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TREE PHOTOSYNTHESIS:

Advanced Tree Biology

(Part 1 of 3)

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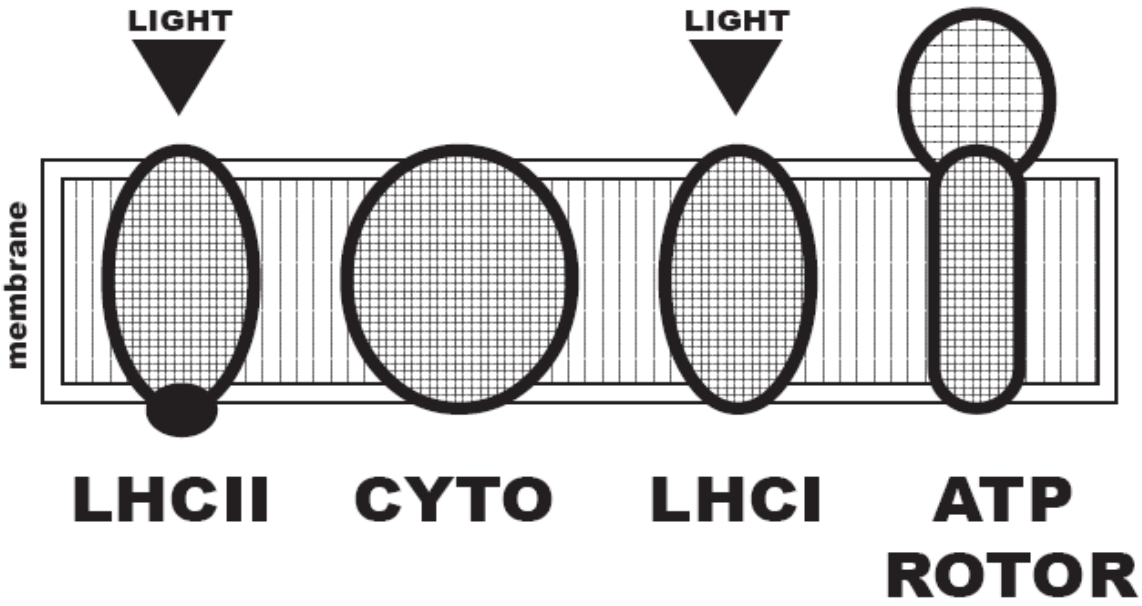

Scope & Disclaimer: This is part 1 of a three part training manual designed for helping advanced tree health care providers and senior community foresters appreciate and understand basic tree physiology -- specifically photosynthesis. This educational product is a synthesis and integration of current research and educational concepts regarding processes allowing trees to survive and thrive. This educational product is for awareness building and professional development at an advanced level. This product does not present detailed tree physiology in depth, nor with complete coverage of the subject. This training manual represents a simple, although strenuous, review drawn from key books and research papers on plant and tree biochemistry, functional physiology, and environmental interactions. This manual is meant as a knowledge foundation guide for understanding tree life.

At the time this third revision was finished, this training manual contained educational models concerning tree physiology thought by the author to provide the best means for considering fundamental tree health care issues surrounding photosynthesis. The University of Georgia, the Warnell School of Forestry & Natural Resources, and the author are not responsible for any errors, omissions, misinterpretations, or misapplications from this educational product. The author assumed professional users would have basic tree biology background. This product was not designed, nor is suited, for non-tree professionals or homeowner use. Always seek the advice and assistance of professional tree health care providers.

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Tree Photosynthesis:
Advanced Tree Biology (Part 1 of 3)

The basic functions of life require organisms to maintain a clear and distinct gradient between living tissue and the outside environment. This gradient is maintained by a water supply system (wet inside / dry outside) and an energy concentration system (energy dense inside / energy sparse outside). This wet energy environment inside is sustained by use of carbon – carbon dioxide (C-CO2) interchanges in an oxygenated space. This is how a tree makes a living.

Limitations

More than 98% of life on Earth depends upon a photosynthesis (Ps) process for survival. All life uses closely related respiration (Rs) processes to live. This part of the manual will concentrate completely upon photosynthesis in woody angiosperm and gymnosperm trees which build their lives by forming three carbon chains (C3 photosynthesis). There are other types of photosynthesis forms which are concentrated in monocots like grass (C4), and succulents like cactus (CAM). Perennial woody tree forms rarely utilize these other forms of photosynthesis.

This manual is a simple, abbreviated review of tree life processes, not technical physiology. Chemical names and notations have been distilled into simple forms and steps. Biochemistry and biophysics are not required here to understand the basics of tree biology. The purpose is to help professional tree health care providers appreciate and understand some of the intricacies, vulgarities, and wonders of tree life. Only tree photosynthesis (Ps) will be reviewed here. As such, this manual will follow carbon and energy manipulations for sustaining tree life.

Light Gathering!

Photosynthesis means "light construction." Photosynthesis is a multi-step process where light energy is used to weld carbon dioxide derived carbons together and bank protons (H^+). Oxygen is produced as a by-product from processing raw materials CO2 and H2O. The carbon containing materials produced comprise more than 99% of everything visible in a tree. These carbon strings are formed, transported and used within a mineral water bath inside living cells.

Most photosynthesis in trees occurs in leaves. Some photosynthesis does occur in leaf petioles, fruits, buds, flowers, twigs, branches, stems, and roots exposed to light. Tissues with green coloration can photosynthesize but may be limited by carbon dioxide (CO2) availability or by the quality and amount of light present. This non-leaf photosynthesis, partially uses CO2 respired (released) inside tree tissues thus recycling carbon.

As much as 50% of stem respired CO2 can be recaptured by photosynthetic tissues (i.e primary and secondary cortex, and non-functional phloem) around the outside of stems, branches, and twigs. In one species, less than 6% of total photosynthesis was from stem, branches, and twig tissues. Even leafless deciduous trees with green twigs under non-freezing conditions can generate significant amounts of carbohydrates.

Light Resources

Sunlight is the ultimate power source in trees. But not all light is usable in trees for sustaining life. Only a narrow band of light energy can be absorbed and converted into chemical energy. Figure 1 shows the spectrum of sunlight we can see, and among which are specific energies of light trees can use in photosynthesis. The shorter the wavelengths, the higher the frequency and the more energy light has as it impacts tree tissue. Beyond biologically useful light energy are x-rays of very shortwave radiation, and radio waves of very longwave radiation.

Sunlight (photons) of various energies stream down. Figure 2 shows the amount of sunlight striking the Earth's surface at each wavelength. The only light energy usable by trees for photosynthesis are in the blue and red areas of the visible spectrum. Most sunlight striking Earth's surface does not significantly impact tree growth except for changes in temperature (longwave radiation -- sensible heat) and damaging radiation (UV).

Blue or Red?

Sunlight strikes the Earth surface along a wide set of wavelengths or energies. Each packet of light (a photon) has an inherent energy level summarized as a wavelength number. Short wavelengths (more wave crests per time) have higher energy than longer wavelengths. Long wavelengths are toward the red end of the spectrum and shorter wavelengths are toward the blue end of the spectrum. The blue end of visible light (shorter wavelength) have more than 1.5 times more energy per photon than longer wavelength red light photons.

Process Equation

Photosynthesis, in the most simple terms, is using light energy to activate carbon in carbon dioxide (CO2) from the air to form sugar (a carbon chain), bank protons, and give off oxygen. This is all done within a mineral water bath where water also chemically participates in sugar synthesis.

A simple equation for photosynthesis is:

CO2	+	H2O	+	(light & chl)	=>	12C	+	O2	+	H+
carbon dioxide gas		water		chloroplasts in living cells		transport sugar		oxygen gas		proton

Clearly there are many complex steps required to complete this simple equation. In slightly more complex terms, the photosynthetic process in trees requires completion of six steps:

1) Water is pulled apart to generate electrons to energize, oxygen to release, and protons to bank.

2) Chlorophyll captures light energy of appropriate wavelength (energy) to energize electrons.

3) Energized electrons are used to transform electron transfer materials into a more energy concentrated state.

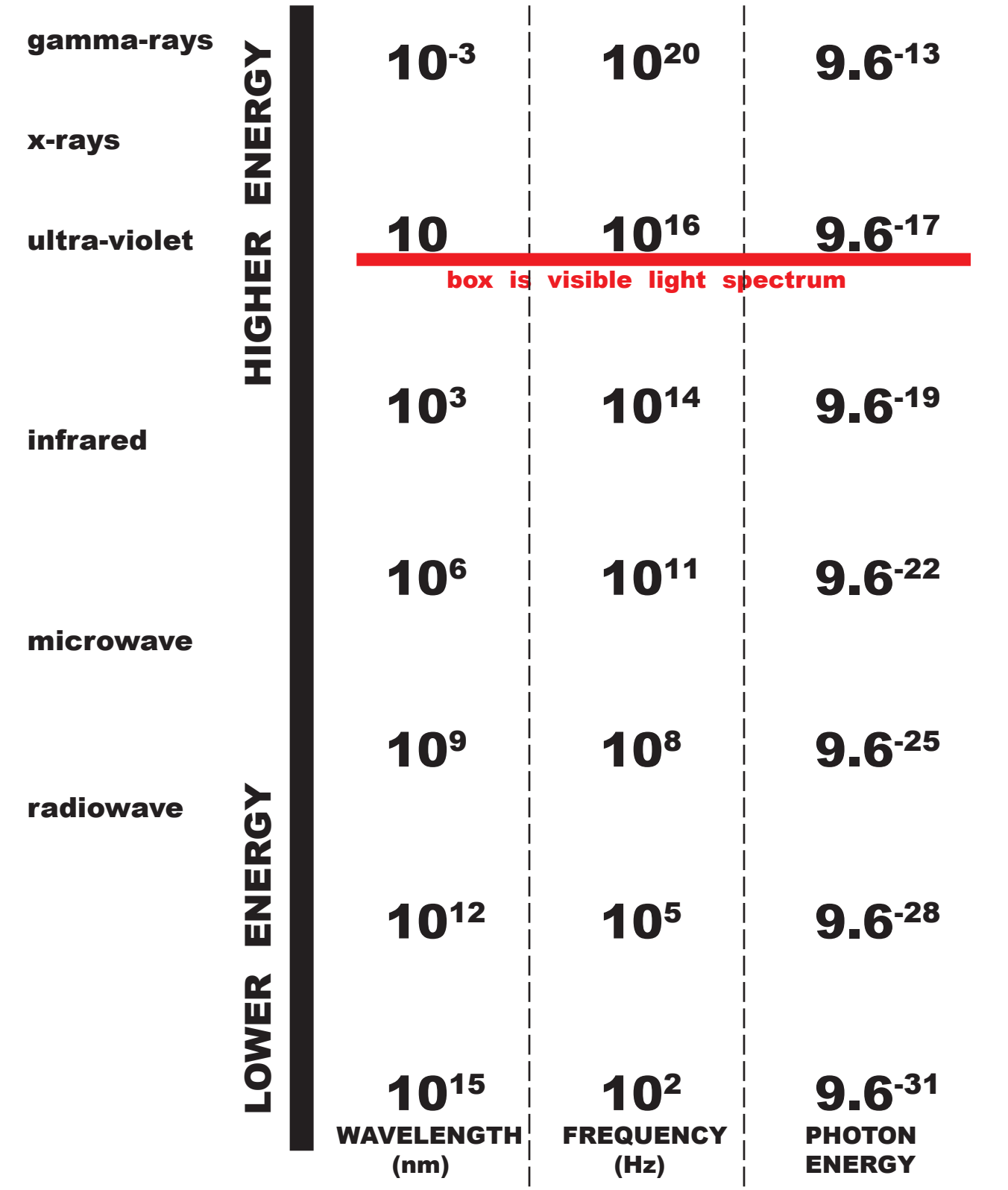


Figure 1: Light radiation wavelengths, frequencies, common names, and energy of one photon.
(modified from Taiz et.al. 2014)

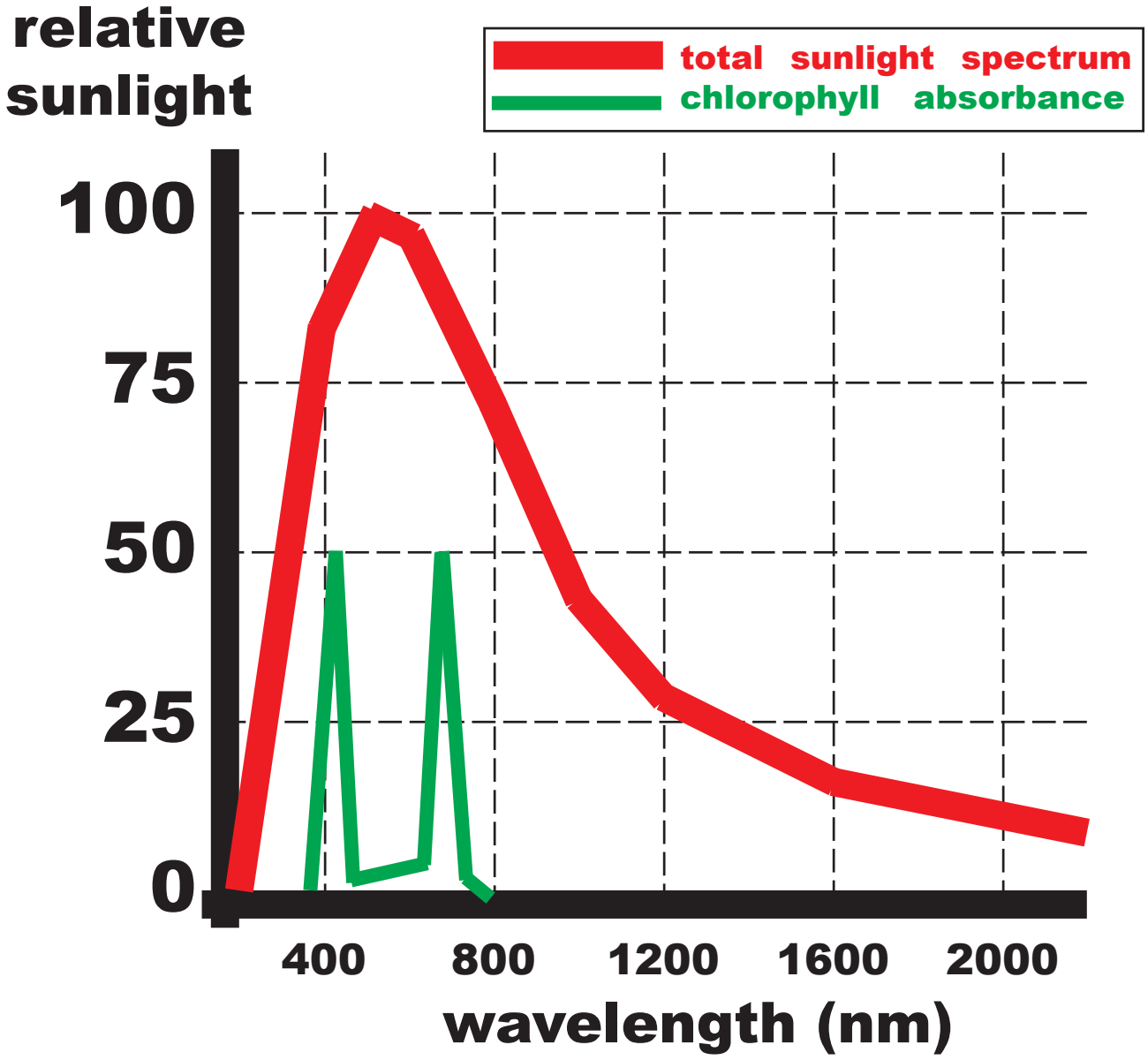


Figure 2: Relative amount of sunlight striking the soil surface by wavelength, and the absorbance of chlorophyll. General curve with no atmospheric absorbance shown. (from Taiz et.al. 2014)

4) Protons (H+) are concentrated by electron transfer and then allowed to escape generating chemical energy.

5) Chemical energy is used to strip carbons from carbon dioxide and string carbons together.

6) Carbohydrates are transported, stored, and/or processed, with additions of various elements and structural modifications, to generate proteins and lipids (and many other things).

In the above list, items 1-4 are light stealing steps occurring in and around chloroplast membranes. Steps 5-6 are part of carbon stealing steps which lead to construction of tree materials.

Light Chemistry

Photochemical reactions involve a photon of light crashing into organic material. The energy exchange in these collisions propel electrons into higher energy positions. These electrons fall back to the state they were in before the collision within a nano-second (10^{-9} second). This short amount of time is not sufficient for chemical reactions within a leaf to harvest energy from the collision. The fast return of an energized electron to its previous energy state can be accompanied by released energy dissipated as heat and/or generation of a photon of a longer (lower energy) wavelength called florescence.

Electrons are the currency of life. Electrons concentrated against an oxidative environment across a membrane defines life. Death is approaching an electron equilibrium with the environment. To gather electrons near an environmental average concentration means there can be no "profit" to complete the work of collection and to power life. If it costs 10 electrons to capture 9 electrons, life can not be sustained. For tree life, many electrons must be collected which are more highly energized than average. Photosynthesis is an electron pump, collecting and boosting electrons within a tree symplast.

Electron Envy

Inside a living tree cell there is a slight negative electrostatic charge (i.e. 100-400milli-volts). This charge is a result of a sharp electron gradient derived from concentrating electrons by photosynthesis. But, electrons can not exist in a free state within a cell. There is no electricity, nor wires to deliver it, within a tree. In order to use a high energy electron, its energy must be bled away in a stepwise fashion by the chemistry of a tree. But, a high energy electron can not be simply plucked from the air. One low energy electron must be boosted in association with another low energy electron being immediately moved in behind to fill the location vacated by the boosted electron. The newly boosted high energy electron must be immediately shifted away upon boosting (energy level elevation). One electron can not move into a place already occupied by an electron.

The plight of life is electrons must be available to be used, and most molecules do not easily give up electrons. Free electrons can not simply "float" around. Free electrons can not exist inside a cell without being encumbered. In photosynthesis, electrons are inserted into a chlorophyll gun which uses sunlight energy to fire an electron into a higher energy state. As soon as an electron is available, it must be used. Once it has been boosted to an elevated energy state, it must be quickly moved away along a series of transport molecules to prevent the boosted electron from falling back to where it was and giving up all its added energy as heat or as a photon (fluorescence).

Photostart

To start electrons moving in photosynthesis, electron ammunition is needed. In an electron barren environment (an oxidative environment), where can these be found? In tree photosynthesis, electrons are broken off of water molecules and move into molecules with electron openings. Electrons can not be stored or pile-up behind a bottle neck. Electrons can only be successfully transferred when they move into a space not occupied by another electron. That available space is made by moving the current electron out of the way in order for a new electron to move in, all within a pico-second (10^{-12} second).

Shifting electrons away in a chain of molecules is key to being able to bring a new high energy electron into the living system. This process is the basis of an electron transfer chain with electron events pushing forward, even though each transfer step loses a small amount of energy (biological friction). If a small amount of energy is lost in an electron transfer from one molecule to another, the electron can not go back without input of new energy. At tree growing temperatures, there is not enough energy to reverse transfers. All boosted electrons tumble forward losing energy in a chain of transfer materials.

H2O Divorce

Key to beginning the energy capture process is firing electrons to a high energy state. In order to have electron ammunition, free electrons must be generated. In photosynthesis, electrons are generated for use by splitting water. Water is split into its component parts including oxygen given off as gas, protons (H+), and electrons.

The process of splitting water to begin photosynthesis is one of the most difficult and unique in all life on Earth. Humans can split water into its component gasses with input of great amounts of energy. Trees accomplish this process of water decay, to a much greater extent and at room temperature. Trees use specialized machinery centered around a manganese-oxygen (Mn-O) lattice with a calcium (Ca) and chlorine (Cl) working site, all held within a special protein caldron. The manganese (Mn) atoms hold and forward electrons, and the calcium (Ca) / chlorine (Cl) site fabricates single oxygen atoms into a gas (O2).

Starting Line

To start photosynthesis in a tree, two water molecules (H2O + H2O) are split at the same time. This produces one molecule of oxygen (O2), four protons banked within the chloroplast, and four available electrons. This water splitting site (or oxygen generating site) acts as a bio-capacitor, briefly holding electrons. The four electrons are forwarded one at a time as ammunition into a chlorophyll boost gun called light harvesting center II (LHCII). Electrons are now available to be energized by light. One oxygen molecule (O2) is generated once every four times this chlorophyll system fires.

Chlorophyll Magic

Once electrons are available, they must be used immediately. Light energy is used to boost the energy level of these electrons. Trees use a complex photochemical system to boost electrons. The primary component in this process in a pigment called chlorophyll. Chlorophyll captures light of two narrow wavelengths and quickly transfers this light energy to electrons and then quickly onto surrounding materials.

Chlorophyll has a compound ring structure. Chlorophyll is a carbon matrix surrounding a magnesium (Mg) atom in a four nitrogen (N) setting. This chlorophyll "head" has many loosely bound and easily movable electrons. Chlorophylls have a long (21C) tail section which attaches chlorophylls in

place on the proteins and membranes of a chloroplast. The head is the functional component of a chlorophyll molecule and acts as an energy race track surrounding a magnesium atom. Figure 3.

Chloroplasts

Photosynthesis occurs within chloroplasts. Chloroplasts are specialized organelles inside a cell which contain photosynthetic machinery, raw materials, finished products, and a sharp pH gradient. Chloroplasts contain their own specialized DNA which is translated to control many parts of their structure and function, while cell nuclear DNA is translated to make a number of key enzymes and structural proteins. New developing chloroplasts (i.e. plastids) in angiosperm trees require light to initiate chlorophyll, while new chloroplasts in gymnosperm trees will generate chlorophyll without exposure to light. A chloroplast is essentially a self-contained organelle derived from free-living bacterial in the evolutionary past.

Reddish Blue / Bluish Red?

Chlorophyll absorbs light energy in very narrow wavelength zones. Light with too much energy (violet wavelengths and smaller) break chlorophyll apart. Light with too little energy (far red wavelengths and longer) can not activate chlorophyll and just generates heat in tissues. The wrong light means chlorophyll damage and repair is a continual chloroplast maintenance task. Chlorophyll is a big, breakable molecule which must be constantly maintained at great expense. As much as 30% of all energy captured by leaves is used to fix broken chlorophyll.

Chlorophyll has two absorption peaks. Figure 4. One peak is in the red area and one in the blue area of the visible spectrum. Blue area photons, because of their high energy, boost electrons in chlorophyll to an extremely high state. This extremely high energy state is unstable and electron energy quickly decays to a lower energy state. This lower energy state is still elevated from unenergized chlorophyll. As electrons fall back to a lower energy level, heat is usually given off. Figure 5. If chlorophyll absorbs a photon of light in the red zone, there is barely enough energy to elevate electrons into the lowest high energy state. Chlorophyll in this state is stable for several nanoseconds (10^{-9} second) and can pass energy onto surrounding materials.

