Paper Code **18BBO25A - ALLIED PAPER - II PLANT STRUCTURE AND FUNCTIONS (For B. Sc. Zoology students)**

Unit - IV

Plant physiology –Absorption of water (active and passive). Types of transpiration. Stomatal movement. Photosynthesis: Light reaction and dark reaction (C_3 Cycle). Phytohormones – Auxins. Plant movements (phototropism and geotropism).

Mechanism of Absorption of Water:

In higher plants water is absorbed through root hairs which are in contact with soil water and form a root hair zone a little behind the root tips (Fig. 4.1). Root hairs are tubular hair like prolongations of the cells of the epidermal layer (when epidermis bears root hairs it is also known as piliferous layer) of the roots. The walls of root hairs are permeable and consist of pectic substances and cellulose which are strongly hydrophilic (water loving) in nature. Root hairs contain vacuoles filled with cell sap.

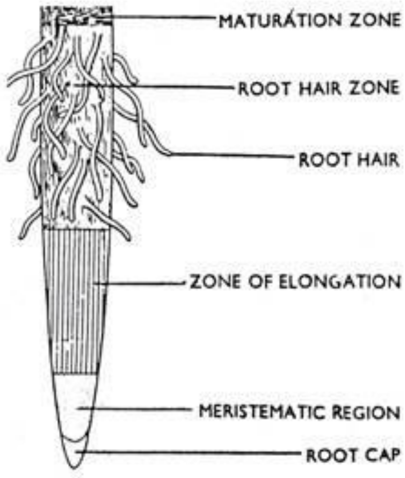


Fig. 4.1. Diagrammatic representation of a root tip showing root hair zone.

When roots elongate, the older hairs die and new root hairs are developed so that they are in contact with fresh supplies of water in the soil.

Mechanism of water absorption is of two types:

(1) Active Absorption of Water:

In this process the root cells play active role in the absorption of water and metabolic energy released through respiration is consumed.

Active absorption may be of two kinds:

(a) Osmotic absorption i.e., when water is absorbed from the soil into the xylem of the roots according to the osmotic gradient.

(b) Non-osmotic absorption i.e., when water is absorbed against the osmotic gradient.

(2) Passive Absorption of Water:

It is mainly due to transpiration, the root cells do not play active role and remain passive.

(1a) Active Osmotic Absorption of Water:

First step in the osmotic absorption of water is the imbibition of soil water by the hydrophilic cell walls of root hairs. Osmotic Pressure (O.P.) of the cell-sap of root hairs is usually higher than the O.P. of the soil water. Therefore, the Diffusion Pressure Deficit (D.P.D.) and the suction pressure in the root hairs become higher and water from the cell walls enters into them through plasma-membrane (semi-permeable) by osmotic diffusion. As a result, the O.P., suction pressure and D.P.D. of root hairs now become lower, while their turgor pressure is increased.

Now, the cortical cells adjacent to root hairs have higher O.P., suction pressure and D.P.D. in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from the root-hairs by osmotic diffusion.

In the same way, the water by cell to cell osmotic diffusion gradually reaches the innermost cortical cells and the endodermis. Osmotic diffusion of water into endodermis takes place through special thin walled passage cells because the other endodermal cells have casparian strips on their walls which are impervious to water (Fig. 4.2).

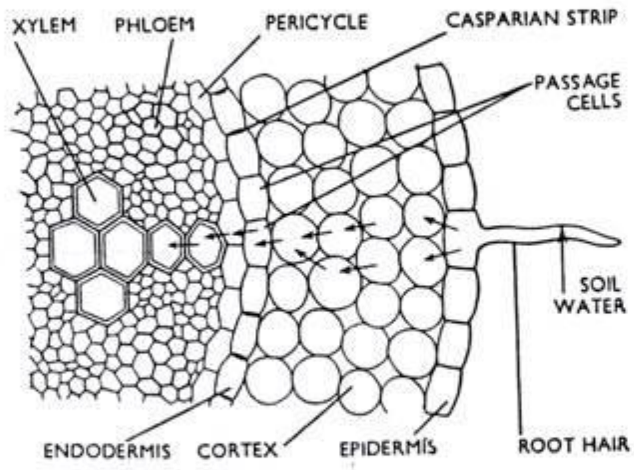


Fig. 4.2. A part of T.S. of typical dicot root. The arrows indicate the path of water.

Water from endodermal cells is drawn into the cells of pericycle by osmotic diffusion which now becomes turgid and their suction pressure is decreased. In the last step, water is drawn into xylem from turgid pericycle cells. (In roots the vascular bundles are radial and protoxylem elements are in contact with pericycle).

It is because in absence of turgor pressure of the xylem vessels (which are non-elastic), the suction pressure of xylem vessels becomes higher than the suction pressure of the cells of the pericycle. When water enters into xylem from pericycle, a pressure is developed in the xylem of roots which can raise the water to a certain height in the xylem. This pressure is called as root pressure.

(1b) Active Non-Osmotic Absorption of Water:

Sometimes, it has been observed that absorption of water takes place even when the O.P. of the soil water is higher than the O.P. of cell-sap. This type of absorption which is non-osmotic and against the osmotic gradient requires the expenditure of metabolic energy probably through respiration.

(i) The factors which inhibit respiration also decrease water absorption.

(ii) Poisons which retard metabolic activities of the root cells also retard water absorption.

(iii) Auxins (growth hormones) which increase metabolic activities of the cells stimulate absorption of water.

(2) Passive Absorption of Water:

Passive absorption of water takes place when rate of transpiration is usually high. Rapid evaporation of water from the leaves during transpiration creates a tension in water in the xylem of the leaves. This tension is transmitted to water in xylem of roots through the xylem of stem and the water rises upward to reach the transpiring surfaces.

As a result, soil water enters into the cortical cells through root hairs to reach the xylem of roots to maintain the supply of water. The force for this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

During absorption of water by roots, the flow of water from epidermis to endodermis may take place through three different pathways:

(i) Apoplastic pathway (cell walls and intercellular spaces),

(ii) Trans-membrane pathway (by crossing the plasma membranes) and

iii) Symplast pathway (through plasmodesmata).

The mechanism of water absorption described earlier, in-fact belongs to the second category. The relative importance of these three pathways in water absorption by roots is not clearly established. However, a combination of these three pathways is responsible for transport of water across the root.

External Factors Affecting Absorption of Water:

1. Available Soil Water:

Sufficient amount of water should be present in the soil in such form which can easily be absorbed by the plants. Usually the plants absorb capillary water i.e., water present in films in between soil particles. Other forms of water in the soil e.g., hygroscopic water, combined-water, gravitational water etc. are not easily available to plants. Increased amount of water in the soil beyond a certain limit results in poor aeration of the soil which retards metabolic activities of root cells like respiration and hence, the rate of water absorption is also retarded.

2. Concentration of the Soil Solution:

Increased conc. of soil solution (due to the presence of more salts in the soil) results in higher osmotic pressure. If the O.P. of soil solution will become higher than the O.P. of cell sap in root cells, the water absorption particularly the osmotic absorption of water will be greatly suppressed. Therefore, absorption of water is poor in alkaline soils and marshes.

3. Soil Air:

Absorption of water is retarded in poorly aerated soils because in such soils deficiency of O_1 and consequently the accumulation of CO_2 will retard the metabolic activities of the roots like respiration. This also inhibits rapid growth and elongation of the roots so that they are deprived of the fresh supply of water in the soil. Water logged soils are poorly aerated and hence, are physiologically dry. They are not good for absorption of water.

4. Soil Temperature:

Increase in soil temperature up to about 30°C favours water absorption. At higher temperatures water absorption is decreased. At low temp, also water absorption decreases so much so that at about 0°C it is almost checked.

This is probably because at low temp:

(i) The viscosity of water and protoplasm is increased,

(ii) Permeability of cell membranes is decreased,

(iii) Metabolic activities of root cells are decreased, and

(iv) Growth and elongation of roots are checked.

Relative Importance of Active and Passive Absorption of Water:

There are two views regarding the relative importance of active and passive absorption of water in the water economy of plants. Many workers in the past regarded the active absorption of water to be the main mechanism of water absorption and gave very little importance to the passive absorption. But according to Kramer (1969) the active absorption of water is of negligible importance in the water economy of most or perhaps all plants.

Ref: https://www.biologydiscussion.com/plants/movement-of-water/movement-of-water-in-plants-with-experiments/14226

STOMATA AND THEIR MECHANISM OF OPENING AND CLOSING

The epidermis of leaves contains pores that provide for the exchange of gases between the internal air spaces and the ambient environment. This minute opening is called stomata (singular stoma). Stomata occur in the epidermis of all parts of the shoot system, even in flower parts such as stamens and pistils. The opening, or stoma, is bordered by a pair of unique cells called **guard cells**. In most cases the guard cells are in turn surrounded by specialized, differentiated epidermal cells called **subsidiary cells**. Subsidiary cells provide a reservoir of water and ions that move into and out of the guard cells as they change shape during stomatal opening and closing. In dicot plants and non-grasses monocots, kidney-shape guard cells occur. Dumbbell shaped guard cells occur mainly in grasses. The stoma, together with its bordering guard cells and subsidiary cells, is referred to as the **stomatal complex**, or **stomatal apparatus**.

