



CRP 101 - FUNDAMENTALS OF CROP PHYSIOLOGY (2+1)

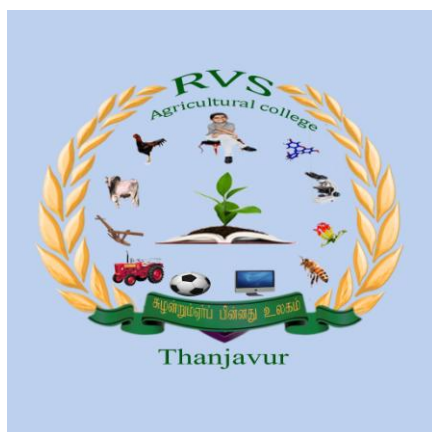
Course Teacher

Dr. G. Karuppusamy, Assistant Professor (Crop Physiology)

RVS AGRICULTURAL COLLEGE

(Affiliated to Tamil Nadu Agricultural University, Coimbatore)

THANJAVUR – 613 402



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Aim

To impart basic knowledge on various functions and processes related to crop production, mineral nutrition, plant growth regulators and environmental stresses.

Theory

Unit I

Introduction to Crop Physiology and importance of Crop Physiology in Agriculture – Plant cell: an overview, organelles- plasma membrane, chloroplast, mitochondria, peroxisome and vacuole, Structure and role of water, water potential and its components, diffusion and osmosis; imbibition, plasmolysis, Field Capacity and Permanent Wilting Point, Absorption of water, Mechanisms of water absorption, Pathways of water movement, Apoplast and symplast, Translocation of water, ascent of sap and its mechanisms - Transpiration and Stomatal physiology: structure of stomatal pore, mechanisms of stomatal opening and closing, guttation, antitranspirants.

Unit II

Mineral nutrition of plants: Criteria of essentiality, classification of nutrients, macro, micro, mobile, immobile and beneficial elements, Physiological functions and deficiency symptoms of nutrients, nutrient uptake mechanism; Hidden hunger, Foliar nutrition, root feeding and fertigation, sand culture, hydroponics and aeroponics.

Unit III

Photosynthesis: Light and dark reactions, Photosystems, red drop and Emerson enhancement effect, Photolysis of water and photophosphorylation, Z scheme, C₃, C₄ and CAM plants; Photosynthetic pathways of C₃, C₄ and CAM plants, difference between three pathways, Factors affecting photosynthesis, Photorespiration – pathway and its significance, Phloem transport, Munch hypothesis, Phloem loading and unloading, Source and sink strength and their manipulations. Respiration: Glycolysis, TCA cycle and electron transport chain; Oxidative phosphorylation – difference between photo and oxidative phosphorylation – energy budgeting - respiratory quotient. Fat metabolism: fatty acid synthesis and breakdown.

Unit IV

Plant growth regulators: physiological roles and agricultural uses, Hormones- classifications - Biosynthetic pathway and role of auxins, gibberellins, cytokinins, ethylene and ABA, Novel and new generation PGRs, Brassinosteroids and salicylic acid, Growth retardants, Commercial uses of PGRs. Photoperiodism - short, long and day neutral plants, Chailakhyan's theory of flowering, Forms of phytochrome, Pr and Pfr, regulation of flowering, Vernalisation - Theories of vernalisation, Lysenko theories, Seed germination - physiological and biochemical changes, seed dormancy and breaking methods, Senescence and abscission, physiological and biochemical changes, Physiology of fruit ripening, climacteric and non-climacteric fruits, factors affecting ripening, Manipulations. Physiological aspects of growth and development of major crops: growth analysis, role of physiological growth parameters in crop productivity.

Unit V

Classification of stresses - Physiological changes and adaptations to drought, flooding, high and low temperature, salinity and UV radiation – compatible osmolytes – membrane properties - compartmentalization – stress alleviation - Global warming – green house gases – physiological effects on crops - Carbon Sequestration.

Practicals

Study of plant cells, structure and distribution of stomata, imbibition, osmosis, plasmolysis, measurement of root pressure, rate of transpiration, Separation of photosynthetic pigments through paper chromatography, Rate of transpiration, photosynthesis, respiration, tissue test for mineral

nutrients, estimation of relative water content, Measurement of photosynthetic CO₂ assimilation by Infra Red Gas Analyser (IRGA).

Theory lecture schedule

1. Introduction and importance of Crop Physiology in Agriculture, an over view of Plant cell.
2. Structure and role of water –water potential and its components – Diffusion – Osmosis – imbibition – Plasmolysis - Field Capacity and Permanent Wilting Point
3. Mechanisms of water absorption – Pathways of water movement – Apoplast and symplast
4. Translocation of water – ascent of sap – mechanisms of xylem transport
5. Transpiration – significance – Stomatal physiology: structure of stomata with mechanisms of stomatal opening and closing – guttation - antitranspirants
6. Mineral nutrition of plants – criteria of essentiality - classification of nutrients – macro, micro, mobile and immobile – beneficial elements, mechanism of nutrient uptake
7. Physiological functions and disorders of macronutrients, Hidden hunger
8. Physiological functions and disorders of micronutrients
9. Foliar nutrition- root feeding and fertigation – sand culture, hydroponics and aeroponics
10. Light reaction of photosynthesis – photolysis of water and photophosphorylation - Z scheme
11. Dark Reaction of photosynthesis - C₃, C₄ and CAM pathways and differences.
12. Factors affecting photosynthesis - Photorespiration – pathway and its significance
13. Phloem transport – Munch hypothesis - Phloem loading and unloading - Source and sink strength and their manipulations
14. Respiration - Glycolysis – TCA cycle.
15. Photo and oxidative phosphorylation - Electron transport chain - energy budgeting - respiratory quotient.
16. Fat metabolism: fatty acid synthesis and breakdown
17. Mid Semester Examination
18. Growth – phases of growth – factors affecting growth.
19. Hormones and plant growth regulators (PGR): physiological roles and agricultural uses - Biosynthetic pathway and role of auxins and gibberellins
20. Plant growth regulators (PGR): physiological roles and agricultural uses - Biosynthetic pathway and role of cytokinin, ethylene and ABA
21. Novel growth regulators viz., Brassinosteroids and salicylic acid – New Generation PGRs - Growth retardants and inhibitors -commercial uses of PGRs
22. Photoperiodism - short, long and day neutral plants – Chailakhyan’s theory of flowering
23. Forms of phytochrome - Pr and Pfr - regulation of flowering
24. Vernalisation - theories of vernalisation – Lysenko and Hormonal theories – devernalization
25. Physiological aspects of growth and development of major crops
26. Growth analysis – role of physiological growth parameters in crop productivity
27. Seed germination - physiological and biochemical changes - seed dormancy and breaking methods
28. Senescence and abscission – physiological and biochemical changes
29. Physiology of fruit ripening- climacteric and non climacteric fruits - factors affecting ripening and manipulations
30. Drought - physiological changes - adaptation – compatible osmolytes - alleviation
31. High and low temperature stress – physiological changes - membrane properties - adaptation
32. Salt stress - physiological changes - adaptation – compartmentalization - alleviation
33. Flooding and UV radiation stresses – physiological changes - adaptation
34. Global warming – green house gases –physiological effects on crop productivity- Carbon Sequestration

Practical schedule

1. Preparation of solutions
2. Study of leaf epidermal, xylem and phloem cells
3. Determination of stomatal index and stomatal frequency
4. Measurement of plant water potential
5. Measurement of water imbibition by seed mass test
6. Estimation of photosynthetic pigments
7. Determination of photosynthetic efficiency in crops
8. Measurement of transpiration and photosynthesis by IRGA
9. Diagnosis of nutritional and physiological disorders in crops
10. Rapid tissue test for mineral nutrients
11. Estimation of relative water content
12. Measurement of osmosis and plasmolysis
13. Growth Analysis
14. Bioassay for gibberellin and cytokinin
15. Estimation of chlorophyll stability index
16. Estimation of proline content
17. Final Practical Examination

Outcome

Students will acquire basic knowledge on various functions and processes related to crop production, mineral nutrition, plant growth regulators and environmental stresses. In addition, hands on exposure to preparation of solutions, analysis of pigment composition, estimation of growth analytical parameters, diagnosis and correction of nutrient deficiencies, enzyme assays and demonstration of plant growth regulator applications.

Text books

1. Salisbury F.B. and C.W.Ross., 1992 (Fourth Edition). Plant Physiology. Publishers: Wadsworth Publishing Company, Belmont, California, USA.
2. Boominathan P., R. Sivakumar, A. Senthil, and D. Vijayalakshmi. 2014. Introduction to Plant Physiology, A.E. Publications. Coimbatore
3. Jain, V.K. 2007. Fundamentals of plant physiology, S.Chand & Company Ltd., New Delhi.
4. Taiz. L. and Zeiger. E., 2015 (Sixth edition). Plant Physiology and Development. Publishers: Sinauer Associates, Inc., Massachusetts, USA.

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- <http://www.plantphys.org>
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- <http://6e.plantphys.net>

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IMPORTANCE OF CROP PHYSIOLOGY IN AGRICULTURE

Plant physiology is a study of vital phenomena in plant. It is the science concerned with

1. Processes and functions
2. The responses of plants to environment and
3. The growth and development that results from the responses

Processes

Processes mean natural containing sequence of events. Examples of processes that occur in living plants are - Photosynthesis, Respiration, Ion absorption, Translocation, Transpiration, Stomatal opening and closing, Assimilation, Flowering, Seed formation and Seed germination.

To describe and explain the plant processes is the first task of plant physiology. Function means natural activity of a cell or tissue, or organ or chemical substances. So the second task of plant physiology is to describe and explain the function of an organ, tissue, cell and cell organelle in plants and also the function of each chemical constituent, whether it may be an ion, molecule or a macro molecule.

Both processes and functions are dependent on the external factors and are modified by the external factors such as light and temperature. Since these two factors are modified by the external factors, the third task of plant physiology is to describe and explain how processes and functions respond to change in the environment. Essentially the overall goal of plant physiology is to evolve a detailed and comprehensive knowledge of all the natural phenomena that occur in living plants and thus to understand the natural of plant growth, development and productivity.

Crop Physiology

Crop physiology can be defined as the science of how crops, as communities of cultivated plants, exploit light, water and nutrients, to grow and generate harvestable yield.

The role of crop physiology in different aspects of agriculture is discussed here.

1. Mineral Nutrition

The detection of deficiencies and toxicities of particular mineral nutrient elements have enabled us to make adequate soil amendments for better plant growth. Several physiological diseases of crop plants such as wheat, rice, pulses and oil seeds have been successfully corrected with the help of knowledge on physiology. For example, application of zinc has corrected khaira disease of paddy. Similarly, knowledge of water relations and mineral utilization has led to improved crop management and now it is possible to grow plants at places where they never grew, by providing proper physiological conditions. Studies on chelates and chelating agents have gone a long way in

making unavailable elements available at functional sites and controlling toxicities of heavy metals.

2. Photoperiodism and Vernalization

Researches on photoperiodism and vernalization have made it possible to grow certain plants and make them flower even in off seasons by suitably altering the photoperiods and providing low temperature treatments.

3. Production Physiology

Carbohydrates are major product of plants and highly valued to human beings. Hence, for increasing its yield capacity, three aspects may be considered: i) production (Photosynthesis) ii) storage (sink potential) and iii) control of distribution in plants, i.e. directing the food material efficiently towards storage organ (translocation of solute). Higher translocation capacity towards storage organs like seeds helps to produce higher yields. In case of rice, the sink capacity of panicles, as well as, the size and longevity of the photosynthetic system after anthesis (flowering) can influence grain yield appreciably.

4. Photosynthesis

Green plants utilise less than one per cent of solar energy for the production of food, and there are two types of plants, C_3 and C_4 based on CO_2 assimilation. C_3 plants are less efficient photosynthesizers than C_4 plants, though these plants are more precious to human beings. C_3 plants include pulses, oilseed crops, fibre crops, important cereals such as wheat, rice, barley etc. Their lower efficiency is due to occurrence of photorespiration which deviates *Rubisco* enzyme from photosynthesis. Therefore, there is a great need to reduce wasteful process of photorespiration or to find out newer crop varieties with low rate of photorespiration.

5. Plant Growth Physiology

Synthetic auxins and related compounds are being used for thinning of crops, prevention of premature fruit drop, promotion of plant growth and yield, induction of seedless or parthenocarpic fruits, promotion of root formation in cuttings for vegetative propagation, budding or sprouting, induction of flowering, control of fruit set and quality, hastening maturity, inducing dormancy in potato, controlling weeds etc.

Gibberellins have found great use in breaking dormancy, inducing uniform crop emergence, producing staminate flowers in cucurbits, loosening fruit clusters, increasing fruit size, hastening maturity, improving fruit quality, production of seedlessness, increasing sugar content in sugarcane, inducing flowering etc.

Cytokinins have been widely used for increasing shelf life of fruits, quickening root induction and producing efficient root system, increasing yield and oil contents of groundnut, breaking dormancy, delaying senescence of living organisms, causing cell division. Ethylene has shown great potentials

in making chemical harvesting possible, thinning by causing abscission, inducing bulbing in onion and tillering in other crops, causing dwarfness of plants, preventing lodging and inducing femaleness.

A number of other chemicals are also being used for causing male sterility, overcoming incompatibility, environmental engineering and land maintenance. In well-developed countries, some growth regulators are frequently used in agriculture. For example, chlormequat (CCC) is used as dwarfing agent in wheat. Ethephon is used to induce flowering in pineapple and as sugarcane ripener. Maleic hydrazide is used as growth retardant, for sucker control on tobacco, and as turf grass growth inhibitor. Daminozide is used to enhance size and colour of various fruits. Glyphosine is used as sugarcane ripener. Mepiquat chloride is a recent addition in the group of growth retardants, having potential use in cotton, ground nut, banana and many vegetable crops.

Role of various hormones like, auxins, gibberellins, cytokinins and ethrel in inducing and promoting flowering is now well documented. Ethrel is widely used to increase the number of female flowers followed by higher yield in cucumber. In several plants such as mango, apple, cotton *etc.*, the fruits abscise and fall before attaining maturity. Auxins have been found successful in preventing immature fall of fruits and thus saving the enormous loss. Planofix (a formulation of NAA) is commonly used in cotton, mango and coconut.

Tissue culture is the technique used to make successful *in vitro* growing of plant parts under controlled aseptic conditions. Tissue culture practices are now widely used and found immensely valuable in crop improvement programmes and hybridization programmes. This technique is commonly used in:

- * Micro propagation in orchids, bananas, potatoes *etc.*
- * Production of disease free plants in potato, cassava, sugarcane, sweet potato *etc.*
- * Androgenic haploid and their use in breeding
- * Embryo rescue for successful hybridization, as in case of interspecific hybridization between *Phaseolus vulgaris* and *P. angustissimus*.
- * Induction and selection of mutants
- * Somoclonal variations, as in case of wheat, potato and tomato
- * Protoplast technology, as in production of pomato (a hybrid of potato and tomato produced by protoplasmic fusion)

6. Environment Physiology

The environmental factors influencing growth and yield of crops include temperature, solar radiation (light), atmospheric carbon dioxide, water supply, air humidity, wind velocity *etc.*

i) Temperature

Extreme temperatures are destructive to plant growth. The critically low and high temperatures normally vary from one stage to another. The critical temperature will be below 20°C and above 30°C for many of the crops. These temperatures also differ according to variety, duration of critical temperature, diurnal changes and physiological status of the plant. Temperature greatly influences the growth rate just after germination. Within a temperature range of 22-31°C, the growth rate increases almost linearly with increasing temperatures. Depending on the growth stages, injury to crop due to low temperature occurs when the daily mean temperature drops below 20°C. Common cool injuries are failure to germinate, delayed seedling emergence, stunting, leaf discolouration, panicle tip degeneration, incomplete panicle exertion, delayed flowering, high spikelet sterility and irregular maturity. On the other hand, high temperatures cause high percentages of spikelet sterility, when the temperatures exceed 35°C at anthesis for more than 1 hour.

Vernalization: This is a method of inducing early flowering in plants by pre-treatment of their seeds at very low temperatures. Practical utility of vernalization are i) crops can be produced earlier ii) crops can be grown in the regions where they do not naturally reproduce and iii) plant breeding work can be accelerated.

ii) Solar Radiation

Most of radiant energy from the sun has a wavelength between 300 and 3000nm, often referred as short wave radiation. Photosynthesis in green leaves uses solar energy in wave lengths from 0.4 to 0.7 µm (400-700 nm), often refer as Photosynthetically Active Radiation (PAR). The solar radiation requirements of a crop differ from one growth stage to another. For example, in rice, shading during the vegetative stage only, slightly affects yield and yield components. Shading during the reproductive stage, however, has a pronounced effect on spikelet number. During ripening, it reduces grain yield considerably because of a decrease in the percentage of filled spikelets.

Flowering

The physiological mechanism responsible for flowering is found to be controlled by duration of light (photoperiodism) and temperature (vernalization).

Photoperiodism: On the basis of length of photoperiod requirement the plants are classified into: short-day plants, long-day plants and day-neutral plants.

Short-day plants: For flowering of short-day plants, the day length must not exceed a certain critical value; the day length required is less than the critical length. Short-day plants will not flower even if a flash of light is provided during the continuous dark period.

eg. Rice, onion, upland cotton and strawberry.

Long-day plants: Long-day plants require a photoperiod of more than a critical length, which may vary from 14 to 18 hours. The best flowering of long day plants usually occurs in continuous light.

eg. Lettuce, radish, alfalfa, sugar beet, spinach etc.

Day-neutral plants: Their flowering is not affected by the length of the day. They can flower even if the light provided is from few hours to continuous illumination. eg. tomato, cucumber, cotton, pea, maize, sun-flower etc.

iii) CO₂ concentration

Being one of the raw materials for photosynthesis, CO₂ concentration affects the rate of photosynthesis markedly. Because of its very low concentration in the atmosphere (360 ppm), it acts as a limiting factor for natural photosynthesis. The rate of photosynthesis increases markedly with increase in the CO₂ level up to a certain extent. Under full sunlight, photosynthesis increases up to 1000 ppm CO₂.

iv) Water Supply

Water stress at any growth stage may reduce yield. The most common symptoms of water deficit are leaf rolling, leaf scorching, and impaired tillering, stunting and delayed flowering, spikelet sterility and incomplete grain filling. Depending on topography and rainfall patterns, low-lying areas may be subjected to different water depths and to different duration. When a crop is submerged for a long time during critical growth stages, the grain yield is reduced.