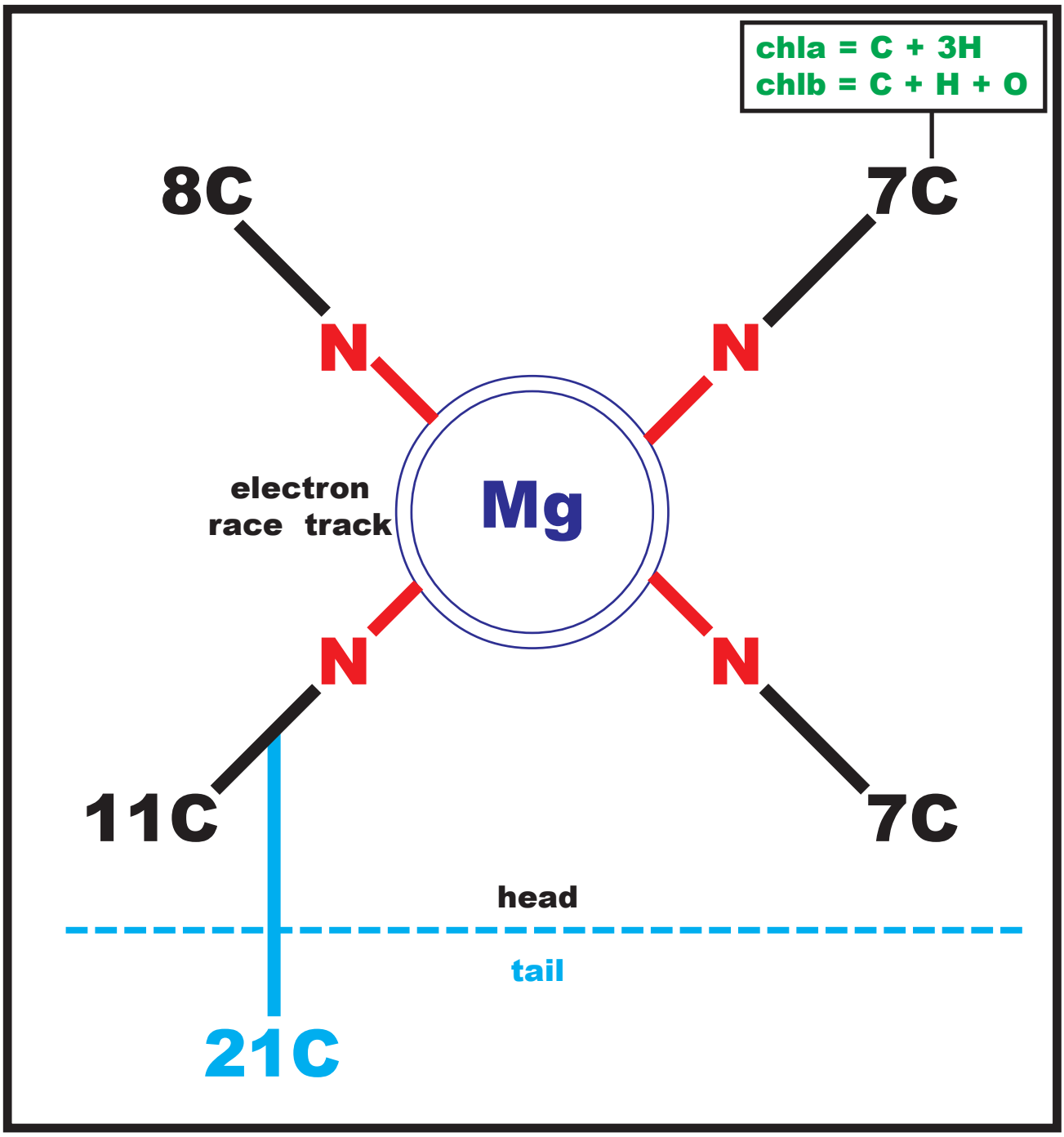
What To Do!

In an energized state, chlorophyll can do four things with captured energy:

1) emit a photon (fluoresce) at a longer wavelength;
2) loose all of its captured energy as heat;
3) transfer energy to any neighboring materials; or,
4) transfer energy to neighboring materials which capture part of the energy chemically.

The first three processes are relatively slow while the fourth photochemical process is much faster (by a factor of 1000X). The preferred flow of photon energy capture by chlorophyll is toward the ultra-fast photochemical capture of energy.

If a photon in the red light zone (680nm wavelength) is absorbed, and the relative energy gained is set to 100%, the amount of energy needed for photosynthesis in a tree is roughly 26.5% of that energy.



(33C in head; 21C in tail)

54C + 4N + 1Mg = chlorophyll a/b

Figure 3: General structure for chlorophyll.

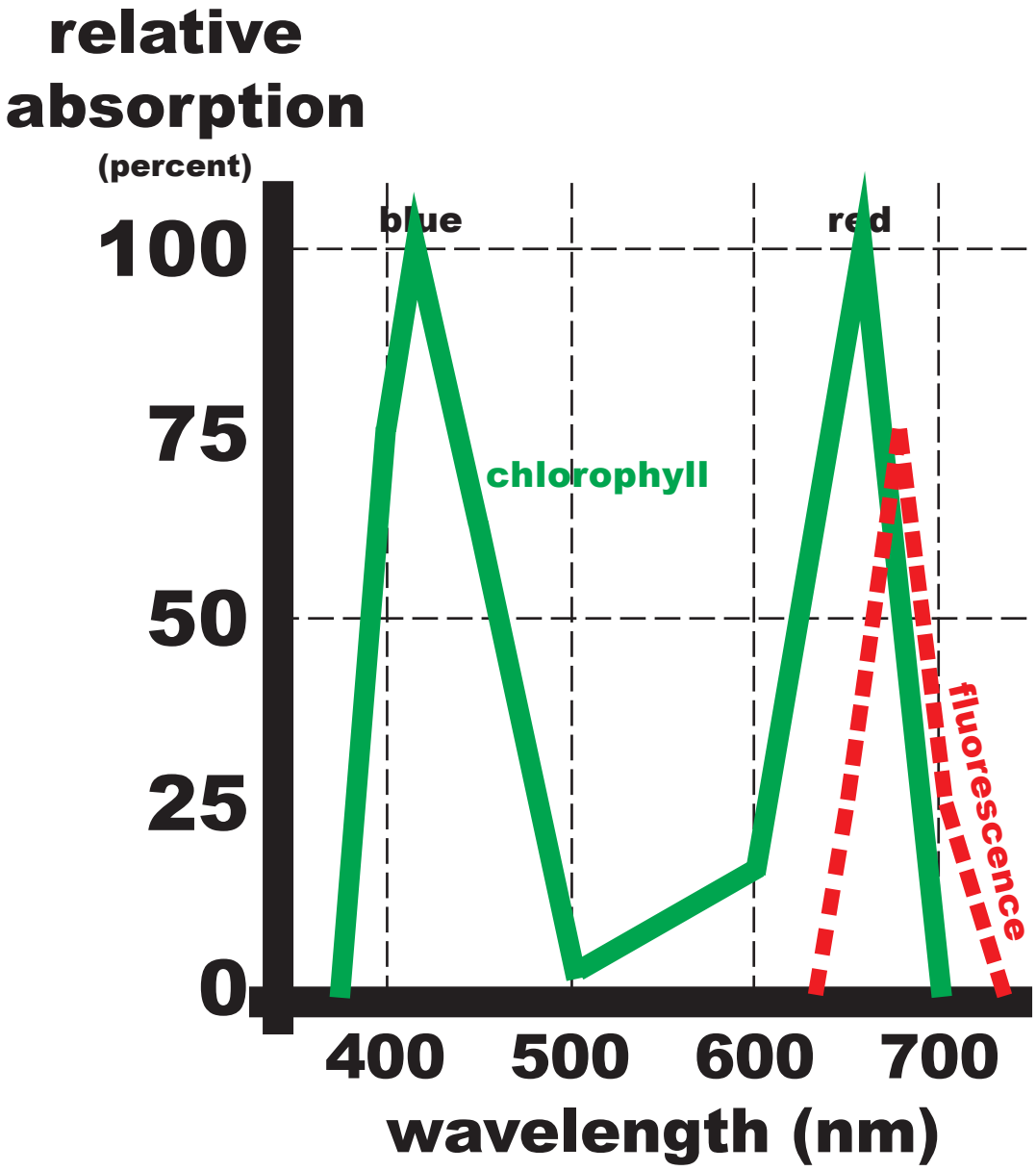


Figure 4: Simplified view of light wavelength absorbance by chlorophyll and its fluorescence.

(from Taiz et.al. 2014)

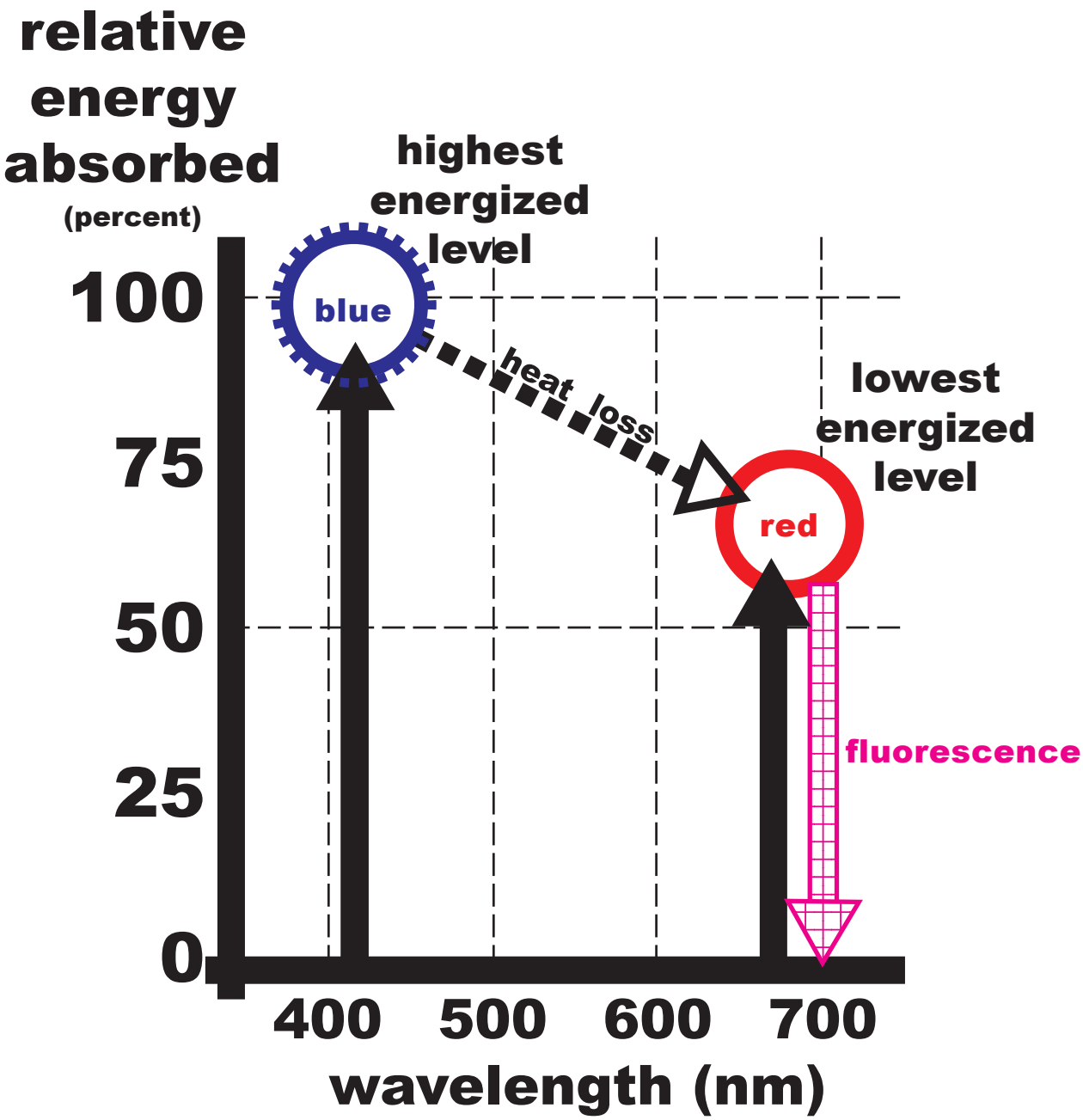


Figure 5: Simplified view of light energy absorbance by chlorophyll at its two absorbance peaks. The highest energized state is unstable and decays to the lowest energized state. (from Taiz et.al. 2014)

Efficient and effective light absorption in the proper wavelengths can provide more than enough energy for trees. The remaining energy will be lost as heat.

Collisions

For photon-electron collision energy to be captured, the electron boosted must be quickly transferred within a pico-second (10^{-12} second) to another slightly lower energy material. This material in turn, must quickly transfer that electron to another lower energy material, assuring a downhill electron flow which prevents any backward electron flow. An electron is boosted while it is prevented from returning to its base level through heat loss and fluorescence. In a tree, this photochemical energy concentration is accomplished through chlorophyll.

A's & B's

Chlorophyll comes in two almost identical forms, chlorophyll a (chla) and chlorophyll b (chlb). Trees have both chlorophylls. The two forms of chlorophyll differ only in two hydrogens and one oxygen at one point opposite from the tail across the pigment's magnesium head. This subtle difference of 3 atoms out of 129 atoms, of which are all in the same configuration, changes the absorption of each chlorophyll slightly.

Chla (~85% of chlorophylls) is called the full sun chlorophyll, and chlb (~15% of chlorophylls) is called the shade chlorophyll. Both absorb light best in two wavelength areas, a blue light zone (420-450nm) and a red light zone (640-660nm). Both reflect light which falls in the center of the visible spectrum light zone (500-600nm or green light zone). Chlorophyll is green colored to our eyes and absorbs light in the blue and red zones. Figure 6.

Selective Filter

As chlorophyll absorbs sunlight, it acts as a filter removing blue and red light wavelengths while passing or reflecting the rest of the spectrum. If chla filters out all usable light, then what will lower positioned chlorophylls and leaves use? Chla captures only a tiny amount of light energy at very narrow wavelength peaks. Much usable energy still remains. Chlb absorbs at slightly different wavelength peaks than chla to avoid self shading effects. Chlb absorbs at slightly longer wavelengths in the blue light zone and at slightly shorter wavelengths in the red light zone (i.e. more shaded conditions). Chlb absorbance peaks nestle just inside chla absorbance peaks by about 20nm.

Other Piggies

Several other pigments occur in the chloroplast. Most closely tied to chlorophyll areas are carotenoids (carotenes and xanthophylls). Carotenoids are 40 carbon long linear molecules with various endcaps. These pigments can have many different reflected colors, but tend to absorb light in the higher energy blue zone. Carotenoids are the original "blue blockers" and serve a chlorophyll protecting role. Figure 7 shows absorption of chlorophylls and carotenoids in a tree. Some types of carotenes can also absorb and transfer captured light energy to neighboring chlorophylls. Carotenes extend the absorbance range of chlorophyll into the blue range where chlorophyll can be unstable.

Carotenoids also help protect chlorophyll from damaging light (wrong wavelengths and too much) which super excites the chlorophyll molecule. Carotenoids dump this excess energy as heat. Some xanthophylls, a close chemical relative to carotenes, have a protective cycle in chloroplasts for

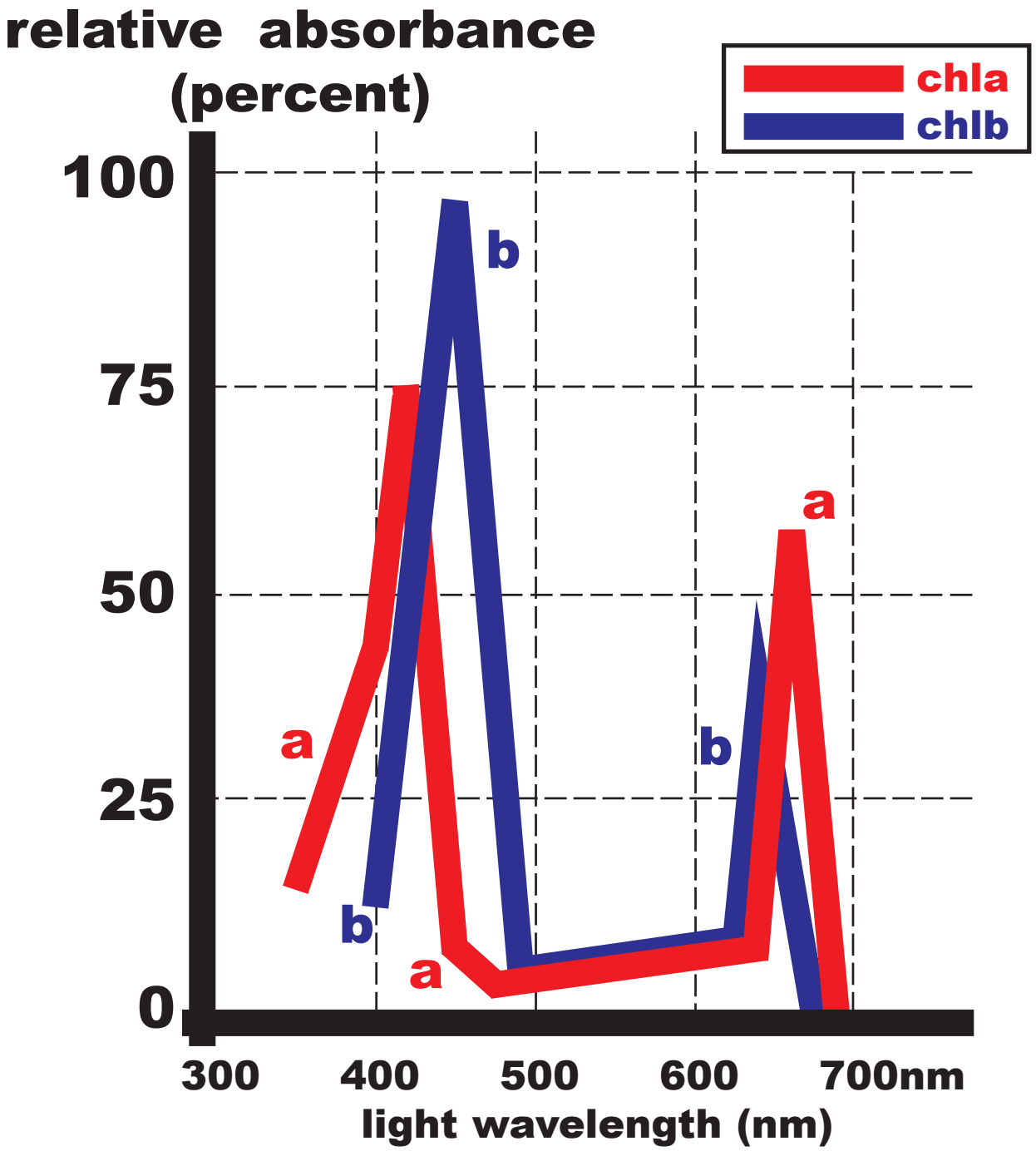


Figure 6: Relative absorbance values for chlorophyll a (chla -- full sun pigment), and for chlorophyll b (chlb -- shade pigment). Chla peaks = 420 & 660nm. Chlb peaks = 450 & 640nm. Average peak absorbances combined: chla = 65% & chlb = 68%.

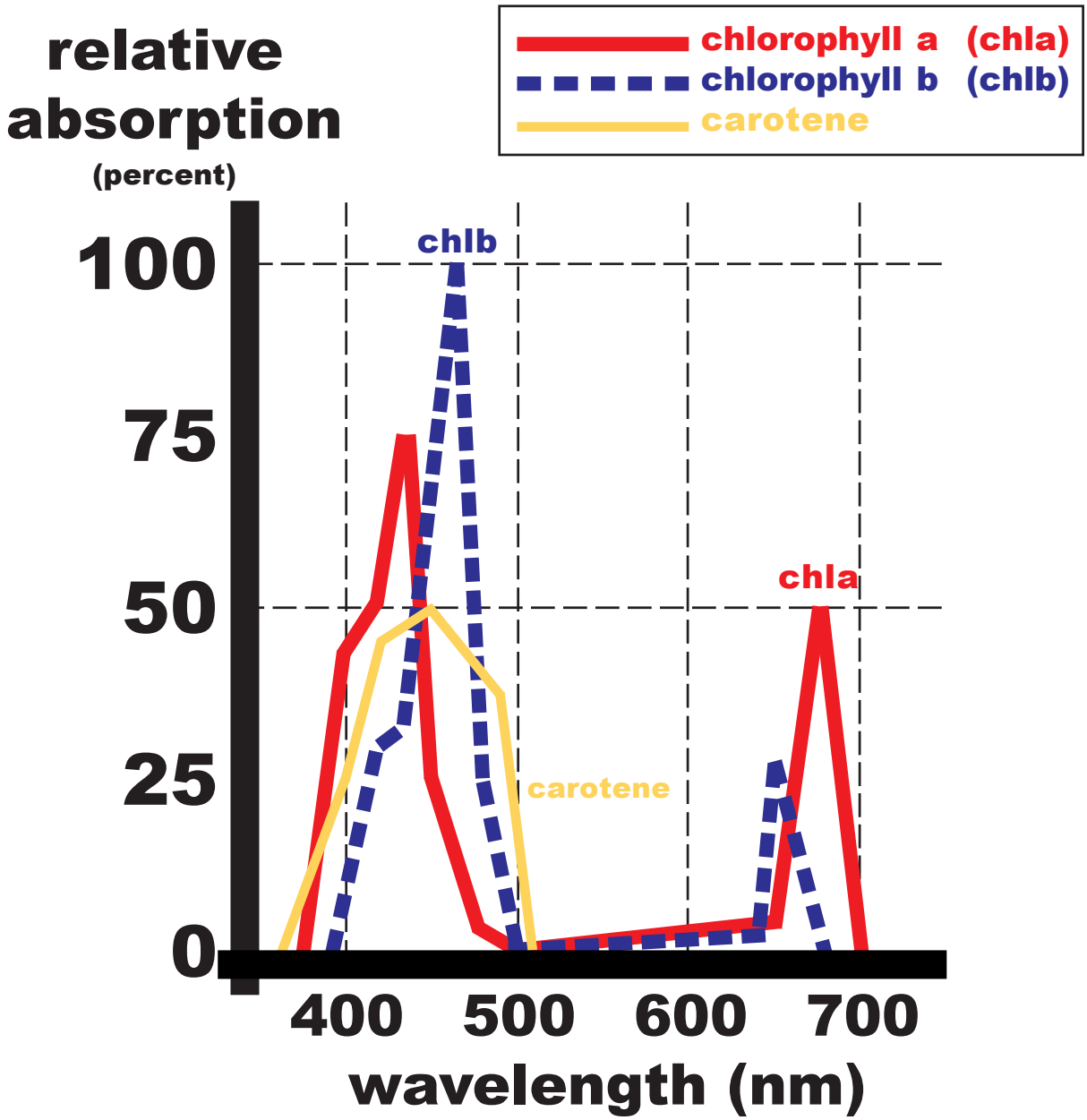


Figure 7: Simplified view of chlorophyll a, chlorophyll b, and carotene absorbance wavelengths. (from Taiz et.al. 2014)

blocking excess usable light and higher energy light from damaging chlorophyll. Xanthophylls funnel excess energy out of the light harvesting systems as heat.

A final pigment set which can color tree leaves in such intensity it shades out the green of chlorophyll, is anthocyanins. These water soluble pigments change color with changing cell pH and sugar content. Anthocyanins are not in the chloroplast, but are held within the central vacuole of a cell. The copper, bronze, red, and purple leaves of some trees are derived from anthocyanins in leaf cells. Anthocyanins block and filter light, protecting chlorophyll and cell materials (especially in new and senescing tissues), but do not participate in energy gathering.

Banging Around

As a photon of appropriate energy (wavelength) slams into a chlorophyll, the chlorophyll shifts its bonds making the area around the magnesium head center similar to an electron raceway or relay, quickly and easily allowing electron energy to transfer to surrounding materials. Energy captured by one chlorophyll is continually passed from one chlorophyll to another until the light energy can be harvested (i.e. an energized electron removed as chemical energy).

A single light harvesting antenna in a chloroplast is made of many chlorophylls and a few carotenoids all sunk into a membrane intertwined with an energy modifying protein. Only a few chlorophylls are involved with the final electron conversion to chemical energy. Most chlorophylls just move energy of a photon along to photosynthesis reaction centers. In these reaction centers, captured light energy is used to fire electrons into higher energy states, which then can be used by biological machinery. Within a tree leaf, photosynthesis is not limited by reaction centers firing electrons, but by having enough photon impacts (i.e. enough light) to keep the system energized. Many chlorophylls absorbing light are needed to keep a select few chlorophylls firing electrons for chemical energy capture.

Big Four!

The light reactions of photosynthesis are processed in four major protein complexes: light harvesting center II (LHCII), cytochrome (CYTO), light harvesting center I (LHCI), and ATP synthesis center. Figure 8 shows a portion of a chloroplast inner membrane and these four protein complexes. Remember these are not found in a one-to-one or side-by-side form. These independent complexes are designed to quickly separate charges (electrons) across membranes to prevent reverse reactions and conserve captured energy.

Antenna

Most chlorophylls and carotenes serve as an antenna or photon net. These nets are composed of arrays of 100-250 pigments which relay energy of photon absorption to reaction centers. Each chlorophyll only absorbs a few photons per second. The capacity of the photochemistry system is more than a million times greater than photons gathered by one chlorophyll. The fast photon absorption reactions from many chlorophylls are funneled to a small number of reaction center chlorophylls. The expensive photochemical machinery needs to be built, maintained and concentrated around only a few chlorophylls in order to capture sunlight energy efficiently.

