Chapter 10

The Plant Cell

10.1. Structure

Plant cells are eukaryotic and have many of the structures found in animal cells.

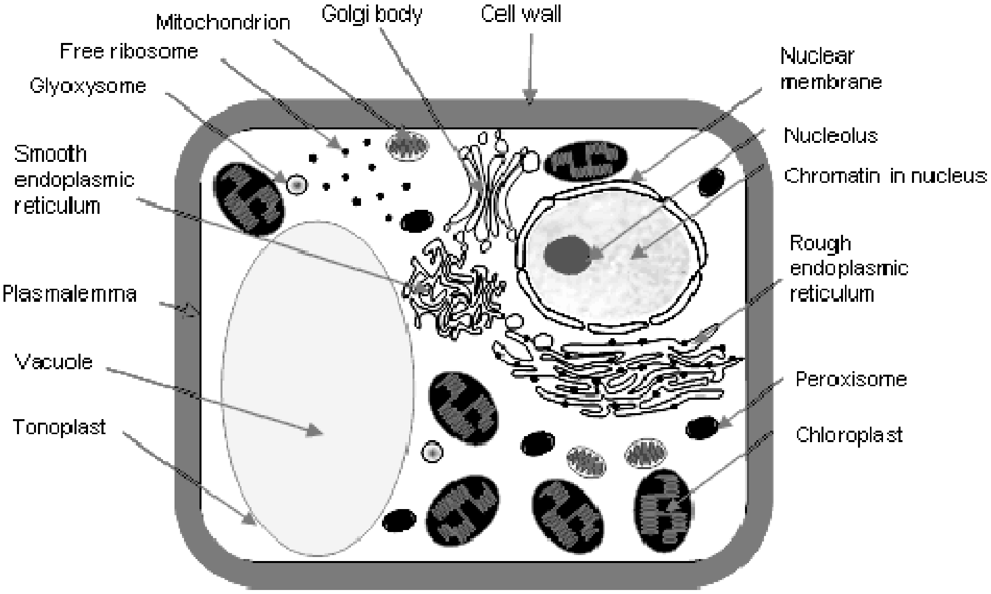

Fig.10.1. The Structure of a Plant Cell

All cells have a Plasma membrane, Nucleus and nucleolus, Mitochondria, Ribosomes, Endoplasmic reticulum, Golgi apparatus, Peroxisomes and Microtubules. Plant cells differ from animal cells in lacking centrioles, intermediate filaments and having plastids, a cell wall and large vacuoles

10.2. The Cell Wall

The rigid cell wall of plants is made of fibrils of cellulose embedded in a matrix of several other kinds of polymers such as pectin and lignin. The linear nature of cellulose molecules and the many opportunities for side-to-side intermolecular **hydrogen bonding** provide just what one would want to build long, stiff fibrils.

(a) Primary Cell Walls

The cell walls of **parenchyma** and **meristems** are uniform in thickness. Although each cell appears encased within a box, in fact primary cell walls are perforated permitting **plasmodesmata** to connect adjacent cells.

(b) Secondary Cell Walls

The cells of **sclerenchyma**, **collenchyma** and **xylem** have secondary deposits of lignified cellulose which provide mechanical strength to the tissue.

10.3. Vacuoles

Vacuoles are bounded by a single membrane. Young plant cells often contain many small vacuoles, but as the cells mature, these unite to form a large **central vacuole**. Vacuoles serve several functions, such as storing foods (e.g., proteins in seeds), storing wastes, storing malic acid in CAM plants, and maintaining turgor in the cell. Plant cells avoid bursting in hypotonic surroundings by their strong cell walls. These allow the build-up of **turgor** within the cell. Loss of turgor causes wilting.

When a freshwater (or terrestrial) plant is placed in sea water, its cells quickly lose turgor and the plant wilts. This is because sea water is **hypertonic** to the cytoplasm. As water diffuses from the cytoplasm into the sea water, the cells shrink - drawing their plasma membrane away from the cell wall.

10.4. Plastids

Chloroplasts are the most familiar plastids. They are usually disk-shaped and about 5-8 µm in diameter and 2-4 µm thick. A typical plant cell has 20-40 of them. Chloroplasts are green because they contain **chlorophylls** - the pigments that harvest the light used in photosynthesis. Chloroplasts are probably the descendants of cyanobacteria that took up residence in the ancestor of the plants. Plant cells that are not engaged in photosynthesis also have plastids that serve other functions, such as storing starch (when they are called **leucoplasts**) and storing the **carotenoids** that give flowers and fruits their colour (when they are called **chromoplasts**).

10.5. Chloroplasts

A typical plant cell (e.g., in the palisade layer of a leaf) might contain as many as 50 chloroplasts.

