UNIVERSITY OF GEORGIA
Warnell School of Forestry & Natural Resources

Publication WSFNR-21-35C

May 2021

# TREE RESPIRATION PROCESS:

## Advanced Tree Biology

### (Part 2 of 3)

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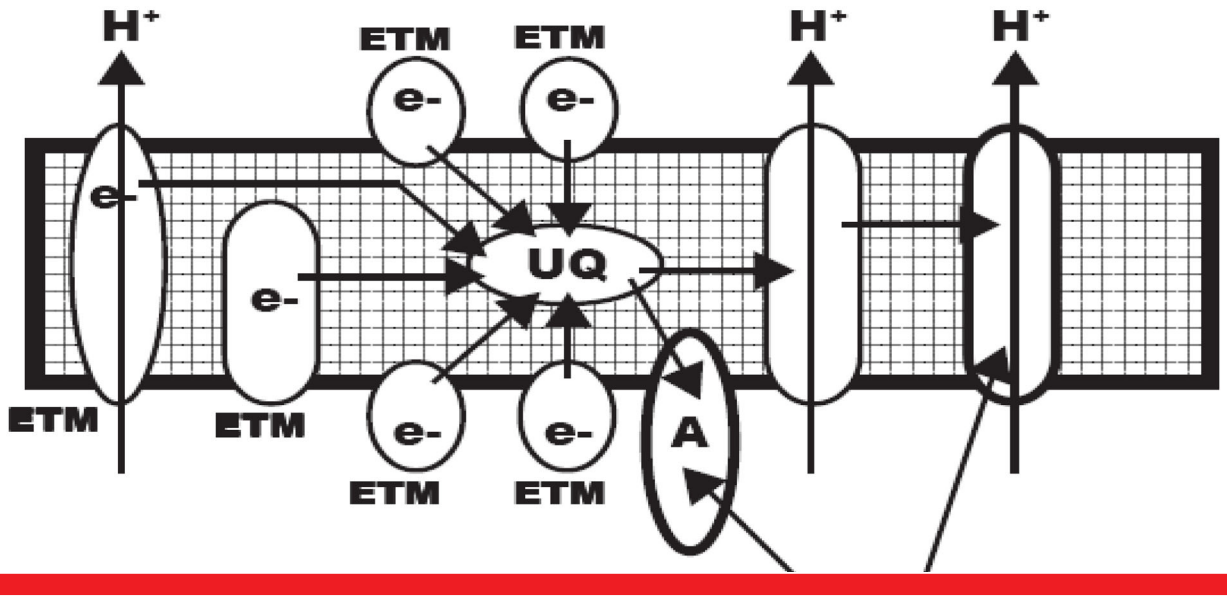

**Scope & Disclaimer:** This is part 2 of a three part training manual designed for helping advanced tree health care providers and senior community foresters appreciate and understand basic tree physiology -- specifically respiration. This educational product is a synthesis and integration of current 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 manual 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 respiration. 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.



Citation For This Revised Publication:

Coder, Kim D. 2021. **Tree Respiration Process: Advanced Tree Biology (Part 2 of 3).** University of Georgia, Warnell School of Forestry & Natural Resources Outreach Manual WSFNR-21-35C. Pp.31.

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# Tree Respiration Process:
## Advanced Tree Biology (Part 2 of 3)

Respiration concerns the transport, release, and use of energy stored in carbohydrate products of photosynthesis in order to grow, maintain, and defend tree life. Tree respiration can be considered the reverse of photosynthesis except for energy wasted through heat and non-sustaining processes. Tree respiration requires oxygen (O2) as a resource onto which to shift electrons. Breaking carbon-carbon bonds regenerates a significant amount of the original energy used to fix carbons together, and in so doing, releases CO2. Other materials are also produced.

Respiration allows energy of the sun to be transported to living cells which can not photosynthesize, are within a tree, or are underground. A leaf array 100 feet in the air can capture, stabilize and ship energy to be used 300 feet away from the stem base and 12 inches below the soil surface. Respiration is the platform which allows life to use carbon chains made in photosynthesis. All living cells in plants and animals respire, whether they have chloroplasts or not.

### In-spiration

Respiration in trees releases energy stored in carbon compounds through a controlled process. Aerobic respiration uses O2 to oxidize organic compounds into CO2 and H2O. Energy released is stored within living cells as ATP, ETM, and a proton bank which are easily used for cell work. Anaerobic respiration oxidizes organic compounds incompletely into alcohol and lactate. Remember, most carbon is not respired away, but is used to maintain tree life and build tree structure.

### Burning Sugar

12C (sucrose), the transport sugar in trees, can be chemically burnt or oxidized in a dish. To start it burning, energy must be added. In this case, all the energy produced is lost to the environment as heat and high temperature gases. 12C in a tree cell is respired or oxidized between 35°F (2°C) and 100°F (38°C). Only a small amount of initial energy is required. Cellular respiration is a carefully controlled process where most of the energy (~66%) is captured as ATP and some lost as heat (~33%).

Tree respiration depends upon enzymes to initiate and catalyze reactions. Enzymes are proteins with special shapes and active sites (sometimes helped by co-factors, co-enzymes, vitamins, or activator ions) which catalyze oxidation processes (as well as catalyzing many other reactions) at ambient temperatures. There are many types of enzymes – common generalists, specific to one organelle, or only needed and produced under dire circumstances. Each step in respiring sucrose into cell energy is moved forward (or sometime reversed) by a specific type of enzyme.

### Not Animal

Tree respiration is similar to respiration in animals. In animals, glucose (6C sugar) is the primary respiration substance. In trees, sucrose (12C double sugar) is the primary transport and initial respiration substance. Sucrose is broken into 6C* units once in a cell. Complete respiration of one sucrose molecule generates 48 protons, 48 electrons and uses 12 O2. The total energy, if released all at once, is enough to damage and destroy cell contents. But tree cells carefully, in a controlled step-by-step process, slowly release this energy for work and allow the rest to escape as heat.

Picture Summary

Figure 1 shows 12C moving into a cell from phloem. Figure 2 shows how starch is broken apart inside storage plastids (amyloplasts) into 6C* components. Some 6C* can be used to make ETMs and generate CO2 in the 5C* shunt. Figure 3 shows the breakdown of 12C or starch into 6C* and 3C* in the cytoplasm of a cell. As in the amyloplast, some of the 6C* in the cytoplasm can be used to make ETMs and generate CO2 in the 5C* shunt. Figure 4 shows glycolysis in the cytoplasm generating 3C as fuel for the mitochondria. The mitochondria uses an oxygen rich Krebs cycle to make ETMs and generate CO2. A build-up of protons (H+) and use of O2 generates ATPs.

Figure 5 shows a combined view of tree cell respiration. A simple summary is 12C is added at the top and CO2 escapes at the bottom in this figure, generating ETMs and ATPs along the way. Although this looks complex and complicated, a simple flow of carbon exists here. Figure 6 presents the two primary components of respiration in trees -- glycolysis and the Krebs cycle.

Mighty Mite

In photosynthesis, the chloroplast is a control and manufacturing facility. In respiration, cytoplasm, plastids, and mitochondria are locations for carbon-carbon bond breakdown. Mitochondria are small oval to oblong organelles found in all cells. Plastids are small, membrane enclosed spaces in a cell where special chemistry reactions take place. There are many types of plastids. Cytoplasm of a cell supports the transport into a cell of 12C and contains a number of metabolite pools and processing enzymes.

Foursome

Now let us examine respiration in living tree cells in more detail. The controlled energy release of respiration is completed in four connected processes:

1) Glycolysis, which occurs in cytoplasm and plastids, where 6C* sugars are partially oxidized to an organic acid (3C) generating a small amount of energy as ATP and an electron transfer molecule (ETM). Figure 7.

2) 5C shunt, which occurs in cytoplasm and plastids (the dominate location), is a side process of glycolysis processing a 6C* and generating 2 electron transfer molecules (ETMs), releasing a CO2, and interconverting carbon chains into a number of forms. Figure 8.

3) Krebs cycle, an organic acid (3C) from glycolysis is completely oxidized to CO2 in the mitochondria which generates electron transfer molecules (ETMs). Figure 9.

4) ATP production occurs along an electron transport chain in the mitochondria which uses ETMs to move electrons to oxygen, produce water, and bank a large number of protons used to generate ATP.

Electro-molecules

Electron transfer molecules (ETM) used in trees insert chemical energy through easily transferable electrons into processes to activate enzymes and energize materials for easier manipulations. These

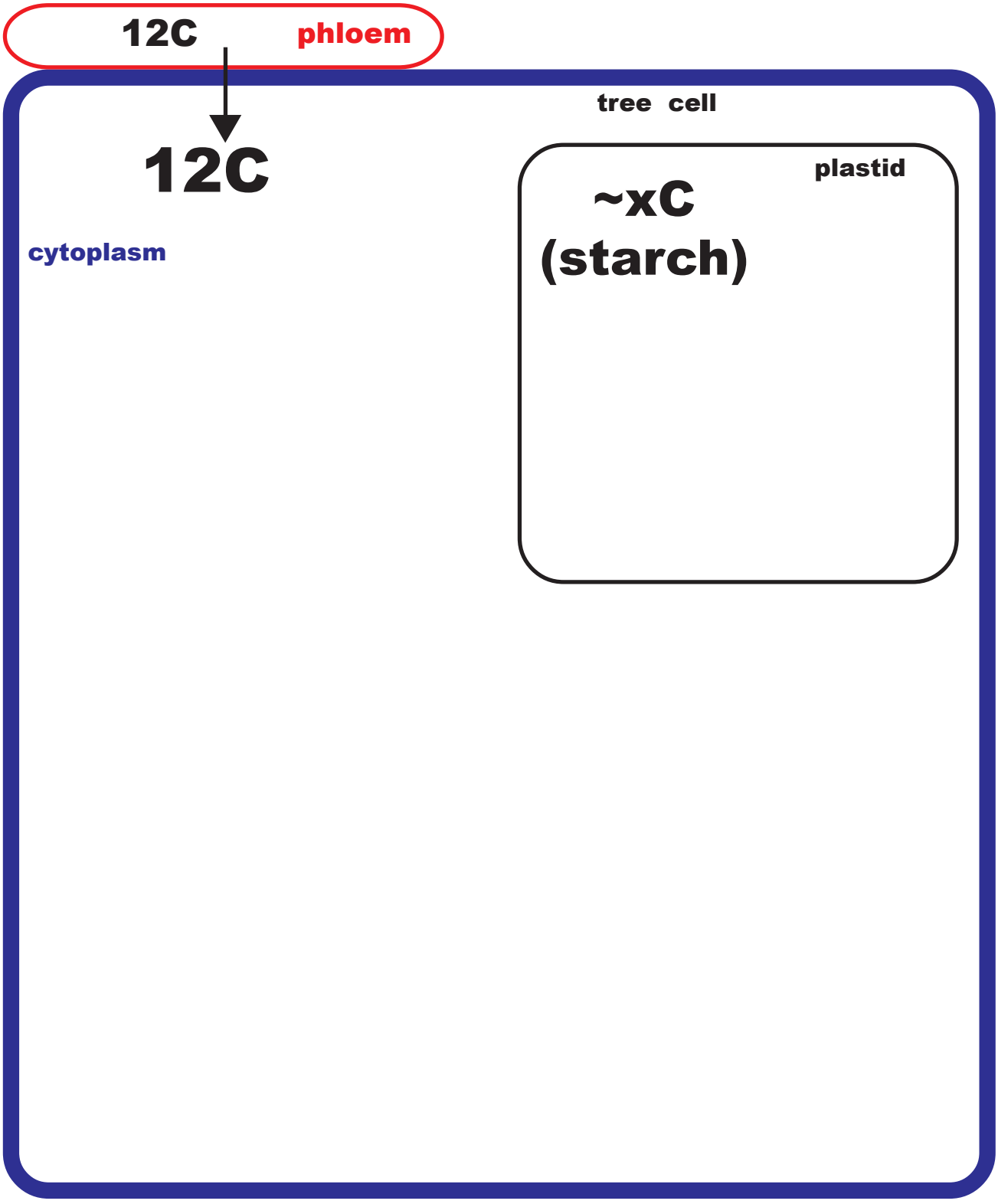


Figure 1: 12C transport in phloem and moving into a cell and starch (stored carbon) in cell plastids. (after Taiz et.al. 2014)