As light is captured by one antenna chlorophyll, its energy gain is passed along by resonance from one molecule to the next. With each pass a small amount of energy is lost as heat. This assures energy initially captured can not move backwards but will always move energetically downhill to chlorophyll reaction centers. Figure 9 shows how energy transfers from pigment to pigment in the antenna by physical resonance. Energy is transferred eventually to the photosynthetic reaction center

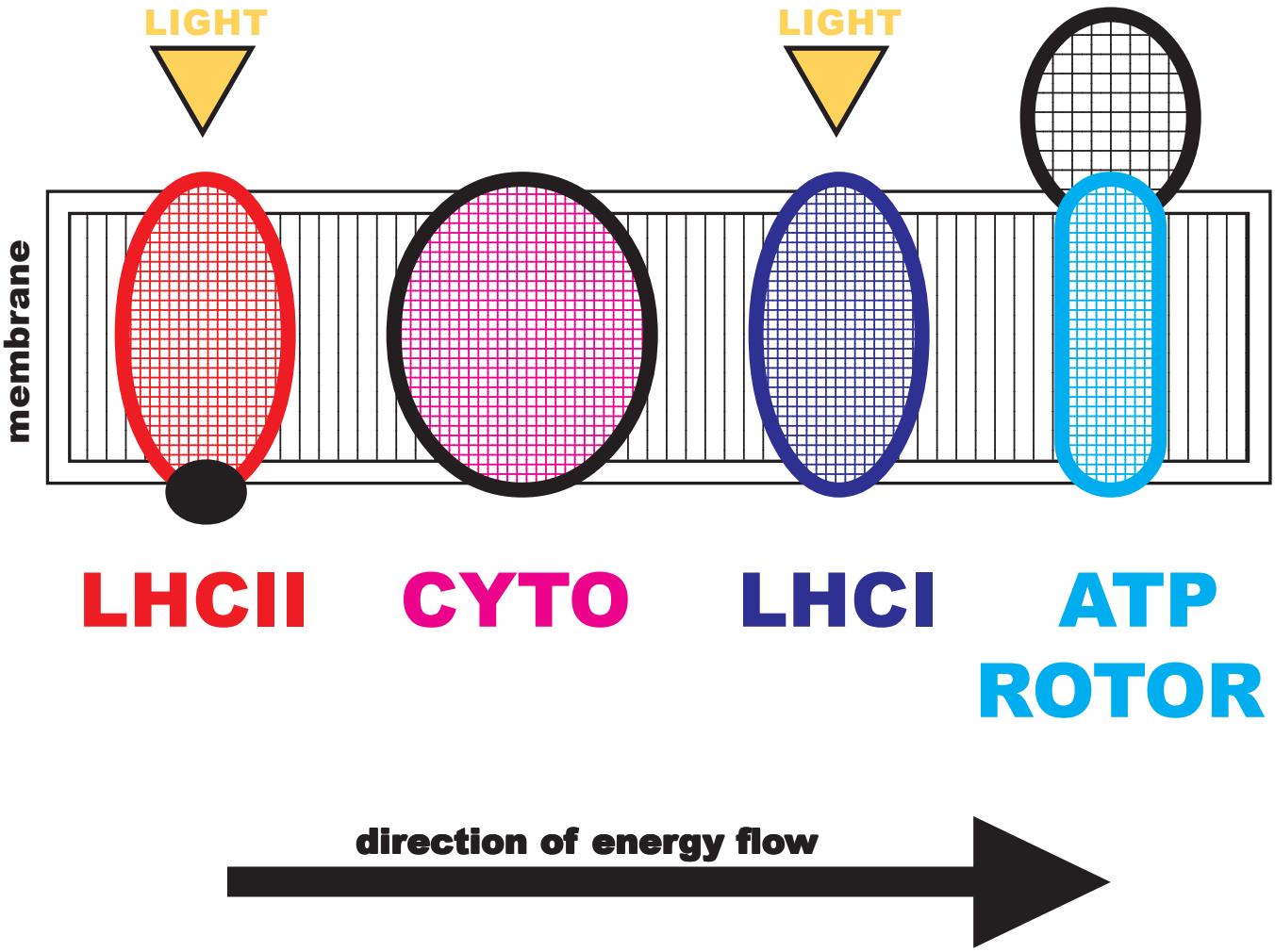


Figure 8: General diagram of the four protein complexes of photosynthesis in tree chloroplasts: LHCII, CYTO, LHCI, and the ATP production rotor. These complexes are physically seperate and independent of each other occurring scattered across chloroplast membrances.

(derived from Taiz et.al. 2014)

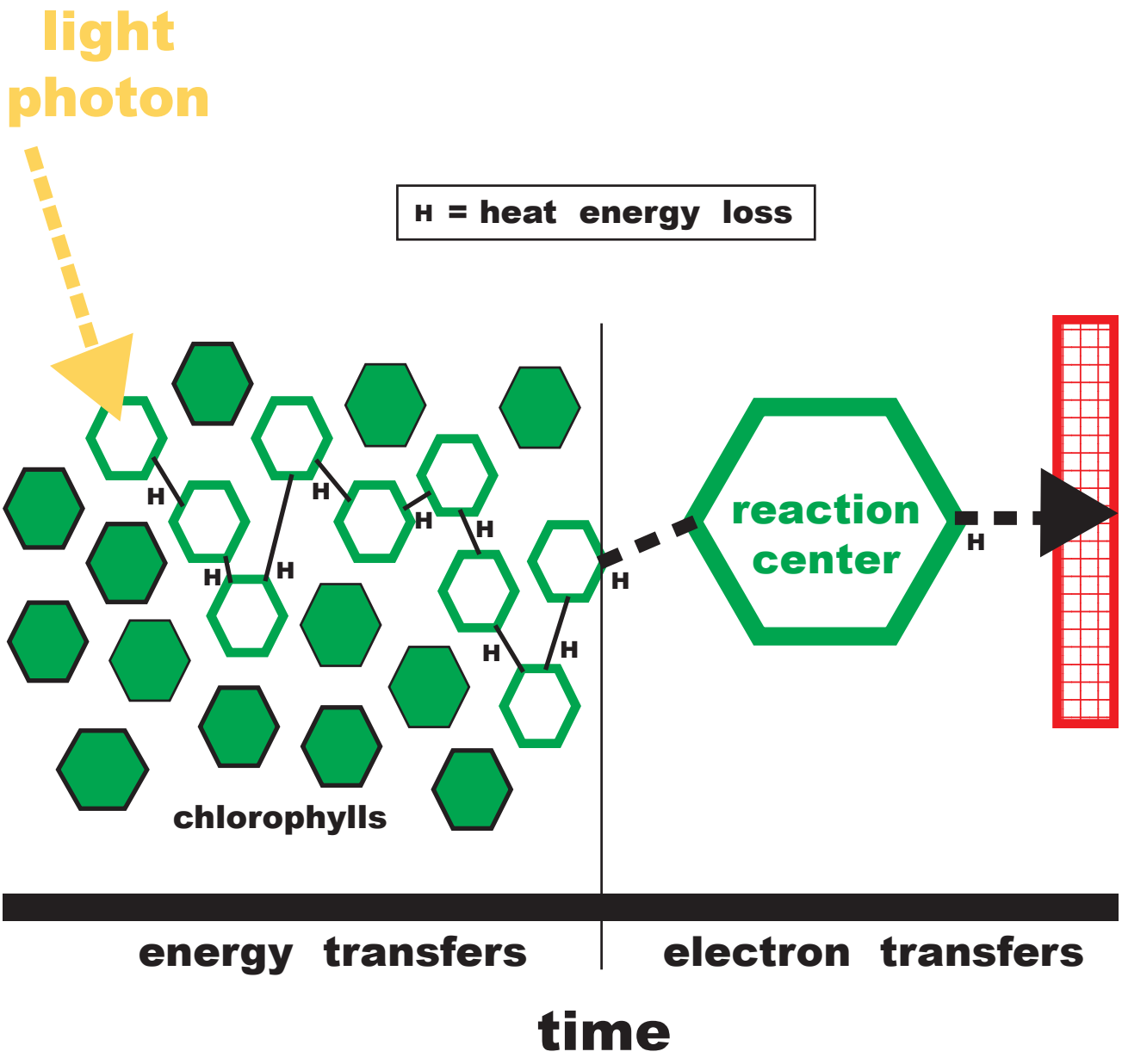


Figure 9: Light energy capture and energy transfer by resonance in chlorophyll antenna, and then electron transfer. (from Taiz et.al. 2014)

which fires an electron into the photochemical machinery. It takes roughly 2,500 chlorophyll molecules absorbing 10 usable photons in a tree leaf to generate one oxygen molecule (O2).

Light Harvesters

Chlorophylls must work together as a integrated unit. A free floating chlorophyll molecule has no place to dump energy and will generate damaging materials. Almost all chlorophylls are attached to a light harvesting center. A light harvesting center is a combination of pigments and proteins. One way to think about a light harvesting center is like many small bird feathers stuck into a mound of clay, where a feather represents chlorophyll and the clay represents protein enclosing the reaction center. Light harvesting centers collectively capture light and pass this energy onto the reaction center.

There is great debate regarding how many chlorophylls comprise each light harvesting center. The light harvesting center surrounding the P680 reaction center LHCII contains a major portion of a cell's chlorophyll (>50%) and protein. LHCII carries 8 chla, 6 chlb, 3 carotenes, and one xanthophyll. At its center are dual photosystem processors called the P680 reaction center (P680 = chlorophyll pigment with absorbance peak at 680nm).

In the light harvesting center for the P700 reaction center in LHCI, there are 56 to 93 chlorophylls with ~21% chlb and ~79% chla. With so many pigment molecules in a small LHCI complex, the absorbance is shifted more toward the red light wavelengths. Light with wavelengths up to 750nm can be captured and used to fire LHCI. At its center are dual photosystem processors called the P700 reaction center.

Distribution

Chlorophyll antennas are positioned in light harvesting centers which ride embedded in internal membranes of chloroplasts and stick out on each side. Each light harvesting center is found independently on the membranes and are surrounded by a variety of other processing machinery. Some parts of the chloroplast membrane are very dense with organized and stacked layers of light harvesting centers (primarily LHCII). The remainder of the inner membranes of chloroplasts are unstacked and loose, composed primarily of LHCI. A specialized electron transfer chain unit (a cytochrome unit) is found evenly distributed along chloroplast membranes. This cytochrome transfers electrons between light harvesting centers I and II.

Harvest Time

All chlorophyll and carotenoid molecules in a single light harvesting unit continue to funnel captured energy to two specific chlorophylls held tightly by their protein bindings. These special chlorophylls are key components of reaction centers. Chloroplasts in trees contain a host of both reactions center complexes for capturing light energy. The two reaction centers are labeled P700 and P680, for the dominant wavelength each absorbs. Remember LHCII (P680) is activated first and LHCI (P700) activates second. The numbering was derived by when each light harvesting center was discovered, not the order used in photosynthesis.

Separation

Light harvesting centers are not side-by-side. Each light harvesting center is separate and found in different spots on inner membranes of chloroplasts. These systems need to be separated in space to prevent short circuiting electron transfers. Figure 10. Each light harvesting center produces an energy

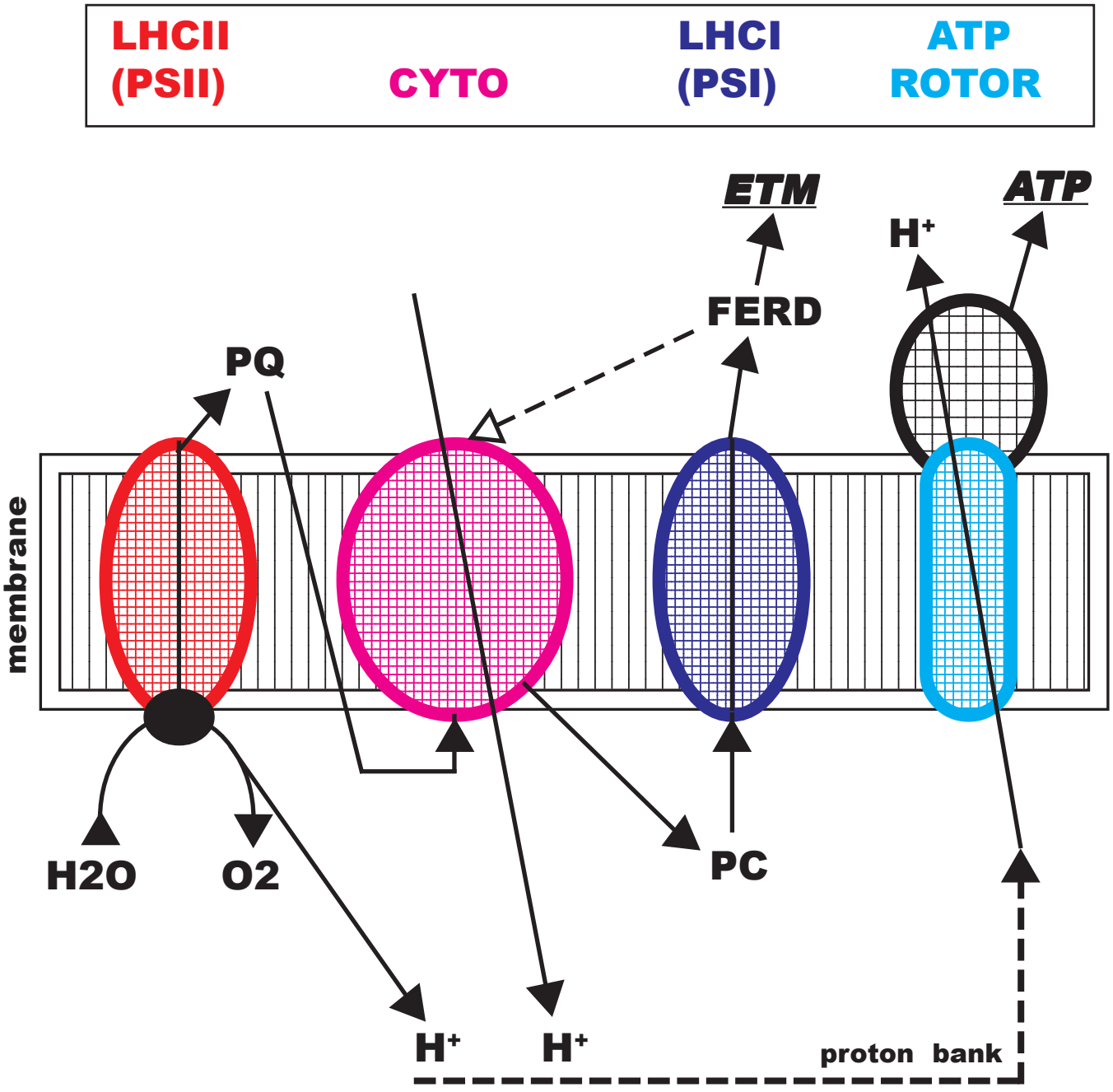


Figure 10: General diagram of input / output products as electrons flow through various components to yield ETM and ATP. (derived from Taiz et.al. 2014)

rich, diffusible material which moves throughout the chloroplast. For example, each LHCI averages 5 electron feeder units (PC) for assuring fast and continuous electron transfer.

A single LHCII is not matched with a single LHCI. LHCII continues to feed energized materials into a common pool. LHCI removes the energized materials from the pool. There is usually more LHCII units than LHCI units with a ratio of 3:2 to 2:1 respectively. This ratio is changed by the tree under different light conditions.

Going Low

Figure 11 graphically shows how light energy is captured and moved to a reaction center, where boosted electrons are used to modify materials. Note the wavelength (energy content) absorbed by different pigments assure a flow from higher to lower energy. Some energy is lost in transfer for each photon, but some energy from each is retained. For a living system in an oxidative environment, this is an efficient energy conserving process.

One or Two?

Conceivably, one short wavelength photon captured could deliver the total amount of energy needed for a tree in one strike. Unfortunately for these single high energy jumps, organic pigments would be constantly ripped apart requiring significant costs in maintenance and repair. Any energy captured in this one-step process would have to be great enough to more than account for all the inefficiencies occurring. One light capture event is not enough unless it is stable under higher energy / shorter wavelength light.

Trees use two light capture events to boost electrons to their final energy level. As electron energy is allowed to dissipate through various materials (called electron transfer chains), energy can either be converted to heat, transferred to a lower energy material, or escape as a photon (fluoresce). Only by quick transfer can energy be conserved for tree life. Two light harvesting centers are needed to both minimize maintenance expenditures and maximize electron movement from split water to electron transfer molecules (ETM).

Energy Bump

In order for cell machinery to function, energy must be captured and retained. One way this energy can be visualized is through measuring changing electron volts (free energy) of materials. When water is cut apart to yield electrons to boost, and oxygen gas is released, its costs (a loss of) about 0.4 e-volts. The electrons from the demise of water are passed to the P680 reaction center in LHCII. The reaction center uses light energy captured in its chlorophyll antenna to boost the energy level of these electrons. This first energy jump in the P680 reaction center increases energy to 2.0 e-volts. This increase in electron energy is quickly pulled away and allowed to partially (a loss of 1.4 e-volts) dissipate.

Electrons remaining after the fall from LHCII still are energized 0.6 e-volt greater than when they started. These elevated energy electrons can now be fed into the P700 reaction center in LHCI. Another light photon of the appropriate energy now boosts these electrons another 1.8 e-volts. Remember the LHCI functions at longer wavelength (lower energy) light. The total gain in energy has now been 2.4 e-volts since electrons from water was split-off. Figure 12.

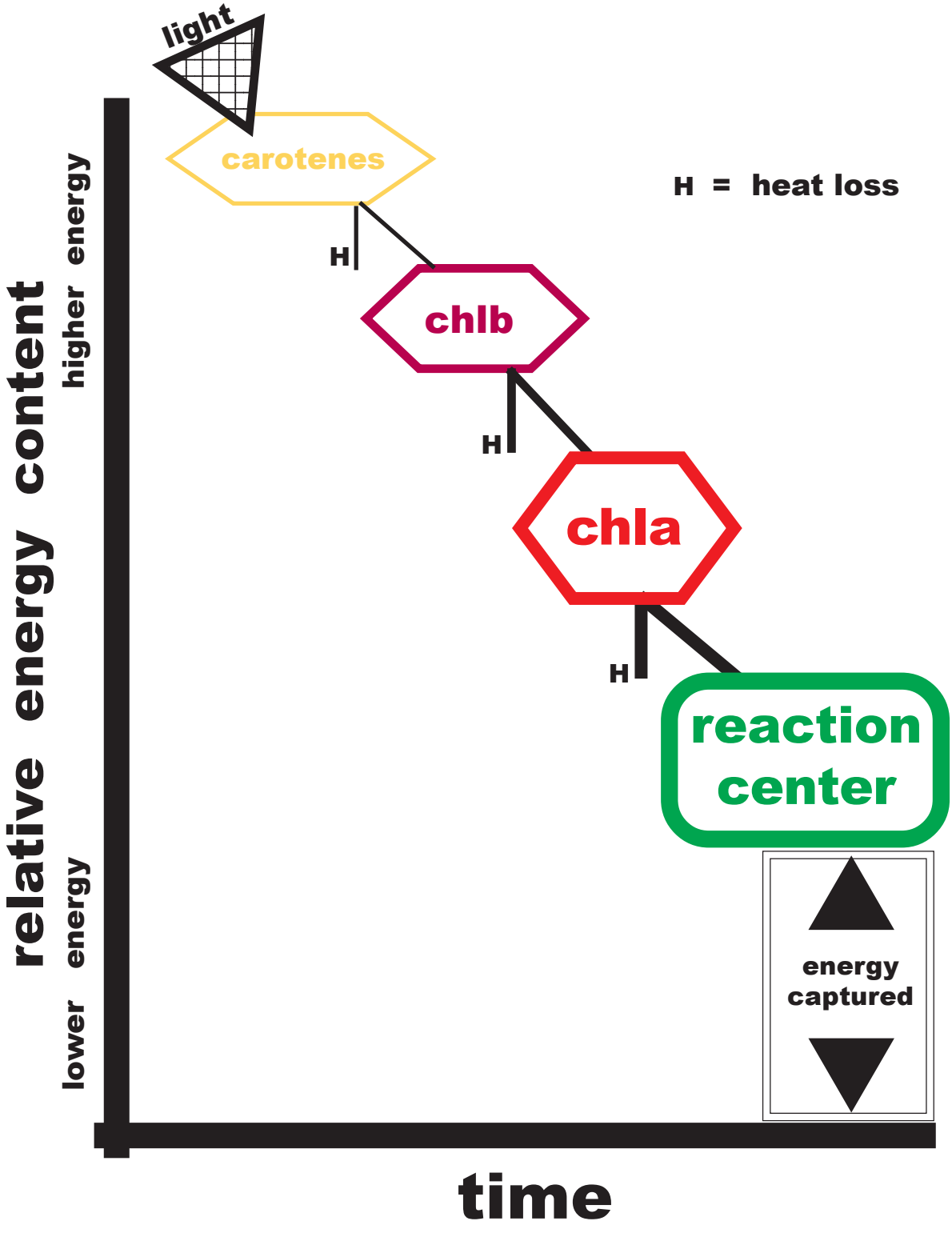


Figure 11: Transfer of light energy through various pigments in an antenna always transferring downslope in energy content with some energy loss by heat.

(from Taiz et.al. 2014)

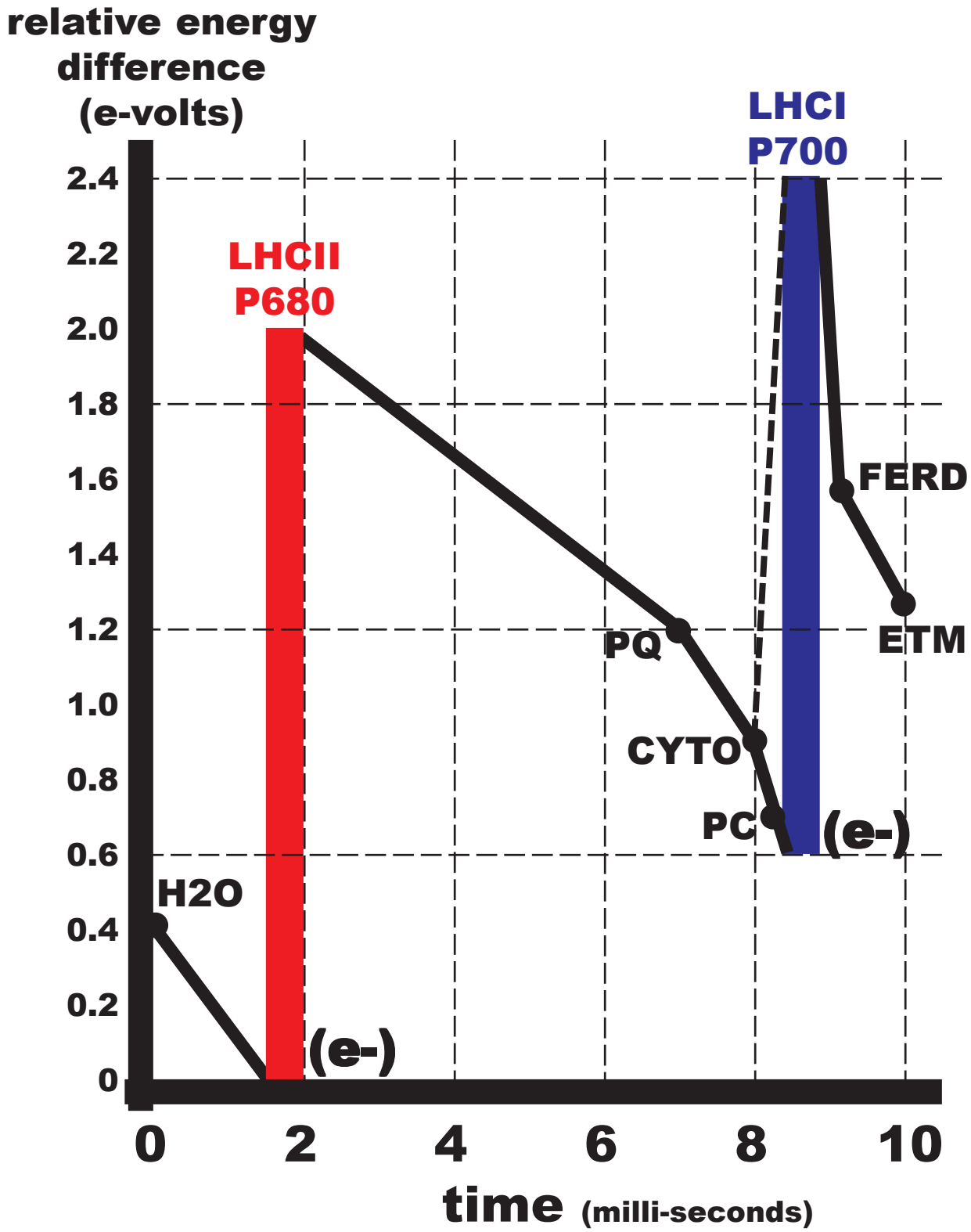


Figure 12: Energy capture sequence over time in tree photosynthesis using two chlorophyll reaction centers (P680 = LHCII; P700 = LHCI). N-scheme definitions in text.