Guard cells are crucially important functional elements: they regulate stomatal apertures, thereby controlling rates of CO_2 uptake and water loss and hence influencing photosynthesis and water status of the plant.

Stomata are especially numerous on the lower epidermis of horizontally oriented leaves—an average of about 100 stomata per square millimetre, although the actual number varies widely—and in many species are located *only* on the lower surface. The lower epidermis of apple (*Malus sylvestris*) leaves, for example, has almost 400 stomata per square millimetre, whereas the upper epidermis has none. This adaptation reduces water loss, in part because stomata on the lower epidermis are shielded from direct sunlight and are therefore cooler than those on the upper epidermis.

Opening and closing of stomata

The alignment of **cellulose microfibrils**, which reinforce all plant cell walls and are an important determinant of cell shape, plays an essential role in the opening and closing of the stomatal pore. In ordinary cells having a cylindrical shape, cellulose microfibrils are oriented transversely to the long axis of the cell. As a result, the cell expands in the direction of its long axis because the cellulose reinforcement offers the least resistance at right angles to its orientation.

An Increase in Guard Cell Turgor Pressure Opens the Stomata

Environmental factors such as light intensity and quality, temperature, relative humidity, and intracellular CO2 concentrations are sensed by guard cells, and these signals are integrated into well-defined stomatal responses. If leaves kept in the dark are illuminated, the light stimulus is perceived by the guard cells as an opening signal, triggering a series of responses that result in opening of the stomatal pore.

Mechanism of Stomatal Opening and Closing

Opening and closing of stomata takes place due to changes in turgor of guard cells. Generally, stomata are open during the day and close at night. The actual mechanism responsible for entry and exit of water to and from the guard cells has been explained by several theories. These theories are described below:

1. **The Starch - Sugar interconversion Theory:** This theory was put forward by Steward in 1964. According to him, during day time phosphorylase enzyme converts the starch into sugar due to which osmotic potential of guard cell increased and allow the entry of water into the cell. During the night same reaction occur in reverse direction which closes the guard cell i.e. stomata is closed during night.

2. **Proton - Potassium Pump Hypothesis:** Levit in 1974 combined the points in Scarth's and Steward's hypothesis and gave a modified version of the mechanism of stomatal movement which was called the proton - potassium pump hypothesis.

   According to this hypothesis K^+ ions are transported into the guard cells in the presence of light. The sequence of events taking place are as follow:

   - Under the influence of light, protons formed by dissociation of malic acid move from cytoplasm in to the chloroplasts of guard cells.
   - To counter the exit of protons, K^+ ions enter the guard cells from the surrounding mesophyll cells.
   - K^+ ions react with the malate ions present in the guard cells to form potassium malate.

- Potassium malate causes increase in the osmotic potential of guard cells causing entry of water into the guard cells as a result of which the stoma opens.
- At night the dissociation of potassium malate takes place and K^+ ions exit out of guard cells causing loss of water from guard cells and so the stoma closes

3. **Synthesis of organic solutes:** blue light also stimulates the starch degradation and malate biosynthesis. Malate is an organic acid. In plants, malate is synthesized in the guard cell cytosol form the compound generated from the hydrolysis of starch. The enzyme phosphoenol pyruvate carboxylase (PEP carboxylase) binds carbon dioxide to PEP to produce oxaloacetate, which is then reduced to malate and stored in the vacuole.

In the presence of light, guard cells also perform photosynthesis. It increases the osmotically active solutes such as sucrose. Thus, in the presence of light, concentration of K^+, Cl^-, malate and sucrose increases. The increase in these osmotically active substances in the guard cells causes water to move passively into these cells and as their turgidity increase, the stomatal pore opens.

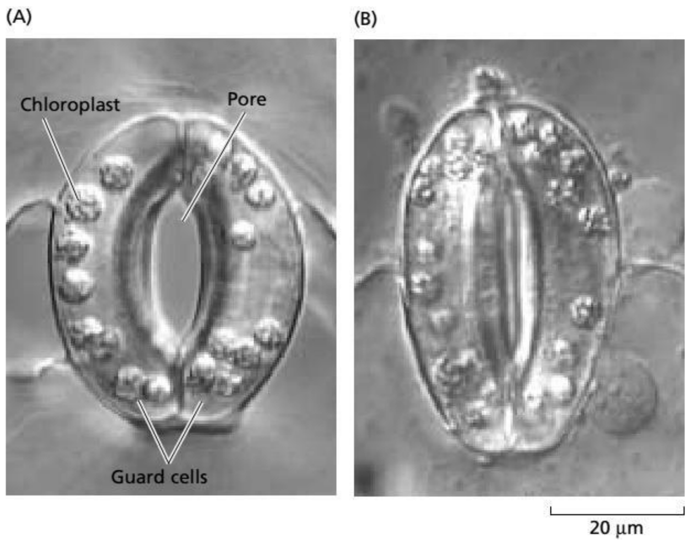
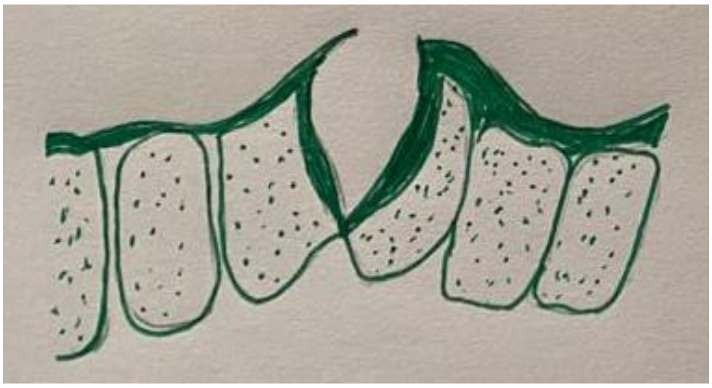
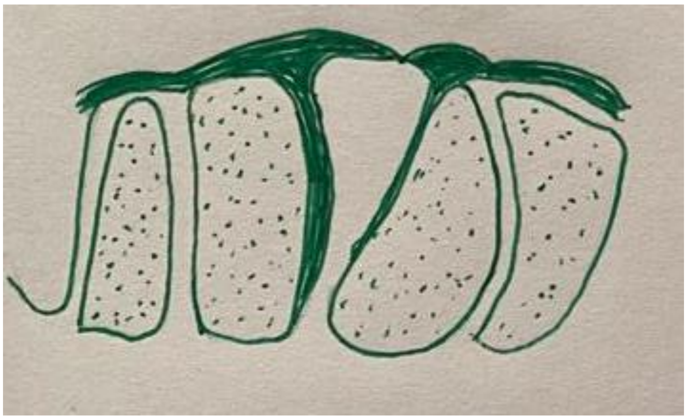


Fig. Light-stimulated stomatal opening in detached epidermis of *Vicia faba*. (A) Open, light-treated stoma. (B) The dark treated, closed state of stomata. Stomatal opening is quantified by microscopic measurement of the width of the stomatal pore.

Opening of Stomata



Closing of Stomata



06. TRANSPIRATION

Although large quantities of water are absorbed by plant from the soil but only a small amount of it is utilized. The excess of water is lost from the aerial parts of plants in the form of water vapours. This is called as transpiration.

Transpiration is of three types

1. Stomatal transpiration

Most of the transpiration takes place through stomata. Stomata are usually confined in more numbers on the lower sides of the leaves. In monocots. Eg. Grasses they are equally distributed on both sides. While in aquatic plants with floating leaves they are present on the upper surface.

2. Cuticular transpiration

Cuticle is impervious to water, even though, some water may be lost through it. It may contribute a maximum of about 10% of the total transpiration.

3. Lenticular transpiration

Some water may be lost by woody stems through lenticells which is called as lenticular transpiration.

Mechanism of stomatal transpiration

The mechanism of stomatal transpiration which takes place during the day time can be studied in three steps.

i. Osmotic diffusion of water in the leaf from xylem to intercellular space above the stomata through the mesophyll cells.

ii. Opening and closing of stomata (stomatal movement)

iii. Simple diffusion of water vapours from intercellular spaces to other atmosphere through stomata.

