Advance Crop Physiology

(PPS500)

Submitted to: Dr. Ali Abdullah Alderfasi

Compiled by: Awais Ahmad (432108560)

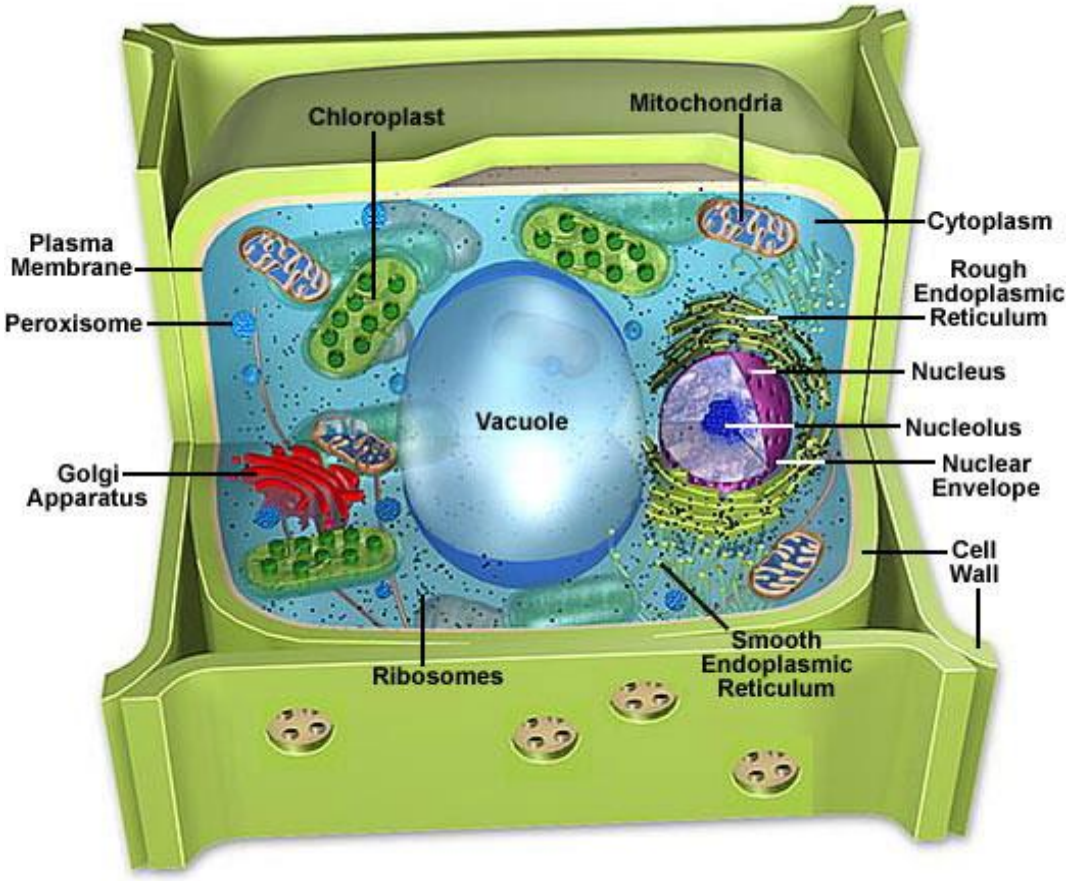
Muhammad Afzal (432108561)

This assignment is submitted as the partial requirement of the course PPS-500

Advanced Crop Physiology, PPS 500

Plant Cell Structure & Functions:

Plants are unique among the eukaryotes, organisms whose cells have membrane-enclosed nuclei and organelles, because they can manufacture their own food. Chlorophyll, which gives plants their green color, enables them to use sunlight to convert water and carbon dioxide into sugars and carbohydrates, chemicals the cell uses for fuel.



Anatomy of the Plant Cell:-

Like the fungi, another kingdom of eukaryotes, plant cells have retained the protective cell wall structure of their prokaryotic ancestors. The basic plant cell shares a similar construction motif with the typical eukaryote cell, but does not have centrioles, lysosomes, intermediate filaments, cilia, or flagella, as does the animal cell. Plant cells do, however, have a number of other **specialized structures**, including a rigid cell wall, central vacuole, plasmodesmata, and chloroplasts. Although plants (and their typical cells) are non-motile, some species produce gametes that do exhibit flagella and are, therefore, able to move about.

Plants can be broadly categorized into two basic types: **vascular and nonvascular**. Vascular plants are considered to be more advanced than nonvascular plants because they have evolved specialized tissues, namely xylem, which is involved in structural support and water conduction, and phloem, which functions in food conduction. Consequently, they also possess roots, stems, and leaves, representing a higher form of organization that is characteristically absent in plants lacking vascular tissues. The nonvascular plants, members of the division Bryophyta, are usually no more than an inch or two in height because they do not have adequate support, which is provided by vascular tissues to other plants, to grow bigger. They also are more dependent on the environment that surrounds them to maintain appropriate amounts of moisture and, therefore, tend to inhabit damp, shady areas.

It is estimated that there are at least 260,000 species of plants in the world today. They range in size and complexity from small, nonvascular mosses to **giant sequoia trees**, the largest living organisms, growing as tall as 330 feet (100 meters). Only a tiny percentage of those species are directly used by people for food, shelter, fiber, and medicine. Nonetheless, plants are the basis for the Earth's ecosystem and food web, and without them complex animal life forms (such as humans) could never have evolved. Indeed, all living organisms are dependent either directly or indirectly on the energy produced by photosynthesis, and the **byproduct** of this process, oxygen, is essential to animals. Plants also reduce the amount of carbon dioxide present in the atmosphere, hinder soil erosion, and influence water levels and quality.

Plants exhibit life cycles that involve alternating generations of diploid forms, which contain paired chromosome sets in their cell nuclei, and haploid forms, which only possess a single set. Generally these two forms of a plant are very dissimilar in appearance. In higher plants, the **diploid generation**, the members of which are known as sporophytes due to their ability to produce spores, is usually dominant and more recognizable than the **haploid gametophyte generation**. In **Bryophytes**, however, the gametophyte form is dominant and physiologically necessary to the sporophyte form.

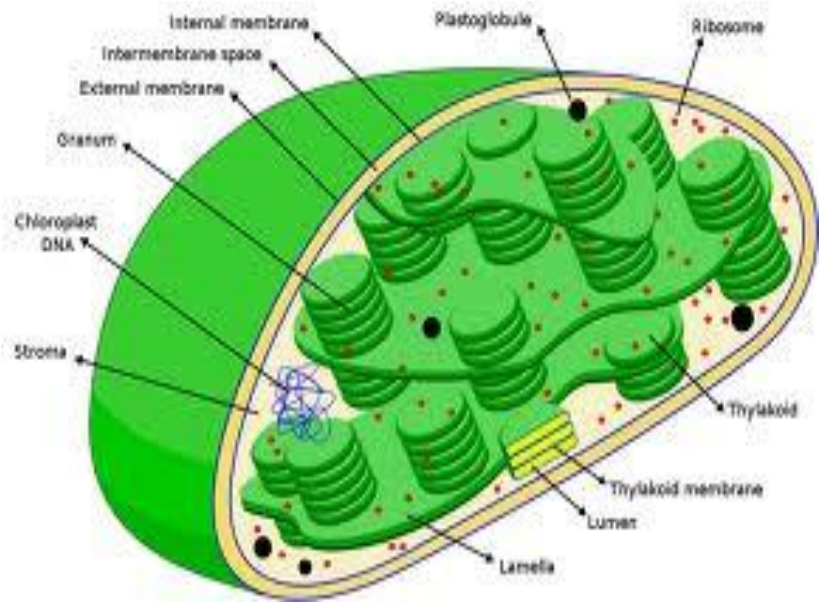
Animals are required to consume protein in order to obtain nitrogen, but plants are able to utilize inorganic forms of the element and, therefore, do not need an outside source of protein. Plants do, however, usually require significant amounts of water, which is needed for the photosynthetic process, to maintain cell structure and facilitate growth, and as a means of bringing nutrients to plant cells. The amount of nutrients needed by plant species varies significantly, but nine elements are generally considered to be necessary in relatively large amounts. Termed **macroelements**, these nutrients include calcium, carbon, hydrogen, magnesium, nitrogen, oxygen, phosphorus, potassium, and sulfur. Seven microelements, which are required by plants in smaller quantities, have also been identified: boron, chlorine, copper, iron, manganese, molybdenum, and zinc.

Thought to have evolved from the green algae, plants have been around since the early **Paleozoic era**, more than 500 million years ago. The earliest fossil evidence of land plants dates to the Ordovician Period (505 to 438 million years ago). By the Carboniferous Period, about 355

million years ago, most of the Earth was covered by forests of primitive vascular plants, such as lycopods (scale trees) and gymnosperms (pine trees, ginkgos). Angiosperms, the flowering plants, didn't develop until the end of the Cretaceous Period, about 65 million years ago—just as the dinosaurs became extinct.

• **Cell Wall** - Like their prokaryotic ancestors, plant cells have a rigid wall surrounding the plasma membrane. It is a far more complex structure, however, and serves a variety of functions, from protecting the cell to regulating the life cycle of the plant organism.

• **Chloroplasts** - The most important characteristic of plants is their ability to photosynthesize, in effect, to make their own food by converting light energy into chemical energy. This process is carried out in specialized organelles called chloroplasts.



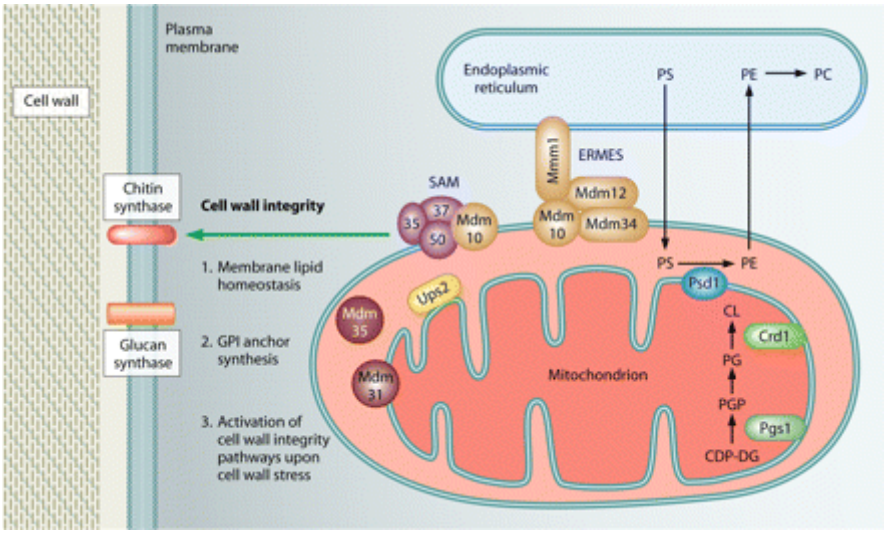
• **Endoplasmic Reticulum** - The endoplasmic reticulum is a network of sacs that manufactures, processes, and transports chemical compounds for use inside and outside of the cell. It is connected to the double-layered nuclear envelope, providing a pipeline between the nucleus and the cytoplasm. In plants, the endoplasmic reticulum also connects between cells via the **plasmodesmata**.

• **Golgi Apparatus** - The Golgi apparatus is the distribution and shipping department for the cell's chemical products. It modifies proteins and fats built in the endoplasmic reticulum and prepares them for export as outside of the cell.

• **Microfilaments** - Microfilaments are solid rods made of globular proteins called actin. These filaments are primarily structural in function and are an important component of the cytoskeleton.

• **Microtubules** - These straight, hollow cylinders are found throughout the cytoplasm of all eukaryotic cells (prokaryotes don't have them) and carry out a variety of functions, ranging from transport to structural support.

• **Mitochondria** - Mitochondria are oblong shaped organelles found in the cytoplasm of all eukaryotic cells. In plant cells, they break down carbohydrate and sugar molecules to provide energy, particularly when light isn't available for the chloroplasts to produce energy.



• **Nucleus** - The nucleus is a highly specialized organelle that serves as the information processing and administrative center of the cell. This organelle has two major functions: it stores the cell's hereditary material, or DNA, and it coordinates the cell's activities, which include growth, intermediary metabolism, protein synthesis, and reproduction (cell division).

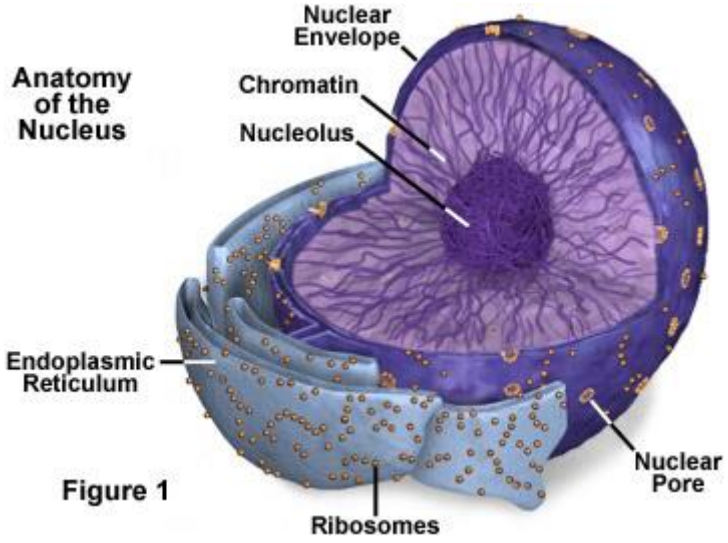
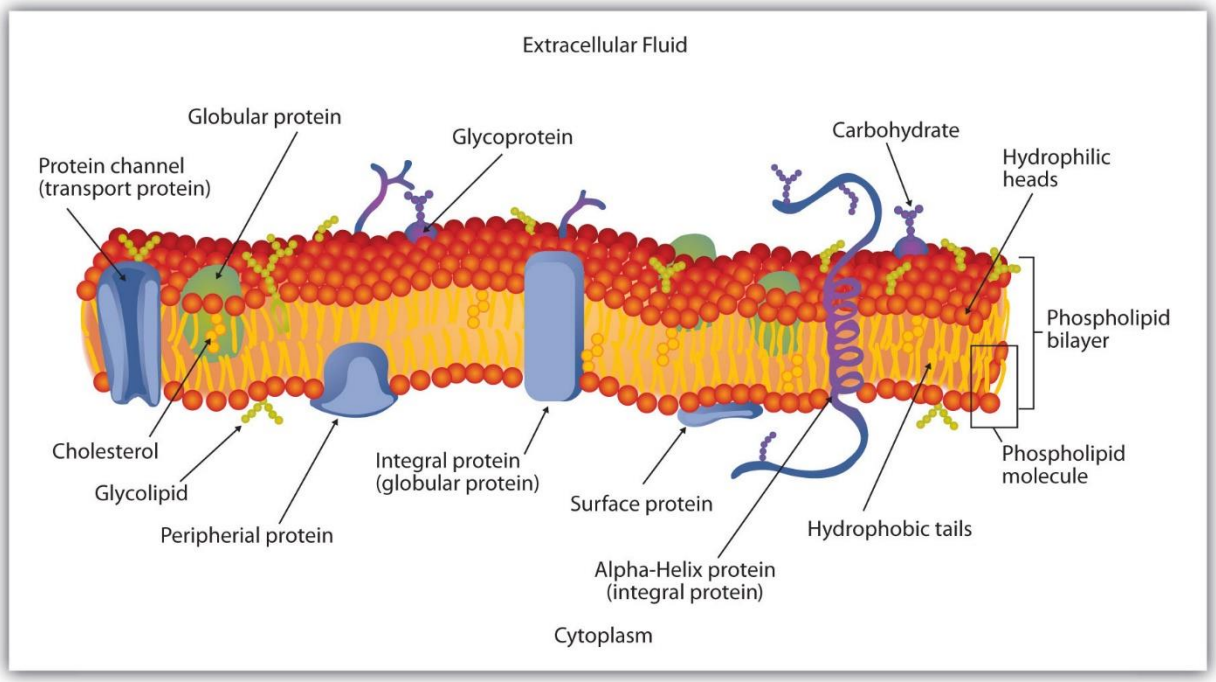


Figure 1

• **Peroxisomes** - Microbodies are a diverse group of organelles that are found in the cytoplasm, roughly spherical and bound by a single membrane. There are several types of microbodies but peroxisomes are the most common. They consist of peroxides and oxidative enzymes.

• **Plasmodesmata** - Plasmodesmata are small tubes that connect plant cells to each other, providing living bridges between cells.

• **Plasma Membrane** - All living cells have a plasma membrane that encloses their contents. In prokaryotes and plants, the membrane is the inner layer of protection surrounded by a rigid cell wall. These membranes also regulate the passage of molecules in and out of the cells.



• **Ribosomes** - All living cells contain ribosomes, tiny organelles composed of approximately 60 percent RNA and 40 percent protein. In eukaryotes, ribosomes are made of four strands of RNA. In prokaryotes, they consist of three strands of RNA.

• **Vacuole** - Each plant cell has a large, single vacuole that stores compounds, helps in plant growth, and plays an important structural role for the plant.

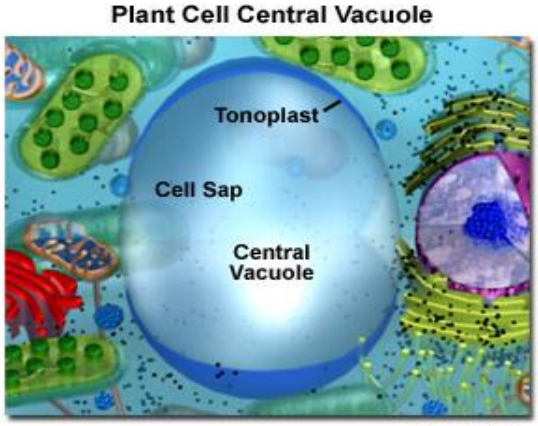
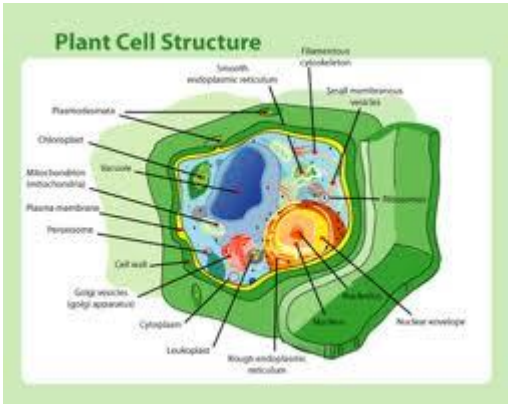


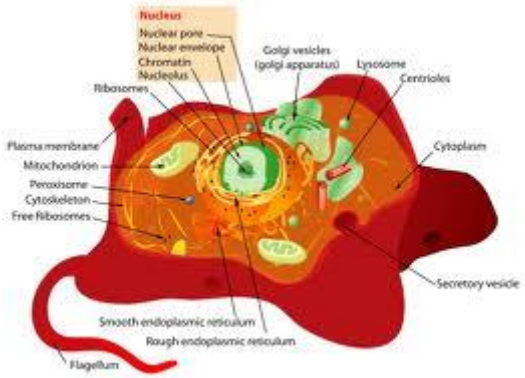
Figure 1

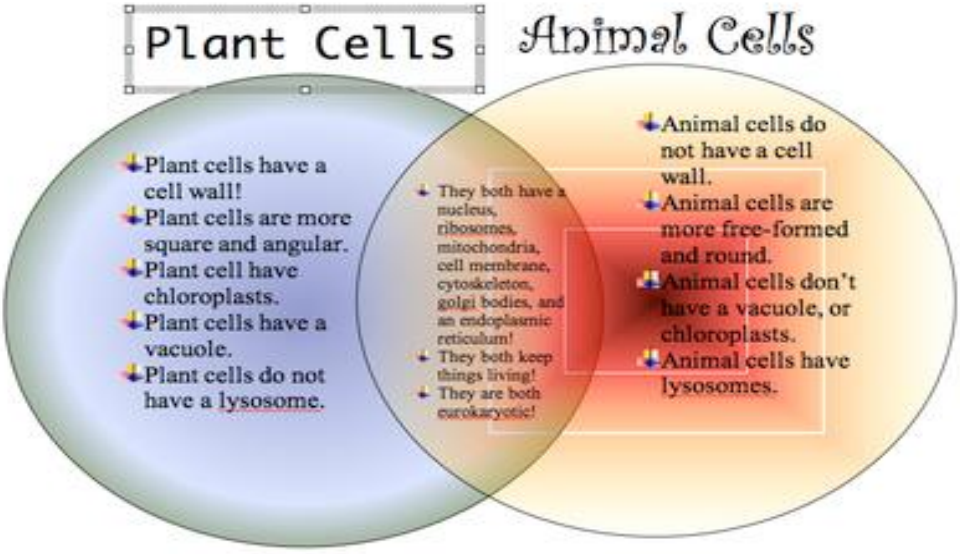
Leaf Tissue Organization - The plant body is divided into several organs: roots, stems, and leaves. The leaves are the primary photosynthetic organs of plants, serving as key sites where energy from light is converted into chemical energy. Similar to the other organs of a plant, a leaf is comprised of three basic tissue systems, including the dermal, vascular, and ground tissue systems. These three motifs are continuous throughout an entire plant, but their properties vary significantly based upon the organ type in which they are located. All three tissue systems are discussed in this section.

Plant and Animal Cell Differences:-

Plant and animal cells have several differences and similarities. For example, animal cells do not have a cell wall or chloroplasts but plant cells do. Animal cells are round and irregular in shape while plant cells have fixed, rectangular shapes.







Comparison chart:-

	Animal Cell	Plant Cell
Cell wall:	Absent	Present (formed of cellulose)
Shape:	Round (irregular shape)	Rectangular (fixed shape)
Vacuole:	One or more small vacuoles (much smaller than plant cells).	One, large central vacuole taking up 90% of cell volume.
Centrioles:	Present in all animal cells	Only present in lower plant forms.
Chloroplast:	Animal cells don't have chloroplasts	Plant cells have chloroplasts because they make their own food
Cytoplasm:	Present	Present
Endoplasmic Reticulum (Smooth and Rough):	Present	Present
Ribosomes:	Present	Present
Mitochondria:	Present	Present
Plastids:	Absent	Present
Golgi Apparatus:	Present	Present
Plasma Membrane:	only cell membrane	cell wall and a cell membrane
Microtubules/ Microfilaments:	Present	Present
Flagella:	May be found in some cells	May be found in some cells
Lysosomes:	Lysosomes occur in cytoplasm.	Lysosomes usually not evident.
Nucleus:	Present	Present
Cilia:	Present	It is very rare

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Plant Cell Water Relations

Water is the most abundant constituent of all physiologically active plant cells. Leaves, for example, have water contents which lie mostly within a range of **55-85%** of their fresh weight. Other relatively succulent parts of plants contain approximately the same proportion of water, and even such largely nonliving tissues as wood may be **30-60%** water on a fresh-weight basis. The smallest water contents in living parts of plants occur mostly in dormant structures, such as mature seeds and spores. The great bulk of the water in any plant constitutes a unit system. This water is not in a static condition. Rather it is part of a **hydrodynamic system**, which in terrestrial plants involves absorption of water from the soil, its translocation throughout the plant, and its loss to the environment, principally in the process known as transpiration.

Importance of Water:-

Water is the major component of living cells and constitutes more than **90%** of protoplasm by volume and weight. In acts as **medium** for all biochemical reaction that takes place in the cell, and also acts a medium of transportation from one region to another region. Water is a remarkable compounded made up of Hydrogen and oxygen (2:1) and it has **high specific heat**, high heat of vaporization, high heat of fusion and expansion (colligative properties). Water because of its **bipolar nature** acts as universal solvent for it dissolves more substances than any other solvent. Electrolytes and non-electrolytes like sugars, and proteins dissolve very well. Even some hydrophobic lipid molecules show some solubility in water.

Water acts as a good **buffer** against changes in the Hydrogen ion concentration (pH). This is because of its ionization property. Certain xerophytes use water as buffer system against high temperature. Water also exhibits viscosity and adhesive properties. Because of **hydrogen bonds**, water molecules are attracted towards each other, they are held to each other with considerable force. This force of attraction is called **cohesive force**. Thus water possesses a high tensile strength. If this water is confined in very narrow columns of dimensions of xylem vessels, its tensile and cohesive forces reach very high values (1000-1200 Gms). And this force is very helpful in **ascent of sap**. Water is of great importance in osmoregulation, particularly in the maintenance of turgidity of cells, opening and closing of stomata and growth of the plant body. Water is an important substrate in photosynthesis, for it provides reducing power in CO_2 fixation; water is also used in **breaking or making** chemical bonds of polypeptides, poly-nucleotides, carbohydrates etc. All the above features clearly indicate that water plays an important role in the regulation of life processes.

To understand plant water relation, it is necessary to be familiar with following few terms and process.

Diffusion:-

If the scent is sprayed in one corner of the room, the smell spreads to all part of the house in no time. If a fire wood is burnt, the black soot goes up and spreads. If a pinch of solid potassium permanganate if dropped into water contained in a beaker, pink color slowly diffuses and spreads

throughout. The above said spreading phenomenon is due to movement of molecules. Having their own kinetic energy, water molecules will be in constant motion randomly.

Diffusion is governed Ficks First Law. It depends upon the rate of transport or Flux density-ds, s-is the substance crossing over a unit area per unit time. **Diffusion coefficient** (Ds), it is proportionality constant Ds that measures how easily a substance moves through a particular medium. The concentration gradient is defined as δcs/δx.

Molecules of a particular species always tend to move or now call it diffuse from higher concentration to lower concentration irrespective of the other types of solutes present in the system; i.e. from higher kinetic energy to lower kinetic energy. However the rate of diffusion is governed by other factors like **(1)** concentration gradient **(2)** temperature **(3)** density of molecules **(4)** pressure and **(5)** medium through which it diffuses.

Diffusion Pressure Deficit (DPD)

In a pure solvent, all molecules will be moving freely by virtue of their chemical potential. This random movement is called diffusion. It further depends upon the concentration of diffusing molecules, which in turn exert a pressure termed diffusion pressure. The direction and rate of diffusion in a pure solvent is random but equal and opposite. Hence the diffusion pressure exerted in such a system can be taken as zero. To such a system, if solute is added, it undergoes solubility, where some freely moving solvent molecules get bound to solute molecules and in fact in some cases they form a shell around such salts. This results in the loss of considerable number of solvent molecules for free diffusion. This loss is called **diffusion pressure deficit**. In this process there is loss of chemical free energy of water because of the binding of solvent to solutes. Thus the DPD is governed by the relative concentration of solute in a given volume of a solution. Increase in the concentration of solute in a known volume of solution increases the DPD of the system. Furthermore increase in solute's concentration also increases OP; hence DPD and OP are related to each other. The water or solvent always moves from lower DPD to higher DPD.

Water Potential (Ψw):

In this context, it is important to be familiar with the term called water potential (Ψw) which refers to the chemical free energy of water. The chemical free energy of pure water or solutes is always expressed in terms pressure units such as bars.1 atmosphere = 14.7 pounds per square inch, = 760mm Hg at sea level, =1.013 bar, = 0.1013 Mpa, = 1.013 x 10^5 Pa (1 bar = 0.987 atmospheric units, 10 bars = 1 Mega Pascal (Mpa). 1 mpa = 106dynes / cm2, under standard conditions). To give a common values for these a car tyre typically pressured at about 0.2Mpa and the water pressure less than 15 feet (5m) of water is about 0.05Mpa.

The chemical free energy of water in its purest form is also called water potential (Ψw). Purest form means there are no other molecules in it. The chemical energy is maximum and its value is given as 0 bars. Addition of solutes to pure solvent decreases the **chemical free energy** of pure water, because certain amount of energy of a number of water molecules is used for binding to the surface of solutes. So the total value of water potential of a solution is less than zero; it is

always expressed in negative pressure values. Here it is equal to DPD; if the water potential of pure water is zero and DPD is also zero. But the water potential of solution is less than zero expressed in **negative value**, but DPD of the solution is expressed in **positive value**.

These energy relations are governed by the said equations, understanding of it is very important.

$\Psi w = \Psi s + \Psi p + \Psi g$

Ψw = water

Ψs = solutes-solutes potential or osmotic potential.

Ψp = pressure-hydrostatic pressure of the solution, it is often called turgour pressure, which can be negative or positive.

Ψg = gravity- will not be considered for normal calculations.

Pure water:

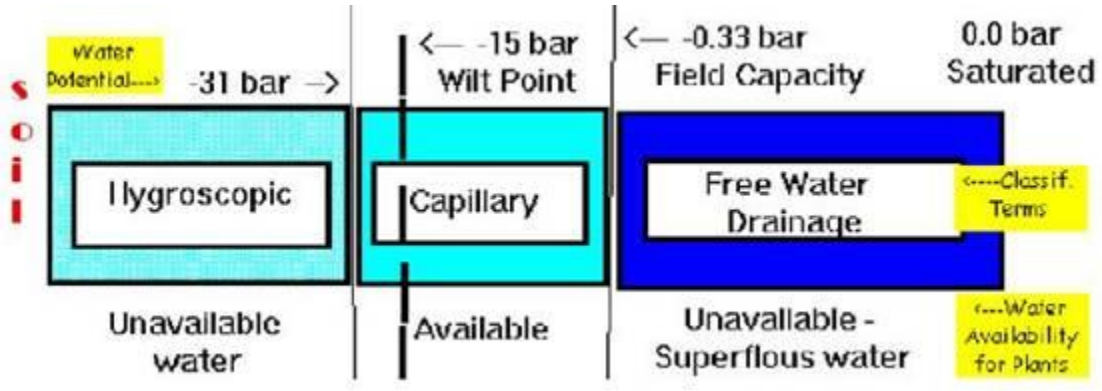
$\Psi p = 0$ Mpa

$\Psi s = 0$ Mpa

$\Psi w = \Psi p + \Psi s = 0$ Mpa

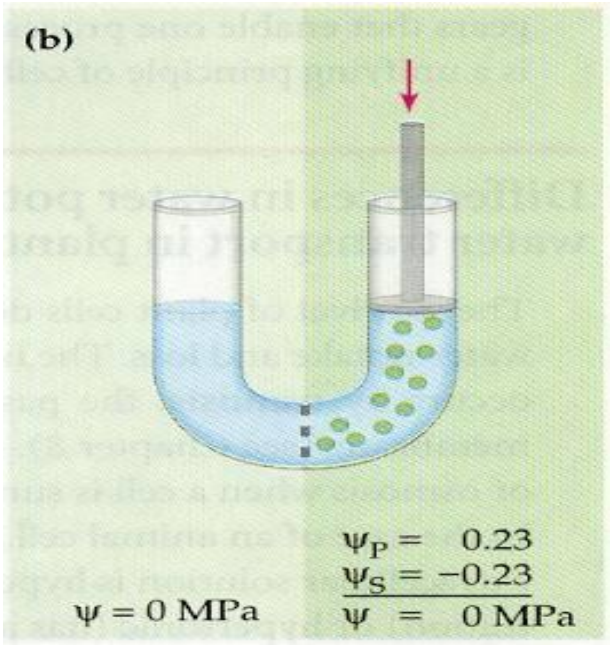
DPD of pure water = 0 bars; DPD of a solution = (+) bars

Ψ w of pure water = 0 bars; ψ w of a solution = (-) bars



Osmosis:-

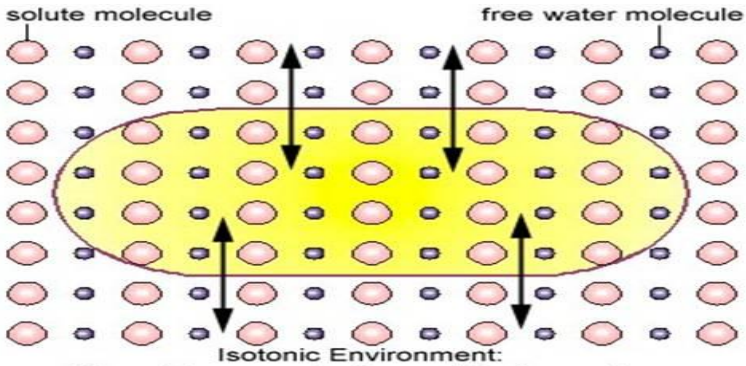
If two solutions of different concentrations are separated by a plasma membrane, which is **semi permeable** as well as **selectively permeable**, the solvent (in this case it is H2O) moves through the membrane from higher concentration towards lower concentration. Here the plasma membrane has a differential permeability, where it allows the diffusion of water molecules to move from higher concentration to lower concentration but it prevents the movement of solute molecules from higher concentration to lower concentration. Such differential diffusion through a semi permeable membrane is called osmosis.



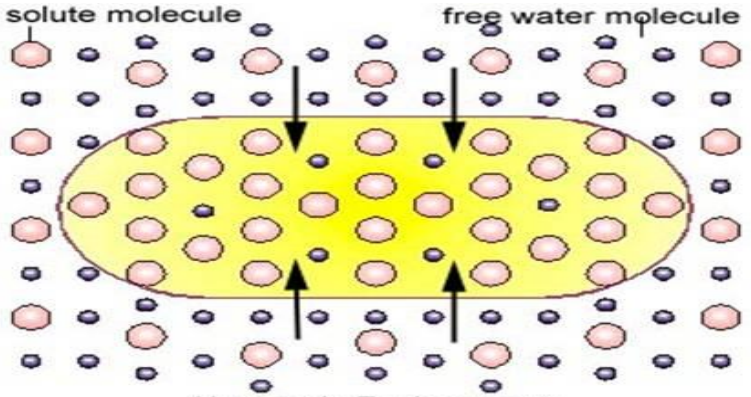
Osmotic potential: Osmosis is always referred to living cells. The movement of water into the cell (endosmosis or plasmolysis) mostly depends upon the concentration of solutes which are of varied types like mineral salts, proteins, carbohydrates, fatty acids etc., and these contribute to the osmotic potential or **osmotic concentration**, which contributes to the osmotic pressure. Higher the concentration of solutes, higher is the osmotic pressure and vice-versa.

A solution is made up of a solvent within which solutes are dissolved or present in soluble form. Basing on the concentration of solute in a given volume of solution, it is referred to as dilute solution or concentrated solution. The **concentration of solutes** in an enclosed system having a constant volume exerts a pressure because of the kinetic movement and collision of the solute molecules. The pressure that is exerted by the solute in a system, either separated or enclosed in a semi permeable membrane is called osmotic pressure. Hence a dilute solution exhibits lower osmotic pressure and concentrated solution shows higher osmotic pressure which is also called osmotic potential.

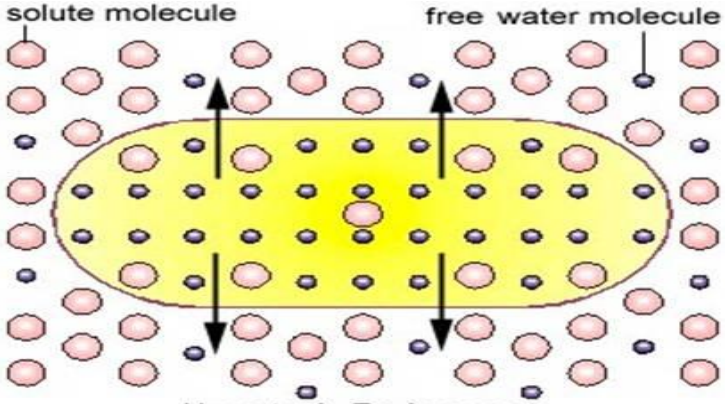
Besides the concentration of solutes, Osmotic potential is governed by other factors life ionizing potential of the solutes, temperature etc.