Nnn Good

The N pattern (i.e. Z scheme or zig-zag pattern) made from diagramming both twin reaction centers boosting electrons to a total of 2.4 e-volts is the beginning of tree life energy. Everything now energetically flows downhill, back to the environmental base. Figure 13. A tree allows this energy drop to slowly occur through many specialized materials and process steps in order to power tree functions. The result is two captured energetic electrons sped away in under 8 micro-seconds with a portion of the original light energy. This energy can be allowed to trickle back out to the oxidative environment and propel tree life.

Between LHCII (reaction center P680) and LHCI (reaction center P700), electrons tumble down an energy gradient through an electron transfer chain. This chain represents electrons from LHCII changing the electronic states of materials which, in turn, change the electronic states of other materials and then return to their original base state. The bottom line is electrons are relayed through several different compounds to LHCI. It is possible electrons boosted by LHCII can trickle back to their ground state through a special cytochrome in order to provide relief under high electron concentrations.

Plasto-

The chain for electron transfer between LHCII and LHCI have three major players – plastoquinone (PQ), a cytochrome iron-sulfur complex (CYTO), and plastocyanin (PC). PQ accepts electrons from LHCII (Figure 14) and transfers them to CYTO, while banking protons. This transfer is the slowest (5X slower) of all electron transfers and can limit quick exchange between light harvesting centers. The pool of PQ in a chloroplast can build up or fall depending upon how well LHCII is working.

PQ passes electrons through CYTO. Figure 15. CYTO, a specialized cytochrome, governs electron flow between light harvesting centers. CYTO is a membrane bound complex evenly distributed along all inner chloroplast membranes. As electrons are passed through CYTO, four protons are banked for every two electrons transferred to PC molecules.

Electrons are next moved through PC. PC is a water soluble, copper-containing protein which feeds electrons quickly (10-20 microseconds) into LHCI. PC is chemically powerful but too large to power cell systems. PC easily gives up electrons (much easier than water) to LHCI (P700 reaction center). Figure 16. As electrons move through this electron transfer chain from LHCII to LHCI, a pH gradient builds (protons are concentrated) within chloroplasts.

Ferre-

Electrons boosted by LHCI can provide energy to two materials. The primary electron acceptor is a stable, small, water soluble iron-sulfur protein (which is actually fourth in line after reaction center P700 fires) called ferredoxin (FERD). Energizing FERD was the goal of all light processes of photosynthesis. Now FERD can power cellular work by energizing small electron transfer molecules (ETM). An ETM is a small molecule which easily passes throughout a cell to energize cellular mechanisms. ETM is used in fixing carbons from carbon dioxide into carbohydrates, and making cellular energy. In addition, FERD can be used to energize nitrate and sulphate for amino acid manufacture.

The secondary acceptor of electrons from LHCI, especially when too much energy is being generated, or if the FERD path is blocked, is back to the cytochrome complex (CYTO). This is called an electron cycle because the end product is not FERD, but a recycling of electrons into LHCI again while adding to the pH gradient (proton banking) developed within the chloroplast.

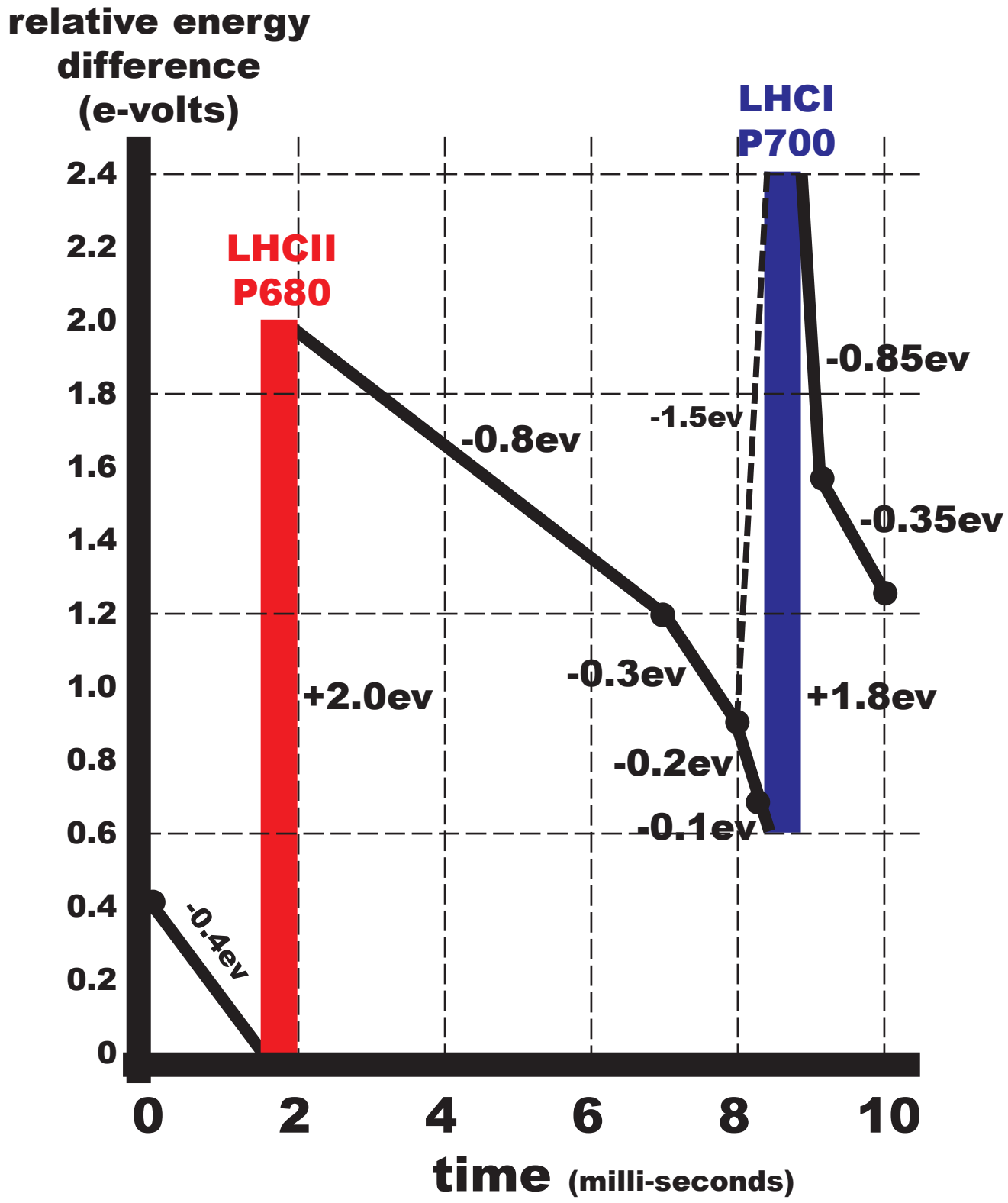


Figure 13: Energy captured and lost over time in the two reaction centers of the N-scheme.
Definition of terms in text.

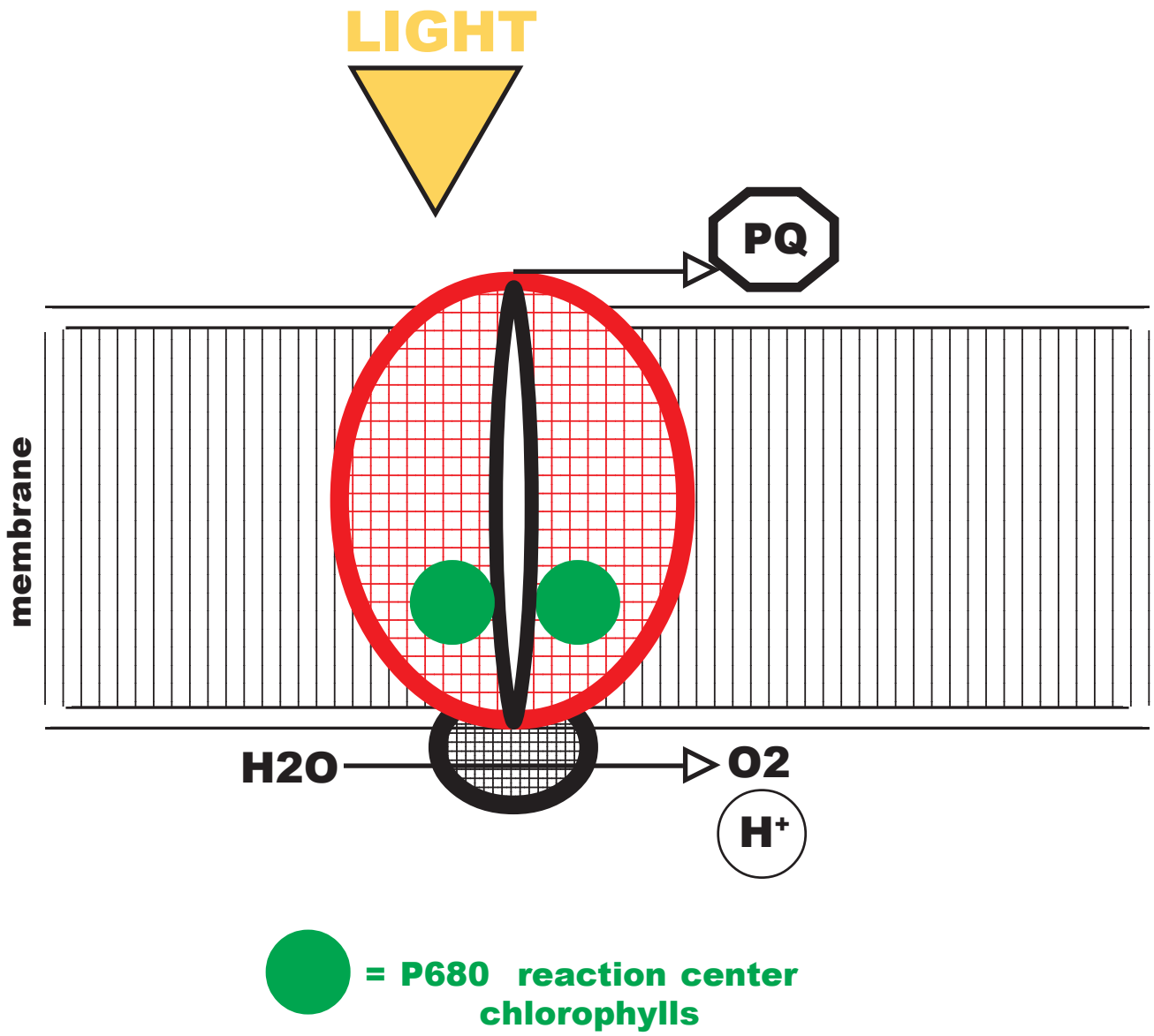


Figure 14: General diagram of light harvesting complex II (LHCII) with input / output products for electron transfer from split water to PQ, and proton banking. (derived from Taiz et.al. 2014)

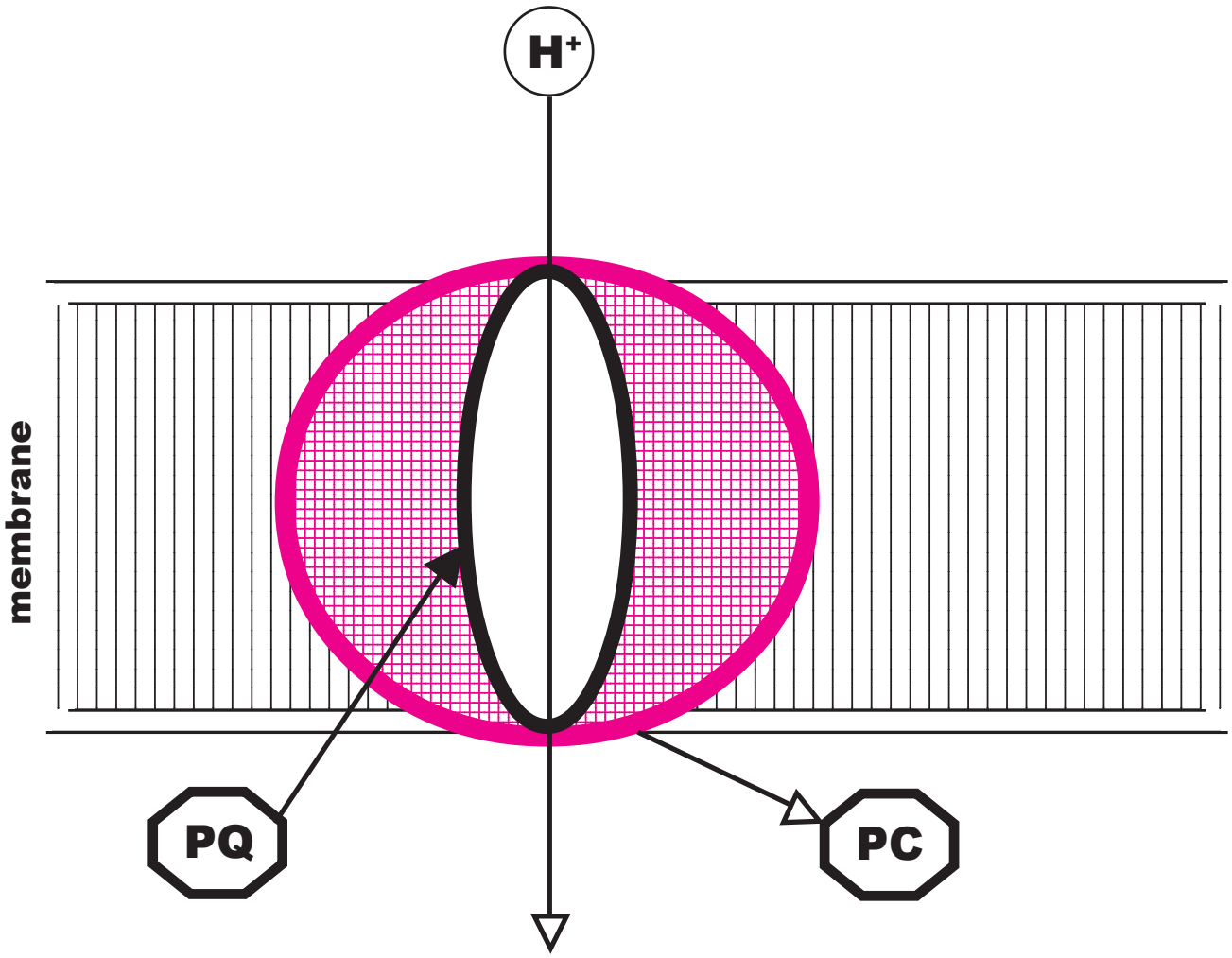


Figure 15: General diagram of CYTO (cytochrome b_6f) system with input / output products for electron transfer from PQ to PC, and proton banking.

(derived from Taiz et.al. 2014)

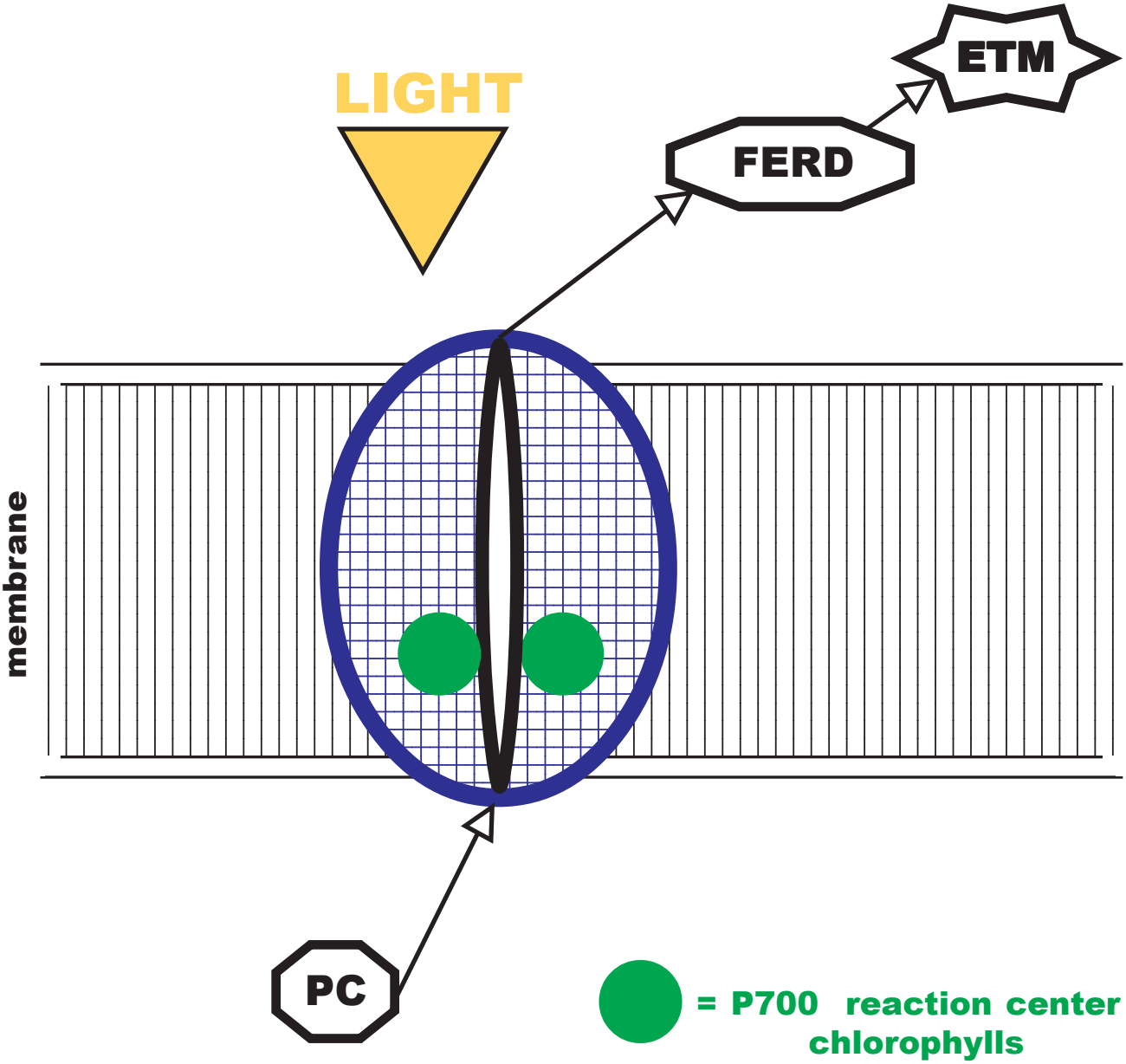


Figure 16: General diagram of light harvesting complex I (LHCI) with input / output products for electron transfer from PC to FERD. FERD energizes ETM. (derived from Taiz et.al. 2014)

Energy Bank

Within living tree cells, raw energy is a ephemeral thing. Electrons can not be held in a pool, but can be concentrated onto different materials. Inside a cell is an electron concentration zone. Outside a cell is an oxidative environment ready to steal any available electron. Within cells electrons can not be pooled, but their counterpart can be (i.e. protons (H^+)). Protons can be pooled, banked, and held for later use.

For example, the four electrons taken from two split water molecules generate four protons banked within the membrane of a chloroplast. In addition, as the four electrons from two split waters move through the electron transfer chain between LHCII and LHCI, 8 additional protons are banked. This concentration of protons generates a proton motive force which is tapped for work energy.

Banking means protons are held and concentrated behind membranes within chloroplasts. Energy of the proton gradient is focused in two forms. The first, and dominant form, is a pH gradient, as proton concentration is measured as a pH value. The second energy form is a gradient of electrostatic charge difference across the membrane measured in milli-volts due to concentration of positive charges of protons. Trees use these two types of potential energy gradients to make ATP.

ATP

Energy for cell functions come from an energized material called adenine triphosphate (ATP). This universal energy source is made in chloroplasts using a proton rotor (i.e. ATP synthase). The rotor complex has 21-24 parts including a magnesium atom. Protons are allowed to trickle through this membrane floating protein, pushed by the proton gradient. Protons rotate an ATP synthesis wheel. As protons move through the rotor, they rachet proteins forward one step in manufacturing ATP. Figure 17 shows a simplified ATP production rotor.

ATP is produced in light, with the process reversible in the dark if needed in order to sustain a proton gradient. It takes 4-5 protons to make and release one ATP. Because this process occurs in chloroplasts, and the proton motive force used is generated by light harvesting centers, it is called photophosphorylation. A similar, but not identical, proton motive force driven process occurs in mitochondria during respiration.

Energy Wages

Splitting two water molecules for their electrons to be piped through LHCII and LHCI generates 2 ETM and releases 12 protons. Approximately 1.5 ATP are produced per ETM. If all the ATP generated by photosynthesis are added up, there is not enough ATP to fix CO2 carbon. In order to generate more ATP, a tree uses cyclic photophosphorylation to bank more protons without making ETM. This ATP production process uses multiple LHCI firings to boost electrons and then cycle them back to CYTO to feed reaction center P700 again while banking protons for ATP production. In a limited way, LHCII can also cycle back electrons through a different cytochrome to bank protons and generate ATP.

Too Much!

Photosynthesis in trees is subject to many limitations. Limitation by too much light (full sunlight or greater than normal light due to site factors) is called “photoinhibition.” Most leaves are photoinhibited. Photosynthesis is also slowed or limited by many stresses other than light intensity. Non-optimal essential elements, water, and temperature all can limit photosynthesis.

Usually photoinhibition is caused by LHCII repeatedly firing in high light levels. If electron energy is not shifted away quickly, excess electrons are captured by single oxygen atoms which cause

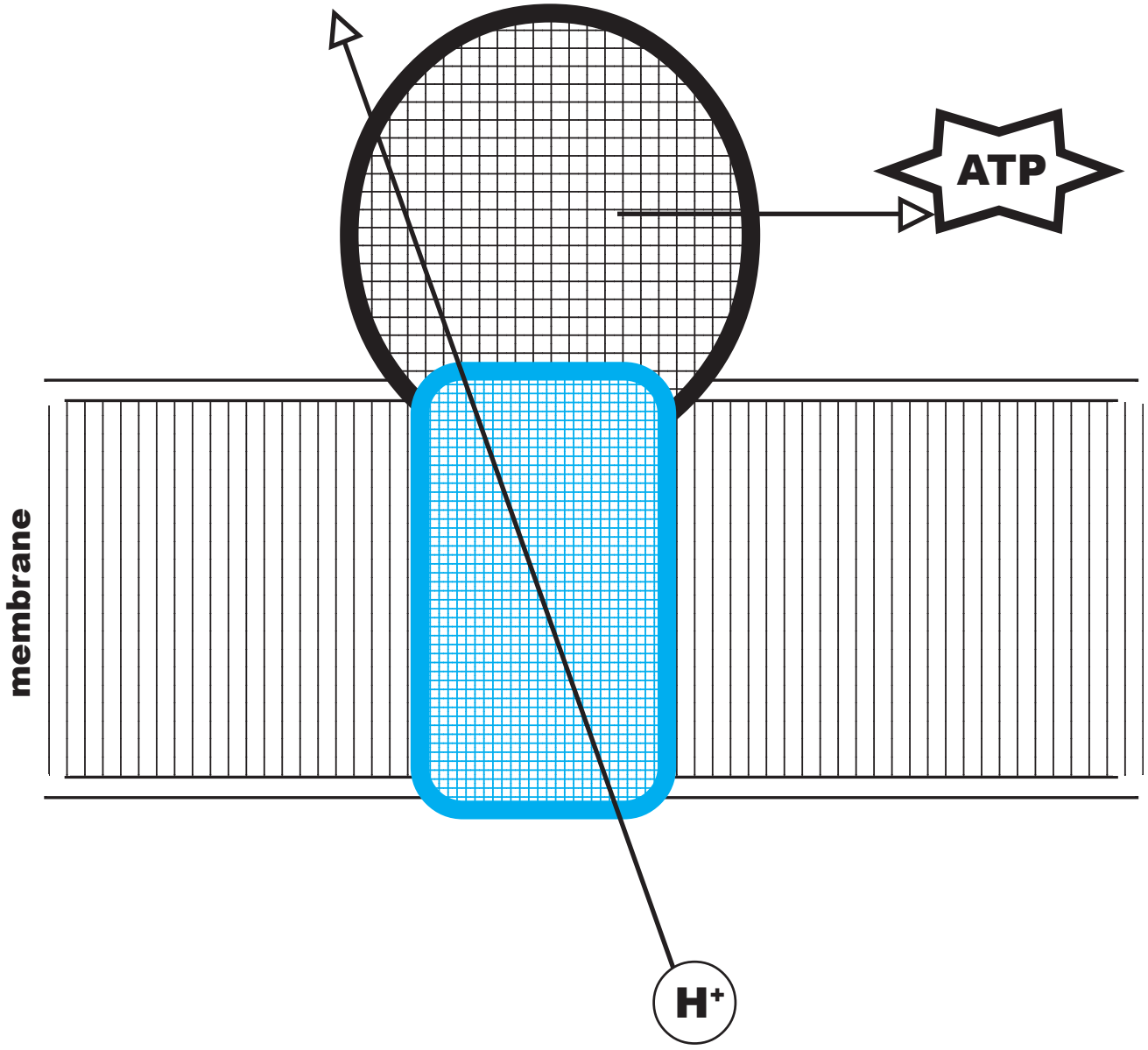


Figure 17: General diagram of ATP synthase with proton flow turning production rotor.