- Inside the leaf the mesophyll cells are in contact
- With xylem, and on the other hand with intercellular space above the stomata

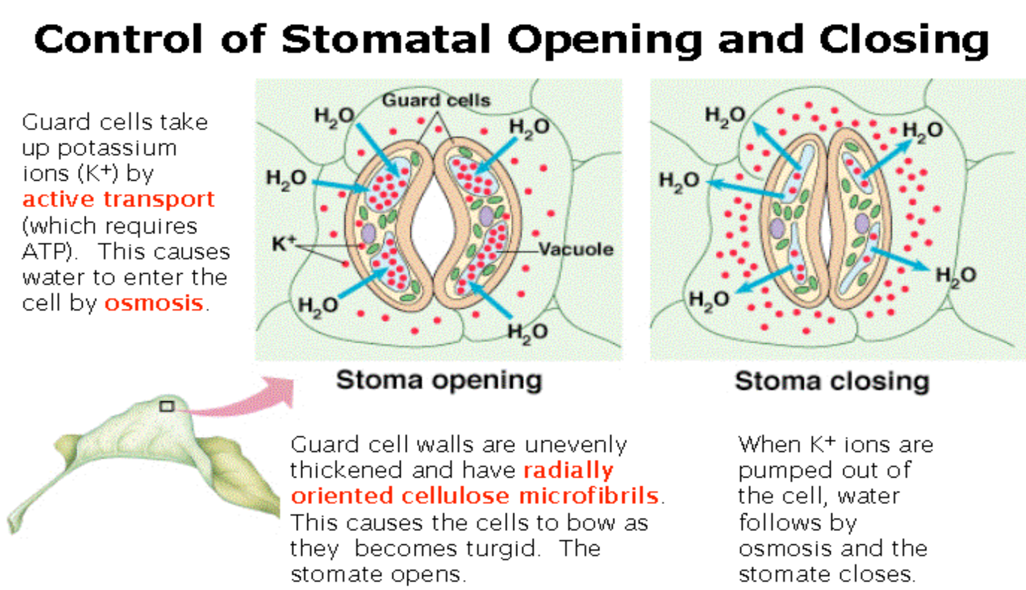
- ♦ When mesophyll cells draw water from the xylem they become turgid and their diffusion pressure deficit (DPD) and osmotic pressure (OP) decreases with the result that they release water in the form of vapour in intercellular spaces close to stomata by osmotic diffusion. Now in turn, the O.P and D.P.D of mesophyll cells become higher and hence, they draw water form xylem by osmotic diffusion.

Opening and closing of stomata (Stomatal movement)

The stomata are easily recognized from the surrounding epidermal cells by their peculiar shape. The epidermal cells that immediately surround the stomata may be similar to other epidermal cells or may be different and specialized. In the latter case, they are called as subsidiary cells.

The guard cells differ from other epidermal cells also in containing chloroplasts and peculiar thickening on their adjacent surface (in closed stomata) or on surfaces.

Consequent to an increase in the osmotic pressure (OP) and diffusion pressure deficit (DPD) of the guard cells (which is due to accumulation of osmotically active substances), osmotic diffusion of water from surrounding epidermal cells and mesophyll



cells into guard cells follows. This increase the turgor pressure (TP) of the guard cells and they become turgid. The guard cells swell, increase in length and their adjacent thickened surfaces starch forming a pore and thus the stomata open.

On the other hand, when OP and DPD of guard cells decrease (due to depletion of osmotically active substances) relative to surrounding epidermal and mesophyll cells, water is released back into the latter by osmotic diffusion and the guard cells become flaccid. The thickened surfaces of the guard cells come close to each other, thereby closing the stomatal pore and stomata.

Osmotic diffusion of water into guard cells occur when their osmotic pressure increases and water potential decreases (i.e become more negative) related to those of surrounding epidermal and mesophyll cells. The guard cells become flaccid when their osmotic pressure decreases relative to the surrounding cells (Movement of water takes place from a region of higher water potential to a region of lower water potential.

These may be several different agents or mechanisms which control stomatal movements.

Hydrolysis of starch into sugars in guard cells

Synthesis of sugars or organic acids in them

The active pumping of K^+ ions in the guard.

1. Hydrolysis of starch into sugars in guard cells

Starch – sugar Inter conversion theory

This classical theory is based on the effect of pH on starch phosphorylase enzyme which reversibly catalyses the conversion of starch + inorganic phosphate into glucose -1 phosphate.

During the day, pH is guard cells in high. This favours hydrolysis of starch (which is insoluble into glucose -1- phosphate (which is soluble) so that osmotic pressure is increased in guard cells.

Consequently water enters, into the guard cells by osmotic diffusion from the surrounding epidermal and mesophyll cells. Guard cells become turgid and the stomata open.

During dark, reverse process occurs. Glucose 1- phosphate is converted back into starch in the guard cells thereby decreasing osmotic pressure. The guard cell release water, become flaccid and stomata become closed.

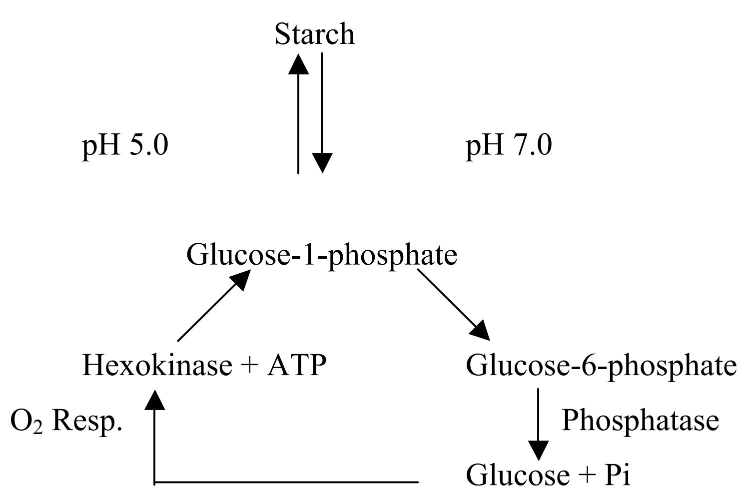
$$\underset{\text{(Insoluble)}}{\text{Starch}} \quad + \text{Pi} \; \underset{\text{Dark low pH}}{\overset{\text{Light high pH}}{\rightleftharpoons}} \; \underset{\text{(Soluble)}}{\text{Glucose-1-phosphate}}$$

According to Steward 91964), the conversion of starch and inorganic phosphate into glucose-1-phosphate does not cause any appreciable change in the osmotic pressure because the inorganic phosphate and glucose-1-phosphate are equally active osmotically.

In this scheme he has suggested that,

Glucose-1-phosphate should be further converted into glucose and inorganic phosphate for the opening of stomata.

Metabolic energy in the form of ATP would be required for the closing of stomata which probably comes through respiration.



2. Synthesis of sugars or organic acids in Guard cells

During day light photosynthesis occurs in guard cells as they contain chloroplast. The soluble sugars formed in this process may contribute in increasing the osmotic potential of guard cells and hence resulting in stomatal opening. However, very small amounts of soluble sugars (osmotically active) have been extracted from the guard cells which are insufficient to affect water potential.

As a result of photosynthesis CO_2 concentration in guard cells decreases which leads to increased pH up of organic acids, chiefly malic acid during this period in guard cells. The formation of malic acid would produce proton that could operate in an ATP-driven proton K^+ exchange pump moving protons into the adjacent epidermal cells and K ions into guard cells and thus may contribute in increasing the osmotic pressure of the guard cells and leading to stomatal opening.

Reverse process would occur in darkness.

3. ATP –Driven proton (H^+) – K exchange pump mechanism in Guard cells

According to this mechanism, there is accumulation of K^+ ions in the guard cells during day light period. The protons (H^+) are 'pumped out' from the guard cells into the adjacent epidermal cells and in exchange K^+ ions are mediated through ATP and thus are an active process. ATP is generated in non-cyclic photophosphorylation in photosynthesis in the guard cells. The ATP required in ion exchange process may also come through respiration.

The accumulation of K ion is sufficient enough to significantly decrease the water potential of guard cells during day light. Consequently, water enters into them from the adjacent epidermal and mesophyll cells thereby increasing their turgor pressure and opening the stomatal pore.

Reverse situation prevails during dark when stomata are closed. There is no accumulation of 'K' in g cells in dark.

(iii) The last step in the mechanism of transpiration is the simple diffusion of water vapours from the intercellular spaces to the atmosphere through open stomata. This is because the intercellular spaces are more saturated with moisture is comparison to the outer atmosphere in the vicinity of stomata.

Significance of Transpiration

Plants waste much of their energy in absorbing large quantities of water and most of which is ultimately lost through transpiration.

Some people thin that – Transpiration as advantageous to plant.

Others regard it as an unavoidable process which is rather harmful.

Advances of transpiration

1. Role of movement of water

Plays an important role in upward movement of water i.e Ascent of sap in plants.

2. Role in absorption and translocation of mineral salts

Absorption of water and mineral salts are entirely independent process. Therefore transpiration has nothing to do with the absorption of mineral salts.