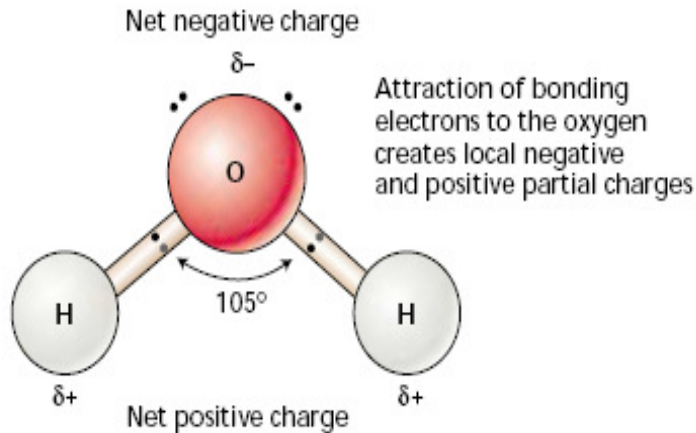
There are number of areas where the subject will have a major impact in agriculture and the following few are the examples.

1. To increase the efficiency of photosynthetic conversion of solar radiation
2. Improved biological fixation of nitrogen
3. To breed desirable strains of crop by utilizing tissue culture and cell fusion
4. Means of avoiding or reducing environmental stresses
5. Crop yields increased by application of plant growth regulator
6. Trait based breeding
7. Breeding for quality
8. To clone genes of relevance in Molecular biology.

UNIT I - PLANT WATER RELATIONS

Chemical Properties of water

Water's chemical description is H_2O . As the diagram below shows, that is one atom of oxygen bound to two atoms of hydrogen. The hydrogen atoms are "attached" to one side of the oxygen atom, resulting in a water molecule having a positive charge on the side where the hydrogen atoms are and a negative charge on the other side, where the oxygen atom is. Since opposite electrical charges attract, water molecules tend to attract each other, making water kind of "sticky." As the diagram 2 shows, the side with the hydrogen atoms (positive charge) attracts the oxygen side (negative charge) of a different water molecule. Oxygen attracts electrons much more strongly than hydrogen, resulting in a net positive charge on the hydrogen atoms, and a net negative charge on the oxygen atom. The presence of a charge on each of these atoms gives each water molecule a net dipole moment. Electrical attraction between water molecules due to this dipole pulls individual molecules closer together, making it more difficult to separate the molecules and therefore raising the boiling point. This attraction is known as hydrogen bonding.



Water is called the "universal solvent" because it dissolves more substances than any other liquid. This means that wherever water goes, either through the ground or through our bodies, it takes along valuable chemicals, minerals, and nutrients. Pure water has a low electrical conductivity, but this increases significantly upon dissolving of a small amount of ionic material in water such as hydrogen chloride. Pure water has a neutral pH of 7, which is neither acidic nor basic.

Physical Properties of water

- Water is unique in that it is the only natural substance that is found in all three states -- liquid, solid (ice), and gas (steam) at the temperatures normally found on Earth. Earth's water is constantly interacting, changing, and in movement.
- Water freezes at 32° Fahrenheit (F) and boils at 212° F at sea level. Water is unusual in that the solid form, ice, is less dense than the liquid form, which is why ice floats.
- Water has high cohesion and high adhesion properties because of its polar nature
- Water has a high specific heat index.
- Water has a very high surface tension. In other words, water is sticky and elastic, and tends to clump together in drops rather than spread out in a thin film. Surface tension is responsible for capillary action, which allows water (and its dissolved substances) to move through the roots of plants.

Importance of water to plants

Water is the main constituent of protoplasm comprising up to about 90-95 per cent of its total weight. In the absence of water, protoplasm becomes inactive and is oven killed.

1. Different organic constituents of plants such as carbohydrates proteins, nucleic acid and enzymes etc. Lose their physical and chemical properties in the absence of water.
2. Water participates directly in many metabolic processes. Inter conversion of carbohydrates and organic acids depend upon hydrolysis and condensation reaction.
3. Water increases the rate of respiration. Seeds respire fast in the presence of water.
4. Water is the source of hydrogen atom for the reduction of CO₂ in the reaction of photosynthesis.
5. Water acts as a solvent and acts as a carrier for many substance. It forms the medium in which several reactions take place.
6. Water present in the vacuoles helps in maintaining the turgidity of the cells which is a must for proper activities of life and to maintain this form and structure.
7. Water helps in translocation of solutes
8. In tropical plants, water plays a very important role of thermal regulation against high temperature.
9. The elongation phase of cell growth depends on absorption of water.

Diffusion, osmosis and imbibitions

The process involved in the absorption of water and dissolved mineral salts by plant cell membrane and the movements within the plant are following:

1. Diffusion
2. Osmosis
3. Imbibitions
4. Plasmolysis

Diffusion

The movement of molecules, atoms or ions, from a region of higher concentration towards a region of lower concentration is known as Diffusion. Energy is not required for the process of diffusion. The process of diffusion stops until the concentration of diffusing particles become uniform throughout the system.

Example: If a crystal of CuSO_4 is placed in a beaker filled with water. At constant temperature copper and sulphate ions will spread out among the water molecules and every part of beaker will contain same copper and sulphate ions.

In **simple diffusion**, molecules which are soluble in lipids simply move between the phospholipids; but for other substance (like ions) it is difficult and these moves by facilitated diffusion.

Facilitated diffusion is a movement in the direction of a concentration gradient; but it involves moving through a channel protein or a carrier protein. A channel protein is merely a pore in the membrane, and is often gated to control movement. A carrier protein has a binding site which the substance attaches to this and then moved through the membrane.

Significance of Diffusion in Plants

- The absorption of CO_2 by the green plant cell takes place by means of diffusion.
- The oxygen produced in green plants cells during photosynthesis is removed out of the cells by diffusion.

Osmosis

Osmosis is the process in which molecules of the solvent move from the region of their higher concentration to the region of their lower concentration through a semi-permeable membrane.

Types of Osmosis

There are two types of osmosis: (i) Exosmosis (ii) Endosmosis

(i) Exosmosis: The outward movement of water from a cell when it is placed in a hypertonic solution is called Exosmosis.

(ii) Endosmosis: The absorption of water by a cell from outside when it is placed in hypotonic solution is called endosmosis.

Plant Cell as an Osmotic System

Due to presence of semi-permeable plasma membrane, osmosis plays an important role in the absorption of water by plant cells. The cell sap contained in the vacuoles is an aqueous solution of salts, sugars and organic acids and possesses a fairly high osmotic pressure. If the cell is in contact with pure water or with hypotonic solution, water will pass into the cell i.e. endosmosis will occur. If it is in contact with isotonic solution, the cell will neither lose nor absorb water and if it is in contact with a hypertonic solution, water will be lost from the cells i.e. exosmosis will occur.

Significance of Osmosis

1. The absorption of water by root hairs from soil is brought about by osmosis.
2. The movement of water from one living cell to another within the plants is brought about by osmosis.
3. Osmosis is responsible for the movement of water from non-living xylem elements into living cells.
4. Osmosis results in turgidity, which is responsible for keeping young stems erect and leaves extended.
5. The turgidity, which depends upon osmosis, makes growth possible.
6. The force developed in young roots growing through the soil is osmotic in nature.
7. Opening and closing of flowers and sleep movements of leaves depends on osmosis.

Plasmolysis

The shrinkage of protoplasm from the cell due to exosmosis known as Plasmolysis. Incipient plasmolysis is stage where protoplasm begins to contract from the cell wall. If a plasmolysed cell in tissue is placed in water, the process of endosmosis take place. Water enters into the cell sap, the cell becomes turgid and the protoplasm again assumes its normal shape and position. This phenomenon is called deplasmolysis.

Advantages of plasmolysis

1. It indicates the semi permeable nature of the plasma membrane.
2. It is used to determine the osmotic pressure of the cell sap.

3. Plasmolysis is used in salting of meat and fishes. Addition of concentrated sugar solution to jam and jellies check the growth of fungi and bacteria which become plasmolysed in concentrated solution.

Imbibition

The swelling up of substances due to absorption of water is known as Imbibitions.

Certain substances if placed in a particular liquid absorb it and swell up. For example, when some pieces of grass or dry wood or dry seeds are placed in water they absorb the water quickly and swell up considerably so that their volume is increased. These substances are called as imbibants and the phenomenon as imbibition, certain force of attraction is exists between imbibants and the substance involved. In plants, the hydrophilic colloids viz., protein and carbohydrates such as starch, cellulose and pectic substance have strong altercation towards water.

Imbibition plays a very important role in the life of plants. The first step in the absorption of water by the roots of higher plants is the imbibition of water by the cell walls of the root hairs. Dry seeds require water by imbibition for germination.

Field capacity and permanent wilting point

After heavy rain fall or irrigation of the soil some water is drained off along the slopes while the rest percolates down in the soil. Out of this water, some amount of water gradually reaches the water table under the force of gravity (gravitational water) while the rest is retained by the soil. This amount of water retained by the soil is called as field capacity or water holding capacity of the soil.

Field capacity is affected by soil profiles soil structure and temperature. The effective depth of a soil, the clay content of the soil within that depth, determines the water holding capacity of the profile. Effective soil depth varies between plant species. Wheat is used as the benchmark plant in this assessment. Available water holding capacity rankings are estimated from soil texture, structure and stone content within the potential root zone of a wheat plant.

Water-holding capacity is controlled primarily by soil texture and organic matter. Soils with smaller particles (silt and clay) have a larger surface area than those with larger sand particles, and a large surface area allows a soil to hold more water. In other words, a soil with a high percentage of silt and clay particles, which describes fine soil, has a higher water-holding capacity. At field capacity, the soil water potential is -0.1 to -0.3 bars.

Permanent wilting percentage or wilting coefficient

The percentage of soil water left after the plants growing in that soil has permanently wilted is called as permanent wiling percentage or the wilting coefficient. All soils retain water that plants

are unable to extract; clays hold the most unavailable water while sands hold the least. The soil water potential at permanent wilting is -15 to -18 bars.

Plant Available Water

This is the water that is considered available for plant use. It is calculated as the difference between the field capacity and wilting point water contents. As noted above it varies for different types of plants and for different types of soils. Though clays hold the most water at both field capacity and wilting point, silt loams hold the most plant available water.

Water potential

Every component of a system possesses free energy capable of doing work under constant temperature conditions. For non-electrolytes, free energy / mole is known as chemical potential. The chemical potential of water is called as water potential. Thus, the water potential is defined as chemical potential of water in a system(soil/leaf/root) in comparison with chemical potential of pure water and it is denoted by a Greek letter Psi (ψ). The water potential of pure water is Zero. The presence of solute particles will reduce the free energy of water or decrease the water potential. Therefore it is expressed in negative value.

It is therefore, water potential is always less than zero. Water potential is determined by three internal factors i.e.

$$\Psi_w = \Psi_s + \Psi_p$$

Ψ_s = is the solute potential or osmotic potential

Ψ_p = pressure potential or turgor potential

Ψ_m = is the matric potential. Matric potential can be measured for the water molecules adhering on the soil particles and cell wall.

In plant system, the matric potential is very less, therefore,

$$\Psi_w = \Psi_s + \Psi_p$$

Osmotic pressure

Osmotic pressure in a solution results due to the presence of solutes and the solutes lower the water potential. Therefore osmotic pressure is a quantitative index of the lowering of water potential in a solution and using thermodynamic terminology is called as osmotic potential. Osmotic pressure and osmotic potential are numerically equal but opposite in sign. Osmotic pressure has positive sign. Osmotic potential has negative sign (ψ_s)

Turgor Pressure (ψ_p)

The hydrostatic pressure exerted by the protoplasm on the cell wall due to entry of water molecules in the cell is known as Turgor Pressure. Turgidity is the state at which cell is fully stretched due to entry of water.

In a normal plant cell, the water potential

$$\psi_w = \psi_s + \psi_p \text{ - partially turgid cell}$$

$$\psi_w = \text{Zero} \text{ - Fully turgid cell, because } -\psi_s = \psi_p \text{ (Highest)}$$

$$\psi_w = \psi_s \text{ - Flaccid cell or plasmolysed cell, where } \psi_p = \text{Zero (Lowest)}$$

Movement of water from high water potential to low water potential

There are 2 cells A and B in contact with each other, cell A has a pressure potential (turgor pressure) of 4 bars and an osmotic potential of -12 bars. Cell B has pressure potential of 2 bars and osmotic potential of -5 bars.

Then,

$$\begin{aligned} \psi_w \text{ of cell A} &= \psi_s + \psi_p \\ &= -12 + (+4) \\ &= -8 \text{ bars} \\ \psi_w \text{ of cell B} &= -5 + (+2) \\ &= -3 \text{ bars} \end{aligned}$$

Hence, water will move from cell B to cell A (i.e., towards lower or more negative water potential) with a form of $(-8 - (-3)) = -5$ bars.

Diffusion Pressure Deficit (DPD) (Suction pressure)

Diffusion pressure of a solution is always lower than its pure solvent. The difference between the diffusion pressure of the solution and its solvent at a particular temperature and atmosphere conditions is called as diffusion pressure deficit (D.P.D). If the solution is more concentrated D.P.D increases but it decreases with the dilution of the solution,

D.P.D of the cell sap or the cells is a measure of the ability of the cells to absorb water and hence is often called as the suction pressure (S.P). It is related with osmotic pressure (O.P) and turgor pressure (T.P) of cell sap and also the wall pressure (W.P) as follows.

$$\text{D.P.D. (S.P)} = \text{O.P} - \text{W.P}$$

But

$$(W.P) = T.P$$

$$D.P.D = O.P - T.P$$

Due to the entry of the water the osmotic pressure of the cell sap decreases while its turgor pressure is increased so much so that in a fully turgid cell T.P equals the O.P

$$O.P = T.P \quad = D.P.D = 0$$

In fully plasmolysed cells: T.P = 0

Therefore, D.P.D = O.P

D.P.D. in case of plant cells is not directly proportional to their osmotic pressure or the concentration of the cell sap but depend both on O.P and T.P. Higher osmotic pressure of the cell sap is usually accompanied by lower turgor pressure so that its D.P.D is greater and water enters into it. But sometimes it is possible that two cells are in contact with each other one having higher O.P and also higher turgor pressure than the other cell and still its does not draw water. It is because of its lower D.P.D., no matter is O.P is higher.

Cell a		Cell b	
O.P = 25 atm.	—————>	O.P = 30 atm	
T.P = 15 atm.		T.P = 10 atm.	A
D.P.D = 10 atm.		D.P.D = 20 atm.	

Entry of water into the cell depends on D.P.D and not on O.P only

ABSORPTION OF WATER

Roots

Often roots are overlooked, probably because they are less visible than the rest of the plant. However, it's important to understand plant root systems because they have a pronounced effect on a plant's size and vigor, method of propagation, adaptation to soil types, and response to cultural practices and irrigation. Roots typically originate from the lower portion of a plant or cutting. They have a root cap, but lack nodes and never bear leaves or flowers directly. Their principal functions are to absorb nutrients and moisture, anchor the plant in the soil, support the stem, and store food. In some plants, they can be used for propagation.

A root's epidermis is its outermost layer of cells. These cells are responsible for absorbing water and minerals dissolved in water. Cortex cells are involved in moving water from the epidermis to the vascular tissue (xylem and phloem) and in storing food. Vascular tissue is located in the center of the root and conducts food and water

Externally, there are two areas of importance: the root cap and the root hairs. The root cap is the root's outermost tip. It consists of cells that are sloughed off as the root grows through the soil. Its function is to protect the root meristem. Root hairs are delicate, elongated epidermal cells that occur in a small zone just behind the root's growing tip. They generally appear as fine down to the naked eye. Their function is to increase the root's surface area and absorptive capacity. Root hairs usually live 1 or 2 days. When a plant is transplanted, they are easily torn off or may dry out in the sun.

Mechanism of water absorption

There are two types active and passive absorption based on energy used in the process.

1. A. Active- Osmotic absorption

Water is absorbed from the soil into the xylem of the roots according to osmotic gradient. 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. First step in osmotic absorption of water is the imbibition of soil water by the hydrophilic cell walls of root hairs. Osmotic pressure of the cell sap of root hairs is usually higher than the OP of the soil water. Therefore, the DPD in the root hairs become higher and water from the cell walls enters into them through plasma membrane by osmotic diffusion. As a result, OP and DPD of root hairs how become lower, while their turgor pressure is increased.

Now the cortical cells adjacent to root hairs have high DPD in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from root hairs by osmotic diffusion. In the same way, by cell to cell osmotic diffusion gradually reaches the inner most cortical cells and

the endodermis. Osmotic diffusion of water into endodermis takes place through special thin walled passage cells because the other endodermis cells have casparian strips on thin walls which are impervious to water. Water from endodermis cells is down into the cells of pericycle by osmotic diffusion which now become turgid and their suction pressure is decreased.

In the last step, water is drawn into xylem from turgid pericycle. It is because the SP of xylem vessels becomes higher than SP 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.

1. B. Active non-osmotic absorption

Water is absorbed against the osmotic gradient. Sometimes, it has been observed that absorption of water takes place even when OP of soil water is high than OP 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.

2. Passive absorption of water

It is mainly due to transpiration, the root cells do not play active role and remain passive. 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 water rises upward to reach the transpiring surfaces. As the 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 of this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

External factors affecting absorption of water

1. Available soil water

Sufficient amount of water should be present in the soil in 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 eg. Hygroscopic water, combined water, gravitational water etc. is 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 soil solution

Due to presence of more salts in the soil results in higher OP. If OP of soil solution will become higher than the OP 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_2 and consequently the accumulation of CO_2 will retard the metabolic activities of roots like respiration. This also inhibits rapid growth and elongation of the roots so that they are deprived of 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 $30^\circ C$ favours water absorption. At higher temperature water absorption is decreased. At low temperature also water absorption decreased so much so that at about $0^\circ C$, it is almost decreased. This is probably because at low temperature.

1. The viscosity of water and protoplasm is increased
2. Permeability of cell membrane is decreased
3. Metabolic activity of root cells are decreased
4. Root growth and elongation of roots are checked.

XYLEM TRANSPORT

Ascent of sap

The water after being absorbed by the roots is distributed to all parts of the plants. In order to reach the topmost part of the plant, the water has to move upward through the stem. The upward movement of water is called as Ascent of sap.

Mechanism of ascent of sap

In small trees and herbaceous plants, the ascent of sap can be explained easily, but in tall trees like Eucalyptus and conifers reaching a height of 300-400 feet), where water has to rise up to the height of several hundred feet, it becomes a problem. To explain the mechanism of Ascent of sap, a number of theories have been put forward.

- a. vital theory
- b. root pressure theory
- c. physical force theory
- d. transpiration pull and cohesion of water theory

A. Vital theories

According to vital theories, the ascent of sap is under the control of vital activities in the stem.