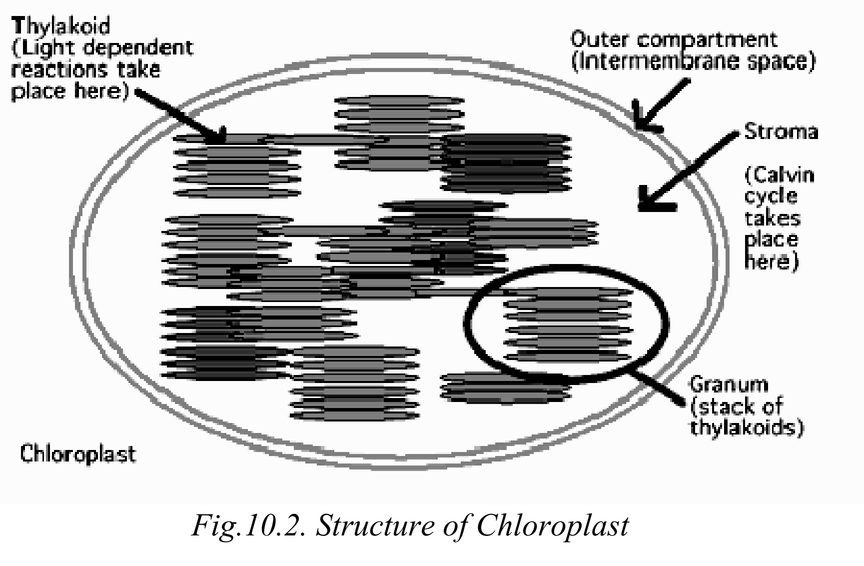

Fig.10.2. Structure of Chloroplast

The chloroplast is made up of 3 types of membrane:

1. A smooth **outer membrane** which is freely permeable to molecules.
2. A smooth **inner membrane** which contains many **transporters**: integral membrane proteins that regulate the passage in an out of the chloroplast of small molecules like

sugars and proteins synthesized in the cytoplasm of the cell but used within the chloroplast

3. A system of **thylakoid membranes**

(a) Thylakoids

The thylakoid membranes enclose a lumen: a system of vesicles (that may all be interconnected). At various places within the chloroplast these are stacked in arrays called **grana** (resembling a stack of coins). Four types of protein assemblies are embedded in the thylakoid membranes:

1. **Photosystem I** which includes chlorophyll and carotenoid molecules
2. **Photosystem II** which also contains chlorophyll and carotenoid molecules
3. **Cytochromes b** and **f**
4. **ATP synthase**

These carry out the so-called **light reactions of photosynthesis**.

(b) Stroma

The thylakoid membranes are surrounded by a fluid **stroma**. The stroma contains:

1. All the enzymes, e.g., RUBISCO, needed to carry out the "dark" reactions of photosynthesis; that is, the conversion of CO_2 into organic molecules like glucose.
2. A number of identical molecules of DNA, each of which carries the complete chloroplast genome. The genes encode some - but not all - of the molecules needed for chloroplast function. The others are
    a. Transcribed from genes in the **nucleus** of the cell
    b. Translated in the cytoplasm and
    c. Transported into the chloroplast.

10.6. Photosynthesis: The Role of Light

The heart of photosynthesis as it occurs in most **autotrophs** consists of two key processes:

1. The removal of hydrogen (H) atoms from water molecules
2. The reduction of carbon dioxide (CO_2) by these hydrogen atoms to form organic molecules.

The second process involves a cyclic series of reactions named (after its discoverer) the **Calvin Cycle**. The electrons (e^-) and protons (H^+) that make up hydrogen atoms are stripped away separately from water molecules.

$$2H_2O \rightarrow 4e^- + 4H^+ + O_2$$

The electrons serve two functions:

1. They reduce $NADP^+$ to **NADPH** for use in the Calvin Cycle.
2. They set up an electrochemical charge that provides the energy for pumping protons from the **stroma** of the **chloroplast** into the interior of the thylakoid.

The protons also serve two functions:

1. They participate in the reduction of $NADP^+$ to NADPH.
2. As they flow back out from the interior of the thylakoid (by facilitated diffusion), passing **down** their concentration gradient), the energy they give up is harnessed to the conversion of ADP to **ATP**. Because it is drive by light, this process is called **photophosphorylation**.

$$ADP + P_i \rightarrow ATP$$

The ATP provides the second essential ingredient for running the Calvin Cycle. The removal of electrons from water molecules and their transfer to $NADP^+$ requires energy. The electrons are moving from a redox potential of about +0.82 volt in water to −0.32 volt in NADPH. Thus enough energy must be available to move them against a total potential of 1.14 volts and the needed energy come **Light**.

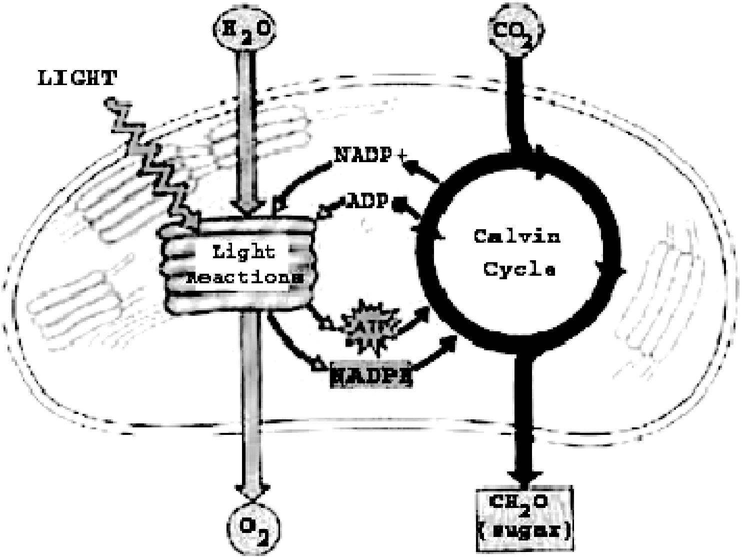

Fig.10.3.Photosynthetic pathways

(a) The Thylakoid Membrane

Chloroplasts contain a system of thylakoid membranes surrounded by a fluid **stroma**.
Six different complexes of **integral membrane proteins** are embedded in the thylakoid membrane. The exact structure of these complexes differs from group to group (e.g., plant vs. alga) and even within a group (e.g., illuminated in air or underwater). But, in general, one finds:

(i) Photosystem I

The structure of **photosystem I** in a cyanobacterium ("blue-green alga") has been completely worked out. It probably closely resembles that of plants as well. It is a homotrimer with each subunit in the trimer containing 12 different protein molecules bound to 96 molecules of **chlorophyll a** 2 molecules of the **reaction centre chlorophyll** $\mathbf{P_{700}}$, 4 accessory molecules closely associated with them, 90 molecules that serve as antenna pigments, 22 **carotenoid** molecules, 4 lipid molecules, 3 clusters of Fe_4S_4 and 2 phylloquinones.

