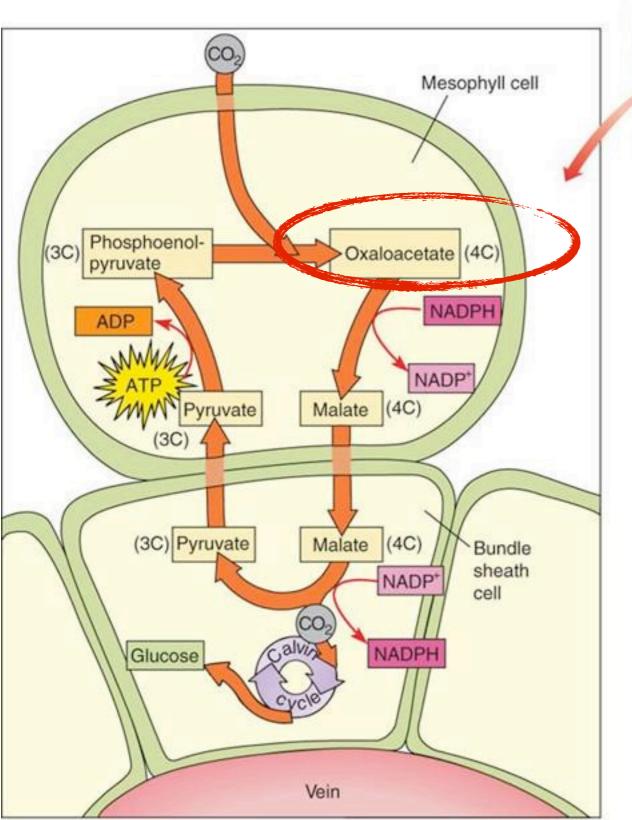
Sorry evolution does not work that way!

Trade Offs (?)

- There is evidence that suggests that photorespiration plays a protective role in some plants.
 - Photorespiration may act to neutralize harmful products that build up during times of low [CO₂].
- This may explain why a seemingly wasteful metabolic pathway has persisted for so long.

However, in other plants where perhaps there are no benefits from photorespiration we find adaptations and mechanisms that minimize photorespiration...