Isotonic Environment:
The solute concentration and the free water concentration are the same inside and outside the cell.
Water flows in and out of the cell at an equal rate.



Hypotonic Environment:
The solute concentration is greater inside the cell; the free water concentration is greater outside.
Free water flows into the cell.



Hypertonic Environment:
The solute concentration is greater outside the cell; the free water concentration is greater inside.
Free water flows out of the cell.

Those solutes which undergo greater **ionization** (electrolytes) exert greater osmotic pressure than non-ionizing substances (non-electrolytes). Similarly **temperature** has a contributing factor for osmotic pressure, because with the increase in temperature, molecular movement increases and so also the collision, hence OP (Osmotic Pressure).

Ex-osmosis, Endosmosis and Turgidity:

When a normal cell is put in a **hypertonic solution** (solution with high concentration of solutes, than the solute concentration of the cells), a water potential or DPD gradient1 is created between the cell and the external solution. Hence the water diffuses out of the cell; the process is called **Exosmosis or Plasmolysis**. As a consequence, the cell collapses and the plasma membrane withdraws from the cell wall and the whole cytoplasm gets concentrated in a corner of the cell. Such a cell is called flaccid cell. In this state, turgour pressure (TP) is zero, and OP is very high, but $\Psi\pi = \Psi w$.

If such a cell is transferred to **hypotonic solution** i.e. (the solute concentration is less than that of a cell. If the solute concentration of the solution is equal to the cell concentration then it is called **Isotonic**) or pure water, again an osmotic gradient is created. Hence, water from external solution enters into the cell. This process is called **Endosmosis or Deplasmolysis**. As a result, the concentration of water or water potential within the cell increases. Increases in the water concentration create its own molecular pressure within the cell and it is called **turgour pressure**. With the increase in turgour pressure, the cytoplasm swells and gradually plasma membrane is pushed towards the cell walls. As more and more water enters, more and more of turgour pressure builds up and the cell goes on increasing in the size. The water potential of the cell increases towards zero value. As turgour pressure exerts its impact outwardly i.e., on to the cell wall, the cell wall being plastic, exerts counter pressure; this is called **wall pressure**. When the TP (Ψp) becomes equal to wall pressure, the water potential within the cell and outside the cell reaches an equilibrium state. Such a cell is called turgid cell and Ψw. The relation can be expressed in the following formulae:

If **DPD = OP - TP** If **$\Psi w = \Psi S + \Psi p$**

By determining OP or P one can determine the DPD or Ψw of any given cell. This can be done by initial plasmolytic method. Where M = molarity at which incipient plasmolysis occurs, t = Room temperature, 273 = Absolute temperature.

$$\Psi\pi = (-)\ mart$$

Where $\Psi\pi$ = osmotic potential, M = molarity at which incipient plasmolysis takes place, I = Ionization constant i.e., one for glucose and sucrose, but for NaCl, it is two, R = gas constant, i.e., 0.083 bars, T = 273 + room temperature say 250C.

Chemical free Energy of Water:

Water, for that matter any solvent in its pure state has its own chemical potential by virtue of which it exhibits random movement. This is referred to as chemical free energy or water potential. If such a solvent is separated from a solution (solvent + solute) by a semi permeable membrane, water molecules move from higher chemical or **water potential** to the lower water potential. In this case pure water has higher chemical energy than the solution, for the solute present in water lowers the free chemical energy of pure solvent of the solution.

Imbibition:-

Hydrophilic substances like polysaccharides, proteins etc. of cell walls and storage tissues attract dipolar water to them. Water molecules in turn bind to the charged surfaces. As a consequences the imbibant swells in volume; such a phenomenon is called **imbibition** and the pressure generated due to imbibition i.e., in the form of swelling force is called **Imbibition pressure**. During this process some amount of energy is lost and it is called **imbibitional energy**. In many cases the imbibition force developed due to the imbibition of water is very high (ranges from 1000 to 10000 bars). The same can be used for breaking big boulders in queries. Even today this method is in practice.

Cellular Water Relations

The typical mature, vacuolate plant cell constitutes a tiny osmotic system, and this idea is central to any concept of cellular water dynamics. Although the cell walls of most living plant cells are quite freely permeable to water and solutes, the cytoplasmic layer that lines the cell wall is more permeable to some substances than to others.

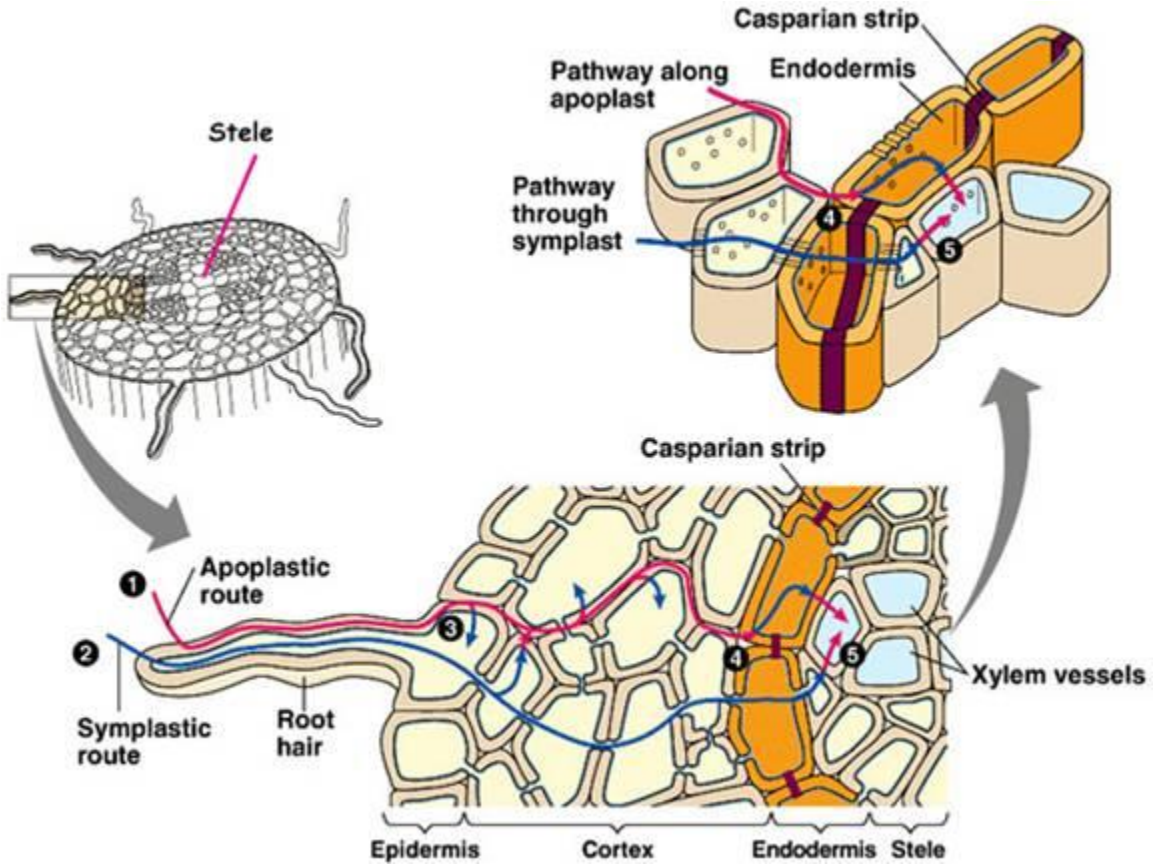
If a plant cell in a **flaccid** condition one in which the cell sap exerts no pressure against the encompassing cytoplasm and cell wall is immersed in pure water, inward osmosis of water into the cell sap ensues. This gain of water results in the exertion of a **turgor pressure** against the protoplasm, which in turn is transmitted to the cell wall. This pressure also prevails throughout the mass of solution within the cell. If the cell wall is elastic, some expansion in the volume of the cell occurs as a result of this pressure, although in many kinds of cells this is relatively small.

If a turgid or partially turgid plant cell is immersed in a solution with a greater osmotic pressure than the cell sap, a gradual **shrinkage** in the volume of the cell ensues; the amount of shrinkage depends upon the kind of cell and its initial degree of turgidity. When the lower limit of cell wall elasticity is reached and there is continued loss of water from the cell sap, the protoplasmic layer begins to recede from the inner surface of the cell wall. Retreat of the protoplasm from the cell wall often continues until it has shrunk toward the center of the cell, the space between the protoplasm and the cell wall becoming occupied by the bathing solution. This phenomenon is called **plasmolysis**. In some kinds of plant cells movement of water occurs principally by the

process of imbibition rather than osmosis. The swelling of dry seeds when immersed in water is a familiar example of this process.

Water Absorption:-

The successively smaller branches of the root system of any plant terminate ultimately in the root tips, of which there may be thousands and often millions on a single plant. Most absorption of water occurs in the **root tip** regions, and especially in the **root hair** zone. Older portions of most roots become covered with cutinized or suberized layers through which only very limited quantities of water can pass.

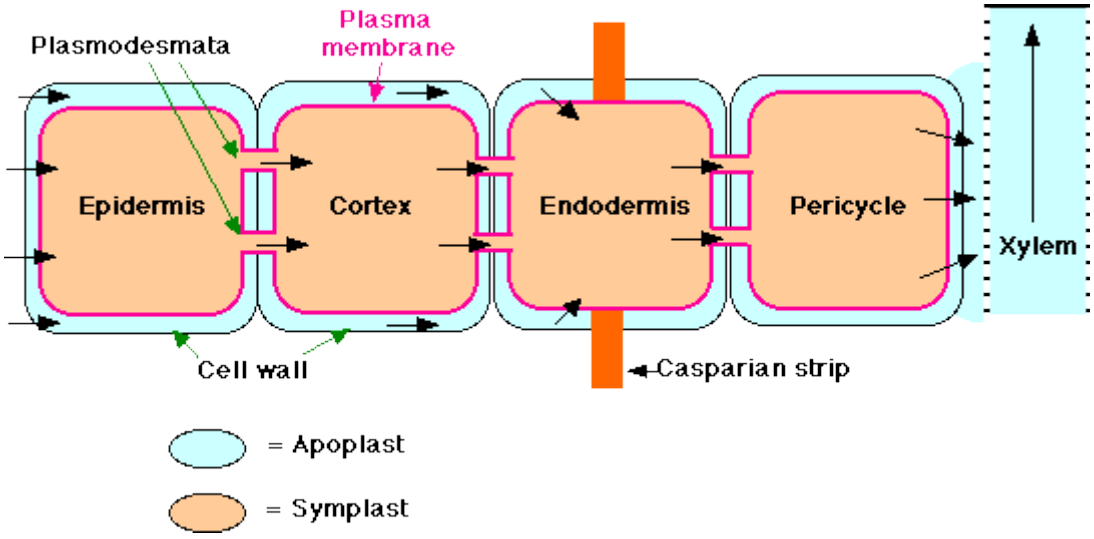


Whenever the water potential in the peripheral root cells is less than that of the soil water, movement of water from the soil into the root cells occurs. There is some evidence that, under conditions of marked internal water stress, the **tension generated** in the xylem ducts will be propagated across the root to the peripheral cells. If this occurs, water potentials of greater negativity could develop in peripheral root cells than would otherwise be possible. The absorption mechanism would operate in fundamentally the same way whether or not the water in the root cells passed into a state of tension. The process just described, often called **passive absorption**, accounts for most of the absorption of water by **terrestrial plants**.

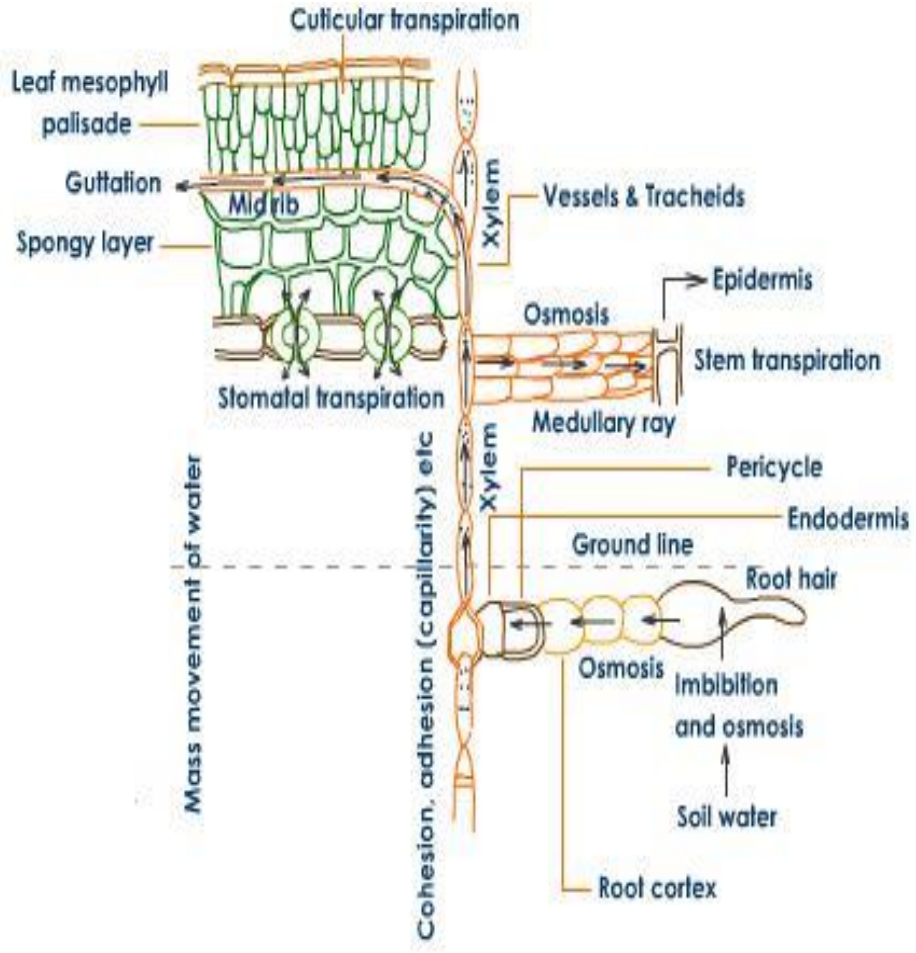
The phenomenon of **root pressure** represents another mechanism of the absorption of water. This mechanism is localized in the roots and is often called **active absorption**. Water absorption of this type only occurs when the rate of transpiration is low and the soil is relatively moist. Although the xylem sap is a relatively dilute solution, its osmotic pressure is usually great enough to engender a more negative water potential than usually exists in the soil water when the soil is relatively moist. A gradient of water potentials can thus be established, increasing in negativity across the epidermis, cortex, and other root tissues, along which the water can move laterally from the soil to the xylem.

Water Translocation:-

In terrestrial rooted plants practically all of the water which enters a plant is absorbed from the soil by the roots. The water thus absorbed is translocated to all parts of the plant. The mechanism of the **"ascent of sap"** (all translocated water contains at least traces of solutes) in plants, especially tall trees, was one of the first processes to excite the interest of plant physiologists.



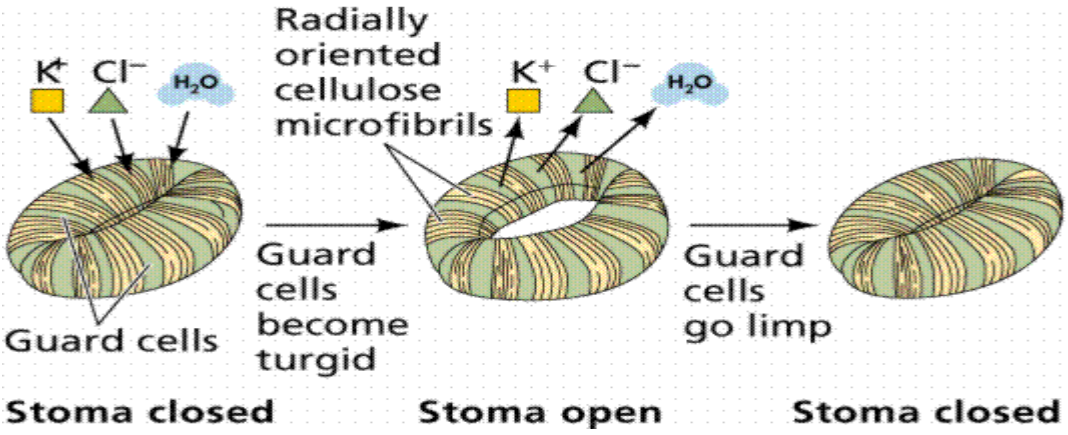
The upward movement of water in plants occurs in the xylem, which, in the larger roots, trunks, and branches of trees and shrubs, is identical with the wood. In the trunks or larger branches of most kinds of trees, however, sap movement is restricted to a few of the outermost annual layers of wood. **Root pressure** is generally considered to be one of the mechanisms of upward transport of water in plants. While it is undoubtedly true that root pressure does account for some upward movement of water in certain species of plants at some seasons, various considerations indicate that it can be only a secondary mechanism of water transport. Upward translocation of water (actually a very dilute sap) is engendered by an increase in the **negativity of water potential** in the cells of apical organs of plants. Such increases in the negativity of water potentials occur most commonly in the **mesophyll cells** of leaves as a result of transpiration.



Stomatal Mechanism:-

Various gases diffuse into and out of physiologically active plants. Those gases of greatest physiological significance are carbon dioxide, oxygen, and water vapor. The great bulk of the gaseous exchanges between a plant and its environment occurs through tiny pores in the epidermis that are called **stomata**. Although stomata occur on many aerial parts of plants, they are most characteristic of, and occur in greatest abundance in, leaves.

Stomatal pores close if excessive water loss occurs. As long as there is sufficient water in the soil to replace the water that is being lost by a plant, stomata stay open. Low concentrations of CO_2 also cause the stomata to open. When guard cells are full of water, they stretch away from each other and the stomata are open. When guard cells are limp, they fall on each other and the stomata are closed. **Potassium ions** play a role in the opening and closing of stomata by changing the concentration of ions in the guard cells. When the potassium ions are in the guard cells, water also flows in the guard cells because of osmosis and the stomata open. When the potassium ions are out of the guard cells, water also flows out of the guard cells because of osmosis and the stomata close.



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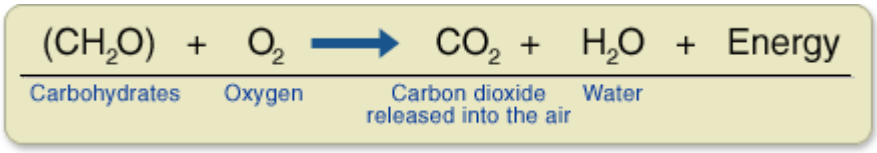
Plant Respiration

Introduction:-

Cellular respiration is the set of the **metabolic** reactions and processes that take place in the cells of organisms to convert biochemical energy from nutrients **into adenosine triphosphate (ATP),** and then release waste products. The reactions involved in respiration are **catabolic reactions**, which break large molecules into smaller ones, releasing energy in the process as they break high-energy bonds. Respiration is one of the key ways a cell gains useful energy to fuel cellular activity. Cellular respiration is considered an **exothermic redox reaction**. The overall reaction is broken into many smaller ones when it occurs in the body, most of which are redox reactions themselves. Although technically, cellular respiration is a combustion reaction, it clearly does not resemble one when it occurs in a living cell. This difference is because it occurs in many separate steps. While the overall reaction is a combustion, no single reaction that comprises it is a combustion reaction. Nutrients that are commonly used by animal and plant cells in respiration include **sugar, amino acids and fatty acids**, and a common oxidizing agent (electron acceptor) is molecular **oxygen (O2).** The energy stored in ATP can then be used to drive processes requiring energy, including biosynthesis, locomotion or transportation of molecules across cell membranes.

Summary:-

Aerobic respiration requires oxygen in order to generate (ATP). Although carbohydrates, fats, and proteins can all be processed and consumed as reactants, it is the preferred method of **pyruvate** breakdown in **glycolysis** and requires that pyruvate enter the mitochondrion in order to be fully oxidized by the Krebs cycle. The product of this process is energy in the form of ATP (adenosine triphosphate), by substrate-level phosphorylation, NADH and FADH2.

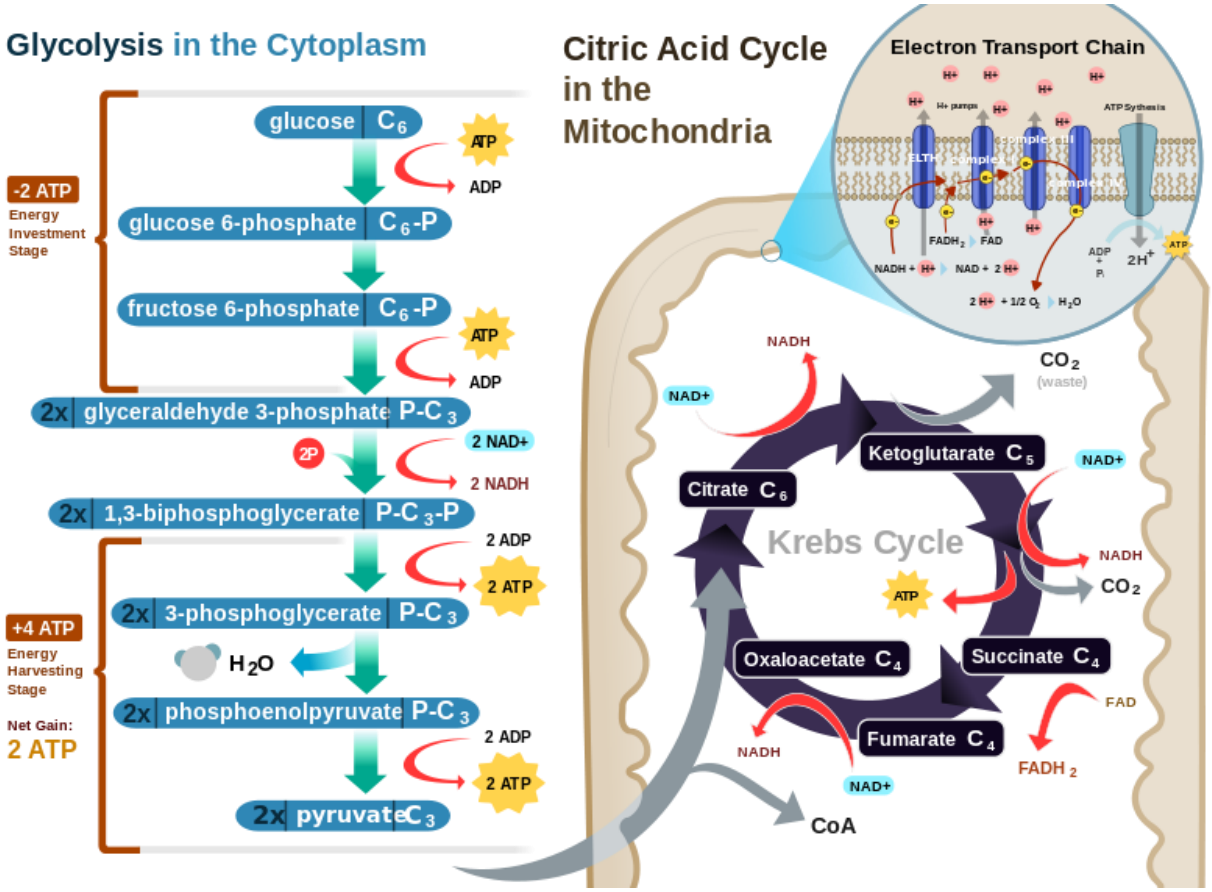


ΔG = -2880 kJ per mole of $C_6H_{12}O_6$

The negative ΔG indicates that the reaction can occur spontaneously.

The reducing potential of NADH and FADH2 is converted to more ATP through an electron transport chain with oxygen as the **"terminal electron acceptor".** Most of the ATP produced by aerobic cellular respiration is made by oxidative phosphorylation. This works by the energy released in the consumption of pyruvate being used to create a chemiosmotic potential by pumping protons across a membrane. This potential is then used to drive ATP synthase and produce ATP

from ADP and a phosphate group. Biology textbooks often state that **38 ATP** molecules can be made per oxidised glucose molecule during cellular respiration (2 from glycolysis, 2 from the Krebs cycle, and about 34 from the electron transport system). However, this maximum yield is never quite reached due to losses (leaky membranes) as well as the cost of moving pyruvate and ADP into the mitochondria's matrix and current estimates range around **29 to 30 ATP** per glucose.



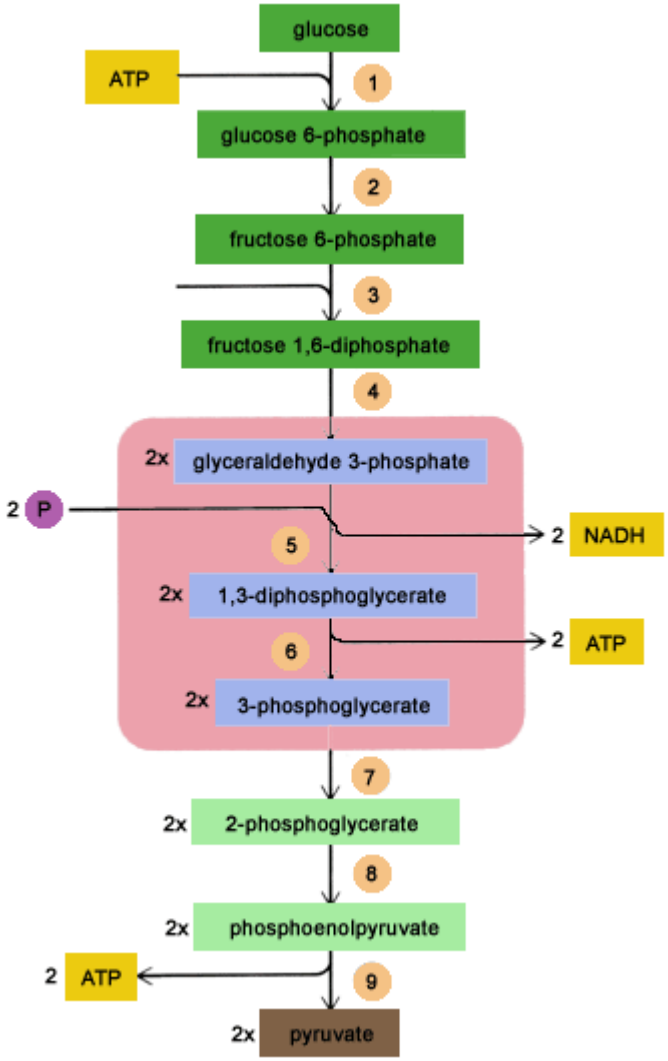
The whole process of respiration actually occurred is steps at different cellular parts, discussed below.

I. Glycolysis:-

Glycolysis is a metabolic pathway that takes place in the **cytosol** of cells in all living organisms. This pathway can function **with or without** the presence of oxygen. Aerobic conditions produce **pyruvate** and anaerobic conditions produce **lactate**. In aerobic conditions, the process converts one molecule of glucose into two molecules of pyruvate (pyruvic acid), generating energy in the form of two net molecules of ATP. Four molecules of ATP per glucose are actually produced; however, two are consumed as part of the preparatory phase. The initial phosphorylation of glucose is required to increase the reactivity (decrease its' stability) in order for the molecule to be cleaved

into two pyruvate molecules by the enzyme **Aldolase**. During the pay-off phase of glycolysis, four phosphate groups are transferred to ADP by substrate-level phosphorylation to make four ATP, and two NADH are produced when the pyruvate are oxidized. The overall reaction can be expressed this way:

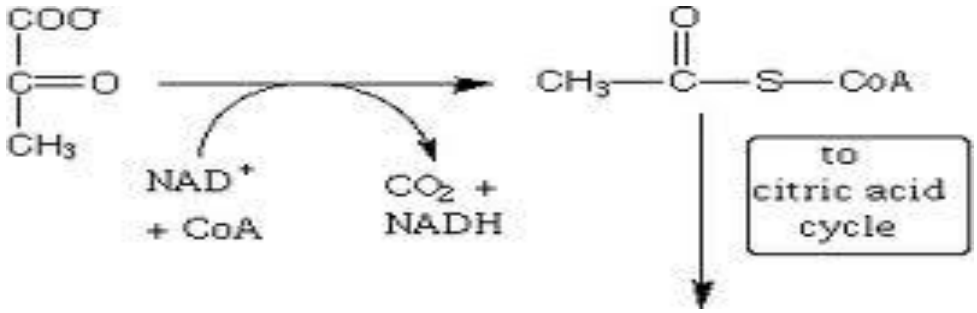
Glucose + 2 NAD+ + 2 Pi + 2 ADP → 2 pyruvate + 2 NADH + 2 ATP + 2 H+ + 2 H2O + heat



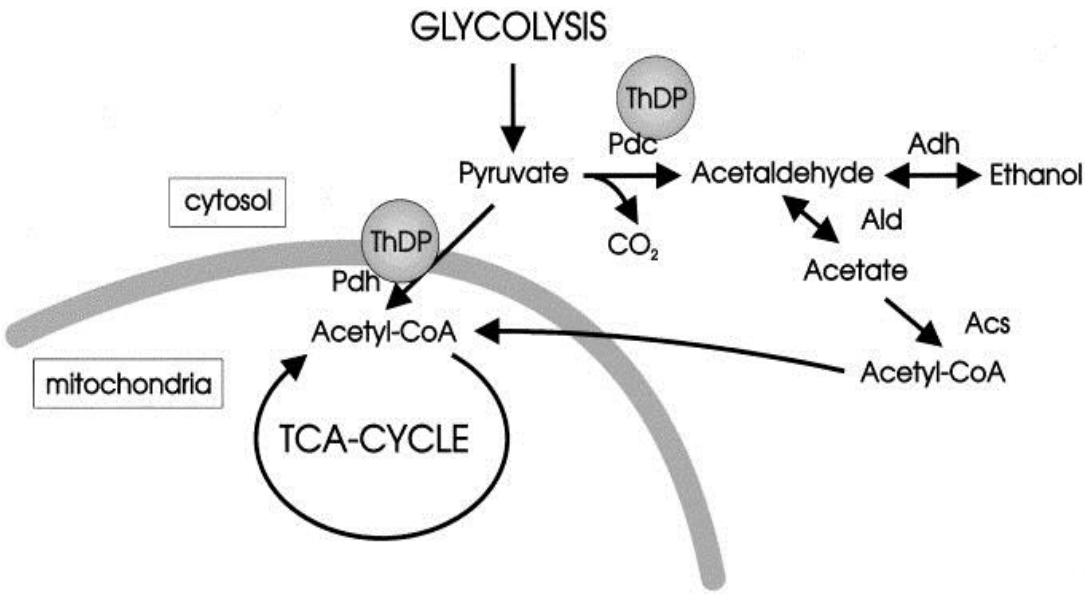
Starting with glucose, 1 ATP is used to donate a phosphate to glucose to produce **glucose 6-phosphate**. Glycogen can change into glucose 6-phosphate as well with the help of **glycogen phosphorylase**. During Energy metabolism, glucose 6-phosphate turns into fructose 6-phosphate. An additional ATP is used to phosphorylate fructose 6-phosphate into fructose **1,6-disphosphate** by the help of **phosphofructokinase**. Fructose 1,6-diphosphate then splits into two phosphorylated molecules with three carbon chains that later degrades into **pyruvate**.

II. Pyruvate decarboxylation:-

Pyruvate is oxidized to **acetyl-CoA** and CO_2 by the **pyruvate dehydrogenase complex (PDC).** The PDC contains multiple copies of three enzymes and is located in the mitochondria of eukaryotic cells and in the cytosol of prokaryotes. In the conversion of pyruvate to acetyl-CoA, one molecule of NADH and one molecule of CO_2 is formed. This step is also known as the **link reaction** or transition step, as it links glycolysis and the Krebs cycle.



Pyruvate to Acetyle-CoA

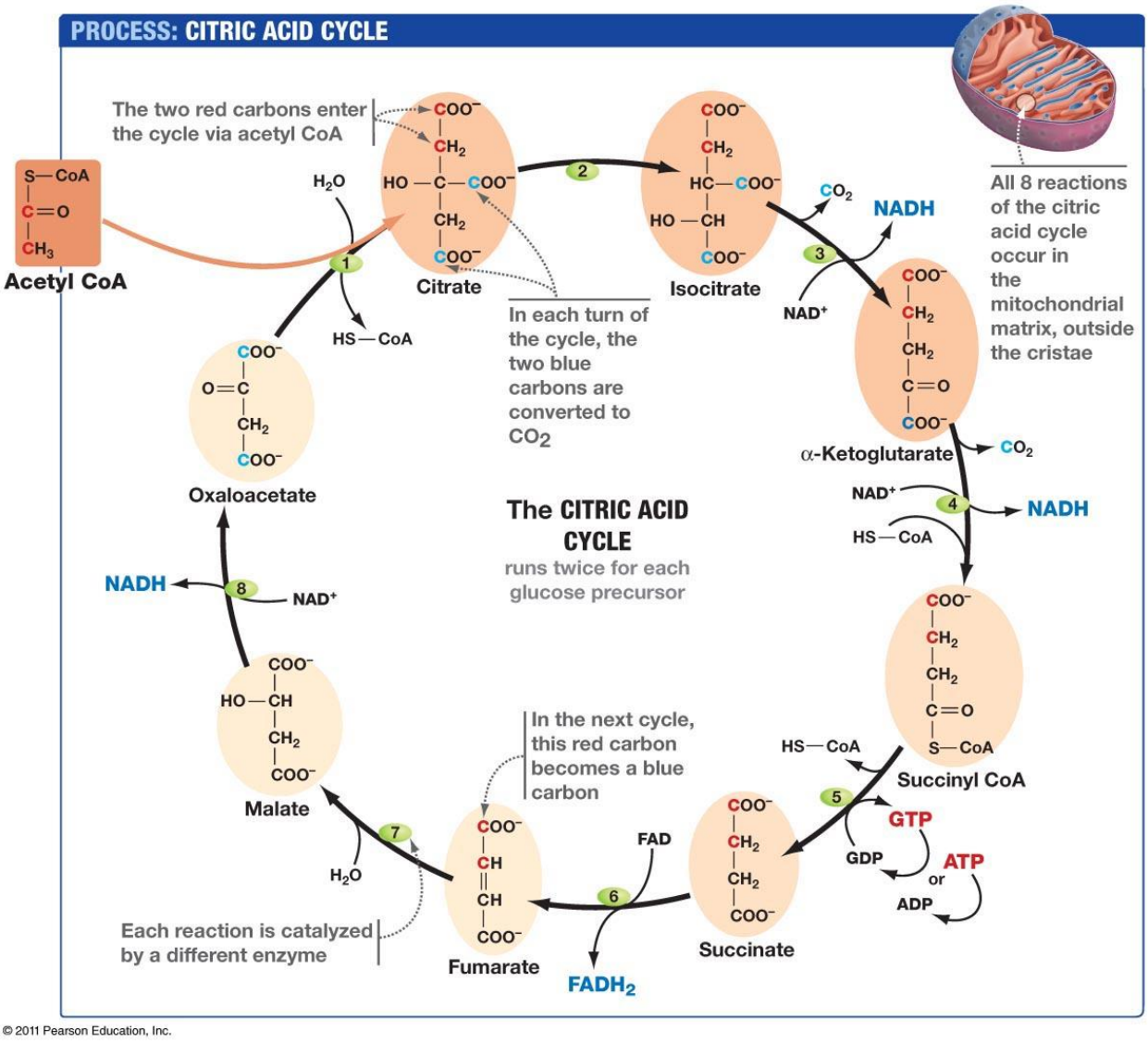


Link reaction between glycolysis and the Krebs cycle

III. Citric Acid Cycle/ Krebs Cycle:-

This is also called the Krebs cycle or the **tricarboxylic acid cycle**. When oxygen is present, acetyl-CoA is produced from the pyruvate molecules created from glycolysis. In the presence of oxygen, when acetyl-CoA is produced, the molecule then enters the citric acid cycle (Krebs cycle) inside the **mitochondrial matrix**, and gets oxidized to CO2 while at the same time reducing NAD to

NADH. NADH can be used by the electron transport chain to create further ATP as part of oxidative phosphorylation. To fully oxidize the equivalent of one glucose molecule, two acetyl-CoA must be metabolized by the Krebs cycle. Two waste products, H_2O and CO_2, are created during this cycle.