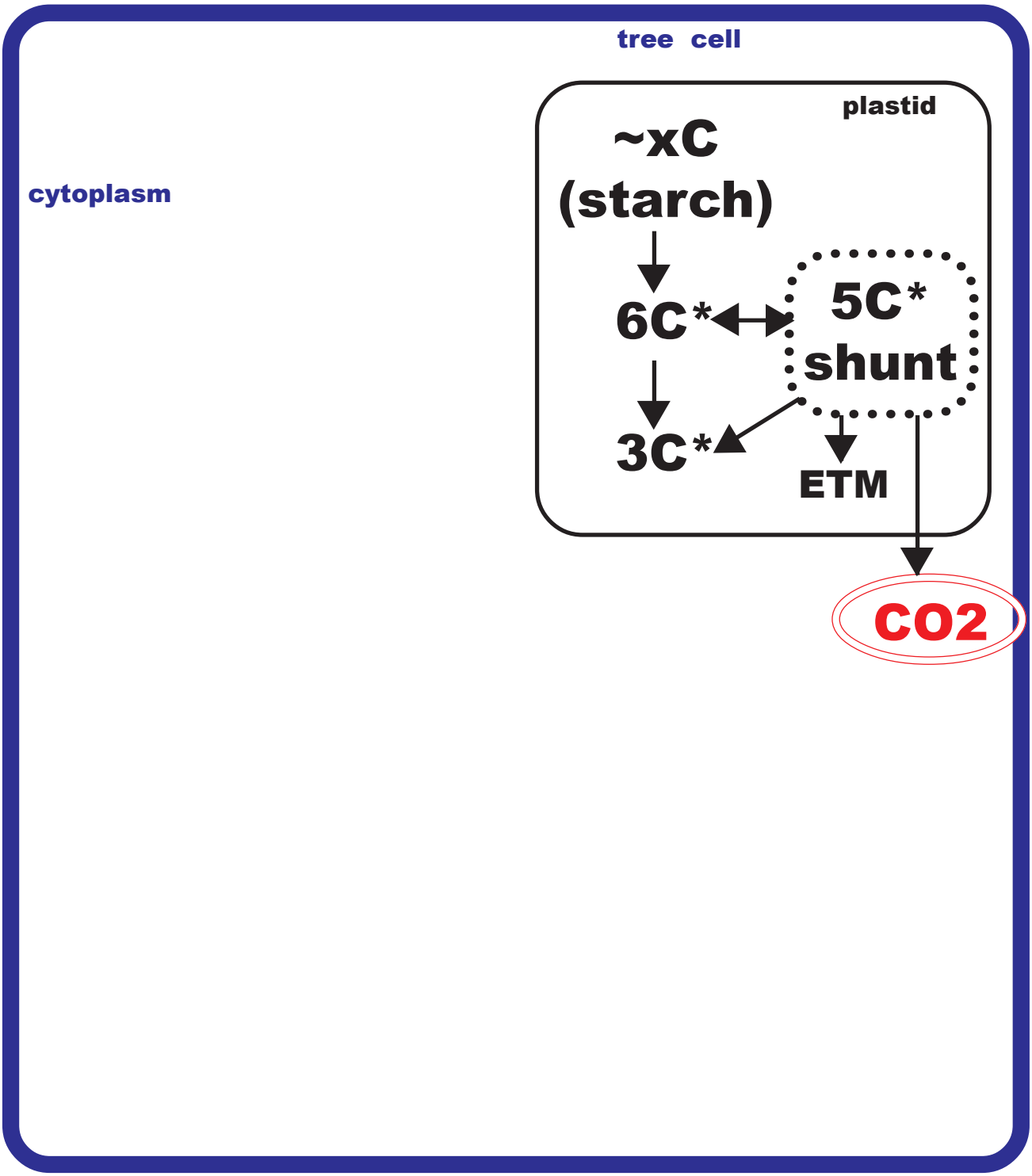


Figure 2: Breakdown of starch in cell plastid into 6C* and then 3C* units. The 5C* shunt can be used to generate ETMs and CO2. (after Taiz et.al. 2014)

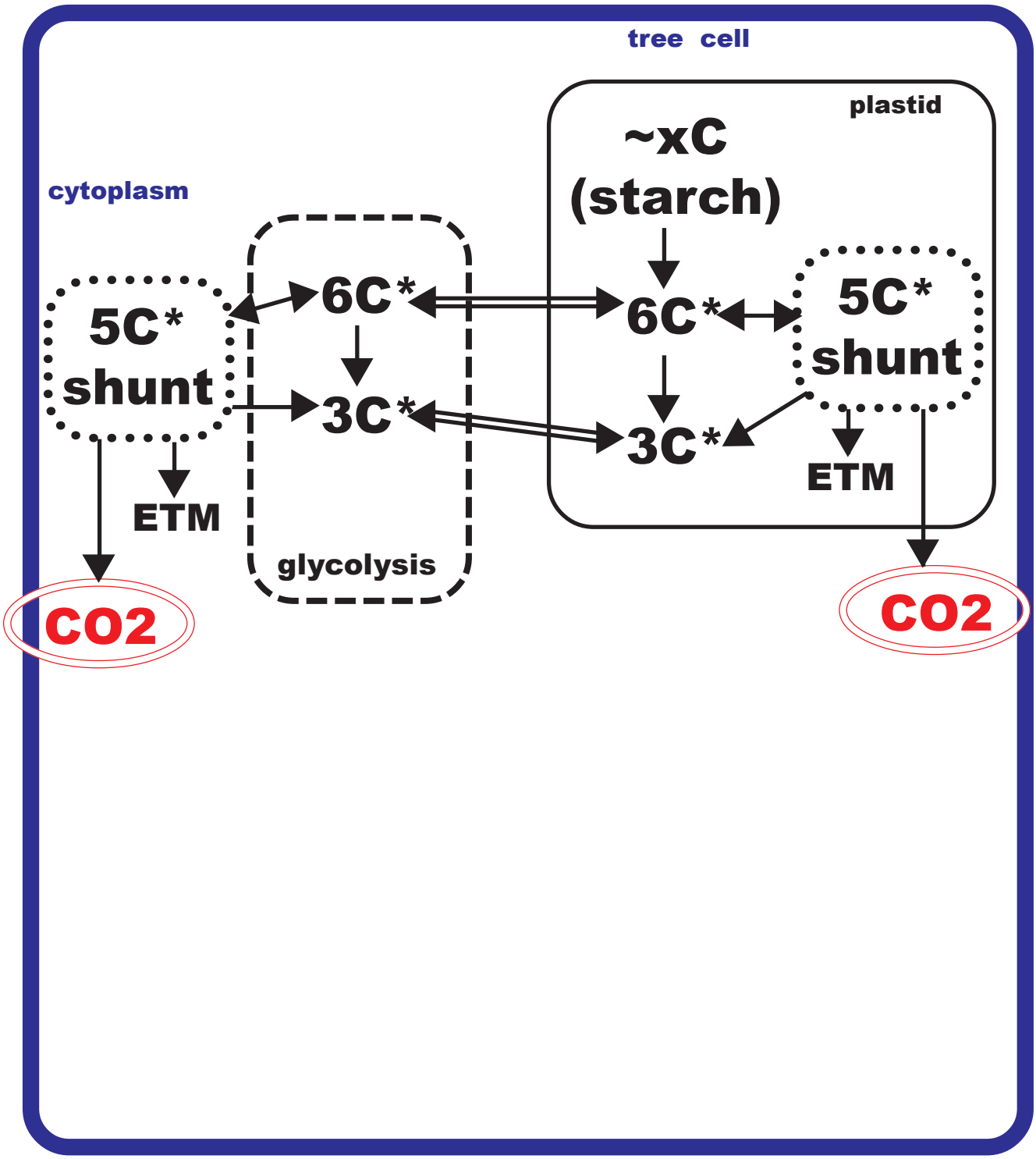


Figure 3: Cytoplasm and plastid centered use of 6C* units generating 3C* units in glycolysis. In addition, each location can generate ETMs and CO2 in the 5C* shunt. (after Taiz et.al. 2014)

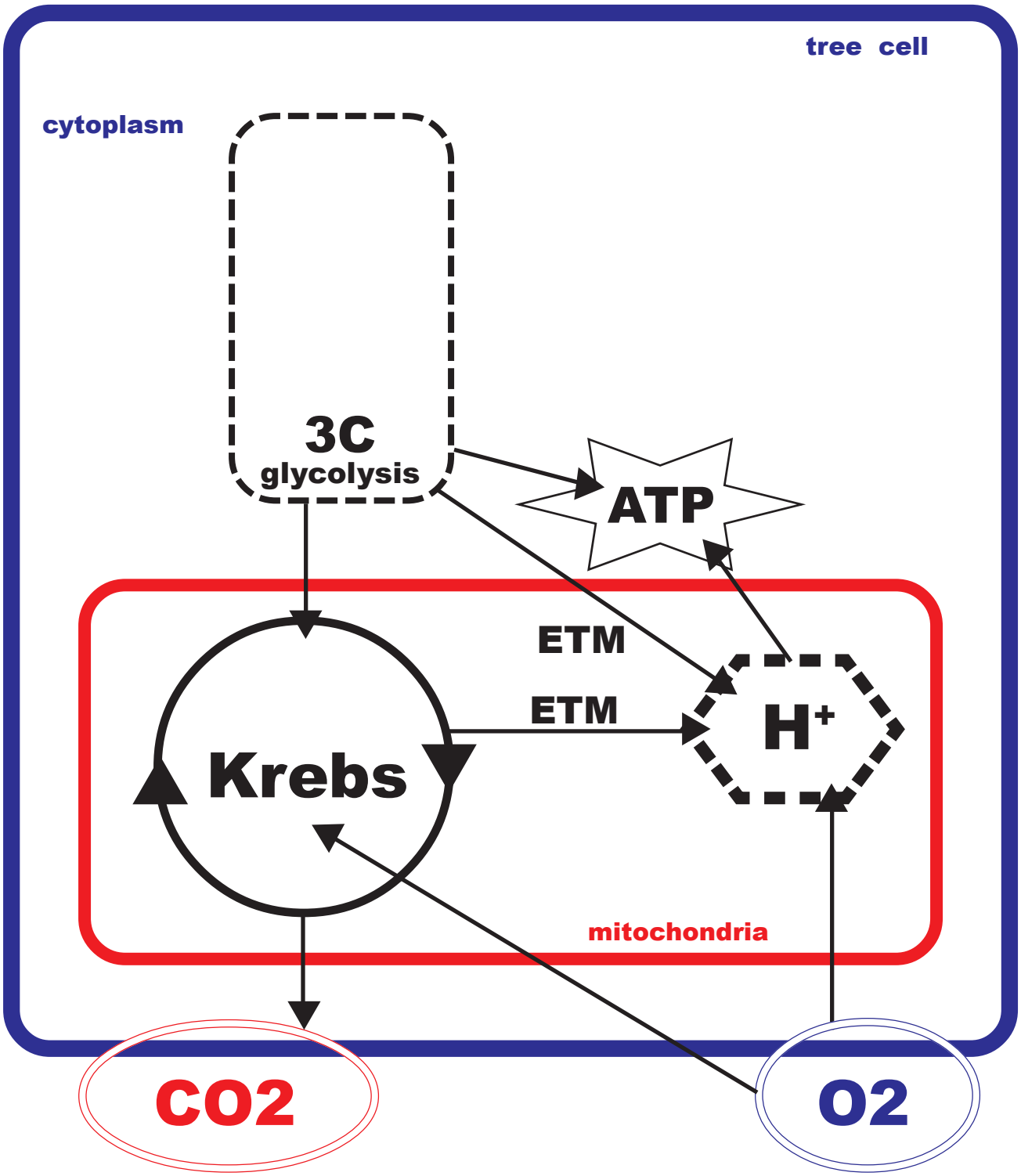


Figure 4: 3C units are feedstock for a mitochondria, allowing for the Krebs cycle, proton banking, and generation of ETMs and ATPs. (after Taiz et.al. 2014)