1. According to Godlewski (1884) - Ascent of sap takes place due to the pumping activity xylem tissues which are living.
2. According to Bose (1923) - Upward translocation of water takes place due to pulsatory activity of the living cells of the inner most cortical layer just outside the endodermis.

B. Root pressure theory

Root pressure is generated by the osmotic pressure of the cortical cells of the root. This theory explains that root pressure is responsible for forcing up water from root to leaves.

Objections

- The force of root pressure rarely exceeds 2 atm axially 6 atm whereas requirement for all plants may be up to 30 atm.
- It is also shows seasonal fluctuations, it is very low in summer when transpiration is high and high in spring when transpiration is slow.
- Also water can rise up in absence of root.

C. Physical force theories

Various physical forces may be involved in Ascent of sap.

1. Atmospheric pressure

This does not seem to be convincing because it cannot act on water present in xylem in roots. In case it is working, and then also it will not be able to raise water beyond 34.

2. Imbibition

Sachs (1878) supported the view that ascent of sap could take place by imbibition through the walls of xylem. But imbibitional force is insignificant in the A. of sap because it takes place through the lumen of xylem elements and not through walls.

3. Capillary force

In plants the xylem vessels are placed one above the other forming a sort of continuous channel which can be compared with long capillary tubes and it was thought that as water rises in capillary tube due to capillary force in the same manner ascent of sap takes place in the xylem.

D. Transpiration pull and cohesion of water theory

This theory was originally proposed by Dixon and Jolly (1894) later supported and elaborated by Dixon (1924). This theory is very convincing and has now been widely supported by many workers.

Due to transpiration, there is continuous loss of water from aerial part of plants. This results in water deficit condition in the mesophyll cell. Due to this condition, cells which lose water withdraw it from adjoining cells and ultimately set up chains which absorb water from the soil through roots. So, a tension develops in xylem a vessel which is known as Transpiration Pull. In plants, water moves in the form of column due to transpiration pull. The water column remains unbroken due to cohesive force of water molecule, which is actually due to formation of hydrogen bonds between molecules. Further studies of Dixon, reveals that cohesive force of water molecule is about 300 atm to 350 atm and the total force needed to raise water column about 350 feet's is 12 atm but due to cross-walls and other resistance's it may reach to 30 atm.

PHLOEM TRANSPORT

Translocation of organic solutes

The movement of organic food materials or the solutes in soluble form from one place to another in higher plants is called as Translocation of organic solutes

Directions of translocation

Translocation of organic solutes may take place in the following directions.

1. Downward translocation

Mostly, the organic material is manufactured by leaves and translocated downward to stem and roots for consumption and storage.

2. Upward translocation

It takes place mainly during the germination of seeds, tubers etc. When stored food after being converted into soluble form is supplied to the upper growing part of the young seedling till it has developed green leaves. Upward translocation of solutes also takes place through stem to young leaves, buds and flowers which are situated at the tip of the branch.

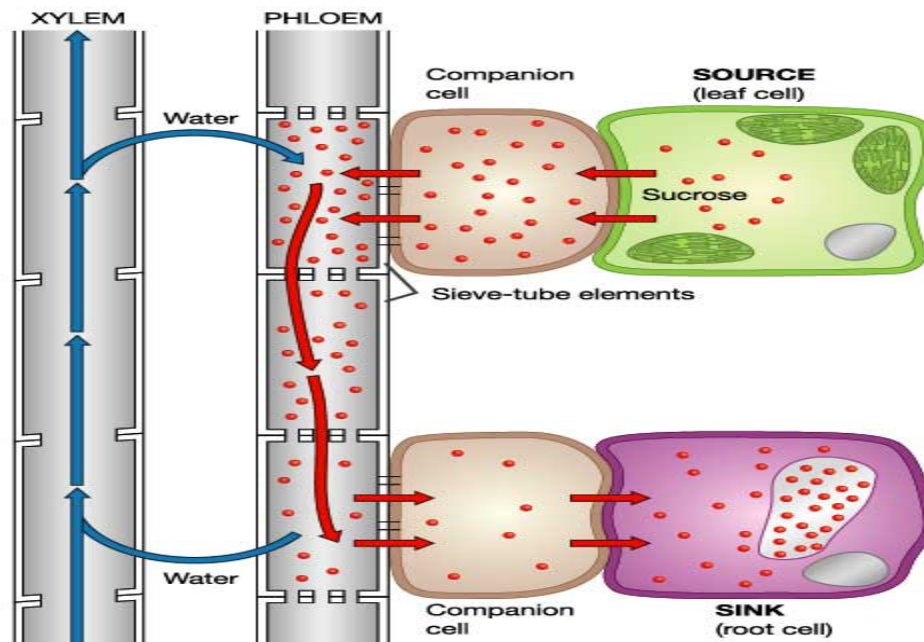
3. Radical translocation

Radical translocation of organic solutes also takes place in plants from the cells of the pith to cortex.

Mechanism of translocation

Various theories have been put forward to explain the mechanism of phloem conduction. Among them Munch's (1930) hypothesis is most convincing.

Munch's mass flow on pressure flow hypothesis



According to this hypothesis put forward by Much (1930) and others, the translocation of organic solutes takes place through phloem along a gradient of turgor pressure from the region of higher concentration of soluble solutes (supply end) to the region of lower concentration (consumption end). According to this theory, Mesophyll cells draw water from the xylem of the leaf due to higher osmotic pressure and suction pressure of their sap so that their turgor pressure is increased. The turgor pressure in the cells of stem and the roots is comparatively low and hence, the soluble organic solutes begin to flow en masse from mesophyll through phloem down to the cells of stem and the roots under the gradient of turgor pressure. In the stem and the roots, the organic solutes are either consumed or converted into insoluble form and the excess water is released into xylem through cambium.

TRANSPIRATION

Transpiration is the loss of water in form of water vapour from plants. It occurs chiefly at the leaves while their stomata are open for the passage of CO₂ and O₂ during photosynthesis. But air that is not fully saturated with water vapor (100% relative humidity) will dry the surfaces of cells with which it comes in contact. So the photosynthesizing leaf loses substantial amount of water by evaporation. This transpired water must be replaced by the transport of more water from the soil to the leaves through the xylem of the roots and stem.

Importance

Transpiration is not simply a hazard of plant life. It is the "engine" that pulls water up from the roots to:

- supply photosynthesis (1%-2% of the total)
- bring minerals from the roots for biosynthesis within the leaf
- cool the leaf

Types of transpiration

There are 3 types of transpiration

1. **Stomatal Transpiration:** it is the most important type of transpiration as constitutes 50-97% of the total transpiration. It takes place through the stomata on leaves.
2. **Cuticular Or Epidermal Transpiration:** it takes place through the epidermal cells of the leaves & other exposed aerial parts like herbaceous stem, flowers, fruits, etc. the permeability of the cuticular layer varies inversely with thickness . The cuticle imbibes water from the epidermal cells & loses the same by evaporation. . It may contribute a maximum of about 10% of the total transpiration.
3. **Lenticular Transpiration:** it is found only in woody stems & some fruits where lenticels occur. Lenticels connect atmospheric air with the water- saturated cortical cells. Water is lost from the cortical cells.

Mechanism of stomatal transpiration

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

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

When mesophyll cells draw water from the xylem they become turgid and their diffusion pressure deficit (DPD) and osmotic pressure (OP) decreases leading to 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 from xylem by osmotic diffusion.

2. Opening and closing of stomata (stomatal movement)

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.

3. Simple diffusion of water vapours from intercellular spaces to other atmosphere through 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).

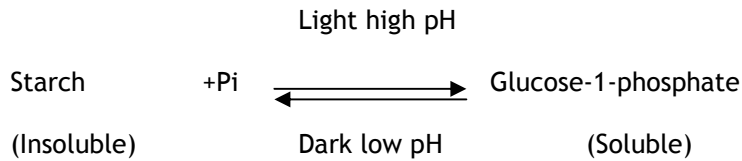
Theories for mechanism of stomatal opening and closing

1. Theory of photosynthesis

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.

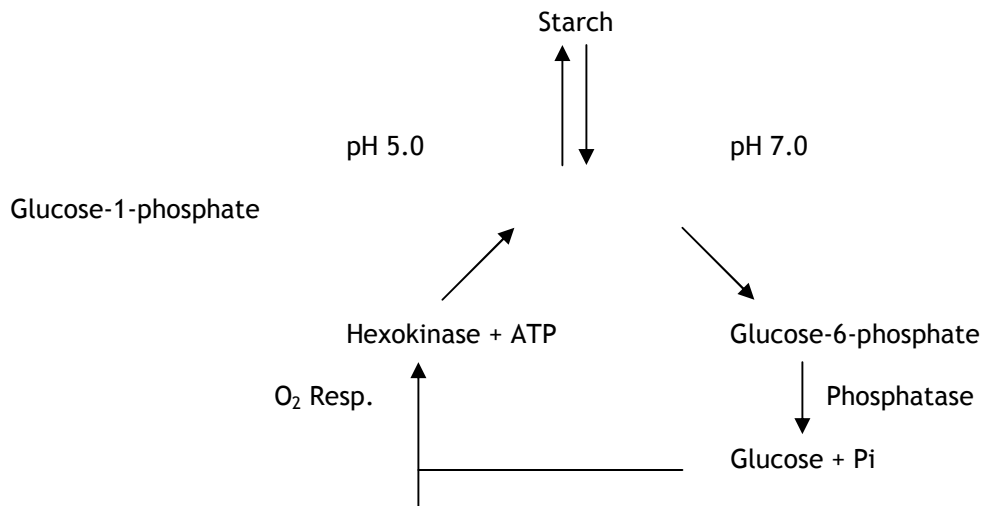
2. Starch - sugar Inter conversion theory- classical theory

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.



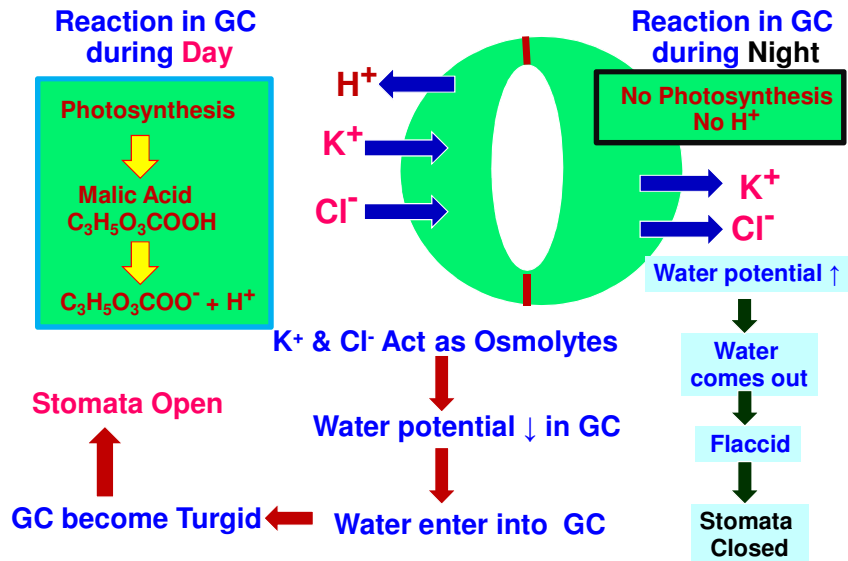
3. Steward theory

According to Steward (1964), 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. 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.



4. Theory of proton transport and hormonal regulation

Proton (H⁺) – K⁺ Exchange Pump



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.

Environmental factors that affect the rate of transpiration

1. **Light:** Plants transpire more rapidly in the light than in the dark. This is largely because light stimulates the opening of the stomata. Light also speeds up transpiration by warming the leaf.
2. **Temperature:** Plants transpire more rapidly at higher temperatures because water evaporates more rapidly as the temperature rises. At 30°C, a leaf may transpire three times as fast as it does at 20°C.
3. **Humidity:** The rate of diffusion of any substance increases as the difference in concentration of the substances in the two regions increases. When the surrounding air is dry, diffusion of water out of the leaf goes on more rapidly. Hence lower humidity leads to higher transpiration.
4. **Wind:** When there is no breeze, the air surrounding a leaf becomes increasingly humid thus reducing the rate of transpiration. When a breeze is present, the humid air is carried away and replaced by drier air.

5. Soil water: A plant cannot continue to transpire rapidly if its water loss is not made up by replacement from the soil. When absorption of water by the roots fails to keep up with the rate of transpiration, loss of turgor occurs, and the stomata close. This immediately reduces the rate of transpiration (as well as of photosynthesis). If the loss of turgor extends to the rest of the leaf and stem, the plant wilts. The volume of water lost in transpiration can be very high. It has been estimated that over the growing season, one acre of corn plants may transpire 400,000 gallons of water. As liquid water, this would cover the field with a lake 15 inches deep. An acre of forest probably does even better.

Advantages of transpiration

1. Role of movement of water

Transpiration is 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.

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 temperature of plants. Transpiration plays an important role in regulating 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.

B. 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 trees have to shed their leaves during autumn to check loss of water.

In spite of the various disadvantages, the plants cannot avoid transpiration due to their peculiar internal structure particularly those of leaves. Therefore, many workers like Curtis (1926) have called transpiration as necessary evil.

Antitranspirants

A substance sprayed on plant leaves to reduce the rate of transpiration and conserve moisture.

Types of antitranspirants

a. stomatal closing type. By spraying certain chemicals, stomata closes and hence transpirations stops.

Eg. Phenyl mercuric acetate, ABA

b. Thin film forming type: These substances form a thin film on the leaf surface

Eg. Wax, rice gruel

C. Reflective type: The principle of using this type of chemicals is to increase the light reflection by the leaved and thus reducing leaf temperature and hence transpiration.

Eg. Kaolin, lime water spray

Guttation

Secretion of water on to the surface of leaves through specialized pores called as hydathodes. The process occurs most frequently during conditions of high humidity when the rate of transpiration is low. Drops of water found on grass in early morning are often the result of guttation, rather than dew. Sometimes the water contains minerals in solution, such as calcium, which leaves a white crust on the leaf surface as it dries.

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
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

UNIT II: NUTRIO PHYSIOLOGY

MINERAL NUTRITION

Plant tissue analysis measures all essential plant nutrients and indicates whether the sample tissue contains an adequate concentration at the current time.

- The chemical compounds required by an organism are termed as nutrients
- Nutrition may be defined as the supply and absorption of chemical compounds needed for plant growth and metabolism
- For plant growth and metabolism, 16 elements are essential. They are C, H, O, N, P, K, Ca, S, Mg, Fe, Mn, Zn, B, Cu, Mo and Cl

Arnon's Essentiality criteria of elements

1. Deficiency of any essential element prevents the plants from completing its lifecycle
2. Essentiality of element is highly specific. This can be corrected only by supplying that specific element
3. The element must have a nutritional growth. It must form a component of plant system or it must have specific biological or physiological function.

Classification of essential elements

a. Classification based on amount required or amount present in the tissue

These essential elements are classified into two groups

1. Major elements (macro nutrients)
2. Minor elements (Micro nutrients) (Trace elements)

Major elements

The essential elements which are required by the plants in comparatively large amounts are called as major elements or macro nutrients. They are C, H, O, N, P, K, Ca, S, Mg. In this C, H, O, N, P and K are called primary elements and Ca, S, Mg are called as secondary elements.

Minor elements

The essential elements which are required in very small amounts or traces by the plants are called as minor elements or micronutrients or trace elements. They are Fe, Zn, Mn, B, Cl, Cu and Mo.

b. Classification based on mobility inside the plant system

Based on the mobility, elements are also classified into three types.

1. Mobile elements : N, P, K, S and Mg

2. Immobile elements : Ca, Fe and B

3. Intermediate in mobility : Zn, Mn, Cu, Mo

c. Classification based on biochemical function

1. Group 1 - major constituent of organic material - N and S

2. Group 2 - Nutrient important for energy storage or structural integrity - P and B

3. Group 3 - Nutrient that remain in ionic form - K, Ca, Mg, Cl, Mn and Na

4. Group 4 - Nutrient that are involved in redox reaction - Fe, Zn, Cu, Ni and Mo

Physiological roles of essential mineral nutrients

Macronutrients

Nitrogen

- Nitrogen is important constituent of proteins, nucleic acids, porphyrins (chlorophylls & cytochromes) alkaloids, some vitamins, coenzymes etc
- Thus N plays very important role in metabolism, growth, reproduction and heredity.

Deficiency symptoms

- Plant growth is stunted because protein content cell division and cell enlargement are decreased
- N deficiency causes chlorosis of the leaf i.e yellowing older leaves are affected first
- In many plants eg. tomato, the stem, petiole and the leaf veins become purple coloured due to the formation of anthocyanin pigments.

Phosphorus

- It is important constituent of nucleic acids, phospholipids, coenzymes NADP, NADP H₂ and ATP
- Phospholipids along with proteins may be important constituents of cell membranes
- P plays important role in protein synthesis through nucleic acids and ATP
- Through coenzymes NAD, NADP and ATP, it plays important role in energy transfer reactions of cell metabolism eg. Photosynthesis, respiration and fat metabolism etc.

Deficiency symptoms

- P deficiency may cause premature leaf fall
- Dead necrotic areas are developed on leave or fruits

- Leaves may turn to dark green to blue green colour. Sometimes turn to purplish colour due to the synthesis and accumulation of anthocyanin pigments.
- Sickle leaf disease

Potassium

- Although potassium is not a constituent of important organic compound in the cell, it is essential for the process of respiration and photosynthesis
- It acts as an activator of many enzymes involved in carbohydrate metabolism and protein synthesis
- It regulates stomatal movement
- Regulates water balance

Deficiency symptoms

- Mottled chlorosis of leaves occurs
- Neurotic areas develop at the tip and margins of the leaf (marginal necrosis)
- Plants growth remains stunted with shortening of internodes.
- Deficiency causes easy lodging in cereals
- Deficiency leads to increase in pest and diseases

Calcium

- It is important constituent of cell wall
- It is essential in the formation of cell membranes
- It helps to stabilize the structure of chromosome
- It may be an activation of many enzymes

Deficiency symptoms

- Calcium deficiency causes disintegration of growing meristematic regions of root, stem and leaves
- Chlorosis occurs along the margins of the younger leaves
- Malformation of young leaves takes place
- Blossom end rot in tomato

Magnesium

- It is very important constituent of chlorophylls
- It acts as activation of many enzymes in nucleic acid synthesis and carbohydrate metabolism
- It plays important role in binding ribosomal particles during protein synthesis.

Deficiency symptoms

- Mg deficiency causes mottled chlorosis with veins green and leaf tissues yellow or white appearing first on older leaves
- Dead necrotic patches appear on the leaves
- In cotton Mg deficiency leads to reddening of leaves and disorder is called as reddening in cotton.