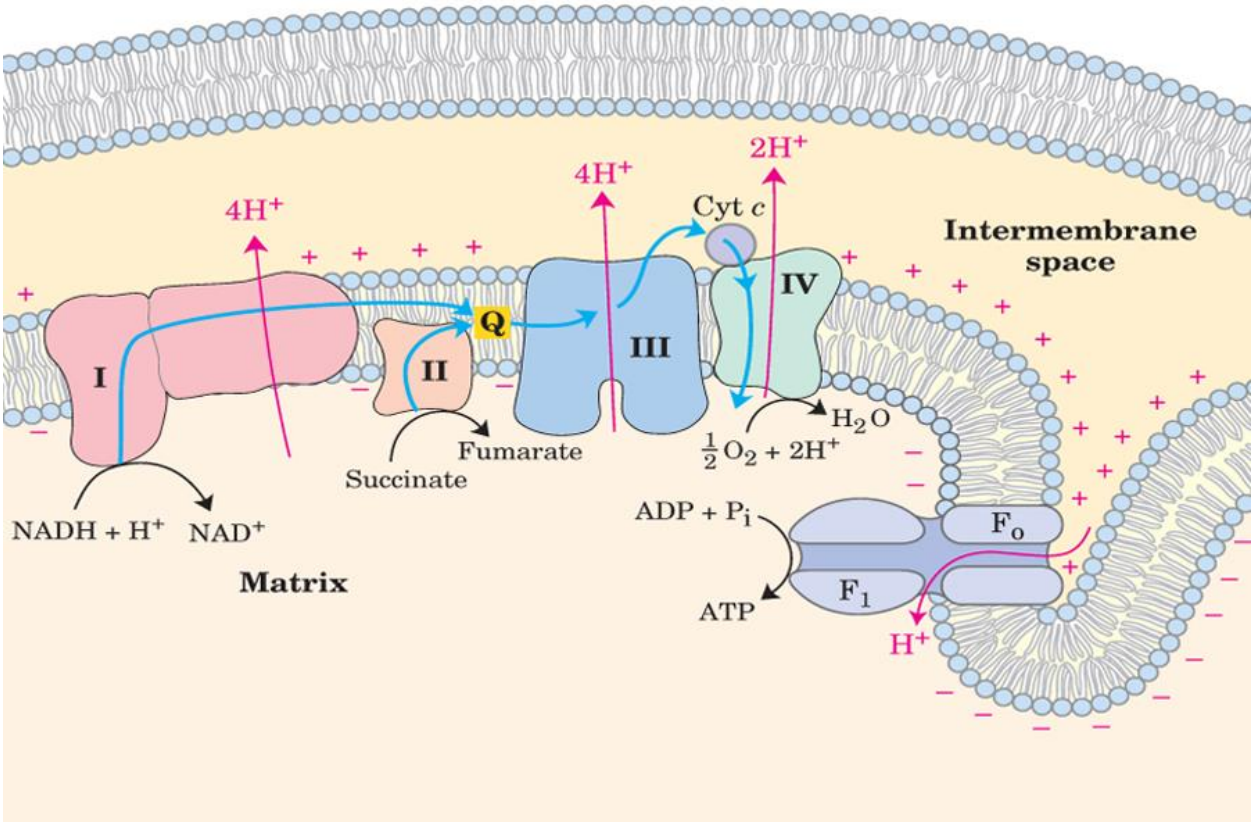


The citric acid cycle is an 8-step process involving different enzymes and co-enzymes. Throughout the entire cycle, acetyl-CoA(2 carbons) + Oxaloacetate(4 carbons). Citrate(6 carbons) is rearranged to a more reactive form called Isocitrate(6 carbons). Isocitrate(6 carbons) modifies to become α-Ketoglutarate(5 carbons), Succinyl-CoA, Succinate, Fumarate, Malate, and finally, Oxaloacetate. The net energy gain from one cycle is **3 NADH, 1 FADH2, and 1 GTP**; the GTP

may subsequently be used to produce ATP. Thus, the total energy yield from one whole glucose molecule (2 pyruvate molecules) is **6 NADH, 2 FADH2, and 2 ATP.**

IV. Oxidative phosphorylation or Electron transport chain:-

In eukaryotes, oxidative phosphorylation occurs in the mitochondrial **cristae**. It comprises the electron transport chain that establishes a proton gradient (chemiosmotic potential) across the inner membrane by oxidizing the NADH produced from the Krebs cycle. ATP is synthesised by the **ATP synthase enzyme** when the chemiosmotic gradient is used to drive the phosphorylation of ADP. The electrons are finally transferred to exogenous oxygen and, with the addition of two protons, water is formed.



Efficiency of ATP Production:-

The table below describes the reactions involved when one glucose molecule is fully oxidized into carbon dioxide. It is assumed that all the reduced coenzymes are oxidized by the electron transport chain and used for oxidative phosphorylation. Although there is a theoretical yield of **38** ATP molecules per glucose during cellular respiration, such conditions are generally not realized due to losses such as the cost of moving pyruvate (from glycolysis), phosphate, and ADP (substrates

for ATP synthesis) into the mitochondria. All are actively transported using carriers that utilise the stored energy in the proton electrochemical gradient.

Overview of Cellular Respiration (with per Glucose ATP Accounting)	
# ATP	**step**
-2	• priming glycolysis
+4	• substrate level phosphorylation (glycolysis)
+6	• 2 NADH produced (glycolysis)
-2	• transportation of two NADH into mitochondria
+6	• 2 NADH produced in conversion of pyruvate to acetyl-CoA
+18	• 6 NADH produced during Kreb's cycle
+4	• 2 2"$FADH_2$ produced during Kreb's cycle
+2	• substrate level phosphorylation (Kreb's cycle)
+36	• total ATPs produced from one glucose from aerobic respiration in eucaryotes. Compare with total from glycolysis alone (i.e., 2 ATP).

Obviously this reduces the theoretical efficiency of the whole process and the likely maximum is closer to **28–30 ATP** molecules. In practice the efficiency may be even lower due to the inner membrane of the mitochondria being slightly leaky to protons. Other factors may also dissipate the proton gradient creating an apparently leaky mitochondria. The potential energy from the proton gradient is not used to make ATP but generates heat. This is particularly important in brown fat thermogenesis of newborn and hibernating plants. According to some of newer sources the ATP yield during aerobic respiration is not 36-38, but only about 30-32 ATP molecules / 1 molecule of glucose, because:

ATP : NADH+H+ and ATP : FADH2 ratios during the oxidative phosphorylation appear to be not 3 and 2, but 2.5 and 1.5 respectively. Unlike in the substrate-level phosphorylation, the stoichiometry here is difficult to establish.

ATP synthase produces 1 ATP / 3 H+. However the exchange of matrix ATP for cytosolic ADP and Pi (antiport with OH- or symport with H+) mediated by ATP–ADP translocase and phosphate carrier consumes 1 H+ / 1 ATP due to regeneration of the transmembrane potential changed during this transfer, so the net ratio is 1 ATP / 4 H+.

The mitochondrial electron transport chain proton pump transfers across the inner membrane 10 H+ / 1 NADH+H+ (4+2+4) or 6 H+ / 1 FADH2 (2+4).

So the final stoichiometry is

1 NADH+H+ : 10 H+ : 10/4 ATP = 1 NADH+H+ : 2.5 ATP

1 FADH2 : 6 H+ : 6/4 ATP = 1 FADH2 : 1.5 ATP

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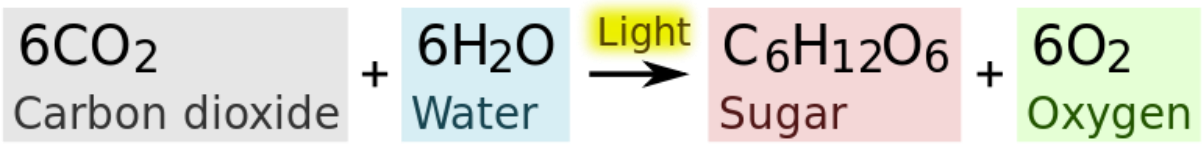
Plant Photosynthesis

Introduction:-

Photosynthesis is a process used by plants and other organisms to convert the light energy captured from the sun into chemical energy that can be used to fuel the organism's activities. Photosynthesis occurs in plants, algae, and many species of bacteria. Photosynthetic organisms are called **photoautotrophs**, since they can create their own food. In plants, algae, and cyanobacteria, photosynthesis uses carbon dioxide and water, releasing oxygen as a waste product. Photosynthesis is **vital** for all aerobic life on Earth. In addition to maintaining normal levels of oxygen in the atmosphere, photosynthesis is the source of energy for nearly all life on earth, either directly, through primary production, or indirectly, as the ultimate source of the energy in their food. The **average rate of energy capture** by photosynthesis globally is immense, approximately **130 terawatts**, which is about **six times larger** than the power consumption of human civilization. As well as energy, photosynthesis is also the source of the carbon in all the organic compounds within organisms' bodies. In all, photosynthetic organisms convert around **100–115 thousand million metric tons** carbon into biomass per year.

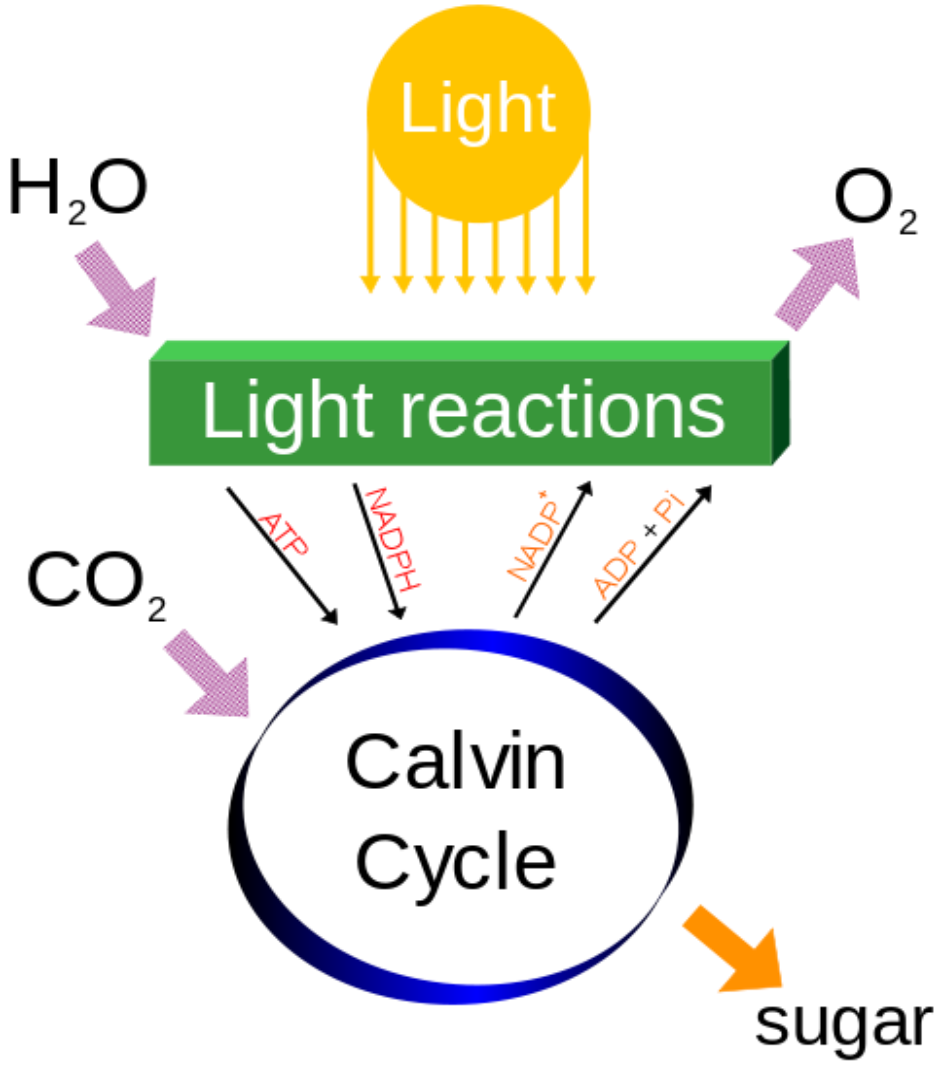
Summary:-

Although photosynthesis can happen in different ways in different species, some features are always the same. For example, the process always begins when energy from **light** is absorbed by proteins called **photosynthetic reaction centers** that contain chlorophylls. In plants, these proteins are held inside organelles called **chloroplasts**, while in bacteria they are embedded in the plasma membrane. Some of the light energy gathered by chlorophylls is stored in the form of **adenosine triphosphate (ATP)**. The rest of the energy is used to **remove electrons** from a substance such as water. These electrons are then used in the reactions that turn **carbon dioxide** into organic compounds. In plants, algae and cyanobacteria, this is done by a sequence of reactions called the **Calvin cycle**. Many photosynthetic organisms have adaptations that concentrate or store carbon dioxide. This helps reduce a wasteful process called **photorespiration** that can consume part of the sugar produced during photosynthesis. This whole process in short usually expressed as an equation.



Schematic of Photosynthesis in Plants:-

The first photosynthetic organisms probably evolved about **3,500 million years ago**, early in the evolutionary history of life. The chloroplasts in modern plants are the descendants of the ancient **symbiotic cyanobacteria**. Photosynthetic organisms are **photoautotrophs**, which means that they are able to synthesize food directly from carbon dioxide and water using energy from light. In plants, algae and cyanobacteria, photosynthesis releases oxygen. Carbon dioxide is converted into **sugars** in a process called **carbon fixation**. Carbon fixation is a **redox reaction**, so photosynthesis needs to supply both a source of energy to drive this process, and the electrons needed to convert carbon dioxide into a carbohydrate, which is a reduction reaction. In general outline, photosynthesis is the opposite of **cellular respiration**, where glucose and other compounds are oxidized to produce carbon dioxide, water, and release chemical energy. However, the two processes take place through a different sequence of chemical reactions and in different cellular compartments.



The general equation for photosynthesis is therefore:

$$2n\ CO_2 + 2n\ DH_2 + photons \rightarrow 2(CH_2O)n + 2n\ DO$$

Carbon dioxide + Electron donor + Light energy → Carbohydrate + Oxidized electron donor

In oxygenic photosynthesis water is the electron donor and, since its hydrolysis releases oxygen, the equation for this process is:

$$2n\ CO_2 + 4n\ H_2O + photons \rightarrow 2(CH_2O)n + 2n\ O_2 + 2n\ H_2O$$

Carbon dioxide + Water + Light energy → Carbohydrate + Oxygen + Water

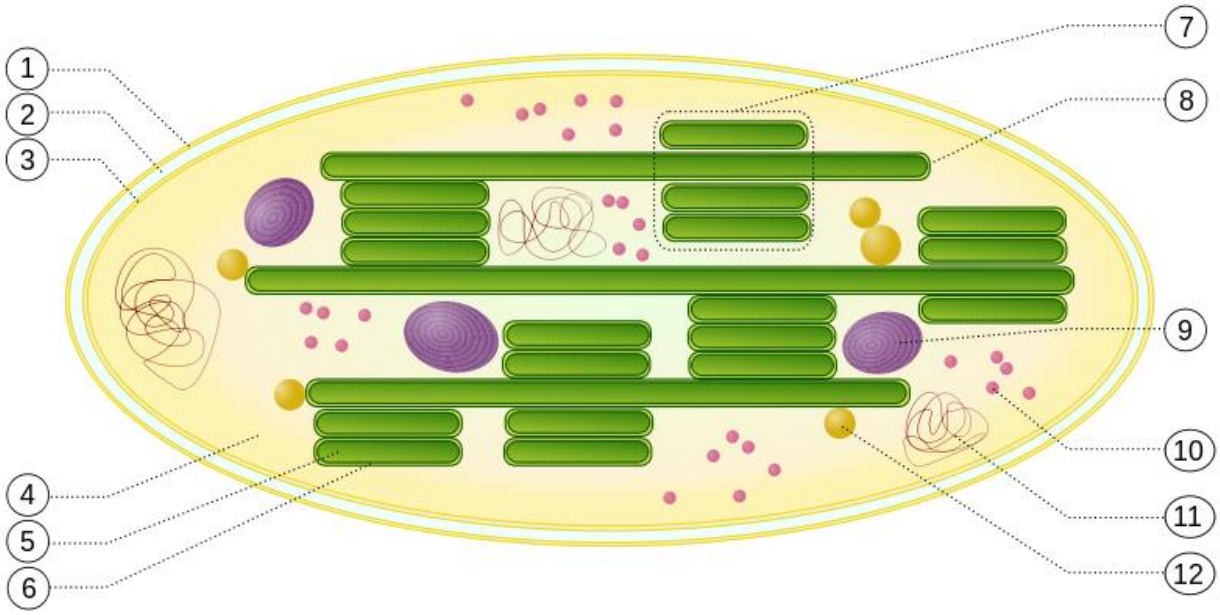
Photosynthesis occurs in two stages. In the first stage, **light-dependent reactions** or light reactions capture the energy of light and use it to make the energy-storage molecules **ATP** and **NADPH**. During the second stage, the **light-independent reactions** use these products to capture and reduce carbon dioxide. Most organisms that utilize photosynthesis to produce oxygen use visible light to do so.

Photosynthetic Membranes and Organelles:-

In plants and algae, photosynthesis takes place in organelles called **chloroplasts**. A typical plant cell contains about **10 to 100** chloroplasts. The chloroplast is enclosed by a membrane **(Tonoplast).** This membrane is composed of a phospholipid inner membrane, a phospholipid outer membrane, and an intermembrane space between them. Within the membrane is an aqueous fluid called the **stroma**. The stroma contains stacks (**grana**) of thylakoids, which are the site of photosynthesis. The **thylakoids** are flattened disks, bounded by a membrane with a **lumen** or thylakoid space within it. The site of photosynthesis is the thylakoid membrane, which contains integral and peripheral membrane protein complexes, including the pigments that absorb light energy, which form the photosystems. Plants absorb light primarily using the **pigment chlorophyll**, which is the reason that most plants have a **green color**. Besides chlorophyll, plants also use pigments such as **carotenes and xanthophylls**. These pigments are embedded in plants and algae in special antenna-proteins. In such proteins all the pigments are ordered to work well together. Such a protein is also called a **light-harvesting complex**.

Although all cells in the green parts of a plant have chloroplasts, most of the energy is captured in the leaves. The cells in the interior tissues of a leaf, called the **mesophyll**, can contain between **450,000 and 800,000** chloroplasts for every **square millimeter** of leaf. The surface of the leaf is uniformly coated with a water-resistant waxy **cuticle** that protects the leaf from excessive evaporation of water and decreases the absorption of **ultraviolet** or blue light to reduce heating. The transparent epidermis layer allows light to pass through to the palisade mesophyll cells where most of the photosynthesis takes place.

Chloroplast ultra-structure:



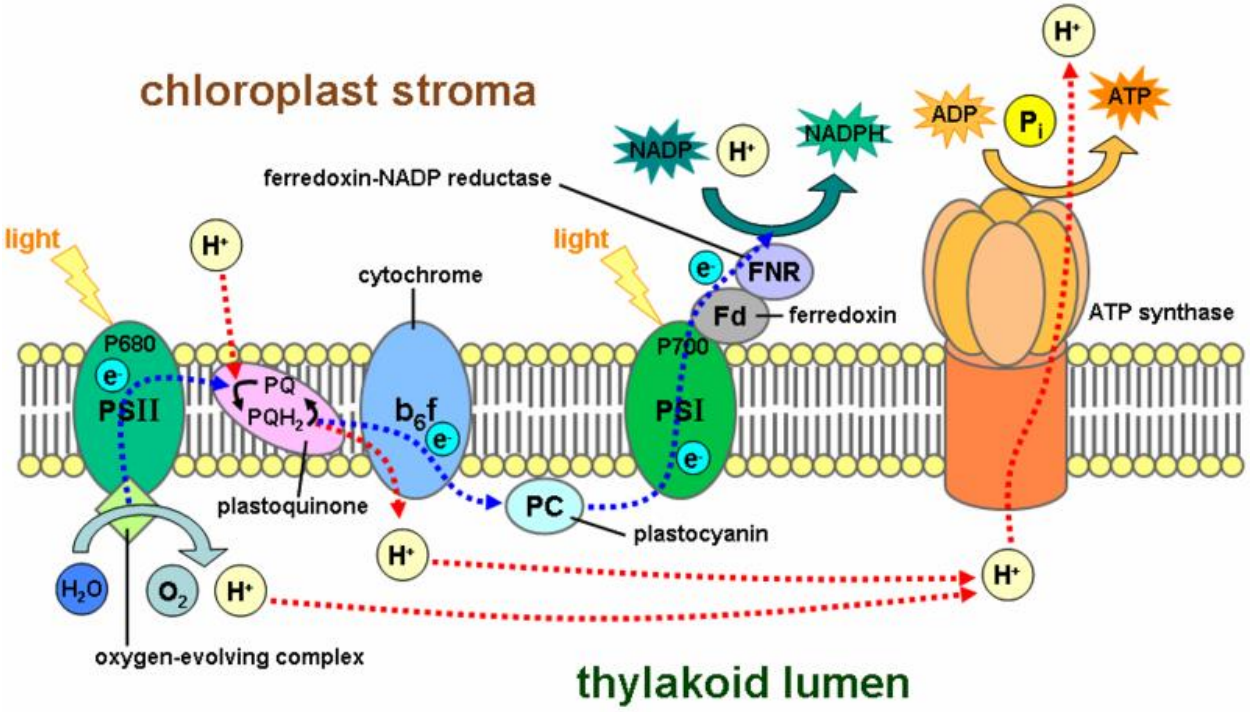
1. Outer membrane
2. Intermembrane space
3. Inner membrane (1+2+3: envelope)
4. Stroma (aqueous fluid)
5. Thylakoid lumen (inside of thylakoid)
6. Thylakoid membrane
7. Granum (stack of thylakoids)
8. Thylakoid (lamella)
9. Starch
10. Ribosome
11. Plastidial DNA
12. Plastoglobule (drop of lipids)

Light-dependent Reactions/ Light Reaction:-

Light-dependent reactions of photosynthesis at the thylakoid membrane.

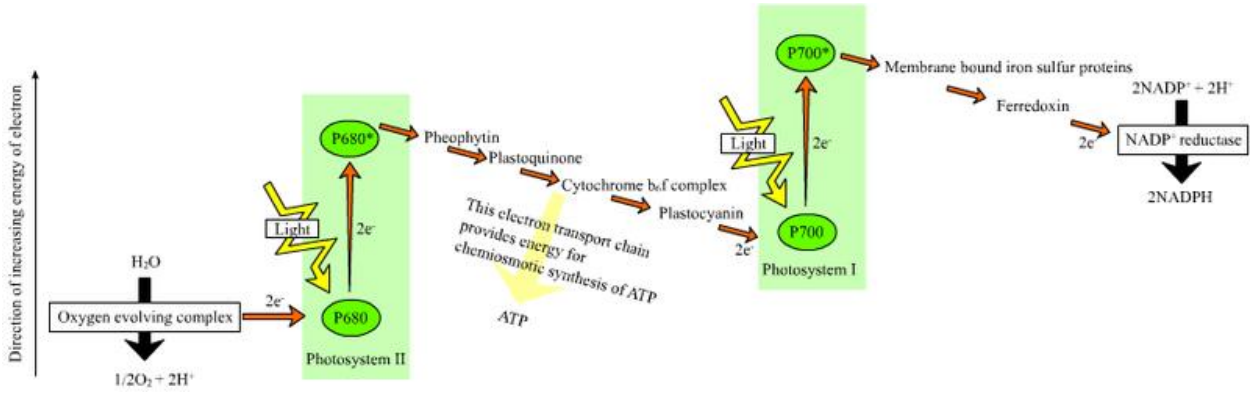
In the light reactions, one molecule of the pigment chlorophyll absorbs one photon and loses one electron. This electron is passed to a modified form of chlorophyll called **pheophytin**, which passes the electron to a **quinone** molecule, allowing the start of a flow of electrons down an electron transport chain that leads to the ultimate reduction of NADP to NADPH. In addition, this creates a **proton gradient** across the chloroplast membrane; its dissipation is used by ATP synthase for the concomitant synthesis of ATP. The chlorophyll molecule regains the lost electron from a water molecule through a process called **photolysis**, which releases a di-oxygen (O2) molecule. The overall equation for the light-dependent reactions under the conditions of non-cyclic electron flow in green plants is…..

$2\ H_2O + 2\ NADP^+ + 3\ ADP + 3\ Pi + light \rightarrow 2\ NADPH + 2\ H^+ + 3\ ATP + O_2$



Not all wavelengths of light can support photosynthesis. The photosynthetic **action spectrum** depends on the type of accessory pigments present. For example, in green plants, the action spectrum resembles the absorption spectrum for chlorophylls and carotenoids with peaks for **violet-blue and red light**. In red algae, the action spectrum overlaps with the absorption spectrum of phycobilins for red blue-green light, which allows these algae to grow in deeper waters that filter out the longer wavelengths used by green plants. The non-absorbed part of the light spectrum is what gives photosynthetic organisms their color (e.g., green plants, red algae, purple bacteria) and is the least effective for photosynthesis in the respective organisms.

The "Z scheme":- In plants, light-dependent reactions occur in the **thylakoid membranes** of the chloroplasts and use light energy to synthesize **ATP and NADPH**. The light-dependent reaction has two forms: **cyclic** and **non-cyclic**. In the non-cyclic reaction, the photons are captured in the **light-harvesting antenna** complexes of **photosystem II** by chlorophyll and other accessory-



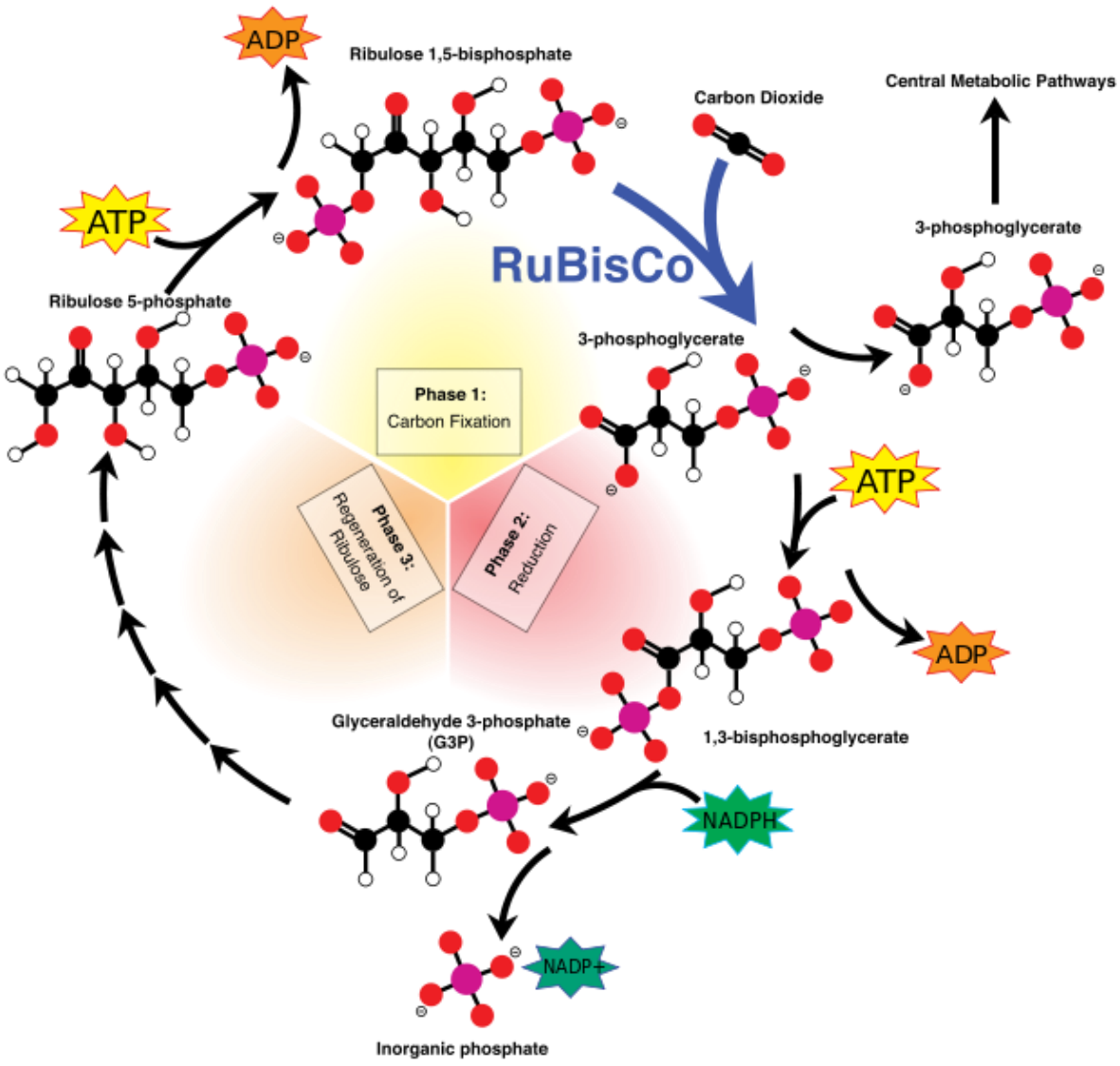
pigments (see diagram). When a chlorophyll molecule at the core of the photosystem II reaction center obtains sufficient excitation energy from the adjacent antenna pigments, an electron is transferred to the primary electron-acceptor molecule, **pheophytin**, through a process called **photoinduced charge separation**. These electrons are shuttled through an electron transport chain, the so-called **Z-scheme** shown in the diagram that initially functions to generate a **chemiosmotic** potential across the membrane. An **ATP synthase enzyme** uses the chemiosmotic potential to make ATP during **photophosphorylation**, whereas NADPH is a product of the terminal redox reaction in the Z-scheme. The electron enters a chlorophyll molecule in **Photosystem I**. The electron is excited due to the light absorbed by the photosystem. A second electron carrier accepts the electron, which again is passed down lowering energies of electron acceptors. The energy created by the electron acceptors is used to move hydrogen ions across the thylakoid membrane into the lumen. The electron is used to reduce the **co-enzyme NADP**, which has functions in the light-independent reaction. The **cyclic reaction** is similar to that of the **non-cyclic**, but differs in the form that it generates only ATP, and no reduced NADP (NADPH) is created. The cyclic reaction takes place only at photosystem I. Once the electron is displaced from the photosystem, the electron is passed down the electron acceptor molecules and returns to photosystem I, from where it was emitted, hence the name cyclic reaction.

Photodissociation and Oxygen Evolution:- The NADPH is the main **reducing agent** in chloroplasts, providing a source of energetic electrons to other reactions. Its production leaves chlorophyll with a deficit of electrons (oxidized), which must be obtained from some other reducing agent. The excited electrons lost from chlorophyll in photosystem I are replaced from the electron transport chain by plastocyanin. However, since photosystem II includes the first steps of the Z-scheme, an external source of electrons is required to reduce its oxidized chlorophyll a molecules. The source of electrons in green-plant and cyanobacterial photosynthesis is water. Two water molecules are oxidized by four successive charge-separation reactions by photosystem II to yield a molecule of diatomic oxygen and four **hydrogen ions**; the electron yielded in each step is transferred to a redox-active **tyrosine** residue that then reduces the photoxidized paired-chlorophyll a species called **P680** that serves as the primary (light-driven) electron donor in the photosystem II reaction center. The oxidation of water is catalyzed in photosystem II by a redox-active structure that contains four **manganese** ions and a **calcium** ion; this oxygen-evolving complex binds two water molecules and stores the four oxidizing equivalents that are required to drive the water-oxidizing reaction. Photosystem II is the only known biological enzyme that carries out this oxidation of water. The hydrogen ions contribute to the **transmembrane chemiosmotic potential** that leads to ATP synthesis. Oxygen is a waste product of light-dependent reactions, but the majority of organisms on Earth use oxygen for cellular respiration, including photosynthetic organisms.