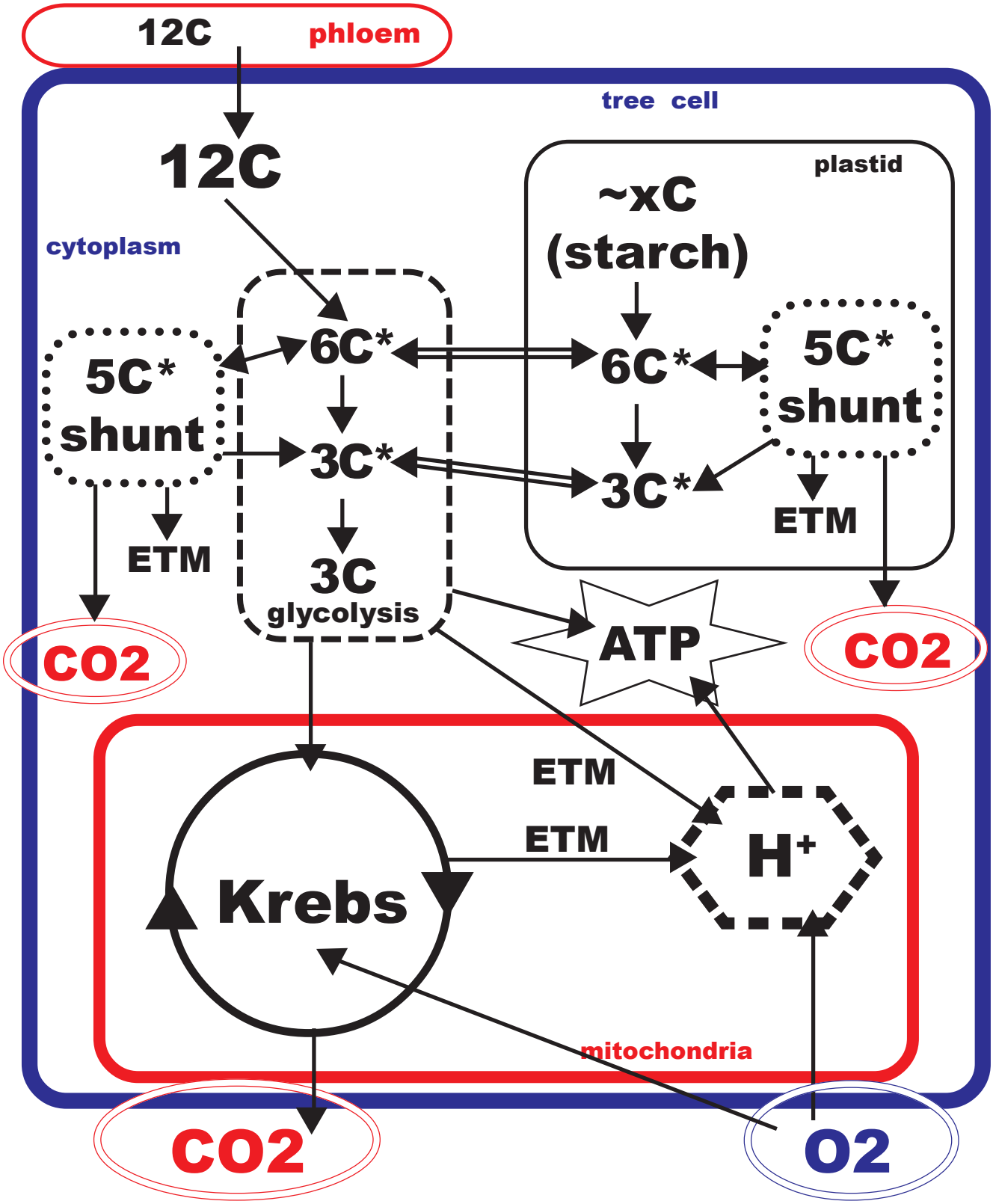


Figure 5: Combined path of 12C and starch input and CO2 output through cell respiration. (after Taiz et.al. 2014)

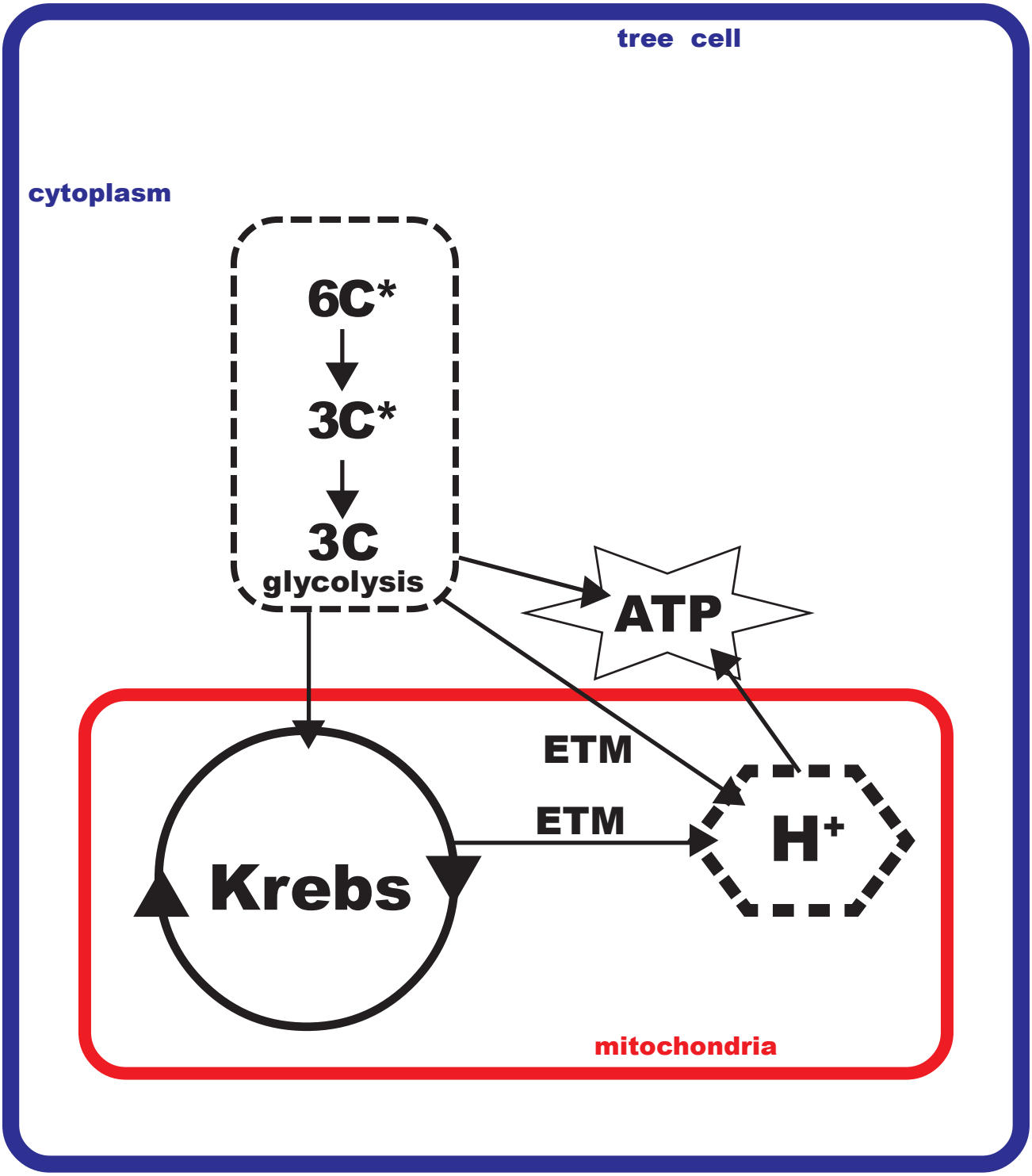


Figure 6: Tree respiration can be summarized as consisting of glycolysis and the Krebs cycle, with each generating ATPs. (after Taiz et.al. 2014)

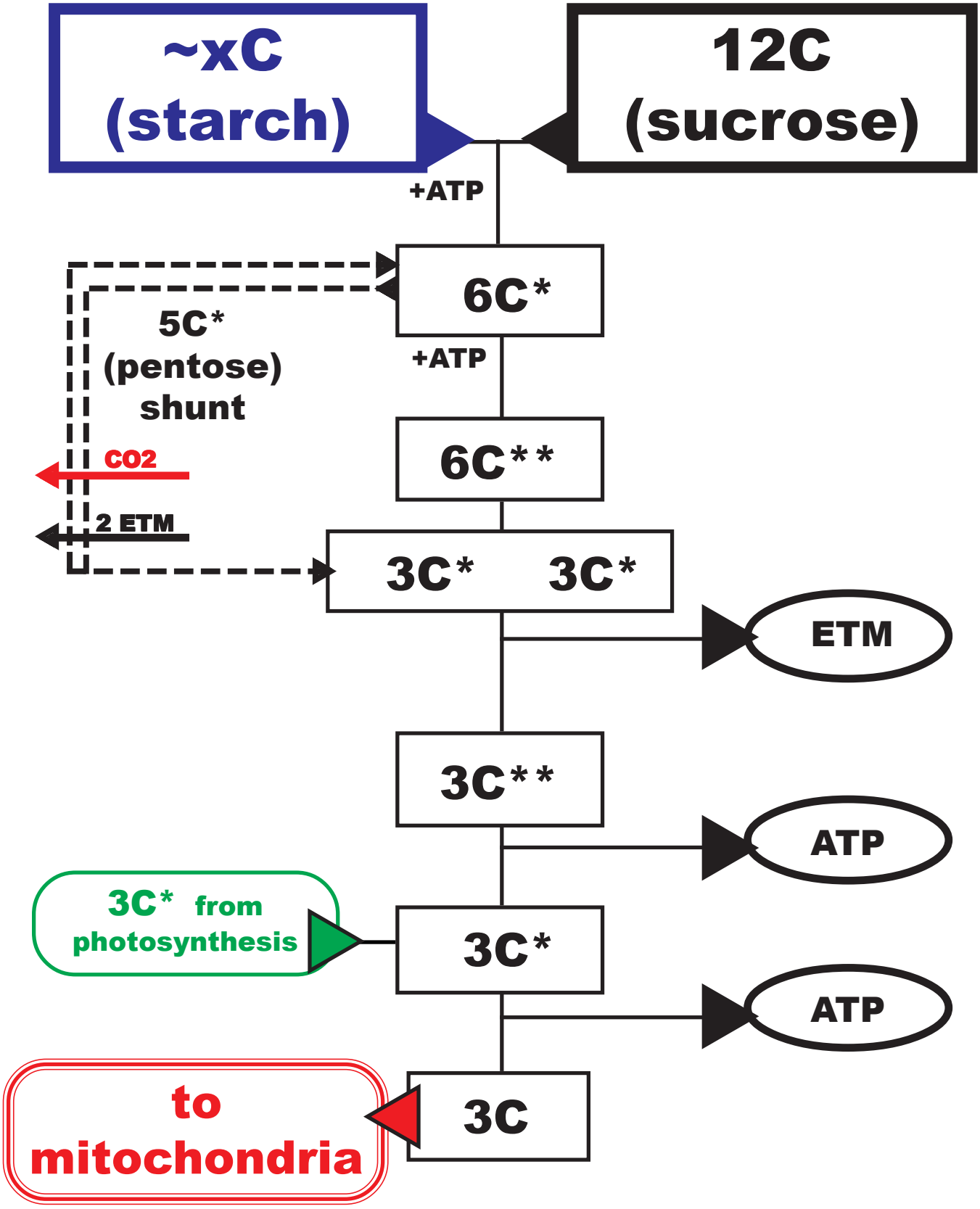


Figure 7: Primary steps of tree glycolysis in cell cytoplasm.