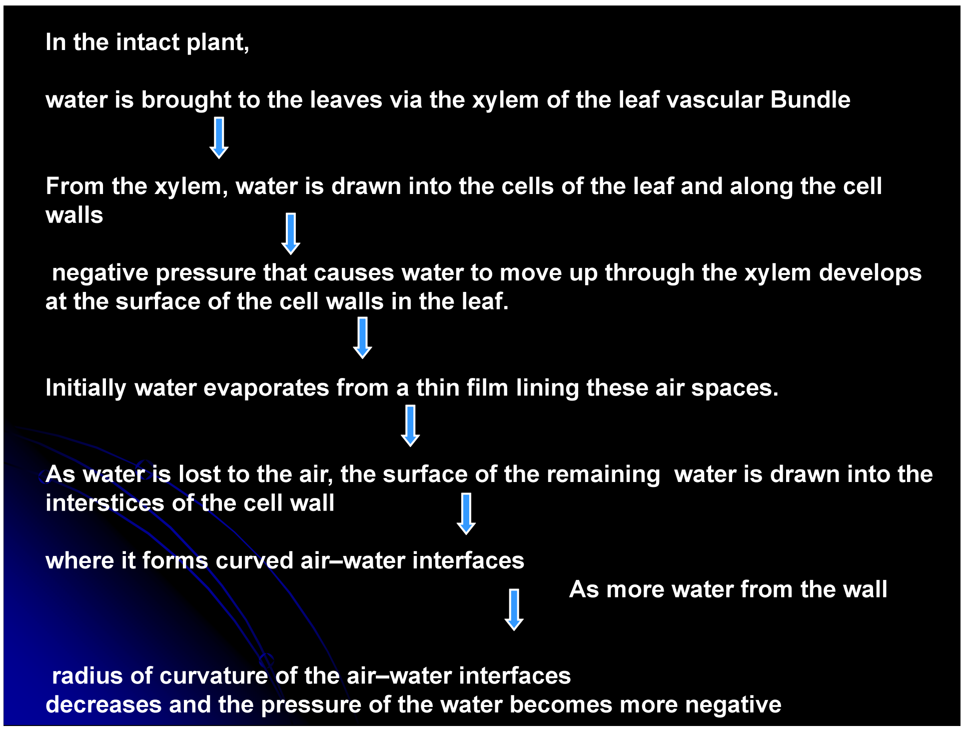
However, once mineral salts have been absorbed by the plants, their further translocation and distribution may be facilitated by transpiration through translocation of water in the xylem elements.

Transpiration from the leaf regulates by

1. **difference in water vapor concentration between the leaf air spaces and the external air**
2. **diffusional resistance (*r*) of this pathway**
3. **leaf stomatal resistance (*r*s)**
4. **leaf boundary layer resistance**
5. **control of stomatal apertures by the guard cells**

3. Role of regulation of temperature

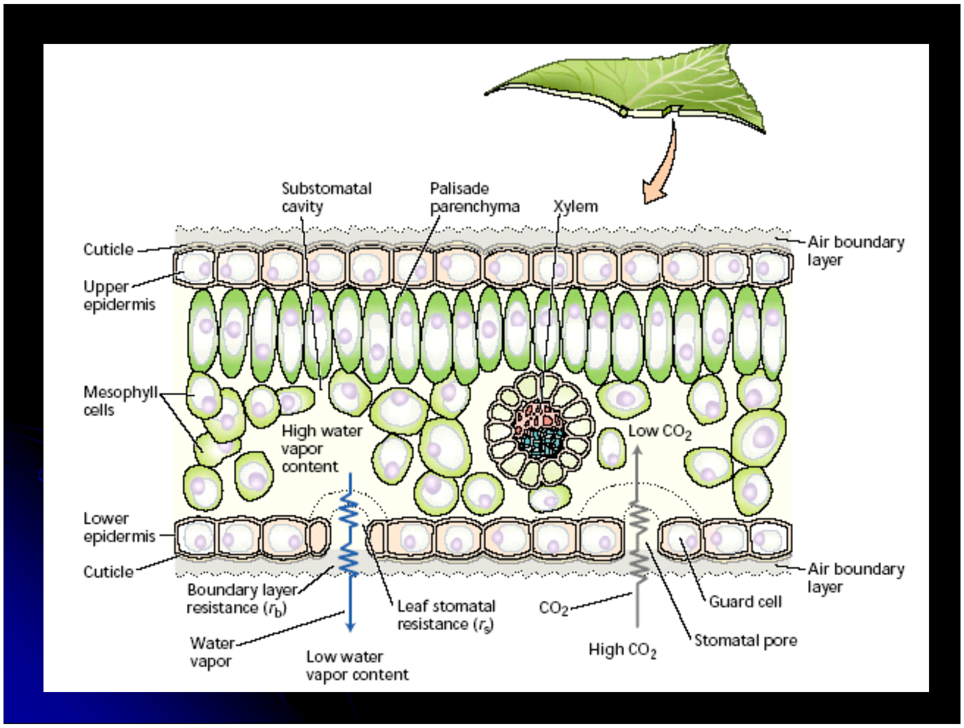
Some light energy absorbed by the leaves is utilized in photosynthesis; rest is converted into heat energy which raises their temperature. Transpiration plays an important role in controlling the temperature of the plants. Rapid evaporation of water from the aerial parts of the plant through transpiration brings down their temperature and thus prevents them from excessive heating.



Transpiration as a necessary evil

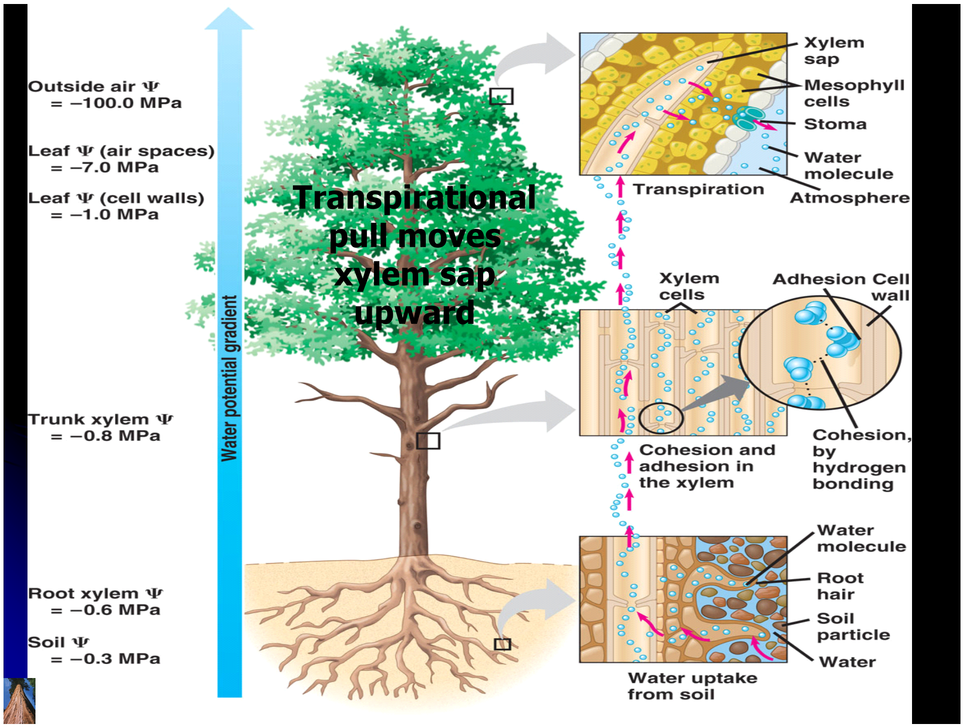
1. When the rate of transpiration is high and soil is deficient in water, an internal water deficit is created in the plants which may affect metabolic processes

2. Many xerophytes have to develop structural modification and adaptation to check transpiration.



3. Deciduous tress has to shed their leaves during autumn to check loss of water.

But, in spite of the various disadvantages, the plants cannot avoid transpiration due to their peculiar internal structure particularly those of leaves. Their internal structure although basically mean for gaseous exchange for respiration, P.S. etc. is such that it cannot check the evaporation of water. Therefore, many workers like Curtis (1926) have called transpiration as necessary evil.



Factors affecting transpiration rate

A. External factors

1. Atmospheric humidity

In humid atmosphere, (when relative humidity) is high), the rate of transpiration decreases. It is because atmosphere is more saturated with moisture and retards the diffusion of water vapour from the intercellular spaces of the leaves to the outer atmosphere through stomata.

In dry atmosphere, the RH is low and the air is not saturated with moisture and hence, the rate of transpiration increases.

2. Temperature

An increase in temperature brings about an increase in the rate of transpiration by

1. lowering the relative humidity
2. Opening of stomata widely

3. Wind

i. When wind is stagnant (not blowing), the rate of transpiration remains normal

ii. When the wind is blowing gently, the rate of transpiration increases because it removes moisture from the vicinity of the transpiration parts of the plant thus facilitating the diffusion of waster vapour from the intercellular spaces of the leaves to the outer atmosphere though stomata.

iii. When the wind is blowing violently, the rate of transpiration decreased because it creates hindrance in the outward diffusion of water vapours from the transpiring part and it may also close the stomata.