Calvin cycle, Carbon Fixation, and Light-independent Reactions (C3):-

In the light-independent (or "dark") reactions, the enzyme **RuBisCO** captures CO_2 from the atmosphere and in a process that requires the newly formed NADPH, called the Calvin-Benson Cycle, releases three-carbon sugars, which are later combined to form sucrose and starch. The overall equation for the light-independent reactions in green plants is….

$$3\ CO_2 + 9\ ATP + 6\ NADPH + 6\ H^+ \rightarrow C_3H_6O_3\text{-phosphate} + 9\ ADP + 8\ Pi + 6\ NADP^+ + 3\ H_2O$$

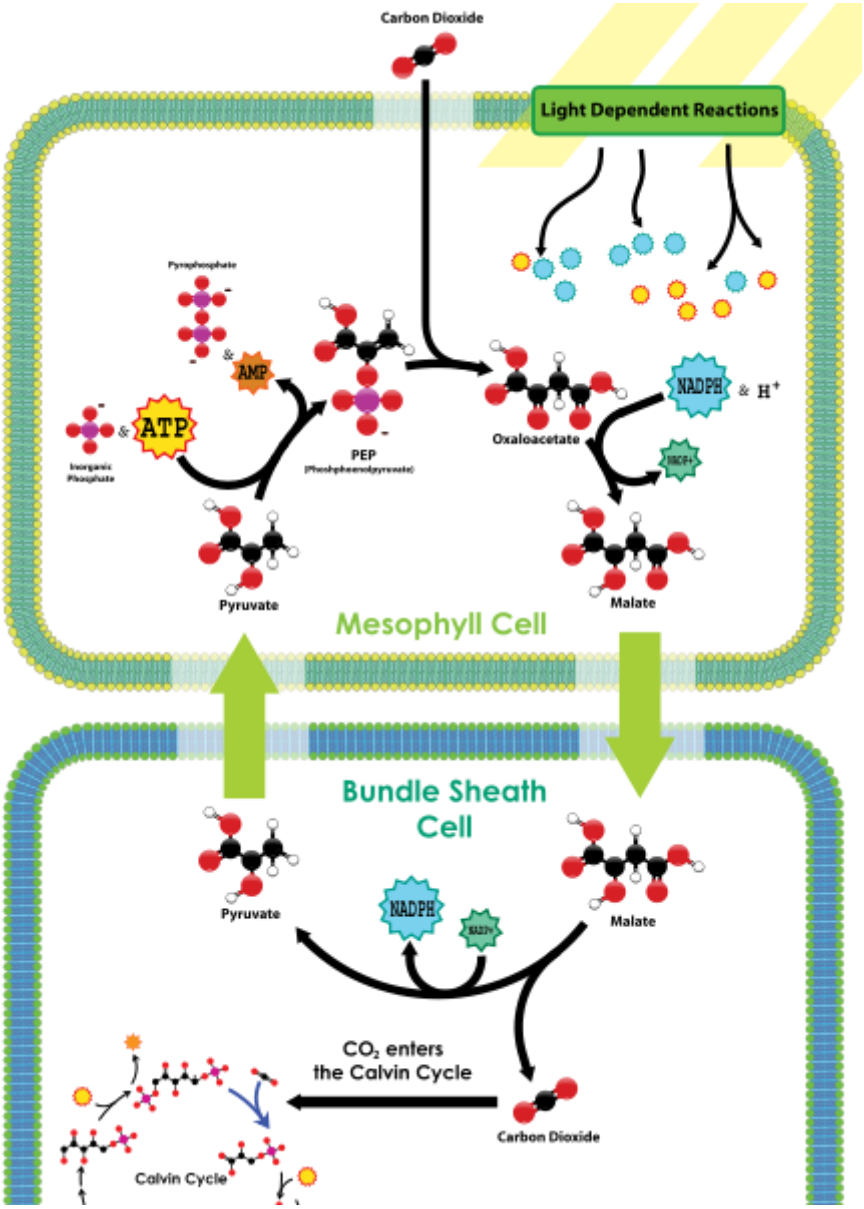


Overview of the Calvin cycle and carbon fixation

To be more specific, carbon fixation produces an intermediate product, which is then converted to the final **carbohydrate** products. The carbon skeletons produced by photosynthesis are then variously used to form other organic compounds, such as the building material cellulose, as precursors for lipid and amino acid **biosynthesis**, or as a fuel in cellular respiration. The latter occurs not only in plants but also in animals when the energy from plants gets passed through a food chain. The fixation or reduction of carbon dioxide is a process in which carbon dioxide combines with a five-carbon sugar, **ribulose 1,5-bisphosphate (RuBP)**, to yield two molecules of a three-carbon compound, glycerate 3-phosphate (GP), also known as **3-phosphoglycerate**

(PGA). GP, in the presence of ATP and NADPH from the light-dependent stages, is reduced to glyceraldehyde 3-phosphate **(G3P)**. This product is also referred to as 3-phosphoglyceraldehyde (PGAL) or even as **triose phosphate**. Triose is a 3-carbon sugar (see carbohydrates). Most (5 out of 6 molecules) of the G3P produced is used to regenerate RuBP so the process can continue (see Calvin-Benson cycle). The 1 out of 6 molecules of the triose phosphates not "recycled" often condense to form hexose phosphates, which ultimately yield sucrose, starch and cellulose. The sugars produced during carbon metabolism yield carbon skeletons that can be used for other metabolic reactions like the production of amino acids and lipids.

Carbon Concentrating Mechanisms (C4 carbon fixation):-



In hot and dry conditions, plants close their stomata to prevent the loss of water. Under these conditions, CO2 will decrease, and oxygen gas, produced by the light reactions of photosynthesis, will decrease in the stem, not leaves, causing an increase of **photorespiration** by the oxygenase activity of **ribulose-1,5-bisphosphate carboxylase/oxygenase** and decrease in carbon fixation. Some plants have evolved mechanisms to increase the CO2 concentration in the leaves under these conditions. **C4** plants chemically fix carbon dioxide in the cells of the mesophyll by adding it to the three-carbon molecule **phosphoenolpyruvate (PEP)**, a reaction catalyzed by an enzyme called **PEP carboxylase**, creating the four-carbon organic acid **oxaloacetic acid**. Oxaloacetic acid or **malate** synthesized by this process is then translocated to specialized bundle sheath cells where the enzyme **RuBisCO** and other Calvin cycle enzymes are located, and where CO2 released by decarboxylation of the four-carbon acids is then fixed by RuBisCO activity to the three-carbon sugar 3-phosphoglyceric acids. The physical separation of RuBisCO from the oxygen-generating light reactions reduces photorespiration and increases CO2 fixation and, thus, photosynthetic capacity of the leaf. C4 plants can produce more **sugar** than C3 plants in conditions of high light and temperature. Many important crop plants are C4 plants, including maize, sorghum, sugarcane, and millet.

	C_3 pathways		**C_4 pathways**
1.	The primary acceptor of CO_2 is RUBP – a six-carbon compound.	**1.**	The primary acceptor of CO_2 is phosphoenol pyruvate – a three-carbon compound.
2.	The first stable product is 3-phosphoglycerate.	**2.**	The first stable product is oxaloacetic acid.
3.	It occurs only in the mesophyll cells of the leaves.	**3.**	It occurs in the mesophyll and bundle-sheath cells of the leaves.
4.	It is a slower process of carbon fixation and photo-respiratory losses are high.	**4.**	It is a faster process of carbon fixation and photo-respiratory losses are low.

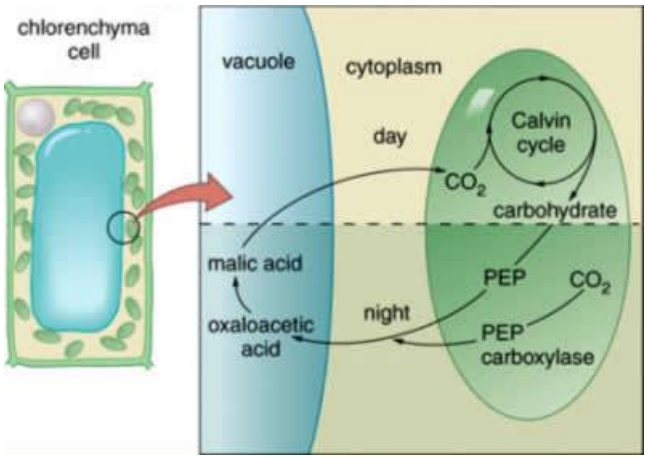
Crassulacean Acid Metabolism (CAM):-

A second alternative photosynthetic pathway, known as crassulacean acid metabolism **(CAM),** exists in succulents such as cacti and other desert plants. These plants have the same two carbon-fixing steps as are present in C4 plants, but rather than being spatially separated between the mesophyll and bundle sheath cells, CAM plants have both carbon dioxide-fixing enzymes **within the same cell**. These enzymes are active at different times, **PEP carboxylase** during the day and **Rubisco** at night. Just as Kranz anatomy is unique to C4 plants, CAM plants are unique in that the **stomata** are open at night and largely closed during the day. The biochemical pathway of photosynthesis in CAM plants begins at night. With the stomata open, carbon dioxide diffuses into

the leaf and into mesophyll cells, where it is fixed by the C4 enzyme PEP carboxylase. The product is **malate**, as in C4 photosynthesis, but it is transformed into **malic acid** (a nonionic form of malate) and is stored in the cell's **vacuoles** (cavities within the cytoplasm) until the next day. Although the malic acid will be used as a carbon dioxide source for the **C3 cycle**, just as in C4 photosynthesis, it is stored until daylight because the C3 cycle requires light as an energy source. The vacuoles will accumulate malic acid through most of the night.

A few hours before daylight, the vacuole will fill up, and malic acid will begin to accumulate in the **cytoplasm** outside the vacuole. As it does, the pH of the cytoplasm will become acidic, causing the enzyme to stop functioning for the rest of the night. When the sun rises the stomata will close, and photosynthesis by the C3 cycle will quickly deplete the atmosphere within the leaf of all carbon dioxide. At this time, the malic acid will be transported out of the vacuole to the cytoplasmof the cell. There it will be broken down, and the carbon dioxide will enter the chloroplast and be used by the C3 cycle; thus, photosynthesis is able to continue with closed stomata.

Crassulacean acid metabolism derives its name from the fact that it involves a daily fluctuation in the level of acid within the plant and that it was first discovered to be common in species within the stonecrop family, **Crassulaceae**. The CAM plants are successful inhabitants of warm, arid sites and include species of 23 or more flowering plant families as well as a few ferns. Many are fleshy succulents like the stonecrops (Crassulaceae) for which the C4 type was named, as well as many cacti, agaves, and lilies.



Environmental Factors Affecting Photosynthesis:-

The term rate always involves time, so the rate of photosynthesis can be considered to be how fast photosynthesis takes place. This can be measured by the amount of **glucose produced** by a plant over a given time. This topic is especially important to scientist and farmers. By understanding the factors that affect the rate of photosynthesis they can do work to try and increase the rate of photosynthesis to increase the yield of a crop.

The three main things affecting the rate of photosynthesis are:

1.Light

2.Temperature

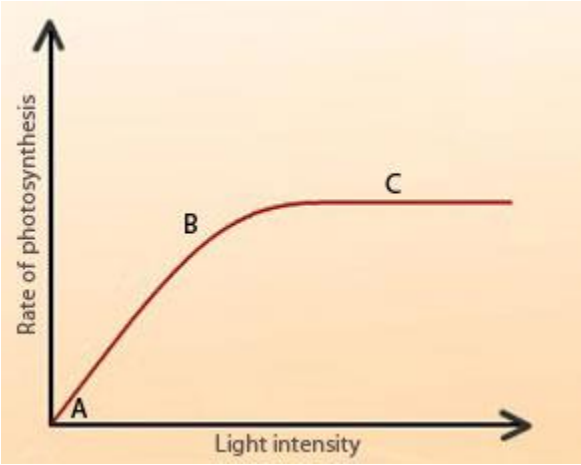
3.Carbon dioxide

These three factors are called **LIMITING FACTORS**.

In a process like photosynthesis which is affected by more than one factor, its rate is limited by the factor which is closest to its minimum value. So at any point in time if one of the three factors is in low supply, this factor will be the limiting factor. Only a change to the limiting factor will increase or decrease the rate of photosynthesis. Changing the other two will have no effect. In addition to the three main factors above are other factors such as chlorophyll concentration, water and pollution. Only the three main factors identified above will be considered in further detail.

1- Light:-

The rate of photosynthesis increases when light gets brighter. The rate of photosynthesis increases linearly with increasing light intensity. Gradually the rate falls of and at a certain light intensity the rate of photosynthesis stay constant. Here a rise in light intensity has no effect on the rate of photosynthesis as the other factors such as temperature and carbon dioxide become limiting.



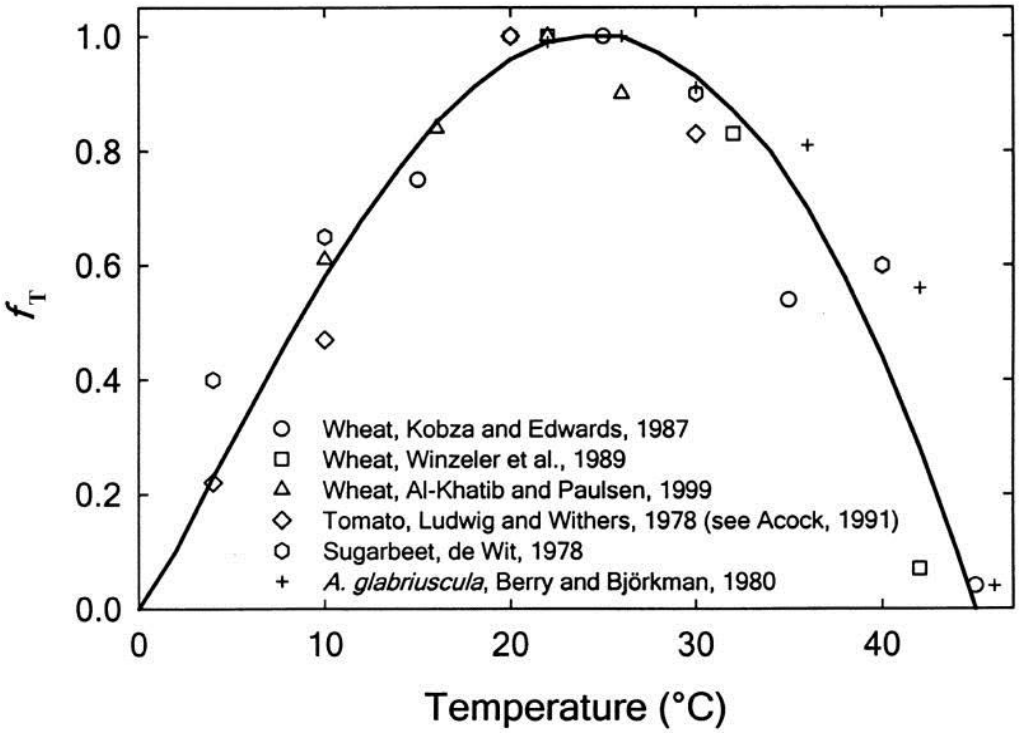
The effects of light on photosynthesis

Many plants spread out their leaves in such a way that each leaf maximises the amount of light falling on them and the lower leaves are not shaded by the ones above. Too much light at a **high intensity** can damage chloroplasts. Some woodland plants photosynthesize more efficiently in dim light and are so called shade plants. The animation above describes an experiment to investigate the effects of light on photosynthesis.

2- Temperature:-

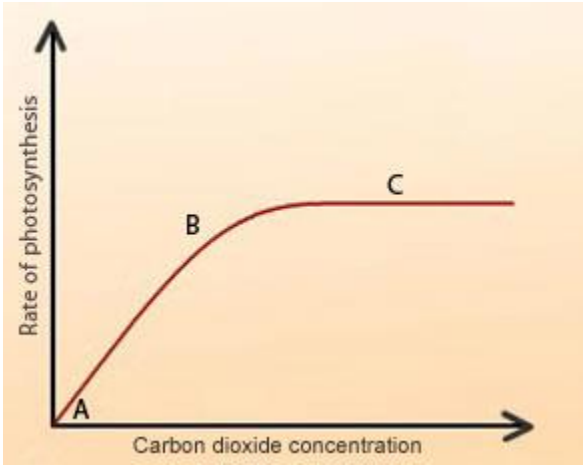
The higher the temperature then typically the greater the rate of photosynthesis, photosynthesis is a chemical reaction and the rate of most chemical reactions increases with temperature. However, for photosynthesis at temperatures above **40°C** the rate slows down. This is because the **enzymes** involved in the chemical reactions of photosynthesis are temperature sensitive and **destroyed** at higher temperatures. To better understand the effects of temperature on photosynthesis it is important to know the effect of temperature on the enzymes involved in photosynthesis. Enzymes are affected a great deal by temperature. If the temperature is too cold the enzymes move around too slowly to meet the substrate and for a reaction to occur. As the temperature increases though, so does the rate of reaction. This is because heat energy causes more collisions between the enzyme and the substrate. However as you will remember all enzymes are proteins and at too high temperatures the **proteins break down**. The active site of the enzyme becomes distorted and so the substrate no longer fits and hence the reaction does not occur. We say that the enzyme has been **denatured**.

Greenhouses are used to capitalize on the effects of higher temperatures increasing the rate of photosynthesis. Plants from regions of warmer climates can successfully grow in colder regions by using greenhouses. The rate of photosynthesis does not increase with higher temperatures for all plants. Plants which grow in colder climates have an optimum rate of photosynthesis at low temperatures. Therefore different types of plants have **optimum** temperatures for photosynthesis.



3- Carbon dioxide:-

Carbon dioxide is used to make sugar in the photosynthesis reaction. The concentration of carbon dioxide in the Earth's atmosphere varies between **0.03% and 0.04%.** An increase in the concentration of carbon dioxide gives an increase in the rate of photosynthesis. It is difficult to do this out in the open air but is possible in a greenhouse.



The rate of photosynthesis increases linearly with increasing carbon dioxide concentration (from point A to B on the graph). Gradually the rate falls of and at a certain carbon dioxide concentration the rate of photosynthesis stays constant (from point B to C on the graph). Here a rise in carbon dioxide levels has no effect on the rate of photosynthesis as the other factors such as light intensity become limiting. Many crops such as tomatoes and lettuce give higher yield when grown in greenhouses. Farmers add additional carbon dioxide into the greenhouse to increase the concentration and so the rate of photosynthesis of the crops. The additional cost of the carbon dioxide is worthwhile because of the increased yield. Some companies have used this to great environmental use. Rather than pump waste carbon dioxide into the atmosphere as a pollutant they redirect it into big greenhouses where plants such as tomatoes use it during photosynthesis. This not only reduces their carbon footprint but gives an additional profitable product.

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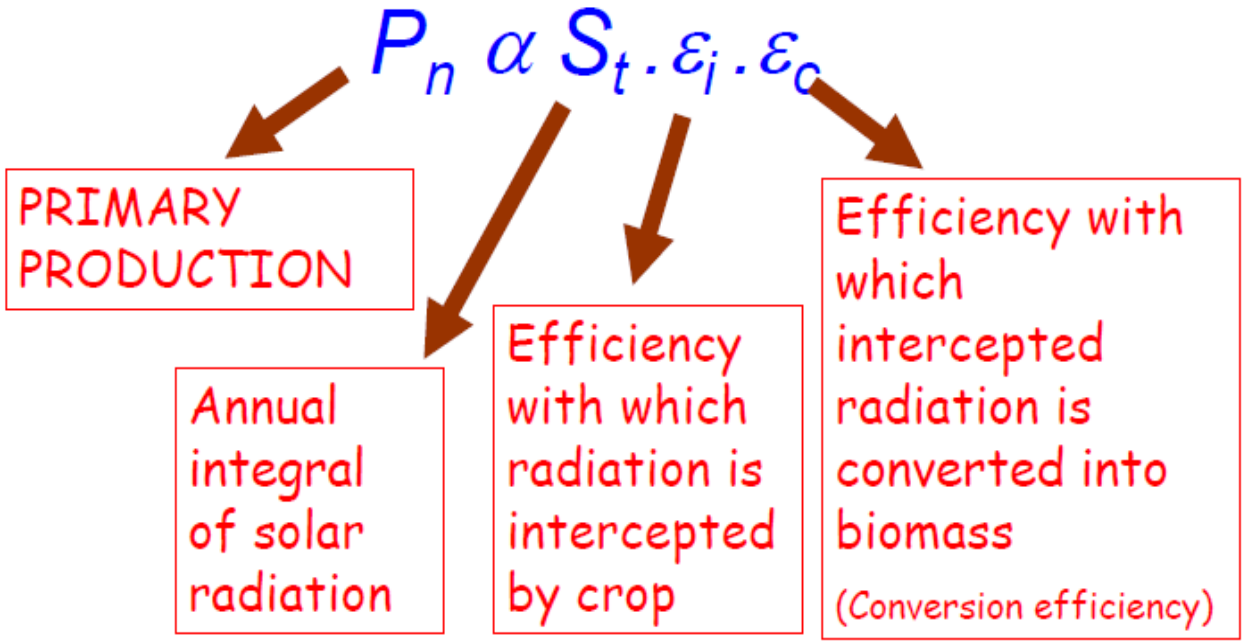
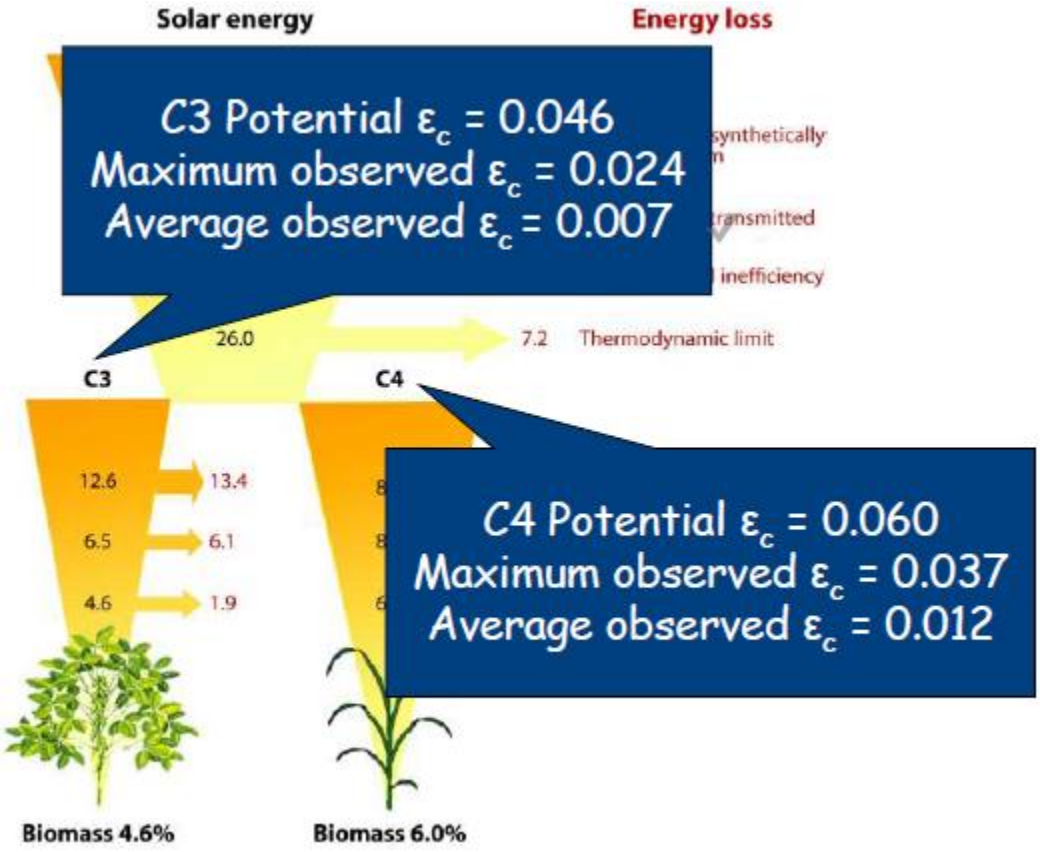
Photosynthetic Efficiency in Agricultural Crops

Increasing the yield potential of the major food grain crops has contributed very significantly to a rising food supply over the past 50 years, which has until recently more than kept pace with rising global demand. Whereas improved **photosynthetic efficiency** has played only a minor role in the remarkable increases in productivity achieved in the last half century, further increases in **yield potential** will rely in large part on improved photosynthesis. Here we examine inefficiencies in photosynthetic energy transduction in crops from **light interception** to carbohydrate synthesis, and how classical breeding, systems biology, and synthetic biology are providing new opportunities to develop more productive germplasm. Near-term opportunities include improving the display of leaves in **crop canopies** to avoid light saturation of individual leaves and further investigation of a **photorespiratory** bypass that has already improved the productivity of model species. Longer-term opportunities include engineering into plants carboxylases that are better adapted to current and forthcoming CO_2 concentrations, and the use of modeling to guide molecular optimization of resource investment among the components of the photosynthetic apparatus, to maximize carbon gain without increasing crop inputs. Collectively, these changes have the potential to more than double the yield potential of our major crops. It can be summarized as:



However a huge difference is present between radiation coming to plants canopy and effect use of the radiation for photosynthesis. These differences varies in C3 and C4 plants as presented below.



Possible increases photosynthetic efficiency to convert CO_2 into biomass: Despite the fact that photosynthesis is the basis of energy capture from the sun in plants, algae and other organisms, it has some fundamental limitations. There are trade-offs in nature which mean that photosynthesis is not as efficient as it could be – for many important crops such as wheat, barley, potatoes and sugar beet, the theoretical maximum is only **5%,** depending on how it is measured. There is scope to improve it for processes useful to us, for example increasing the amount of food crop or energy biomass a plant can produce from the same amount of sunlight. For this purpose genetic or physiological improvements for canopy architecture, leaf area, leaf arrangements, RuBP activity, light interception and C4 mechanism can significantly improve the photosynthetic efficiency in agricultural crops. A brief table below is presenting the potential of these fundamental modifications to increase photosynthetic efficiency under a given amount of light.

Modification	Estimated % increase in ε_c	Speculated Time
Increased rate of regeneration of RuBP by SBPase overexpression	30%	Near-term
Improved canopy architecture	30%	Near-term
Photorespiration by-pass	13%	Near-term
Engineering higher catalytic rate foreign forms of Rubisco	25%	Mid-term
Improved recovery from photoprotection	15%	Mid-term
C4 photosynthesis engineered into C3 crops	30%	Long-term
Rubisco with decreased oxygenase activity without decrease in catalytic rate	30%	Long-term
Improved regulatory and acclimatory responses	?	Long-term

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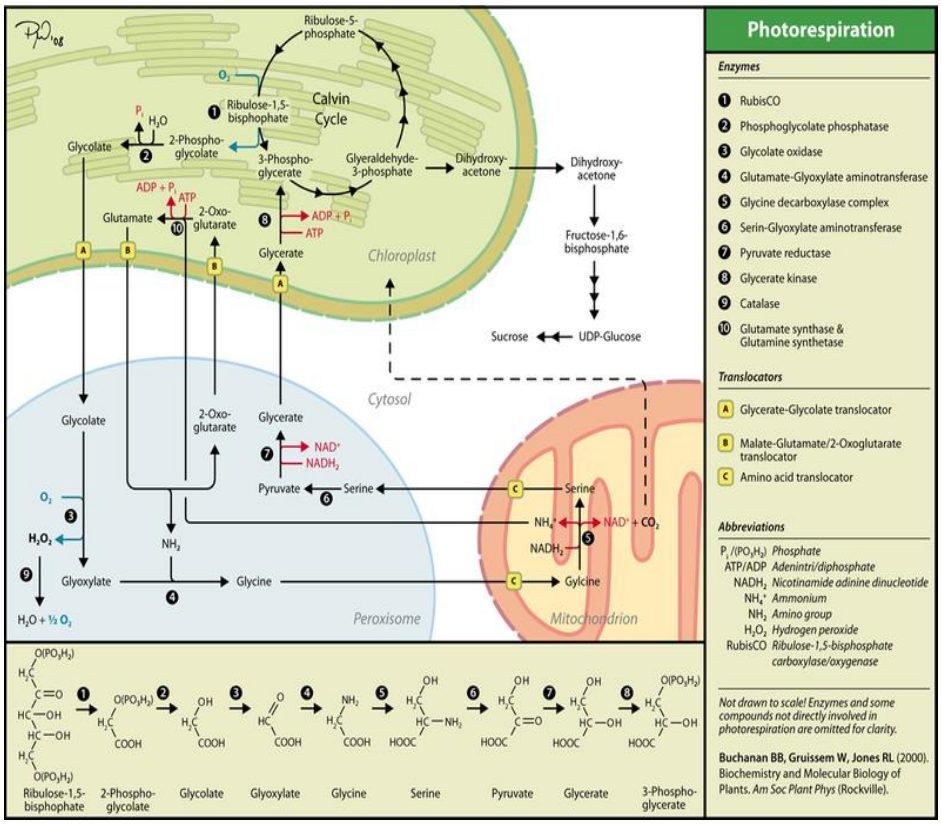
Modified from Zhu et al. (2010) Annu Rev Plant Biology 61, 235-261.

1-Photorespiration:-

Photorespiration, or "'photo-respiration"', is a process in plant metabolism by which RuBP (a sugar) has oxygen added to it by the enzyme (**rubisco**), instead of carbon dioxide during normal photosynthesis. This is the beginning step of the Calvin-Benson cycle. This process reduces efficiency of photosynthesis in **C3** plants.

Biochemistry of the reaction in brief: Rubisco favors carbon dioxide as a ligand to oxygen, however, photorespiration occurs when there is a high concentration of oxygen relative to carbon dioxide. The first reaction produces phosphoglycerate (PGA) and phosphoglycolate (PPG); PGA re-enters the **Calvin cycle** and is simply converted back to RuBP. **PPG**, however, is more difficult to recycle and has to move from the chloroplast to the peroxisomes, and then to the mitochondria, undergoing many reactions on the way, before the atoms can return into the Calvin cycle.



Why Photorespiration Occurs:-

Several theories have been proposed to explain why plants photorespire. One possibility is that when plants first evolved, conditions on the primitive earth were very different from what they are now. The early atmosphere contained little oxygen, so the inability of **Rubisco** to distinguish between oxygen and carbon dioxide was not a problem. As the oxygen level in the atmosphere

gradually increased, the formation of **glycolate** during photosynthesis began to occur, and this led to the problem of photorespiration. The glycolate pathway then developed as a mechanism for salvaging some of the material that leaves the Calvin cycle in the form of glycolate ultimately, returning a portion of it to the cycle. Seen in this context, the real culprit in photorespiration is the formation of glycolate by Rubisco, while the **glycolate pathway** is an evolutionary adaptation for making the best of a bad situation. Perhaps, millions of years in the future, plants will evolve a form of Rubisco that can more effectively distinguish between these two gases.

An alternative theory about why plants photorespire is that the process does, in fact, perform an important function: protecting the plant from the harmful effects of very high internal concentrations of oxygen or energy storage molecules. This high concentration could occur when the plant is exposed to high light intensities, causing photosynthesis to generate these substances very rapidly. Photorespiration would then consume some of the excess oxygen and energetic molecules, depleting them to levels that would not be harmful to the plant. It has not yet been conclusively shown, however, that photorespiration really does play such a protective role. Further research will be required before scientists know whether photorespiration is beneficial to the plant.

Conditions Under Which Photorespiration Occurs:-

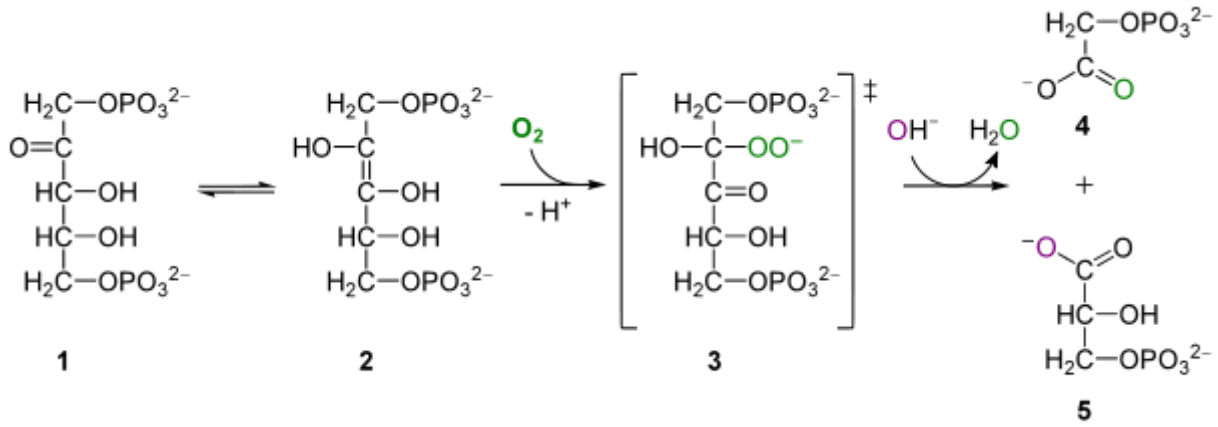
Photorespiration can occur when carbon dioxide levels are low, for example, when the stomata are closed to prevent water loss during drought. In most plants, photorespiration increases as temperature increases. Photorespiration produces no ATP and leads to a net loss of carbon and nitrogen (as ammonia), slowing plant growth. Potential photosynthetic output may be reduced by photorespiration by up to **25%** in C3 plants.

The Glycolate Pathway:-

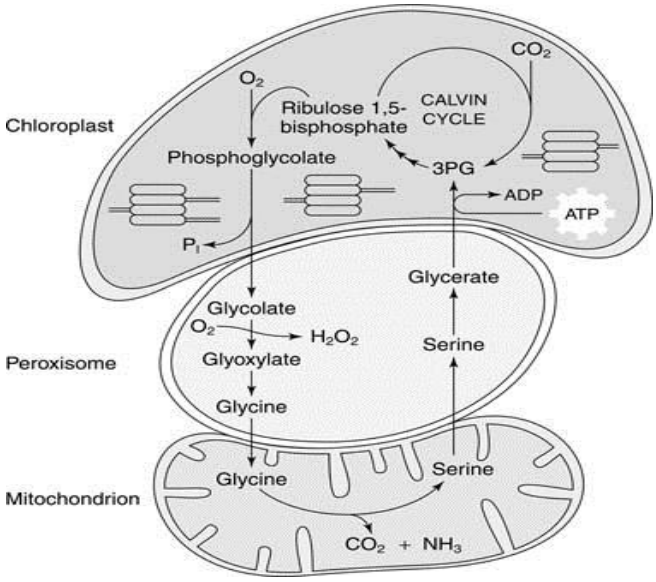
The oxidative photosynthetic carbon cycle reaction is catalyzed by RuBP oxygenase activity:

$$\mathbf{RuBP + O_2 \rightarrow Phosphoglycolate + 3\text{-}phosphoglycerate + 2H^+}$$

The phosphoglycolate is salvaged by a series of reactions in the peroxisome, mitochondria, and again in the peroxisome where it is converted into serine and later glycerate. Glycerate reenters the chloroplast and, subsequently, the Calvin cycle by the same transporter that exports glycolate. A cost of 1 ATP is associated with conversion to 3-phosphoglycerate (PGA) (Phosphorylation), within the chloroplast, which is then free to reenter the Calvin cycle. One carbon dioxide molecule is produced for every 2 molecules of O_2 that are taken up by RuBisCO.



Oxidation of **ribulose-1,5-bisphosphate** by Rubisco produces a 3-carbon compound, 3-phosphoglycerate, and a 2-carbon compound, phosphoglycolate. Because carbon is oxidized, the process is termed **photorespiration**. Photorespiration reduces the efficiency of photosynthesis for a couple of reasons. First, oxygen is added to carbon. In other words, the carbon is oxidized, which is the reverse of photosynthesis—the reduction of carbon to carbohydrate. Secondly, it is now necessary to resynthesize the ribulose bisphosphate and to reduce the phosphoglycolate. The 3-phosphoglycerate from photorespiration can reenter the **Calvin-Benson Pathway**, but the phosphoglycolate must be recycled to make a useful compound. This recycling takes place in a specialized organelle termed the **peroxisome**. Peroxisomes lie between chloroplasts and mitochondria in the plant cell and serve to pass the 2-carbon products of oxygenation on for further metabolism. In the chloroplast, the phosphoglycolate is dephosphorylated. Glycolate is transported to the peroxisome where molecular oxygen further oxidizes it to glyoxylate. The product is hydrogen peroxide, H_2O_2, (the term peroxisome comes from this product) which is rapidly broken down by catalase to water and oxygen.