C₄ Plants & CAM Plants

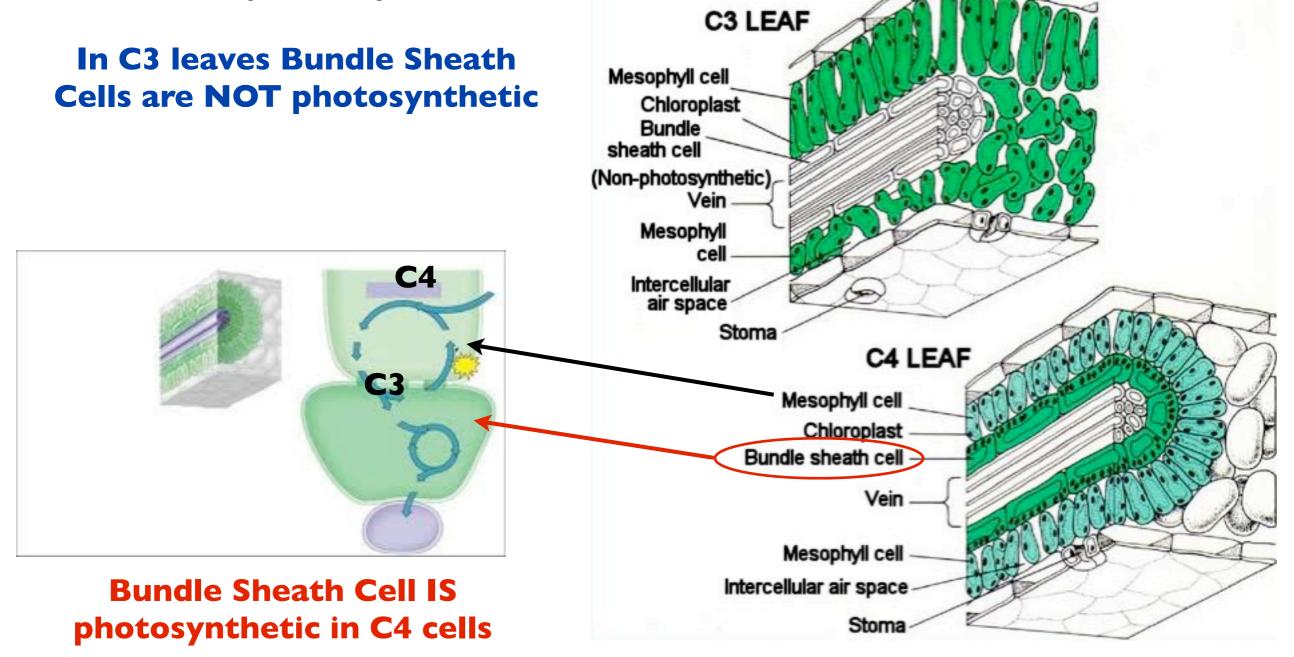


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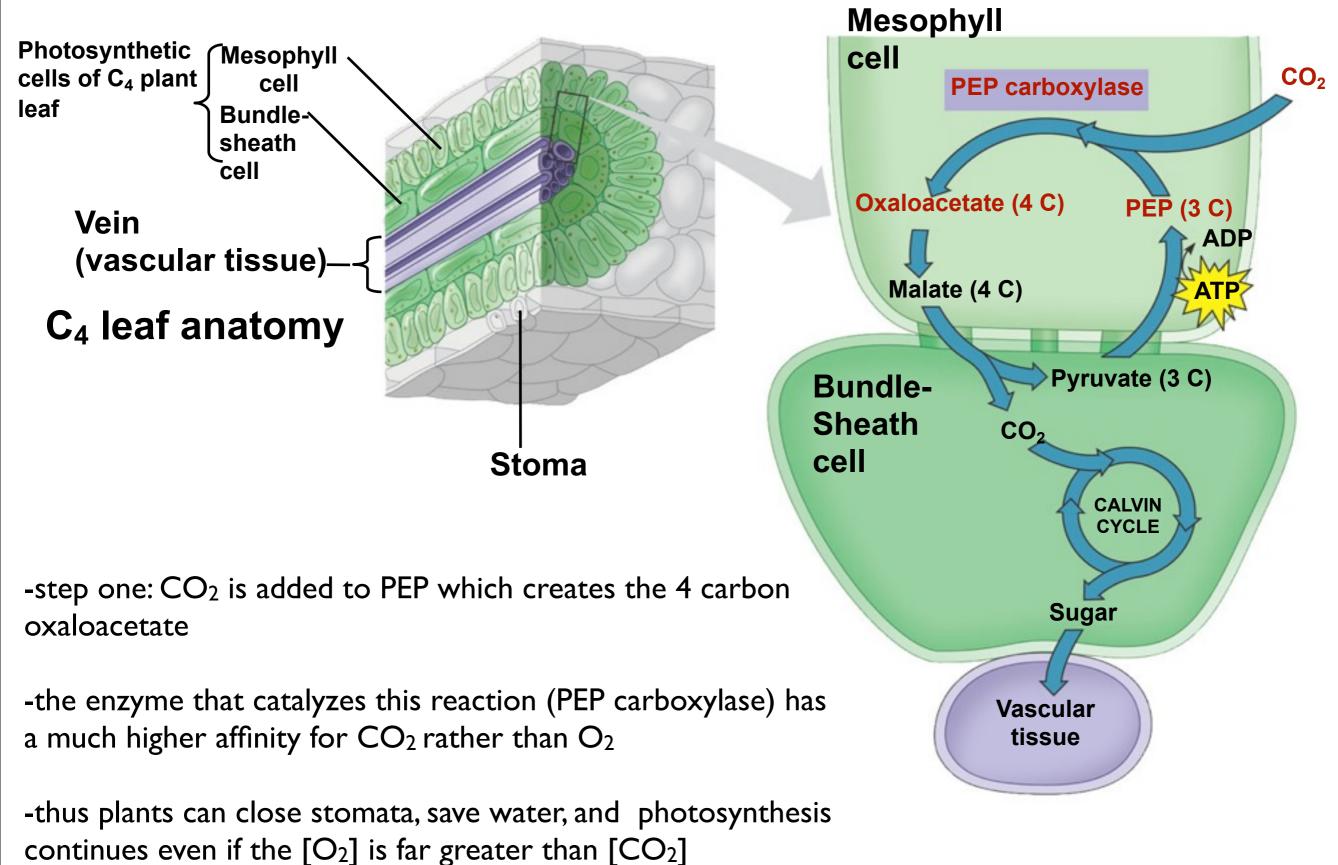
Thousands of so called C₄ plants preface the Calvin Cycle with an alternate mode of carbon fixation that consequently results in a product with 4 carbon atoms.

> Examples Include: Sugarcane Corn Grasses

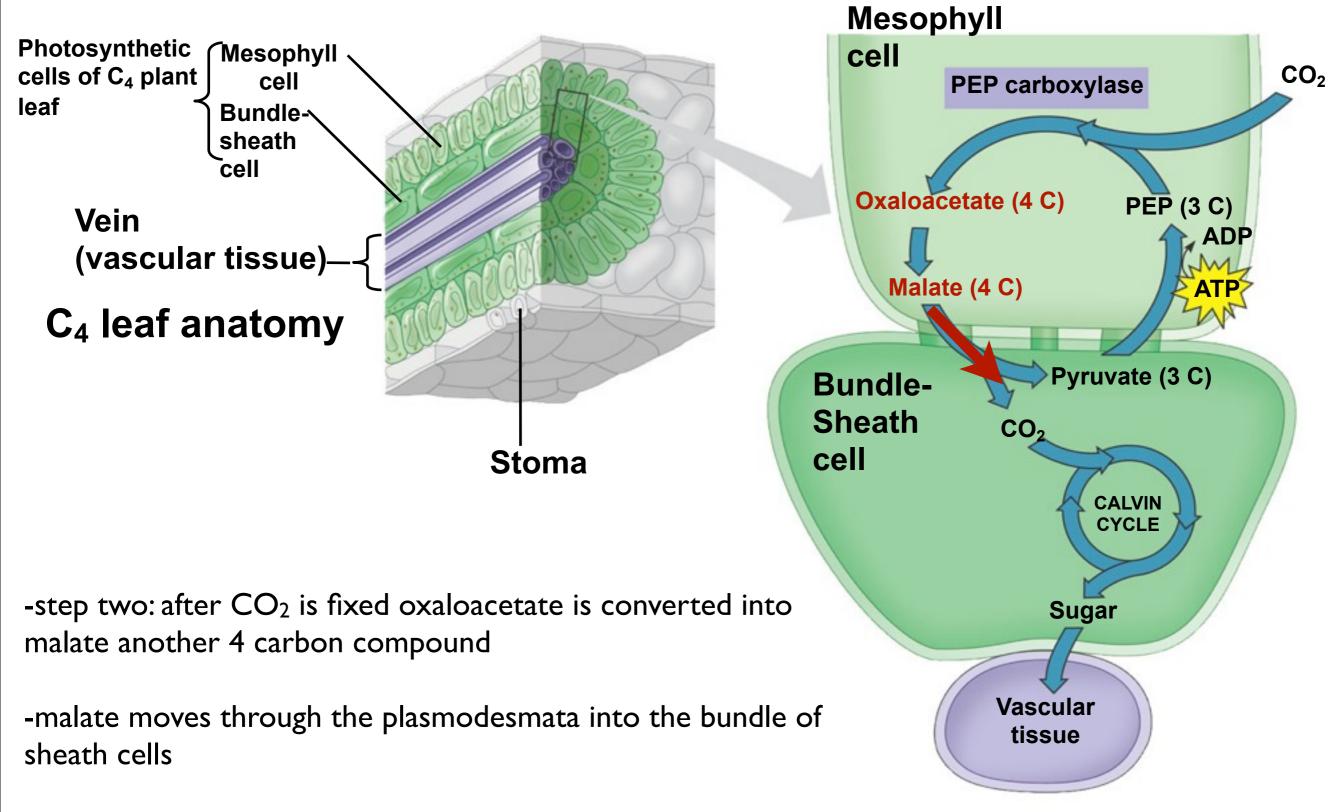
- It is easy to see from the last slide that this adaptation has its own unique metabolic pathway
- It is however a unique anatomy that enables the success of the metabolic pathway