(ii) Photosystem II

Photosystem II is also a complex of more than 20 different protein molecules bound to 50 or more **chlorophyll a** molecules, 2 molecules of the **reaction centre chlorophyll** $\mathbf{P_{680}}$, 2 accessory molecules close to them, 2 molecules of pheophytin (chlorophyll without the Mg^{++}). The remaining molecules of **chlorophyll a** serve as **antenna pigments**. Some half dozen **carotenoid** molecules also serve as antenna pigments and 2 molecules of **plastoquinone**

(b) Light-Harvesting Complexes (LHC)

1. LHC-I associated with photosystem I
2. LHC-II associated with photosystem II

These LHCs also act as **antenna pigments** harvesting light and passing its energy on to their respective photosystems. The LHC-II of spinach is a homotrimer, with each monomer containing a single polypeptide, 8 molecules of chlorophyll a, 6 molecules of chlorophyll b, 4 carotenoid molecules, 5. Cytochromes b_6 and f and 6. ATP synthase.

(c) How the System Works

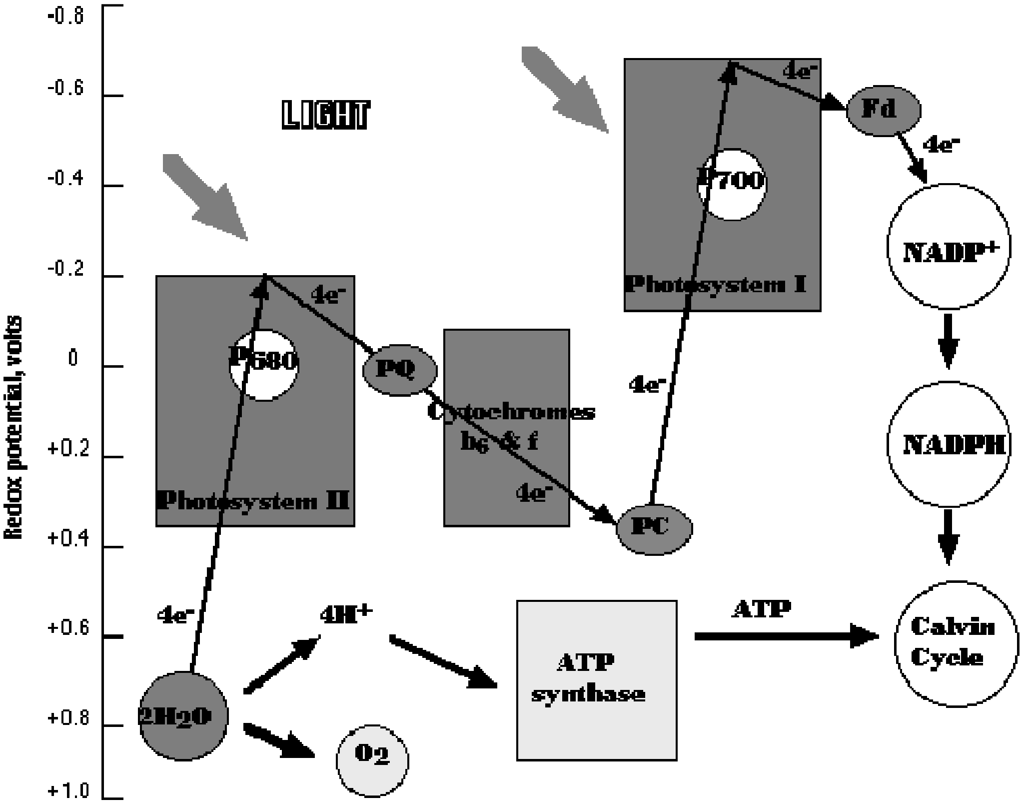

Fig.10.4. The Z-Diagram

Light is absorbed by the antenna pigments of **photosystems II** and **I**. The absorbed energy is transferred to the reaction centre pigment, $\mathbf{P_{680}}$ in photosystem II, $\mathbf{P_{700}}$ in photosystem I. Activation of $\mathbf{P_{680}}$ in Photosystem **II** removes an electron from it. With its resulting positive charge, P_{680} is sufficiently **electronegative** that it can remove electrons from water. These electrons are transferred (by way of **plastoquinone** — **PQ** in fig. 10.4) to the **cytochrome $\mathbf{b_6}$/f** complex where they provide the energy for **chemiosmosis**. Activation of $\mathbf{P_{700}}$ in photosystem **I** enables it to pick up electrons from the cytochrome b_6/f complex (by way of plastocyanin — **PC** in fig. 10.4) and raise them to a sufficiently high redox potential that, after passing through **ferredoxin** (**Fd** in the figure), they can reduce $NADP^+$ to **NADPH**. The sawtooth shifts in redox potential as electrons pass from P_{680} to $NADP^+$ have caused this system to be called the **Z-Scheme** (although the diagram looks more like an "N"). It is also called **noncyclic photophosphorylation** because it produces ATP in a one-way process (unlike **cyclic photophosphorylation** and **pseudocyclic photophosphorylation**).