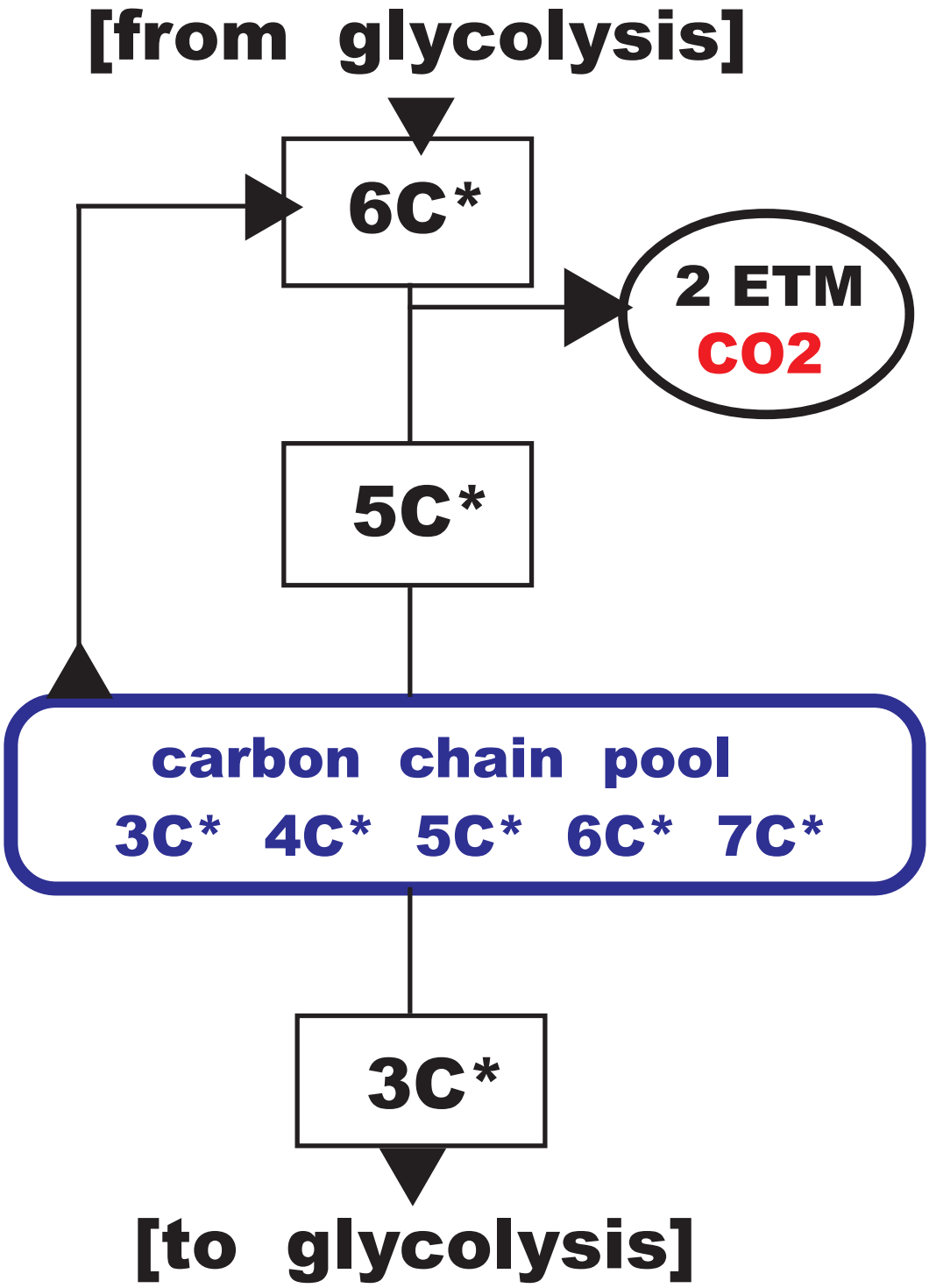


Figure 8: A side respiration chain from mainline glycolysis called the 5C* (pentose) shunt.

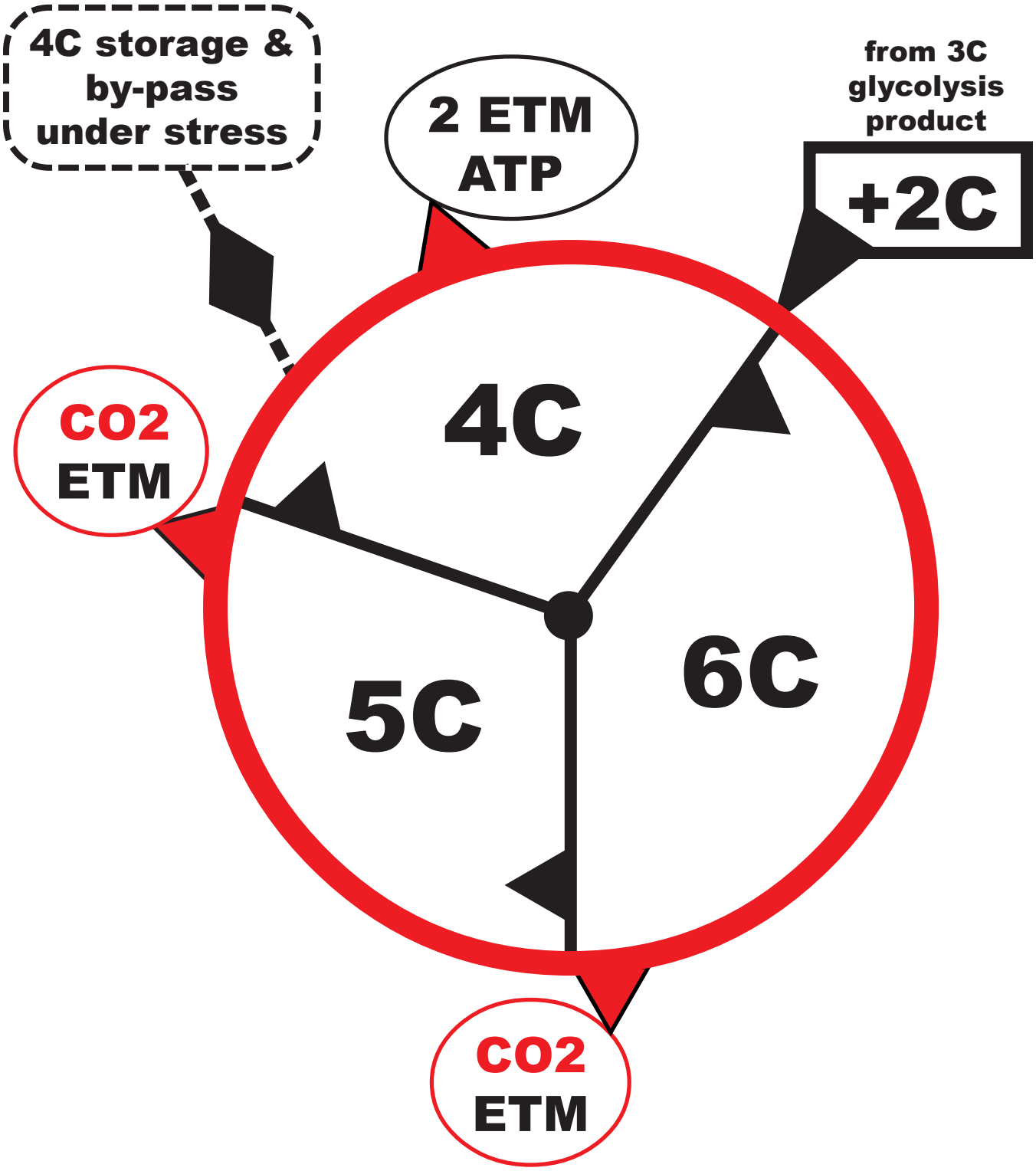


Figure 9: Primary steps of the Krebs cycle within tree mitochondria.

electron transfer molecules are usually NADPH2, NADH, and FADH2. For example, NADH (nicotinamide adenine dinucleotide) is a coenzyme which reversibly provides and takes up two electrons.

Electron transfer molecules are used to capture energy released during sugar oxidation in glycolysis and the Krebs cycle. These molecules then insert electrons into the electron transfer chain used to bank protons. The proton gradient developed from these electron transfers, ending with electrons transferred to oxygen, are used to generate ATP. From one sucrose (12C), as many as 60 ATPs can be produced.

Glycolysis

Glycolysis begins with the breakdown of 12C into two 6C*, and ends with one of two end-products -- a 3C or 4C organic acid. The 4C product can be stored and used to jump-start the Krebs cycle. The 3C product is the normal input into a mitochondria. Having two glycolysis end products is a great advantage for a tree, compared with glycolysis in an animal with only one end product. Trees have great flexibility in processing carbon chains, sustaining process cycles, and generating energy.

The primary purpose of glycolysis is to break down carbon chains and activate materials for insertion into the Krebs cycle. In this process some ATPs are needed and electron transfer molecules are energized. Glycolysis is divided into two halves, a carbon chain preparation portion and an energy extraction portion. In the first half, (Figure 10) glycolysis acts to process a variety of carbon chains like 6C* from stored starch and 12C transport sugars into 3C** generating an ETM and using 2-4 ATP.

Part II

The second half of glycolysis conserves energy. Figure 11. Here 3C** is used. Each 3C** (four generated from one 12C) generates an ATP yielding a 3C*. Under various stress conditions especially phosphorus deficiency, tree cells may bypass the 3C** step losing an ETM and ATP. The final step of glycolysis generates ATP from processing 3C* to 3C (4 more ATP for each 12C entering glycolysis). The 3C pool of molecules can then be transported into a mitochondria. Glycolysis extracts about 25% of the energy in 12C bonds leaving the rest bound in four 3C.

3C* can also be converted into a 4C unit with addition of energy from an electron transfer molecule and an addition of CO2. Figure 12. The 4C organic acid can be stored in a cell vacuole or shipped directly into the mitochondria for processing in the Krebs cycle. The 4C storage and bypass option provides flexibility in energizing materials and providing feedstock carbon chains for other processes, particularly under phosphorus deficiency. The second portion of glycolysis and the 4C storage / bypass process is shown in Figure 13.

No Go

Anaerobic conditions (<5% O2) shuts down the Krebs cycle and almost all ATP production. Any small amount of energy generated comes only from glycolysis. Figure 14. Anaerobic respiration or fermentation occurs, like glycolysis, within the cytoplasm, and generates energy through electron transfer molecules. The energy generated under anaerobic conditions is about 4% normal amounts. At first under oxygen deficiencies, cells increase respiration rates (increase CO2 release) attempting to maintain survival level ATP production. This process quickly collapses with continued lack of O2.

The final end product generated partially determines cellular damage levels. Generally in trees, ethanol producers are more flood tolerant or are low oxygen tolerant trees because ethanol evaporates away and can be reprocessed quickly with any change in oxygen concentrations. Lactate is stuck in a

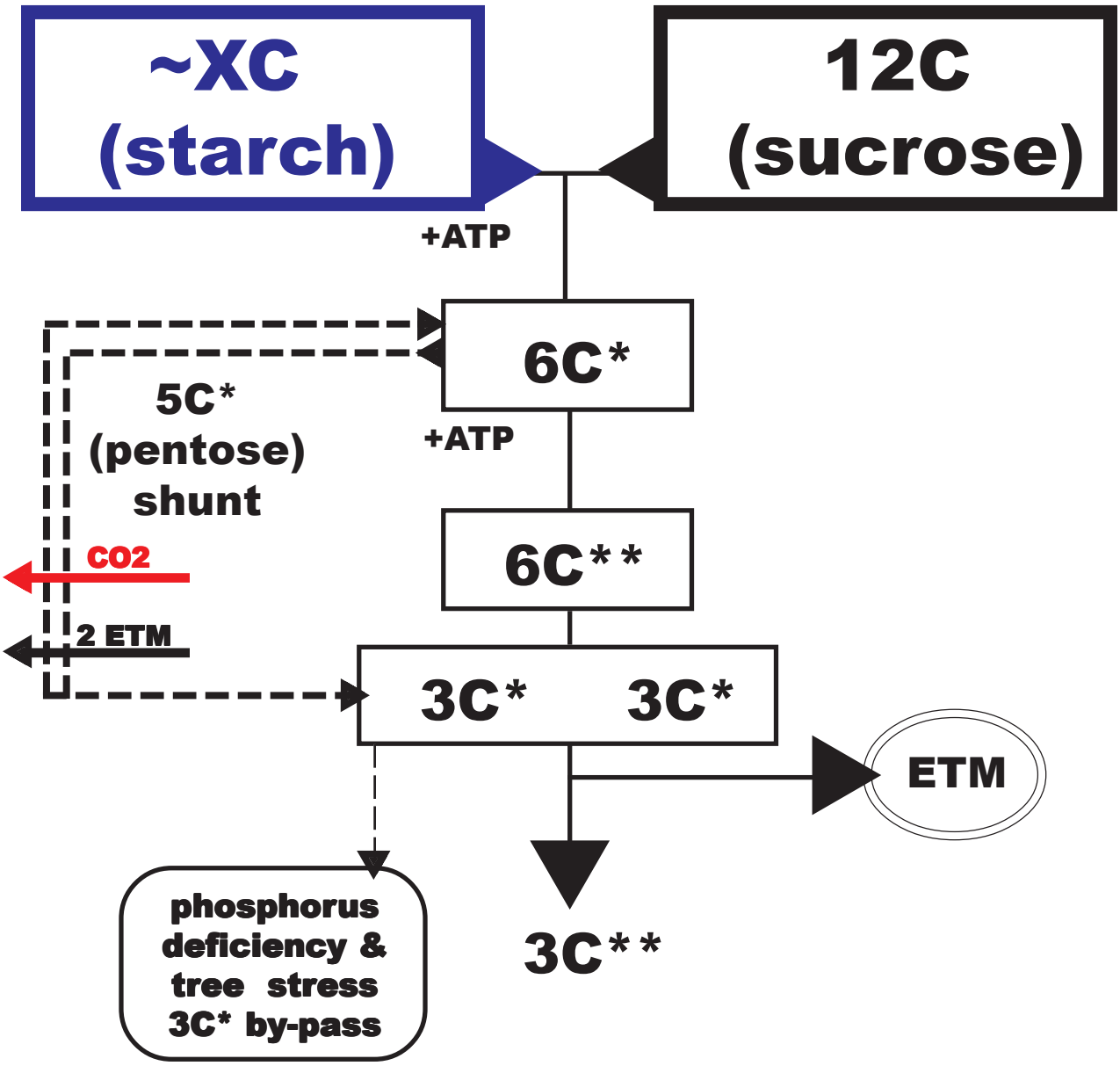


Figure 10: First portion of tree glycolysis in cell cytoplasm used to process carbon chains into tree fuel. Also shown is the 5C* shunt which generates 2ETMs and CO2.