4. Light

Light increases the rate of transpiration because,

In light stomata open; It increases the temperature

In dark, due to closure of stomata, the stomatal transpiration is almost stopped.

5. Available soil water

Rate of transpiration will decrease if there is not enough water in the soil in such from which can be easily absorbed by the roots.

6. CO_2

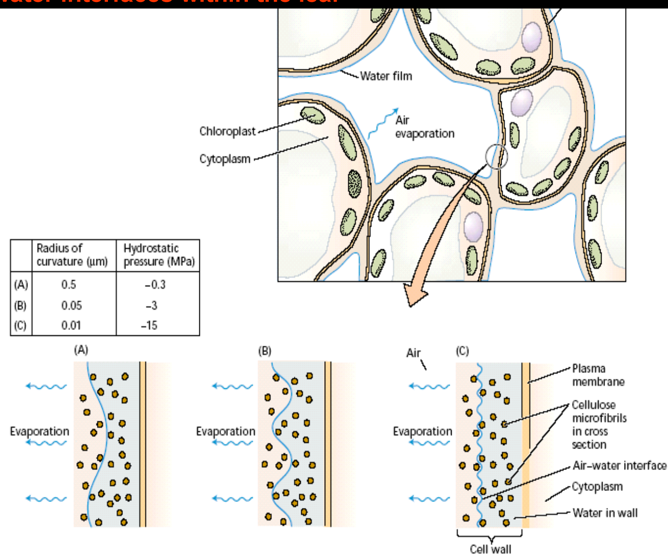
An increase in CO_2 concentration in the atmosphere (Ova the usual concentration) more so inside the leaf, leads towards stomatal closure and hence it retards transpiration.

B. Internal factors

1. Internal water conditions

It is very essential for transpiration. Deficiency of water in the plants will result in decrease of transpiration rate. Increase rate of transpiration containing for longer periods often create internal water deficit in plants because absorption of water does not keep pace with it.

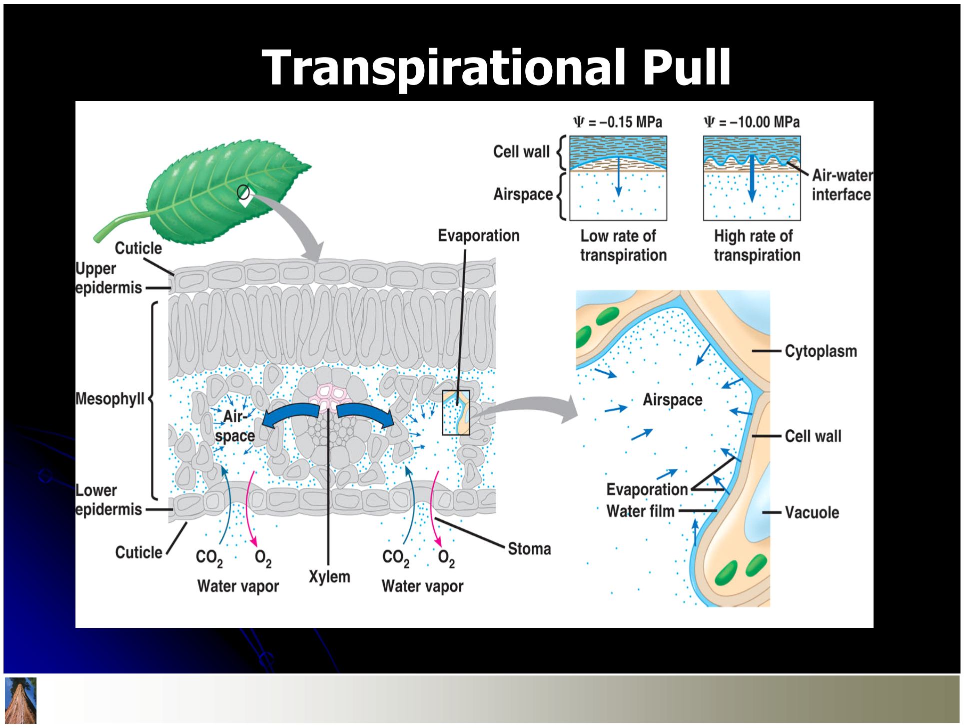
Motive force for xylem transport is generated at the air–water interfaces within the leaf



	Radius of curvature (μm)	Hydrostatic pressure (MPa)
(A)	0.5	−0.3
(B)	0.05	−3
(C)	0.01	−15

2. Structural features

The number, size, position and the movement of stomata affect rate of transpiration. In dark stomata are closed and stomatal transpiration is checked. Sunken stomata help in reducing the rate of stomatal transpiration. In xerophytes the leaves are reduced in size or may even fall to check transpiration. Thick cuticle on presence of wax coating on exposed parts reduces cuticles transpiration.

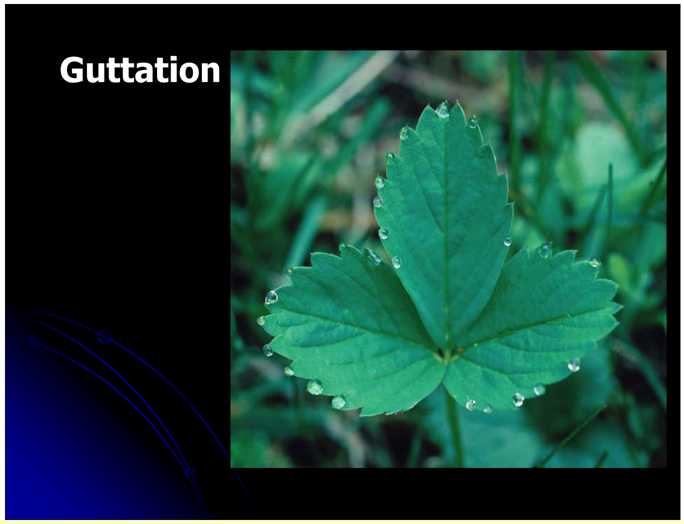


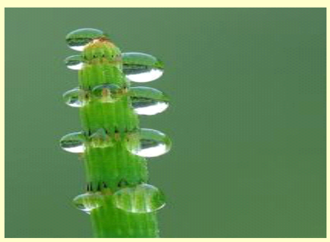
Antitranspirants

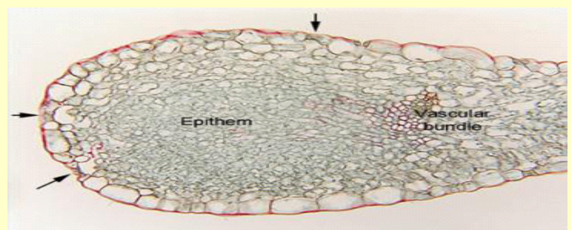
A number of substances are known which when applied to the plants retard their transpiration. Such substances are called as antitranspirants. Some examples of antitranspirants are colourless plastics, silicone, oils, low viscosity waxes, phenyl mercuric acetate, abscisic acid, CO_2, etc. Colourless plastic, silicone oils and low viscosity waxes belong to one group as these are sprayed on the leaves, form after film which is permeable to O_2 and CO_2 but not to water.

Fungicide phenyl mercuric acetate, when applied in low concentration (10^{-4} m), it exercised a very little toxic effect on leaves and resulted in partial closure of stomatal pores for a period of two weeks. Similarly ABA a plant hormone also induces stomatal closure. CO_2 is an effective antitranspirants. A little rise in CO_2 concentration from the natural 0.03% to 0.05% induces partial closure of stomata. Its higher concentration cannot be used which results in complete closure of stomata affecting adversely the photosynthesis and respiration.

GUTTATION







In some plants such as garden nasturtium, tomato, colocasia etc, water drops ooze out from the uninjured margins of the leaves where a main vein ends. This is called as guttation and takes place usually early in the morning when the rate of absorption and root pressure are high while the transpiration is very low.

The phenomenon of guttation is associated with the presence of special types of stomata at the margins of the leaves which are called as **water stomata or hydathodes**. Each hydathode consists of a water pore which remains permanently open.

Below this there is a small cavity followed by a loose tissue called as epithem. This epithem is in close association with the ends of the vascular elements of veins. Under high root pressure the water is given to the epithem by the xylem of the veins. From epithem water is released into the cavity. When this cavity is completely filled with watery solution, the later begins to ooze out in the form of watery drops through the water pore.