10.7. Chemiosmosis in Chloroplasts

The energy released as electrons pass down the gradient between photosystem II and photosystem I is harnessed by the cytochrome b_6/f complex to pump **protons** (**H^+**) **against** their concentration gradient from the stroma of the chloroplast into the interior of the thylakoid (an example of **active transport**). As their concentration increases inside (which is the same as saying that the **pH** of the interior decreases), a strong diffusion gradient is set up. The only exit for these protons is through the **ATP synthase** complex. As in **mitochondria**, the energy released as these protons flow down their gradient is harnessed to the synthesis of **ATP**. The process is called **chemiosmosis** and is an example of facilitated diffusion.

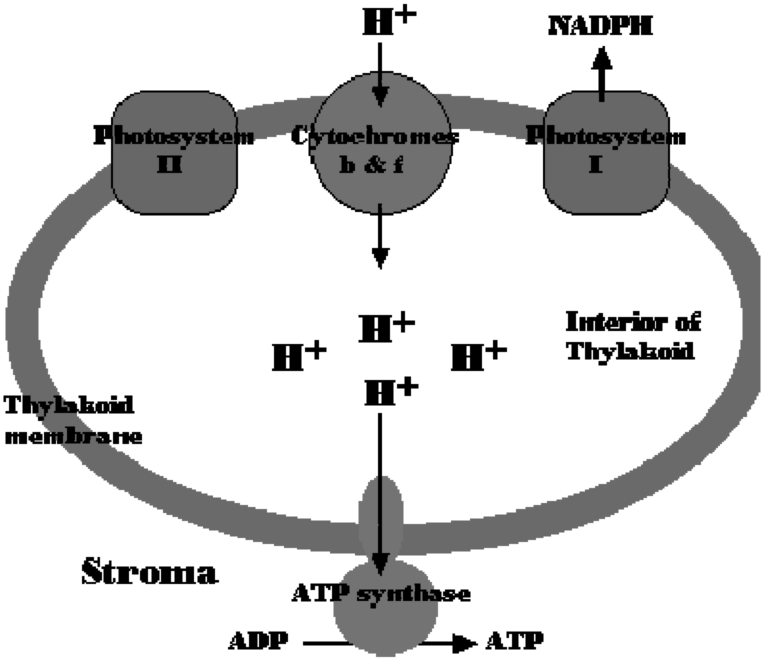

Fig.10.5. Chemiosmosis in Chloroplasts

(a) Cyclic Photophosphorylation

Each CO_2 taken up by the **Calvin cycle**) requires 2 NADPH molecules and 3 ATP molecules. Each molecule of oxygen released by the light reactions supplies the 4 electrons needed to make 2 NADPH molecules. The chemiosmosis driven by these 4 electrons as they pass through the cytochrome b_6/f complex liberates only enough energy to pump **12** protons into the interior of the thylakoid. But in order to make 3 molecules of ATP, the ATPase in chloroplasts appears to have **14** protons (H^+) pass through it. So there appears to be a deficit of 2 protons which is made up by **cyclic photophosphorylation**. In cyclic photophosphorylation, the electrons expelled by the energy of light absorbed by **photosystem I** pass, as normal, to **ferredoxin** and may even go on to reduce **$NADP^+$** to **NADPH**. But instead of then going on to the **Calvin cycle**, they pass instead to **plastoquinone** and on back into the **cytochrome b_6/f complex**. Here the energy each electron liberates pumps 2 protons (H^+) into the interior of the thylakoid — enough to make up the deficit left by noncyclic photophosphorylation. This process is truly cyclic because no outside source of electrons is required. Like the photocell in a light meter, **photosystem I** is simply using light to create a flow of current. The only difference is that instead of using the current to move the needle on a light meter, the chloroplast uses the current to help synthesize ATP.

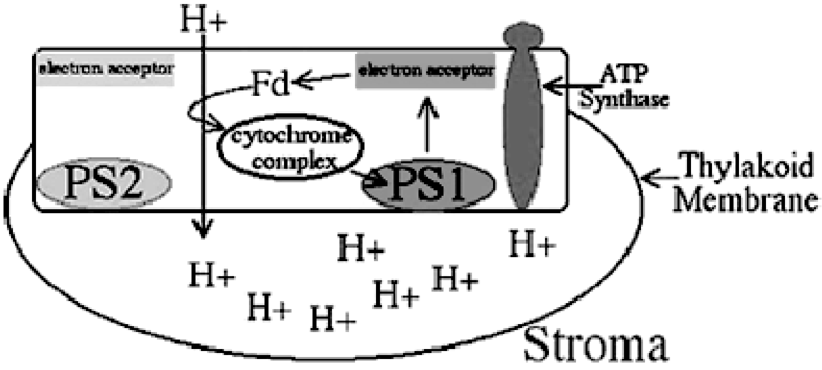

Fig.10.6. Cyclic Photophosphorylation

(b) Pseudocyclic Photophosphorylation

Some workers believe that cyclic photophosphorylation is simply an artifact of the preparations studied in the laboratory. They think that the deficit is made up instead by a process called **pseudocyclic photophosphorylation** in which some of the electrons passing to **ferredoxin** then reduce molecular **oxygen** back to **H_2O** instead of reducing **$NADP^+$** to **NADPH**. At first glance, this might seem a fruitless undoing of all the hard work of photosynthesis. But look again. Although the electrons cycle from water to ferredoxin and back again, part of their pathway is through the chemiosmosis-generating stem of cytochrome b_6/f. Here, then, is another way that simply by turning on a light, enough energy is imparted to electrons that they can bring about the synthesis of ATP.