The glyoxylate is **amidated** to the amino acid glycine in the **peroxisome**. **Glycine** is then transported to the **mitochondrial matrix** where the conversion of two glycines to one **serine** occurs with the loss of CO_2 and NH_3 from the pool of fixed molecules. The serine is transported into the peroxisome, where it is deaminated to glycerate. The glycerate is transported back to the chloroplast, where it is phosphorylated to **3-phosphoglycerate** for the **Calvin-Benson cycle**. This set of reactions is very detrimental to the efficiency of photosynthesis. Oxygen is added to carbon, CO_2 is lost, energy is consumed, and ribulose bisphosphate is destroyed. For a plant to be able to increase the discrimination of Rubisco for CO_2 would obviously be advantageous, but that hasn't happened, either naturally or through the efforts of scientists. An increased concentration of CO_2 in the atmosphere may lead to increased photosynthesis and decreased photorespiration, but high CO_2 concentrations would also contribute to global warming (and the increased photosynthetic carbon fixation would not likely reduce the amount of co_2 in any event).

Role of Photorespiration:-

Although the functions of photorespiration remain controversial, it is widely accepted that this pathway influences a wide range of processes from bioenergetics, photosystem II function, and carbon metabolism to nitrogen assimilation and respiration. The photorespiratory pathway is a major source of $\mathbf{H_2O_2}$ in photosynthetic cells. Through H_2O_2 production and pyridine nucleotide interactions, photorespiration makes a key contribution to cellular redox homeostasis. In so doing, it influences multiple signaling pathways, in particular, those that govern plant hormonal responses controlling growth, environmental and defense responses, and programmed cell death. Another theory postulates that it may function as a "safety valve", preventing the excess of reductive potential coming from an over reduced NADPH-pool from reacting with oxygen and producing free radicals, as these can damage the metabolic functions of the cell by subsequent oxidation of membrane lipids, proteins or nucleotides.

Mechanisms to Minimize Photorespiration:-

Since photorespiration requires additional energy from the light reactions of photosynthesis, some plants have mechanisms to reduce uptake of molecular oxygen by RuBisCO. They increase the concentration of $\mathbf{CO_2}$ in the leaves so that Rubisco is less likely to produce glycolate through reaction with $\mathbf{O_2}$.

C4 plants capture carbon dioxide in cells of their mesophyll (using an enzyme called Phosphoenolpyruvate carboxylase), and oxaloacetate is formed. This oxaloacetate is then converted to malate and is released into the **bundle sheath cells** (site of carbon dioxide fixation by RuBisCO) where oxygen concentration is low to avoid photorespiration. Here, carbon dioxide is removed from the malate and combined with **RuBP** in the usual way, and the **Calvin cycle proceeds** as normal. This ability to avoid photorespiration makes these plants more hardly than other plants in dry and hot environments, wherein stomata are closed and internal carbon dioxide levels are low. C4 plants include sugar cane, corn (maize), and sorghum.

CAM plants, such as cacti and succulent plants, use the enzyme **PEP carboxylase** (which catalyzes the combination of carbon dioxide with a compound called Phosphoenolpyruvate or PEP) in a mechanism called **Crassulacean acid metabolism**, or CAM, in which PEP carboxylase

sequesters carbon at night and releases it to the photosynthesizing cells during the day. This provides a mechanism for reducing high rates of water loss (transpiration) by stomata during the day.

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2-The Potential for Increasing Crop Photosynthesis:-

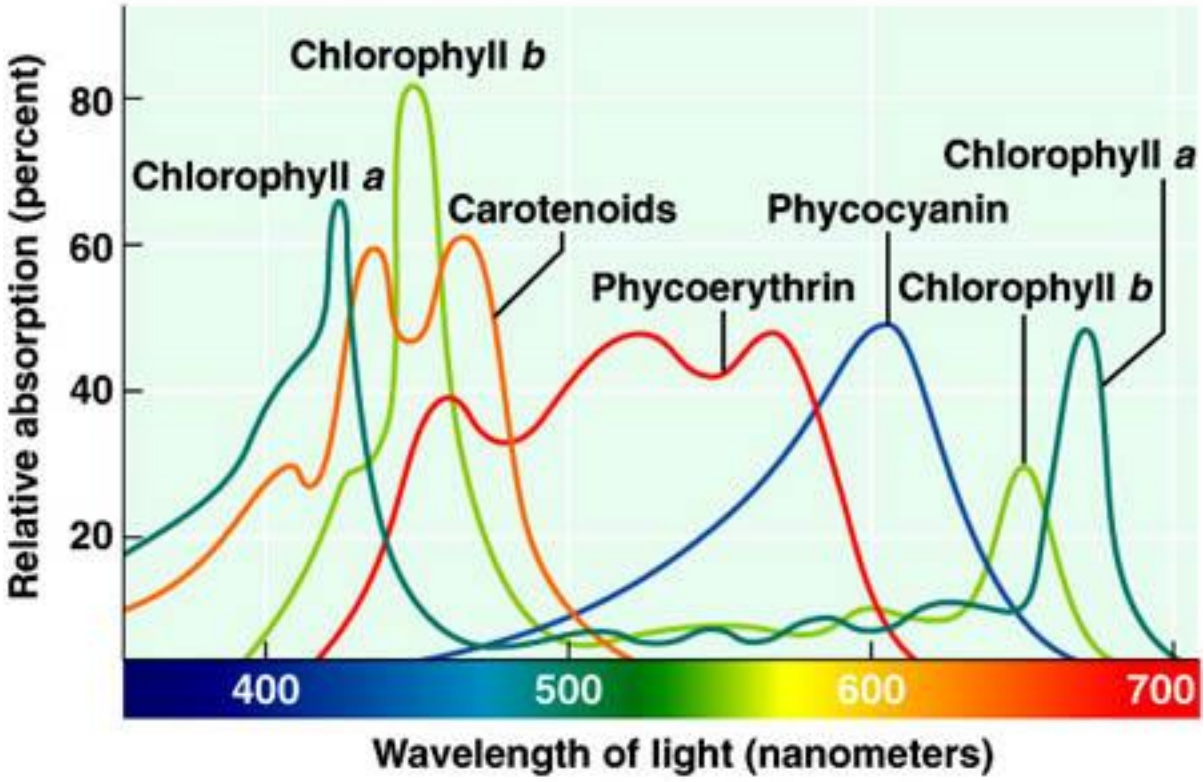
The process of photosynthesis is pivotal to the production of food and fiber as it provides the raw materials for all plant products. The average global grain yield per unit area of the major staple crops, wheat, rice and maize, more than doubled in the period between 1940 and 1980 and this trend continues. This doubling of grain yield coincided with the period when the understanding of photosynthesis exploded. Advances in photosynthesis research continue with a new wave of excitement brought on by the advances in **molecular biology**. There are two rather surprising features of the yield increases. **Firstly**, the greater understanding of photosynthesis has not yet contributed to yield increases. **Secondly**, a genetic increase in the rate of photosynthesis has not been required to achieve the increased productivity. Increased yields have been achieved by **(i)** increased or extended photosynthesis per unit land area and **(ii)** increased partitioning of crop biomass to the harvested product. The first has mainly been achieved by irrigation schemes and improved agronomic practices, in particular the use of inorganic fertilizers, but also to elevated atmosphere CO2 concentrations, whereas the second has largely been due to plant breeding. Despite intense selection for increased yield by plant breeders this century, selection has not resulted in a genetic increase in photosynthesis per unit leaf area. On the contrary, in many crops photosynthesis per unit leaf area has declined with intensive breeding! Nevertheless, plant breeding has been successful in extending the duration of photosynthesis in many crops although much of this has been assisted by genetic improvements in disease resistance.

Maximizing the photosynthetic potential:

Maximizing photosynthesis in an indoor garden is dependent on a number of factors: the **correct wavelength spectrum** (as explained earlier, these days that means full-spectrum lamp outputs), **sufficient intensity of light** for the stage of plant development, **CO2 replacement** or enrichment to levels over 1,000 ppm, sufficient **warmth** to maximize the rate of photosynthesis, good rates of **water uptake** and cell turgor, **overall plant health** and sufficient **nutrition**. Providing all these factors will allow plants to take full advantage of those cellular reactions which provide both energy and assimilate for maximum growth and development.

1- Correct wavelength spectrum:

Using a spectrophotometer, it is possible to see how much light chlorophyll will absorb at various wavelengths. The resulting **absorption spectrum** indicates the wavelengths of light absorbed by the pigment. Note the absorption spectrum presented in the figure below Figure. Chlorophyll exists in two forms, chlorophyll a (the primary photosynthetic pigment) and chlorophyll b. Please make note in the figure that both **chlorophyll a** and **chlorophyll b** absorb primarily **blue** and **red** wavelengths of light. Such a situation indicates that plants use primarily blue and red wavelengths of light to facilitate the overall process of photosynthesis. You should note that the overall process of photosynthesis is not entirely reflective of the absorption spectrum of chlorophyll a. This is due to the presence of **accessory pigments** such as chlorophyll b, the **carotenoids**, **phycoerythrin** and **phycocyanin**. Accessory pigments serve to capture light energy and transfer this energy to chlorophyll. Once absorbed the energy associated with the photon is used to begin the process of photosynthesis.

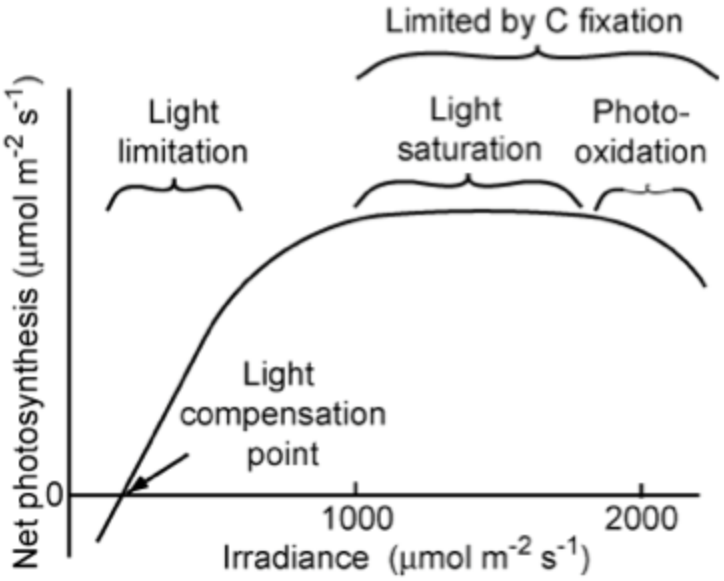


From the above research it's cleared that plants can only absorb a specific quality of light. All other wavelengths **reflected back** into the atmosphere or just used to generate heat. Genetic modifications in plants are still needed to enable them to filter the light or efficiently absorb the specific quality of light.

2- Sufficient intensity of light:

At low to moderate light levels, leaves have a near linear response to light intensity. The rate of change of net photosynthesis in this region to irradiance is the quantum yield of photosynthesis. This is similar for all C3 plants (in the absence of environmental stresses) at around 6%. At **higher light levels**, saturation occurs as the efficiency of the photosynthetic mechanism is reduced. At higher levels still, net photosynthesis can decline as a result of photorespiration as described above. Plants have some capacity to respond to changes in light conditions over time scales of days to months, such as by having leaves in more direct sunlight with more cell layers and higher photosynthetic capacity than shade leaves by acclimation or adaptation over longer time periods. Respiration rate depends on tissue protein content so shade leaves with low photosynthetic capacity generally have a lower protein content to minimize respiration losses.

Light response curves measures plants response to light intensity.



"Relationship of net photosynthetic rate to photosynthetically active radiation and the processes that limit photosynthesis at different irradiances. The linear increase in photosynthesis in response to increased light (in the range of light limitation) indicates relatively constant light use efficiency. The light compensation point is the minimum irradiance at which the leaf shows a net gain of carbon. "

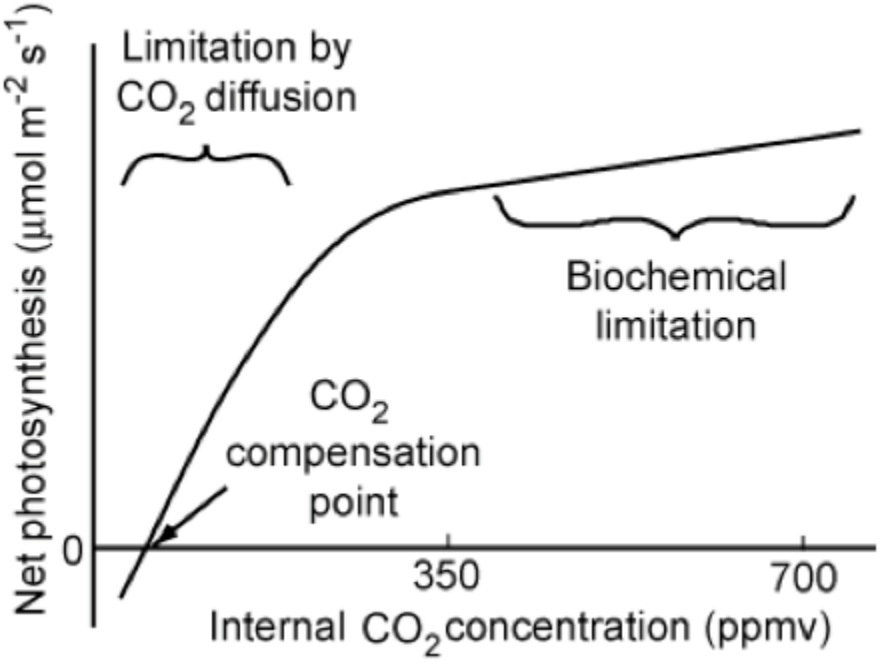
Certain modifications should be conducted to protect the terrestrial plants especially hot climate plants to thicker the **cuticle layer** or deposit an **additional layer** to safe their leaves from high light intensity as some plants have produced proteins to save regulate the high or low light intensity.

3- CO_2 absorption limitations:

Although we have noted spatial and temporal variations in CO2 concentrations, the variation is in fact only quite small, being of the order of **4%** and insufficient to cause significant regional variations in photosynthesis. Further, although photosynthesis locally depletes the CO2 pool, it is not to a sufficient extent that it significantly affects the amount available.

The response curve of net photosynthesis to CO2 concentration inside the leaf of a C3 plant is shown above. At low levels, CO2 diffusion limits photosynthesis. With current atmospheric CO2 levels of around **390 ppmv** most **C3** plants would show an increase in photosynthetic rate with further increases. The magnitude of this is however uncertain due to plant acclimation and other factors. Over the long term, it is likely that indirect effects of elevated CO2 concentrations may be more important than increased net photosynthesis rates, such as thoise arising from changes to the water cycle. C4 plants are relatively unresponsive to changing CO2 concentrations, which

could possibly affect their competitiveness with C3 plants with rising CO2, but again, indirect effects are likely to be important and are hard to predict.

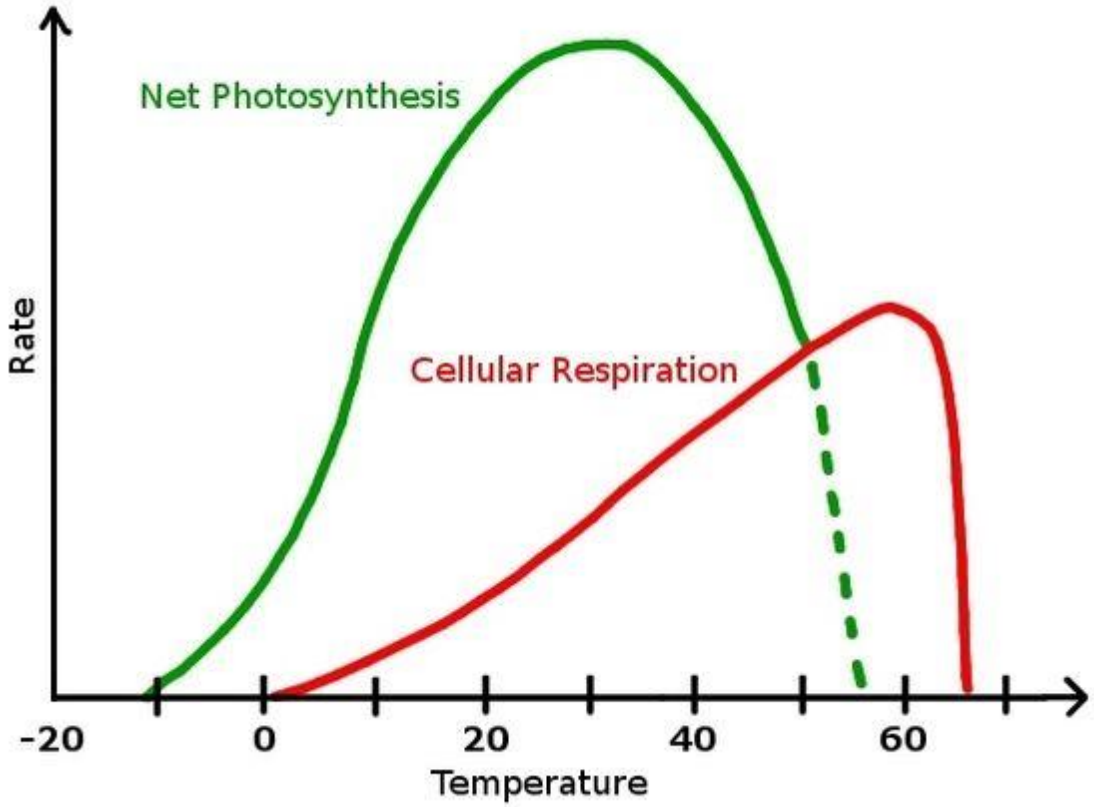


"Relationship of the net photosynthetic rate to the CO2 concentration inside the leaf. Photosynthetic rate is limited by the rate of CO2 diffusion into the chloroplast in the initial (left-hand side) linear portion of the CO2 response curve and by biochemical processes at higher CO2 concentrations. The CO2 compensation point is the minimum CO2 concentration at which the leaf shows a net gain of carbon. "

In above research plants cannot afford or utilized CO2 concentration more than **350 ppmv**, whereas genetically some plants have a potential to photosynthesize upto **1000 ppmv CO2** but due to some **biochemical limitations** as expressed above, they are unable to use it. Hence with this reference there is still hey huge gap to increase photosynthetic efficiency by decreasing biochemical limitation of CO2 absorption.

4- Canopy temperature:

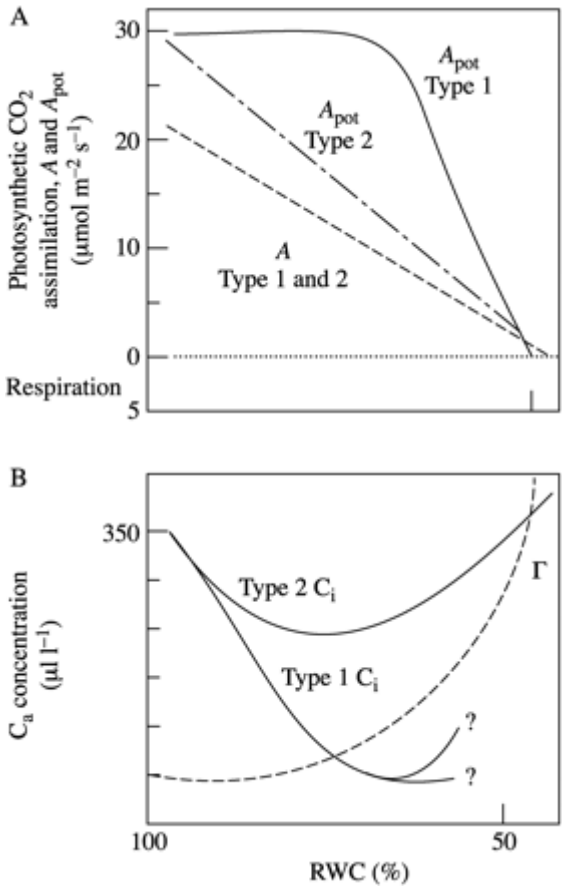
Initially, increasing temperature causes net photosynthesis to increase. More kinetic energy leads to more collisions between the reactants in photosynthesis. Cellular respiration increases in the same way, at the same time, for the same reason. Then, net **photosynthetic activity** reaches a peak. Increasing cellular respiration has limited the accumulation of photosynthetic products. **Denatured enzymes** do not yet limit photosynthesis. If they did, then cellular respiration also would be limited. Finally, too much heat denatures the enzymes that catalyze both photosynthesis and cellular respiration. Photosynthesis is severely limited, as is **cellular respiration**.



Heat shock proteins (HSP) are a class of functionally related proteins involved in the folding and unfolding of other proteins. Their expression is increased when cells are exposed to elevated temperatures or other stress. **Salt and lipids** accumulation along with heat shock proteins may **thermo-regulate** the cell temperature as being done in many desert plants. Genetic modifications may increase the plant photosynthetic activity even under high temperature like Tropical. Similarly some plants are able to escape from **chilling effect** of lower temperature by **K^+ or lipids** accumulation in cell sap.

5- Water uptake/ availability:

Water limitation reduces the capacity of leaves to match CO2 supply with light availability. Water stress is manifested as a decrease in leaf relative water content (RWC). Decreasing RWC progressively decreases **stomatal conductance** which slows **CO2 assimilation** (lower photosynthetic capacity), although different studies show different responses for **RWC** between **100% and 70%** (type 1 and 2 responses below). In plants that are acclimated and adapted to dry conditions, plants reduce photosynthetic capacity and leaf N concentrations to give a low stomatal conductance that conserves water. Such plants also minimize **leaf area** (shedding or lower leaf production rates) to minimize water loss. Some such plants also minimize shortwave radiation absorption by higher reflectance at the leaf surface and or by having more vertically-inclined (erectophile) leaves.



"A, Schematic of the basic responses of actual photosynthetic rate (A) in air (360 umol CO2 m-2s-1) and potential photosynthetic rate (Apot) measured at elevated CO2 concentration, to relative water content (RWC). Type 1 and 2 responses of Apot are shown. In the Type 1 response, Apot is unaffected until a 20-30 % decrease in RWC occurs, when it becomes metabolically limited. In Type 2, the change is linear, showing progressive metabolic limitation. In both types in well-watered leaves, photosynthetic rate (A) is stimulated by elevated CO2. Elevated CO2 maintains A at the potential rate (Apot) in the Type 1 response as RWC decreases; but at RWC below approx. 80 % Apot decreases in Type 1. Elevated CO2 simulates A progressively less as RWC decreases in Type 2, showing that Apot is inhibited. B, Scheme of the changes in CO2 inside the leaf (Ci) during steady-state A, as stomatal conductance (gs) decreases with falling RWC, associated with Type 1 or Type 2 photosynthetic response (1 with Ci decreasing to compensation point; 2 with Ci decreasing but not to compensation point). The equilibrium compensation point, Gamma, associated with Type 1 response is indicated. There are differences between experiments, with Ci not decreasing, or decreasing somewhat, or substantially. This may reflect different methods of assessing Ci."

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Canopy Architecture and Interception of Solar Radiation

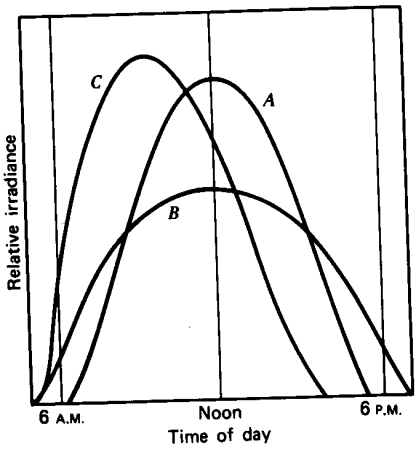
The canopy is the aboveground portion of a plant community or crop, formed by plant crowns. Canopy structure is the organization or spatial arrangement (three-dimensional geometry) of a plant canopy. Leaf area index (LAI), leaf area per unit ground area, is a key measure used to understand and compare plant canopies.

There are some very common questions about light and plant:

- What factors determine how much light a plant receives at a particular location in the canopy or a leaf at a particular location on the plant?
- Why is light distribution in the canopy important? How do plants response to these differences and how does this relate to productivity, species composition (competition), etc?
- How much light is received?

The cosine law: Light incident on a leaf varies with leaf angle and canopy position: Lambert's cosine law:

I = COSθ (theta)



Canopy composition and distribution:

This affects both light quantity and light quality

Light quantity diminishes through the canopy but all canopies are not equal.

Incident light **(PAR)** at the forest floor may be 50 –80 % in a leafless forest.

10 –15 % in an even aged pine stand.

1 to 5 % temperate forest.

0.2 to 0.4 % in a dense beech stand in Michigan.

0.1 to 2 % in a tropical forest.

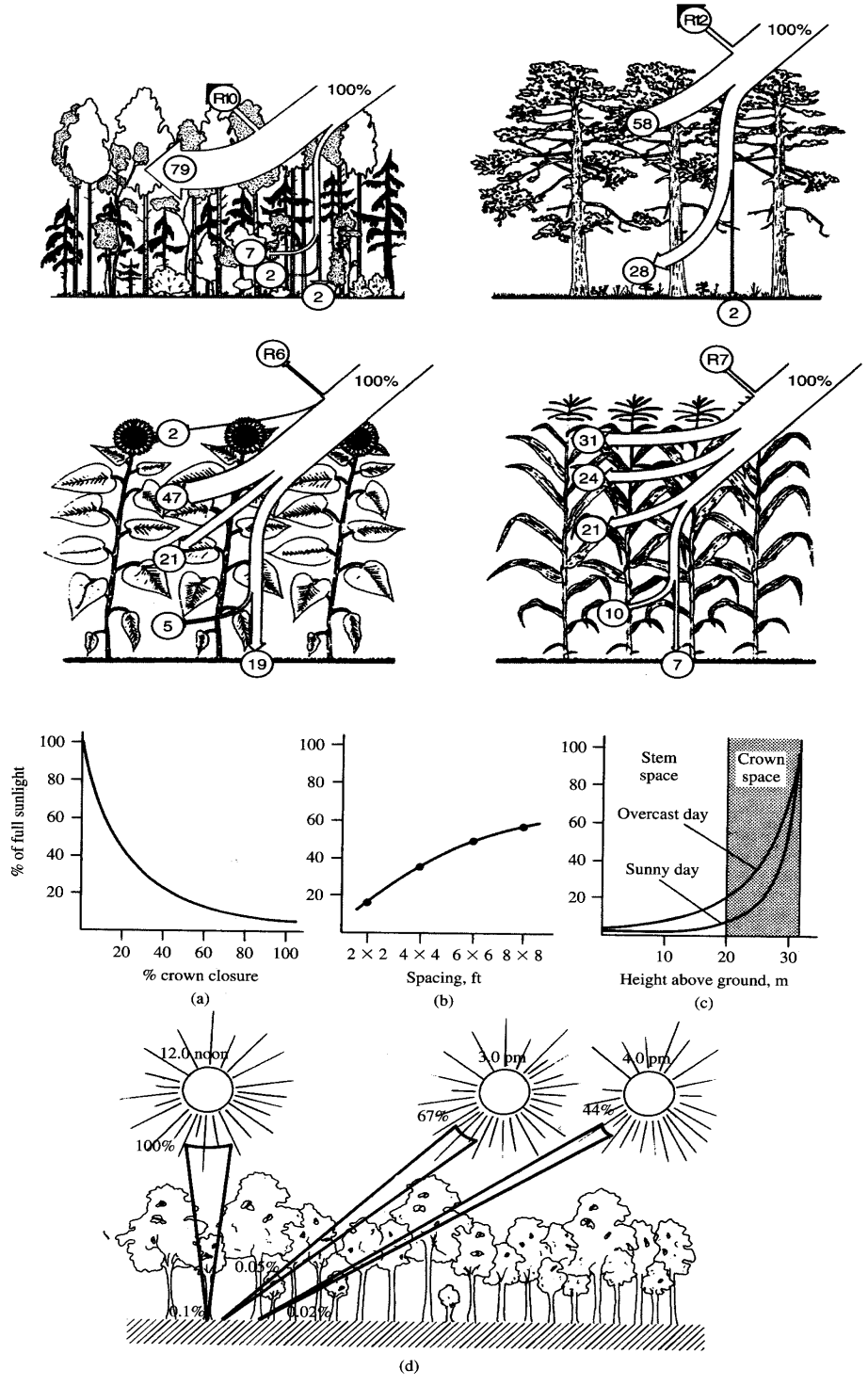


Figure 7-7 Effect of forest canopy on the intensity of solar radiation reaching the forest floor

Plant canopies are structurally diverse due to unique spatial patterns that different species adopt for **intercepting light** and an even diversity of plant species which occupies a natural community. For example, there is considerable penetration of sunlight through the canopy of a dry eucalypt forest. The first reason is simply based on **canopy density** or the quantity of **leaf area** per unit canopy volume. The second reason relates to the display of the foliage. Many species display their leaves at shallower angles to the horizontal thereby absorbing a larger proportion of incident radiation and preventing much of the incident light and energy being transmitted to the ground.

The Beer–Lambert Law, which describes absorption of light by plant pigments in solution, provides a simple approach which has been applied widely to a range of canopies. This function demonstrates that the absorption of light will be more or less exponential with increasing **intercepting area** down through the canopy. Absorption of sunlight by photosynthesis occurs within a well-defined spectral band **(400–700nm)** and matches a peak in energy distribution across the wavelength spectrum of sunlight transmitted to the earth's surface through our atmospheric window. Sunlight in this waveband can be represented as either a **quantum flux** or a radiant energy flux. Quantum flux, or more explicitly, **photosynthetic photon flux density** (PPFD), is simplified here to '**photon irradiance' (Q)** and has units of μmol quanta m^{-2} s^{-1} ('μmol quanta' rather than 'μmol photons' because quantum energy derived from photons drives photosynthesis). For the sake of making a clear distinction, radiant energy flux is simplified to '**irradiance**'. In the present example, irradiance coincides with **photosynthetically active radiation** (PAR) and is expressed as joules (J) per square metre per unit time. Depending on the application, time can span seconds, days or years, and is then coupled with either joules, megajoules (MJ) or gigajoules (GJ).

On clear days, PAR represents about **half of the total** shortwave (solar) radiation or radiant energy flux I (expressed as J m–2 s–1) incident on a canopy, and is totally responsible for photosynthesis. If changes in the spectral distribution of energy as it passes through the canopy are ignored, I and PPFD can be used interchangeably in the analysis below. In practice PPFD is attenuated more rapidly than I (that is, there is a proportionally larger change in **PAR** than total **solar radiation (I)** in moving from top to bottom) because leaves are relatively transparent to the **near-infrared** part of the solar beam. Application of the Beer–Lambert Law shows that at any level of cumulative area **F** within the canopy, the rate of change of photon irradiance, **Q**, within the canopy is given by:

$$\mathbf{dQ/dF = -kQF \quad (12.5)}$$

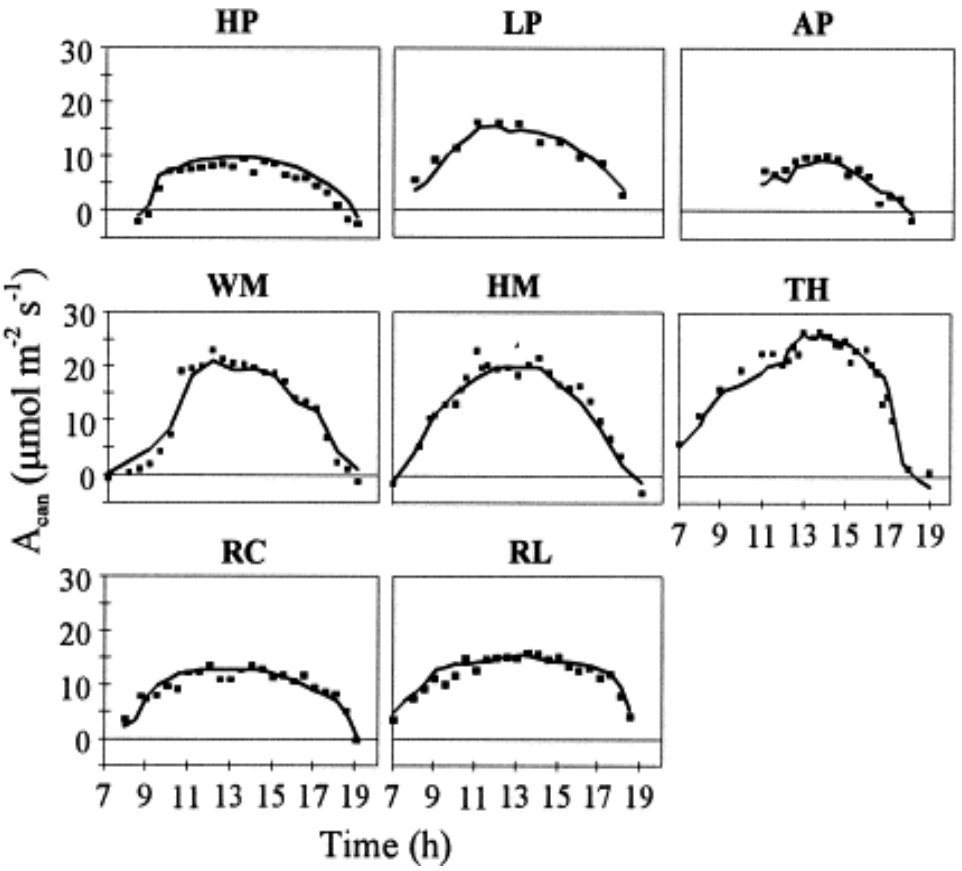
Where **k** is the extinction or foliar absorption coefficient, a dimensionless parameter. k measures the fraction of incident photons absorbed by a unit of leaf area or conversely the fraction of leaf area projected onto the horizontal from the direction of the incident beam. For many species, foliage in the vertical plane is distributed approximately symmetrically about the midpoint of the canopy and most absorption of light will occur in the middle of the canopy. After integration, QF at any level F is given by:

$$\mathbf{QF = Q0e–kF \quad (12.6)}$$

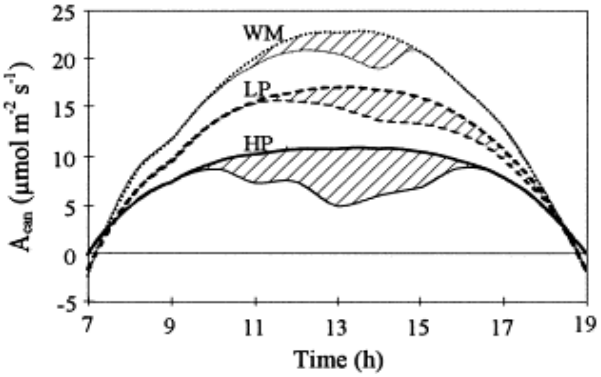
Where Q_0 is the PAR incident at the top of the canopy. At the base of the canopy F is equal to the leaf area index (LAI), a dimensionless number which expresses total projected leaf area of the canopy as a ratio of the ground area over which it is displayed. Thus the level of interceptance is an exponential function of the product kF. If a value of 0.5 is assigned to k, then 95% light interception occurs at kF = 3 which is equivalent to an LAI of 6 m^2 leaf area m^{-2} ground area. Maximum values of LAI vary with species, site, stress and season.