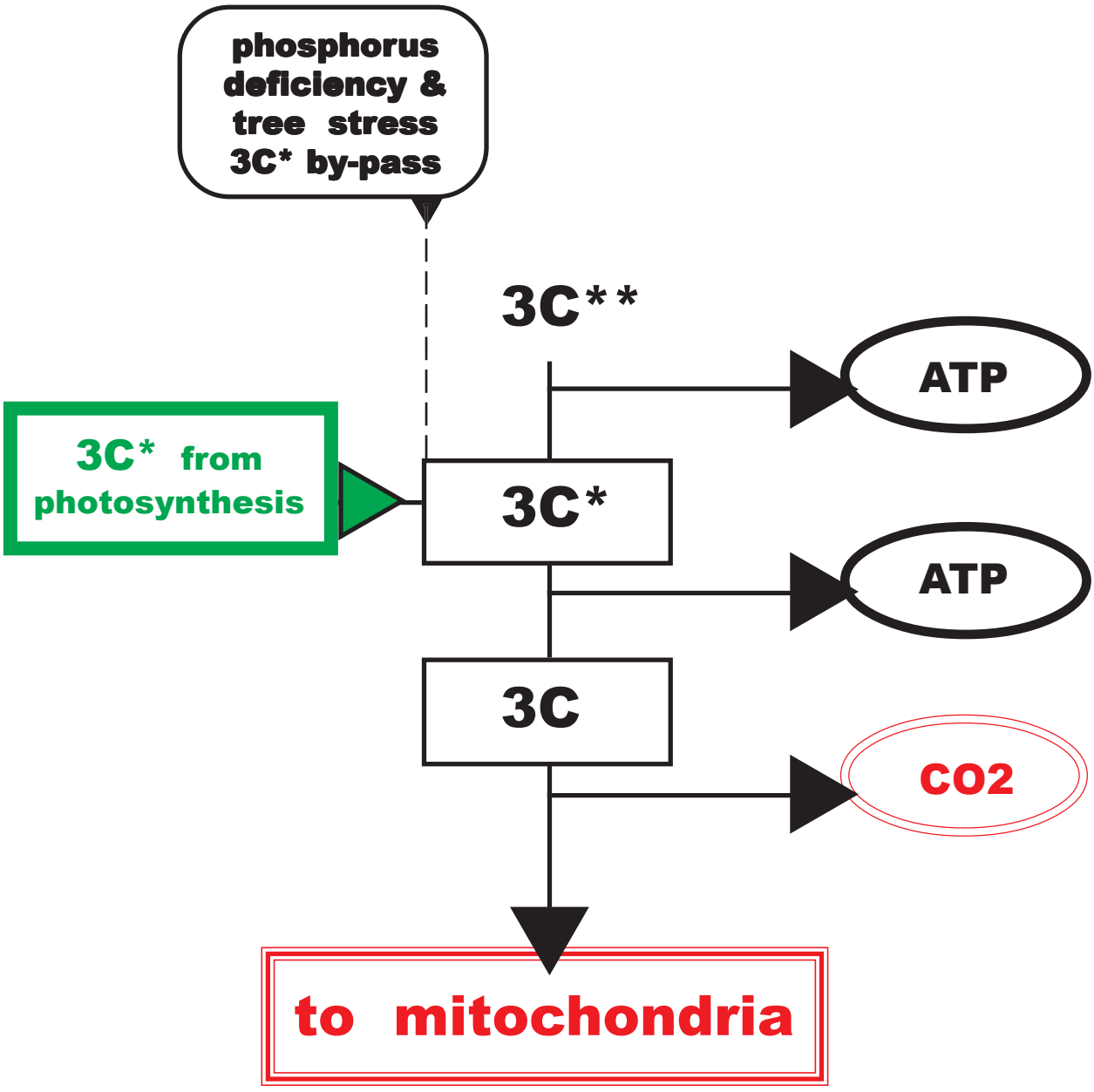


Figure 11: The second portion of tree glycolysis in cell cytoplasm used to conserve energy before 3C transfer to mitochondria.

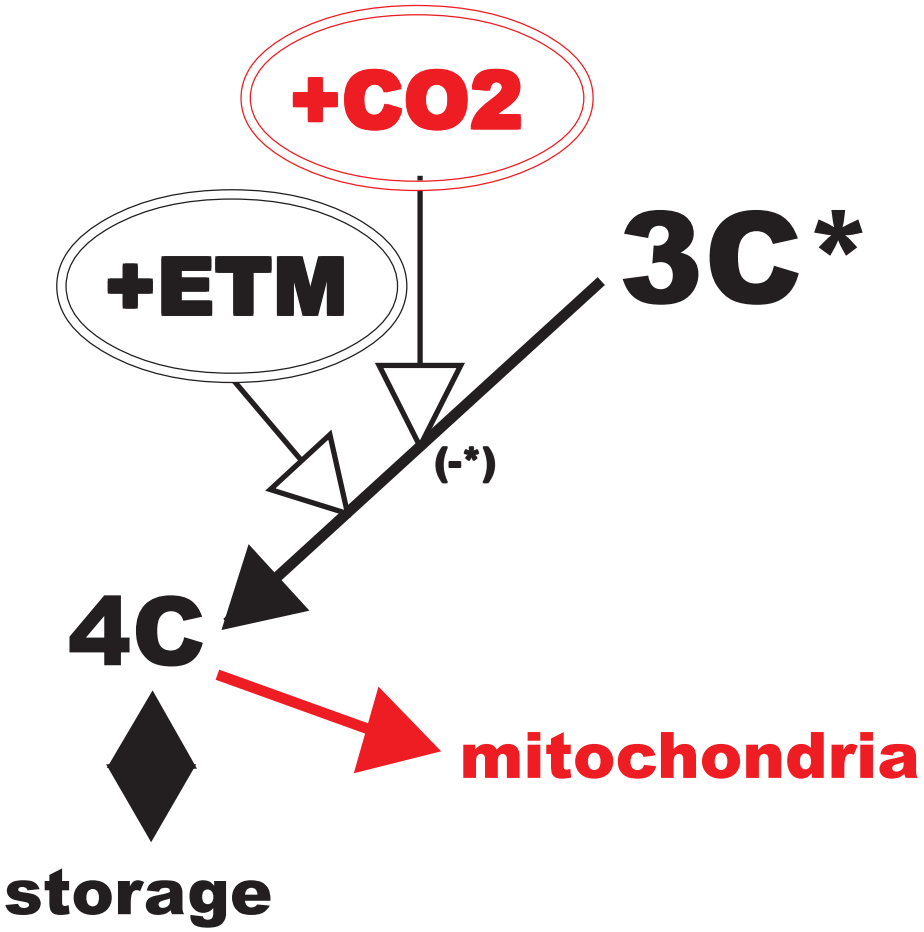


Figure 12: An energy requiring storage system of 4C branches from 3C* and bypasses normal entry material into mitochondria. This system is used under phophorus deficiencies and other stress problems.
(after Bowshur & Tobin 2021; Taiz et.al. 2014)

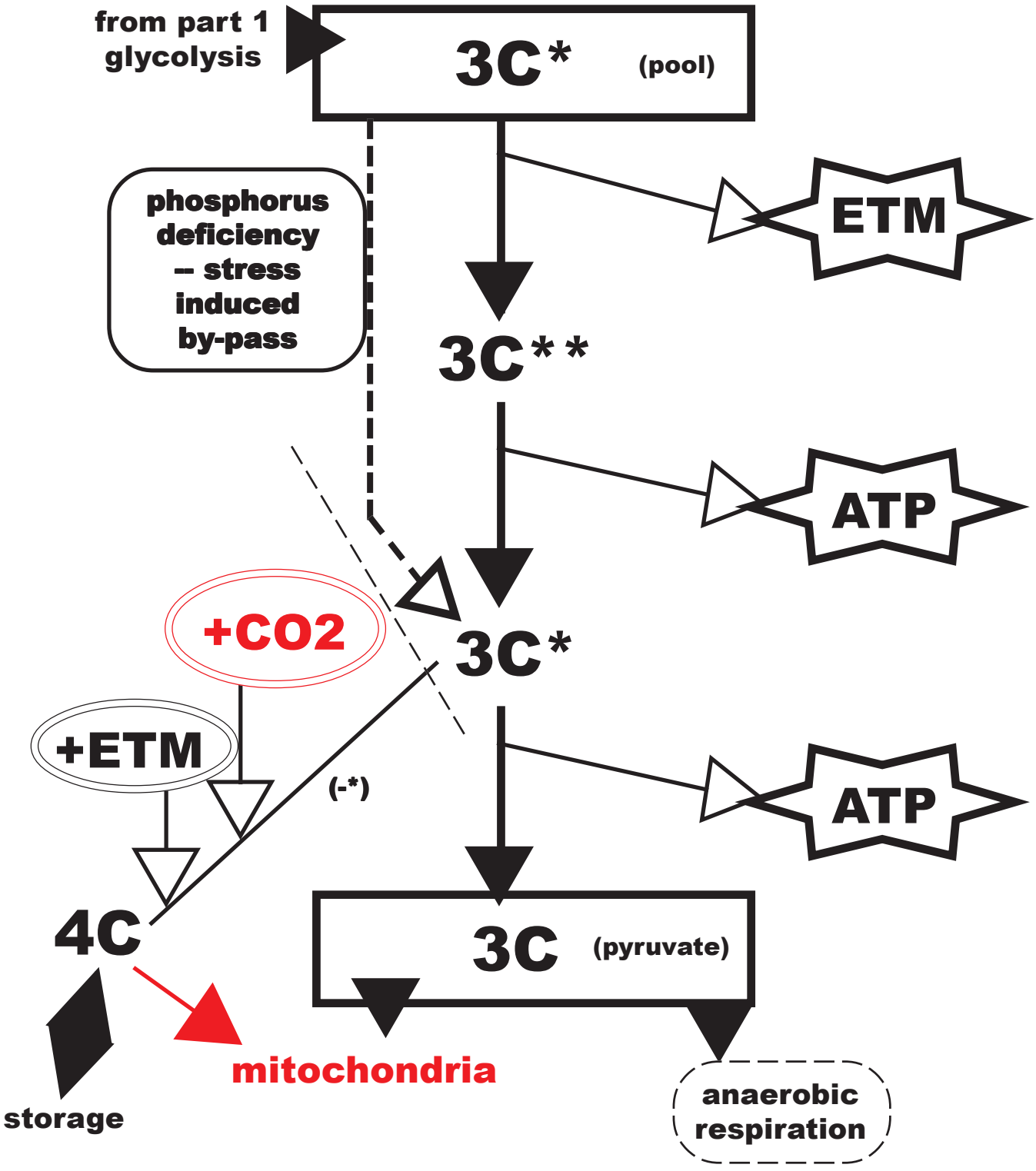


Figure 13: Combined part 2 of gycolysis generating 3C fuel for mitochondria and a 4C storage / bypass system.
(after Bowshur & Tobin 2021; Taiz et.al. 2014)