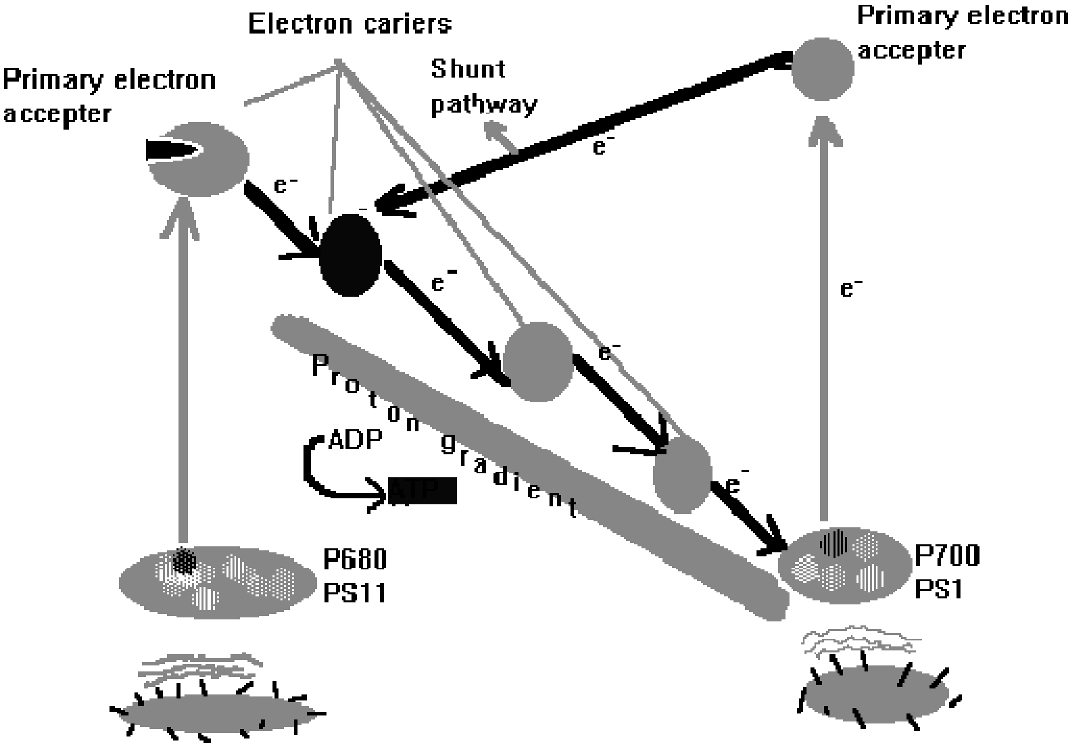

Fig.10.7. Pseudocyclic Photophosphorylation

(c) Antenna Pigments

Chlorophylls a and b differ slightly in the wavelengths of light that they absorb best (although both absorb red and blue much better than yellow and green). Carotenoids help fill in the gap by strongly absorbing green light. The entire complex ensures that most of the energy of light will be trapped and passed on to the reaction centre chlorophylls.

10.8. Photosynthesis: Pathway of Carbon Fixation

Photosynthesis is the synthesis of organic molecules using the energy of light. For the sugar glucose (one of the most abundant products of photosynthesis) the equation is:

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

Light provides the energy to transfer electrons from water to **Nicotinamide Adenine Dinucleotide Phosphate** (**NADP$^+$**) forming **NADPH**; **ATP** and **NADPH** provide the energy and electrons to reduce carbon dioxide (CO_2) to organic molecules.

The Steps in this process are as follows:

1. CO_2 combines with the phosphorylated 5-carbon sugar **ribulose bisphosphate**.
2. This reaction is catalyzed by the enzyme **ribulose bisphosphate carboxylase oxygenase** (**RUBISCO**)(an enzyme which can fairly claim to be the most abundant protein on earth).
3. The resulting 6-carbon compound breaks down into two molecules of **3-phosphoglyceric acid** (**PGA**).
4. The PGA molecules are further phosphorylated (by **ATP**) and are reduced (by **NADPH**) to form **phosphoglyceraldehyde** (**PGAL**).
5. Phosphoglyceraldehyde serves as the starting material for the synthesis of **glucose** and **fructose**.
6. Glucose and fructose make the disaccharide **sucrose**, which travels in solution to other parts of the plant (e.g., fruit, roots).
7. Glucose is also the monomer used in the synthesis of the **polysaccharides starch** and **cellulose**.