In practice **k is not a constant value** for any canopy and varies with solar elevation, the ratio of direct to diffuse beam irradiance and any changes in **canopy structure** or **leaf inclination** and orientation which occur seasonally or in response to the movement of leaves (e.g. heliotropism). For the majority of canopies, **k varies from 0.3 to 1.3**. Canopies with **erectophile** leaves (e.g. grasses) and high leaf angles to the horizontal or with a clumped distribution have a lower k and intercept less light per unit of foliage compared to canopies with **planophile** leaves (e.g. clovers) and low leaf angles or a regular distribution. The cumulative leaf area required to intercept 95% of the radiation incident at the top of the canopy will be greater for canopies dominated by erectophile leaves or having a clumped distribution. In many species and plant communities leaf inclination may change from erectophile at the top of the canopy to planophile at the bottom. This allows more even distribution and interception of light and reduces the proportion of leaves which is exposed at the top of a canopy to levels of light which are saturating for photosynthesis and, conversely, reduces the proportion of leaves at the bottom of a canopy which is exposed to levels below the light-compensation point for photosynthesis. For a canopy with leaves distributed randomly with respect to orientation and inclination, **k is approximately 0.5** and this value is commonly assigned to k in the literature.

Canopy architecture and leaves arrangement directly affect the amount of radiations intercepted. To investigate this effect an experiment was conducted in realtion to canopy strcture and radiation effect was estimated by photosynthetic rate by measuring CO_2. Effects of both classical parameters of canopy structure (vertical distribution of leaf area, plant area and leaf inclination) and of leaf dispersion on were analyzed by means of a relatively simple canopy **photosynthesis model**. This model was designed for photosynthetic input parameters based on measured field parameters. Eight structurally different species-rich seminatural and natural plant communities (used and abandoned pastures, hay meadows, tall herbs and dwarf shrubs) were investigated. The validation by means of a micrometeorological approach showed that the estimate of Acan in the model corresponds well with the measurements in very differently structured, species-rich plant communities. Simulations showed that the significance of canopy properties for canopy photosynthesis essentially depends on the **vertical distribution** of the leaf area. Therefore this parameter was used for classifying the canopies investigated.

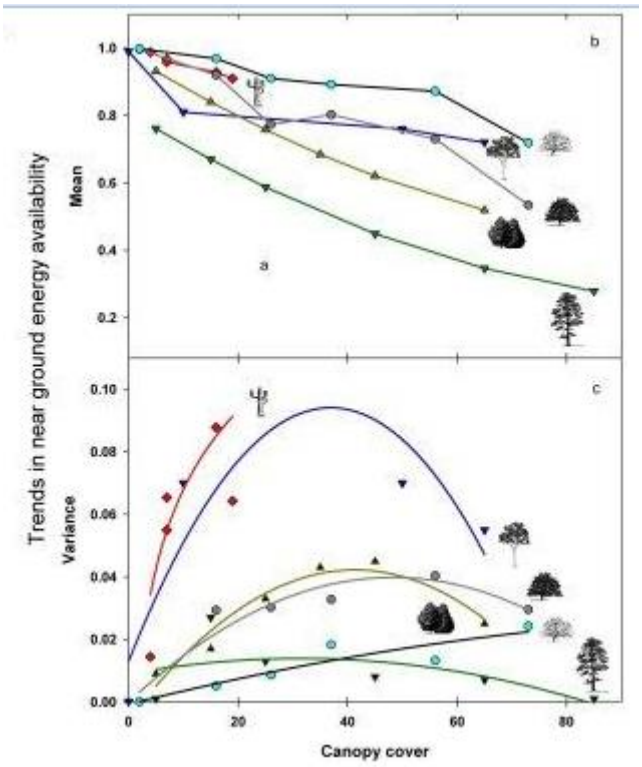


"Model validation for comparable clear days showing diurnal courses of whole apparent canopy photosynthesis (expressed on a ground area basis, Acan, μmol CO2 m−2 s−1). Points are values measured, in which Acan results from the difference of the CO2 flux from the atmosphere measured by a micrometeorological approach (Bowen-ratio energy-balance) and the CO2 output of the soil measured in situ by IRGA techniques. Lines are model predictions using measured structural and microclimatic data as inputs. Experimental sites: HP, heavily stocked pasture; LP, lightly stocked pasture; AP, abandoned pasture; WM, wet meadow; HM, hay meadow; TH-tall herb community; RC, evergreen Rhododendron shrub community; RL, deciduous Rhododododendron shrub community."



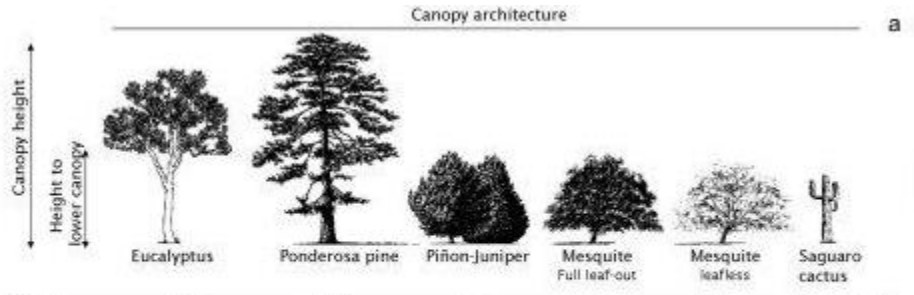
Reduction (hatched area) of whole apparent canopy photosynthesis (expressed on a ground area basis, Acan) in the diurnal course, due to high leaf temperatures measured on a clear day on the wet meadow (WM), the lightly (LP) and the heavily (HP) stocked pasture. Simulations were performed with measured (thin line) and hypothetical (bold line) leaf temperatures. Leaf temperatures above 20° were substituted by the optimum temperature of single leaf photosynthesis.

Another very clear evidence of canopy architecture's effect on solar radiation interception and finally on photo synthesis can be seen under this research analysis.



Trends in near-ground solar radiation along different grassland–forest continuum types with (a) different canopy architectural characteristics, corresponding to (b) mean, and (c) variance values of direct site factor (DSF).

The control of canopy architecture is very **complex** as it is determined by the expression of many separate traits all of which show large interactions between the **plant genotype**, the natural **environment** and **agronomy**. In addition, these traits are frequently quantitative characters controlled by many genes.



Height	High	High	Low	Low	Low	Intermediate
Height to lower canopy	High	Intermediate	Very low	Low	Low	Intermediate to lower branch
Canopy density	Intermediate	High	High	Intermediate	Low	Not applicable

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Optimum and Maximum Leaf Area Indices

Forestry scientists often define **Leaf Area Index** as the one-sided green leaf area per unit ground surface area.

LAI is used to predict **photosynthetic primary production**, evapotranspiration and as a reference tool for crop growth. As such, LAI plays an essential role in theoretical production ecology. An inverse exponential relation between **LAI and light interception**, which is linearly proportional to the primary production rate, has been established.

$$P=P_{max}\ (1-e^{-c.\ LAI})$$

Where P_{max} designates the **maximum primary production** and **c** designates a **crop-specific growth coefficient**. This inverse exponential function is called the **primary production function**.

Determining LAI:- "LAI is determined directly by taking a statistically significant sample of foliage from a plant canopy, measuring the leaf area per sample plot and dividing it by the plot land surface area. Indirect methods measure canopy geometry or light extinction and relate it to LAI."

- **Direct methods:** Direct methods require **stripping** and measuring the foliage of plant canopy samples. LAI for clip plots or individual plants is measured by hand or by using an LAI meter. Traditional LAI meters require each plant leaf to be stripped and fed through the entrance of the machine, which can be likened to a kind of crude image scanner. The disadvantage of the direct method is that it is destructive, time consuming and expensive, especially if the study area is very large.
- **Indirect methods:** A **hemispherical photograph** of forest canopy. The ratio of the area of canopy to sky is used to approximate LAI. The **LAI-2200** calculates LAI and other canopy structure attributes from solar radiation measurements made with a wide-angle optical sensor. Measurements made above and below the canopy are used to determine canopy light interception at five angles, from which LAI is computed using a model of **radiative transfer** in vegetative canopies. The **LP-80** calculates LAI by means of measuring the difference between light levels above the canopy and at ground level, and factoring in the leaf angle distribution, solar zenith angle, and plant extinction coefficient. Such indirect methods, where LAI is calculated based upon observations of other variables (canopy geometry, light interception, leaf length and width etc.) are generally faster, amenable to automation, and thereby allow for a larger number of spatial samples to be obtained. For reasons of convenience when compared to the direct (destructive) methods, these tools are becoming more and more important. The **disadvantage** of the indirect method is that in some cases it can underestimate the value of LAI in very dense canopies, as it does not account for leaves that lie on each other, and essentially act as one leaf according to the theoretical LAI models.

Interception of **PAR** by a crop canopy is strongly related to total leaf area. A crop will thus intercept more PAR and hence grow faster if it develops leaf area rapidly. This principle applies

to both annual crops which are usually planted at the beginning of a growing season and to perennial crops which resume growth after a dormant season. Leaf area development of sugar cane, for example, is generally slower in the year of planting compared with a subsequent ratooned crop where canopy regrowth is enhanced by stored photoassimilate. By analogy with early canopy expansion, retention of green leaves late in a growing season also extends **sunlight interception**.

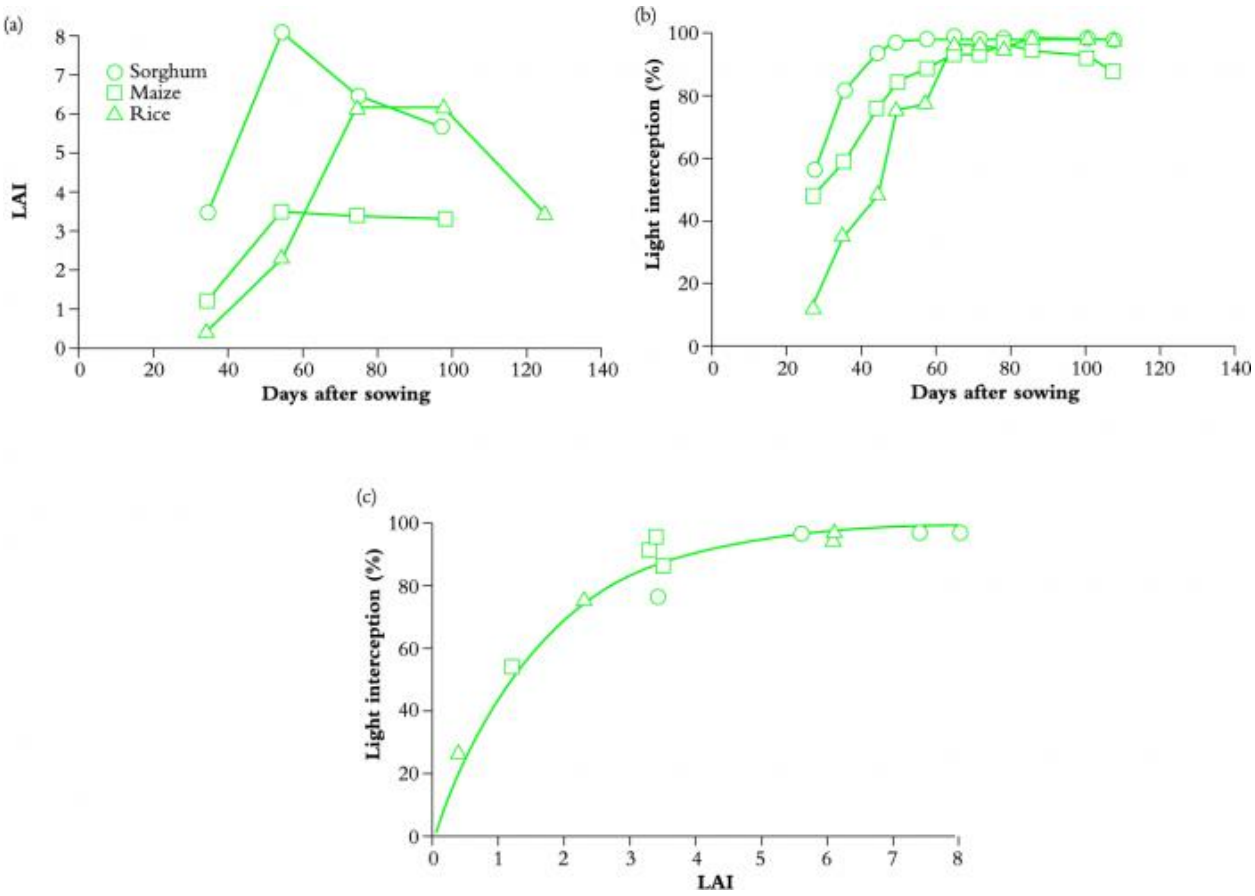

Figure: Changes in (a) leaf area index (LAI), (b) light interception, and (c) the overall relationship between light interception and LAI for all three species, sorghum, maize and rice. (All grown in southeast Queensland)

The **leaf area index (LAI)** is the ratio of total projected leaf area (one side only) per unit ground area, and is widely used to characterise canopy **light climate**. A canopy where LAI equals 1 has a leaf area equal to the soil surface area on which it grows, but this does not mean all PAR is intercepted because some leaves overlap, leaving gaps. Moreover, not all leaves are positioned at right angles to incident radiation. A crop under favourable growing conditions increases LAI rapidly during early development to a **maximum of 3 to 7**. An example of LAI development of three tropical cereal crops grown under well-watered conditions in southeast Queensland is given

in Figure. Sorghum showed a more rapid increase in LAI than did maize largely because of a higher sowing density (33 v. 5.6 plants m–2). A late maturing rice crop showed slowest leaf area development during early stages of growth, but maximum LAI was none the less higher in rice than in maize. As a general rule**, maximum LAI is achieved just prior to flowering in cereal crops**. By that stage, growing points are differentiating floral rather than leaf primordia, and initiation of new leaves has ceased.

Some cereal crops lose leaves and LAI declines during **grain filling** as crops mature. Differences in LAI development among the three crops are evident in **PAR interception** by respective canopies, interception prior to 60 d was highest in sorghum and lowest in rice. However, in all three crops, canopy PAR interception increased rapidly during early stages of growth. Incident radiation was almost completely intercepted once high LAI had been achieved.

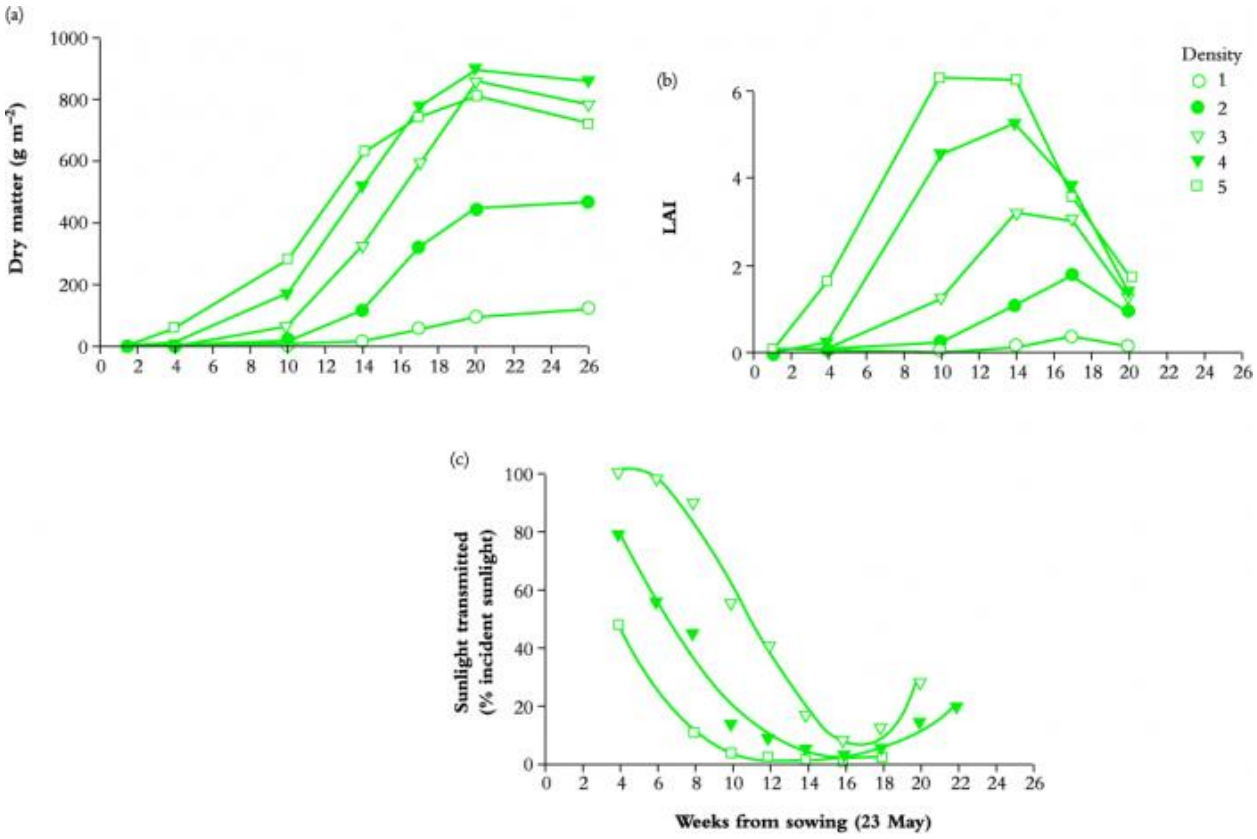

Figure: Changes in (a) dry matter, (b) leaf area index (LAI), and (c) photon irradiance at ground level for wheat crops grown at five different planting densities, 1.4, 7, 35, 184 and 1078 plants m-2 for treatments 1 to 5 respectively. Some self-thinning occureed in plots sown at higher densities, and by 26 weeks after sowing treatment densities were 1.4, 7, 35, 154 and 447 plants m-2 respectively.

Despite wide variation in crop phenology, sunlight interception and LAI maintain a tight relationship. Interception increases sharply with increase in LAI to about 90% once LAI exceeds 4, and approaches an asymptote at higher LAI. Such a relationship applies to many crops, and emphasises (1) the importance of a rapid increase in LAI during early stages of growth, and (2) a requirement for only moderate LAI to achieve effective interception. Indeed, excessive leaf area development can be counter-productive because reproductive development, and hence economic yield, may be reduced due to self-shading and resource allocation to leaf production.

The time-course of radiation interception during crop growth can be manipulated to some extent by farmers. For example, seeding rate is an important management option which affects interception and subsequent crop growth and yield. A higher seeding rate would produce a higher plant population density and a higher LAI at crop establishment. This hastens canopy interception and hence biomass pro-duction would be promoted. Any advantage of a high plant density may disappear with time during crop growth because radiation interception of a medium plant density may eventually catch up with that of the high density. In this case, density 3 (35 plants m–2) was sufficient for radiation interception and plant dry matter production. If plant density is very low, shown as density 1 (1.4 plants m–2) or density 2 (7 plants m–2) in Figure 12.21, LAI never exceeded 2 and final biomass at harvest was much smaller than values returned from higher densities. Solar radiation was wasted at low planting density, and potential yield (dry mass produced per unit area) was never realised. Shown in above figure.

As solar radiation penetrates a crop canopy, PAR is intercepted by leaves and photon irradiance commonly declines exponentially with cumulative leaf area (i.e. depth in Figure 12.23), according to the simple relationship:

$$\mathbf{I = I_0 \exp(-kL)} \quad \mathbf{(12.5)}$$

Where **I** is horizontal photon irradiance within a canopy, $\mathbf{I_0}$ is horizontal photon irradiance above that canopy, **L is LAI** from the top of the canopy to the point where I is determined, and **k** is an extinction coefficient.

Large k values imply that photon irradiance decreases rapidly with depth, whereas a canopy with a small k would allow solar radiation to penetrate deeply, for a similar leaf area profile. Variation in k value is commonly associated with leaf angle. Canopies with more horizontal leaves, such as sun-flower or cotton, have large k values, often 0.7–1.0, whereas those with more erect leaves, such as barley and sugar cane, have small values, often 0.3–0.6.

The growth rate of the crop is closely related to the amount of solar radiation captured by the leaves. Depending on variety and sowing date, between 9 and 30 leaves are produced on each main stem. The maximum size of individual leaves on the plant in the absence of stress is around 200 cm^2. The development of **leaf area index (LAI)** for a short season canola crop in Western Australia and in a long season environment in New South Wales are illustrated in Figure below.

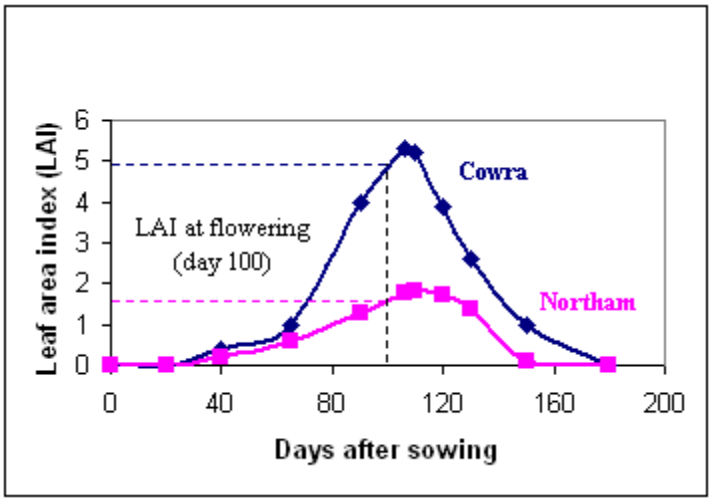

Figure: Leaf area index of a canola crop at Northam, Western Australia, and at Cowra, New South Wales.

Initially, LAI increases slowly in the autumn and winter, then increases rapidly in spring to a maximum just after flowering commences. A leaf area index of about 4 is required for the crop canopy to intercept about **90%** of the incoming solar radiation. Leaves senesce and are shed rapidly from late flowering onwards. At full flower, the canopy of flowers can intercept or reflect up to **60%** of the **incoming radiation**, causing potential shortages of photosynthate to the early developing pods underneath. After flowering, a dense layer of green pods provides a photosynthetic canopy up to mid pod filling. Researchers in Australia and Britain have explored ways of improving the structure and efficiency of the crop from flowering onwards. Limiting the number of branches, flowers and pods set can improve the radiation environment and hence rate of seed retention. Removing the petals from flowers (apetalous types) has been shown to also allow more radiation into the crop canopy, to prolong leaf life and improve seed retention. Different pod types, including fewer but longer pods, and more acute angles of insertion on the stems, can also play a role in more efficient crop canopies for photosynthesis in the same way that narrow, upright leaves improve canopies in rice and wheat.

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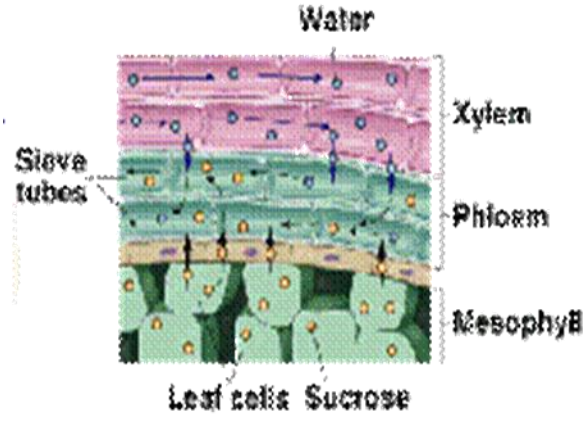
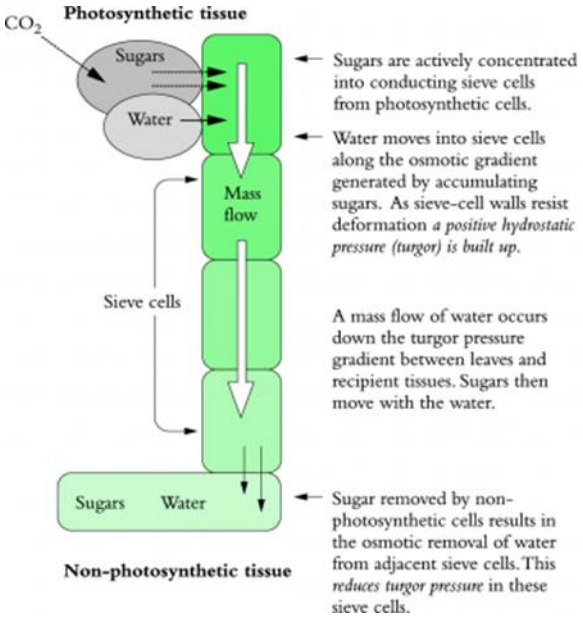
Translocation in phloem

Translocation is the movement of materials from leaves to other tissues throughout the plant. Plants produce carbohydrates (sugars) in their leaves by photosynthesis, but no photosynthetic parts of the plant also require carbohydrates and other **organic** and nonorganic materials. For this reason, nutrients are trans-located from sources (regions of excess carbohydrates, primarily mature leaves) to sinks (regions where the carbohydrate is needed). Some important sinks are roots, flowers, fruits, stems, and developing leaves. Leaves are particularly interesting in this regard because they are sinks when they are young and become sources later, when they are about half grown.

Phloem Structure and Function: The tissue in which nutrients move is the phloem. The phloem is arranged in long, continuous strands called vascular bundles that extend through the roots and stem and reach into the leaves as veins. Vascular bundles also contain the **xylem,** the tissue that carries water and dissolved minerals from the roots to the shoots. When plants increase in diameter (secondary growth) they do so by divisions of a layer of cells just under the bark; this cell layer makes new xylem to the inside (forming the wood of the tree trunk) and a thin, continuous cylinder of new phloem to the outside. The contents of the phloem can be analyzed by cutting off the stylets (mouth parts) of phloem-feeding insects such as aphids and collecting the drops of sap that exude. Phloem sap is composed largely of sugar dissolved in water. All plants translocate sucrose (table sugar) and some also transport other sugars such as stachyose, or sugar alcohols such as sorbitol. Many other organic compounds are found, **including amino acids**, **proteins, and hormones**. In order to accommodate the flow of sap, the internal structure of the conducting cells of the phloem, the **sieve elements**, is drastically altered. As the sieve elements mature, they lose many of the **organelles** commonly found in living cells and they modify others. The nucleus disappears, as do the vacuoles, microfilaments, microtubules, ribosomes, and Golgi bodies. Therefore, the inside (lumen) of the cell is left essentially.





Translocation in phloem sap:

The sieve elements are greatly elongated in the direction of transport and are connected to one another to form long **sieve tubes**. Large pores perforate the end walls of the sieve elements to facilitate flow through the tube. The connecting walls thus look like a sieve, giving the cell type its name. Some sieve elements can live for a long time, as many as one **hundred years** in palm trees, even though they have no nucleus or any of the machinery needed for protein synthesis. Cells closely associated with them, called **companion cells**, apparently keep them alive. The association of sieve elements and companion cells is one of the most intimate and complex in nature, and one of the least understood. It now appears that both small and large molecules can move from companion cells to sieve elements through the **plasmodesmata** that connect them. Plasmodesmata are minute pores that traverse the common walls between plant cells. They have an intricate internal structure. Interest in plasmodesmata is high because viruses move through them to cause infections. If a virus enters the phloem this way it will travel with the sap, spread widely around the plant, and infect **sink organs.** Since viruses are much larger than plasmodesmata, they must be disassembled in one cell and reassembled when they get to their destination. Sugars synthesized in the chloroplasts are actively pumped into the sieve tubes. Water follows by **osmosis**, creating high pressure. Sugar is then removed by active transport, and water again by osmosis, lowering the pressure in the sieve tube.

Pressure Flow Mechanism:

The rate of translocation in angiosperms (flowering plants) is approximately **1 meter per hour**. In conifers it is generally much slower, but even so this is far too fast to be accounted for by diffusion. Instead, the sap flows, like a river of dilute syrup water. What is the force that drives the flow of material in the phloem? It is pressure, generated in the sieve elements and companion cells in source tissues. In leaves, sugar is synthesized in mesophyll cells (the middle layer of the leaf), and is then actively pumped into the phloem, using metabolic energy. By using energy, the sugar is not only transferred to the phloem but is also **concentrated**. When a solute such as sugar is concentrated inside cells, water enters the cells by **osmosis**. Since the plant cells have a rigid cell wall, this influx of water creates a great deal of internal pressure, over ten times the pressure in an automobile tire. The pressure causes sap to move out through the pores of the sieve element, down the tube. At the other end of the transport stream, in the sinks, sugar is constantly leaving the phloem and being used by surrounding cells. Some is consumed as an energy source, some is stored as sugar or starch, and some is used to make new cells if the **sink tissue** is growing. Since sugar leaves the phloem in the sink, water exits too (again by osmosis) and the pressure goes down. Therefore, there is a difference in pressure between source and sink phloem. This causes the solution to flow, just as water flows along a pressure gradient in a garden hose. This process is known as the pressure-flow mechanism.

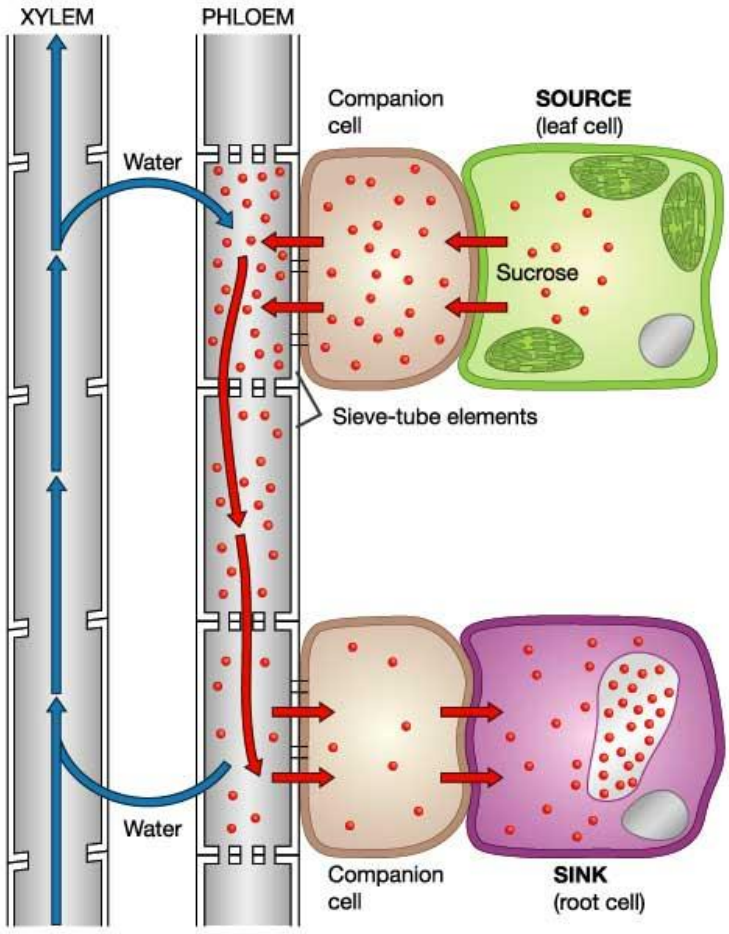
The **pressure-flow hypothesis** can be modelled using the relationship that rate of mass flow **(F_f)** of a substance is given by the product of speed **(S)** of solution flow, path cross-sectional area **(A)** and its concentration **(C).** That is:

$$F_f = S.A.C$$

Speed (m s^{-1}) has the same units as **volume flux** (Jv — m^3 m^{-2} s^{-1}) of solution passing through a transport conduit. Poisseuille's Law describes the volume flux (Jv) of a solution of a known **viscosity** (h) driven by a **pressure difference** (DP) applied over the **length** (l) of pathway of radius (r) as:

$$Jv = \pi r^4 \Delta P / 8\eta l$$

The term $\pi r^4/8\eta l$ in above Equation provides an estimate of hydraulic conductivity **(Lp)** of the sieve-tube conduit which is set by the radius of the sieve pores. Raised to the fourth power, small changes in the sieve-pore radius will exert profound effects on the hydraulic conductivity of the sieve tubes. The viscosity of sieve-tube sap is determined by the chemical species (particularly sugars) and their concentrations in the phloem sap.



Sugar Loading and Unloading: Sugar actively pumped (loaded) into the phloem? There are two known mechanisms, operating in different species. In one, sucrose enters the cell walls near the phloem in the smallest (minor) veins of the leaf. It then enters the phloem by attaching to sucrose transporter proteins embedded in the plasma membranes of the sieve elements and companions

cells. In the second mechanism, sucrose enters the companion cells of the minor vein through small **plasmodesmata**, and is converted to larger sugars, **raffinose**, and **stachyose**. These larger sugars are unable to diffuse back through these plasmodesmata due to their size. Therefore they are trapped in the phloem of the leaf and build up to high concentration. They enter the sieve elements through larger plasmodesmata and are carried away toward the sinks. When sugars and other nutrients arrive in sink tissues they unload from the phloem and enter surrounding cells, either through plasmodesmata or by crossing from one cell to another across the cell walls. The size and metabolic activity of the different sinks determines the amount of material that is delivered to them. Thus, the use of sugar in the **sinks** determines how much sugar flows to them.

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Source-Sink Relationship

The term **source–sink relationship** refers to "the integration of suger and amino acid production in photosynthesis with sugar and amino acid utlisation in growth, storage, maintenance and production."

Plants grown in elevated CO2 for extended durations often, but not always, exhibit some degree of photosynthetic acclimation or down regulation, which is typically characterized by reduced rates of photosynthesis resulting from decreased activity and/or amount of the primary plant carboxyl ting enzyme rubisco. When this phenomenon occurs, leaf nitrogen content often decreases, as nitrogen previously invested in rubisco is transferred to other parts of the plant. Photosynthetic acclimation to elevated CO2 can be induced by insufficient plant sink strength, which often leads to carbohydrate accumulation in source leaves and reductions in net rates of photosynthesis. **Acclimation** can also result from the physical constraints of growing plants in pots or by limiting their access to important nutrients such as nitrogen. In this summary, we review the results of various studies of source: sink relationships on plant growth responses to atmospheric CO2 enrichment. Within a plant, the "**source**" may be defined as a photosynthesizing tissue or organ with export of carbon skeletons, the "**sink**" as one requiring import of carbon, the "**sink strength**" as the ability of a tissue or an organ to mobilize photo-assimilates, the "sink capacity (or sink size)" as the capacity of a tissue or organ to import and store further compounds from the source(s) and the "**sink activity**" by the rate of respiration. Plant growth and development are normally limited by photosynthetic resources, i.e. are "**source-limited**".

Source-sink relation in plants

Picture: Visualization of invertase activity in an Arabidopsis seedling.