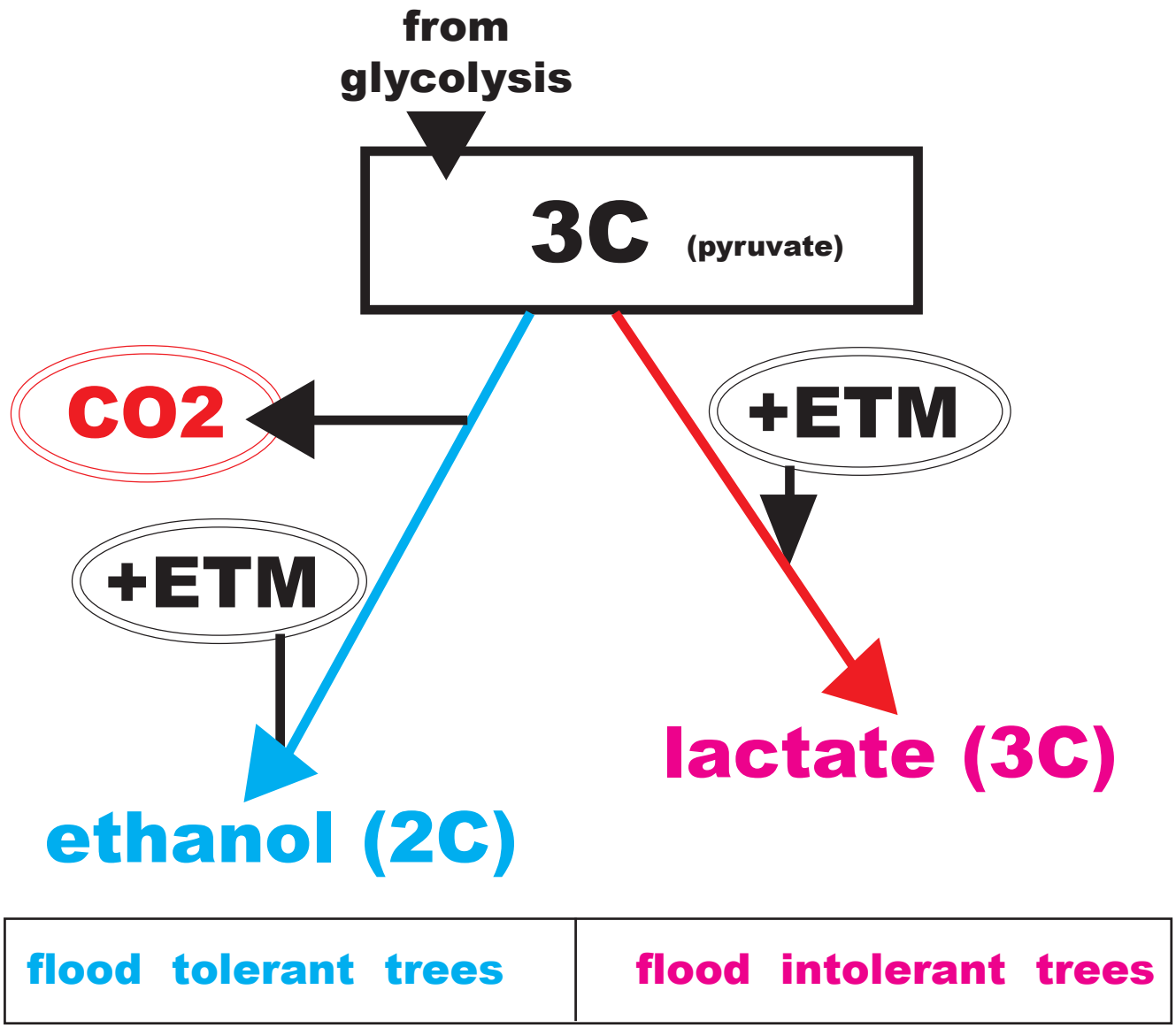


Figure 14: Anaerobic respiration (fermentation) process and end products. (after Taiz et.al. 2014)

cell and generates more severe damage the longer its residence time. Figure 15 provides an overview of anaerobic respiration compared with aerobic respiration including by-products generated and energy production.

Pentose For Your Thoughts

The 5C shunt is a side pathway off of glycolysis occurring in both cytoplasm and plastids. Processing in plastids is the dominate location. Figure 16. A 6C* from the first half of glycolysis is used to energize two electron transfer molecules while losing a CO2. The resulting 5C* pool of molecules can then be attached and separated in many ways to generate various sized carbon chains for manufacture of many other materials. 3C*, 4C*, 5C*, 6C*, and 7C* are all generated along this pathway. One of these materials generated is 6C*, the starting material of this pathway and feedstock to glycolysis.

For every six 6C* in this pathway, five 6C*, 6CO2, and 12 electron transfer molecules are generated. Glycolysis remains the main pathway (85%) along which carbon follows. The value of the 5C shunt is to:

a) energize electron transfer molecules for manufacturing other products and making ATP;

b) provide shorter carbon chains for RNA / DNA, phenolics, lignin, and some amino acids; and,

c) provide Calvin cycle (Ps) intermediates for Spring or seed start-up.

The 5C* shunt is controlled by electron transfer molecules – the greater concentration of energized electron transfer molecules, the less carbon shunted off into this pathway. Many tree stresses accelerate this pathway.

Big Show

The Krebs cycle, also called the tricarboxylic acid cycle (TCA) or the citric acid cycle, generates a great deal (>75%) of a cell's energy. The Krebs cycle occurs inside a mitochondria and requires plenty of O2. The 3C from glycolysis is stripped of one of its carbons as CO2 and an electron transfer molecule is energized. The 2C product is then combined with a 4C to generate a 6C molecule which is systematically torn up one carbon at a time until the starting 4C is generated. Figure 17. Three CO2 are produced for each 3C entering the mitochondria. The energy from these three fixed carbons have energized 5 electron transfer molecules and one ATP.

Unique in trees, compared with respiration in animals, is a 4C recycling process. A 4C from the Krebs cycle can be stripped of a carbon and energize an electron transfer molecule returning to the initial 3C organic acid which entered the mitochondria. This pathway assures the Krebs cycle can continue for a while without glycolysis delivering 3C to the mitochondria.

Making Stuff

Most carbon fixed in a tree (55%) is not used in respiration of a tree, but maintains and builds tree life. Figure 18 shows where carbon chains begin their journey to many other products in a tree. Some products are structural like cellulose and lignin. Other materials go to regulate and control tree life like forming DNA or the growth regulator auxin. The tree you see is a result of this building process, from chlorophylls to ATP.

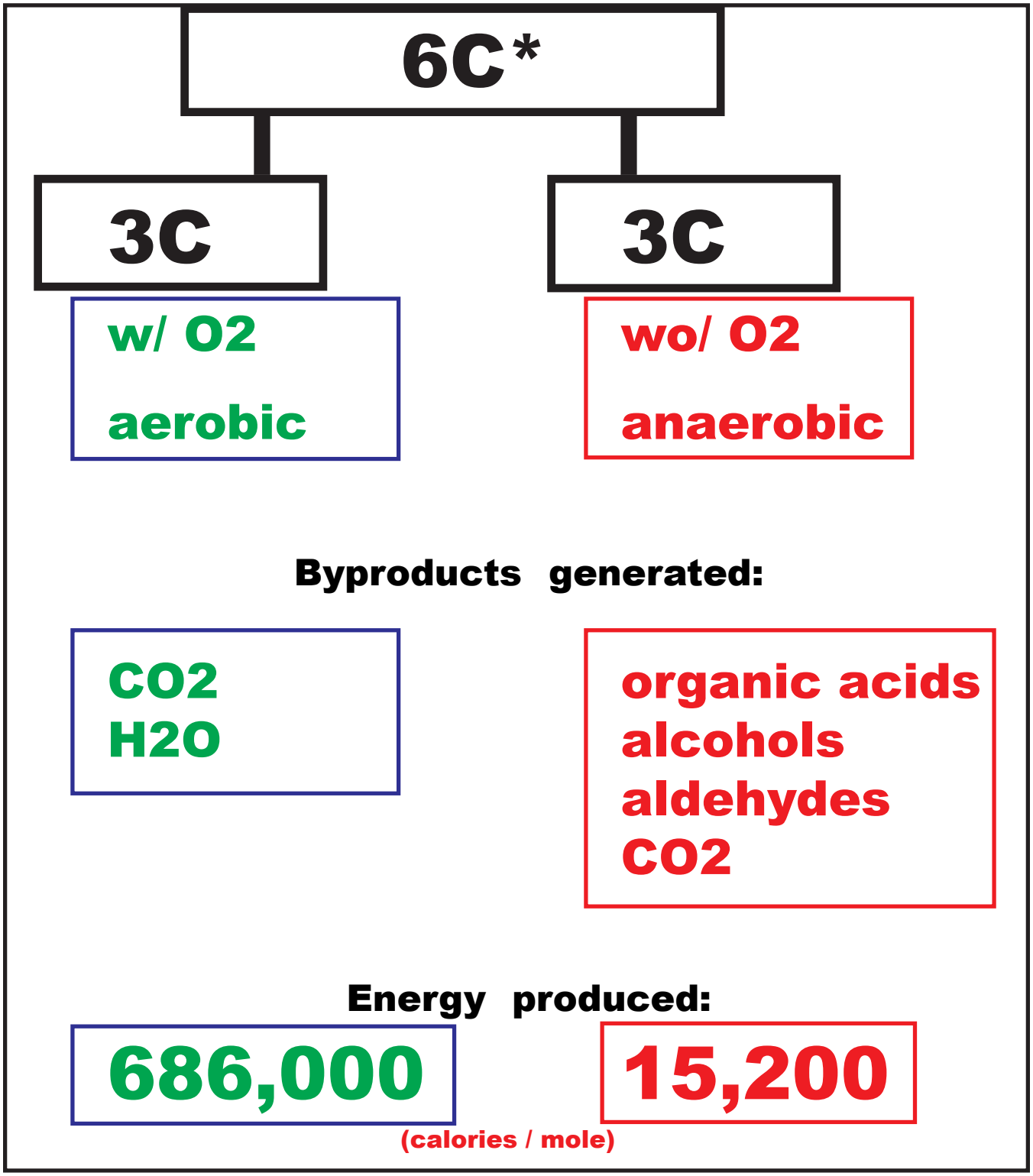


Figure 15: Difference between aerobic and anaerobic respiration conditions in trees. Anaerobic respiration generates only 2-4% the energy of aerobic respiration.

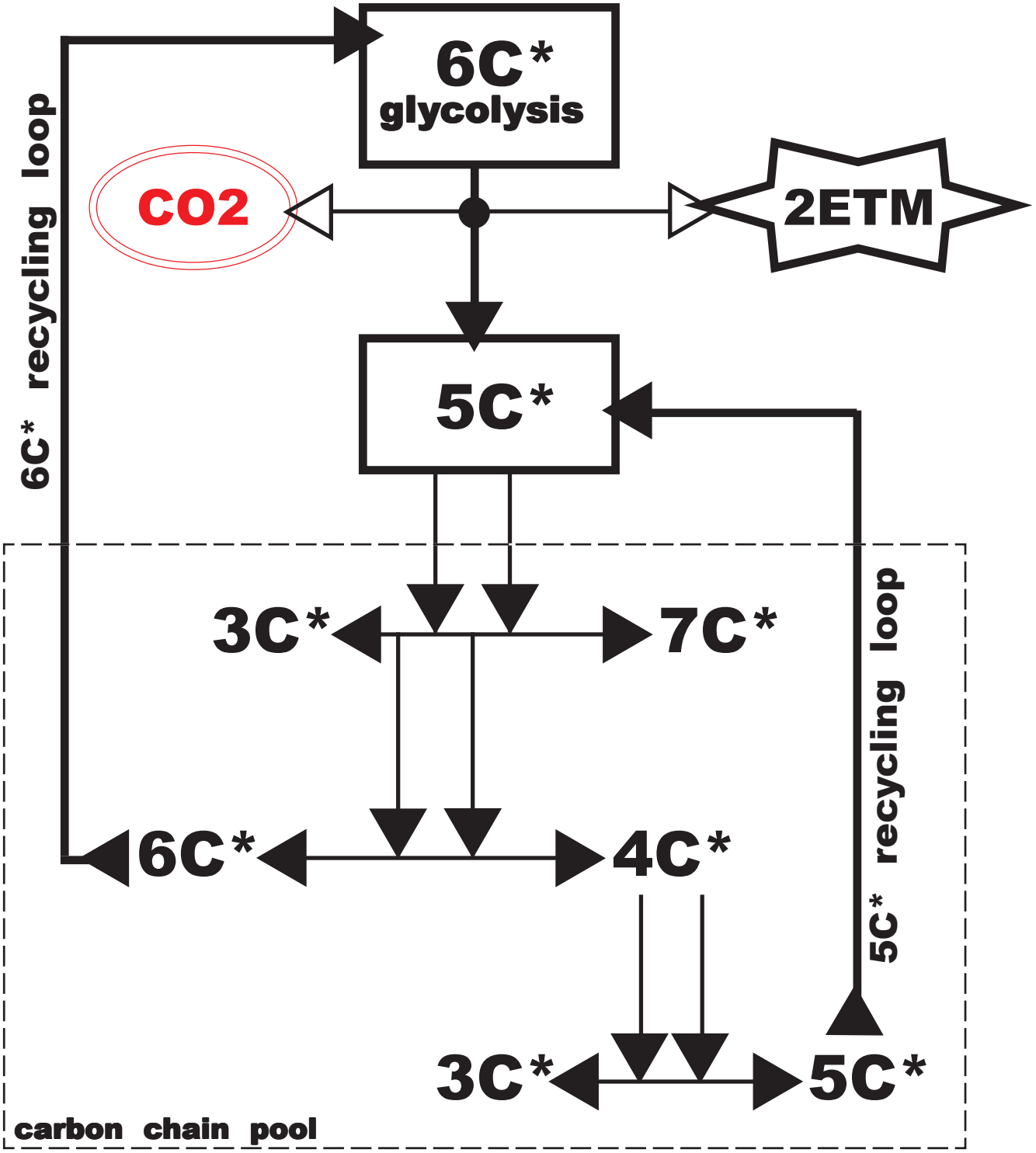


Figure 16: Reactions in the 5C* shunt. (after Taiz et.al. 2014)