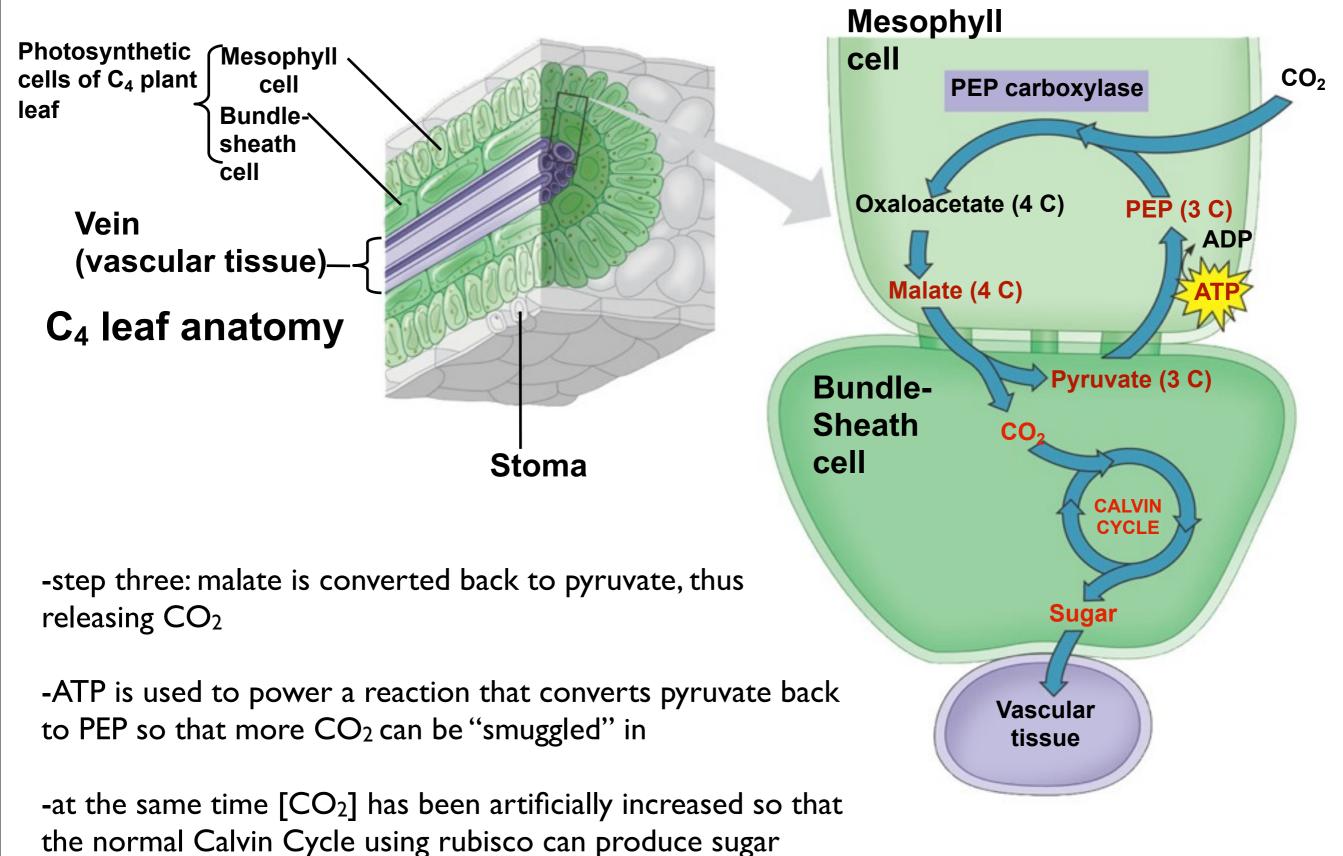
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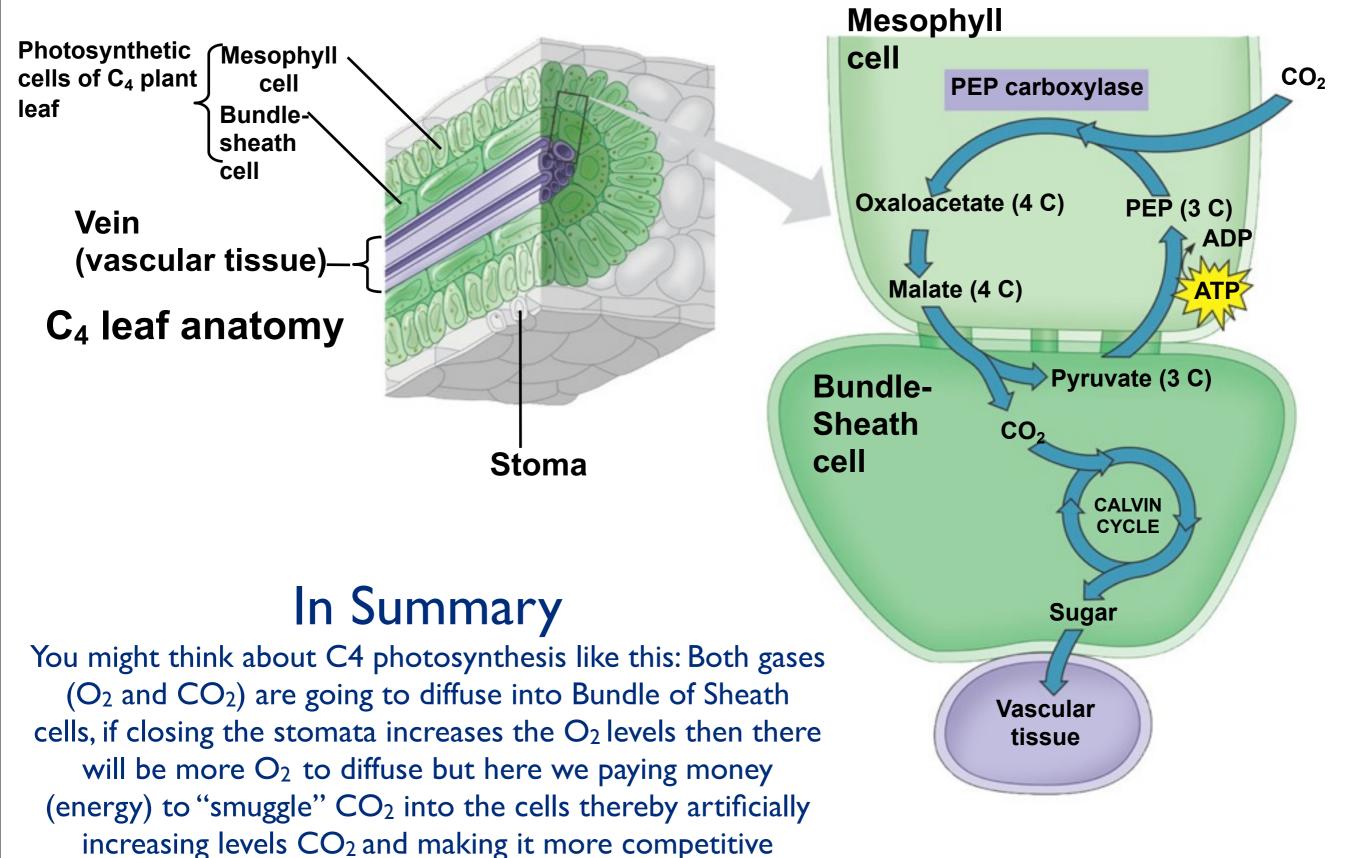
