Photosynthesis

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There are many photosynthetic species, ranging in complexity from photosynthetic bacteria to plants. Bacteria do not have chloroplasts, of course, so they must use a single memnbrane to accomplish what eukaryotic photosynthesizers require doubly membrane-bounded organelles to do. Prokaryotic photosynthesis is therefore slightly different from eukaryotic photosynthesis. The latter is treated in this course.

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The major organ of photosynthesis in most plants is the leaf. The mesophyl layer of a leaf is made up of cells rich in chloroplasts, the organelles of photosynthesis. A chloroplast is bounded by two membranes. The inner membrane is highly elaborated, forming many disc-like sacs, called thylakoids, arranged in stacks called grana. The chloroplastic fluid outside of the thylakoids is called the stroma, whereas fluid enclosed by thlylakoids fills the thylakoid space.

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Though photosynthesis occurs as a complex set of chemical reactions, it can be summarized by a single (one-step) reaction equation:

$$6\ CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$

This summary reaction is the reverse of the summary reaction for the combustion of glucose (glycolysis and cellular respiration), illustrating the reciprocal relationship between these processes. In photosynthesis, water is both a reactant and a product, but more water is required than is produced. The oxygen produced by photosynthesis comes from water, whereas the oxygen in the glucose that is produced comes from carbon dioxide.

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Photosynthesis occurs entirely within a chloroplast. The overall process consists of two component processes:

- In the light-dependent reactions, photons are absorbed by chlorophyll and other pigment molecules, exciting their electrons. This leads to transfer of electrons along electron transport chains, and the harnessing of the energy released by electron transport allows for phosphorylation of ADP into ATP and for reduction of $NADP^+$ into $NADPH+H^+$. In the process, water provides a source for replacement of electrons and is converted into oxygen.
- In the Calvin cycle (or light-independent reactions), inorganic carbon (in carbon dioxide molecules) gets incorporated (or fixed) into the carbon skeletons of carbohydrate molecules that can then be used to form glucose or other organic molecules. The production of glucose from carbon dioxide is an endergonic process. The sources of energy to power the Calvin cycle are the ATP and the $NADPH+H^+$ that are produced in the light-dependent reactions.

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Light is electromagnetic radiation having both wavelike and particle-like properties. Electromagnetic radiation occurs as a spectrum, ranging from high-energy, short-wavelength gamma rays to low-energy, long-wavelength radio waves. Different types of electromagnectic radiation differ only in wavelength. The humanly visible spectrum is a tiny fraction of the overal spectrum. Wavelengths outside of that range do not cause the necessary intractions with our eyes for us to see those types of light. Photosynthetic organisms absorb light for photosynthesis, and that light also happens to be humanly visible.

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In addition to having wave-like properties, light has particle-like properties. Particles of light are called photons. When a photon encounters a material particle it can be transmitted (passed through the particle), reflected (bounced off), or absorbed by the particle. If a photon is absorbed, it ceases to exist, but the nergy is not destroyed. Substances that abosrb photons in the humanly visible range are called pigments. Chlorophyll is an example of a pigment. It apears green to humans, because white light (a mixture of all colors of light) that shines on a chloroplast gets depleted of its reddish and bluish photons (which are abosorbed), and the only photons reflected to our eyes are in the green range.

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An absorption spectrum is a plot of the absorbance of light by a pigment versus the wavelength of light. Each pigment absorbs well at only certain wavelengths. The pigments involved in photosynthesis (chlorophyll *a*, chlorophyll *b*, and carotenoids) absorb light well in the blue and red ranges, but do not absorb light well in the green range. Therefore, photosynthesis proceeds well when a plant is exposed to blue or red light, but not when it is exposed to green light only.

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A chlorophyll molecule consists of a light-absorbing head and a hydrocarbon tail. The non-polarity of the hydrocarbon tail allows the chlorophyll molecule to remain embedded in the phospholipid bilayer of the thylakoid membrane, where chlorophyll molecules function by absorbing photons.

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Ordinarily when a pigment absorbs a photon (destroys the photon), the release of energy formerly carried by that photon excites one of the electrons in that pigment, causing the electron to move to a higher atomic energy level. This is a highly unstable condition, so the electron immediately moves back to the lower energy level. This releases energy in the form of heat and in the form of a new photon that is created and emitted by the pigment. This is called fluorescence. A solution of chlorophyll molecules isolated from a plant will fluoresce when illuminated. But plants do not fluoresce (which would serve no purpose for photosynthesis), because the chlorophyll molecules in intact plants are complexted with proteins in specialized structures called photosystems. These photosystems allow the light energy to be harnessed for producing carbohydrates rather than being wasted in fluorescence.

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Each photosystem (of the millions that occur in the thylakoids) consists of a reaction center surrounded by several light-harvesting complexes. The light harvesting complexes contain a mixture of protein and pigment molecultes. If a photon strikes one of the pigment molecules in a light-harvesting complex, the excited pigment molecule will transfer the excitation to a nighboring pigment molecule via a mechanism called resonance energy transfer. Adjacent pigment molecules become sequentially excited until the excitation gets passed to chlorophyll that is part of the reaction center. When the chlorophyll in the reaction center becomes excited, its excited electron entirely leaves the chlorophyll and gets transferred to a molecule called the primary electron acceptor. This provides a source of high-energy electrons for the electron transport portion of the light-dependent reactions.