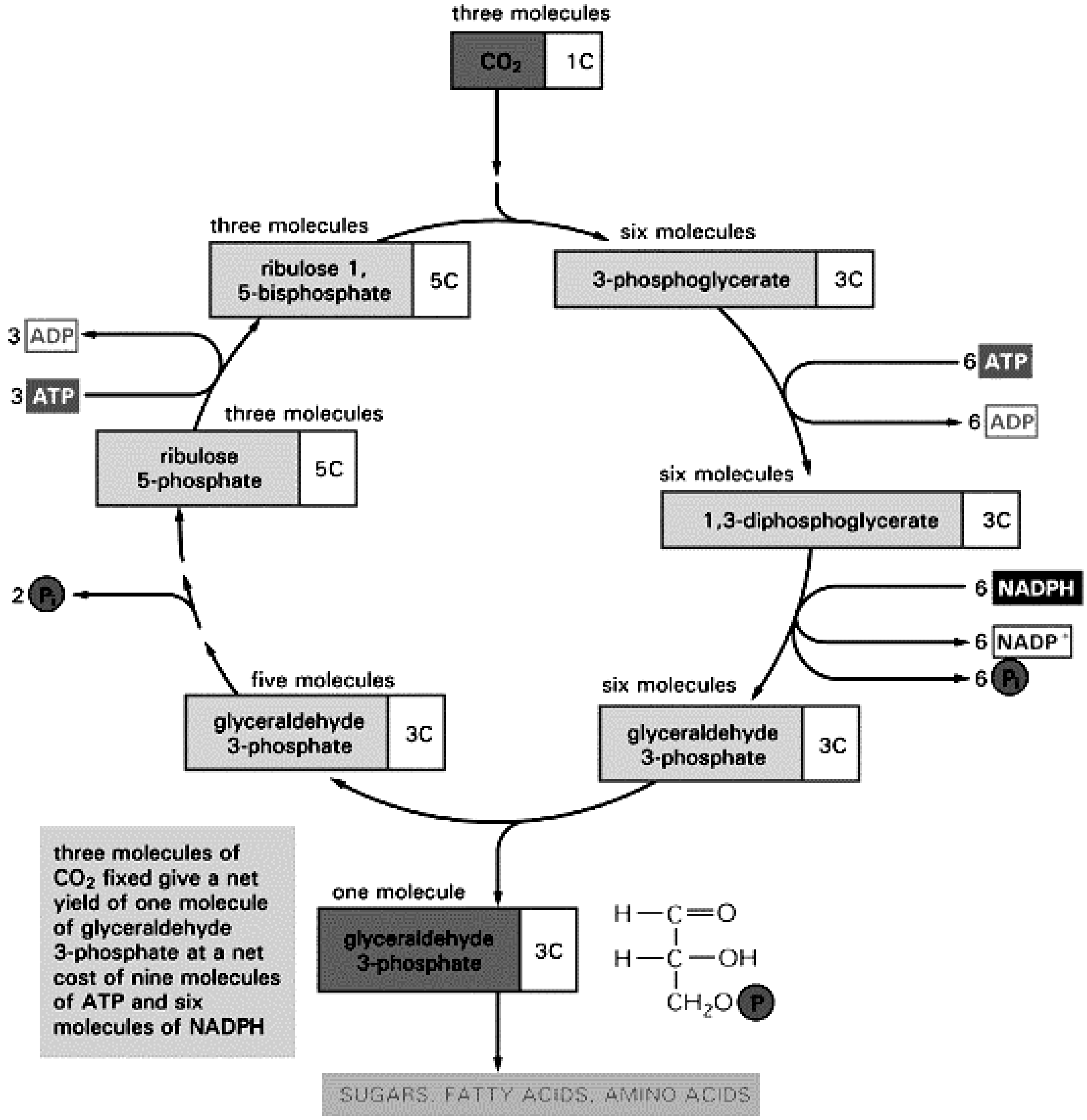

Fig.10.8. The Calvin Cycle

The graphic shows the steps in the fixation of carbon dioxide during photosynthesis. These steps were worked out by **Melvin Calvin** and his colleagues at the **University of California** and, for this reason, are named the Calvin cycle.

10.9. The Energy Relationships in Cellular Respiration and Photosynthesis: The Balance Sheet

The respiration (or burning) of a **mole** of glucose releases 686 kcal of energy. This value represents the difference between the energy needed to break the bonds of the reactants (glucose and oxygen) and the energy liberated when the bonds of the products (H_2O and CO_2) form. Conversely, the photosynthesis of a mole of glucose requires the input of 686 kcal of energy. The reasons: water and carbon dioxide the differences in **electronegativity** between their atoms are high so they have **polar covalent bonds** with high **bond energies** these are strong bonds broken with difficulty and liberating copious amounts of energy when they form glucose and oxygen the differences in electronegativity between their atoms tend to be lower so they form covalent bonds with average bond energies on the low side these are broken with relative ease. The diagram shows the details.