Difference between transpiration and Guttation

Transpiration	Guttation
1. Water is lost from aerial parts of plants in the form of invisible water vapours	Watery solution oozes out from uninjured margins of aerial leaves only
2. Transpiration occurs mostly through stomata. It may also takes place through cuticle and lenticels	It occurs only through hydathodes (water stomata)
3. It takes place throughout the day, its rate being maximum at noon.	It takes place only early in the morning when root pressure and the rate of water absorption are higher

Photosynthesis

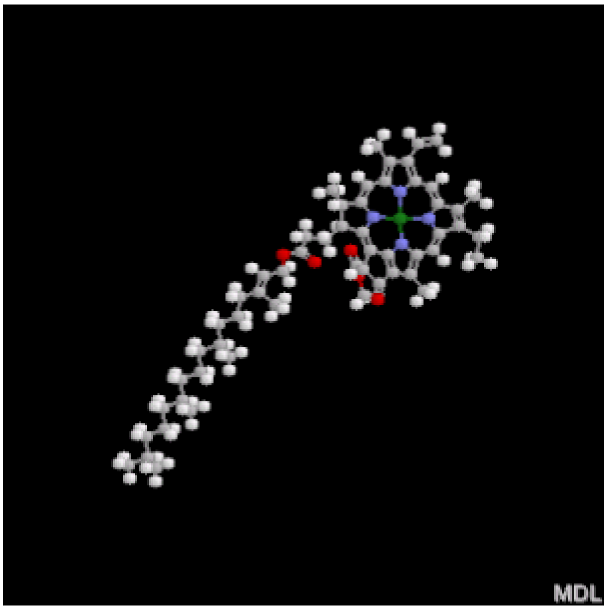
Photosynthesis is the process by which plants, some bacteria and some protistans use the energy from sunlight to produce glucose from carbon dioxide and water. This glucose can be converted into pyruvate which releases adenosine triphosphate (ATP) by cellular respiration. Oxygen is also formed.

Photosynthesis may be summarised by the word equation:

$$\text{carbon dioxide + water} \xrightarrow[\text{chlorophyll}]{\text{sunlight}} \text{glucose + oxygen}$$

The conversion of usable sunlight energy into chemical energy is associated with the action of the green pigment chlorophyll.

Chlorophyll is a complex molecule. Several modifications of chlorophyll occur among plants and other photosynthetic organisms. All photosynthetic organisms have chlorophyll a. Accessory pigments absorb energy that chlorophyll a does not absorb. Accessory pigments include chlorophyll b (also c, d, and e in algae and protistans), xanthophylls, and carotenoids (such as beta-carotene). Chlorophyll a absorbs its energy from the violet-blue and reddish orange-red wavelengths, and little from the intermediate (green-yellow-orange) wavelengths.



Chlorophyll

All chlorophylls have:

- a lipid-soluble hydrocarbon tail ($C_{20}H_{39}$ -)
- a flat hydrophilic head with a magnesium ion at its centre; different chlorophylls have different side-groups on the head

The tail and head are linked by an ester bond.

Leaves and leaf structure

Plants are the only photosynthetic organisms to have leaves (and not all plants have leaves). A leaf may be viewed as a solar collector crammed full of photosynthetic cells.

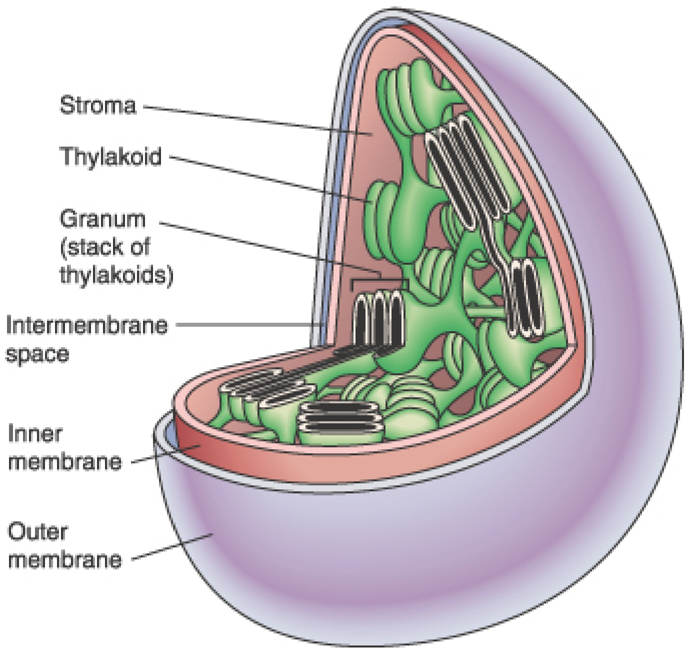
The raw materials of photosynthesis, water and carbon dioxide, enter the cells of the leaf, and the products of photosynthesis, sugar and oxygen, leave the leaf.

Water enters the root and is transported up to the leaves through specialized plant cells known as xylem vessels. Land plants must guard against drying out and so have evolved specialized structures known as **stomata** to allow gas to enter and leave the leaf. Carbon dioxide cannot pass through the protective waxy layer covering the leaf (**cuticle**), but it can enter the leaf through the **stoma** (the singular of stomata), flanked by two guard cells. Likewise, oxygen produced during photosynthesis can only pass out of the leaf through the opened stomata. Unfortunately for the plant, while these gases are moving between the inside and outside of the leaf, a great deal of water is also lost. Cottonwood trees, for example, will lose 100 gallons (about 450 dm^3) of water per hour during hot desert days.

The structure of the chloroplast and photosynthetic membranes

The thylakoid is the structural unit of photosynthesis. Both photosynthetic prokaryotes and eukaryotes have these flattened sacs/vesicles containing photosynthetic chemicals. Only eukaryotes have chloroplasts with a surrounding membrane.

Thylakoids are stacked like pancakes in stacks known collectively as grana. The areas between grana are referred to as stroma. While the mitochondrion has two membrane systems, the chloroplast has three, forming three compartments.



Structure of a chloroplast

Stages of photosynthesis

When chlorophyll a absorbs light energy, an electron gains energy and is 'excited'. The excited electron is transferred to another molecule (called a primary electron acceptor). The chlorophyll molecule is oxidized (loss of electron) and has a positive charge. Photoactivation of chlorophyll a results in the splitting of water molecules and the transfer of energy to ATP and reduced nicotinamide adenine dinucleotide phosphate (NADP).

The chemical reactions involved include:

- condensation reactions - responsible for water molecules splitting out, including phosphorylation (the addition of a phosphate group to an organic compound)
- oxidation/reduction (redox) reactions involving electron transfer

Photosynthesis is a two stage process.

The **light dependent reactions**, a light-dependent series of reactions which occur in the **grana**, and require the direct energy of light to make energy-carrier molecules that are used in the second process:

- light energy is trapped by chlorophyll to make ATP (photophosphorylation)
- at the same time water is split into oxygen, hydrogen ions and free electrons:

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

- the electrons then react with a carrier molecule nicotinamide adenine dinucleotide phosphate (NADP), changing it from its oxidised state ($NADP^+$) to its reduced state (NADPH):

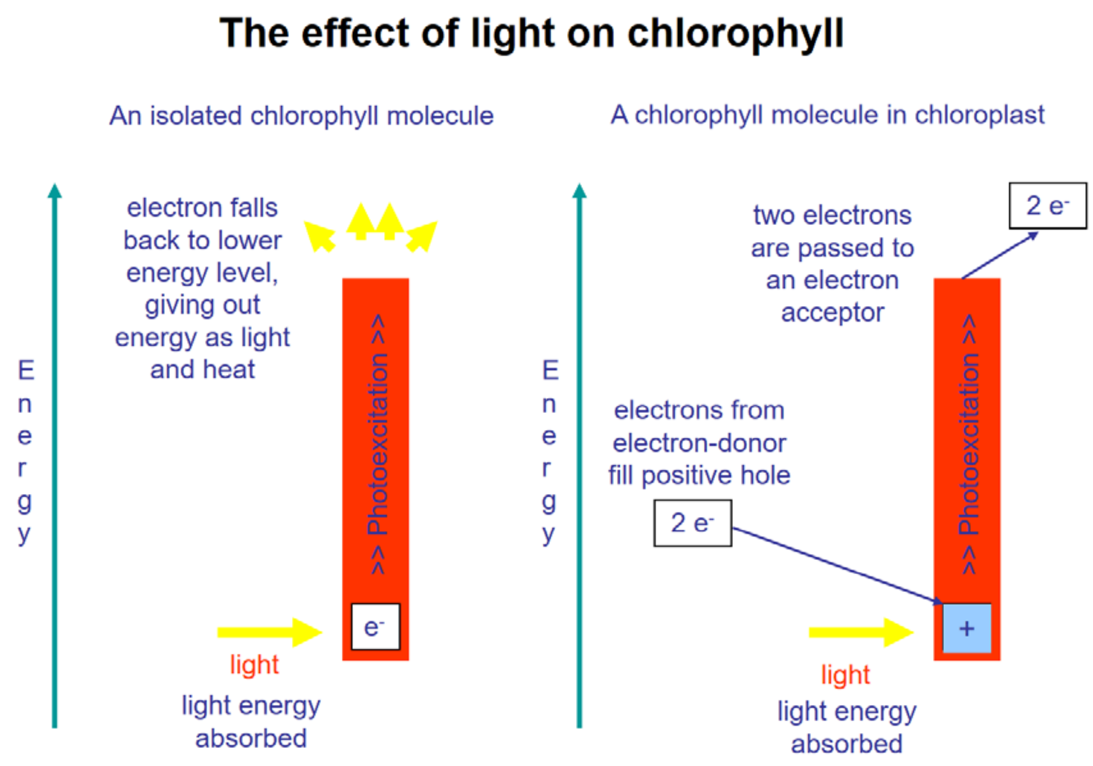
  $NADP^+ + 2e^- + 2H^+ \rightarrow NADPH + H^+$

The **light-independent reactions**, a light-independent series of reactions which occur in the stroma of the chloroplasts, when the products of the light reaction, ATP and NADPH, are used to make carbohydrates from carbon dioxide (reduction); initially glyceraldehyde 3-phosphate (a 3-carbon atom molecule) is formed.