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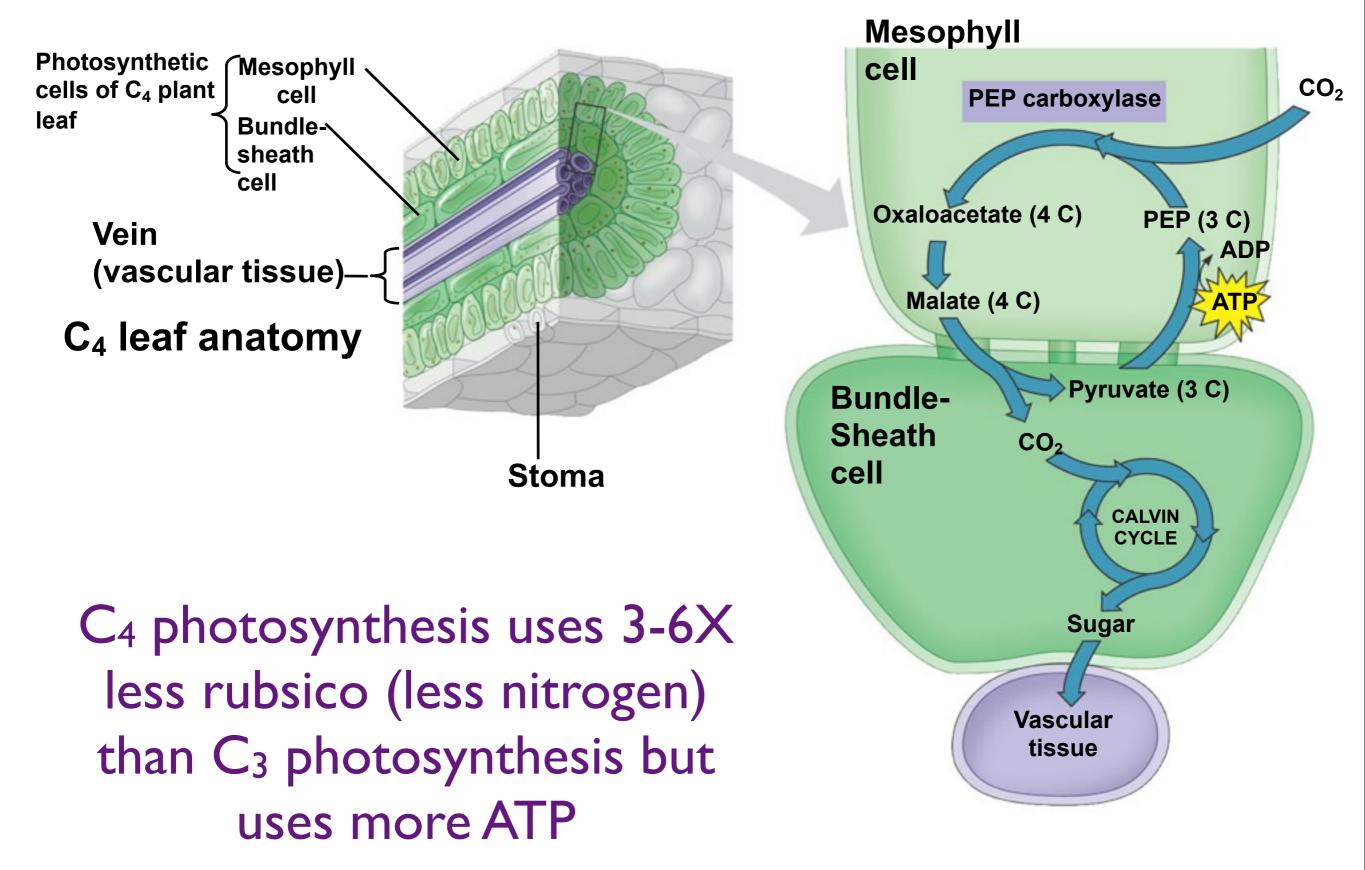