(derived from Taiz et.al. 2014)

severe damage to LHCII proteins and a poor connection to PQ which exasperates electron transfer problems further. A tree continually attempts to tear apart, repair, and reassemble this damage.

LHCI under high light intensities can handle more excess electrons because energy can be shifted in two directions, either recycling back through CYTO or pushed quickly into ETM. Any additional electrons not used immediately will charge oxygen and produce peroxides and other destructive ions which tear apart membranes. Other associated pigments and materials in chloroplasts are designed to quench excess energy.

Changing Leaves

Leaves develop photosynthetic systems carefully tuned for the light environment in which they grow. In some species, leaf preparation begins in the bud as the light environment is sensed. Shade tolerant trees, and trees grown in shade of other trees, can have photosynthetic machinery slowed or damaged by too much additional light. Trees develop two primary types of leaves, continuously change chlorophylls, and constantly shift light harvesting centers to assure photosynthesis is tuned to current light availability.

Leaf types developed to process various amounts and quality of light are termed sun leaves and shade leaves. Because of structural and photosynthetic differences, shade leaves placed into full sun quickly slow photosynthesis (photoinhibition). If returned to shaded conditions, leaves begin to recover. Sun leaves recover faster from light overexposure than shade leaves.

Protective Measures

For trees it is critical to keep both light harvesting centers functioning at the same level, where energy is not accumulated in excess around either. This regulation process includes coarse controls like venting energy away as heat, quenching damaging energy using carotenoids and special enzymes, and disassembly of damaged materials for reprocessing and repair.

Chloroplasts have several means of protection from over-excited chlorophylls. As chlorophylls are activated by excessive light, the photosynthetic system first attempts to push electrons more quickly into normal pathways. As these normal pathways flood with electrons, excess energy is allowed to quickly dissipate by conversion into heat or through fluorescence. Leaves will physically move chloroplasts closer to cell wall edges under excess light producing self shading within each cell. Leaves can also lower turgor pressure which causes drooping of leaf blades and petioles which change leaf orientation and decrease sunlight impacts.

Optimize!

The balance between the two light harvesting centers is important for proper electron processing and preventing buildup of damaging materials. There can be no “perfect” configuration of light harvesting center numbers and locations to optimize energy conservation. As sunlight during a day changes, from sun to cloud, and full sun to shade, coupled with resource limitations under drought or essential element shortages, each moment requires slightly different configurations of light harvesting centers. At highly variable light intensities and differing stress conditions, chloroplasts can change the ratio between LHCII and LHCI from between a 5:1 ratio down to 1:1.

On The PQ

One form of chloroplast optimization and control of electron movement between light harvesting centers is based upon PQ. PQ accumulation means LHCII is firing more than LHCI. With PQ

accumulation, a shift enzyme is activated which causes LHCII to shift outward away from light harvesting stacks which allows more excess energy to be expelled as heat and through fluorescence, as well as slowing LHCII firings.

The net result of moving LHCII out is proportionally more LHCI firing. If PQ is in short supply because LHCI is firing more than LHCII, the shift enzyme becomes inactive and LHCII migrates back to the concentrated stacks which accelerates LHCII firing. This optimization process occurs over a single day and over a growing season to maximize throughput of electrons and minimize excess energy damage.

Proton Excesses

Another optimization process in chloroplasts is tuned in by pH changes. At high light intensities, pH inside chloroplast membranes fall rapidly and cause protein changes which shutdown and protect photosynthetic machinery. A finely tuned energy quenching system is associated with xanthophyll pigments in LHCII. This is a photochemistry reaction control process similar to control rods in a nuclear reactor, quickening or slowing reactions.

As pH falls (i.e. more protons banked) the xanthophyll protection system is turned up. Low pH cause xanthophylls to change forms and slow associated LHCII. As pH climbs at night, the xanthophyll system reverses. Xanthophylls are essential to tree photosynthesis and life. As seen in laboratory mutations, trees without the xanthophyll protection system are only able to handle low light intensities under conditions of low or no oxygen.

Xan-Who?

There are many forms of xanthophyll pigments, which are oxygenated carotenes. Xanthophylls absorb light in wavelengths chlorophylls can not, and pass some energy to light harvesting centers. Xanthophylls primary role is to protect photosynthesis from overexposure to light. Xanthophylls act as filters of blue spectrum light (blue-blocker) and actively dissipate extra energy. Leaves in full sun usually have a significant amounts of xanthophyll pigments.

In trees, most xanthophyll in the morning is violaxanthin. As light intensity and ultraviolet light increases, violaxanthin (a light yellow colored pigment) is converted to antheraxanthin (a darker yellow colored pigment) which provides greater light screening and cell protection. As sunlight intensity peaks, zeaxanthin (an orange colored pigment) is generated from antheraxanthin providing even more protection for photosynthetic machinery. Lower pH (more protons) quickens the xanthophyll cycle toward zeaxanthin. Overnight most of the xanthophylls are converted back to violaxanthin. This progressive protective process is called the xanthophyll cycle. Figure 18.

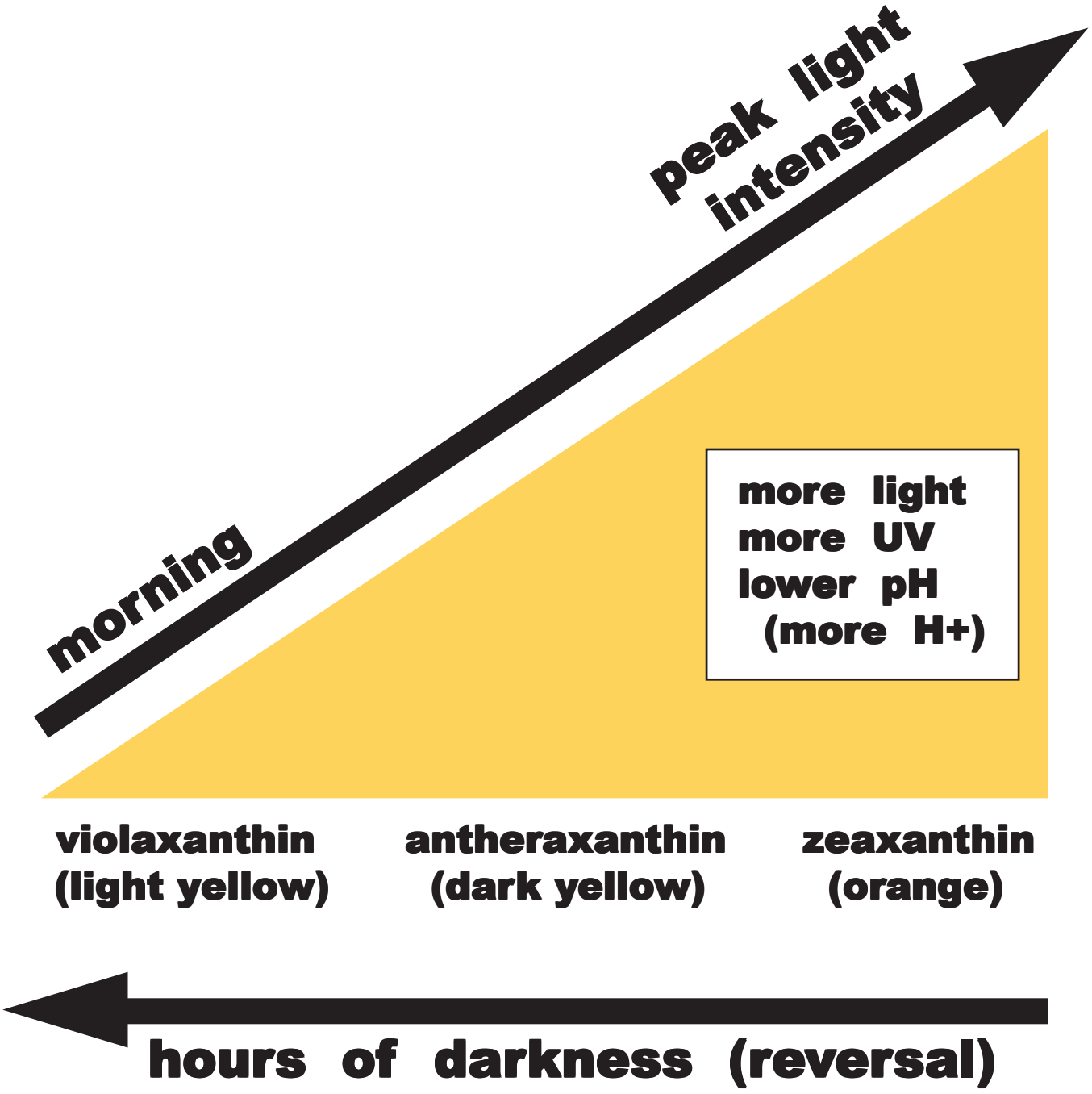


Figure 18: The xanthophyll cycle for photosynthetic system protection in a tree. Colored pigments of xanthophyll are converted to darker, more light blocking forms over a day and returned to their starting color overnight.

Carbon Grabbing !

Sunlight has now completed its energy supplying task in photosynthesis. Sunlight was needed to generate energy to be used to extract carbon (C) from carbon dioxide (CO2). Now carbons must be grabbed from air and strung together in a process called carbon fixation. Sunlight is still needed for carbon fixation because some enzymes and processing can only occur during daylight. A few secondary processes only occur at night. Figure 19.

The carbon fixation portion of photosynthesis will take carbon from carbon-dioxide and meld it into a carbohydrate (CHO). Most (80%) of a tree is carbohydrate. The rest of a tree comes from soil water (19%) and soil elements (1%). Carbon fixation in trees is accomplished through the Calvin cycle (i.e. Calvin-Benson or C3 cycle).

Counting Carbons

In order to follow processing of carbon, a special notation is used here. The two most critical elements in a tree is carbon and nitrogen. An accounting of both these elements must always be provided because they both require a tremendous amount of energy to secure. Phosphorus provides a way of changing shapes and activities of proteins, providing activation energy, and by acting as a "handle" to manipulate materials. Here phosphorus attachments will be denoted as an asterisk (*) along with the number of carbons and nitrogens present. An asterisk means a carbon compound has been energized. A plus sign (+) denotes a carbon compound energized by an electron transfer molecule (ETM). Figure 20 gives an example of this special accounting notation.

Basic "C"

This new notation is being used to simplify chemical processing. For most processes in a tree, biochemistry can be visually daunting with material names, reaction directions, and enzyme names. Here just the most basic names will be used and usually only carbon content will be given. As long as addition and subtraction, plus a little simple division, is used accurately, carbon and nitrogen flow in a tree can be appreciated and followed.

For example, Figure 21 shows three 6C materials (hexose sugars or sugars made of six carbons) which are continually transformed between each other based upon internal pool contents. For purpose here, it is not critical to know names, their interconversion process, or enzymes which manipulate them. To approach a basic understanding of tree physiology, this type of traditional chemistry notation and physiology sequencing is discarded. There are many fine textbooks covering at great depth plant and tree physiology and biochemistry which can be used to fill in details, if required.

Come On In

Outside a leaf, the atmosphere contains valuable carbon dioxide (CO2) in small amounts (0.033%). Gas exchange in a leaf occurs through stomates on the underside of broadleaf surfaces and along the length of needles. Figure 22 shows a diagrammatic view of the underside of a leaf with stomates in various stages of opening. Stomates open in the morning as guard cells sense light and swell. Water evaporates from wet surfaces of mesophyll cells lining the sub-stomatal cavity. Figure 23 shows a cross section of a sub-stomatal cavity on the underside of a tree leaf. Note how loosely packed mesophyll cells are compared to palisade cells.

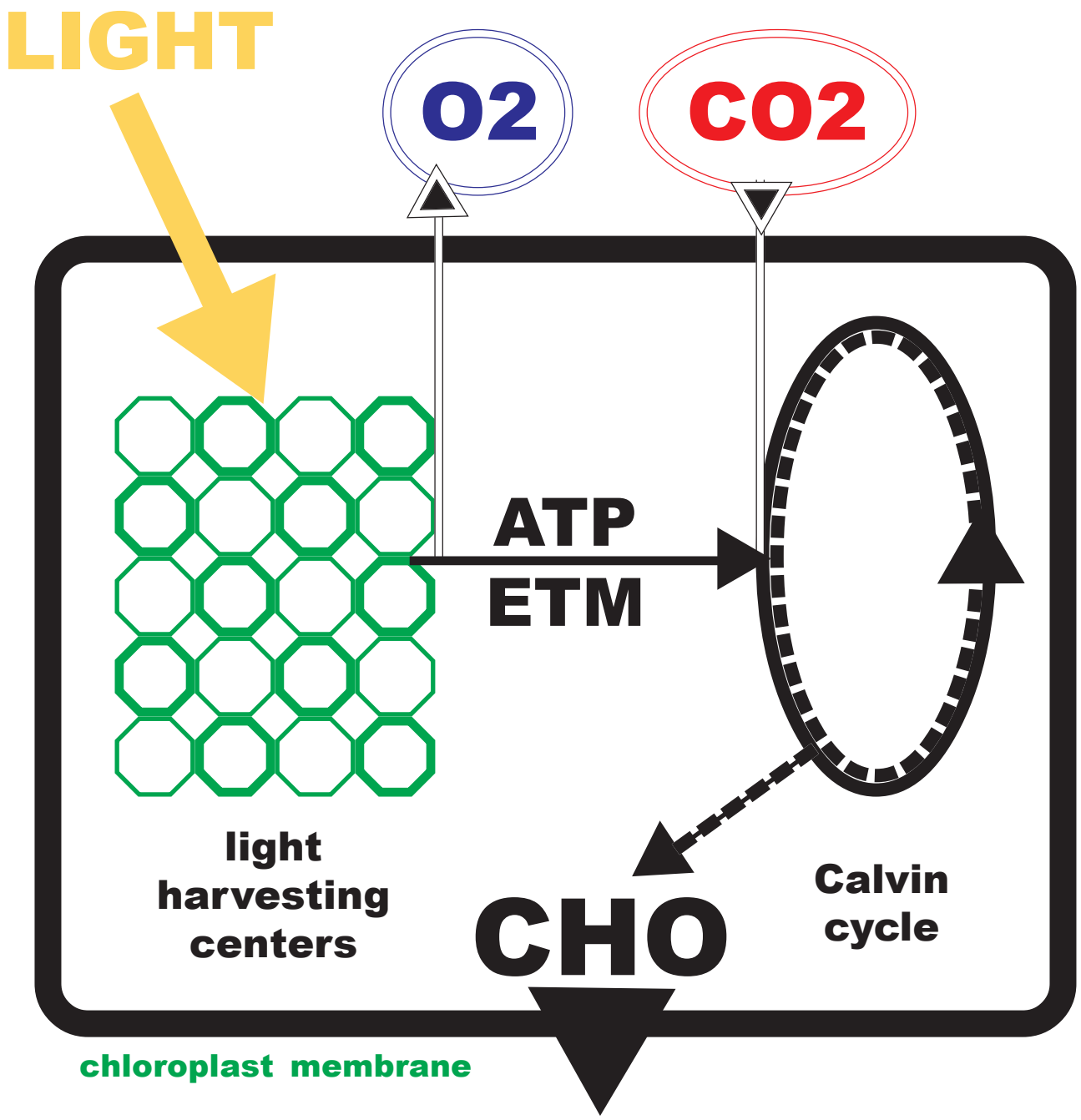


Figure 19: The light energy capture and the carbon fixation process inside a tree chlorplast.

(after Taiz et.al. 2014)

key

C	=	a single fixed carbon atom
2C	=	a pair of fixed carbon atoms
5C	=	a chain of five fixed carbon atoms
5C*	=	a chain of five fixed carbon atoms energized by an ATP
5C*+	=	a chain of five fixed carbon atoms energized by an ATP and by an ETM

addition

C	+	C		=	2C
C	+	C	+ C	=	3C
2C	+	3C		=	5C
2C*	+	3C		=	5C*
2C*	+	3C*		=	5C**
2C**	+	3C		=	5C**
2C1N	+	3C		=	5C1N
2C1N	+	3C1N		=	5C2N

Figure 20: Simplified chemical notation used for following carbon and nitrogen atoms undergoing enzymatic modifications in a tree. Ring structures, conformation effects, substitution changes, and enzyme names are not identified with this notation.

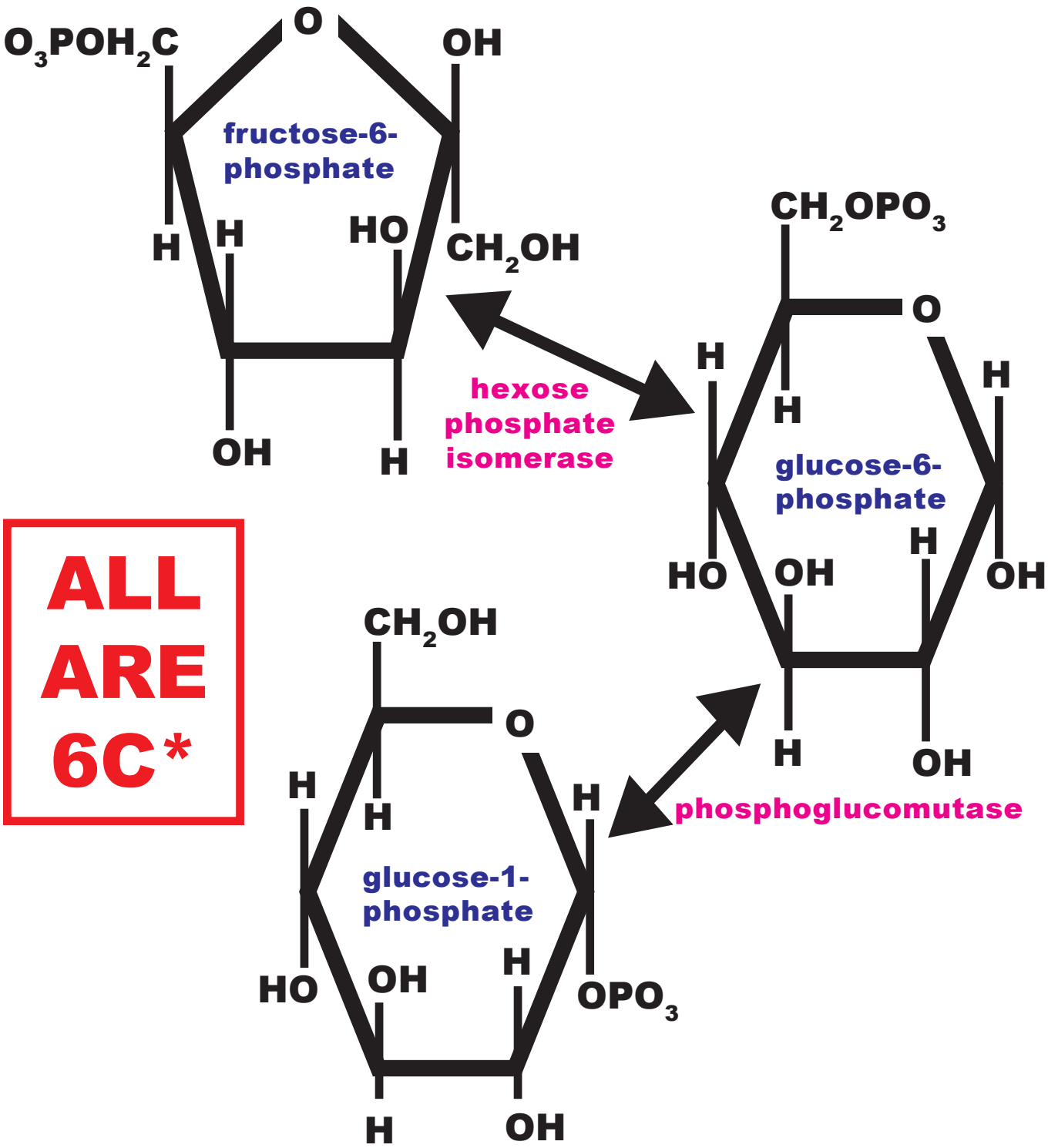


Figure 21: Traditional chemical notation for three different hexose phosphates. All are interconvertable without energy input using the enzymes listed. All three of this group is summarized here simply as 6C*.

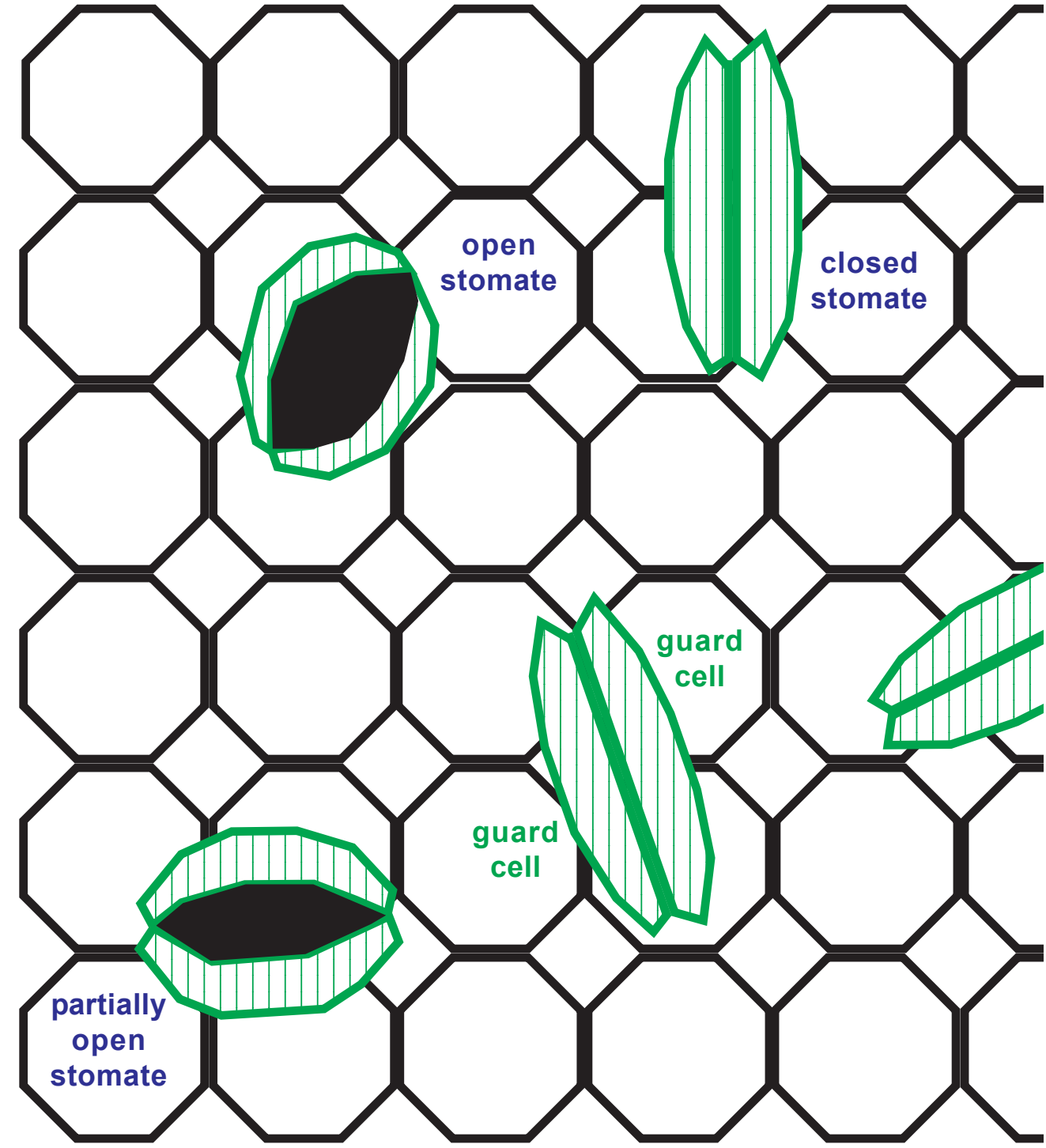


Figure 22: Idealized diagram showing open and closed stomates on underside of a tree leaf blade. The geometric pattern background represents leaf epidermis cells covered by a waxy cuticle.