The light-dependent reactions

When light energy is absorbed by a chlorophyll molecule its electrons gain energy and move to higher energy levels in the molecule (photoexcitation). Sufficient energy ionises the molecule, with the electron being 'freed' leaving a positively charged chlorophyll ion. This is called photoionisation.

In whole chloroplasts each chlorophyll molecule is associated with an **electron acceptor** and an **electron donor**. These three molecules make up the core of a **photosystem**. Two electrons from a photoionised chlorophyll molecule are transferred to the electron acceptor. The positively charged chlorophyll ion then takes a pair of electrons from a neighbouring electron donor such as water.



An electron transfer system (a series of chemical reactions) carries the two electrons to and fro across the thylakoid membrane. The energy to drive these processes comes from two photosystems:

- Photosystem II (PSII) (P680)
- Photosystem I (PSI) (P700)

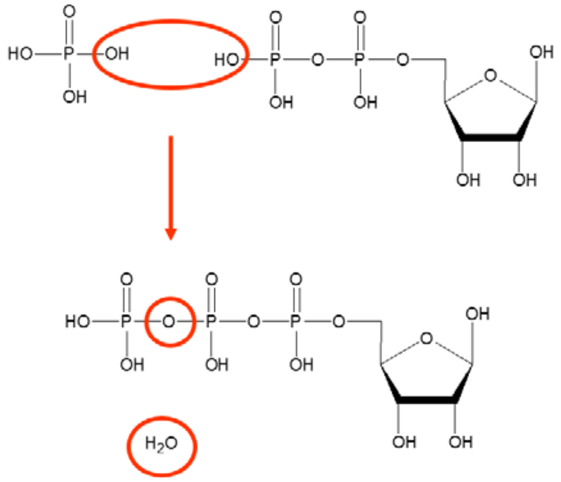
It may seem confusing, but PSII occurs *before* PSI. It is named because it was the second to be discovered and hence named second.

The energy changes accompanying the two sets of changes make a Z shape when drawn out. This is why the electron transfer process is sometimes called the Z scheme. Key to the scheme is that sufficient energy is released during electron transfer to enable ATP to be made from ADP and phosphate.

Synthesis of ATP from ADP

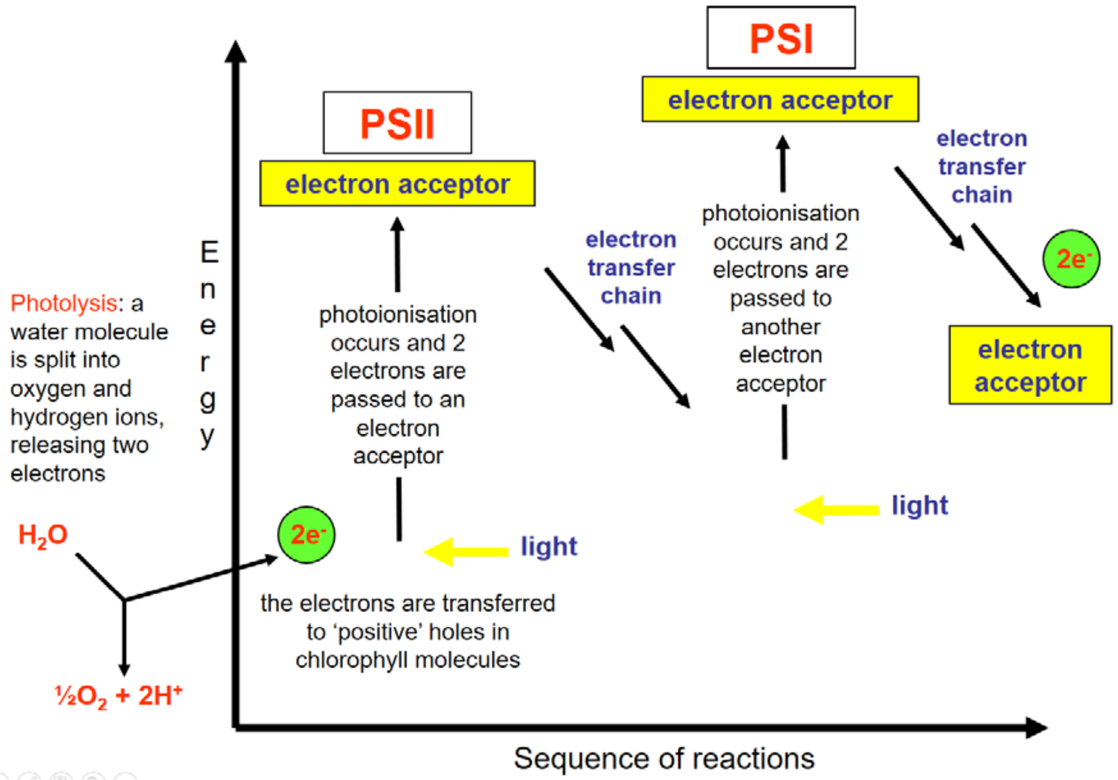
Phosphoric acid and ADP undergo a condensation reaction

Water is eliminated and ATP is formed



A condensation reaction has led to phosphorylation.

PSII and PSI: the Z scheme

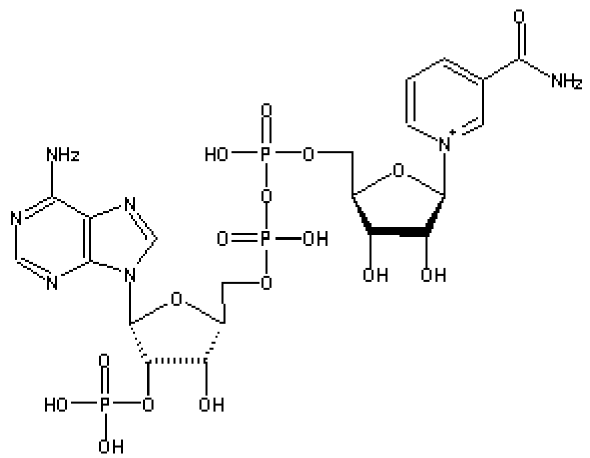


Non-cyclic phosphorylation (the Z scheme)

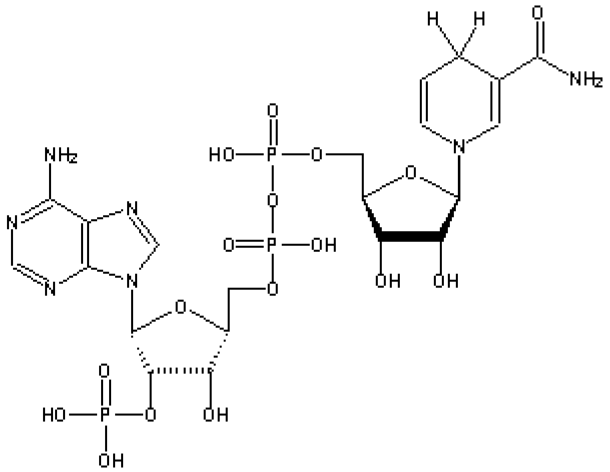
Both adenosine triphosphate (ATP) and NADPH are produced.