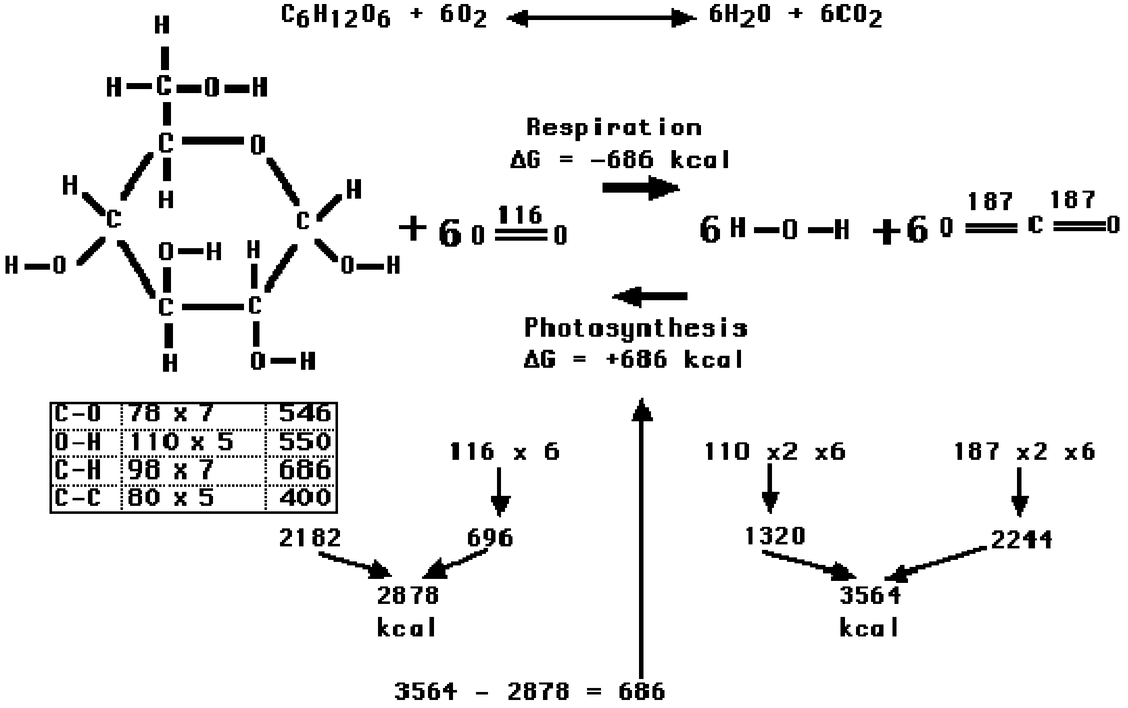

Fig.10.9. Energy Balance Sheet

The overall equation for each process is the same; only the direction of the arrow differs. (The actual equation is:

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

but we shall ignore the six molecules of water that occur on each side as they "cancel out".) The structural formulas are shown as well as the average bond energies for each bond involved.

(a) Cellular Respiration

As you can see, the 24 moles of covalent bonds in a mole of glucose require a total of 2182 kcal to be broken. The 6 double bonds of oxygen require another 696. Thus a grand total of 2878 kcal is needed to break all the bonds of the reactants in cellular respiration. As for the products, The formation of 6 moles of CO_2 involves the formation of 12 double polar covalent bonds each with a bond energy of 187 kcal/mole; total = 2244. The formation of 6 moles of H_2O involves the formation of 12 O-H bonds each with an energy of 110 kcal/mole; total = 1320. Thus a grand total of 3564 kcal is released as all the bonds of the products form. Subtracting this from the 2878 kcal needed to break the bonds of the reactants, we arrive at -686 kcal, the free energy change of the oxidation of a mole of glucose. This value holds true whether we oxidize glucose quickly by burning it or in the orderly process of **cellular respiration.** The minus sign indicates that free energy has been removed from the system.

(b) Photosynthesis

The details of the energy budget are just the same. The only difference is that now it takes 3564 kcal to break the bonds of the reactants and only 2878 kcal are released in forming glucose and oxygen. So we express this change in free energy (+686 kcal) with a plus sign to indicate that energy has been added to the system. The energy came from the sun and now is stored in the form of bond energy that can power the needs of all life.

10.10. The Chloroplast Genome

The genome of the chloroplasts found in **Marchantia polymorpha** (a liverwort, one of the Bryophytes) contains 121,024 base pairs in a closed circle. These make up some 128 genes which include duplicate genes encoding each of the four subunits (23S, 16S, 4.5S, and 5S) of the **ribosomal RNA** (**rRNA**) used by the chloroplast. 37 genes encoding all the transfer RNA (tRNA) molecules used for **translation** within the chloroplast. 4 genes encoding some of the subunits of the RNA polymerase used for **transcription** within the chloroplast. A gene encoding the large subunit of the enzyme **RUBISCO** (ribulose bisphosphate carboxylase oxygenase), 9 genes for components of **photosystems I and II**, 6 genes encoding parts of the chloroplast ATP synthase and genes for 19 of the ~60 proteins used to construct the chloroplast ribosome

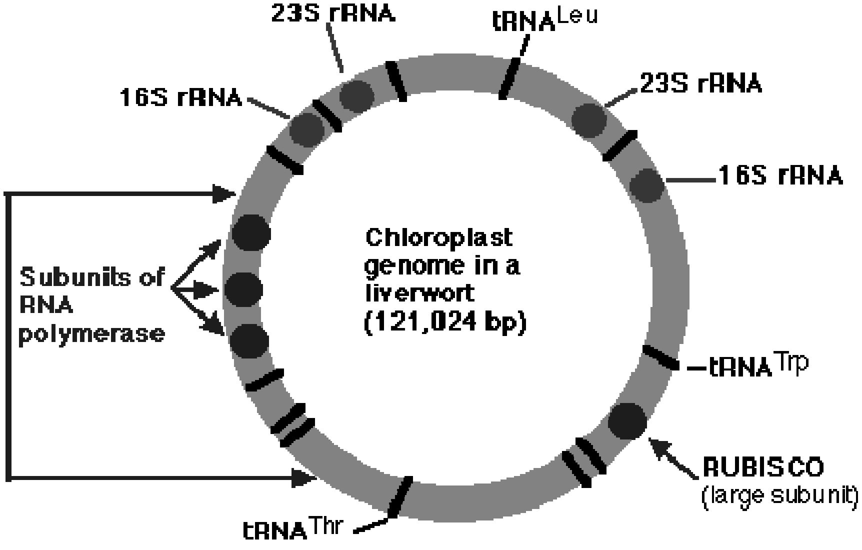

Fig.10.10. Chloroplast Genomes

All these gene products are used within the chloroplast, but all the chloroplast structures also depend on proteins encoded by nuclear genes translated in the cytosol, and imported into the chloroplast. **RUBISCO**, for example, the enzyme that adds CO_2 to ribulose bisphosphate to start the **Calvin cycle**, consists of multiple copies of two subunits:

1. A large one encoded in the chloroplast genome and synthesized within the chloroplast, and
2. A small subunit encoded in the nuclear genome and synthesized by ribosomes in the cytosol. The small subunit must then be imported into the chloroplast.