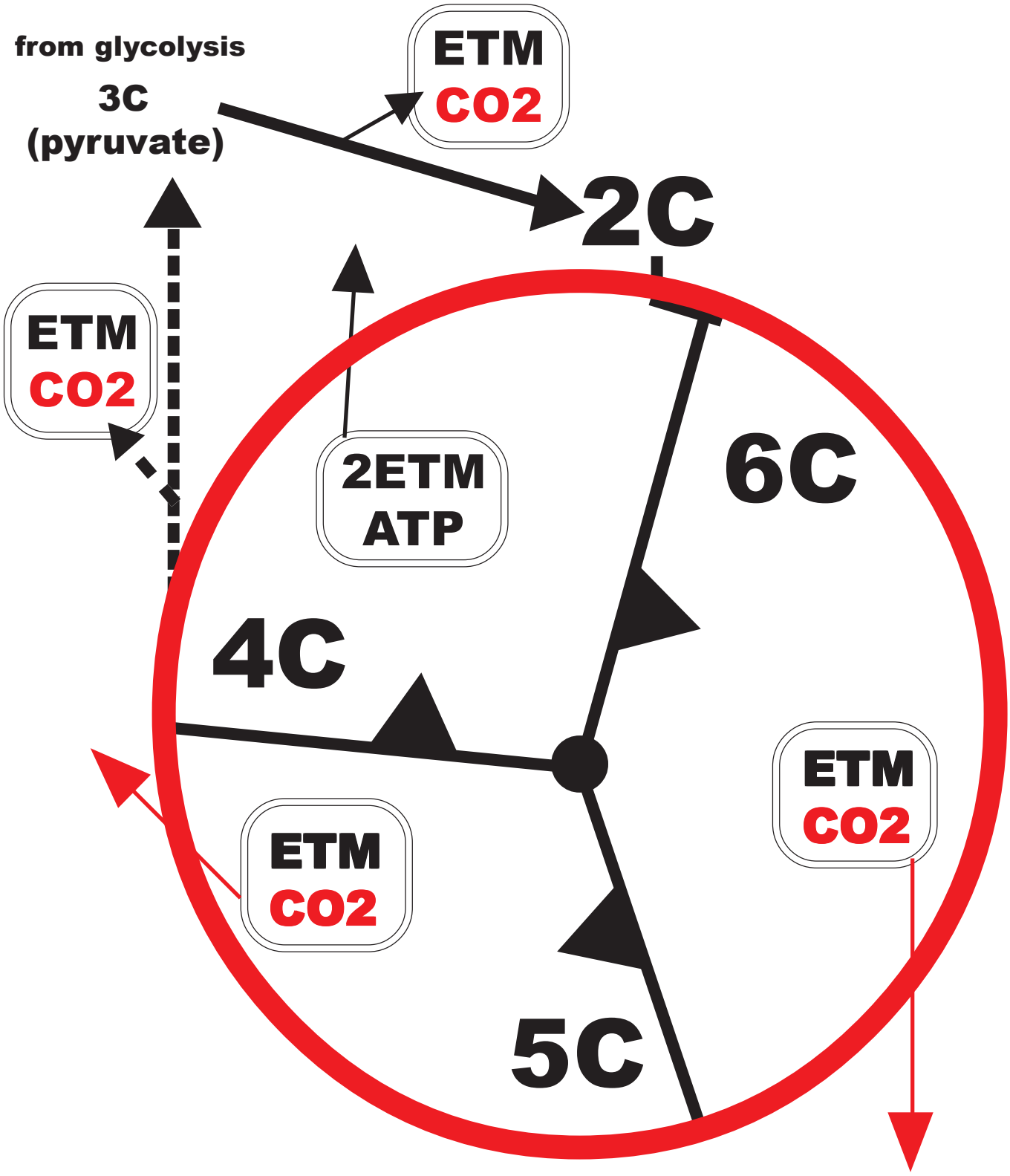


Figure 17: The Krebs cycle in trees.

(after Bowshur & Tobin 2021; Taiz et.al. 2014)

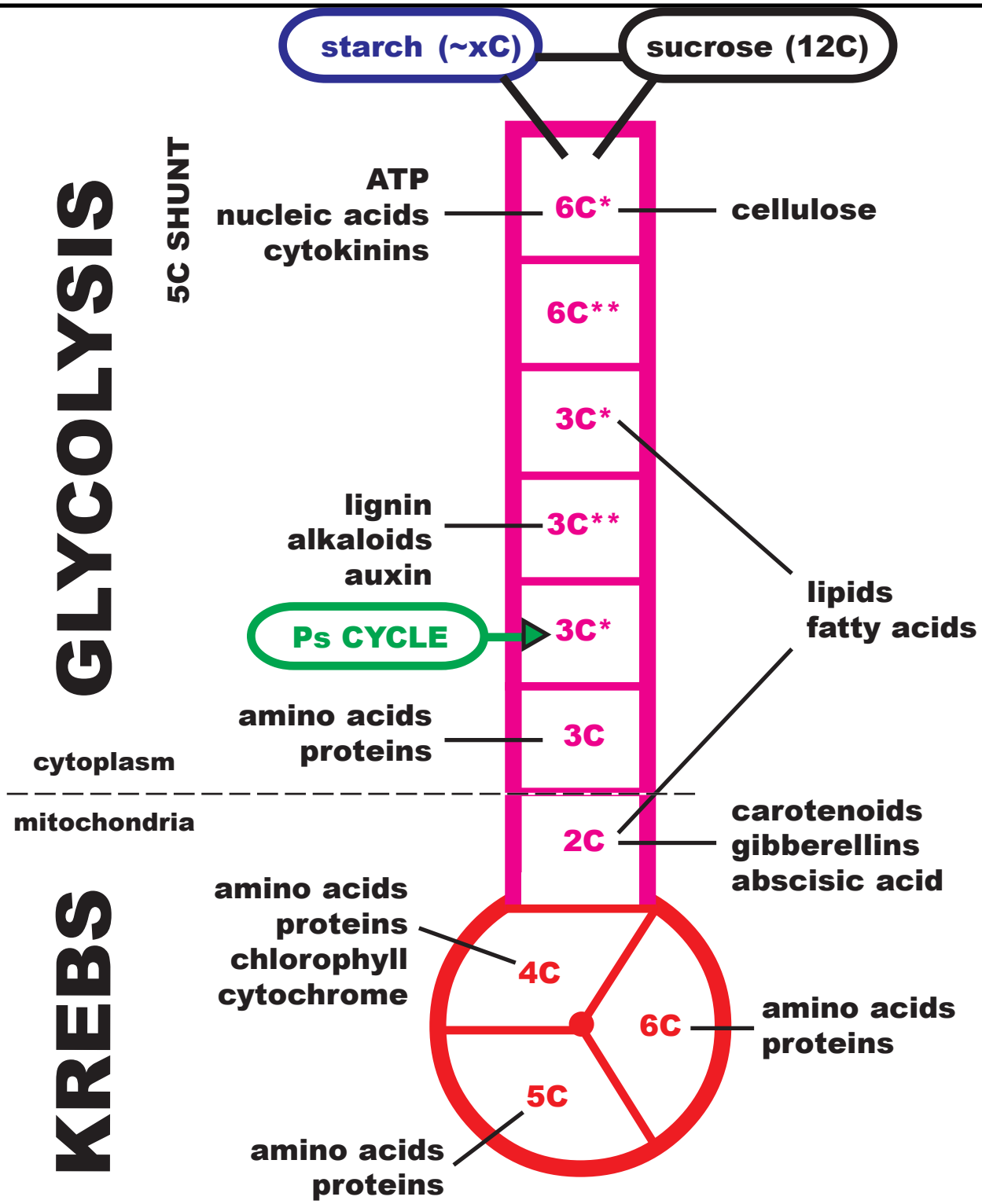


Figure 18: Selected physiological pathways in trees streaming from the respiration cycle.
(Pallardy 2008; Taiz et.al. 2014)

Some needed materials are extremely expensive for a tree to manufacture (i.e. phenolic substances and fats). Figure 19. For example, to make one unit of a carbohydrate requires 1.2 units of 6C and 0.1 unit of O2, and venting of 0.15 units of CO2. To make one unit of lipid (membrane material) requires 3 units of 6C and 0.3 units of O2, and venting of 1.5 units of CO2. The difference between making a carbohydrate and a lipid is roughly three times the inputs and 10 times the output (i.e. fixed carbon lost) for lipid manufacture. Lignin, a basic components of wood structure in trees, is also expensive to produce.

Meaning of Life

ATP powers life. Energized electron transfer molecules must have their energy converted to ATP for cell use. Electron transfer molecules give up electrons in what is called an electron transport chain. Production of ATP must occur under large oxygen concentrations because oxygen is used to accept electrons and form water. Water splitting to provide electrons for photosynthesis has now returned to making water at the final step in respiration. (Water to water -- dust to dust!)

In a general sense, the electron transfer chain of respiration is the same in all aerobes. Trees do have some significant differences compared with animal respiration. Trees have four additional sites for de-energizing electron transfer molecules and one additional site which transfers electrons to oxygen and makes water. For every 12C moving through glycolysis and the Krebs cycle, 24 energized electron transfer molecules are produced. These molecules must be de-energized or the entire respiration process will slowdown.

Herding Electrons

The electron transport chain in respiration takes electrons from energized electron transfer molecules and use released energy to pump protons (H+) into a collection pool or bank. This proton gradient can then be tapped to generate ATP. The electron transport system is attached to and through internal membranes within a mitochondria. There are four main components of the electron transport chain in trees labeled from complex I to complex IV. Figure 20.

Complex I = takes electrons from energized electron transfer molecules and moves them to ubiquinone (UQ) at the same time pumping four proton into the proton concentration bank. UQ is an electron carrier found inside mitochondria membranes.

Complex II = takes electrons from one type of 4C from the Krebs cycle and moves them to UQ with no protons concentrated.

Complex III = takes electrons from UQ and moves them to Complex IV while pumping four protons across the membrane into the proton bank.

Complex IV = is a double copper cytochrome which takes four electrons from complex III and moves them to oxygen making two water molecules and pumping four protons across the membrane (i.e. two protons pumped per every two electrons). This is the point where cyanide and carbon-monoxide stop respiration in animals.

| | shoot percent | total sugar used | tree sugar cost | CO2 produced | CO2 / sugar |
|---|---|---|---|---|---|
| **lipids**<br>fatty & resin acids<br>membrane material | 5.3 | 3.02 | 0.57 | 1.50 | 0.50 |
| **phenolics** | 20.0 | 1.92 | 0.10 | 0.56 | 0.29 |
| **lignin** | 23.3 | 1.90 | 0.08 | 0.27 | 0.14 |
| **nitrogen products**<br>aminoacids<br>protein<br>nucleic acids | 8.4 | 1.58 | 0.19 | 0.40 | 0.25 |
| **organic acids** | 3.5 | 1.48 | 0.42 | 0.48 | 0.32 |
| **carbohydrates**<br>sucrose<br>cellulose<br>hemicellulose<br>pectin<br>sugars | 38.0 | 1.18 | 0.03 | 0.14 | 0.12 |
| **minerals** | 1.5 | --- | --- | --- | --- |

Figure 19: Respiration costs for producing essential materials in live shoots of pine, placed in order of largest sugar-using product to least sugar-using product.

Note sugar cost (column 3) is column 2 / column 1.

Note CO2 / sugar (column 5) is column 4 / column 2.