Plant performance -how does a plant grow under various conditions- depends on the acquisition of raw material (carbon fixation and mineral uptake), the allocation of this material over the plant organs, and the ability to cope with environmental stresses. Although this is a gross oversimplification, it provides a useful scheme to approach plant performance. For total biomass

production, photosynthetic carbon dioxide fixation is by far the most important process. However, mineral nutrition, although contributing a much smaller proportion in terms of weight, is also essential for plant growth. Functionally a plant can be divided into source and sink, sources being the parts where net **fixation of carbon dioxide** occurs, and sinks being the sites where **assimilates are stored or used**. Allocation of assimilates between plant parts occurs via transport in the phloem. Much of the present research uses the model species **Arabidopsis thaliana**, because of its obvious advantages: small size, sequenced genome, availability of mutants, etc. However, in other projects we try to exploit the knowledge, as obtained in Arabidopsis, to other species, e.g. tomato and potato.

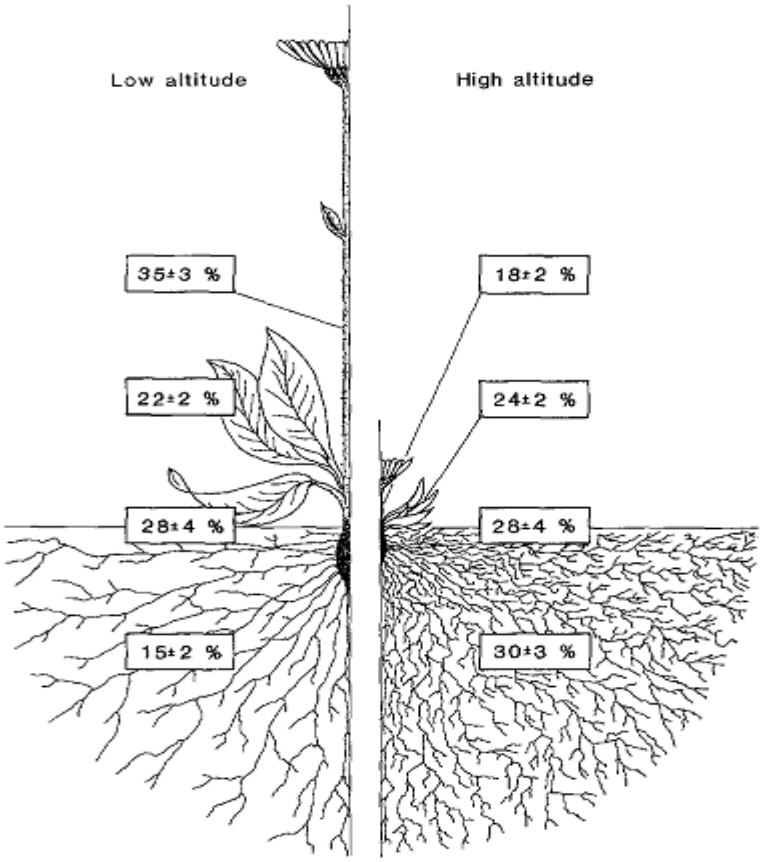

Fig. 1. Summary of dry matter partitioning in perennial herbaceous plants of the Alps. Mean relative portions (±s.e.) allocated to each compartment in 22 low (600 m) and 27 high altitude (2600–3200 m) plant species. Note similar fractions in green leaves

Leaf photosynthesis is normally down-regulated by the sink and the presence of sinks viz fruit prohibits or retards **leaf senescence**; several sinks can compete for photo-assimilates; after fruit removal, i.e. harvest, the roots become the dominant sink. In **apple**, fruit removal led to starch accumulation in the leaf chloroplasts, while the **soluble sugars** remained largely unaffected. In **tomato**, fruit harvest lead to an instant decline in photosynthesis, carbohydrate surplus, release of vacuolar nitrate into the cytoplasm with nitrate assimilation by cytoplasmic nitrate reductase as a

consequence. The sink or presence of **fruit** increased the stomatal conductance of the leaves, enhanced transpiration, uptake and transport of water and nutrients and evapotranspiration cooling, but also required more water supply for the leaves and the fruit; a water potential gradient enables water flux into the fruit. Overall, the fruit or sink down-regulated leaf photosynthesis, increased photosynthesis, Rubisco in vivo activity, dark respiration, stomatal conductance (to water), transpiration and water use efficiency (wue) and prevented or retarded leaf senescence, then modified by the environment.

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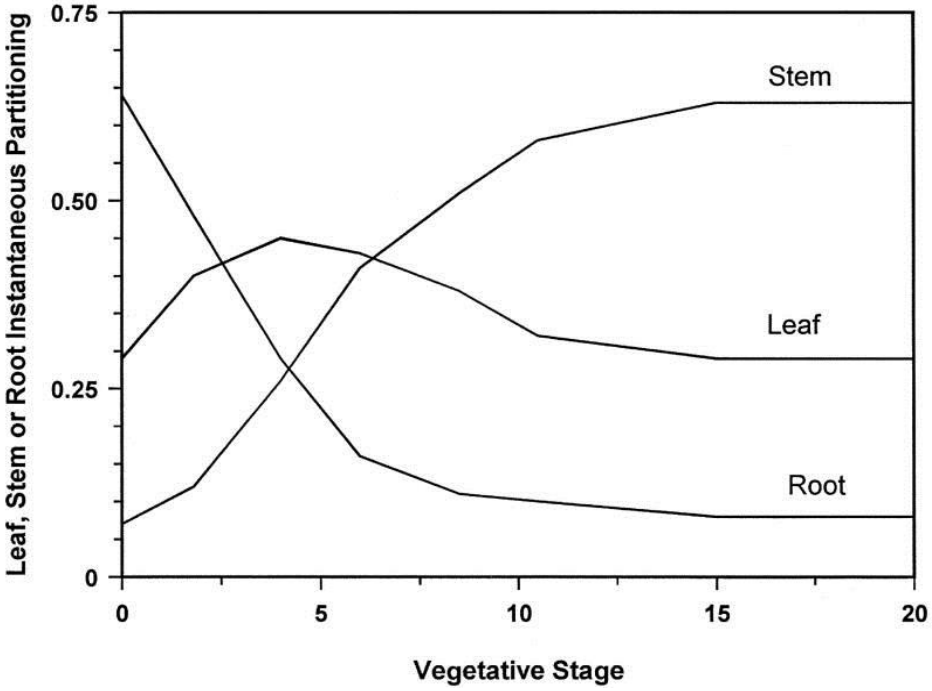
Dry-matter Partitioning

Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. The dry matter partitioning among the sinks of a plant is primarily regulated by the **sinks** themselves. The effect of source strength on dry matter partitioning is often not a direct one, but indirect via the formation of **sink organs**. Although the translocation rate of assimilates may depend on the transport path, the transport path is only of minor importance for the regulation of dry matter partitioning at the whole plant level. To understand the regulation of dry matter partitioning by the sinks, a parameter like **sink strength** is needed that describes **"**a sink's ability to influence assimilate**"** import and is independent of the rest of the plant. The term sink strength can be defined as **"the competitive ability of an organ to attract assimilates**." However, there is much debate and confusion about the term sink strength because this term is often not clearly defined. Sink strength has been proposed to be the product of **sink size** and **sink activity**. Although cell number is often considered as a suitable measure of sink size, it appears not always to be an important determinant of sink size. Moreover, sink strength may depend on sink age rather than sink size. A model for dry matter partitioning into generative plant parts, which is based on sink strengths of the organs, is described. The potential growth rate (potential capacity to accumulate assimilates) has been shown to be an important parameter that quantitatively reflects the sink strength of an organ. The potential growth rates of the plant's organs are not static but change dynamically. The potential growth rate of a fruit is a function of both its age and temperature.



Instantaneous daily partitioning of dry matter among vegetative components (leaf, stem, and root) of faba bean as a function of vegetative stage (number of main-axis nodes).

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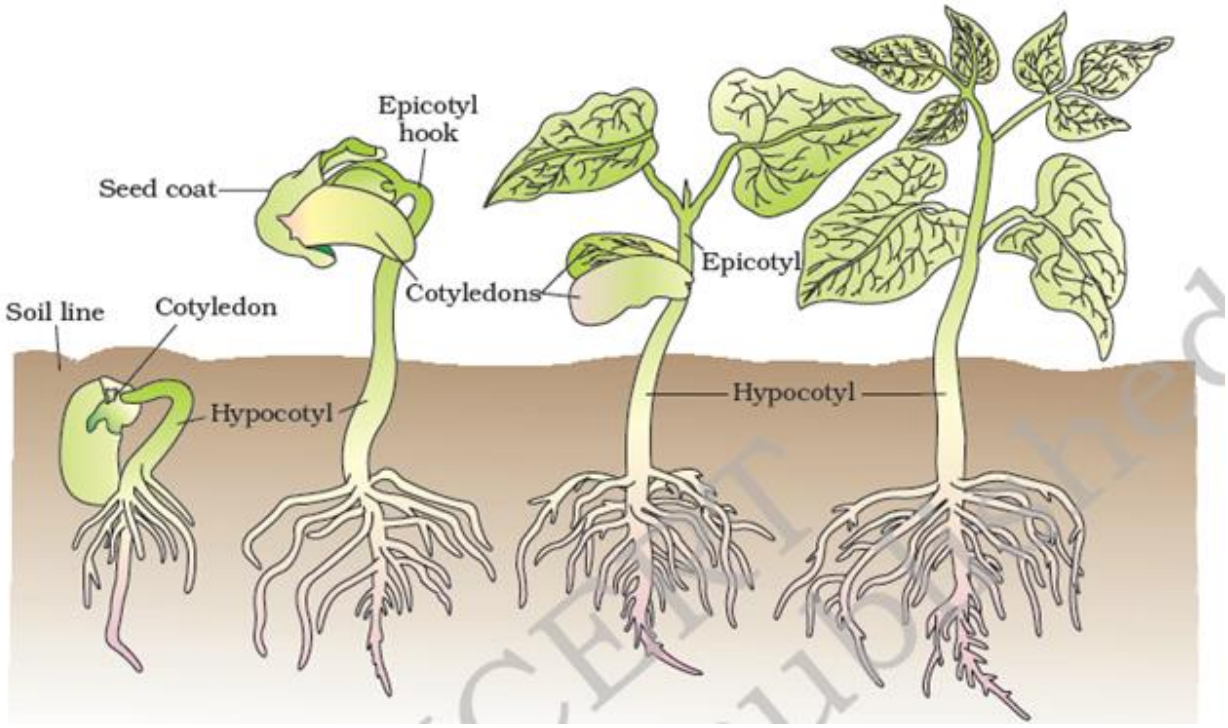
Growth and Development

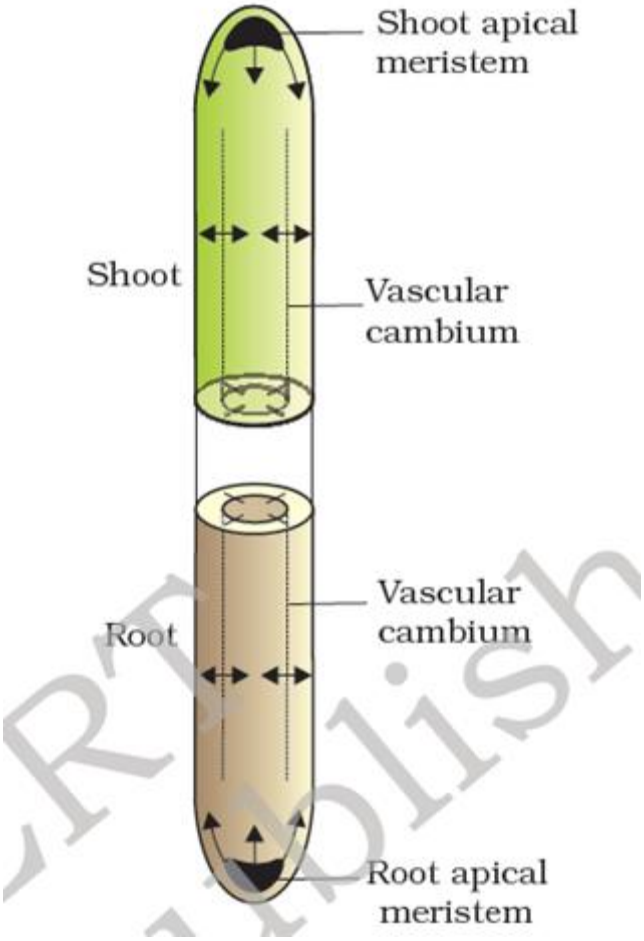
"Development" and "growth" are sometimes used interchangeably in conversation, but in a botanical sense they describe separate events in the organization of the mature plant body.

Growth: "Growth is the irreversible increase in mass that results from cell division (number) and cell expansion (size)."



Growth is regarded as one of the most fundamental and conspicuous characteristics of a living being. What is growth? Growth can be defined as an irreversible permanent increase in size of an organ or its parts or even of an individual cell. Generally, growth is accompanied by metabolic processes (both anabolic and catabolic), that occur at the **expense of energy**. Therefore, for example, expansion of a leaf is growth. How would you describe the swelling of piece of wood when placed in water?

Plant Growth Generally is Indeterminate: Plant growth is unique because plants retain the capacity for unlimited growth throughout their life. This ability of the plants is due to the presence of **meristems** at certain locations in their body. The cells of such meristems have the capacity to divide and self-perpetuate. The product, however, soon loses the capacity to divide and such cells make up the plant body. This form of growth where in new cells are always being added to the plant body by the activity of the meristem is called the open form of growth.



Types of plant growth: plant growth activity may be summarized in two main categories,

a) Primary Growth
b) Secondary Growth

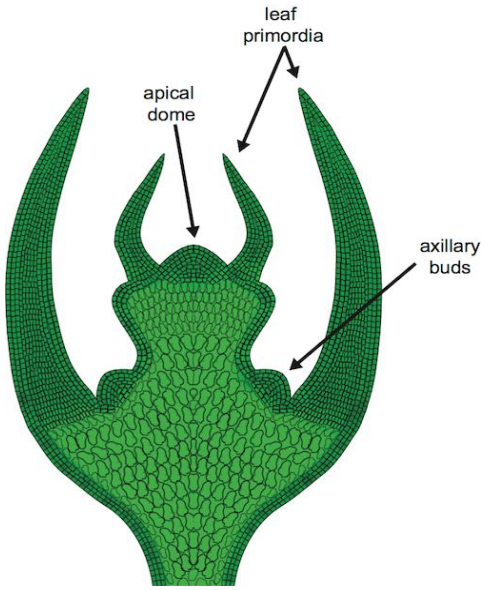
Primary Growth: The entire **shoot system**, no matter how large or small, owes its beginnings to a small region of the plant called the shoot apical meristem. An apical meristem is a region of high cell division (lots and lots of mitosis) that contributes to the extension of the plant. The parts of a shoot system under primary growth are the:

- Stem (nodes + internodes)

  - nodes are where leaves attach to the stem

  - internodes are the spaces on the stem in between the leaves;

- Leaf (petiole + blade);
- Branches, which grow out of axillary buds;
- Reproductive parts (the flowers and fruit)

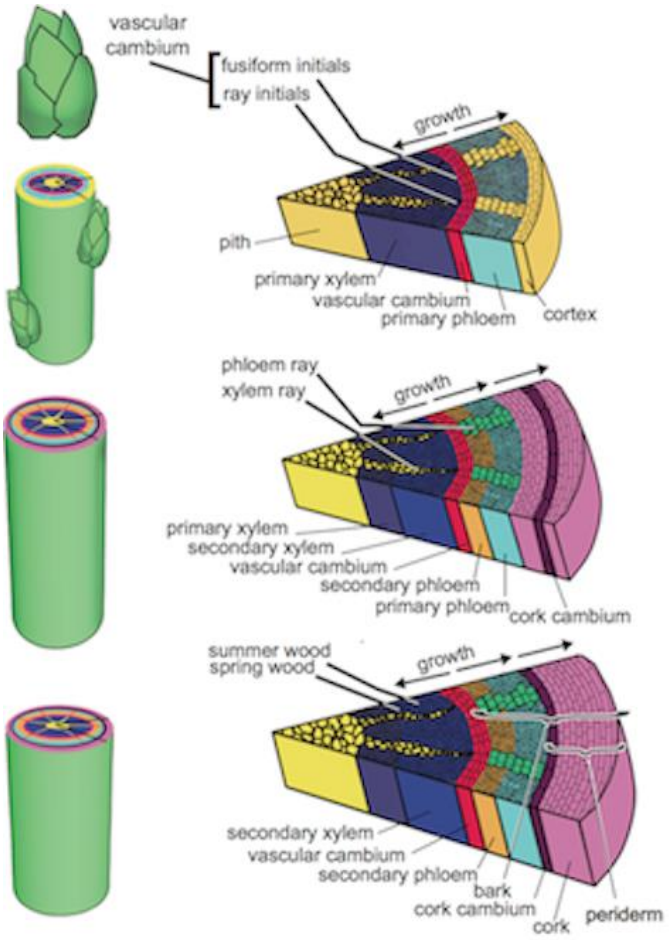


Most of the parts named above are visible as they originate on the shoot apical meristem. The shoot apical meristem is comprised of leaf primordia, which turn into leaves, and the apical dome, where the stem elongates. Under a microscope, the tip of a plant shoot looks like this.

The **root system** also has an apical meristem, known as the **root apical meristem**. This acts in much the same way as the shoot apical meristem, causing extension growth. The main difference is this growth goes down into the ground, and roots, not leaves and branches, come from the root apical meristem. As roots grow, they travel **downward** through the soil, dodging rocks and other obstacles that might be in their way. Just as you should wear a helmet when riding a motorcycle or playing hockey, roots have their own type of helmet: a **root cap**. The root cap protects the root apical meristem as the root pushes its way through the soil. It also secretes slimy ooze that lubricates the soil around the tip of the root, aiding the root on its journey through the harsh soil. Roots can take on many different forms, and root form depends on whether the plant is a eudicot or **monocot**. In eudicots, the first root to form is the **primary root**. It grows straight down and is the dominant root, also known as a taproot. The taproot can produce lateral roots that grow out to the sides. Common eudicots include tomato plants, roses, maple trees, oak trees, and raspberry bushes. In eudicots, branch roots soon join the t**aproot** in its hunt for nutrients. These branch roots form from an area called the **pericycle**. Branch roots don't grow as long as taproots, but they expand the plant's ability to take up water and nutrients from the ground.

In **monocots**, the primary root usually dies soon after the plant germinates and is replaced by roots that form on the stem, called adventitious roots. **Adventitious roots** are lateral roots that anchor the plant. Monocots don't have taproots but instead have shallow, **fibrous root systems** that trap lots of soil. Some examples of monocots are corn, orchids, lilies, and magnolias. When seeds first start to germinate, the most important thing for the young plant is to get a good hold in the ground. The plant produces more roots than shoots when it is young, but as it gets older the amount of root structure is roughly the same as the amount of shoot structure. In fact, the underground root system often mirrors the aboveground shoot system.

Secondary Growth: The width of a plant, or its **girth**, is called **secondary growth** and it arises from the **lateral meristems** in stems and roots. As with apical meristems, lateral meristems are regions of high cell division activity. However, the cells they make grow outward rather than upward or downward. The lateral meristems that produce secondary growth are called **cambiums**, which just means a tissue layer that adds to plant growth. The two important ones for secondary growth are the **vascular cambium** and the **cork cambium**. The vascular cambium produces more vascular tissue (xylem and phloem), which provide support for the shoot system in addition to transporting water and nutrients. Because the xylem and phloem that come from the vascular cambium replace the original (primary) xylem and phloem, and add to the width of the plant, they are called **secondary xylem and secondary phloem**.

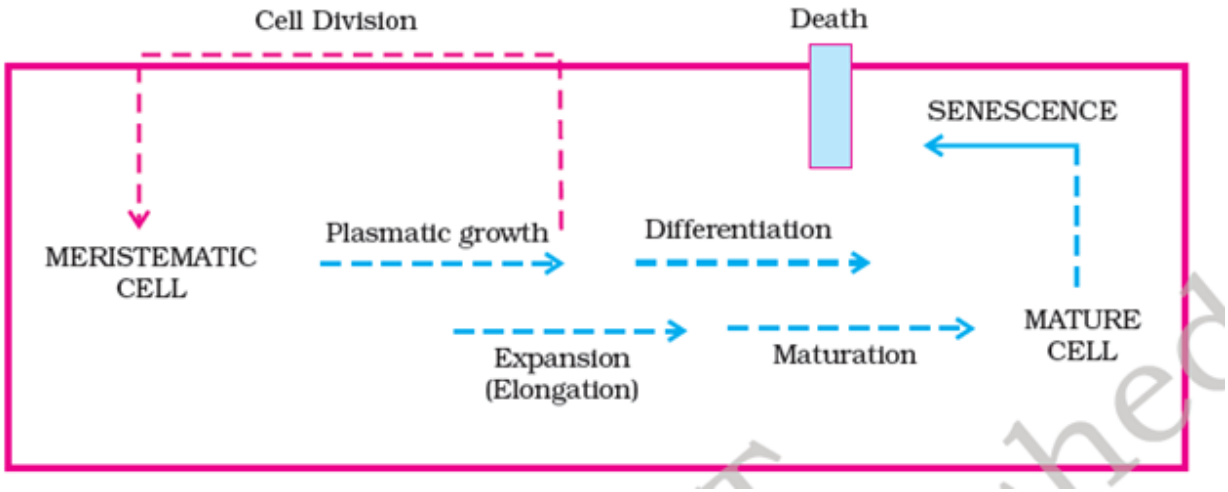


The vascular cambium is only one cell thick and forms a **ring** (called as **Annual Rings** in large trees) around the stem of a plant. On its interior, it adds secondary xylem and on its exterior, it adds secondary phloem. In trees, the layers of secondary xylem form wood. The layers of the secondary phloem form **bark**. Over time, the tree sheds older layers of bark and replaces them with newer layers. Over time, the older wood in the inner part of the trunk goes becomes transformed. It doesn't turn into an alien and fight Decepticons, but it does increase its defenses. The inner wood goes through a genetic process that makes it harder and more resistant to decay. The wood's cells are **dead**, and it is now called **heartwood**. Heartwood is sometimes, but not

always, darker than the surrounding wood. The wood that surrounds the heartwood is called **sapwood**. Sapwood is the living wood where transport of water occurs. Sapwood, unlike heartwood, is vital to the tree's health because it is carrying the water and nutrients the tree needs to survive.

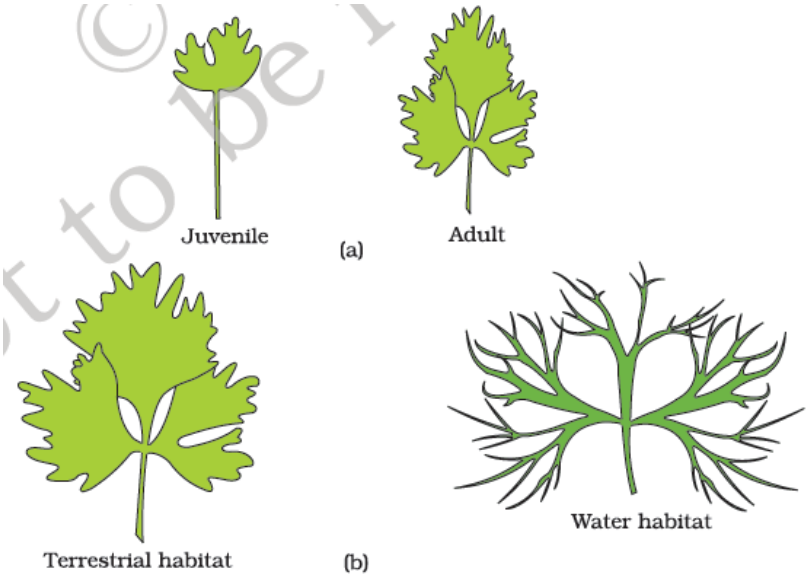
In this cross section of a stem, the stuff in the middle, labeled **Pi**, is called the pith. The pith is made up of primary cells (originating from an apical meristem). The area labeled with an **X** is the xylem, and the **P** is the phloem. The area labeled **BF** is a region of bast fibers, which are strong supporting fibers in the phloem. These are not present in all plants. The outer dark region labeled **C** is the cortex, which surrounds the vascular tissue. And last but not least is the epidermis, which is the outermost layer of cells.

Development: is the progression from earlier to later stages in maturation, e.g. a fertilized egg develops into a mature tree. It is the process whereby tissues, organs, and whole plants are produced. It involves: **growth, morphogenesis** (the acquisition of form and structure), and **differentiation**. The interactions of the environment and the genetic instructions inherited by the cells determine how the plant develops. Development is a term that includes all changes that an organism goes through during its **life cycle** from germination of the seed to senescence. Diagrammatic representation of the sequence of processes which constitute the development of a cell of a higher plant. It is also applicable to tissues/organs.



Sequence of the developmental process in a plant cell

Plants follow different pathways in response to environment or phases of life to form different kinds of structures. This ability is alled plasticity, e.g., heterophylly in cotton, coriander and larkspur. In such plants, the leaves of the juvenile plant are different in shape from those in mature plants. On the other hand, difference in shapes of leaves produced in air and those produced in water in buttercup also represent the heterophyllous development due to environment. This phenomenon of heterophylly is an example of plasticity.



Thus, growth, differentiation and development are very closely related events in the life of a plant. Broadly, development is considered as the sum of growth and differentiation. Development in plants (i.e., both growth and differentiation) is under the control of intrinsic and extrinsic factors. The former includes both intracellular (genetic) or intercellular factors (chemicals such as plant growth regulators) while the latter includes light, temperature, water, oxygen, nutrition, etc.

Differentiation: is the process in which generalized cells specialize into the morphologically and physiologically different cells. Since all of the cells produced by division in the meristems have the same genetic makeup, differentiation is a function of which particular genes are either expressed orrepressed. The kind of cell that ultimately develops also is a result of its location: Root cells don't form in developing flowers, for example, nor do petals form on roots. Mature plant cells can be stimulated under certain conditions to divide and differentiate again, i.e. to dedifferentiate. This happens when tissues are wounded, as when branches break or leaves are damaged by insects. The plant repairs itself by dedifferentiating parenchyma cells in the vicinity of the wound, making cells like those injured or else physiologically similar cells

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Growth Measurements and Analysis

Growth, at a cellular level, is principally a consequence of increase in the amount of protoplasm. Since increase in protoplasm is difficult to measure directly, one generally measures some quantity which is more or less proportional to it. Growth is, therefore, **measured** by a variety of parameters some of which are: increase in fresh weight, dry weight, length, area, volume and cell number. Some methods for growth **analysis** are briefly described below.

Parameter	Symbol	Unit
Crop Growth Rate	CGR	g (crop) m^{-2} d^{-1}
Leaf Area Index	LAI	m^2 (leaf) m^{-2}
Specific Leaf Area	SLA	m^2 (leaf) g^{-1} (leaf)
Relative Growth Rate	RGR	g (crop) g^{-1} (crop) d^{-1}
Net Assimilation Rate	NAR	g (crop) m^{-2} (leaf) d^{-1}

Growth Measurement

1- Weighing Plants: Fresh vs. Dry Weight:

Measuring Fresh Weight: While you can technically measure the fresh weight of plants without harming them, the simple act of removing a plant from its growing "medium" can cause trauma and affect the ongoing growth rate and thus your experiment. Measuring the fresh weight of plants is tricky and should probably be saved as a final measure of growth at the end of the experiment. Here is the process for measuring fresh weight:

- Remove plants from soil and wash off any loose soil.
- 2. Blot plants gently with soft paper towel to remove any free surface moisture.
- 3. Weigh immediately (plants have a high composition of water, so waiting to weigh them may lead to some drying and therefore produce inaccurate data).

Measuring dry weight: Since plants have a high composition of water and the level of water in a plant will depend on the amount of water in its environment (which is very difficult to control), using dry weight as a measure of plant growth tends to be more reliable. You can only capture this data once as a final measure at the conclusion of your experiment.

- Remove the plants from the soil and wash off any loose soil.
- Blot the plants removing any free surface moisture.
- Dry the plants in an oven set to low heat (100° F) overnight.
- Let the plants cool in a dry environment (a Ziploc bag will keep moisture out) - in a humid environment the plant tissue will take up water. Once the plants have cooled weigh them on a scale.

- Plants contain mostly water, so make sure you have a scale that goes down to milligrams since a dry plant will not weight very much.

2- Root Mass:

Root mass is recommended as a final measurement as the plant must be removed from its growing medium in order to capture accurate data. There are quite a few different methods for measuring root mass depending on the type and structure of the roots**.**

Grid intersect technique:

- Remove the plant from the soil.
- If you are working with thin or light roots, you may want to die the roots using an acidic stain.
- Lay the roots on a grid pattern and count the number of times the roots intersect the grid.
- Trace the roots on paper, measure each of the tracings, and calculate root length from the tracings.
- Count the number of roots.
- Measure the diameter of the root. This is especially useful for root vegetables such as beets, carrots, potatoes, etc. that have a large root.

3- Root Shoot Ratio:

Roots allow a plant to absorb water and nutrients from the surrounding soil, and a healthy root system is key to a healthy plant. The root:shoot ratio is one measure to help you assess the overall health of your plants. Your control group of plants will provide you with a "normal" root:shoot ratio for each of your plant types, any changes from this normal level (either up or down) would be an indication of a change in the overall health of your plant. It is important to combine the data from the root:shoot ratio with data from observations to get an accurate understanding of what is happening with your plants. For example, an increase in root:shoot ratio could be an indication of a healthier plant, provided the increase came from greater root size and NOT from a decrease in shoot weight. To measure the root:shoot ratio:

- Remove the plants from soil and wash off any loose soil.
- Blot the plants removing any free surface moisture.
- Dry the plants in an oven set to low heat (100° F) overnight.
- Let the plants cool in a dry environment (a Ziploc bag will keep moisture out) - in a humid environment the tissue will take up water. Once the plants have cooled weigh them on a scale.
- Separate the root from the top (cut at soil line).
- Separately weigh and record the root and top for each plant. (Dry weight for roots/dry weight for top of plant = root/shoot ratio)
- The root/shoot ratio can be calculated for each treatment.
- Plants contain mostly water, so make sure you have a scale that goes down to milligrams since a dry plant will not weight very much.

Growth Analysis

1- Relative Growth Rate (RGR):

Relative growth rate is the growth rate relative to the size of the population. It is also called the **exponential growth rate**, or the continuous growth rate. In terms of differential equations, if **P** is the population, and **dP/dt** its growth rate, then its relative growth rate is **1/PdP/dt**. If the relative growth rate is constant, i.e., **1/PdP/dt=k**, it is not difficult to verify that the solution to this equation is **P(t) = exp(kt).** When calculating or discussing relative growth rate, it is important to pay attention to the units of time being considered.

In plant physiology, **Relative Growth Rate (RGR)** is also a measure used to quantify the speed of plant growth. It is measured as the **mass increase per aboveground biomass per day**, for example as g g^{-1} d^{-1}. It is considered to be the most widely used way of estimating plant growth, but has been criticised as calculations typically involve the destructive harvest of plants.

RGR is calculated using the following equation:

$$\mathbf{RGR = (\ln W_2 - \ln W_1)/(t_2-t_1)}$$

Where:

ln = natural logarithm

t_1 = time one (in days)

t_2 = time two (in days)

W_1 = Dry weight of plant at time one (in grams)

W_2 = Dry weight of plant at time two (in grams)

2- Crop Growth Rate (CGR):

Crop growth rate is a measure of the increase in size, mass or number of crops over a period of time. The increase can be plotted as a logarithmic or exponential curve in many cases. The absolute growth rate is the slope of the curve. Relative growth rate is the slope of a curve that represents logarithmic growth over a period of time. An exponential growth rate is not sustainable over time. The curve typically flattens out, representing a saturation in growth at a certain point in time. The crop growth rate calculation is dependent on the values of NAR (Net Assimilation Rate) and LAI (Leaf Area Index) of the crop. Can be measured as:

$$\mathbf{CGR = W_2\text{-}W_1/T_2\text{-}T_1}$$

Or

$$\mathbf{CGR = NAR * LAI}$$

Where NAR is net assimilation ration while LAI is leaf area index.

3- Leaf Area Index (LAI):

LAI was first defined in 1947 as the total one-sided area of photosynthetic tissue per unit ground surface area. After reviewing various other definitions (some measurement approach – dependent), concluded that in current literature, LAI is defined as "one half of the total leaf area per unit ground surface area." They also noted that different definitions can result in significant differences between calculated LAI values. LAI is a dimensionless quantity (or m2/m2).

$$\mathbf{LAI = LA/\ GA}$$

LAI is determined directly by taking a statistically significant sample of foliage from a plant canopy, measuring the leaf area per sample plot and dividing it by the plot land surface area. Indirect methods measure canopy geometry or light extinction and relate it to LAI.

Direct methods: Direct methods require stripping and measuring the foliage of plant canopy samples. LAI for clip plots or individual plants is measured by hand or by using an LAI meter. Traditional LAI meters require each plant leaf to be stripped and fed through the entrance of the machine, which can be likened to a kind of crude image scanner. The **disadvantage** of the direct method is that it is destructive, time consuming and expensive, especially if the study area is very large.

Indirect methods: A hemispherical photograph of forest canopy. The ratio of the area of canopy to sky is used to approximate LAI. Indirect methods of estimating LAI in situ can be divided in two categories: **(1)** indirect contact LAI measurements such as plumb lines and inclined point quadrats and **(2)** indirect non-contact measurements. Due to the subjectivity and labor involved with the first method, indirect non-contact measurements are typically preferred. Non-contact **LAI** tools, such as **hemispherical photography**. Hemispherical photography methods estimate LAI and other canopy structure attributes from analyzing upward-looking fisheye photographs taken beneath the plant canopy. The **LAI-2200** calculates LAI and other canopy structure attributes from solar radiation measurements made with a wide-angle optical sensor. Measurements made above and below the canopy are used to determine canopy light interception at five angles, from which LAI is computed using a model of radiative transfer in vegetative canopies. The **LP-80** calculates LAI by means of measuring the difference between light levels above the canopy and at ground level, and factoring in the leaf angle distribution, solar zenith angle, and plant **extinction coefficient**. Such indirect methods, where LAI is calculated based upon observations of other variables (canopy geometry, light interception, leaf length and width etc.) are generally faster, amenable to automation, and thereby allow for a larger number of spatial samples to be obtained. For reasons of convenience when compared to the direct (destructive) methods, these tools are becoming more and more important. The d**isadvantage** of the indirect method is that in some cases it can underestimate the value of LAI in very dense canopies, as it does not account for leaves that lie on each other, and essentially act as one leaf according to the theoretical LAI models.

4- Specific Leaf Area (SLA):

Specific leaf area is defined as the ratio of leaf area to dry weight.

$$\mathbf{SLA = LA/LW}$$

Specific leaf area can be used to estimate the reproductive strategy of a particular plant based upon light and moisture (humidity) levels, among other factors.[4] Specific leaf area (SLA) is one of the most widely accepted key leaf characteristics used during the study of leaf traits. Portable leaf area meters can be used to provide a rapid, non-destructive measurement of leaf surface area, length, width and perimeter. Some can also measure diseased area by altering the sensitivity of the detecting system. These instruments have the ability to record the measured parameters as well as store a digital image of the leaf scanned.