Sulphur

- It is important constituent of some amino acids (cystine, cysteine and methionine) with which other amino acids form the protein
- S helps to stabilize the protein structure
- It is also important constituent of vitamin i.e biotin, thiamine and coenzyme A
- Sulphydryl groups are necessary for the activity of many enzymes.

Deficiency symptoms

- Deficiency causes chlorosis of the leaves
- Tips and margins of the leaf roll in ward
- Stem becomes hard due to the development of sclerenchyma.

Micronutrients

Iron

- Important constituent of iron porphyrin - proteins like cytochromes, peroxidases, catalases, etc.
- It is essential for chlorophyll synthesis
- It is very important constituent of ferredoxin which plays important role in photochemical reaction in photosynthesis and in biological nitrogen fixation.

Deficiency symptoms

- Iron deficiency causes chlorosis of young leaves which is usually interveinal.

Zinc

- It is involved in the biosynthesis of growth hormone auxin (indole 3 acetic acid)
- It acts activator of many enzymes like carbonic anhydrase and alcohol dehydrogenase, etc.

Deficiency symptoms

- Zinc deficiency causes chlorosis of the young leaves which starts from tips and the margins
- The size of the young leaves is very much reduced. This disorder is called as 'little leaf disease'
- Stalks will be very short.
- In rice deficiency leads to "Khaira disease"

Manganese

- It is an activator of many respiratory enzymes
- It is also an activator of the enzyme nitrite reductase
- It is necessary for the evolution of oxygen (photolysis) during photosynthesis

Deficiency symptoms

- The young leaves are affected by mottled chlorosis
- Veins remain green
- Small necrotic spots developed on the leaves with yellow strips

Copper

- It is an important constituent of plastocyanin (copper containing protein)
- It is also a constituent of several oxidizing enzymes.

Deficiency symptoms

- Copper deficiency causes necrosis of the tip of the young leaves
- It also causes die-back of citrus and fruit trees
- Also causes reclamation disease or white tip disease of cereals and leguminous plants.

Boron

- Boron facilitates the translocation of sugars by forming sugar borate complex.

- It involves in cell differentiation and development since boron is essential for DNA synthesis
- Also involves in fertilization, hormone metabolism etc.

Deficiency symptoms

- Boron deficiency causes death of shoot tip
- Flower formation is suppressed
- Root growth is stunted
- The other diseases caused by B deficiency is
- Heart rot of beet
- Stem crack of celery
- Brown heart of cabbage
- Water core of turnip
- Internal cork formation in apple
- Hen and chicken in grapes

Molybdeneum

- It is constituent of the enzyme nitrate reductase and thus plays an important role in nitrogen metabolism
- It is essential for flower formation and fruit set.

Deficiency symptoms

- Molybdenum deficiency causes interveinal chlorosis of older leaves
- Flower formation is inhibited

Causes whiptail disease in cauliflower plant

NUTRITIONAL DISORDERS

When a nutrient element insufficiency (deficiency and/or toxicity) occurs, visual symptoms may or may not appear, although normal plant development will be slowed. When visual symptoms do occur, such symptoms can frequently be used to identify the source of the insufficiency.

Deficiency Symptoms

- Stunted or reduced growth of the entire plant with the plant itself either remaining green or lacking an over-all green color with either the older or younger leaves being light green to

yellow in color.

- Chlorosis of leaves, either interveinal or of the whole leaf itself, with symptoms either on the younger and/or older leaves, or both (chlorosis due to the loss or lack of chlorophyll production).
- Necrosis or death of a portion (margins or interveinal areas) of a leaf, or the whole leaf, usually occurring on the older leaves.
- Slow or stunted growth of terminals (rosetting), the lack of terminal growth, or death of the terminal portions of the plant.
- A reddish purpling of leaves, frequently more intense on the under side of older leaves due to the accumulation of anthocyanin (Mottling)

Chlorosis is caused by the deficiency of mineral elements such as Mn, K, Zn, Fe, Mg, S and N. Mottling is caused due to the deficiencies of N, Mg, P, S and *Necrosis* due to the deficiency of Mg, K, Zn, Ca and Mo.

Toxicity Symptoms

Visual symptoms of toxicity may not always be the direct effect of the element in excess on the plant, but the effect of the excess element on one or more other elements. For example, an excessive level of potassium (K) in the plant can result in either magnesium (Mg) and/or calcium (Ca) deficiency, excess phosphorus (P) can result in a zinc (Zn) deficiency and excess Zn in an iron (Fe) deficiency. These effects would compare to elements, such as boron (B), chlorine (Cl), copper (Cu), and manganese (Mn), which create visual symptoms that are the direct effect of an excess of that element present in the plant. Some elements, such as aluminum (Al) and copper (Cu) can affect plant growth and development due to their toxic effect on root development and function.

Hidden Hunger

In some instances, a nutrient element insufficiency may be such that no symptoms of stress will visually appear with the plant seeming to be developing normally. This condition has been named hidden hunger, a condition that can be uncovered by means of either a plant analysis and/or tissue test.

A hidden hunger occurrence frequently affects the final yield and the quality of the product produced. For grain crops, the grain yield and quality may be less than expected; for fruit crops, abnormalities, such as blossomed rot and internal abnormalities may occur, and the post harvest characteristics of fruits and flowers will result in poor shipping quality and reduced longevity. Another example is potassium (K) insufficiency in corn, a deficiency that is not evident until at maturity when plants easily

PHYSIOLOGICAL DISORDERS

Physiological disorder is the abnormal growth pattern or abnormal external or internal conditions due to adverse environmental conditions such as deviation from normal state of temperature, light, moisture, nutrient, harmful gases and inadequate supply of growth regulators.

Disorders associated with low temperature

1. Leaf chlorosis and frost banding

Chlorosis was caused by a disruption of chloroplasts caused by winter cold. Green chlorophyll pigments are often converted in to yellow pigment. Leaf may appear with distinct bleached bands across the blade of young plants called frost banding e.g.: sugarcane, wheat and barley.

2. Leaf necrosis and malformations

Spring frost causes various types and degree of injury including cupping, crinkling finishing and curling of leaves of apple trees and stone fruits. The distortion is caused by death of the developed tissues before the expansion of leaves.

3. Stem disorders

Frost cracks develop when tree trunk or limbs lost their heat too rapidly. The outer layer of bark and wood cool most rapidly and subjected to appreciable tension causing marked shrinkage and cracking following a sudden temperature drop. Affected timber is of poor quality.

Disorders associated with high temperature

1. Leaf scorch

High temperature causes leaf scorch directly or indirectly by stimulating excessive evaporation and transpiration. Tip burn of potato is a widespread example for this disorder.

2. Sunscald

In leaf vegetable crops like lettuce and cabbage, when leaves on the top of the head are exposed to intense heat, water soaked lesions or blistered appearance occur These irregular shaped areas become bleached and parched later.

3. Water core

In fruit crop like Tomato, exposure to high temperature causes death of the outer cells of fruit skin. Subsequently corky tissue occurs beneath the skin, with watery appearance of the flesh near the core of the fruits faster. Often light stress is coupled with heat stress e.g. sun scald of bean, sun burning of soybean and cowpea. In flower crop like chrysanthemum, increase in light intensity affects flower bud formation. Reproduction phase does not commence and modified into leaf like bracts.

Disorders caused by light stress:

Adverse light intensity causes impaired growth and reduced vigour. Subsequently leaves gradually lose green colour, turning pale green to yellow, stems may dieback little every year. Insufficient light limits photosynthesis, causing food reserves to be depleted.

Identification of Physiological Disorders and Corrective Measures

Crop	Malady	Corrective measure
Rice	Severe chlorosis of leaves	1% super phosphate and 0.5% ferrous
Rice	Irregular flowering and chaffiness	1% super phosphate and magnesium
Rice	Tip drying and marginal scoring and	1% super phosphate and 0.5% zinc
Maize	Chlorosis	A spray solution containing 0.5% ferrous
Maize	'White bud' yellowing in the bud leaves	0.5% zinc sulphate spray with 1% urea.
Maize	Tip drying and marginal scoring pinkish	1% super phosphate and 0.5% zinc
Maize	Marginal scorching and yellowing.	0.5% ferrous sulphate and 1% urea
	Irregular drying of tips and margins	25 kg of zinc sulphate / ha
Sorghum	Chlorosis of younger leaves	Spray of 0.5% ferrous sulphate with
Cowpea	Water soaked necrotic spots on leaf	Spray containing sulphate and zinc
Groundnut	Chlorosis of terminal leaves	0.5% ferrous sulphate and urea 1%

Foliar Nutrition

Foliar nutrition is fertilizing certain crop plants through aerial spraying. Penetration of the spray solution or nutrient solution occurs through cuticle the layer of polymerized wax which occurs on outer surface of the epidermal cells of leaves. After penetration in the cuticle, further penetration take place through fine, thread like semi-microscopic structure called ectodesmata. This extends through the outer epidermal cell wall, from the inner surface of the cuticle to the plasma membrane. When the substance reaches plasma membrane of an epidermal cell, it will be observed by mechanism similar to those which operate in root cells.

Advantages

1. Foliar nutrition may serve as a mean of applying supplemental macronutrients during critical growth periods when it is impracticable to apply fertilizers to soil. Eg. Unusual period of dry weather.

2. Foliar nutrition may afford a remedy for the time lag between soil applied and plant absorbed. Time is too long because of fast growing rates.
3. Cost effective because the concentration used in foliar spray is much lower than soil application.
4. It act as a quick remedial measures
5. Loss of nutrients relatively less

SOILLESS GROWTH OR HYDROPONICS

The practice of growing plants in nutrient enriched water without soil is called as soilless growth or hydroponics. However, the term hydroponics is now being applied to plants rooted in sand, gravel or other similar matter which is soaked with a recycling flow of nutrient - enriched water. According to a recent limited nations report on hydroponics: In area of tropics, where the water deficiency is the limiting factor in crop production, the soilless methods hold out much promise because of the more economical use of water.

The report also indicated that in some areas, lack of fertile soil or very thin soil layers may also move soilless methods worth serious consideration. Besides these the other advantages of growing cucumbers, egg plants, peppers, lettuces, spinach and other vegetables hydroponically under controlled environment are

1. The regulation of nutrients
2. Control of pests and diseases
3. Reduction of labour cost
4. Sometimes quicker yield

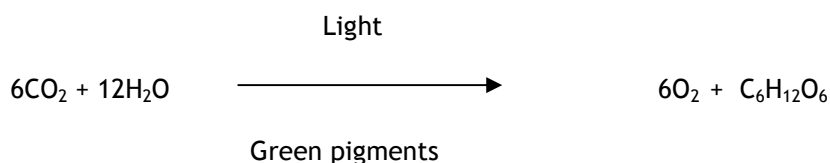
But there is two main drawbacks of hydroponics farming.

1. Firstly the cost of settling up the system is very high
2. Secondly it requires skills and knowledge its operation

UNIT III: CARBON FIXATION

PHOTOSYNTHESIS

Photosynthesis is a vital physiological process where in the chloroplast of green plants synthesizes sugars by using water and carbon dioxide in the presence of light. Photosynthesis literally means synthesis with the help of light i.e. plant synthesize organic matter (carbohydrates) in the presence of light. Photosynthesis is sometimes called as carbon assimilation (assimilation: absorption into the system). This is represented by the following traditional equation.



During the process of photosynthesis, the light energy is converted into chemical energy and is stored in the organic matter, which is usually the carbohydrate. One molecule of glucose contains about 686 K Calories energy. CO_2 and water constitute the raw material for this process and oxygen and water are formed as the byproducts during photosynthesis. *Stephen Hales* (1727) first explained the relationship between sunlight and leaves and *Sachs* (1887) established that starch was the visible product of photosynthesis.

Photosynthetic apparatus

In plants photosynthesis takes place primarily in **leaves**. Almost all of the photosynthetic reactions take place in the **chloroplast**. Chloroplasts are small, ellipsoidal organelles about 5 μm in diameter. There are about 5 billion chloroplasts in an average size leaf, and these are present mainly in the **mesophyll** toward the upper leaf surface. The chloroplast is composed of several "compartments" each with its own set of metabolic functions.

- **Outer envelope** - the outermost membrane, which is permeable to most substances, is "the skin that holds everything in"
- **Inner envelope** - the inner membrane, which is impermeable to most molecules, contains transport proteins that control the movement of substances into and out of the chloroplast
- **Thylakoids** - system of internal membranes that contain the photosystems and components of the electron transport chain. Site of the "light" reactions or light dependent reaction of photosynthesis. Thylakoids are organized into stacked and unstacked regions. Stacked regions are called **grana**. Thylakoids enclose a continuous fluid space known as the **lumen**.

- **Stroma** - a protein filled gel that contains water soluble enzymes and metabolites. Site of the "light-independent" or "dark" reactions of photosynthesis, known as the **Calvin cycle** or the photosynthetic carbon reduction or **PCR cycle**. The major protein in the stroma is the carboxylating enzyme **Rubisco**.

Photosynthetic pigments

Photosynthetic pigments are of three types; Chlorophylls, Carotenoids and Phycobillins.

- Chlorophylls and Carotenoids are insoluble in water and can be extracted only with organic solvents such as acetone, petroleum ether and alcohol.
- Phycobillins are soluble in water
- Carotenoids include carotenes and xanthophylls. The xanthophylls are also called as *carotenols*.

1. Chlorophylls (green pigments)

Chlorophyll consists of a **tetrapyrrole ring** coordinated to a **magnesium atom** via the ring nitrogens. It also contains a "**phytol tail**" (derived from the terpenoid pathway). This makes the molecule very hydrophobic.

The molecular formula for chlorophyll *a*: $C_{55}H_{72}O_5N_4 Mg$ and chlorophyll *b*: $C_{55}H_{70}O_6N_4 Mg$. The two chlorophylls differ because in chlorophyll *b* there is a -CHO group instead of CH_3 group at the 3rd C atom in pyrrol ring II. Chlorophyll is formed from protochlorophyll in light. The protochlorophyll lacks 2H atoms one each at 7th and 8th C atoms in pyrrol ring IV.

2. Carotenoids (yellow or orange pigments)

1. **Carotenes:** Carotenes are hydrocarbons with a molecular formula $C_{40}H_{56}$

2. Xanthophylls (carotenols)

They are similar to carotenes but differ in having two oxygen atoms in the form of hydroxyl or carboxyl group. The molecular formula is $C_{40}H_{56}O_2$. The role of Carotenoids is absorption of light energy and transfer the light energy to chlorophyll *a* molecules. They also play a very important role in preventing photodynamic damage within the photosynthetic apparatus. Photodynamic damage is caused by O_2 molecules which is very reactive and is capable of oxidizing whole range of organic compounds such as chlorophylls and thereby making them unfit for their normal physiological function.

3. Phycobillins (red and blue pigments)

These also contain four pyrrol rings but lack Mg and the phytol chain.

Location of photosynthetic pigments in chloroplast

The photosynthetic pigments are located in grana portions of the chloroplast. They are present in the thylakoids membrane or membrane of grana lamella. The membrane of thylakoids is made up of proteins and lipids. The hydrophilic *heads* of the chlorophyll molecules remain embedded in the protein layer while lipophilic phytol tail in the lipid layer. The other pigments are thought to be present along with chlorophyll molecules.

Distribution of photosynthetic pigments in plant kingdom

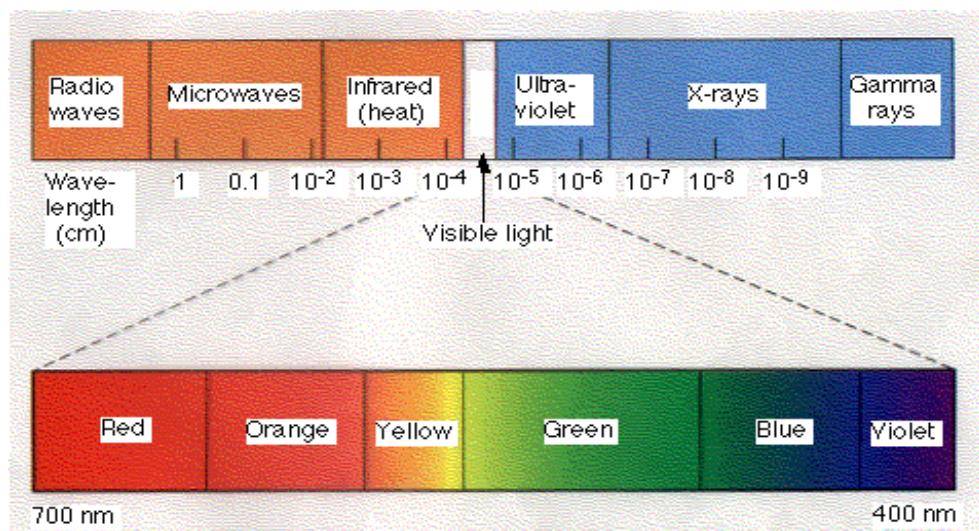
Pigments	Distribution in plant kingdom
Chlorophylls	
Chlorophyll <i>a</i>	All photosynthesizing plants except bacteria
Chlorophyll <i>b</i>	Higher plants and green algae
Chlorophyll <i>c</i>	Diatoms and brown algae
Chlorophyll <i>d</i>	Red algae
Bacteria chlorophylls	Purple and green bacteria
Carotenoids	
Carotenes (α and β)	Higher plants and algae
Xanthophylls	Higher plants and algae
Lutein	Green leaves and Green and Red algae
Violaxanthin	Green leaves
Fucoxanthin	Brown algae
Phycobillins	
Phycocyanins	Blue green algae and red algae
Phycoerythrins	Blue green algae and Red algae
Allophycocyanin	Blue - green and Red algae

Light

Light has both wave-like and particle-like properties. Light can be considered as one form of electromagnetic radiation, and as such it can be described by its wavelength and frequency.

The Electromagnetic Spectrum

- The EM spectrum spans from very high frequency (short wavelength) radiation such as gamma and cosmic rays to very low frequency (long wavelength) radiation such as radio waves. The numbers in the diagram above refer to wavelength in centimeters.
- PAR = "photosynthetically active radiation" (400-700 nm). This is the part of the spectrum that is detected as "visible light"
- 400 nm = blue light, 700 nm = red light
- The region of 400 to 700 nm is the predominant waveband that reaches the surface of the Earth. Other regions of the spectrum are absorbed by molecules in the atmosphere.
- Pigments are molecules that absorb specific wavelengths of light. **Chlorophyll** and its associated accessory pigments absorb radiation predominantly in the region of PAR.
- Chlorophyll absorbs mainly blue and red photons.