In the first photosystem (Photosystem II, PSII):

- photoionisation of chlorophyll transfers excited electrons to an electron acceptor
- photolysis of water (an electron donor) produces oxygen molecules, hydrogen ions and electrons, and the latter are transferred to the positively-charged chlorophyll
- the electron acceptor passes the electrons to the electron transport chain; the final acceptor is photosystem PSI
- further absorbed light energy increases the energy of the electrons, sufficient for the reduction of $NADP^+$ to NADPH



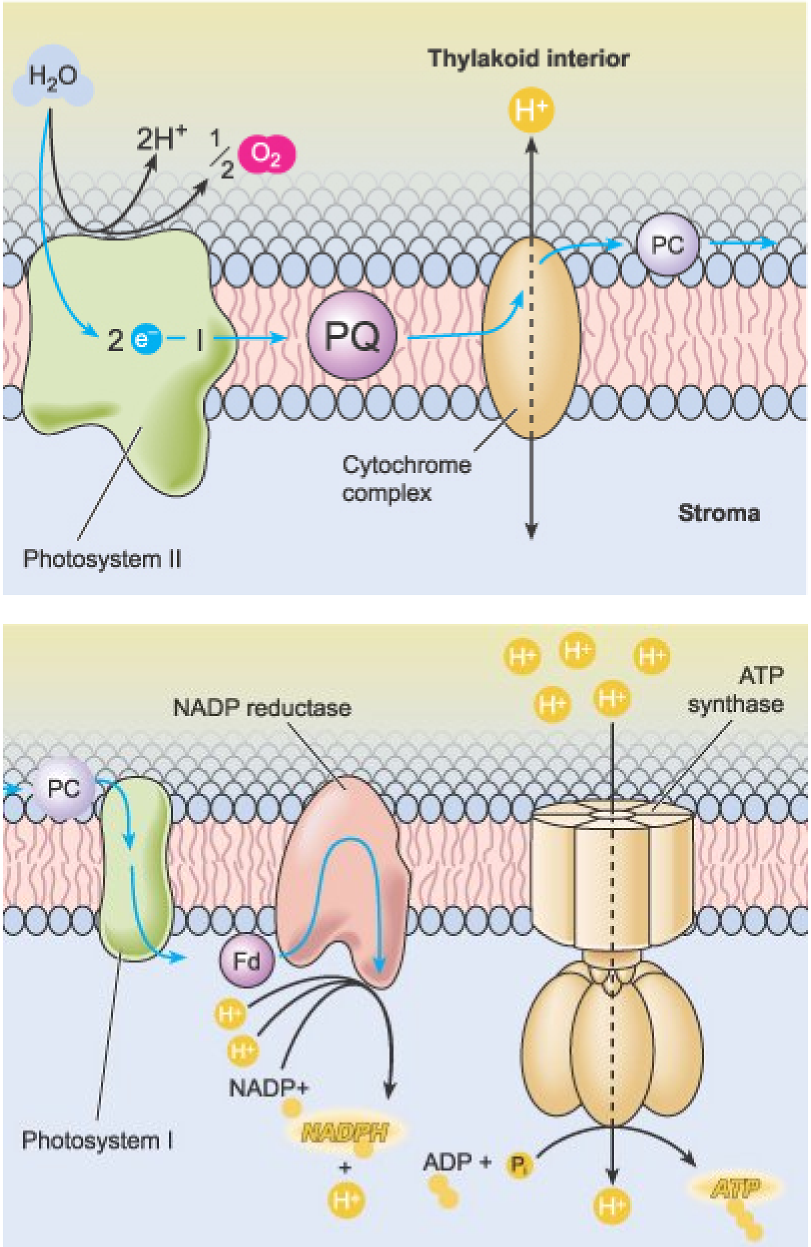
The oxidised form of nicotinamide adenine dinucleotide phosphate ($NADP^+$)



The reduced form of nicotinamide adenine dinucleotide phosphate (NADPH)

Chemiosmosis and ATP synthesis

The components of non-cyclic phosphorylation are found in the thylakoid membranes of the chloroplast. Electrons passing through the transport chain provide energy to pump H^+ ions from the stroma, across the thylakoid membrane into the thylakoid compartment. H^+ ions are more concentrated in the thylakoid compartment than in the stroma. We say there is an electrochemical gradient. H^+ ions diffuse from the high to the low regions of concentration. This drives the production of ATP.



Chemiosmosis as it operates in photophosphorylation within a chloroplast

Cyclic phosphorylation

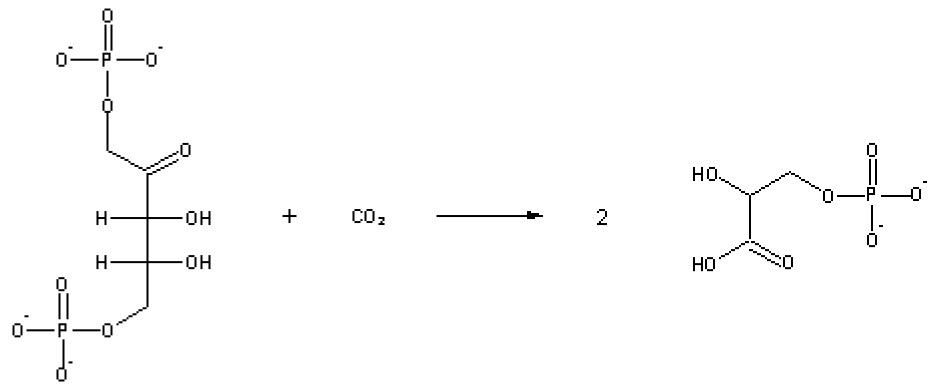
The net effect of non-cyclic phosphorylation is to pass electrons from water to NADP. Energy released enables the production of ATP. But much more ATP is needed to drive the light-independent reactions.

This extra energy is obtained from cyclic phosphorylation. This involves only Photosystem I which generates excited electrons. These are transferred to the electron transport chain between PSII and PSI, rather than to $NADP^+$ and so no NADPH is formed. The cycle is completed by electrons being transported back to PSI by the electron transport system.

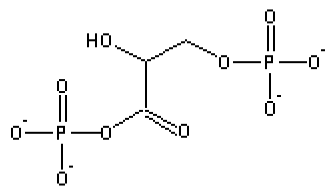
The light-independent reactions

In the Light-Independent Process (the Dark reaction) carbon dioxide from the atmosphere (or water for aquatic/marine organisms) is captured and modified by the addition of hydrogen to form carbohydrates. The incorporation of carbon dioxide into organic compounds is known as **carbon fixation**. The energy for this comes from the first phase of the photosynthetic process. Living systems cannot directly utilize light energy, but can, through a complicated series of reactions, convert it into C-C bond energy that can be released by glycolysis and other metabolic processes.

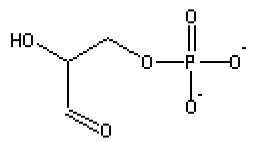
Carbon dioxide combines with a five-carbon sugar, ribulose 1,5-biphosphate (RuBP). A six-carbon sugar forms but is unstable. Each molecule breaks down to form two glycerate 3-phosphate (GP) molecules.



These glycerate 3-phosphate (GP) molecules are phosphorylated by ATP into glycerate diphosphate molecules.

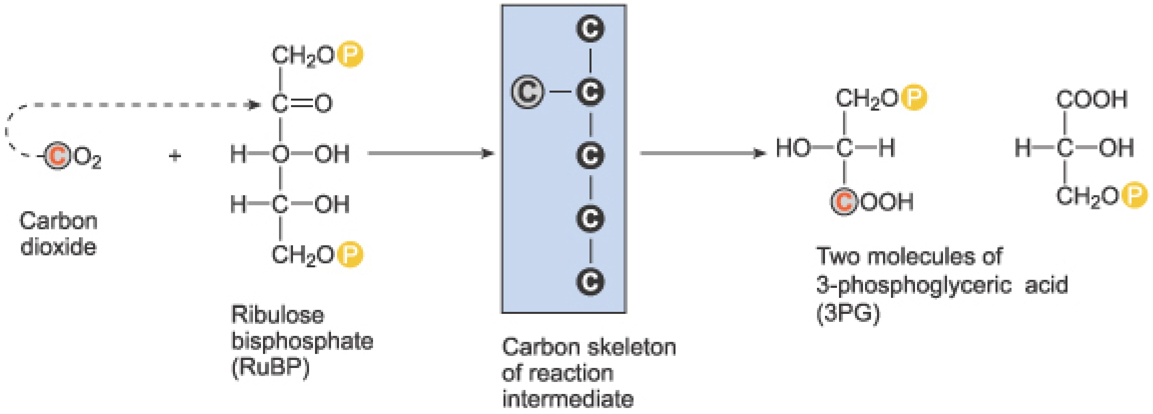


These are reduced by NADPH to two molecules of glyceraldehyde 3-phosphate (GALP).



Of each pair of GALP molecules produced:

- one molecule is the initial end product of photosynthesis; it is quickly converted to glucose and other carbohydrates, lipids or amino acids
- one molecule forms RuBP through a series of chemical reactions



The first steps in the Calvin cycle

The first stable product of the Calvin Cycle is phosphoglycerate (PGA), a 3-C chemical. The energy from ATP and NADPH energy carriers generated by the photosystems is used to phosphorylate the PGA. Eventually there are 12 molecules of glyceraldehyde phosphate (also known as phosphoglyceraldehyde or PGAL, a 3-C), two of which are removed from the cycle to make a glucose. The remaining PGAL molecules are converted by ATP energy to reform six RuBP molecules, and thus start the cycle again.

Summary of stages of photosynthesis