5- Net Assimilation Rate (NAR):

NAR measures the accumulation of plant dry weight per unit leaf area per unit time. It is a measure of efficiency of production.

$$\mathbf{NAR = W_2 - W_1 / LA_2 - LA_1 \quad X \quad \ln W_2 - \ln W_1 / t_2 - t_1}$$

Units = g cm-2 day-1 or g/cm2/day.

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Factors Affecting Growth

Growth is defined as an irreversible change in the size of a cell, organ or whole organism. It may also be the increase in cell number without changes in volume or weight. Commonly, growth is the increase in the amount of living material (protoplasm) which leads to an increase in cell size and ultimately cell division. The increase in protoplasm is brought about as water, carbon dioxide and inorganic salts are transformed into living material. Growth occurs only in living cells by metabolic processes involved in the synthesis of proteins, nucleic acids, lipids, and carbohydrates at the expense of metabolic energy provided by photosynthesis and respiration.

Factors affecting plant growth can be summarized under these main groups.

a) Biotic Factors
b) Internal Factors
c) External Factors
d) Nutritional Factors

Biotic Factors

- Plants compete with other plants for space, water, light and nutrients. Plants can be so crowded that no single individual makes normal growth.
- Many plants rely on birds and insects to effect pollination.
- Grazing animals may affect vegetation.
- Soil fertility is influenced by the activity of bacteria and fungi.
- Bacteria, fungi, viruses, nematodes and insects can parasitize plants.
- Some plant roots require an association with fungi to maintain normal activity (mycorrhizal association).

Internal Factors

- **Genetic** - The genetic compliment of a plant is acquired when the zygote is formed from male and female gametes. The genetic information is duplicated and passed on with subsequent cell divisions. As the plant enlarges to its mature size some genes are activated while others are inactivated. Certain genes direct the synthesis of enzymes that catalyze specific biochemical reactions required for growth and differentiation. The genes involved in protein synthesis are referred to as structural genes. Regulatory and operator genes regulate the activity of the structural genes. The signals that stimulate the regulatory genes are believed to be growth regulators, inorganic ions, coenzymes and environmental factors such as temperature and light.
- **Growth hormones** participate in both genetic and environmental control of growth and differentiation. The pattern of distribution of growth hormones in the plant is controlled by interactions between the environment and genetic factors in the plant. They may be either

growth inhibitors or promotors depending on the site of action and concentration of the substance. There are 5 major types of plant hormones: auxins, cytokinins, gibberellins, abscisic acid and ethylene. They will be discussed in detail later.

External Factors

Plant growth and development are influenced by physical and chemical components in the plants environment. Any factor in the plants' environment that is less than optimum, whether it is deficient or in excess, will limit plant growth.

- **Light**: Adequate light is perhaps one of the most important factors influencing plant growth and it is he quantity, quality and duration of light exposure is what matters. Various light sources can be used to provide light to the plants and the sources of light can be classified as natural and artificial sources. The natural source of light is the sun whereas the artificial sources include various types of lighting equipment. Blue light is essential for the growth of the leaves whereas a combination of red and blue light promotes flowering of plants. The artificial light sources can be manipulated to adjust the intensity of the light as well. While it is always good to rely on the natural source of light, during extreme weather conditions and lack of sunlight artificial light is the best option. Also there are certain plants, which require less light for the growth, in such cases the light can be filtered using protective shelters for the plants to allow minimum required amount of sunlight exposure.

- **Temperature:** Temperature is a crucial element that influences the growth of plants. Temperature of the surrounding atmosphere as well as the temperature of the soil matters for the plant growth. Optimum temperature is one of the pre-requisites for many of the plant processes, like photosynthesis, respiration, germination, and flowering. Although the values differ for various plants usually cool season plants have 55-65 degrees Fahrenheit as the optimum temperature for germination whereas warm-season plants germinate at 65-75 degrees Fahrenheit. The temperature ranges for optimum photosynthesis and respiration vary with the species of plants and their individual requirements.

- **Relative Humidity:** Moisture is a very important factor in growth of plants and is defined as the ratio of water vapor in the air to the amount of water in the air. The relative humidity in the air is used by the plants and is crucial for the transpiration of the plants. Transpiration is at its peak cutting hot, windy and dry days while transpiration slows down during cool and humid days.

- **Carbon dioxide and Oxygen** The manufacturing of sugar by plants requires the presence of carbon dioxide and hence it is one of the vital elements for plant growth. It is a known fact that plants can use as much as 1500 parts per million of carbon dioxide. In case the natural carbon dioxide available in the air is not enough, there exist Carbon dioxide injectors that promote enhanced plant growth. Oxygen is essential for plant respiration and utilization of photosynthesis byproducts.

- **Soil:** Soil with proper humidity, and the right balance of all the minerals and nutrients is one of the essential factors instrumental in plant growth. The type of soil and the quality and the nutrients required in it vary according to the plant species. The right pH balance, which measures the alkalinity or acidity of the soil and presence of certain chemicals, is also instrumental in the growth of plants.

- **Air pollutants:** Air pollution is an important problem for producers of greenhouse crops. The sources of air pollution are increasing as new industries and highways are built. This is a particular problem for horticultural operations near urban and industrial areas. Among the phytotoxic pollutants are ozone, peroxyacel nitrates, oxides of sulfur, hydrocarbons, fluorides, carbon monoxide, herbicides, fumigants, mercury vapors (do not use mercury thermometers in greenhouses), and phytotoxic gases produced from incomplete combustion of CO2 generators. It may be necessary for greenhouse owners to move to areas where phytotoxic gases are not present, or to grow species that are less sensitive to these substances. Often leaves and flowers are first to show signs of air pollution. Unusual discolorations, spotting, twisting or turning of leaves and abortion of flowers followed by poor growth are symptoms of air pollution.

Nutritional Factors

There are several aspects of plant nutrition, which need to be considered for better growth of plants. The basic nutrients required for plant growth are divided into two main categories namely micronutrients and macronutrients. Here is the information about the important plant growth factors based on nutrient intake:

- **Macronutrients:** The nutrients that are required by plants in larger quantities are termed as the macronutrients. There are six elements in the soil that are termed as macronutrients these are nitrogen, potassium, magnesium, calcium, phosphorus, and sulfur.

- **Micronutrients:** The nutrients that are required in smaller quantities by the plants are called the micronutrients. There exist eight elements, which are termed as the micronutrients. The eight micronutrients include iron, zinc, molybdenum, manganese, boron, copper, cobalt, and chlorine.

- **Water:** A majority of growing plants contains as much as 90 percent water. Water is one of the most essential factors required in growth of plants. Water plays a crucial role for efficient photosynthesis, respiration, transpiration and transportation of minerals and other nutrients through the plant. Water is responsible for functioning of the stomatal opening of leaves and also the source of pressure for the directed growth of roots through the soil.

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Chemical Growth Regulators

The plant growth regulators **(PGRs)** are small, simple molecules of diverse chemical composition. They could be indole compounds (indole-3-acetic acid, IAA); adenine derivatives (N6-furfurylamino purine, kinetin), derivatives of carotenoids (abscisic acid, ABA); terpenes (gibberellic acid, GA3) or gases (ethylene, C2H4). Plant growth regulators are variously described as plant growth substances, plant hormones or phytohormones in literature.

The PGRs can be broadly divided into two groups based on their functions in a living plant body. One group of PGRs are involved in growth **promoting activities**, such as cell division, cell enlargement, pattern formation, tropic growth, flowering, fruiting and seed formation. These are also called plant **growth promoters**, e.g., auxins, gibberellins and cytokinins. The PGRs of the other group play an important role in plant responses to wounds and stresses of biotic and abiotic origin. They are also involved in various **growth inhibiting** activities such as dormancyand abscission. The PGR abscisic acid belongs to this group. The gaseous PGR, ethylene, could fit either of the groups, but it is largely an inhibitor of growth activities.

As in animals, plant hormones are chemicals for communication. **Hormone** is a chemical released from one cell that affects growth, development of target cells which have appropriate receptors. However unlike animal, hormones that act on distant cells, plant hormones can act on adjacent cells as well as distant ones

There are five known categories of plant hormones:

1- Auxins:

An auxin, indole-3-acetic acid (IAA), was the first plant hormone identified. It is manufactured primarily in the **shoot tips** (in leaf primordia and young leaves), in **embryos**, and in parts of developing **flowers and seeds**. Its transport from cell to cell through the parenchyma surrounding the vascular tissues requires the expenditure of ATP energy. **IAA** moves in one direction only—that is, the movement is polar and, in this case, downward. Such downward movement in shoots is said to be basipetal movement, and in roots it is acropetal.

Auxins alone or in combination with other hormones are responsible for many aspects of plant growth. IAA in particular:

- Activates the differentiation of vascular tissue in the shoot apex and in calluses; initiates **division of the vascular cambium** in the spring; **promotes growth** of vascular tissue in healing of wounds.
- Activates cellular **elongation** by increasing the **plasticity** of the cell wall.
- Maintains **apical dominance** indirectly by stimulating the production of ethylene, which directly inhibits **lateral bud** growth.
- Activates a gene required for making a protein necessary for growth and other genes for the synthesis of **wall materials** made and secreted by dictyosomes.
- Promotes initiation and growth of **adventitious roots** in cuttings.

- Promotes the growth of many **fruits** (from auxin produced by the developing seeds).
- Suppresses the **abscission** (separation from the plant) of fruits and leaves (lowered production of auxin in the leaf is correlated with formation of the abscission layer).
- Inhibits most **flowering** (but promotes flowering of pineapples).
- Activates **tropic responses**.
- Controls **aging and senescence, dormancy** of seeds.

Synthetic auxins are extensively used as **herbicides**, the most widely known being **2,4-D** and the notorious **2,4,5-T**, which were used in a 1:1 combination as Agent Orange during the Vietnam War and sprayed over the Vietnam forests as a defoliant.

2- Cytokinins:

Named because of their discovered role in **cell division** (cytokinesis), the cytokinins have a molecular structure similar to **adenine**. Naturally occurring zeatin, isolated first from corn (Zea mays), is the most active of the cytokinins. Cytokinins are found in sites of active cell division in plants—for example, in root tips, seeds, fruits, and leaves. They are transported in the **xylem** and work in the presence of auxin to promote cell division. Differing cytokinin:auxin ratios change the nature of organogenesis. If kinetin is high and auxin low, shoots are formed; if kinetin is low and auxin high, roots are formed. Lateral bud development, which is retarded by auxin, is promoted by cytokinins. Cytokinins also delay the senescence of leaves and promote the expansion of cotyledons.

3- Gibberellins:

Gibberellins are another kind of **promotery PGR**. There are more than **100** gibberellins reported from widely different organisms such as fungi and higher plants. They are denoted as **GA1**, **GA2, GA3** and so on. However, **Gibberellic acid** (GA3) was one of the first gibberellins to be discovered and remains the most intensively studied form. All GAs are **acidic**. They produce a wide range of physiological responses in the plants. Their ability to cause an increase in **length of axis** is used to increase the length of grapes stalks. Gibberellins, cause fruits like apple to elongate and **improve its shape**. They also **delay senescence**. Thus, the fruits can be left on the tree longer so as to extend the market period. GA3 is used to speed up the malting process in **brewing industry**. Sugarcane stores carbohydrate as sugar in their stems. Spraying sugarcane crop with gibberellins increases the **length of the stem**, thus increasing the yield by as much as **20 tonnes per acre.** Spraying **juvenile conifers** with GAs hastens the maturity period, thus leading to early seed production. Gibberellins also **promotes bolting** (internode elongation just prior to flowering) in beet, cabbages and many plants with rosette habit.

4- Ethylene:

Ethylene is a simple gaseous PGR. It is synthesised in large amounts by tissues undergoing **senescence and ripening fruits**. Influences of ethylene on plants include horizontal growth of seedlings, swelling of the axis and **apical hook** formation in dicot seedlings. Ethylene promotes senescence and abscission of plant organs especially of leaves and flowers. Ethylene is highly effective in **fruit ripening**. It enhances the respiration rate during ripening of the fruits. This rise in rate of respiration is called **respiratory climactic**. Ethylene breaks seed and **bud dormancy**, initiates germination in **peanut seeds**, sprouting of potato **tubers**. Ethylene promotes rapid **internode/petiole elongation** in deep water rice plants. It helps leaves/ upper parts of the shoot to remain above water. Ethylene also promotes root growth and **root hair formation**, thus helping the plants to increase their **absorption surface**.

Ethylene is used to initiate flowering and for synchronising fruit-set in pineapples. It also induces flowering in mango. Since ethylene regulates so many physiological processes, it is one of the most widely used PGR in agriculture. The most widely used compound as source of ethylene is **ethephon**. Ethephon in an aqueous solution is readily absorbed and transported within the plant and releases ethylene slowly. Ethephon hastens fruit ripening in tomatoes and apples and accelerates abscission in flowers and fruits (thinning of cotton, cherry, walnut). It promotes female flowers in cucumbers thereby increasing the yield.

5- Abscisic acid:

Abscisic acid **(ABA)** was discovered for its role in **regulating abscission and dormancy**. But like other PGRs, it also has other wide ranging effects on plant growth and development. It acts as a general plant **growth inhibitor** and an inhibitor of plant **metabolism**. ABA inhibits seed **germination**. ABA stimulates the closure of stomata in the epidermis and increases the **tolerance** of plants to various kinds of stresses. Therefore, it is also called the **stress hormone**. ABA plays an important role in seed development, maturation and dormancy. By inducing dormancy, ABA helps seeds to withstand desiccation and other factors unfavourable for growth. In most situations, ABA acts as an antagonist to GAs.

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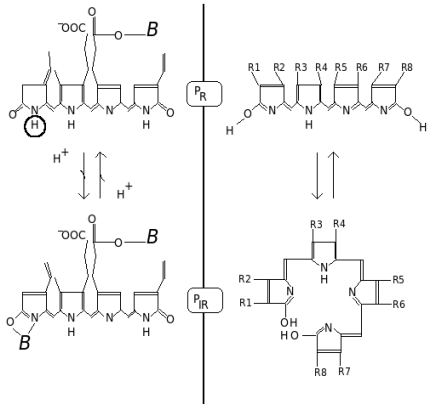
Phytochrome

Phytochrome is a **photoreceptor**, a pigment that plants use to detect light. It is sensitive to light in the **red and far-red** region of the visible spectrum. Many flowering plants use it to regulate the time of flowering based on the length of day and night **(photoperiodism)** and to set **circadian rhythms**. It also regulates other responses including the **germination of seeds** (photoblasty), elongation of seedlings, the size, shape and number of leaves, the synthesis of chlorophyll, and the straightening of the **epicotyl or hypocotyl hook** of dicot seedlings. It is found in the leaves of most plants.

Biochemically, phytochrome is a **protein** with a **bilin chromophore**. Phytochrome has been found in most plants including all higher plants; very similar molecules have been found in several bacteria. A fragment of a bacterial phytochrome now has a solved three-dimensional protein structure. Phytochrome consists of two identical chains (A and B). Each chain has a PAS domain and **GAF domain**. The PAS domain serves as a signal sensor and the GAF domain is responsible for binding to **cGMP** and also senses light signals. Together, these subunits form the phytochrome region, which regulates physiological changes in plants to changes in red and far red light conditions. In plants, red light changes phytochrome to its biologically active form, while far red light changes the protein to its biologically inactive form.



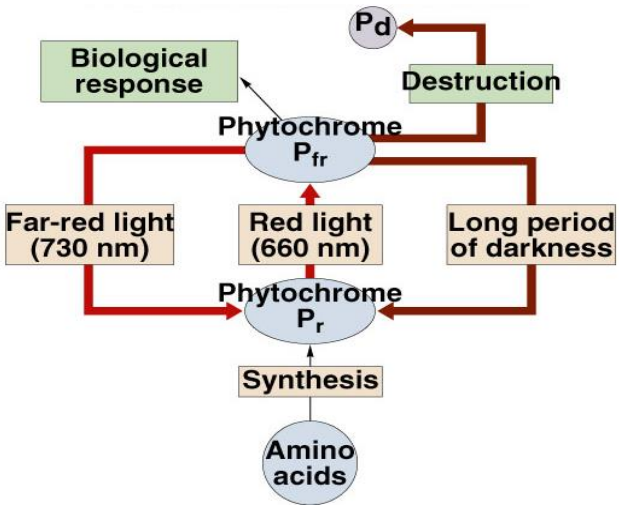
Two hypotheses, explaining the light - induced phytochrome conversions (PR - red form, PIR - far red form, B - protein). Left - H+ dissociation. Right - formation of the chlorophyll - like ring.

Chemically, phytochrome consists of a chromophore, a single bilin molecule consisting of an open chain of four pyrrole rings, bonded to the protein moiety. It is the chromophore that absorbs light, and as a result changes the conformation of **bilin** and subsequently that of the attached protein, changing it from one state or isoform to the other. The phytochrome chromophore is usually phytochromobilin, and is closely related to phycocyanobilin (the chromophore of the phycobiliproteins used by cyanobacteria and red algae to capture light for photosynthesis) and to the bile pigment bilirubin (whose structure is also affected by light exposure, a fact exploited in

the phototherapy of jaundiced newborns). The term "bili" in all these names refers to bile. Bilins are derived from the closed tetrapyrrole ring of haem by an oxidative reaction catalysed by haem oxygenase to yield their characteristic open chain. Chlorophyll too is derived from haem (Heme). In contrast to bilins, haem and chlorophyll carry a metal atom in the center of the ring, iron or magnesium, respectively.

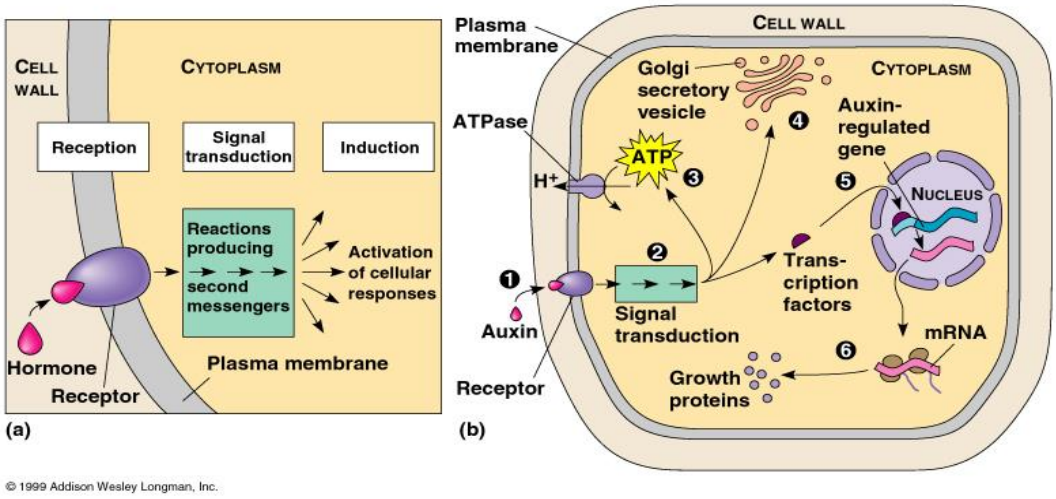
- Phytochrome in **etiolated** plants (type I) is slightly larger and absorbs light maximally at a longer wavelength than phytochrome from light-grown plants (type II).
- Differ mainly in apoprotein
- At least five different proteins that can be identified **immunologically**; proteins are about **50%** similar to one another.
- Proteins are coded by 5 different genes called phy A - phy E. The phytochrome they make is called PHY A etc
- PHY A is found only in dark-grown seedlings (Type 1); the other four types occur in both etiolated and green (light-grown) plants. Interestingly, PHY A is unstable. The PHY A is probably important for detecting the presence of light while the others monitor its quality.

How they work: Plants, like all organisms, must be able to monitor and respond to environmental conditions. For example, a dark-grown seedling "knows" that it has a limited time to get to light until it runs out of energy. In response, an "etiolated" plant exhibits a variety of features in response to darkness including expanded internodes for rapid growth, an **apical hook** (in eudicots), unexpanded leaves, no chlorophyll. A brief exposure to light causes internode elongation to slow, the hook to uncurl, leaves to expand and chlorophyll synthesis to begin. Thus, light has an obvious impact on the form of the plant (photo morphogenesis).



The signal: red & far-red light: In many photo morphogenetic responses, red and far-red light are important environmental signals. For example, from studies of light sensitive lettuce seed germination, Borthwick and Hendricks concluded that: **(1)** germination is dependent upon which

wavelength of light is received last; and that **(2)** this response is the product of a photo-reversible pigment.



The receptor: Phytochrome: The best characterized, and most important receptor for light-induced growth responses is phytochrome. The absorption spectrum of phytochrome closely matches the action spectrum implicating it in these processes.

Photo reversibility: The unique feature of phytochrome is that it exhibits photo reversibility; it exists in two forms that are interchangeable. Pr - red light absorbing form and Pfr - far red light absorbing form. When Pr absorbs red light (ca. 660 nm) it is converted into Pfr. When Pfr absorbs far red light (ca. 730 nm) it is converted into Pr. In short, phytochrome acts like a light switch. This can be depicted:

Pr ↔ Pfr

The absorption spectrum for phytochrome will be provided. Note that there is some overlap in the spectra and also note that there is some absorption of blue light.

Chemical Changes During Photo Reversibility: The main difference between the two forms is a cis-trans isomerization that occurs between one pair of tetrapyrolles. This change has the effect of extending or opening up the chromophore. The protein also undergoes a conformation change. One piece of evidence that supports this is that the protein is more readily digested in the Pfr form.

Efficiency of Photo Conversion: Phytochrome acts like a weird light switch that only turns off/on a portion of the lights. In other words, red light treatment of Pr results in about 85% Pfr + 15% Pr; far red light treatment of Pfr results in 97% Pr + 3% Pfr. Thus, at photo-equilibrium not all the phytochrome is interconverted. The reason for this is because the absorption spectra for the two pigments overlap.

Light-sensitive seed germination: Note that many seeds require light for germination (like lettuce), whereas others are inhibited by light (wild oats, Phacelia, Royal Paulownia). Phytochrome presumably stimulates GA synthesis/release which in turn, stimulates the mobilization of stored reserves (recall the GA lecture). This provides energy for the germinating seed and also decreases

the solute potential for water uptake necessary for providing the force for the radicle to push its way through the seed.

Reversal of etiolation: Recall that etiolated plants are those that have been grown in the dark and exhibit a series of characteristics including elongated internodes, no chlorophyll, apical hook or unopened coleoptile, unexpanded or coiled leaves. These are all adaptations to save energy and get to the light asap. Light stimulates increased [cytokinin] which stimulates cell division and greening; increases [GA] which presumably stimulates IAA oxidase production to get rid of excess IAA that causes the long spindly growth. Also, IAA stimulates ethylene synthesis which maintains the apical hook. Treating the apical hook with red light + ethylene maintains the hook.

Change surface charge: In a classic experiment, Tanada (1968) observed that red light-treated barley root tips adhered to the sides of a beaker (with a negatively charged surface) but released after far red treatment. It was subsequently show that red light caused the surface to become positively charged and far red light negatively charged. Red light causes a depolarization of membranes and far-red reverses or even causes a slight hyperpolarization.

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Carbon Isotopic Discrimination and Water Use Efficiency in Plants

There are two naturally occurring stable isotopes of carbon, ~2C and ~3C. Most of the carbon is **12C (98.9%),** with **1.1%** being **13C**. The isotopes are unevenly distributed among and within different compounds, and this isotopic distribution can reveal information about the physical, chemical, and metabolic processes involved in carbon transformations. The overall abun-dance of 13C relative to ~2C in plant tissue is commonly less than in the carbon of atmospheric carbon dioxide, indicating that carbon isotope discrimination occurs in the incorporation of CO2 into plant biomass. Because the isotopes are stable, the information inherent in the ratio of abundances of **carbon isotopes**, presented by convention as **~3C/~2C**, is invariant as long as carbon is not lost. Numerous contributions have been made to our understanding of carbon isotope discrimination in plants since this area was extensively re-viewed by O'Leary . Here we discuss the physical and enzymatic bases **carbon isotope discrimination** during **photosynthesis**, noting how knowledge of discrimination can be used to provide additional insight into photosynthetic metabolism and the environmental influences on that process.

Isotopic composition and discrimination:

Definitions: Farquhar & Richards proposed that whole plant processes should analyzed in the same terms as chemical processes. From Equation 1 it is evident that this requires measurements of isotopic abundance of both source and product. For plants this means measuring **Ra** (isotopic abundance in the air) and **Rp** (isotopic abundance in the plant, where the plant can be considered the product referred to in Equation 1). For numerical convenience, instead of using the isotope effect **(a = Ra/gp),** Farquhar & Richards (39) proposed the use of **A**, the deviation of a from unity, as the measure of the carbon isotope discrimination by the plant.

$$\Delta = \alpha - 1 = \frac{R_a}{R_p} - 1.$$

The absolute isotopic composition of a sample is not easy to measure directly. Rather, the **mass spectrometer** measures the deviation of the isotopic com-position of the material from a standard.

$$\delta_p = \frac{R_p - R_s}{R_s} = \frac{R_p}{R_s} - 1$$

Environmental Effects on Carbon Isotope Discrimination:

Goudriaan & van Laar, K6rner et al, and Wong et al among the first to note a **strong correlation** between the photosynthetic rate and leaf conductance. This correlation was maintained over a wide variety of plant species and under a diversity of environmental treatments, implying some level of regulation between **COz** demand by the **chloroplasts** and Coz supply by **stomatal control**. If in fact there were no deviations from the slope of the photosynthesis-versus-conductance relationship and if the intercept were zero (as was the case in the original papers), then the intercellular **CO2 pressure (Pi)** of all plants would have been constant, dependent only **photosynthetic pathway**. This constancy was mistakenly suggested in at least one early review. Although a number of studies that followed showed significant tendency for photosynthesis and conductance to be correlated, many of these data sets exhibited some deviation from a linear relationship or a nonzero intercept. It is unfortunate that in the search for general patterns the variance in Pi was, for a time, ignored. When it was recognized that there was a fundamental relationship between A or 6p and Pi, more effort was put into documenting and understanding the isotopic variation at both the **environmental and genetic** (intra- and interspecific) levels. In the next sections, we describe what is known about the relationship between pi (as measured by isotope discrimination) and environmental parameters.

Water-Use Efficiency of C3 Species Transpiration Efficiency and Carbon Isotope Discrimination:

Measurements of A in C3 species may usefully contribute to the selection for transpiration efficiency--i.e, the amount of carbon biomass produced per unit water transpired by the crop.

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Stress Physiology

Stress' in plants can be defined as any external factor that negatively influences plant growth, productivity, reproductive capacity or survival. This includes a wide range of factors which can be broadly divided into two main categories: abiotic or environmental stress factors, and biotic or biological stress factors called stress physiology. And the physiological study of plants under stress is called as "**stress physiology**. "

Physiological Aspects of Air Pollution Stress in plants

Physiological Aspects of Air Pollution Stress in plants Responses of plants to air pollutants may vary widely and these variations can be caused by many factors, such as Differences in pollutant concentrations Distribution in time, The genetic origin, Physiological activity, Phonological stage, Nutritional status of plants as well as effects of various environmental factors.

Air pollutants:

Air pollutants Air pollutants affect plants worldwide (IUFRO 1993). These effects may be severe or subtle. Various air pollutants have been identified as phytotoxic agents. Phytotoxicity of sulfur dioxide (SO2) has been recognized for about a century. Effects of ozone (O3) for more than 30 years. Acidic precipitation for almost 20 years (LIKENS & al. 1979). Effects of elevated levels of nitrogen compounds (nitrogen oxides [NOX] and ammonia [NH3]) in the last decade (NIHLGARD 1985). Importance of other pollutants such as peroxyacetyl nitrate (PAN), fluorides or heavy metals has also been recognized.

How to determine effects of air pollutants on plants:

How to determine effects of air pollutants on plants under field conditions detection of physiological changes in plants and identification of their causes is difficult. Therefore visible symptoms of injury are most commonly used for detecting air pollution damage. However, changes in physiology of plants may occur before visible, morphological damage takes place.

Pollutant deposition to plants:

Pollutant deposition to plants Pollutants can be deposited to plants as 1- gases. 2- wet precipitation. 3- Particulate matter. Gaseous pollutants may be taken up by plants via 1- stomata or 2- cuticle. The effects of pollutants can be observed at various levels of biological Organization like: a- subcellular, b - cellular, c- plant organ, d- whole plant, e- plant population f- community.

Pollutant deposition to plants:

Pollutant deposition to plants the flux (act of moving) of pollutants from the atmosphere to plant cells follows the same pathway as carbon dioxide (CO2). Each pollutant has a different diffusion constant for movement through air, solubility constant for movement across Apo plastic water,

and hydrophobic or hydrophilic properties that affect the rate of transfer across cell walls and membranes. I nternal pollution dose: Concentrations of pollutants and the degree of stomatal opening determine the internal pollution dose and subsequent plant response.

Mechanisms of air pollution toxicity:

Mechanisms of air pollution toxicity once pollutants enter the plant cell a suite of primary and secondary metabolic reactions as well as defense reactions start taking place (BYTNEROWICZ & GRULKE 1992). Knowledge of the mechanisms of air pollution phytotoxicity is still incomplete and continues to develop. Toxic effects of O3 and peroxyacetyl nitrate PAN have been explained by the formation of highly phytotoxic free radicals in plant cells that may damage most of the cell components.

Mechanisms of air pollution toxicity:

Mechanisms of air pollution toxicity to some extent the phytotoxic effects of SO2 can also be explained by-free radical toxicity (WELLBURN 1988). Phytotoxicity of SO2 mainly results from accumulation of the immediate SO2 metabolite, sulfite (ZIEGLER 1973, MILLER & XERIKOS 1979). Secondary sulfur metabolites such as sulfoxides (R-SO-R1) and sulfones (R-SO2-R') are highly phytotoxic .The chloroplast is considered to be a primary site of SO2 toxicity.

Trees Damaged by Sulfur Emissions

Czech Republic

Effects of biotic and abiotic factors:

Effects of biotic and abiotic factors Biotic factors such as insects, various pathogens, mycorrhizal associations and genetic variation can influence physiological responses of plants to air pollutants. Secondary damage: Chronic exposure to air pollutants may also incline plants to bark beetle attacks, e.g. a situation commonly occurring in the ozone-stressed ponderosa pine trees in southern California (MILLER 1983). Plants can be affected by various stresses either simultaneously or sequentially. Some of the most important stresses which may interact with air pollutants include:

increasing concentrations of CO2, elevated ultraviolet B (UV-B) radiation, high nitrogen deposition, nutrient deficiencies, drought, or temperature extremes.

Effects of age and stage of plant development:

Effects of age and stage of plant development Very young seedlings usually are more sensitive to air pollution than mature trees. Seedlings at the cotyledon stage of development often grow at threshold levels of available carbohydrates, hormones, and mineral nutrients and are especially susceptible to air pollution. Despite the high sensitivity of young seedlings to air pollution, older plants near the air pollution point sources are often more injured than young trees. This is probably because the crown canopy serves as a filter and the young trees are less exposed to the pollutant. L ow stomatal conductance of the shaded, understory plants result in low rates of absorption of gaseous pollutants.

Effects of age and stage of plant development:

Effects of age and stage of plant development studied the effect of plant age on susceptibility of giant sequoias to elevated concentrations of ozone. The authors concluded that giant sequoia seedlings were sensitive to ozone until they were about 5 years old. It was studied that low stomatal conductance, high water use efficiency, and compact mesophyll cells all contributed to a natural ozone tolerance or defense, or both, in foliage of older plants.

Examples of physiological changes in trees caused by air pollution:

Examples of physiological changes in trees caused by air pollution In general, exposure to air pollutants changes the net carbon balance of a plant through effects on: 1- the light reactions or enzymatic functions, 2- Increased respiration from repair activities, or decreases in stomatal and mesophyll conductance's . In addition, effects of low doses of pollutants may be stimulatory, but pollutant doses over a certain threshold become deleterious. Changes in photosystems of plants caused by air pollution may be reflected by A- Deterioration of photosynthetic pigments B- Reduced efficiency of photochemical reactions. C- In many studies decreases of chlorophylls and carotenoids have been associated with pollutant exposure.

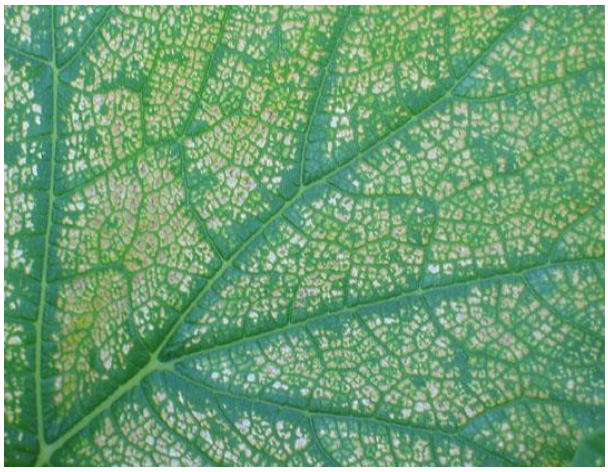
Examples of physiological changes in trees caused by air pollution:

Examples of physiological changes in trees caused by air pollution Chlorophyll fluorescence: also proved to be a good indicator of ozone effects. Under the conditions of a well-defined ozone stress ponderosa pine seedlings showed a wide range of responses: 1- Gradual increase of visible injury (chlorotic mottle) was accompanied by reduction of net photosynthesis , stomatal conductance , starch accumulations and pigment concentrations. 2- More pronounced reduction of net photosynthesis than stomatal conductance suggested that ozone injury to mesophyll, carboxylation, or excitation components of the CO2 diffusion pathway were greater than injury to the stomata. As a result of all these changes plants reduced their growth and biomass production.

Ozone injury to soybean foliage:

Acute sulfur dioxide injury to raspberry. The injury occurs between the veins and that the tissue nearest the vein remains healthy. Acute sulfur dioxide injury to raspberry. The injury occurs

between the veins and that the tissue nearest the vein remains healthy. Fluoride injury to plum foliage. The fluoride enters the leaf through the stomata and is moved to the margins where it accumulates and causes tissue injury. Note, the characteristic dark band separating the healthy (green) and injured (brown) tissues of affected leaves.



Ozone injury in a pumpkin leaf

Fluoride injury to plum foliage:

The fluoride enters the leaf through the stomata and is moved to the margins where it accumulates and causes tissue injury. Note, the characteristic dark band separating the healthy (green) and injured (brown) tissues of affected leaves. Severe ammonia injury to apple foliage and subsequent recovery through the production of new leaves. Severe ammonia injury to apple foliage and subsequent recovery through the production of new leaves. Cement-dust coating on apple leaves and fruit. The dust had no injurious effect on the foliage, but inhibited the action of a pre-harvest crop spray. Cement-dust coating on apple leaves and fruit. The dust had no injurious effect on the foliage, but inhibited the action of a pre-harvest crop spray.

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