Below 280 nm	-	X rays, Gamma rays and Cosmic rays
280-390 nm	-	Ultra violet radiation
400-510 nm	-	Blue light
510-610 nm	-	Green light
610-700 nm	-	Red light
700-1000 nm	-	Far red light (IR)

} Visible light (PAR)
(VIBGYOR)

Photosynthetic pigments absorb light energy only in the visible part of the spectrum. The earth receives only about 40% (about 5×10^{20} K cal) of the total solar energy. The rest is either absorbed by the atmosphere or scattered into the space. Only about 1% of the total solar energy received by the earth is absorbed by the pigments and utilized in photosynthesis.

Absorption spectra of chlorophyll

The absorption of different wavelengths of light by a particular pigment is called absorption spectrum. Chlorophylls absorb maximum light in the violet blue and red part of the spectrum. The absorption peaks of chlorophyll *a* are 410 and 660; for chlorophyll *b* 452 and 642. Carotenoids absorb light energy in blue and blue green part of the spectrum.

Transfer of light energy absorbed by accessory pigments to photo systems

The light energy absorbed by accessory pigments is transferred to **specialized chlorophyll a called photo systems**. The transfer of light energy from accessory pigments to chlorophyll a is called as resonance transfer and takes part in primary photochemical reaction in photosynthesis. Chlorophyll a molecules also absorb light energy directly. As a result of absorbing the light energy, the chlorophyll molecule gets excited.

The excited molecule or the atom may return to the ground state in three ways.

1. By losing its remaining extra energy in the form of heat
2. By losing extra energy in the form of radiant energy (*phosphorescence*) and the chlorophyll molecules emit phosphorescent light even after the incident radiant light is cut off. The phosphorescent light is of longer wavelength than incident light and also fluorescent light.
3. Electrons carrying the extra energy may be expelled from the molecule and is consumed in some further photochemical reaction and the fresh normal electron returns to the molecule (electron transfer)

Quantum requirement and quantum yield

Light rays consist of tiny particles called *photons* and the energy carried by a photon is called *quantum*. The number of photons (quantum) required to release one molecule of oxygen in photosynthesis is called *quantum requirement*. On the other hand, the number of oxygen molecules released per photon of light in photosynthesis is called as *quantum yield*. The quantum yield is always in fraction of one.

MECHANISM OF PHOTOSYNTHESIS

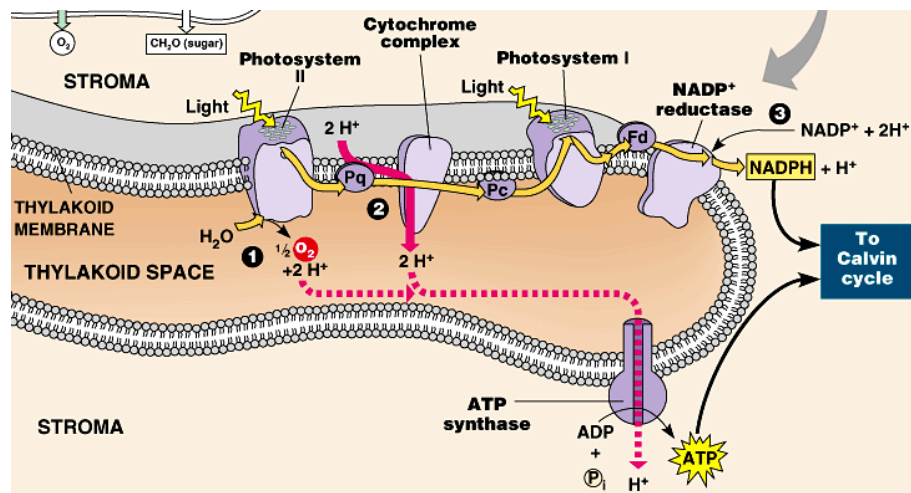
The discovery of red drop and the Emerson's enhancement effect led the scientists to suggest that photosynthesis is driven by two photochemical processes. These processes are associated with two groups of photosynthetic pigments called as *pigment system I* and *pigment system II*. Wavelength of

light shorter than 680 nm affect both the pigments systems while wavelength longer than 680 nm affect only pigment system I.

The biosynthesis of glucose by the chloroplast of green plants using water and CO₂ in the presence of light is called photosynthesis. Photosynthesis is a complex process of synthesis of organic food materials. It is a complicated oxidation- reduction process where water is oxidized and CO₂ is reduced to carbohydrates. The mechanism of photosynthesis consists of two parts.

1. Light reaction / Primary photochemical reaction / Hill's reaction/ Arnon's cycle
2. Dark reaction / Black man's reaction / Path of carbon in photosynthesis.

Light reaction

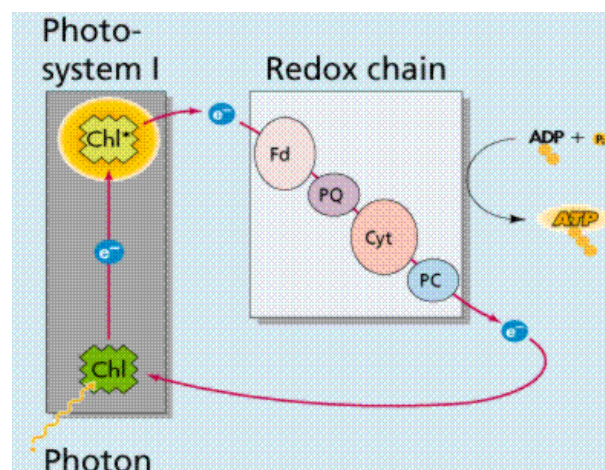


- The light absorption by reaction centre in photosystem II results in excitation and under excitation state it loses a electron into electron transport chain
- Photosystem in turn derives electron from water (ultimate donor of electron) leading to spilling up of water into electrons and protons
- When an electron is removed from a molecule, it is said to be OXIDIZED. Thus, the reaction center chlorophyll becomes **photo-oxidized**. This is a fundamental part of the photosynthetic process.
- plastocyanin, PSI, and ferredoxin.

- Each of the components of the electron transport chain has the ability to transfer an electron from a DONOR to an ACCEPTOR. (Plastoquinone also transfers a proton). That is, each carrier undergo successive rounds of OXIDATION AND REDUCTION.
- The electron then moves through the **electron transport system** and is ultimately transferred to NADP. The product, NADPH, is a source of **photochemical reducing power**.
- Components of the electron transport system (in order) are PSII, plastoquinone, cytochrome b/f complex,
- The terminal or ultimate electron **acceptor** is NADP. The product, **NADPH** is a form of **electrochemical reducing power** used to convert CO₂ to carbohydrate. NADPH is also used in many other biosynthetic reactions besides photosynthesis.
- There is vectorial translocation of protons into the lumen from stroma and water as electrons move from water to NADP. This sets up a **transmembrane electrochemical proton gradient**, or more simply, **delta pH**. This creates a force called **proton motive force (PMF)**
- The delta pH is required to synthesize ATP. The enzyme that carries out this reaction is a multi-subunit protein complex known as the **ATP synthase**. It is bound to the thylakoid membrane.
- Thus the products of the light reactions are NADPH and ATP.

Photophosphorylation

The production of ATP using the energy of sunlight is called **photophosphorylation**. The above series of reactions is referred to as **linear electron transport** since it involves the transfer of electrons from a donor molecule (water) to an acceptor molecule (NADP). ATP formation in this process is referred to as **non-cyclic photophosphorylation**. The other type is **cyclic photophosphorylation** which involves cyclic electron transport around PSI. The purpose of cyclic electron flow is to maintain a pH gradient to supply the "extra" ATP required in the dark reaction.



Significance of cyclic photophosphorylation

1. During cyclic phosphorylation, photolysis of water, O_2 evolution and reduction of NADP do not take place.
2. The electron returns or cycles back to original position in the P700 . Here, chlorophyll molecule serves both as donor and acceptor of the electron.
3. It generates energy rich ATP molecules at two sites

Non cyclic photophosphorylation

The electron released from photosystem II goes to photosystem I. The main function of non cyclic electron transport is to produce the assimilatory powers such as $NADPH_2$ and ATP. In this scheme of electron transport, the electron ejected from pigment system II did not return to its place of origin, instead it is taken up by pigment system I. Similarly, the electron ejected from pigment system I did not cycle back and was consumed in reducing NADP. Therefore, this electron transport has been called as non-cyclic electron transport and accompanying phosphorylation as non-cyclic photophosphorylation.

The non cyclic photophosphorylation takes the shape of Z and hence it is called by the name Z-scheme. Non cyclic photophosphorylation and O_2 evolution are inhibited by CMU and DCMU.

Significance of non cyclic electron transport

1. It involves PS I and PSII
2. The electron expelled from P680 of PSII is transferred to PS I and hence it is a non cyclic electron transport.
3. In non cyclic electron transport, photolysis of water (Hill's reaction and evolution of O_2) takes place.
4. Phosphorylation (synthesis of ATP molecules) takes place at only one place.
5. The electron released during photolysis of water is transferred to PS II.
6. The hydrogen ions (H^+) released from water are accepted by NADP and it becomes $NADPH_2$
7. At the end of non cyclic electron transport, energy rich ATP, assimilatory power $NADPH_2$ and oxygen from photolysis of water are observed.
8. The ATP and $NADPH_2$ are essential for the dark reaction wherein, reduction of CO_2 to carbohydrate takes place.

Comparison of cyclic and non cyclic electron transport and photophosphorylation in chloroplasts

1	Cyclic electron transport and photo phosphorylation in chloroplasts	Non cyclic electron transport and photo phosphorylation in chloroplasts
2	Associated with pigment system I	Associated with pigment system I and II
3	The electron expelled from chlorophyll molecule is cycled back	The electron expelled from chlorophyll molecule is not cycled back. But, its loss is compensated by electron coming from photolysis of water
4	Photolysis of water and evolution of O ₂ do not take place	Photolysis of water and evolution of O ₂ take place
5	Phosphorylation takes place at two places	Phosphorylation takes place at only one place
6.	NADP ⁺ is not reduced	NADP ⁺ is reduced to NADPH ⁺ + H ⁺

Red drop and Emerson's enhancement effect

Robert Emerson noticed a sharp decrease in quantum yield at wavelength greater than 680 nm, while determining the quantum yield of photosynthesis in chlorella using monochromatic light of different wavelengths. Since this decrease in quantum yield took place in the red part of the spectrum, the phenomenon was called as red drop. Later, they found that the inefficient far-red light beyond 680 nm could be made fully efficient if supplemented with light of shorter wavelength (blue light). The quantum yield from the two combined beams of light was found to be greater than the sum effects of both beams used separately. This enhancement of photosynthesis is called as Emerson's Enhancement.

PHOTOSYNTHETIC PATHWAYS - C₃, C₄ AND CAM

Dark reaction or Blackman's reaction or Path of carbon in photosynthesis

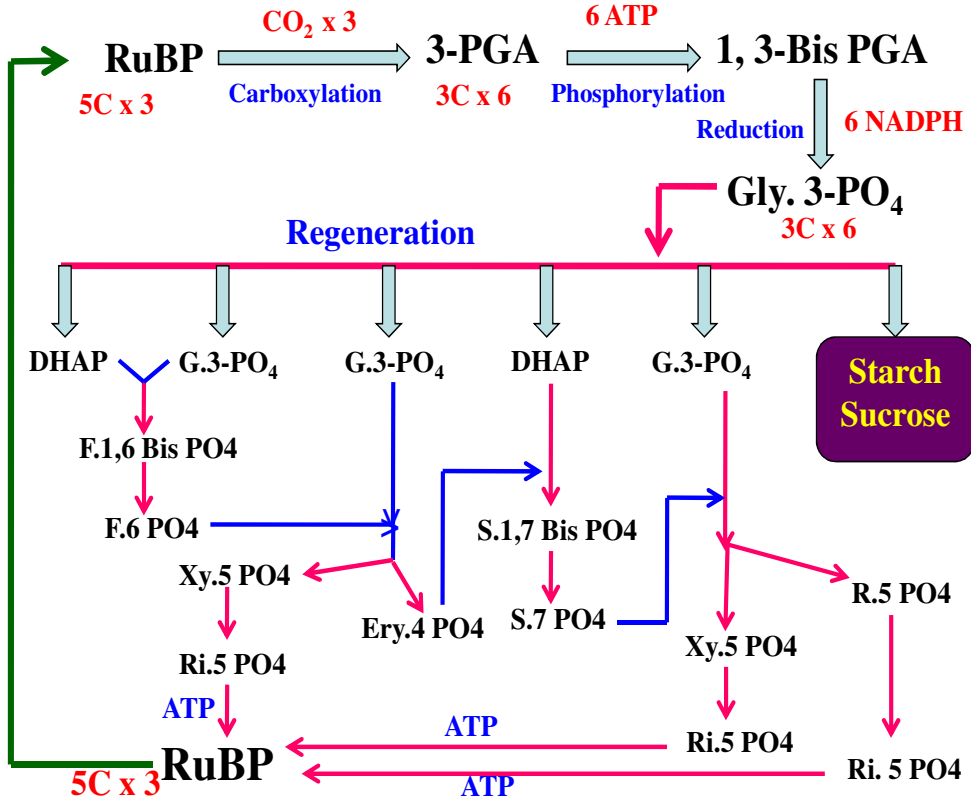
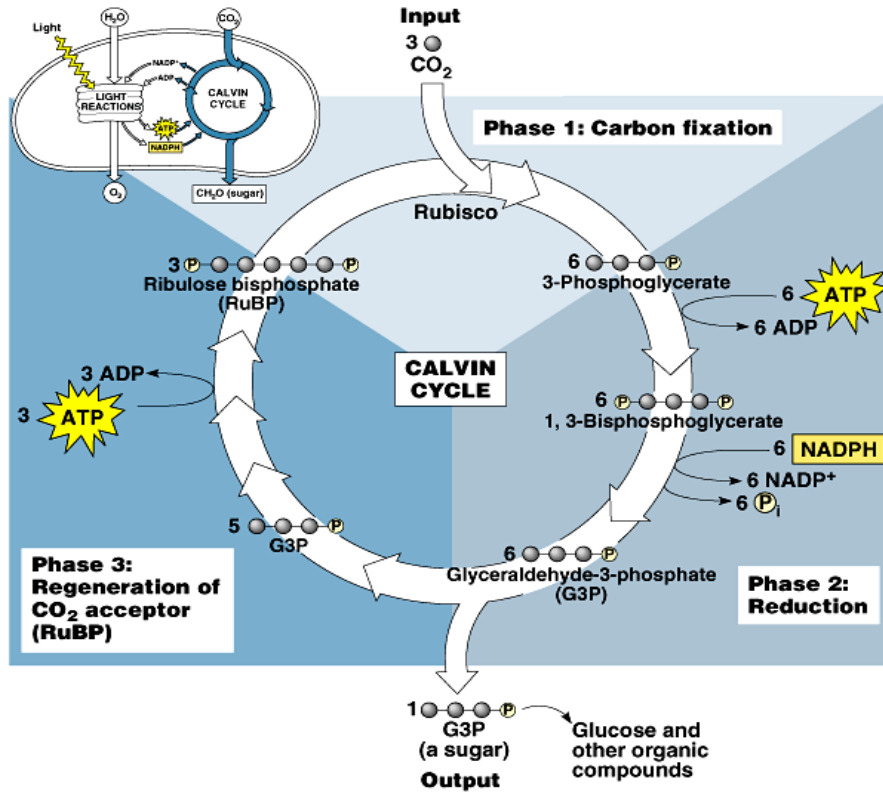
This is the second step in the mechanism of photosynthesis. The chemical processes of photosynthesis occurring independent of light is called dark reaction. It takes place in the stroma of chloroplast. The dark reaction is purely enzymatic and it is slower than the light reaction. The dark reactions occur also in the presence of light where the sugars are synthesized from CO₂. The energy poor CO₂ is fixed to energy rich carbohydrates using the energy rich compound, ATP and the assimilatory power, NADPH₂ of light reaction. The process is called carbon fixation or carbon assimilation. Since Blackman demonstrated the existence of dark reaction, the reaction is also called as Blackman's *reaction*. In dark reaction two types of cyclic reactions occur

1. Calvin cycle or C₃ cycle
2. Hatch and Slack pathway or C₄ cycle

Calvin cycle or C₃ cycle

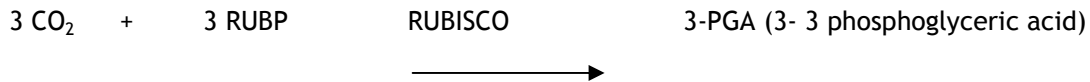
It is a cyclic reaction occurring in the dark phase of photosynthesis. In this reaction, CO₂ is converted into sugars and hence it is a process of carbon fixation. The Calvin cycle was first observed by Melvin Calvin in chlorella, unicellular green algae. Calvin was awarded Nobel Prize for this work in 1961. Since the first stable compound in Calvin cycle is a 3 carbon compound (3 phosphoglyceric acid), the cycle is also called as C₃ cycle. The reactions of Calvin's cycle occur in three phases.

1. Carboxylation
2. Reduction
3. Regeneration



1. Carboxylative phase

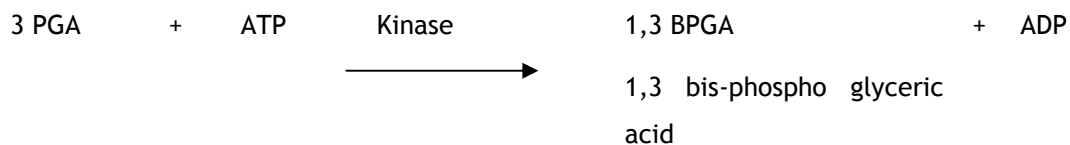
Three molecules of CO_2 are accepted by 3 molecules of 5C compound v ribulose bis-phosphate (RUBP) to form three molecules of an unstable intermediate 6C compound. This reaction is catalyzed by the enzyme, RUBISCO. Ribulosebiphosphate Carboxylase Oxygenase is a bifunctional enzyme. It can do both carboxylation and oxygenation function.



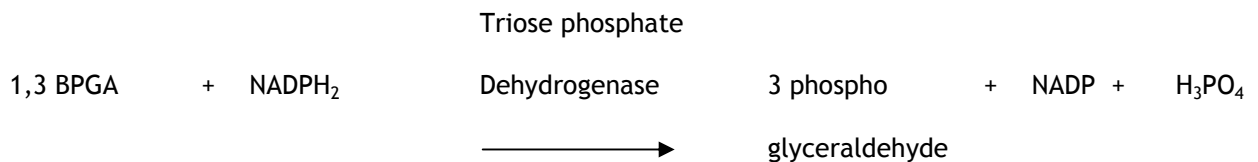
3 phosphoglyceric acid (PGA) is the first stable product of dark reaction of photosynthesis and since it is a 3 carbon compound, this cycle is known as C3 cycle.