The arrangement of genes shown in fig 0.10 is found not only in the Bryophytes (mosses and liverworts) but also in the lycopsids (e.g., **Lycopodium** and **Selaginella)**. In all other plants, however, the portion of DNA bracketed by the red arrows on the left is inverted.

The same genes are present but in inverted order. The evolution of eukaryotic chloroplasts by the **endosymbiosis of cyanobacteria** seems to have occurred on three different occasions producing as separate events the **green algae** and plants as described above, **red algae** and glaucophytes; a small group of **unicellular algae.**

10.11. Secondary Endosymbiosis

This Involves Eukaryotes Engulfing Eukaryotes

(a) The Nucleomorph

Once both heterotrophic and photosynthetic eukaryotes had evolved, the former repeatedly engulfed the latter to exploit their autotrophic way of life. Many animals living today engulf algae for this purpose. Usually the partners in these mutualistic relationships can be grown separately. However, a growing body of evidence indicates that the **chloroplasts** of some algae have not been derived by engulfing cyanobacteria in a primary endosymbiosis like those discussed above, but by engulfing **photosynthetic eukaryotes**. This is called **secondary endosymbiosis**. It occurred so long ago that these **endosymbionts** cannot be cultured away from their host. In two groups, the eukaryotic nature of the endosymbiont can be seen by its retention of a vestige of a nucleus (called its **nucleomorph**).

1. A group of unicellular, motile algae called **cryptomonads** appear to be the evolutionary outcome of a nonphotosynthetic eukaryotic flagellate (i.e., a protozoan) engulfing a **red alga** by endocytosis.
2. Another tiny group of unicellular algae, called **chlorarachniophytes**, appear to be the outcome of a flagellated protozoan having engulfed a **green** alga.

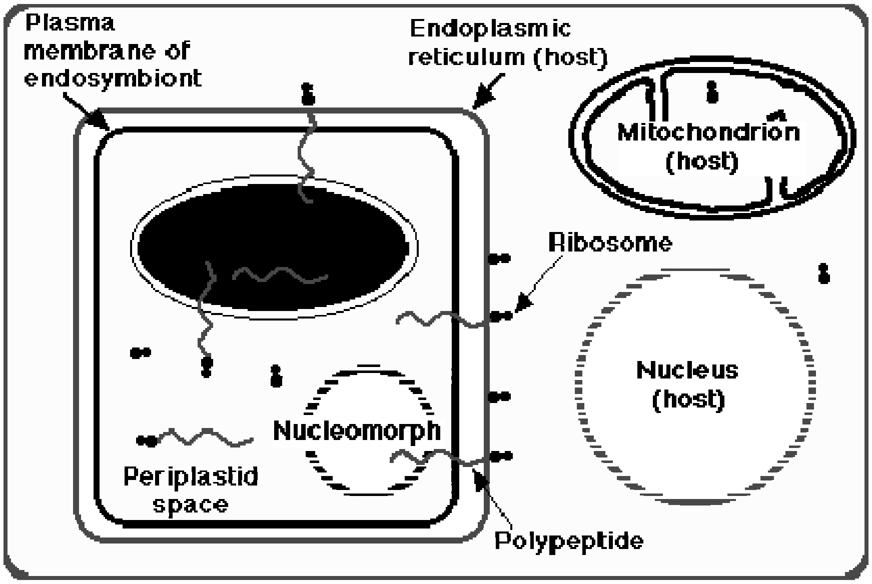

Fig.10.11. Secondary Endosymboisis

The result in both cases: a motile, autotrophic cell containing its own nucleus, its own mitochondria and its own endoplasmic reticulum, which contains the endosymbiont with its own plasma membrane, its own cytoplasm, the **periplastid space**, its own ribosomes, its own chloroplast, and its **nucleomorph** - only a vestige of its original nucleus, but still surrounded by a nuclear envelope perforated with **nuclear pore complexes** and containing a tiny but still-functioning genome.

(b) The Apicoplast

The apicoplast (short for "apicomplexan plastid") is a solitary organelle found in the **apicomplexan protists**: "sporozoans" like ***Plasmodium falciparum*** (and the other agents of malaria) and ***Toxoplasma gondii***. Features include Essential - the organisms cannot survive without it; Encased by 4 membranes, Contains its own genome, a circular molecule of DNA (35,000 base pairs) which encodes ~ 30 proteins, a full set of tRNAs plus some other RNAs. Only a few functions have been discovered, but these include, **anabolic metabolism** such as the synthesis of **fatty acids**; **repair**, **replication, transcription,** and **translation** of its genes. Clearly 30 proteins are not enough to accomplish so many functions so the apicoplast has to import from the cytosol ~500 nuclear-encoded proteins. The apicoplast is the product of an ancient endosymbiosis in which the eukaryotic ancestor engulfed a unicellular alga — probably a red alga — with a solitary chloroplast. Over time, the nucleus was lost (no residual nucleomorph) as well as many features of the chloroplast (including its ability to perform photosynthesis).

(c) Evidence of Secondary Symbiosis Today

Two Japanese scientists have discovered a heterotrophic flagellate that engulfs a unicellular **green alga** that lives freely in the surrounding water. Once inside,

- the alga loses its flagella and cytoskeleton;
- the host loses its feeding apparatus;
- the host switches from heterotrophic to autotrophic nutrition (photosynthesis);
- the host becomes capable of phototaxis.

When the host divides by mitosis, only one daughter cell gets the plastid. The other cell re-grows the feeding apparatus and is ready to engulf another alga.