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There are two types of photosystems (II and I) that are linked by an electron-transport chain occurring between photosystem II (which operates first) and photosystem I. When the chlorophyll in the reaction center of photosystem II loses its electron (because of excitation) to the primary electron acceptor, that primary electron acceptor quickly passes that electron to the electron transort chain between the photosystems. The transfer of electrons along the chain powers oxidative phosphorylation (just as during cellular respiration in a mitochondrion) to produce ATP. Meanwhile, photons being absorbed by pigment molecules in the light-harvesting complexes of photosystem I will cause excitation of chlorophyll in photosystemI's own reaction center. This will cause transfer of an electron from the chlorophyll to the primary electron acceptor of photosystem I, which quickly passes the electron to a second electron transport chain. The second chain does not operate for oxidative phosphosylation. Instead, the electron is transferred along the second chain to $NADP^+$, reducing it to NADPH. The elctron removed from photosystem I is replaced by an electron traveling along the first chain from photosystem II to photosystem I. The electron originally lost from Photosystem II is replaced when photosystem II enzymatically splits water into oxygen, electrons, and protons. The oxygen is released as photosynthetic waste. The operation of both photosystems and both electron transport chains is called noncyclic electron flow. Electrons that are stripped from water get transferred to NADPH, and later (in the Calvin cycle), those electrons (along with protons) will be incorporated into a sugar molecule as hydrogen.

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The operation of the light reactions is schematized in cartoon form.

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Noncyclic electron flow produces ATP and NADPH in equal amounts for the Calvin cycle to use as a source of energy to make sugar. However, the Calvin cycle requires more ATP than NADPH. When NADPH builds up (making $NADP^+$ unavailable), the second electron transport chain in the light reactions shuts down (having no $NADP^+$ to which to pass electrons). This causs the electron from photosystem I to cycle back into the first chain, producing more ATP without producing NADPH. This is called cyclic electron flow. Photosystems switch back and forth between noncyclic and cyclic electron flow to produce the correct ratio of ATP to NADPH for the Calvin cycle to operate.

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The oxdative phosphorylation that occurs in a chloroplast for photosynthesis is just like the oxidative phosphorylation that occurs in a mitochrondrion for celluar respiration. In a mitochondrion, protons are pumped by the electron transport chain from the matrix, through the inner mitochondrial membrane, into the intermembrane space. The protons diffuse back into the matrix through ATP synthase to produce ATP. In a chloroplast, protons are pumped by the electron transport chain from the stroma, through the thylakoid membrane, into the thylakoid space. The protons diffuse back into the stroma through ATP synthase to produce ATP.

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The operation of the light-dependent reactions requires energy from photons to transfer electrons that are removed from water along electron transoprt chains to produce ATP and NADPH, both of which are required by the Calvin cycle.

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The purpose of the Calvin cycle is to incorporate carbon atoms from an inorganic source (carbon dioxide) into the carbon skeleton of an organic compound (sugar). This occurs in three phases:

- In carbon fixation, carbon dioxide is received by a carbon dioxide acceptor, ribulose bisphophate, to produce a six-carbon intermediate. This step is catalyzed by an enzyme called ribulose bisphophate carboxylase oxygenase (RuBisCO).
- In the reduction step, three-carbon intermediates (from the splitting of the six-carbon intermediate from the previous step) are reduced. This requires ATP and NADPH, and it produces three-carbon sugars (glyceraldehyde-3-phosphate, or G3P), some of which are taken out of the Calvin cycle to be made into glucose and other organic molecules.
- In the final step (regeneration of ribulose bisphosphate), some of the G3P from the second step is used to make more ribulose bisphospate, which can then receive carbon dioxide to continue the cycle. This final regeneration step also requires ATP.

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RuBisCO is able to attach either carbon dioxide or oxygen to ribulose bisphosphate. However, if oxygen is used, the compound that resuls cannot be used by the Calvin cycle, so it does not lead to sugar production. Instead, the plant must spend energy (in the form of ATP) to convert that compound back into ribulose bisphosphate. This wasteful incorporation of oxygen instead of carbon dioxide is called photorespiration. In the early history of photosynthesis, this was not much of a problem, because atmospheric oxygen levels were very low. Millions of years of photosynthesis dumped a huge amount of oxygen into the atmosphere, making photorespiration a problem. Eventually, some plants evolved mechanisms to get around the problem. In a C_4 plant, the fixation of carbon is separated from operation of the Calvin cycle by having carbon-fixation occur in a superficial layer of cells (mesophyl cells). The CO_2 is incorporated into an intermediate that travels to a deeper layer of cells (bundle sheath cells). The intermediate then releases the CO_2 to the bundle sheath cells where the CO_2 is used by the Calvin cycle to produce sugar. This avoids photorespiration, because the deep bundle sheath cells are shielded from oxygen by the superficial mesophyl cells.

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Whereas C_4 plants avoid photorespiration by spatially spearating carbon fixation from carbohydrate production, another group of plants avoid photorespiration by temporally separating carbon fixation from carbohydrate production. These plants are called CAM plants (short for crassulacean acid metabolism, named for the group of plants in which the process was discovered). A CAM plant opens its stomata only at night. This allows CO_2 to enter the mesophyl cells. Instead of being directly incorporated into the Calvin cycle, the CO_2 is incorpoated into organic acid molecules that accumulate overnight. At dawn, the stomata close (disallowing oxygen from entering) and sunlight powers the light-dependent reactions to produce ATP and NADPH for the Calvin cycle. The organic acid moleucles that accumulated overnight release the CO_2 to the Calvin cycle for production of sugar without costly photorespiration.

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Photosynthesis is schematically summarized.