2. Reductive phase

Six molecules of 3PGA are phosphorylated by 6 molecules of ATP (produced in the light reaction) to yield 6 molecules of 1-3 diphospho glyceric acid and 6 molecules of ADP. This reaction is catalyzed by the enzyme, Kinase



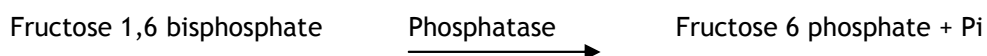
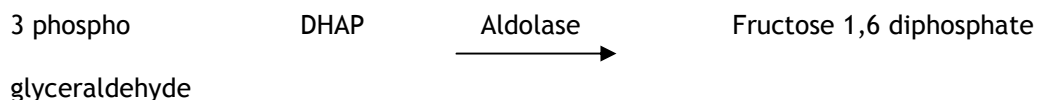
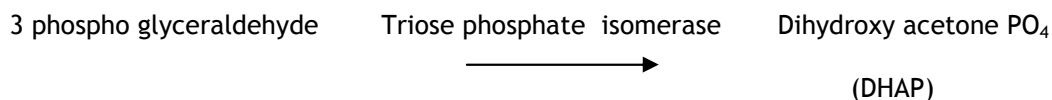
Six molecules of 1,3 BPGA acid are reduced with the use of 6 molecules of NADPH_2 (produced in light reaction) to form 6 molecules of 3 phospho glyceraldehyde. This reaction is catalysed by the enzyme, triose phosphate dehydrogenase.



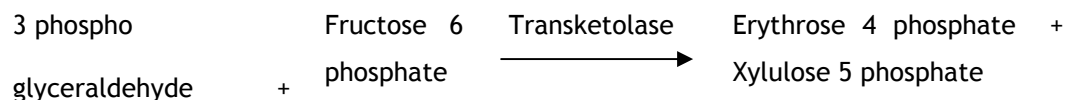
3. Regenerative phase

In the regenerative phase, the ribose diphosphate is regenerated. It involves the following steps.

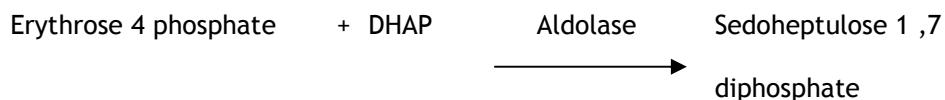
- Some of the molecules of 3 phospho glyceraldehyde into dihydroxy acetone phosphate. Both 3 phospho glyceraldehyde and dihydroxy acetone phosphate then unite in the presence of the enzyme, aldolase to form fructose, 1-6 diphosphate.



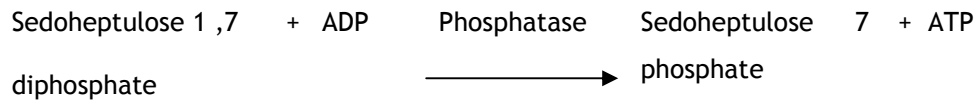
- 3 phospho glyceraldehyde reacts with fructose 6 phosphate in the presence of enzyme transketolase to form erythrose 4 phosphate (4C sugar) and xylulose 5 phosphate(5C sugar)



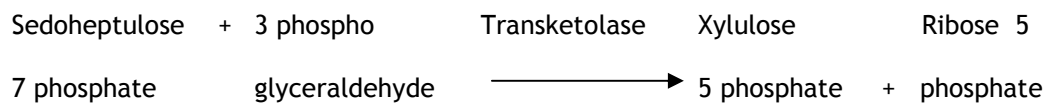
- Erythrose 4 phosphate combines with dihydroxy acetone phosphate in the presence of the enzyme aldolase to form sedoheptulose 1,7 diphosphate(7C sugar)



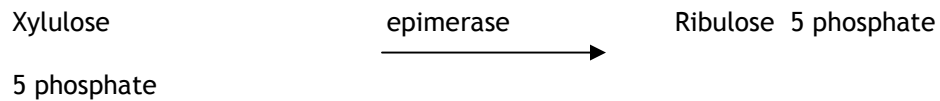
- Sedoheptulose 1, 7 diphosphate loses one phosphate group in the presence of the enzyme phosphatase to form sedoheptulose 7 phosphate.



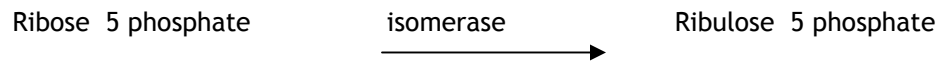
- Sedoheptulose phosphate reacts with 3 phospho glyceraldehyde in the presence of transketolase to form xylulose 5 phosphate and ribose 5 phosphate (both % c sugars)



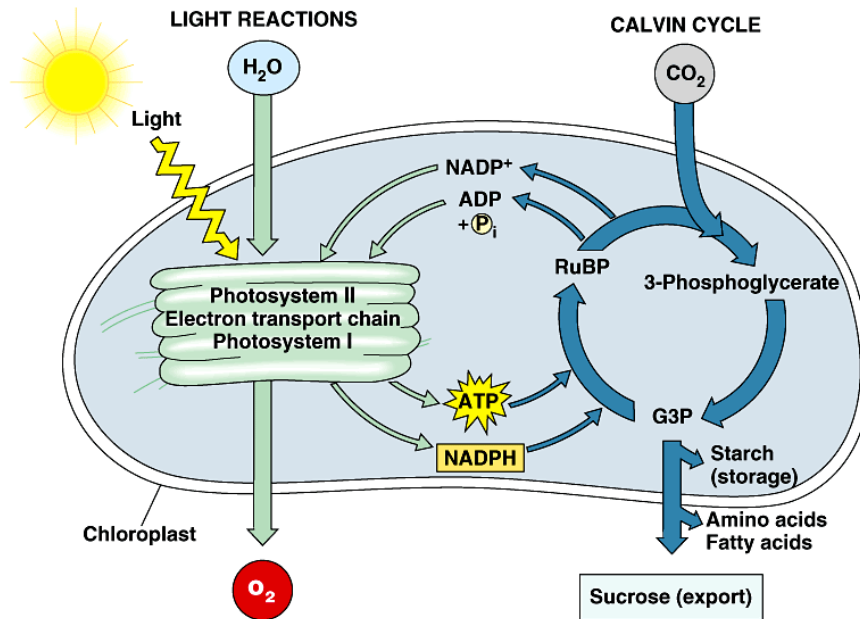
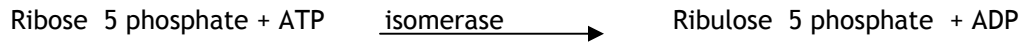
- Formation of Ribulose 5 phosphate from xylulose 5 phosphate.



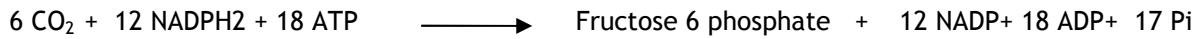
- Formation of Ribulose 5 phosphate from Ribose 5 phosphate



- Formation of Ribulose 1,5 bis phosphate from ribulose 5 phosphate



In the dark reaction, CO₂ is fixed to carbohydrates and the CO₂ acceptor ribulose diphosphate is regenerated. In Calvin cycle, 12 NADPH₂ and 18 ATPs are required to fix 6 CO₂ molecules into one hexose sugar molecule (fructose 6 phosphate).



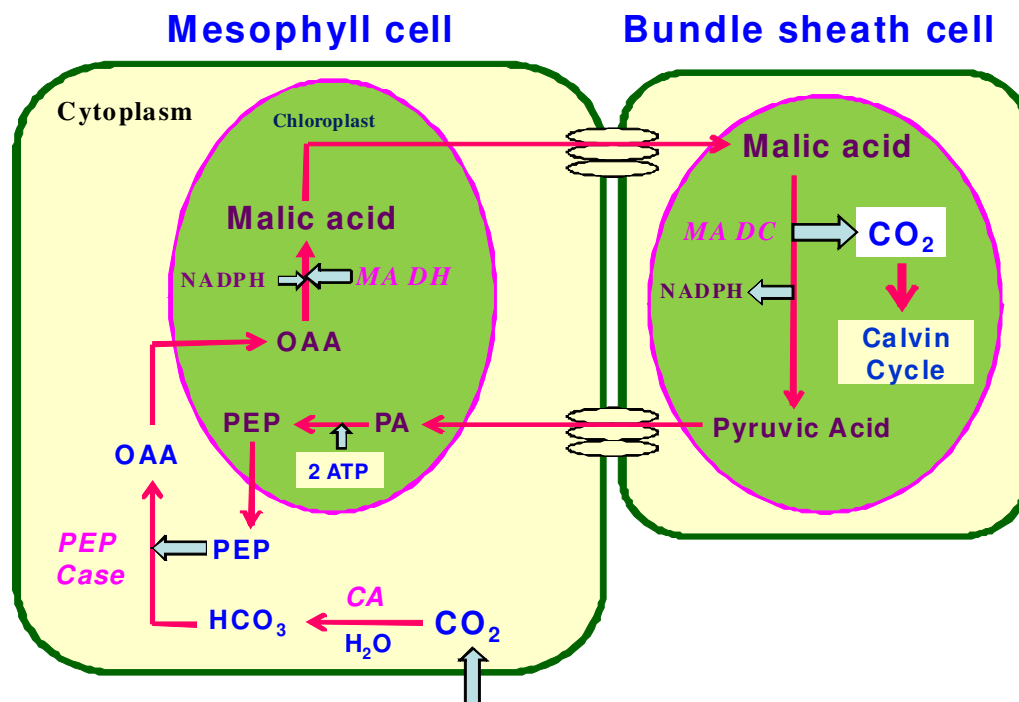
C4 CYCLE OR HATCH AND SLACK PATHWAY

It is the alternate pathway of C₃ cycle to fix CO₂. In this cycle, the first formed stable compound is a 4 carbon compound viz., oxaloacetic acid. Hence it is called C₄ cycle. The path way is also called as Hatch and Slack as they worked out the pathway in 1966 and it is also called as C₄ dicarboxylic acid pathway. This pathway is commonly seen in many grasses, sugar cane, maize, sorghum and amaranthus.

Characteristics feature of C₄ plants

1. Most are tropical in origin
2. They have high temperature optima for growth and high light intensity for photosynthesis.
3. They have very high Water Use Efficiency and high Nitrogen Use Efficiency
4. Have high crop growth rate
5. Thrive well in low water, low Nitrogen soil
6. They have kranz anatomy

Eg. Maize, Sugarcane, Millets, Bajra, Sorghum



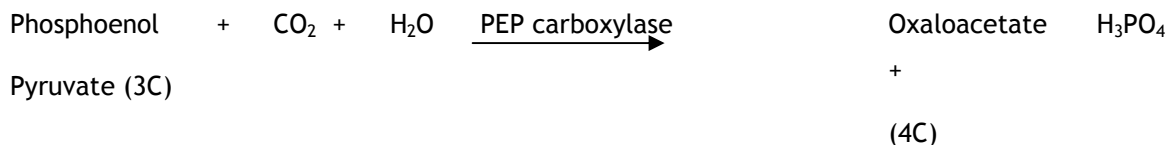
The C₄ plants show a different type of leaf anatomy. The chloroplasts are dimorphic in nature. In the leaves of these plants, the vascular bundles are surrounded by bundle sheath of larger parenchymatous cells. These bundle sheath cells have chloroplasts. These chloroplasts of bundle

sheath are larger, lack grana and contain starch grains. The chloroplasts in mesophyll cells are smaller and always contain grana. This peculiar anatomy of leaves of C4 plants is called Kranz anatomy. The bundle sheath cells are bigger and look like a ring or wreath. Kranz in German means wreath and hence it is called Kranz anatomy. The C4 cycle involves two carboxylation reactions, one taking place in chloroplasts of mesophyll cells and another in chloroplasts of bundle sheath cells. There are four steps in Hatch and Slack cycle:

1. Carboxylation
2. Breakdown
3. Splitting
4. Phosphorylation

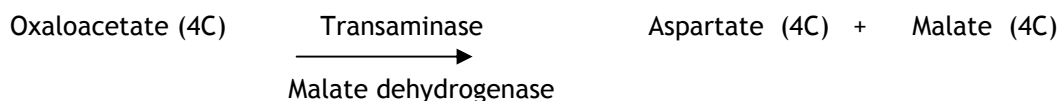
1. Carboxylation

It takes place in the chloroplasts of mesophyll cells. Phosphoenolpyruvate, a 3 carbon compound picks up CO₂ and changes into 4 carbon oxaloacetate in the presence of water. This reaction is catalysed by the enzyme, phosphoenol pyruvate carboxylase.



2. Breakdown

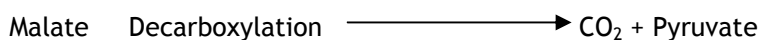
Oxaloacetate breaks down readily into 4 carbon malate and aspartate in the presence of the enzyme, transaminase and malate dehydrogenase.



These compounds diffuse from the mesophyll cells into sheath cells.

3. Splitting

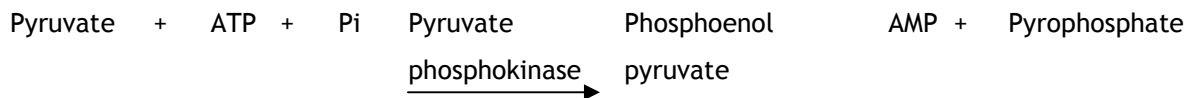
In the sheath cells, malate and aspartate split enzymatically to yield free CO₂ and 3 carbon pyruvate. The CO₂ is used in Calvin's cycle in the sheath cell.



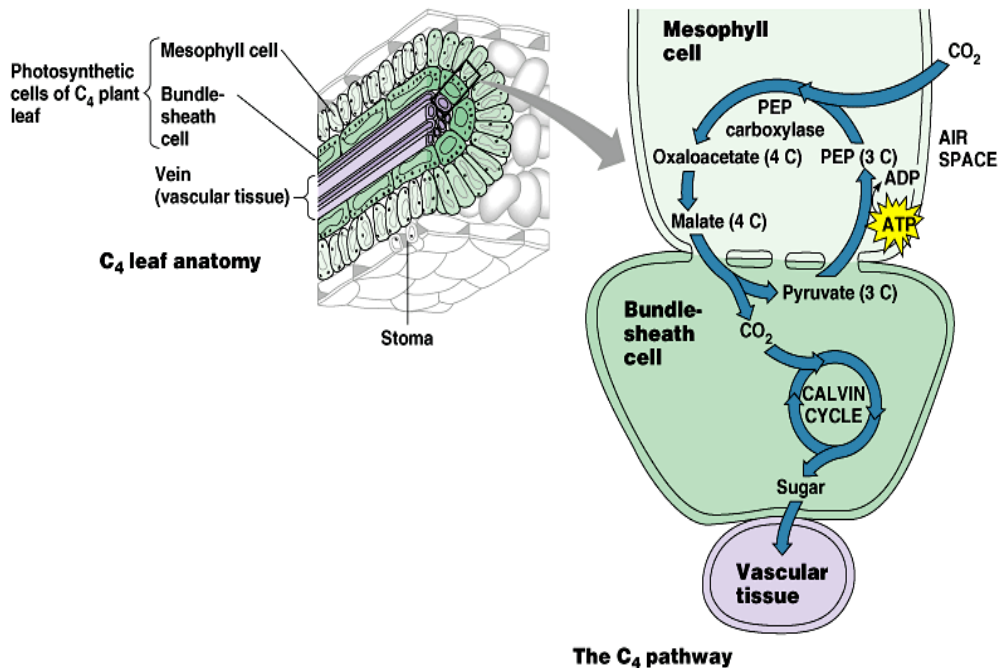
The second Carboxylation occurs in the chloroplast of bundle sheath cells. The CO₂ is accepted by 5 carbon compound ribulose diphosphate in the presence of the enzyme, carboxy dismutase and ultimately yields 3 phosphoglyceric acid. Some of the 3 phosphoglyceric acid is utilized in the formation of sugars and the rest regenerate ribulose diphosphate.

4. Phosphorylation

The pyruvate molecule is transferred to chloroplasts of mesophyll cells where, it is phosphorylated to regenerate phosphoenol pyruvate in the presence of ATP. This reaction is catalysed by pyruvate phosphokinase and the phosphoenol pyruvate is regenerated.



In Hatch and Slack pathway, the C₃ and C₄ cycles of carboxylation are linked and this is due to the Kranz anatomy of the leaves. The C₄ plants are more efficient in photosynthesis than the C₃ plants. The enzyme, phosphoenol pyruvate carboxylase of the C₄ cycle is found to have more affinity for CO₂ than the ribulose diphosphate carboxylase of the C₃ cycle in fixing the molecular CO₂ in organic compound during Carboxylation.



CRASSULACEAN ACID METABOLISM (CAM) CYCLE

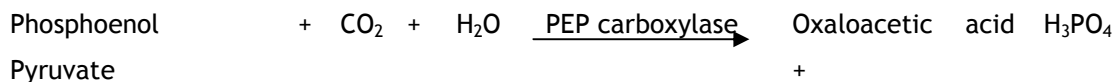
CAM is a cyclic reaction occurring in the dark phase of photosynthesis in the plants of Crassulaceae. It is a CO₂ fixation process wherein, the first product is malic acid. The plants exhibiting CAM cycle are called CAM plants. Most of the CAM plants are succulents e.g., Bryophyllum, Kalanchoe, Crassula, Sedium, Kleinia etc. It is also seen in certain plants of Cactus e.g. Opuntia, Orchid and Pine apple families. CAM plants are usually succulents and they grow under extremely xeric conditions. In these plants, the leaves are succulent or fleshy. The mesophyll cells have larger number of chloroplasts and the vascular bundles are not surrounded by well defined bundle sheath cells. In these plants, the stomata remain open during night and closed during day time. The CAM plants are adapted to photosynthesis and survival under adverse xeric conditions. CAM plants are not as efficient as C₄ plants in photosynthesis. But they are better suited to conditions of extreme desiccation.

CAM involves two steps:

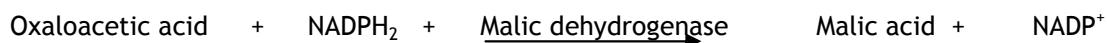
1. Acidification
2. Deacidification

Acidification

In darkness, the stored carbohydrates are converted into phosphoenol pyruvic acid by the process of Glycolysis. The stomata in CAM plants are open in dark and they allow free diffusion of CO₂ from the atmosphere into the leaf. Now, the phosphoenolpyruvic acid carboxylated by the enzyme phosphoenol pyruvic acid carboxylase and is converted into oxaloacetic acid.



The oxaloacetic acid is then reduced to malic acid in the presence of the enzyme malic dehydrogenase. The reaction requires NADPH produced in Glycolysis.