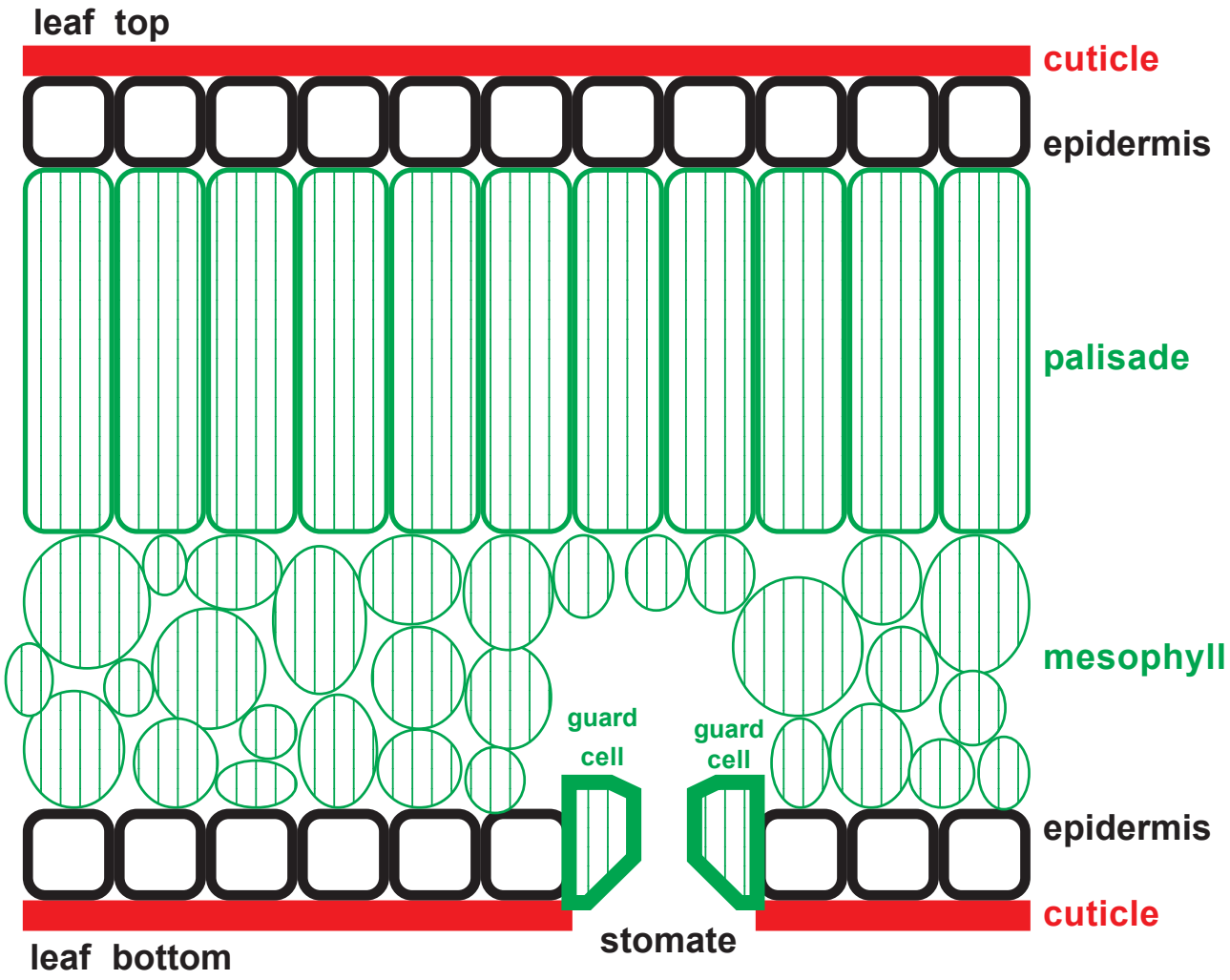


Figure 23: An idealized cross-sectional diagram of a tree leaf blade showing different non-vascular cell layers and a stomate. Cells with shading have chlorophyll. The top and bottom leaf surface is covered with a wax cuticle.

Problems

A tree can have both water and CO2 problems. Leaves must have carbon from CO2 for carbohydrate manufacture, and so, stomates must open. When stomates are open, water vapor pours out because the atmosphere, even in the middle of a Summer rain, can be 100-500 times drier than inside a leaf. Usually the atmosphere is 400-2,000 times drier than inside a leaf. This moisture gradient is so large it drags water quickly from a leaf through open stomates. Trees use this evaporative "pull" of the transpiration stream to transport water and essential elements from roots to leaves. Only a tiny portion of water is used biochemically, but that tiny bit is essential to start photosynthesis. Photosynthesis only works under high moisture concentrations.

As water evaporates, carbon dioxide gas (CO2) from the atmosphere is drawn rapidly in through open stomates. Because chloroplasts are within leaf cells, CO2 must first enter a cell then enter a chloroplast dissolved in water. CO2 gas dissolves on wet surfaces of leaf mesophyll cells. Mesophyll cells are small, have large intercellular spaces, and limited cell wall surface connections with each other (when turgid). These mesophyll features provide a large wet surface area open to stomatal cavity atmosphere. CO2 diffuses 7,000 to 10,000 times slower into water than in air. Because diffusion in water operates well only across short distances, leaf structure assures very short dissolved CO2 paths into chloroplasts.

Carbonated Water

CO2 use by a leaf is not limited by movement into a stomate, but by diffusion across membranes of living cells in a water solution. Inside a chloroplast, a enzymatic process continues to drive CO2 absorption. A chloroplast quickly converts dissolved CO2 into HCO3- (bicarbonate ion). As more CO2 is converted, more CO2 diffuses inward. A chloroplast tries to maintain 40-50 times more bicarbonate ions than CO2. But it is CO2 which is used in the fixation process. As more CO2 is converted, a diffusional "pull" is generated. Because of this active process, partial stomatal opening impacts water loss much more than CO2 gain, something antitranspirants depend upon.

Fixation

The carbon fixation portion of photosynthesis requires energy captured from light. Carbons are strung together using this energy. Fixation occurs in three steps:

1) Carbon from CO2 is placed on the end of a five carbon chain (5C) to make a six carbon chain (6C);
2) The six carbon chain (6C) splits into two 3C units which can be used as a feed stock for many processes in tree cells; and,
3) The original five carbon chain (5C) is regenerated in order to grab another CO2 carbon.

These steps all together are called the Calvin cycle. The Calvin cycle can only occur in sunlight and requires constant energy inputs to fix carbon. Figure 24.

Calvin Summary

The Calvin cycle "begins" with a 5C** sugar prepared in the chloroplast. The 5C** sugar is combined with a carbon from CO2 by use of a key enzyme called Rubisco, and then splits to generate two 3C* molecules. Rubisco can combine either CO2 or O2 onto a 5C** in a nonreversible reaction. If Rubisco captures CO2, it is called the carbon fixation portion of photosynthesis. If Rubisco captures

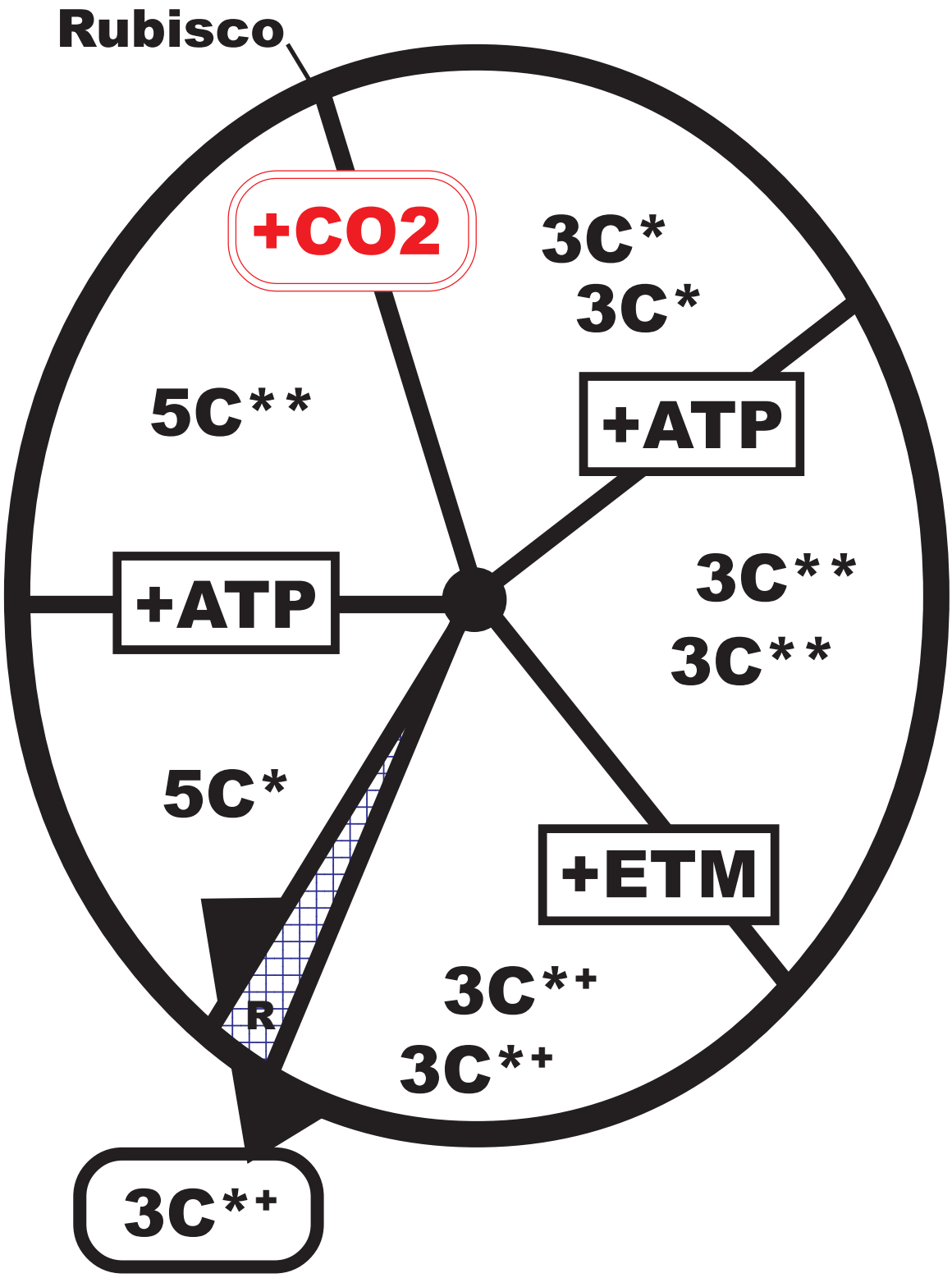


Figure 24: Capture of carbon dioxide (CO2) carbon using light derived energy in the Calvin cycle. "R" is the carbon chain regeneration phase

O2, it is called photorespiration or carbon loss cycle. Note the carbon loss cycle requires O2, loses carbon as CO2, and uses ATP. It is not actual "respiration" as used in a mitochondria. Figure 25.

Take Ruby Aside

Rubisco is a specialized protein (enzyme) in photosynthetic cells. Rubisco's chemical name is ribulose bisphosphate carboxylase / oxygenase. It is a large, slow reacting (i.e. 3 CO2 per second are processed which is 10,000 times slower than most enzyme reactions) protein which comprises almost half of all protein in a chloroplast. It is activated by CO2, high magnesium (Mg) levels, and by increasing pH (less protons), all of which occur under photosynthesis inhibition. Calculations show this protein to be the most abundant protein in tree leaves.

Rubisco combines CO2 carbon with a highly energized five carbon sugar (5C**) which is split into two 3C* units, or Rubisco can process O2 as part of the same five carbon sugar which splits into one 3C* unit and one 2C* unit. If Rubisco captures O2 by mistake, 50% less 3C* is produced. A great deal of fixed carbon can be lost through this process. Figure 26 provides the general pathway split for photosynthesis and the carbon loss cycle (photorespiration).

Calvin Continued

Each 3C* molecule is energetically boosted with ATP producing 3C**, and then each 3C** is energized further with use of a ETM (and loses a phosphorus), producing a $3C^{*+}$. A $3C^{*+}$ can be used for many construction and maintenance jobs in cells and can be shipped out from the chloroplast. Generally, a $3C^{*+}$ combines with other $3C^{*+}$ to produce 6C (hexose sugar), 12C (sucrose sugar), ~xC (starch), or regenerates a 5C* (pool sugar). The $3C^{*+}$ products can be used, stored, or shipped, while a 5C* is energized with ATP to produce 5C** (binding sugar), the place where the cycle began. In regenerating 5C** binding sugars, many valuable intermediates are produced (i.e. 3C*, 4C*, 5C*, 6C*, 6C**, 7C*, 7**). Figure 27.

To make three of the starting sugars (5**) and producing one $3C^{*+}$ carbohydrate for use by a tree, requires 3CO2 + 9ATP + 6 ETM – a tremendous amount of energy and specialized chemistry. About 83% of all energy needed for the Calvin cycle is from ETM. From a sunlight perspective, 8-10 photons of 680nm light is required to fix one carbon with 66% of this energy lost in making ATP and ETM. Only one of every sixth $3C^{*+}$ manufactured can be removed from the Calvin cycle. The Calvin cycle must fix a lot of carbon for a tree to show any progress!

Carbon Gaming

Here is a test. Can you find an easier and more effective way to grab carbons and take them away for use in tree growth? Figure 28 shows a pool of 3C components (without phosphorus attachments). Your task is to combine and split carbon chains until you can run the Calvin cycle by taking away one 3C unit for use in a tree and regenerate the starting CO2 binding materials. The simple rules are given in the figure. Remember no single carbon can be split off as it will be converted to CO2 and lost. The minimum size carbon chain which can be split off has two carbons (2C). The maximum size carbon chain you may create is 14C. After you have attempted the carbon reallocation problem, see how a tree regenerates 5C* in five steps from $3C^{*+}$ shown in Figure 29.

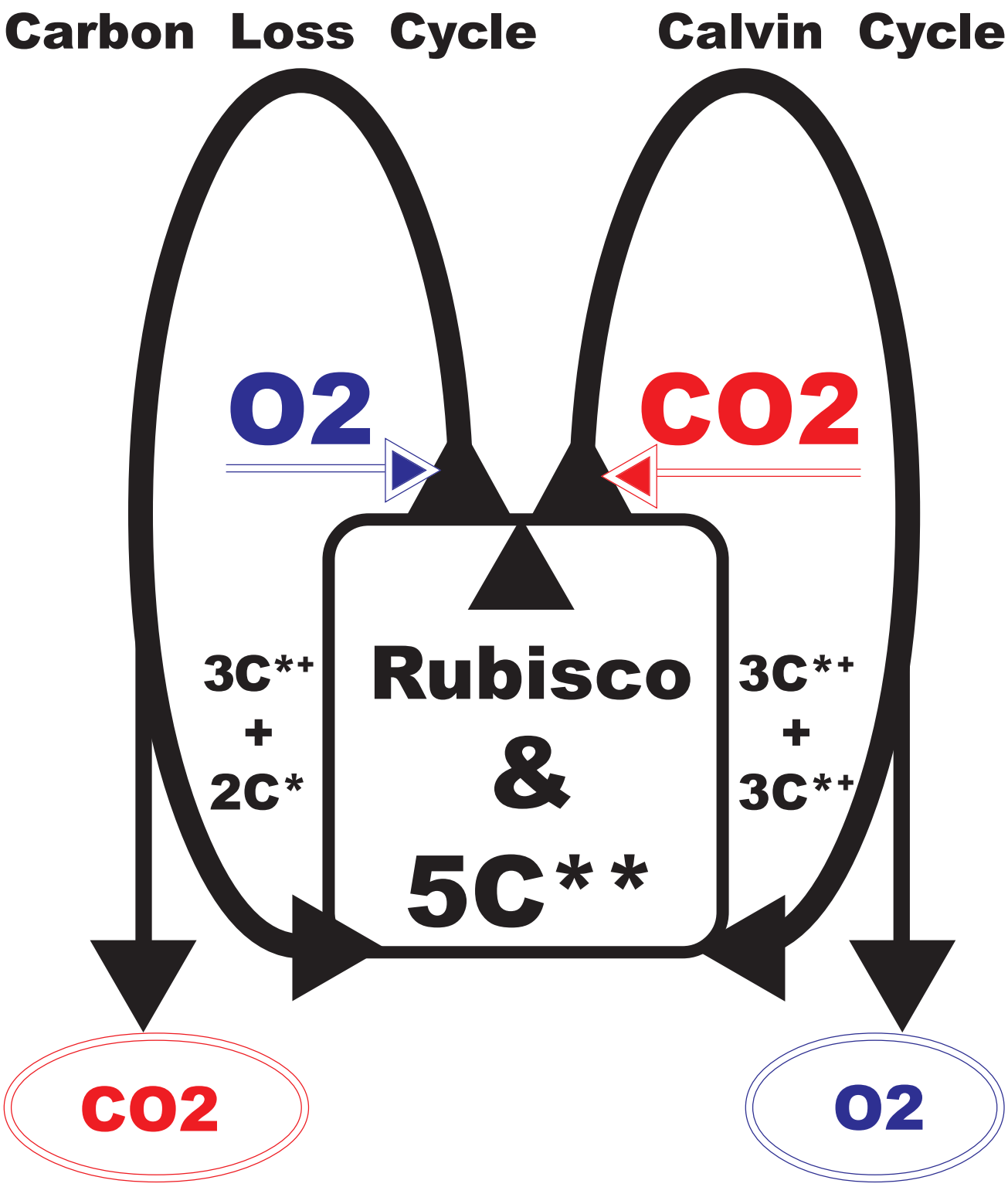


Figure 25: How the carbon loss cycle (photorespiration) overlaps with the Calvin cycle through Rubisco.

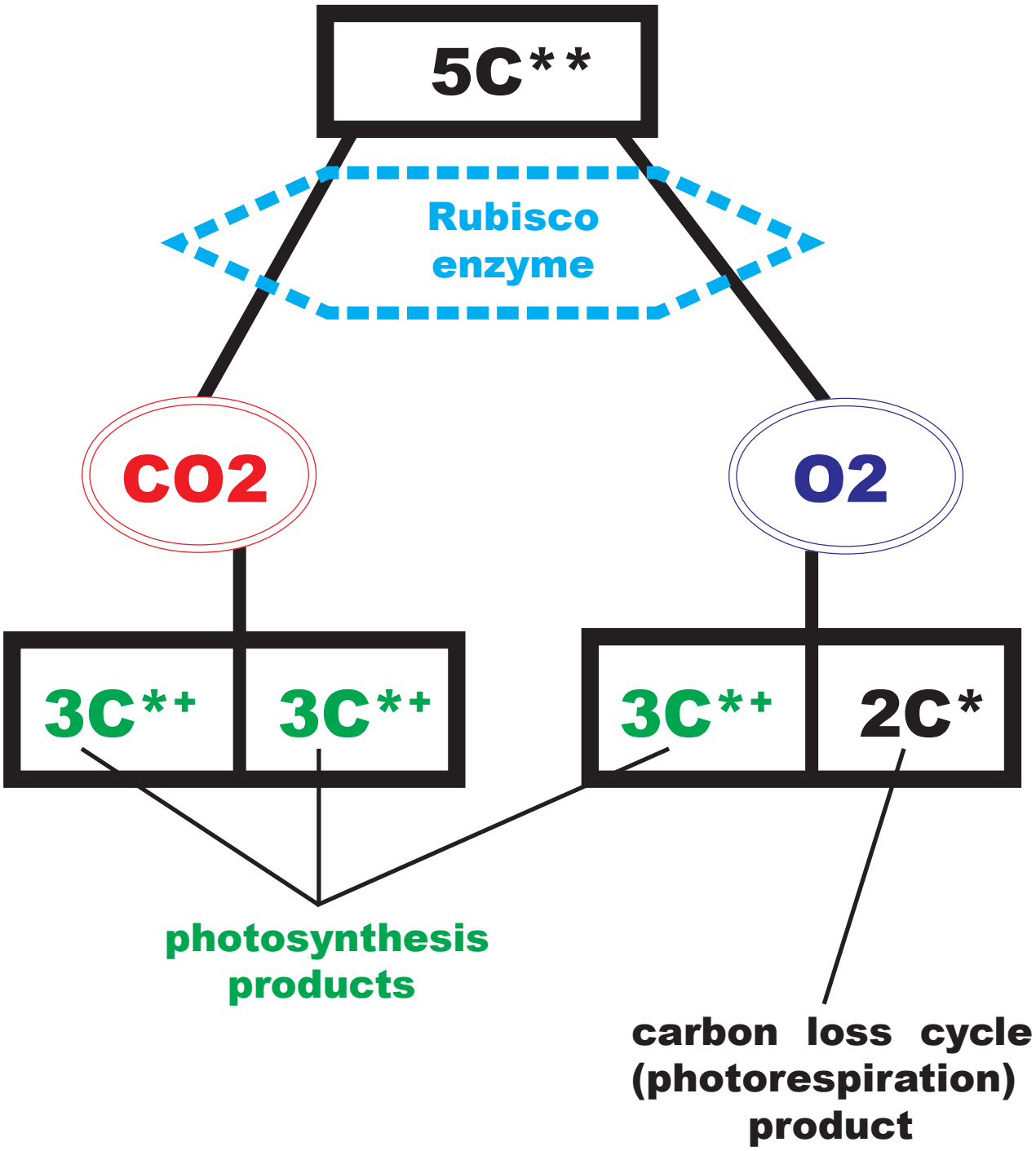


Figure 26: Rubisco processing CO2 and O2 onto 5C** and then splitting to generate $3C^{*+}$ and 2C* products.

(derived from Bowshur & Tobin 2021)

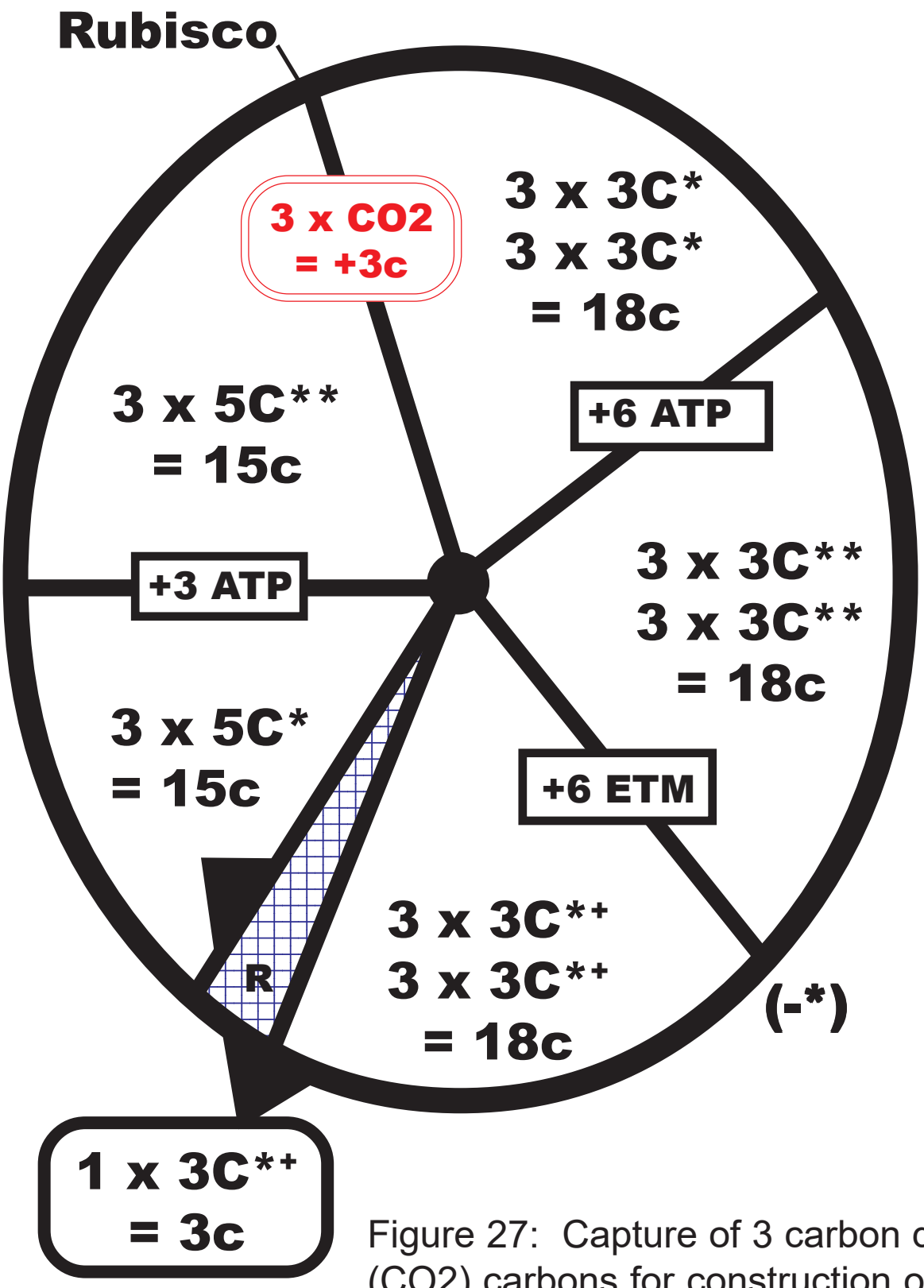


Figure 27: Capture of 3 carbon dioxide (CO_2) carbons for construction of one $3C^{*+}$ product while regenerating three 5C* in the Calvin cycle.