-the [CO₂] is artificially being increased by "smuggling" in CO₂

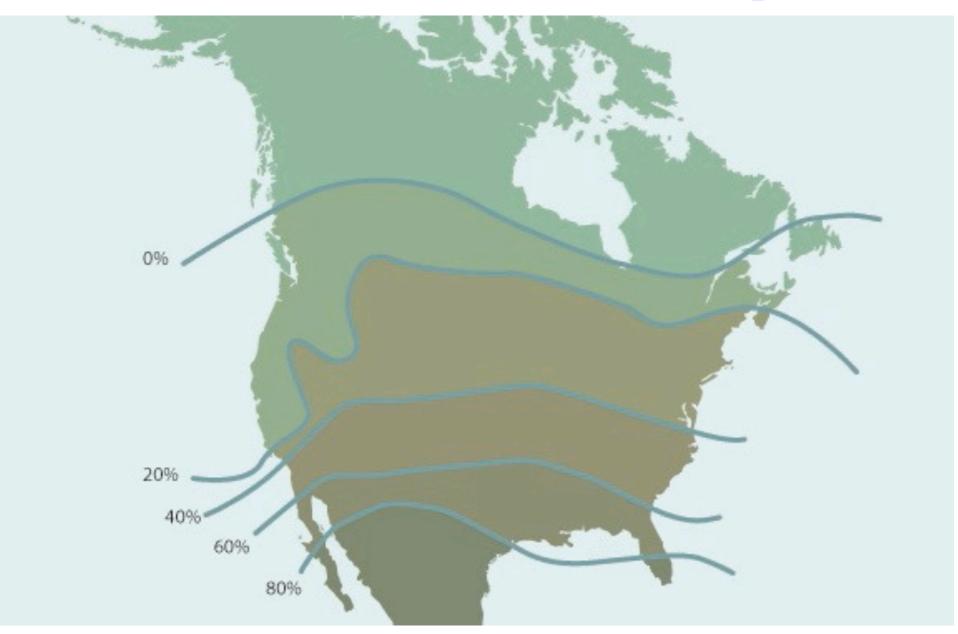


Tuesday, January 22, 2013





Distribution of C₄ Photosynthesis



Use this map of C₄ plant distribution to answer the following. Describe the effect of each variable: abundance of light, water availability and temperature on the distribution of C₄ and C₃ plants (assume the % difference are C₃ plants)? C₄ Photosynthesis Trade Offs