The malic acid produced in dark is stored in the vacuole. The malic acid increases the acidity of the tissues.

Deacidification (Decarboxylation)

During day time, when the stomata are closed, the malic acid is decarboxylated to produce pyruvic acid and evolve carbon dioxide in the presence of the malic enzyme. When the malic acid is removed, the acidity decreases the cells. This is called deacidification. One molecule of NADP^+ is reduced in this reaction.



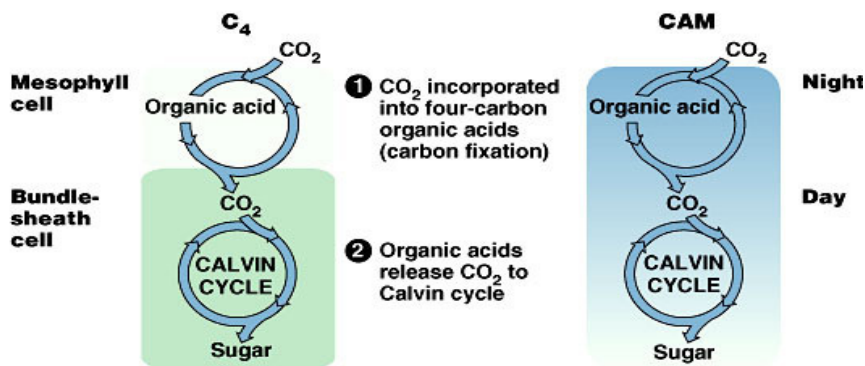
The pyruvic acid may be oxidized to CO_2 by the pathway of Krebs's cycle or it may be reconverted to phosphoenol pyruvic acid and synthesize sugar by C_3 cycle. The CO_2 released by deacidification of malic acid is accepted by ribulose diphosphate and is fixed to carbohydrate by C_3 cycle.

CAM is a most significant pathway in succulent plants. The stomata are closed during day time to avoid transpiration loss of water. As the stomata are closed, CO_2 cannot enter into the leaves from the atmosphere. However, they can carry out photosynthesis during the day time with the help of CO_2 released from organic acids. During night time, organic acids are synthesized in plenty with the help of CO_2 released in respiration and the CO_2 entering from the atmosphere through the open stomata. Thus, the CO_2 in dark acts as survival value to these plants.



Sugarcane

Pineapple



(a) Spatial separation of steps

(b) Temporal separation of steps

Comparison of the plants of C₃ and C₄ cycle

	C ₃ Plant	C ₄ Plant
1.	Only C ₃ cycle is found	Both C ₄ and C ₃ cycles are found.
2.	The efficiency of CO ₂ absorption at low concentration is far less and hence, they are less efficient.	The efficiency of CO ₂ absorption at low concentration is quite high and hence, they are more efficient plants.
3.	The CO ₂ acceptor is Ribulose-1, 5-diphosphate.	The CO ₂ acceptor is phospho enol pyruvate.
4.	The first stable product is phospho glyceric acid (PGA).	Oxaloacetate (OAA) is the first stable product.
5.	Plants show one type of chloroplast (monomorphic type).	Plants show dimorphic type of chloroplast. The chloroplast of parenchymatous bundle sheath is different from that of mesophyll cells (dimorphic type).
6.	In each chloroplast, two pigment systems (Photosystem I and II) are present.	In the chloroplasts of bundle sheath cells, the photosystem II is absent. Therefore, these are dependent on mesophyll chloroplasts for the supply of NADPH + H ⁺ .
7.	The Calvin cycle enzymes are present in mesophyll chloroplast. Thus, the Calvin cycle occurs.	Calvin cycle enzymes are absent in mesophyll chloroplasts. The cycle occurs only in the chloroplasts of bundle sheath cells.
8.	The CO ₂ compensation point is 50-150 ppm CO ₂ .	The CO ₂ compensation point is 0-10 ppm CO ₂ .
9.	Photorespiration is present and easily detectable.	Photorespiration is present only to a slight degree or absent.

10.	The CO ₂ concentration inside leaf remains high (about 200 ppm).	The CO ₂ concentration inside the leaf remains low (about 100 ppm).
11.	The ¹³ C/ ¹² C ratio in C-containing compounds remains relatively low	The ratio is relatively high, <i>i.e.</i> C ₄ plants are more enriched with ¹³ C than C ₃ plants.
12.	Net rate of photosynthesis in full sunlight (10,000 - 12,000 ft. c.) is 15-25 mg. of CO ₂ per dm ² of leaf area per hour.	It is 40-80 mg. of CO ₂ per dm ² of leaf area per hour. That is, photosynthetic rate is quite high. The plants are efficient.
13.	The light saturation intensity reaches in the range of 1000-4000 ft. c.	It is difficult to reach saturation even in full sunlight.
14.	Bundle sheath cells are unspecialized.	The bundle sheath cells are highly developed with unusual construction of organelles.
15.	The optimum temperature for the process is 10-25°C.	In these plants, it is 30-45°C and hence, they are warm climate plants. At this temperature, the rate of photosynthesis is double than that is in C ₃ plants.
16.	18 ATPs are required to synthesize one glucose molecule.	30 ATPs are required to synthesize one glucose molecule.

Factors affecting photosynthesis

I. External factors

1. Light

It is the most important factor of photosynthesis. Any kind of artificial light such as electric light can induce photosynthesis. Out of the total solar energy, only 1-2 % is used for photosynthesis and the rest is used for other metabolic activities. The effect of light on photosynthesis can be studied under three categories.

a. Light intensity

Wolkoff (1966) found that the rate of photosynthesis is directly proportional to light intensity. But at the extremely high light intensities do not favor for higher photosynthetic rates. The high light intensity which fails to accelerate photosynthesis is called light saturation intensity. Of the light falling on a leaf, about 80 per cent is absorbed, 10 per cent is reflected and 10 % is transmitted. The rate of photosynthesis is greater in intense light than in diffused light. The plants are grouped into two types on the basis of light requirement.

i. Heliophytes (Sun plants)

ii. Sciophytes (Shade plants)

At a specific light intensity, the amount of CO₂ used in photosynthesis and the amount of CO₂ released in respiration are volumetrically equal. This specific light intensity is known as light compensation point.

At very high light intensity, beyond a certain point, the photosynthetic cells exhibit photo oxidation. This phenomenon is called solarisation and as a result of this, inactivation of chlorophyll molecules, bleaching of chlorophyll molecules and even inactivation of some enzymes take place resulting in the destruction of whole photosynthetic apparatus. In general, low light intensity favours stomatal closure and in turn reduced rate of photosynthesis.

b. Light quality (wavelength)

Photosynthesis occurs only in the visible part of the light spectrum i.e., between 400 and 700 nm. The maximum rate of photosynthesis occurs at red light followed by blue light. The green light has minimum effect and photosynthesis cannot take place either in the infrared or in the ultraviolet light.

c. Light duration

In general tropical plants get 10-12 hours of light per day and this longer period of light favours photosynthesis.

2. Carbon dioxide

CO₂ is one of the raw materials required for photosynthesis. If the CO₂ concentration is increased at optimum temperature and light intensity, the rate of photosynthesis increases. But, it is also reported that very high concentration of CO₂ is toxic to plants inhibiting photosynthesis.

3. Temperature

The rate of photosynthesis increases by increase in temperature up to 40 °C and after this, there is reduction in photosynthesis. High temperature results in the denaturation of enzymes and thus, the dark reaction is affected. The temperature requirement for optimum photosynthesis varies with the plant species. For example, photosynthesis stops in many plants at 0 °C but in some conifers, it can

occur even at -35°C . Similarly photosynthesis stops beyond $40-50^{\circ}\text{C}$ in certain plants; but certain bacteria and blue green algae can perform photosynthesis even at 70°C .

4. Water

Water has indirect effect on the rate of photosynthesis although it is one of the raw materials for the process. The amount of water utilized in photosynthesis is quite small and even less than 1 per cent of the water absorbed by a plant. Water rarely acts as a limiting factor for photosynthesis. During water scarcity, the cells become flaccid and the rate of photosynthesis might go down.

5. Oxygen

Oxygen is a byproduct of photosynthesis and an increase in the O_2 concentration in many plants results in a decrease in the rate of photosynthesis. The phenomenon of inhibition of photosynthesis by O_2 was first discovered by Warburg (1920) in green alga *Chlorella* and this effect is known as Warburg's effect. This is commonly observed in C_3 plants.

In plants, there is a close relationship between Warburg's effect and photorespiration. The substrate of photorespiration is glycolate and it is synthesized from some intermediates of Calvin's cycle. In plants that show Warburg's effect, increased O_2 concentration result in diversion of these intermediates of Calvin cycle into the synthesis of glycolate, thereby showing higher rate of photorespiration and lower photosynthetic productivity.

6. Mineral elements

The elements like Mg, Fe, Cu, Cl, Mn, P etc are involved in the key reactions of photosynthesis and hence, the deficiency of any of these nutrients caused reduction in photosynthesis.

7. Chlorophyll content

It is very much essential to trap the light energy. In 1929, Emerson found direct relationship between the chlorophyll content and rate of photosynthesis. In general, the chlorophyll sufficient plants are green in colour showing efficient photosynthesis. The chlorotic leaves due to irregular synthesis of chlorophyll or breakdown of chlorophyll pigment exhibit inefficient photosynthesis.

8. Leaf

The leaf characters such as leaf size, chlorophyll content, number of stomata. Leaf orientation and leaf age are some of the factors that are responsible for photosynthesis. The maximum photosynthetic activity is usually seen in the physiologically functional and full size leaves (usually third/fourth leaf from the tip of the shoot system).

9. Carbohydrates

If the accumulated carbohydrates are not translocated, the photosynthetic rate is reduced and respiration is increased. Sugar is converted into starch and gets accumulated in the chloroplasts. This reduces the effective surface in the chloroplast and the rate of photosynthesis is decreased.

10. Phytohormones

Treharne (1970) reported first that photosynthesis may be regulated by plant hormone system. He found that gibberellic acid and cytokinin increase the carboxylating activity and photosynthetic rates. Meidner (1967) also reported that kinetin @ $3\mu\text{m}$ causes 12 per cent increase in photosynthesis within one hour of the treatment.

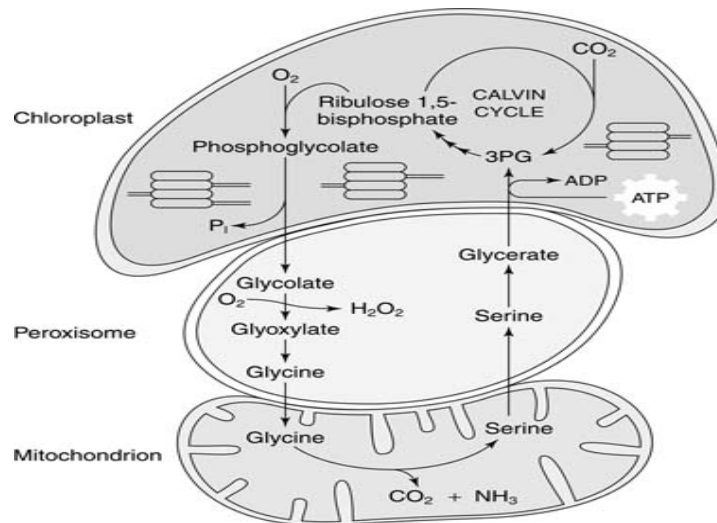
PHOTORESPIRATION

The excessive respiration that takes place in green cells in the presence of light is called as photorespiration. Decker (1955) discovered the process and it is also called as C₂ cycle as the 2 carbon compound glycolic acid acts as the substrate in photorespiration. In general, respiration takes place under both light and dark conditions. However in some plants, the respiration is more in light than in dark. It is 3-5 times higher than the rate of respiration in dark. Photorespiration is carried out only in the presence of light. But the normal respiration is not light dependent and it is called dark respiration.

In photorespiration, temperature and oxygen concentration play an important role. Photorespiration is very high when the temperature is between 25 and 30 °C. The rate of photorespiration increases with the increase in the concentration of oxygen. Three cell organelles namely chloroplast, peroxisome and mitochondria are involved in the photorespiration. This kind of respiration is seen in plants like cotton, pulses, capsicum, peas, tomato, petunia soybean, wheat, oats, paddy, chlorella etc and it is absent in grasses. Generally, photorespiration is found in C₃ plants and absent in C₄ plants.

Warberg effect: The competition between CO₂ and O₂ with CO₂ promoting photosynthesis and inhibiting glycolate formation inhibiting photorespiration and O₂ promoting glycolate formation and inhibiting photosynthesis is known as Warberg effect.

Mechanism



1. In the presence of excess oxygen and low CO_2 , ribulose 1,5 diphosphate produced in the chloroplast during photosynthesis is split into 2 phosphoglycolic acid and 3 phosphoglyceric acid by the enzyme, ribulose 1,5 diphosphate oxygenase
2. The 3 phosphoglyceric acid enters the Calvin cycle.
3. In the next step, phosphate group is removed from 2 phosphoglycolic acid to produce glycolic acid by the enzyme, phosphatase.
4. Glycolic acid then it come out of chloroplast and enter the peroxisome. Here, it combines with oxygen to form glyoxylic acid and hydrogen peroxide. This reaction is catalyzed by the enzyme, glycolic acid oxidase. Hydrogen peroxide is toxic and it is broken down into water and oxygen by the enzyme, Catalase. Photorespiration is an oxidation process. In this process, glycolic acid is converted into carbohydrate and CO_2 is released as the by product. As glycolic acid is oxidized in photorespiration, it is also called as glycolate metabolism.
5. The glyoxylic acid converted into glycine by the addition of one amino group with the help of the enzyme, amino transferase.
6. Now, the glycine is transported from the peroxisome into the mitochondria. In the mitochondria, two molecules of glycine condense to form serine and liberate carbon dioxide and ammonia.
7. Amino group is removed from serine to form hydroxyl pyruvic acid in the presence of the enzyme, transaminase.
8. Hydroxy pyruvic acid undergoes reduction with the help of NADH to form glyceric acid in the presence of enzyme alpha hydroxyl acid reductase.
9. Finally, regeneration of 3 phosphoglyceric acid occurs by the phosphorylation of glyceric acid with ATP. This reaction is catalyzed by the enzyme, Kinase.
10. The 3 phosphoglyceric acid is an intermediate product of Calvin cycle. If it enters the chloroplast, it is converted into carbohydrate by photosynthesis and it is suppressed nowadays with the increased CO_2 content in the atmosphere.

In C_4 plants, photo respiratory substrate, phosphoglycolate is not produced. Due to carbon dioxide enrichment mechanisms in C_4 plants, high carbon dioxide is maintained in bundle sheath cells, where RuBisCo is located. High CO_2 inhibit oxygenase reaction. Therefore no phosphoglycolate, so no photorespiration.

Carbon dioxide compensation point

The carbon dioxide concentration at which the rate of uptake of carbon dioxide will become equal in the rate of photo respiratory carbon dioxide release is called carbon dioxide compensation point. Carbon dioxide compensation point will be high where photorespiration is high.

Significance of photorespiration

1. Carbon dioxide is evolved during the process and it prevents the total depletion of CO₂ in the vicinity of chloroplasts.
2. The process causes oxidation of glycolic acid which arises as an unwanted byproduct of photosynthesis. The glycolic acid after oxidation is converted into carbohydrate but the remainder is converted into CO₂.
3. Photorespiration uses energy in the form of ATP and reduced nucleotides, but normal respiration yields ATP and reduced nucleotides.
4. It is believed that photorespiration was common in earlier days when CO₂ content was too low to allow higher rates.

Source sink relationship

Photosynthates: The product of photosynthesis or which are formed during photosynthesis, generally glucose/fructose is called photosynthates. Photosynthates are transported from leaf to different parts.

Source: A plant tissue or an organ which synthesis photosynthates and translocate to other developing tissue or storage organs.

Source strength: size x activity

Differences in CO₂ fixation (Rubisco & PEPCase)

Leaf characters - size, thickness, mesophyll size, compaction, vascular bundle

Carrying capacity of sieve element (temp., H₂O, nutrients, hormone)

Sink : A plant tissue or an organ which receives photosynthates for its metabolic activity leading to its growth and development or storage function.

Sink strength - size x activity

Potential capacity of the sink to accumulate assimilates

Competition among different sink

Movement of photosynthates from source to sink (in phloem) and movement of ions or nutrients from root to shoot (xylem) is known as **translocation**.

Identification of source and Sink limited conditions

- Defoliation studies - Under defoliated condition, if there is no reduction in yield indicates sink is limiting and not source

- Carbon di oxide enrichment studies - When the plants is exposed to higher concentration of CO₂, if there is an increase in yield indicates source limited condition especially in C₄ plants

UNIT IV: GROWTH PHYSIOLOGY

Growth is defined as a vital process that brings about a permanent and irreversible change in any plant or its part in respect to its size, form, weight and volume. Growth is restricted only to living cells and is accomplished by metabolic processes involving synthesis of macromolecules, such as nucleic acids, proteins, lipids and polysaccharides at the expense of metabolic energy.

Growth at cellular level is also accompanied by the organization of macromolecules into assemblages of membranes, plastids, mitochondria, ribosome and other cell organelles. Cells do not definitely increase in size but divide, giving rise to daughter cells. An important process during cell division is synthesis and replication of nuclear DNA in the chromosomes, which is then passed into the daughter cells. Therefore, the term growth is used to denote an increase in size by cell division and cell enlargement, together with the synthesis of new cellulose materials and the organization of cellular organelles.

Growth regions

Typical growth regions in plants are the apices of shoot and root. Such growing regions are known as apical meristems, primary meristems or regions of primary growth. These apical meristems are responsible for the increase in length, differentiation of various appendages and formation of plant tissues.

Phases of growth

Growth is not a simple process. It occurs in meristematic regions where the meristematic cell has to pass through the following 3 phases.