(derived from Chung & Barnes 1977)

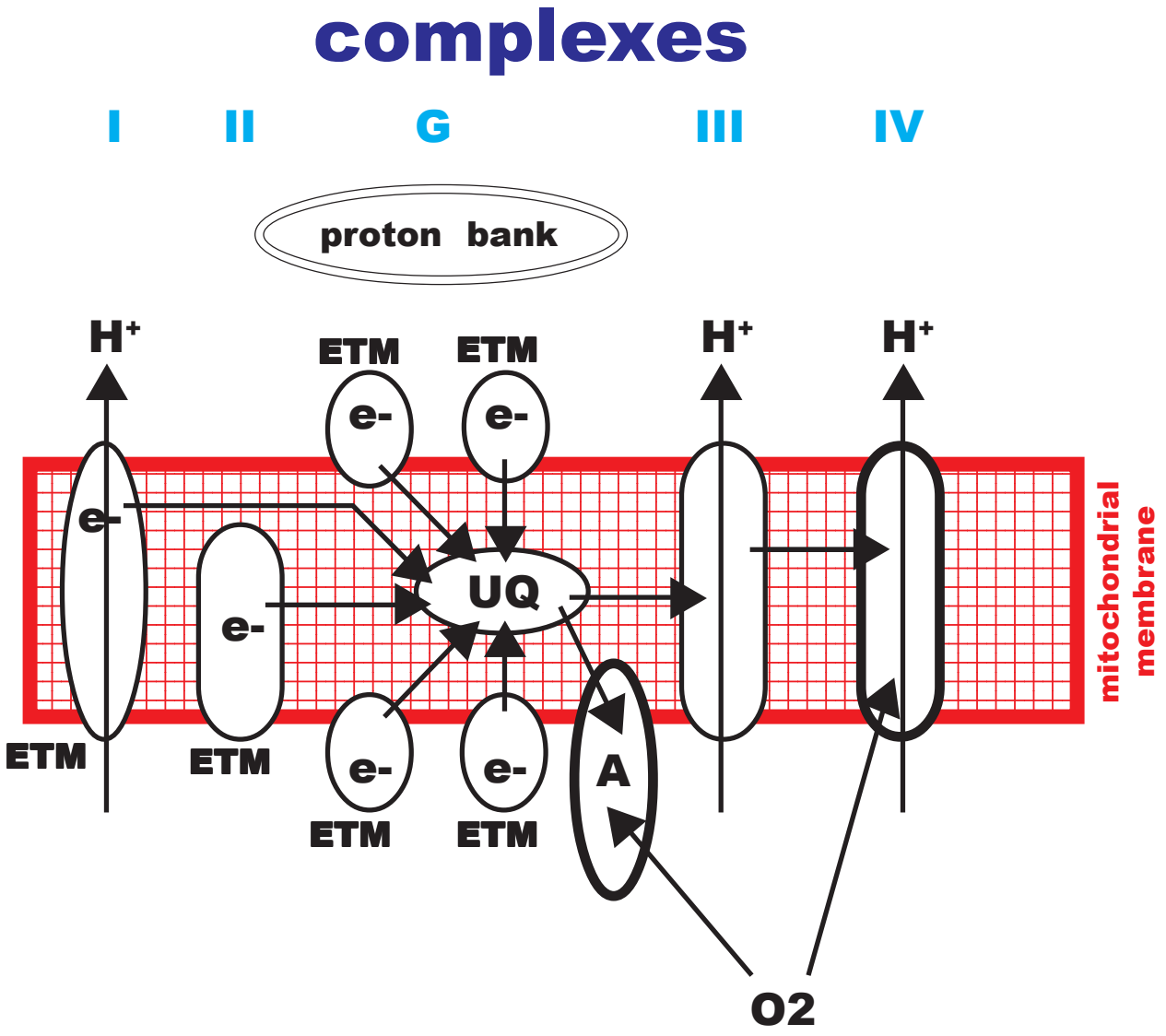


Figure 20: Electron transport chain (complexes I-IV) and four electron generators (G) on tree mitochondria membranes. ETM = electron transfer molecule; UQ = ubiquinone; A = alternative final oxygen using step; $e^-$ = electron; $H^+$ = proton. (after Bowshur & Tobin 2021; Taiz et.al. 2014)

New & Different

Trees have four unique enzyme systems (complex G) on mitochondrial membranes which take electrons from energized electron transfer molecules and move them to UQ without pumping protons. These pathways accelerate when complex I is overloaded. Because they do not pump protons, a significant portion of electron transport chain energy (as much as 40%) can be lost through this electron complex.

Trees have a second form (A) of the final step in the electron transport chain which moves electrons onto oxygen making water, similar to complex IV, but this alternative step does not pump protons. This alternative pathway plays a protective role in consuming excess electrons and removing damaging oxygen ions. It is not sensitive to cyanide or carbon-monoxide poisoning. Available energy developed as electrons pass through this alternative terminal step must be dissipated as heat, as no proton pumping and ATP production occurs. If excess ATP is produced, this alternative final water producing step will be facilitated to drain away electrons and prevent over-excitation of UQ . Various types of tree stress can accelerate the alternative step to minimize respiration complex damage.

ATP Magic

The energy of a living cell is derived from ATP (adenosine triphosphate). Release of the most exterior phosphate bond, and associated rearrangement of remaining electrons, can amount to between 7,300 to 11,000 calories per mole of ATP used. ATP is the battery power of a cell but can not leave the cell or be shipped elsewhere. ATP activates and energizes materials to react. For example, an ATP can be used to activate a 6C sugar by increasing its energy content denoted as 6C*. The phosphate portion added to the compound, in essence, acts as an energy handle with which an enzyme can manipulate 6C* to react.

ATP is made by slowly easing the proton bank gradient across chloroplast or mitochondria membranes. The proton gradient is subject to strong electro-chemical forces trying to equalize protons on both sides of a membrane. A tree cell allows a trickle of protons to run through a special production rotor (called ATP synthase) to make ATP.

ATP Genesis

ATP synthase in the mitochondria is similar, not identical, to the one in chloroplasts. ATP synthase is mitochondria membrane complex V. The number of ATP generated by proton gradient easing for every two electrons passing through complex I to complex IV is approximately 2.5. The cost in protons per ATP generated and shipped is roughly 4, if electrons are passed through complex I to complex IV.

In other word, the complete electron chain generates 10 protons for every two electrons moved and 2.5 ATP. If complex I is bypassed by G enzymes, only 6 protons for every two electrons are generated yielding 1.5 ATP. If the alternative terminal water making step is used after two electron are moved through G, no protons are concentrated and no ATP is made.

Micro-Motor

ATP is generated by the ATP synthase rotor moving at up to 18,000rpm. Figure 21 shows complex V. Protons move through this enzyme (complex V) and ratchet the production head to make ATP. The proton gradient across the membrane provides energy for this production step. A strong proton gradient provides a difference across a membrane in electrical charge (>$H^+$ amounting to -200mV

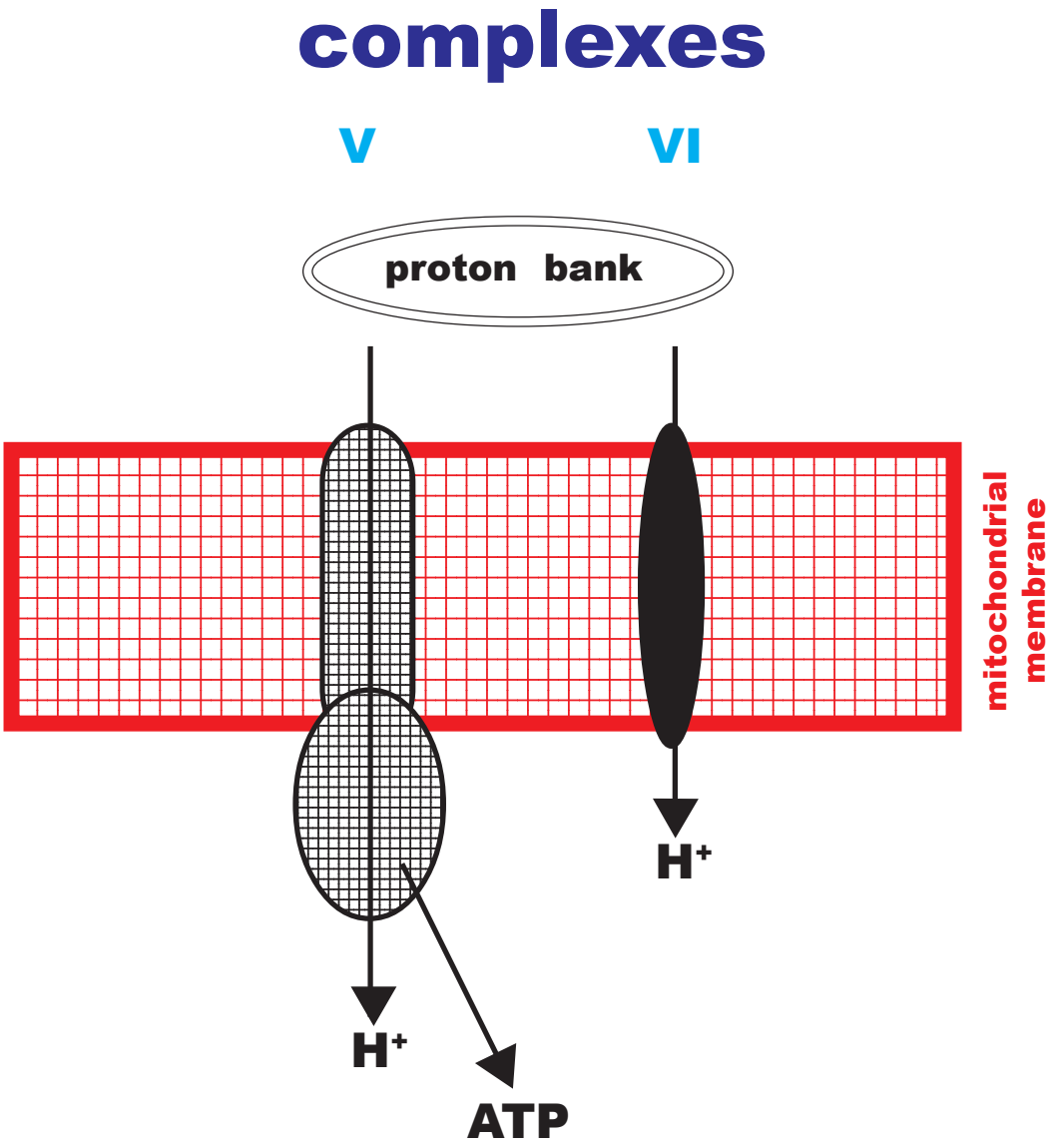


Figure 21: ATP synthase (complex V) and a proton release valve (complex VI) on a tree mitochondria membrane.

(after Taiz et.al. 2014)

difference) and in proton concentration (<pH). In a mitochondria, most proton force is provided by the difference in electrical potential, where in the chloroplast the pH difference is primarily responsible for proton motive force.

About 52 ATP is generated per 12C (sucrose) in the electron transport chain and another 8 in direct contact exchange in glycolysis and the Krebs cycle. These 60 ATP molecules comprise about 52% of the energy in a 12C. The rest of the energy fixed in 12C is lost as heat.

Spell Relief?

The last fail-safe enzyme complex in a tree mitochondria is a proton relief valve across the membrane which passively reduces high proton concentrations (i.e. complex VI in Figure 21). This complex can reduce the proton gradient, generating less ATP and more heat. Different types of tree stress constraints accelerate this function. Complex VI prevents over excitation and damage to the electron transport chain and mitochondria membranes.

Regs.

Respiration rates are controlled in a tree by build-up of products near the end of a process inhibiting processing steps closer to the beginning. For example, excess ATP slows down the electron transport chain. A slowed electron transport chain inhibits energized electron transfer molecules (EMTs) from being stripped of electrons, and so, inhibits the Krebs cycle and 2C units accumulate. As 2C units increase, the first 6C molecules of the Krebs cycle build-up and slows glycolysis at the 3C* step. Excess 3C* inhibits the earlier 6C* step from being energized with ATP. ETMs must be quickly moved away to the electron transport chain or they will inhibit the Krebs cycle. All material and energy transfer step inputs / outputs are all subject to feedback control.

To summarize, excess materials later in the respiration process inhibit earlier enzymes and product formation. Any place / pool with material contents out-of-balance from normal processing will slow the entire respiration process. For example, within photosynthetic cells in light, increasing magnesium (Mg) in the chloroplast and increasing ammonium in mitochondria stimulates ATP and fatty acid production while slowing the Krebs cycle. These same cells in the dark will have falling levels of ATP and decreasing ammonium in mitochandria, and combined with lowered mangnesium (Mg) in the chloroplast, will stimulate starch breakdown and increased glycolysis.

Concluding Rs

Respiration processes allow energy to be transfered to specialized molecules which cells use to power life. Respiration represents a slow trickling of electrons out of the symplast -- electrons originally concentrated by photosynthesis. Holding and transporting electrons within carbon chains, and concentrating protons within cell organelles, allow for tree life. Symplastic respiration processes allow proton gradients to be slowly reduced and electron holdings to be shifted to oxygen -- the net result is cellular work energy generated from using the apoplastic oxidative environment.

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