Not subject to Photorespiration

Energetically expensive

C₃ Photosynthesis Trade Offs



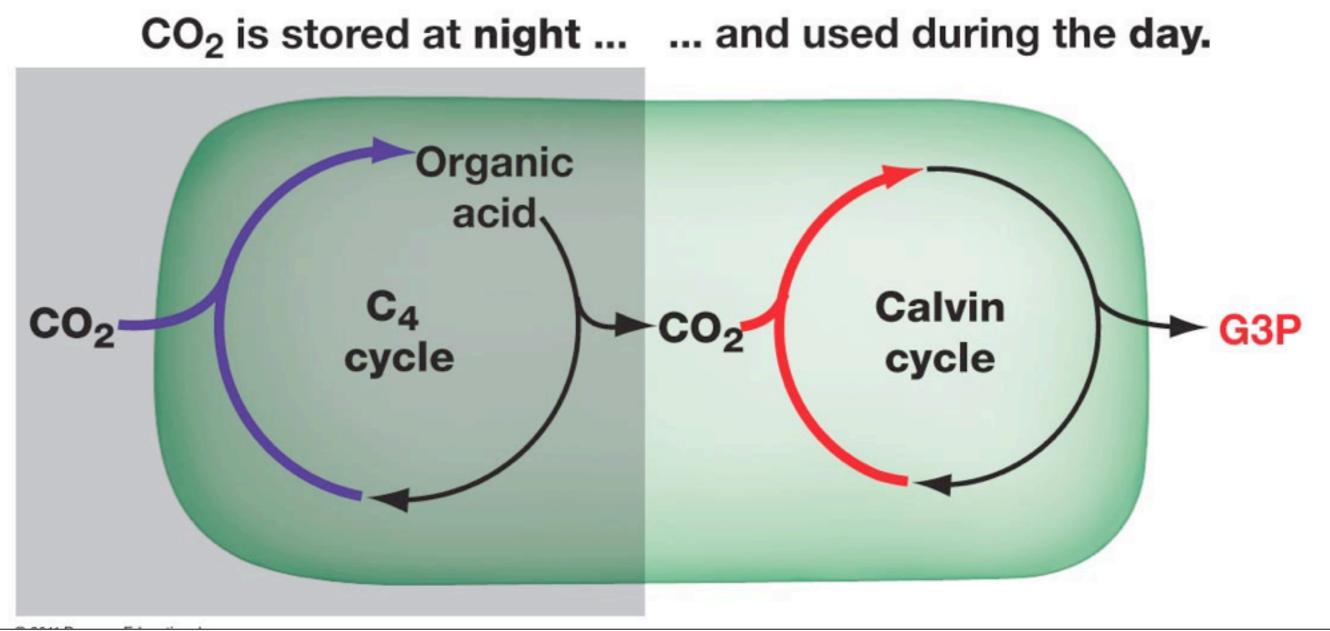


Energetically Inexpensive

Subject to Photorespiration

CAM Photosynthesis (crassulacean acid metabolism)

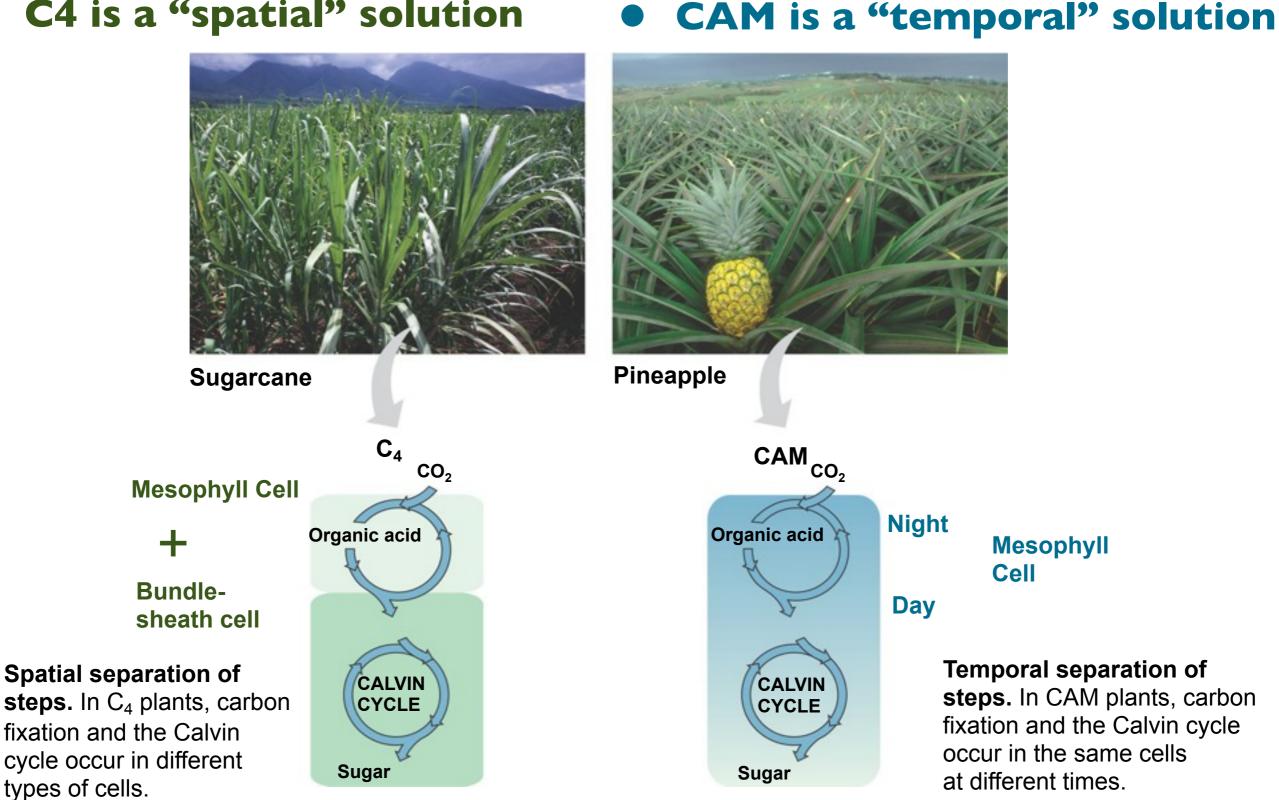
- These plants open there stomata at night and close them in the day (opposite of most plants).
 - Examples Include: Pineapple, Cacti, Succulents