Rules:
1. no single carbons allowed (they go into CO2 and are lost).
2. no carbon chains longer than 14 carbons.
3. minimize carbon use and leftovers.

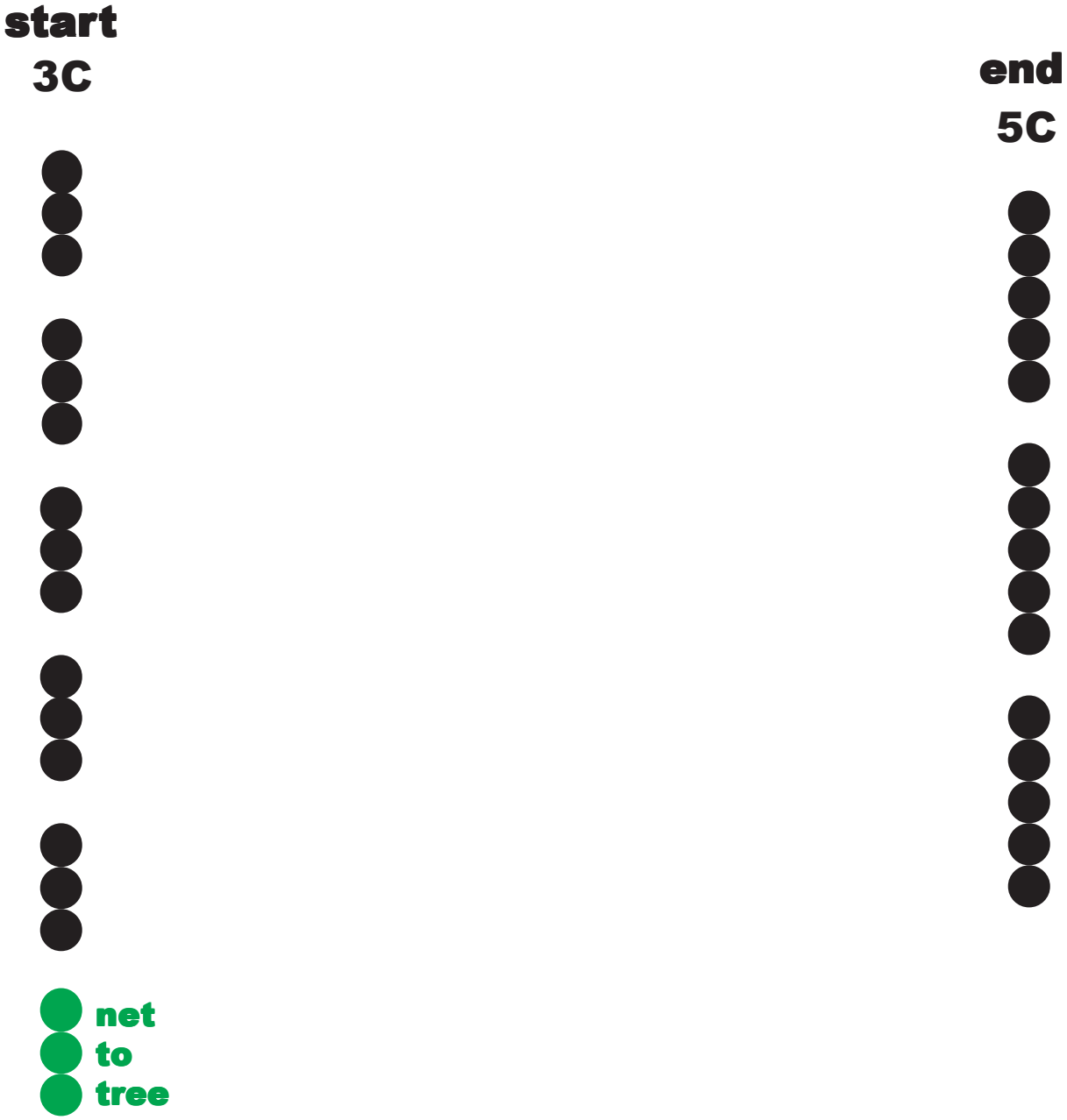


Figure 28: Calvin cycle carbon sort game (regeneration phase). Start with a pool of 3C and attempt to regenerate three 5C in the fewest and simplist steps. Can you do better than a tree? (after Bowshur & Tobin 2021)

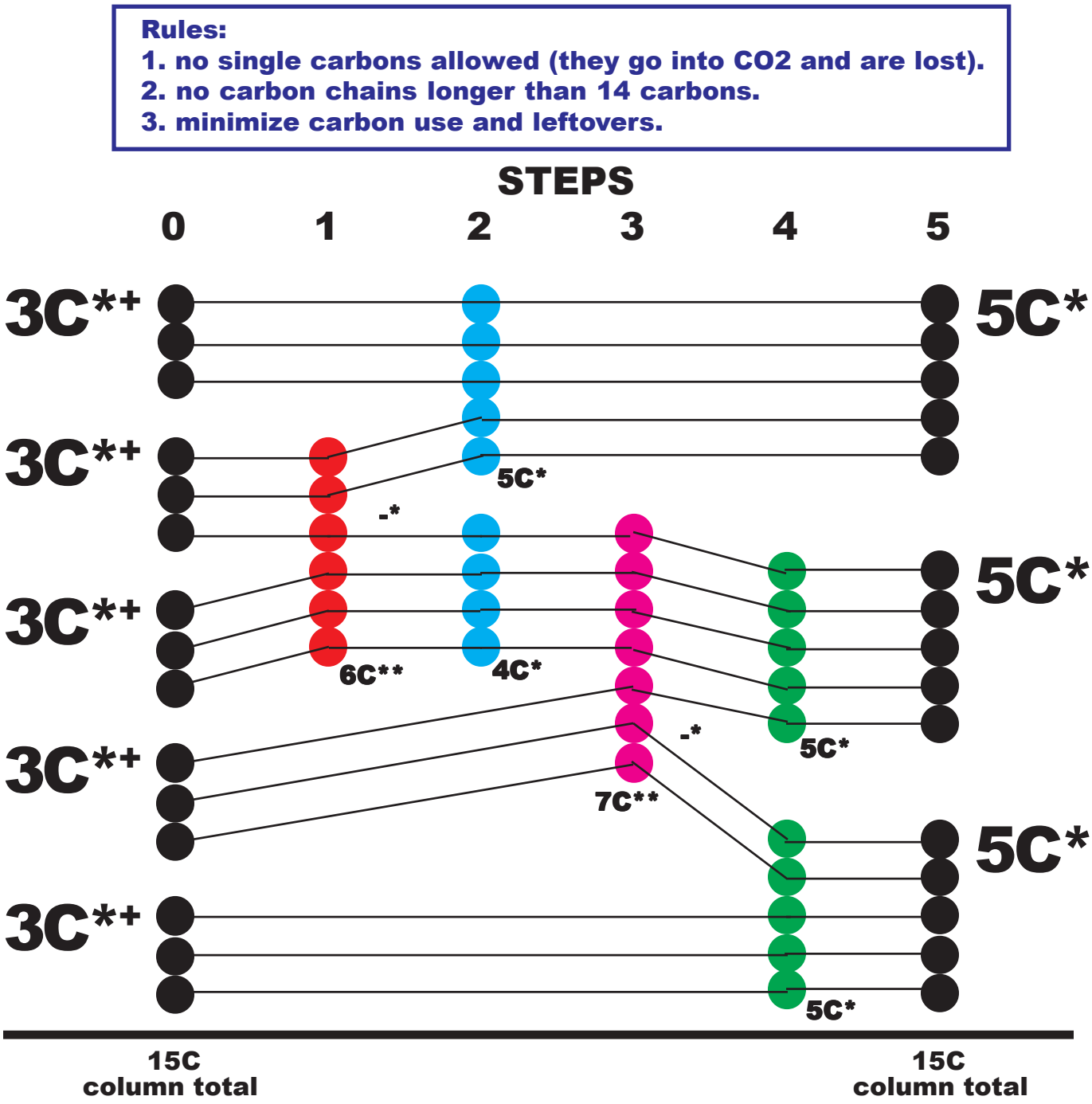


Figure 29: The tree solution to the Calvin cycle carbon sort game. This represents the regeneration portion of the Calvin cycle. This process generates a pool of 4C*, 5C*, 6C*, 6C**, 7C*, and 7C** components.
(after Bowsher & Tobin 2021)

Carbon Leakage

Because of the expense in maintaining all Calvin cycle components, they are turned off in the dark. At one point in the Calvin cycle (in the regeneration process) a 6C* product can be shifted away in the dark to the pentose (5C*) shunt. This dark process uses fixed carbon in a 6C* and releases one C as CO2, makes 2 ETMs, and generates a pool of carbon chains 3C* to 7C* in length. This carbon cycling inside a cell can be shifted either way by photosynthetic constraints. Figure 30. This is a means to quickly harvest energy in the dark by releasing a CO2. The 5C* shunt functions on 6C* in chloroplasts or in the cytoplasm.

Photo Disaster

As mentioned earlier, the carbon loss cycle (photorespiration) is a constant drain on tree photosynthesis just because of the non-selective nature of Rubisco. Because Rubisco will accept CO2 or O2, carbon dioxide and oxygen are competitors for the same site. Rubisco in trees accepts an average of 84% CO2 to 16% O2. The carbon loss cycle actually recovers lost carbon by recycling some (as much as 75%) of the 2C* carbons back into the Calvin cycle. It still does lose some carbon as carbon dioxide and loses energy. This photorespiration scavenges (i.e. uses up) excess ATP in high light, temperature extremes, drought, and other environmental stress conditions when light harvesting systems are capturing too much energy for cell requirements.

Various stress problems can increase O2 acceptance by Rubisco and cause fixed carbon loss. If different ratios of CO2 to O2 are present, it changes the rate of the carbon loss cycle. For example, a decrease in atmospheric O2, or an increase in atmospheric CO2, stimulates more efficient photosynthesis by more than 25%. Figure 31. The carbon loss cycle does play a role in a tree by producing essential amino acids and releasing CO2 for use by the photosynthetic system (a protective role under high light intensities and when stomates are closed by drought or other stress).

Figure 32 shows the pathway of the carbon loss cycle. This cycle starts with Rubisco and traces a path through three separate cell organelles -- chloroplasts, peroxisomes, and mitochondria. The pathway loses a CO2 in the mitochondria and requires an ATP on return to the chloroplast. High temperatures and high light intensities accelerate photorespiration in trees. Figure 33 traces the carbon path in the carbon loss cycle (photorespiration). Up to 50% of all CO2 carbon fixed in photosynthesis could be reprocessed through photorespiration and released into CO2 again.

Carbon Paths

Once CO2 carbon is fixed onto a carbon structure in a chloroplast, three pathways are possible. Each pathway is controlled by tree needs:

A) One path generates cell sugars and transport sugars -- multiple $3C^{*+}$ units are exported from the chloroplast and combined into 6C*, and then into 12C (sucrose) units in a cell. Sucrose is an easily transportable and relatively inert form of carbon.

B) One path regenerates starting materials of carbon fixation -- combining $3C^{*+}$ units together to produce a 5C* pool sugar used to regenerate the 5C** binding sugar needed for carbon fixing.

C) One path generates starch -- uses 6C* units to produce starch (~xC). Figure 34.

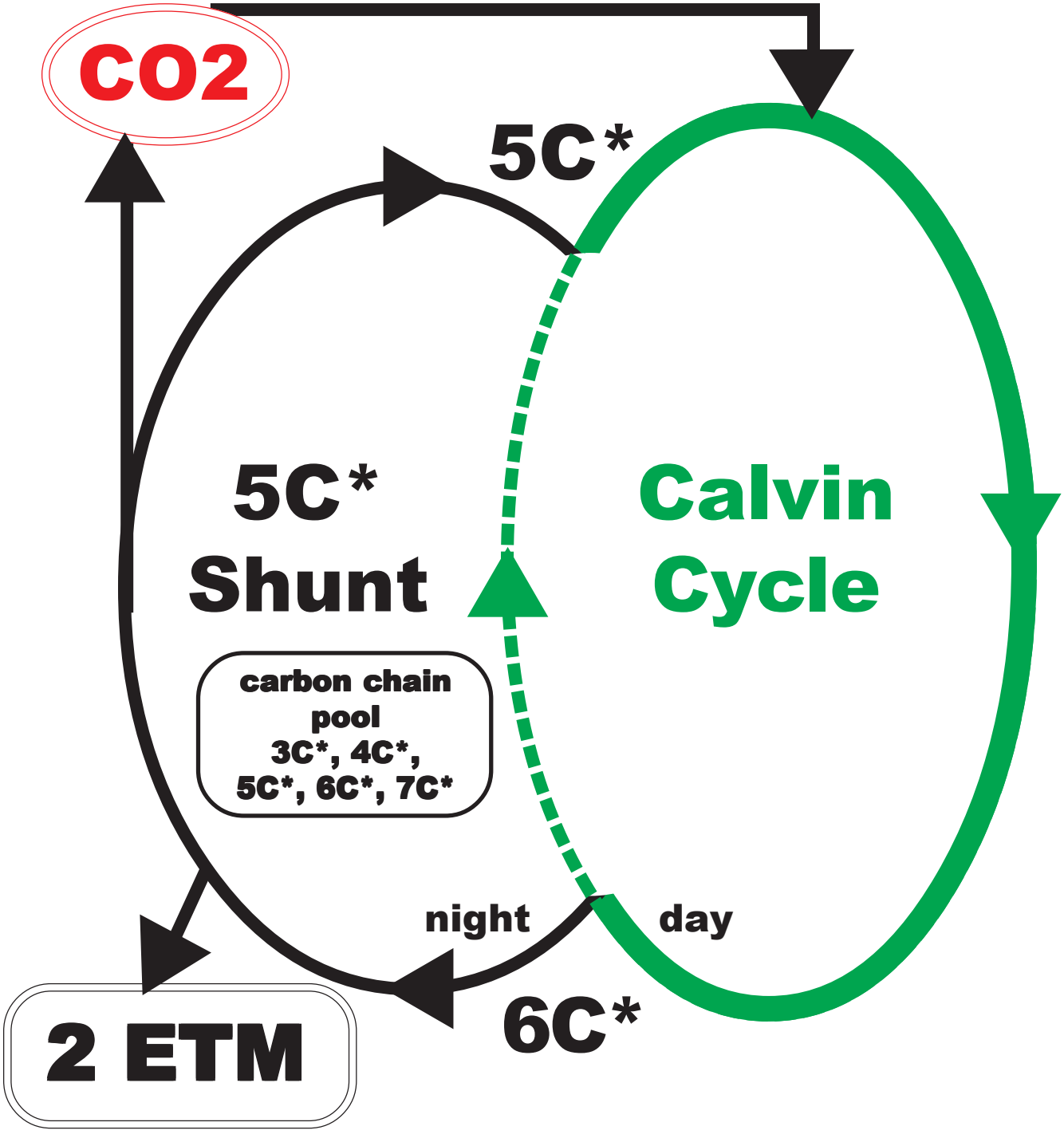


Figure 30: Endless cycling process between Calvin cycle (in daylight) and 5C* (pentose) shunt pathway (at night). The 5C* shunt consumes fixed carbon from the Calvin cycle and generates energy along with an assorted pool of valuable carbon chains. (after Bowsher & Tobin 2021)

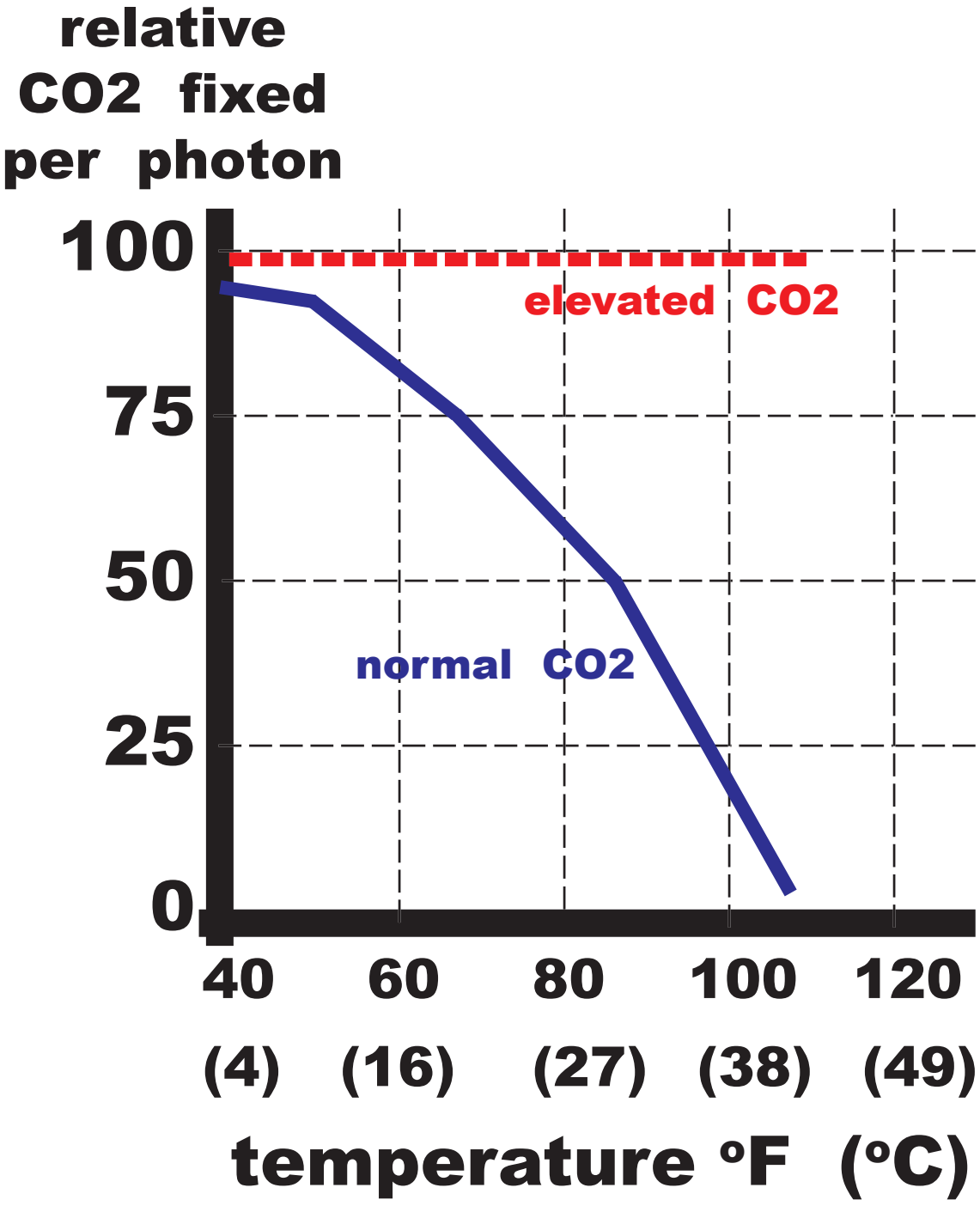


Figure 31: Temperature impacts on photosynthesis efficiency at average CO2 and at elevated (1%) CO2. (derived from Jones et.al. 2000)

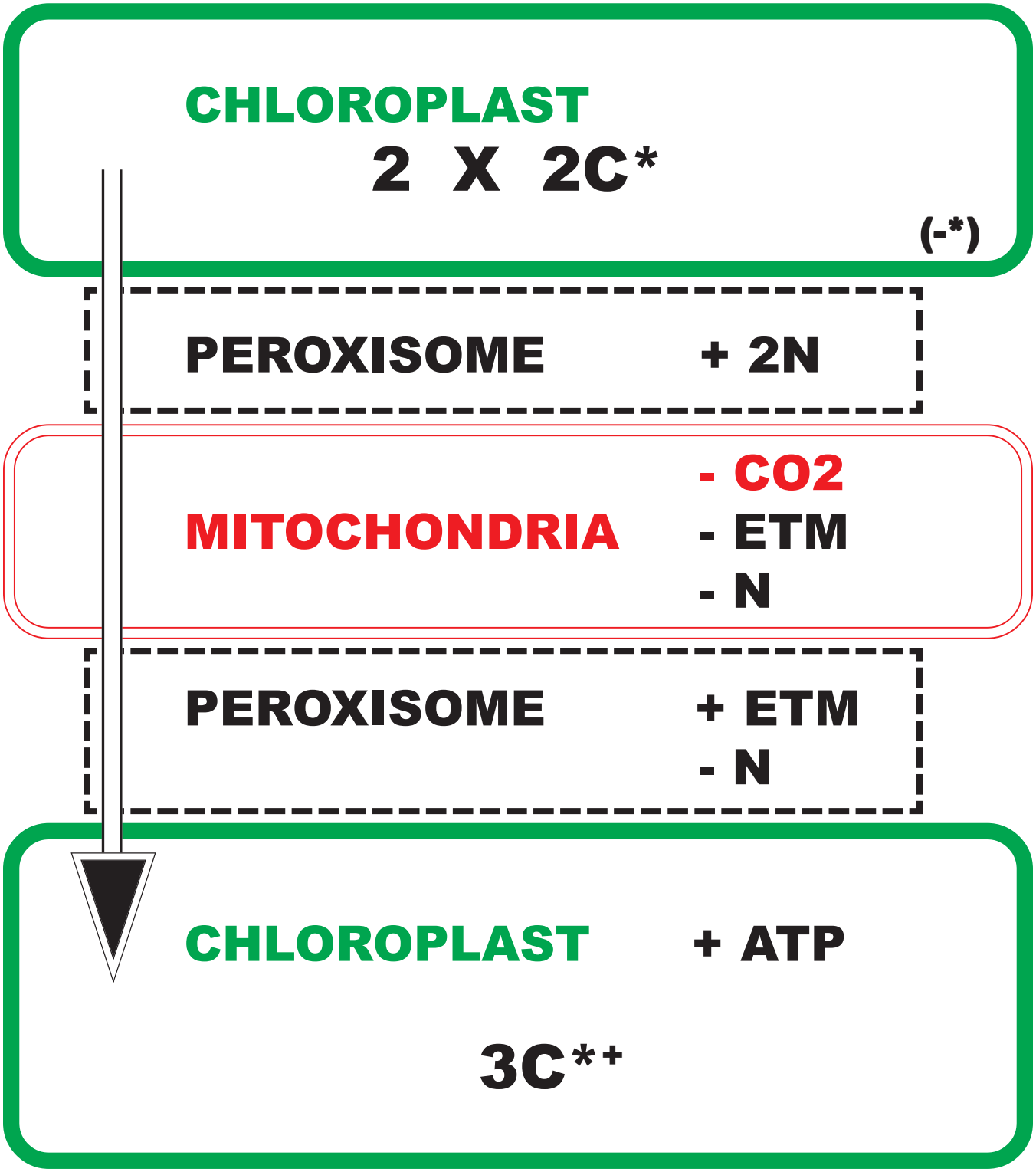


Figure 32: Carbon loss cycle flow through various cell organelles. Net change is CO2 lost and ATP used.