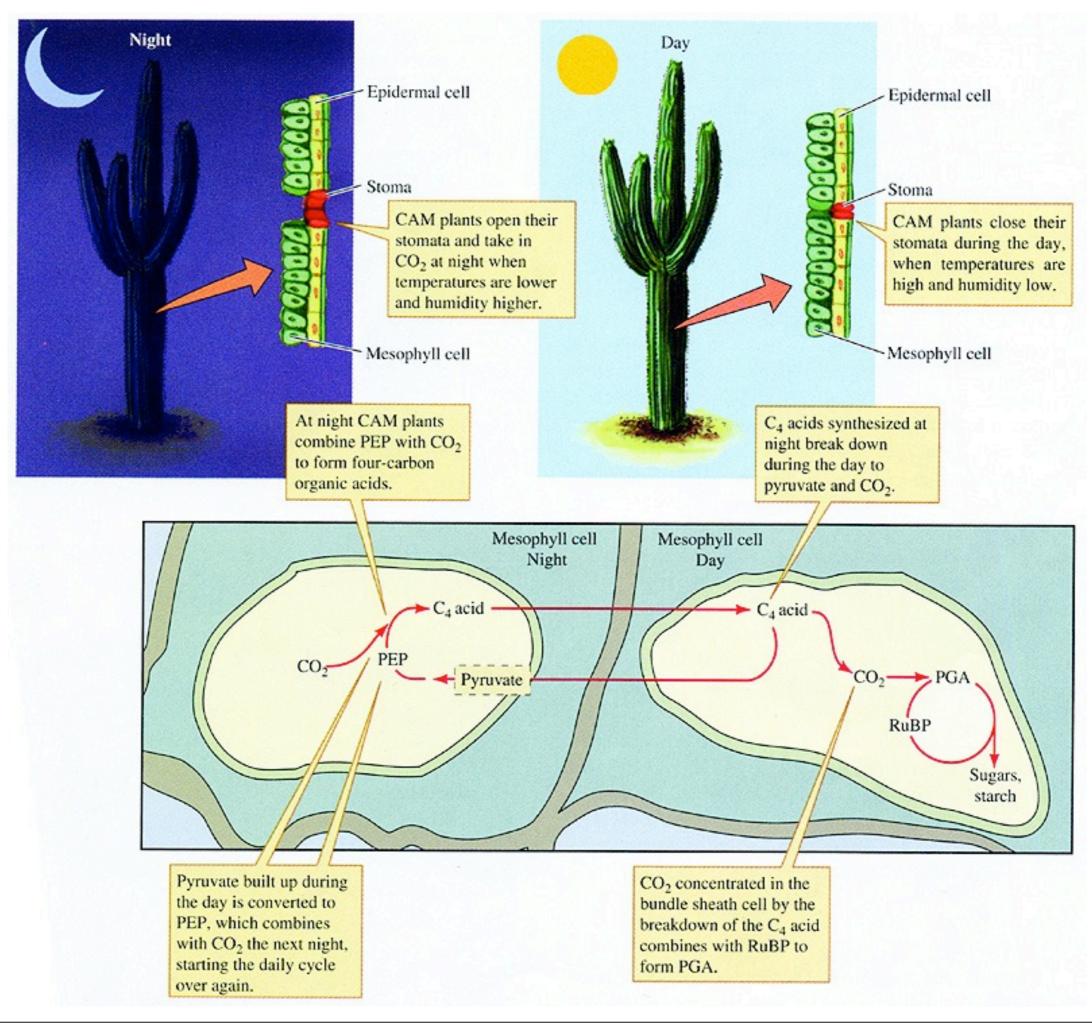


Tuesday, January 22, 2013

CAM Photosynthesis

C4 is a "spatial" solution





CAM Photosynthesis

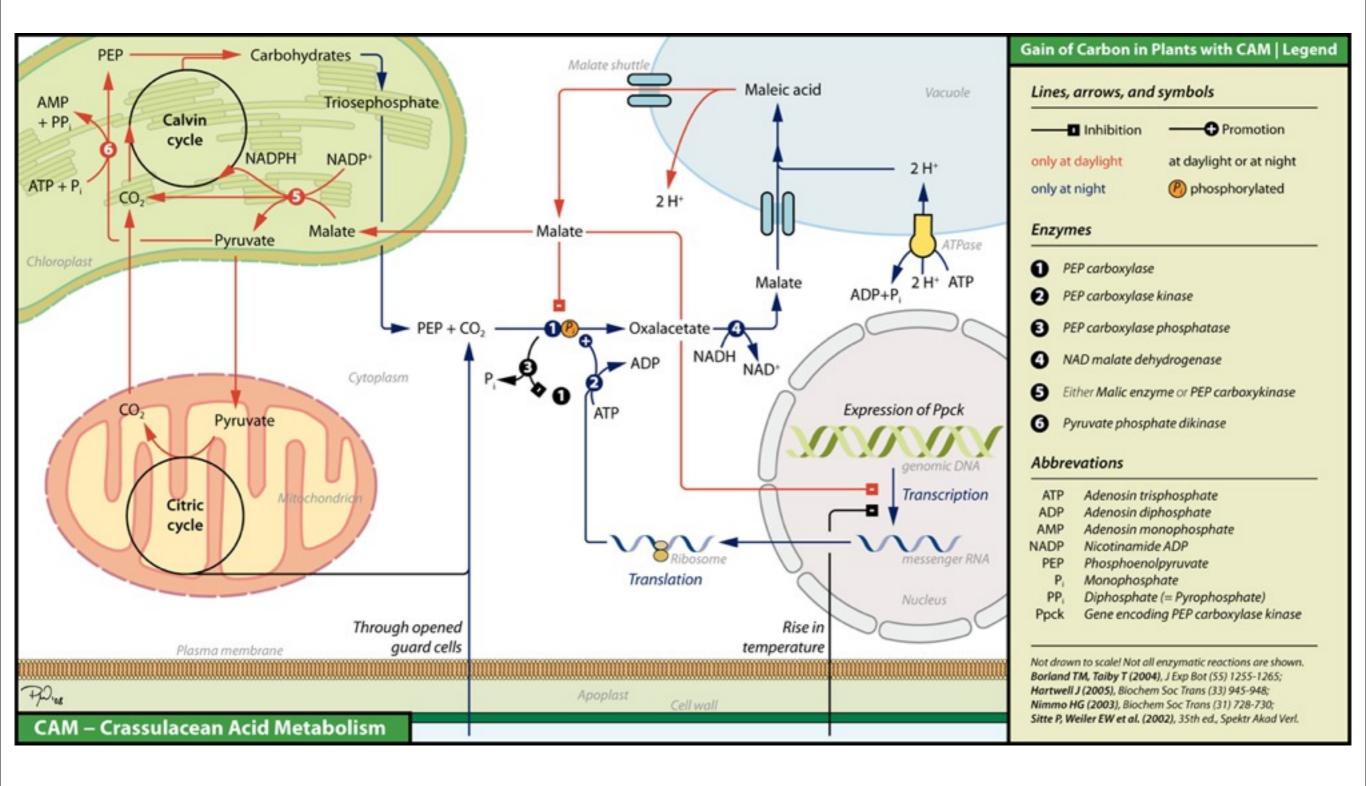
- The distribution of CAM plants are generally correlate with arid areas of the world.
- There is one notable exception...**epiphytes** found in tropical rain forests.



Why would plants in the wet, damp and shaded portion of the rainforest use CAM?

Their structure dictates such, they have no roots and as a result get little water through the humid air

CAM Photosynthesis



CAM Photosynthesis Trade Offs

PROS

Not subject to Photorespiration

Can live through extended periods of drought <u>CONS</u>

Energetically expensive

Low photosynthetic capacity, slow growth

Structure Dictates Function

What is unique about a succulent plant's appearance? They have thick, fleshy, water storing leaves or stems

Where do CAM plants store there acids over night?

In their vacuoles

What other common molecule do you find in vacuoles?

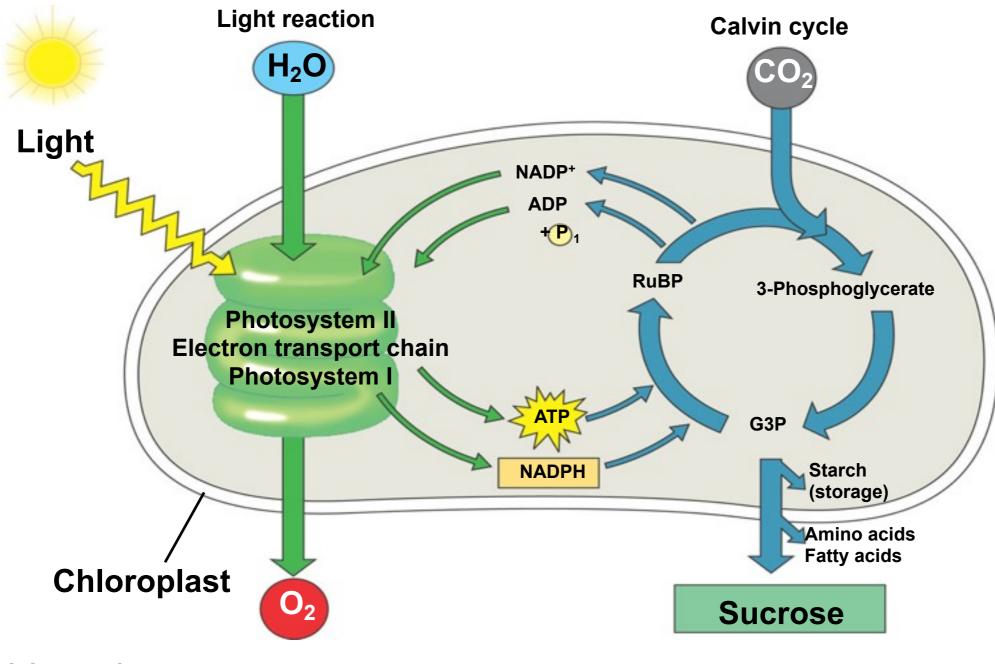
Water

Do you see it yet?

The more acids you can store at night, the more sugars you make in the day. To store more acids you need big vacuoles, the bigger the vacuoles the more water you have thus...thick, fleshy anatomy

Tuesday, January 22, 2013

Photosynthesis in Review



Light reactions:

- Are carried out by molecules in the thylakoid membranes
- Convert light energy to the chemical energy of ATP and NADPH
- Split H₂O and release O₂ to the atmosphere

Calvin cycle reactions:

- Take place in the stroma
- Use ATP and NADPH to convert CO_2 to the sugar G3P
- Return ADP, inorganic phosphate, and NADP+ to the light reactions

Importance of Photosynthesis

- 100% of the sugar made by photosynthesis provides the entire plant with carbon building blocks and energy.
- 50% of the sugar is used by the mitochondria for fuel.
 - Sugar leaves the "photosynthetic cells" as sucrose, the other cells use this for energy or to build a variety of other molecules
- Most plants, most of the time produce more sugar than they use per day.
 - The sugar is stored in chloroplasts, roots, tubers, seeds and fruits.

Importance of Photosynthesis

- On a global scale photosynthesis is responsible for our oxygen rich atmosphere.
- Photosynthesis collectively produces 160 billion metric tons of carbohydrate per year.
 - mass equivalent to I 7 stacks of your textbook from here to the sun.
- No other chemical process on earth can match this output!
- No other chemical process is more important to the welfare of life on earth.