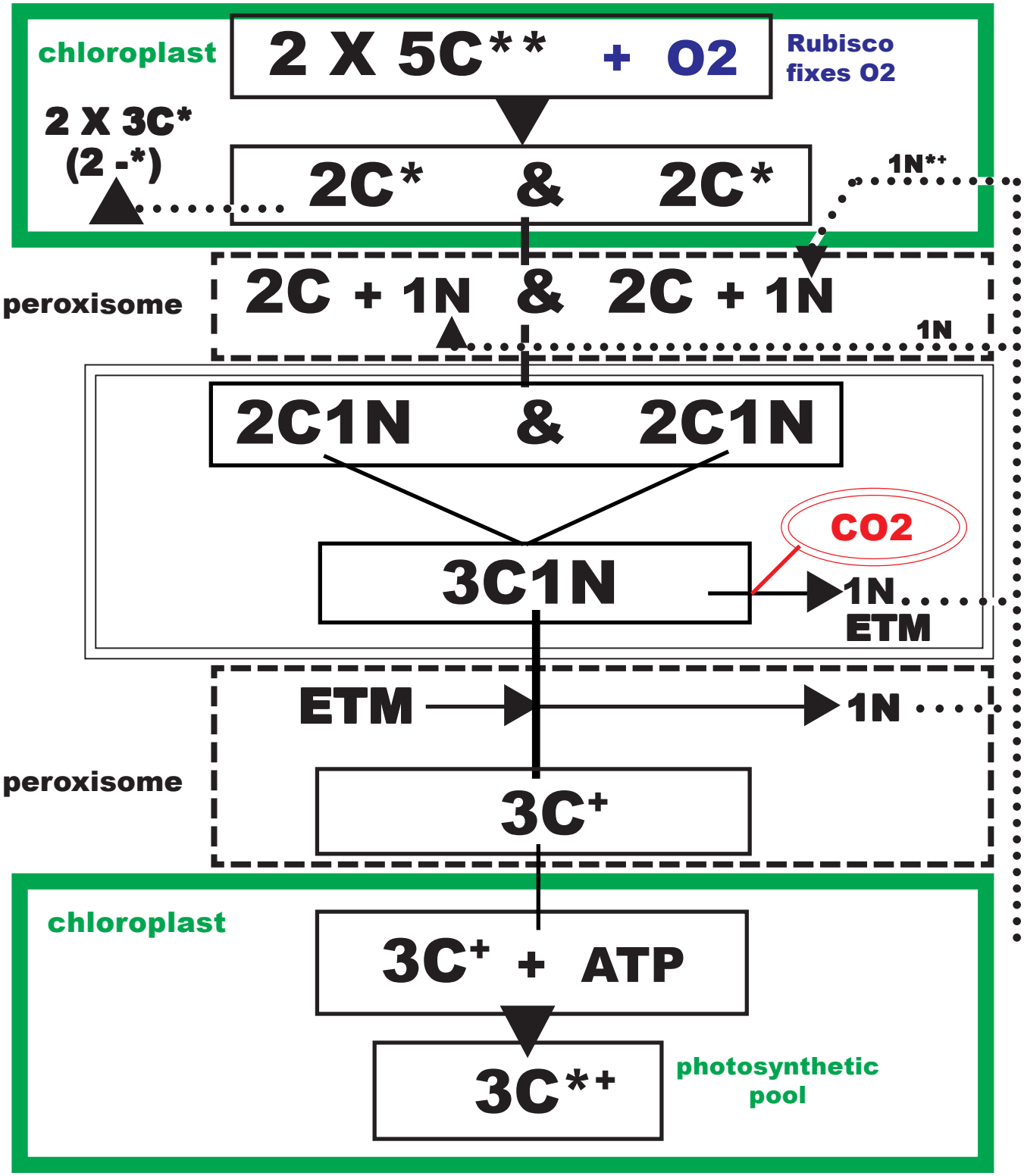


Figure 33: The carbon loss cycle (photorespiration).

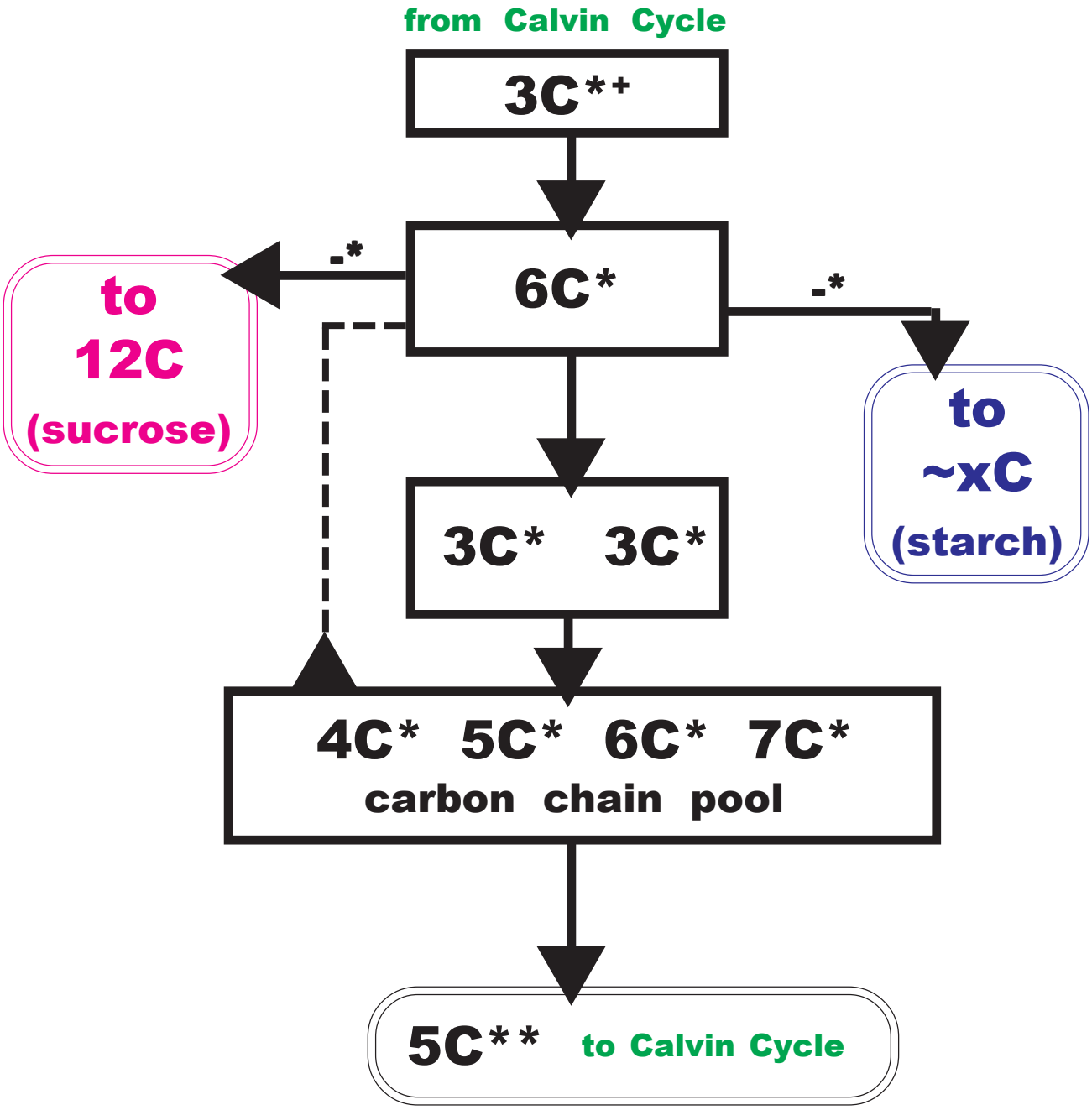


Figure 34: Regeneration phase of Calvin cycle using 3C* pool to build back initial 5C** units while also generating 12C (transport sugar sucrose) and ~xC (starch).

Starch Saving

Starch is multiple carbon strings and clumps made and stored within a chloroplast. For non-photosynthetic cells, starch is stored in amyloplast. Two starch types occur in trees -- amylose (~25% straight carbon chain) and amylopectin (~75% highly branched carbon chain). Both are made by combining 6C* units in chains. Starch is deposited in granules in chloroplasts. Starch accumulates in daytime and is disassembled at night. Starch is used to keep fixed carbon and energy flowing at all times out of a leaf. If sugar supplies are low, leaf cells increase photosynthesis and mobilize starch. Under stress, trees may shift some of the starch to 6C*. If sugar supply is plentiful, growth and health maintenance processes are facilitated and starch is stored. Figure 35.

Sugar Shipping

The primary form of transport sugar coming from leaf cells is sucrose (12C). Figure 36. One 6C* is combined with a 6C to generate 12C (sucrose) and loses a phosphorus. Transport 12C units either come from starch breakdown at night or carbon fixation in daytime. There is a much greater rate of 12C production in light than in darkness. The 12C is transported in phloem to meristems and tissues with large demands (as called for by growth regulator production). Upon arrival, 12C can be split into two 6C.

Sugar and starch generation are separate pathways, with sucrose generated in cell cytoplasm and starch produced inside chloroplasts. In sunlight, 12C (sucrose) is exported from leaves, while ~xC (starch) builds up in the chloroplast. With darkness, starch is broken apart in order to continue to ship 12C out of a cell. Meso-phyll cells continue to push 12C (sucrose = transport sugar) into leaf phloem. Figure 37.

Shipping & Handling

Translocation of 12C in trees moves from sources (mature leaves) to sinks (growth areas or storage). Photosynthetic cells relay 12C along symplast paths toward vascular tissue. At the vascular phloem in a leaf, depending upon tree species, 12C may be moved temporarily into the apoplast for final loading into phloem or may simply move into phloem directly. Energy is required for crossing apoplast / symplast boundaries and for unloading 12C at its destination. Growth regulators map the paths for phloem shipments. 12C is transported in the stem, with other growth materials, in the newest phloem cells just outside the vascular cambium. Only a very thin layer of stem phloem actually participates in transport. 12C can be moved in phloem about 3 feet a hour.

Carbon Compass

The production of starch and sucrose is carefully regulated by a tree. If there are large demands for food, $3C^{*+}$ is quickly moved to cell cytoplasm and converted to transportable 12C (sucrose). If there are small demands for food in a tree, $3C^{*+}$ and 3C** accumulate in the chloroplast. This accumulation stimulates starch production and any starch grains present increase in size. If starch grains grow too large and $3C^{*+}$ continues to accumulate, photosynthesis is slowed. Photosynthesis under starch excess is slowed by a combination of a lack of phosphorus (tied up in existing sugars) for energy transfer and an associated reduction of CO2 carbon fixed.

Macro Control

Photosynthesis has multiple macro-controls and micro-controls. Macro-controls are demands (signaled through growth regulators) of tissues needing carbohydrates, referred to as “sinks.” Anytime

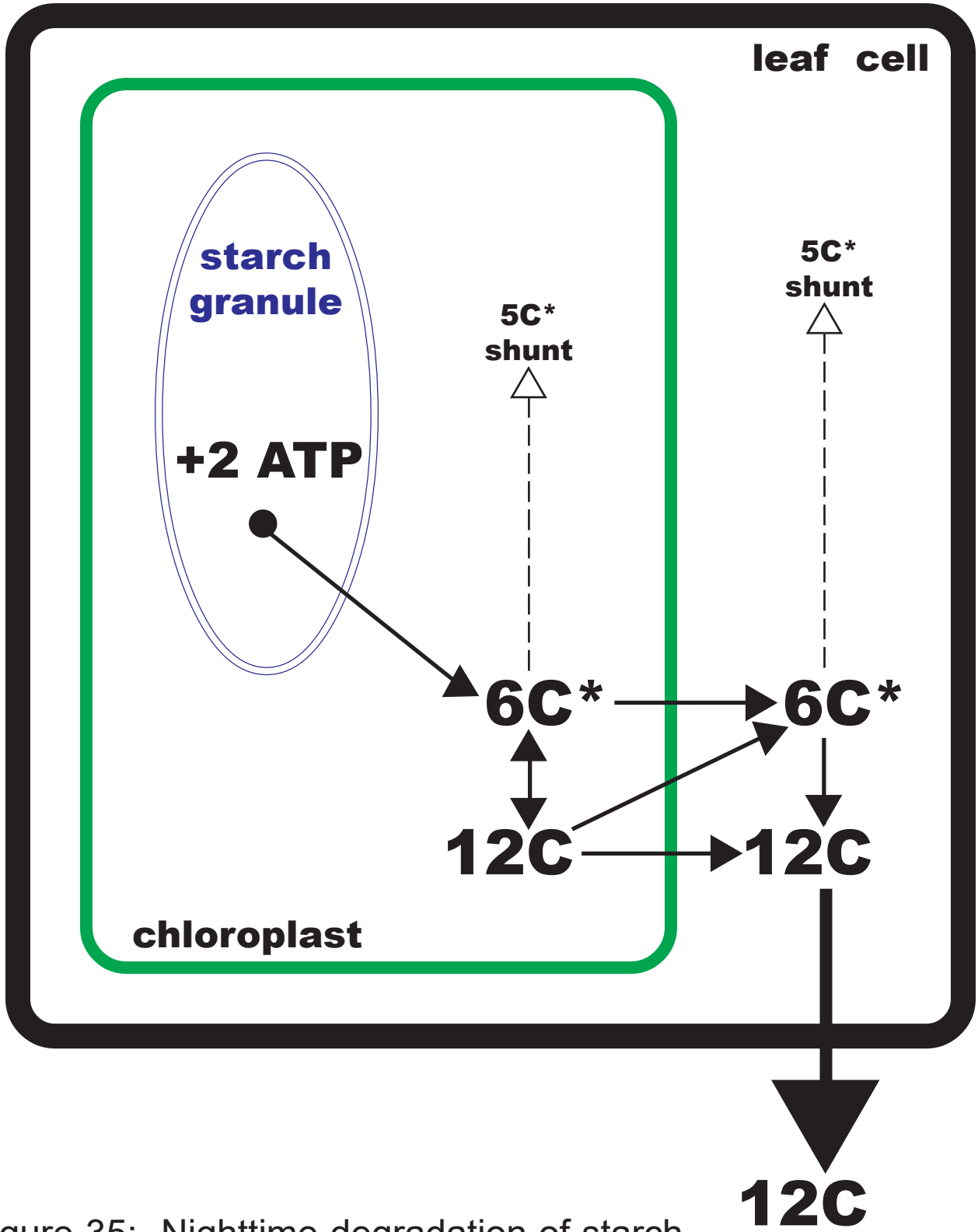


Figure 35: Nighttime degradation of starch (~xC) granule in tree leaf cell. Note this is an energy requiring process. (after Taiz et.al. 2014)

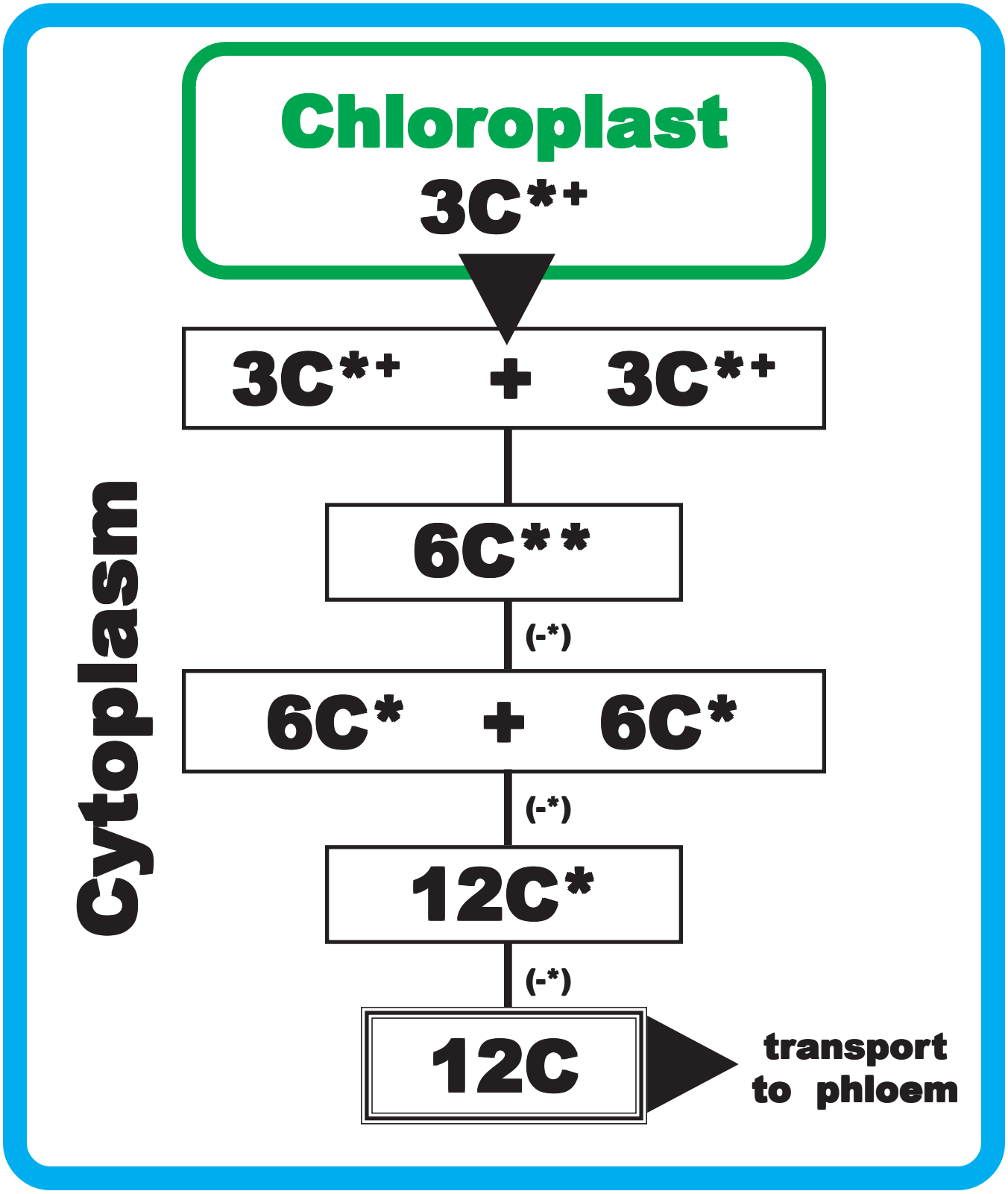


Figure 36: Primary transport sugar in trees is 12C (sucrose). 12C is assembled using $3C^{*+}$ and 6C* components.

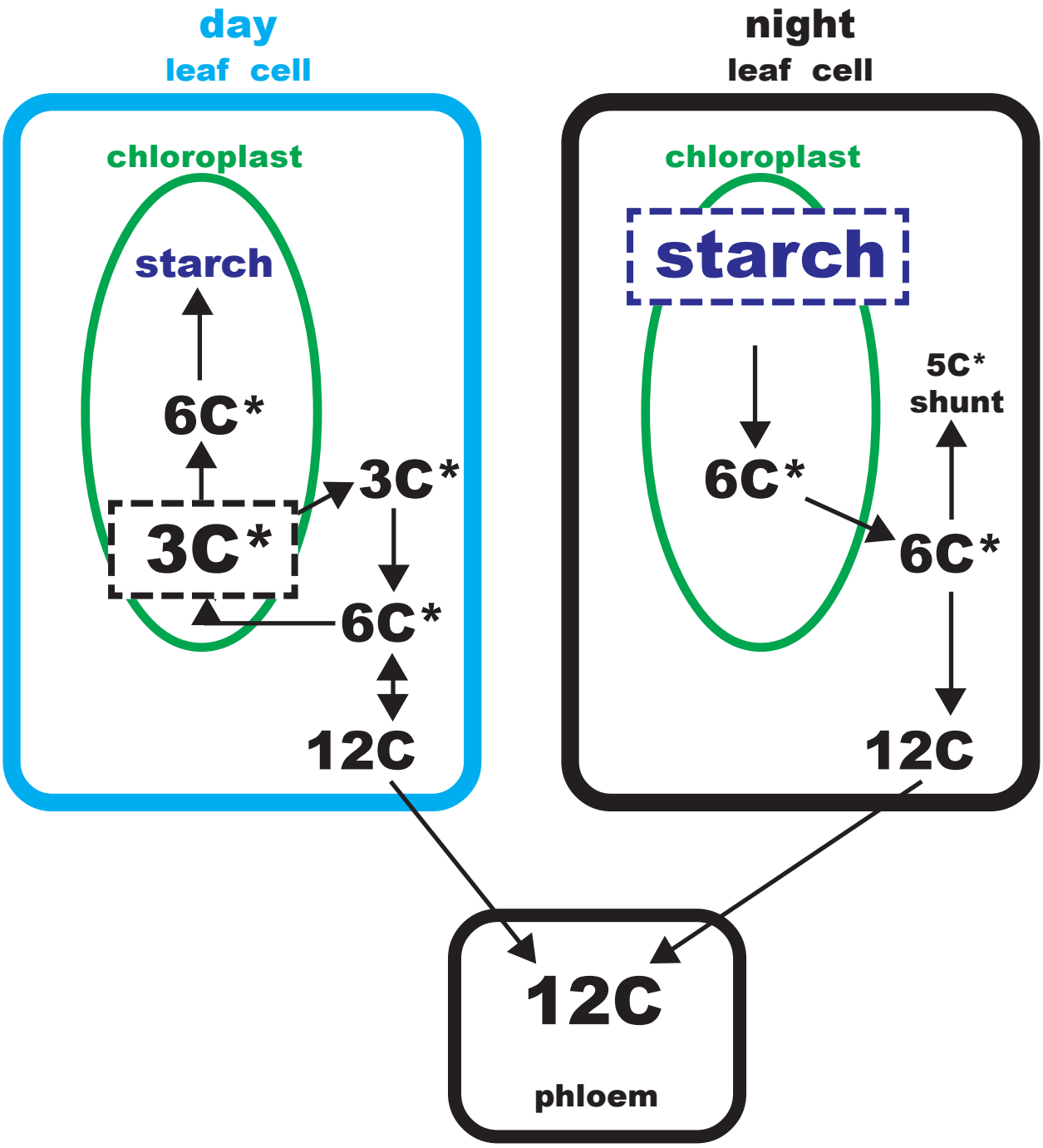


Figure 37: Carbon sources and transport from tree leaf cell chloroplast in daylight (3C*+ source from photosynthesis) and at night (starch (~xC) source).

(after Taiz et.al. 2014)

meristems are dividing and expanding, their sink demands are great. The associated response to increased sink demand is to increase the rate of photosynthesis.

Examples:

a) Trees leaves attacked by defoliator pests increase photosynthesis in remaining leaves.

b) Pruning greater than 33% of live crown reduces photosynthesis in most trees for various lengths of time.

c) Pruning 25% or less of live crown in otherwise healthy trees tends to increase photosynthesis capacity in remaining leaves.

d) Root pruning, and subsequent increase in new roots, tend to increase photosynthesis.

e) Reproductive tissues, like fruits with viable embryos, tend to generate a high sink demand.

Micro Control

Micro-controls on photosynthesis are centered at three major physiological points:

1) Plastoquinone (PQ) in the electron transfer chain between LHCII and LHCI -- Excess electrons feeding into PQ stimulates LHCI proteins to be made in a short time (minutes). Lack of electrons for PQ stimulates LHCII proteins.

2) Presence of sugar and available phosphorus levels in cells and chloroplasts -- As sugars increase within a leaf, associated with a reduction in available phosphorus, photosynthesis capacity declines.

3) Growth regulator cytokinin -- Cytokinins are required for meristems to divide and expand. Cytokinins are shipped along primary transport lines developed by the growth regulator auxin generated from carbon sinks. Cytokinins stimulate photosynthesis and can modify stomate control.

Concluding Ps

Photosynthesis is an electron and proton pump which concentrates electrons and protons inside a tree within the symplast. Holding electrons within carbohydrates and banking protons within cell organelles allow for tree life. Symplastic processes called respiration allow proton gradients to be reduced and electrons to be shifted to oxygen. The net result is energy is allowed to trickle out into an oxidative environment in order to power tree life.

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