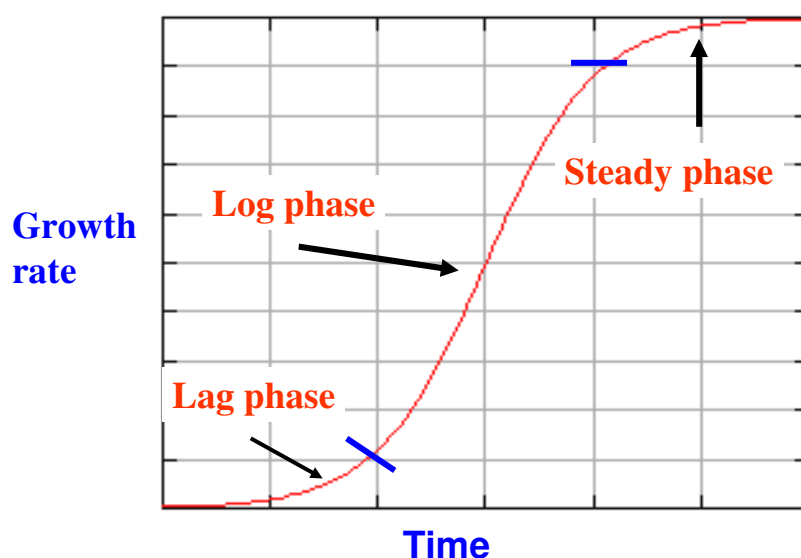
1. Cell formation phase
2. Cell elongation phase
3. Cell differentiation (cell maturation)

The cell formation phase is represented by meristematic zone and cell enlargement phase by cell elongation zone. The dividing meristematic cells are thin walled and have dense protoplasm with a large nucleus and with or without very small vacuoles. The intercellular spaces are also absent. The newly formed cells after the first phase of cell division have to pass through the second phase of cell enlargement. During the second phase of cell elongation on account of large quantities of solutes inside the growing cell, water enters the cell due to osmotic effect resulting in the increased turgidity and expansion and dilation of the thin and elastic cell wall. This phase also results in appearance of large vacuoles. In the last phase or cell maturation, the secondary walls are laid down and cell matures and gets differentiated into permanent tissue.

Growth curve

Growth curve is a graph obtained by plotting the growth rate of a plant against time factor. The growth rate of a cell, a plant organ, a whole plant or the whole life cycle of plant is measured in terms of length, size, area, volume or weight. It has been found that different growth phases result in 'S' shaped curve or sigmoid curve. In initial stages during the phase of cell formation, the growth rate increases slowly while it increases rapidly during the phase of cell elongation or cell enlargement and again slows down during the phase of cell maturation.

GROWTH RATE PHASES - GROWTH CURVE



The period during which the course of growth takes place is known as grand period of growth. Thus, in a standard growth curve, three well marked regions can be observed, the initial growth stage (lag phase), the grand period of growth (exponential or log phase) and the steady stage (maturity stage or senescence or stationary phase). The overall growth may be affected by external or internal factors but the S-shaped curve of grand period of growth is never influenced. This growth curve suits well to the entire life of an annual plant when measured in terms of dry weight against time. Early growth of the plant is limited by the amount of food reserves in the seed. When the emerged seedlings develop an adequate root system and enough leaf surfaces to support vigorous photosynthesis and anabolism, a period of rapid increase in size is possible.

High metabolic rates are not maintained indefinitely and eventually processes are set in motion that leads to cessation of growth. The factors responsible for the decrease in growth are competition for essential metabolites, growth substances, water, light or the accumulation of inhibitors, toxic substances or waste materials.

Blackman (1919) suggested that the growth of the plants can be represented by equation.

$$W_1 = W_0 e^{rt}$$

Where, W_1 is the final size (Wt, ht etc) after time t . W_0 is the initial size at the beginning of the time period. r is the rate at which plant substance is laid down during time t and e is the base of natural logarithm. Blackman pointed out that equation describes the way in which money placed at compound interest increases with time; the term compound interest law is used to describe such phenomenon. In banks, compound interest is usually applied quarterly or annually so that the increase in amount occurs as a jump. With plant system, compound interest is applied continuously and size increase follows a smooth curve.

From the equation, the final size of an organism (W_1) depends on the initial size (W_0). Larger seed give a larger plant. In addition, equation shows that plant size also depends on the magnitude of r , the relative growth rate. Blackman suggested that r might be used as a measure of the ability of the plant to produce new plant material and called r as the efficiency index. The plants with high efficiency index could be expected to outperform plants with low efficiency index.

Measurement of growth

The measurement of growth is possible in terms of either increase in weight or increase in volume or area. The common and simplest method for the measurement of growth can be a direct method by which the growth is measured by a scale at regular intervals from beginning to end. The other methods that can be used are horizontal microscope, auxanometers.

Factors influencing growth

Growth is affected by all factors that affect the activity of protoplasm. Both physiological and environmental factors such as water, minerals, photosynthesis, respiration, climate and edaphic factors significantly influence the growth. In general, factors can be grouped into external and internal factors.

External factors

1. Light

It has direct effect on photosynthesis and transpiration. Light in terms of intensity, quality and periodicity influence the growth very much.

Light intensity: A weak light promotes shortening of internodes and affects expansion of leaf. Very weak light reduces the rate of over all growth and also photosynthesis due to poor development of chlorophyll and higher rate of water loss from the plant.

Light quality: The different wavelengths of light have different responses to growth. In blue violet radiation, the internodal growth is pronounced while green colour light promotes the expansion of

leaves as compared to complete spectrum of visible light. The red light favours the growth while infra red and UV is detrimental to growth.

Light duration: There is remarkable effect of the duration of light on the growth. The induction and suppression of flowering depend on duration

2. Temperature

The plants have different temperature requirements based on the region where they are grown. In general, best growth takes place between 28 and 33 C. and it varies from temperate to tropical conditions. The optimum temperature requirement is essential for seed germination, growth, metabolic activities, flowering and yield.

3. Oxygen

The growth of the plant is directly proportional to the amount of oxygen which is essential for respiration during which the food materials are oxidized to release energy.

4. Carbon dioxide

It is one of the major factors that influence the photosynthesis. The rate of photosynthesis increases as the availability of CO₂ increases while other factors are not limiting.

5. Water

Water is an essential factor for growth. It is essential for uptake of nutrients, translocation of nutrients and food materials, regulating transpiration and for various physiological processes like photosynthesis, respiration and enzymatic activities.

6. Nutrients and food materials

The rate of growth is directly proportional to the availability of nutrients and food materials. The shortage of food supply affects the growth as it provides the growth material to the growing region and also it provides the potential energy to the growing region.

Internal factors

1. Growth hormones and their availability
2. Resistance to climatic, edaphic and biological stresses
3. Photosynthetic rate and respiration
4. Assimilate partitioning and nitrogen content
5. Chlorophyll and other pigments
6. Source-sink relationship and enzyme activities

Growth analysis

Growth analysis can be used to account for growth in terms that have functional or structural significance. The type of growth analysis requires measurement of plant biomass and assimilatory area (leaf area) and methods of computing certain parameters that describe growth. The growth parameters that are commonly used in agricultural research and the name of the scientists who proposed the parameters are given below.

LAI	-	Williams (1946)
LAR	-	Radford (1967)
LAD	-	Power <i>et al.</i> (1967)
SLA	-	Kvet <i>et al.</i> (1971)
SLW	-	Pearce <i>et al.</i> (1968)
NAR	-	Williams (1946)
CGR	-	Watson (1956)
RGR	-	Williams (1946)
HI	-	Nichiporovich (1951)

i. Leaf Area

This is the area of photosynthetic surface produced by the individual plant over a period of interval of time and expressed in $\text{cm}^2 \text{ plant}^{-1}$.

ii. Leaf Area Index (LAI)

Williams (1946) proposed the term, Leaf Area Index (LAI). It is the ratio of the leaf of the crop to the ground area over a period of interval of time. The value of LAI should be optimum at the maximum ground cover area at which crop canopy receives maximum solar radiation and hence, the TDMA will be high.

$$\text{LAI} = \frac{\text{Total leaf area of a plant}}{\text{Ground area occupied by the plant}}$$

iii. Leaf Area Ratio (LAR)

The term, Leaf Area Ratio (LAR) was suggested by Radford (1967), expresses the ratio between the area of leaf lamina to the total plant biomass or the LAR reflects the leafiness of a

plant or amount of leaf area formed per unit of biomass and expressed in $\text{cm}^2 \text{g}^{-1}$ of plant dry weight.

$$\text{LAR} = \frac{\text{Leaf area per plant}}{\text{Plant dry weight}}$$

iv. Leaf Weight Ratio (LWR)

It was coined by (Kvet *et al.*, 1971) Leaf weight ratio is expressed as the dry weight of leaves to whole plant dry weight and is expressed in g g^{-1} .

$$\text{LWR} = \frac{\text{Leaf dry weight}}{\text{Plant dry weight}}$$

v. Leaf Area Duration (LAD)

To correlate dry matter yield with LAI, Power *et al.* (1967) integrated the LAI with time and called as Leaf Area Duration. LAD takes into account, both the duration and extent of photosynthetic tissue of the crop canopy. The LAD is expressed in days.

$$\text{LAD} = \frac{L_1 + L_2}{2} \times (t_2 - t_1)$$

L_1 = LAI at the first stage

L_2 = LAI at the second stage, $(t_2 - t_1)$ = Time interval in days

vi. Specific Leaf Area (SLA)

Specific leaf area is a measure of the leaf area of the plant to leaf dry weight and expressed in $\text{cm}^2 \text{g}^{-1}$ as proposed by Kvet *et al.* (1971).

$$\text{SLA} = \frac{\text{Leaf area}}{\text{Leaf weight}}$$

vii. Specific Leaf Weight (SLW)

It is a measure of leaf weight per unit leaf area. Hence, it is a ratio expressed as g cm^{-2} and the term was suggested by Pearce *et al.* (1968). More SLW/unit leaf area indicates more biomass and a positive relationship with yield can be expected.

$$\text{SLW} = \frac{\text{Leaf weight}}{\text{Leaf area}}$$

viii. Absolute Growth Rate (AGR)

AGR is the function of amount of growing material present and is influenced by the environment. It gives Absolute values of biomass between two intervals. It is mainly used for a single plant or single plant organ e.g. Leaf growth, plant weight etc.

$$\text{AGR} = \frac{h_2 - h_1}{t_2 - t_1} \quad \text{cm day}^{-1}$$

Where, h_1 and h_2 are the plant height at t_1 and t_2 times respectively.

ix. Net Assimilation Rate (NAR)

The term, NAR was used by Williams (1946). NAR is defined as dry matter increment per unit leaf area or per unit leaf dry weight per unit of time. The NAR is a measure of the average photosynthetic efficiency of leaves in a crop community.

$$\text{NAR} = \frac{(W_2 - W_1)}{(t_2 - t_1)} \times \frac{(\log_e L_2 - \log_e L_1)}{(L_2 - L_1)}$$

Where, W_1 and W_2 is dry weight of whole plant at time t_1 and t_2 respectively

L_1 and L_2 are leaf weights or leaf area at t_1 and t_2 respectively

t_1 . t_2 are time interval in days

NAR is expressed as the grams of dry weight increase per unit dry weight or area per unit time ($\text{g g}^{-1} \text{day}^{-1}$)

x. Relative Growth Rate (RGR)

The term was coined by Williams (1946). Relative Growth Rate (RGR) expresses the total plant dry weight increase in a time interval in relation to the initial weight or Dry matter increment per unit biomass per unit time or grams of dry weight increase per gram of dry weight and expressed as unit dry weight / unit dry weight / unit time ($\text{g g}^{-1}\text{day}^{-1}$)

$$\text{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

Where, W_1 and W_2 are whole plant dry weight at t_1 and t_2 respectively

xi. Crop Growth Rate (CGR)

The method was suggested by Watson (1956). The CGR explains the dry matter accumulated per unit land area per unit time ($\text{g m}^{-2}\text{day}^{-1}$)

$$\text{CGR} = \frac{(W_2 - W_1)}{\rho (t_2 - t_1)}$$

Where, W_1 and W_2 are whole plant dry weight at time $t_1 - t_2$ respectively

ρ is the ground area on which W_1 and W_2 are recorded.

CGR of a species are usually closely related to interception of solar radiation

xii. Total dry matter production (TDMP) and its distribution

The TDMP is the biomass accumulated by the whole plant over a period of interval of time and its distribution (allocation) to different parts of the plant such as roots, stems, leaves and the economic parts which controls the sink potential.

xiii. Translocation percentage (TP)

The term translocation percentage indicates the quantum of photosynthates translocated from source (straw) to the grain (panicle/grains) from flowering to harvest.

$$\text{TP} = \frac{\text{Straw weight at flowering} - \text{straw weight at harvest}}{\text{Panicle weight at flowering} - \text{panicle weight at harvest}}$$

xiv. Light extinction coefficient

It is the ratio of light intercepted by crop between the top and bottom of crop canopy to the LAI.

$$K = \frac{\log_e I / I_0}{LAI}$$

Where, I_0 and I are the light intensity at top and bottom of a population with LAI

xv. Light Transmission Ratio (LTR)

It is expressed as the ratio of quantum of light intercepted by crop canopy at top to the bottom. Light intensity is expressed in K lux or $W m^{-2}$

$$LTR = I / I_0$$

Where, I : light intercepted at the bottom of the crop canopy

I_0 : light intercepted at the top of the crop canopy

xvi. Dry Matter Efficiency (DME)

It is defined as the percent of dry matter accumulated in the grain from the total dry matter produced over the crop growth period.

$$DME = \frac{\text{Grain yield}}{\text{TDMP}} \times \frac{100}{\text{Duration of crop}}$$

xvii. Harvest Index

The harvest index is expressed as the percent ratio between the economic yield and total biological yield and was suggested by Nichiporovich (1951).

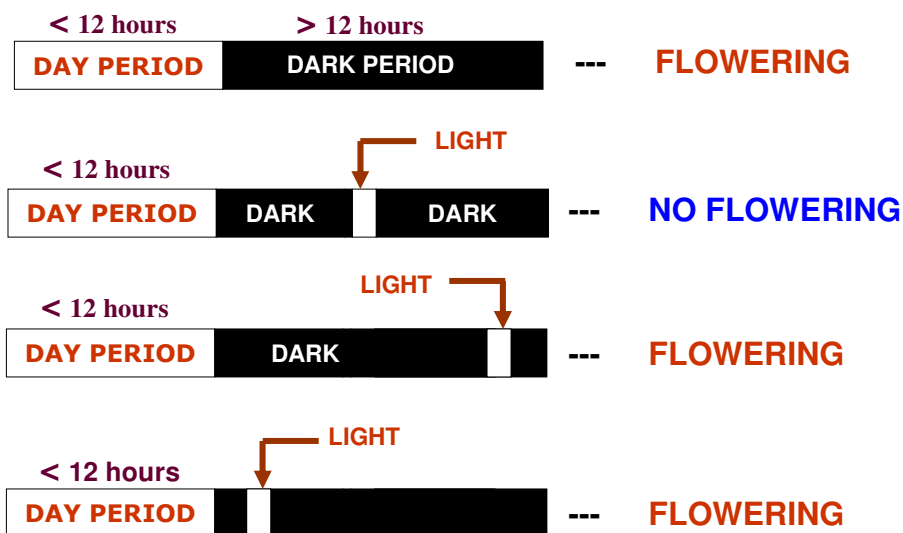
$$HI = \frac{\text{Economic yield}}{\text{Total biological yield}} \times 100$$

PHOTOPERIODISM

Photoperiodism is the phenomenon of physiological changes that occur in plants in response to relative length of day and night (i.e. photoperiod). The response of the plants to the photoperiod, expressed in the form of flowering is also called as photoperiodism. The phenomenon of photoperiodism was first discovered by Garner and Allard (1920). Depending upon the duration of photoperiod, the plants are classified into three categories.

1. Short day plants (SDP)
 2. Long day plants (LDP)
 3. Day neutral plants (DNP)
1. Short day plants

SHORT DAY PLANTS

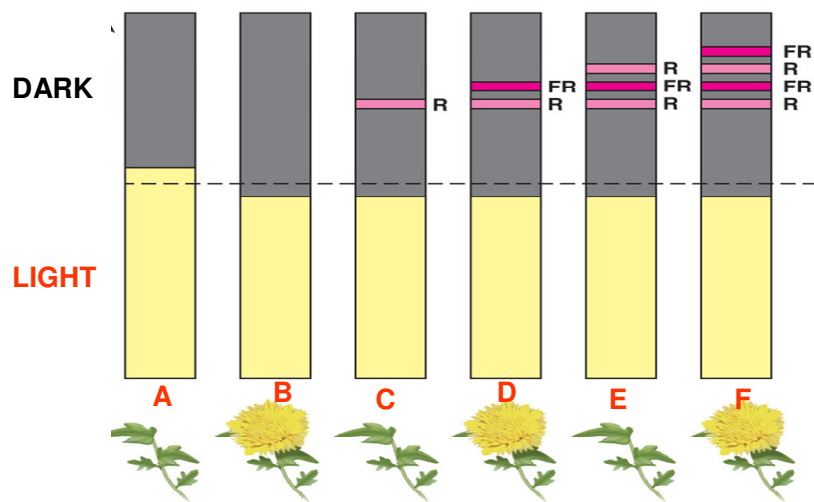


These plants require a relatively short day light period (usually 8-10 hours) and a continuous dark period of about 14-16 hours for subsequent flowering. These plants are also known as long-night plants

E.g. Rice, coffee, soybean, tobacco and chrysanthemum

- In short day plants, the dark period is critical and must be continuous. If this dark period is interrupted with a brief exposure of red light (660-665 nm wavelength), the short day plant will not flower.

- Maximum inhibition of flowering with red light occurs at about the middle of critical dark period.
- However, the inhibitory effect of red light can be overcome by a subsequent exposure with far-red light (730-735 nm wavelength)
- Interruption of the light period with red light does not have inhibitory effect on flowering in short day plants.
- Prolongation of the continuous dark period initiates early flowering.



SHORT DAY PLANTS - FLOWERING

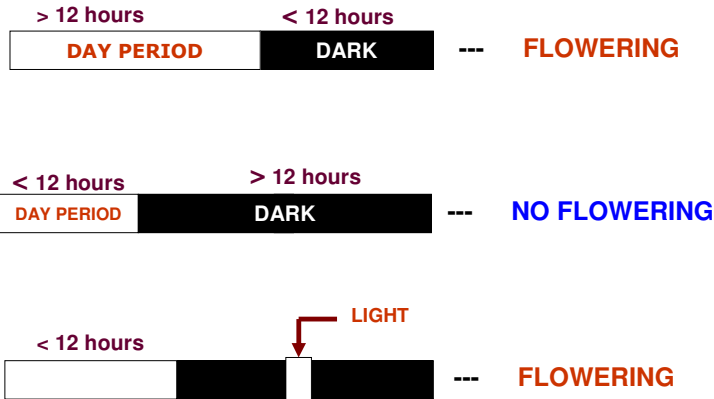
2. Long day plants

These plants require longer day light period (usually 14-16 hours) in a 24 hours cycle for subsequent flowering. These plants are also called as short night plants.

E.g. Wheat, radish, cabbage, sugar beet and spinach.

- In long day plants, light period is critical
- A brief exposure of red light in the dark period or the prolongation of light period stimulates flowering in long day plants.

LONG DAY PLANTS



3. Day neutral plants

These plants flower in all photoperiod ranging from 5 hours to 24 hours continuous exposure.

E.g. Tomato, cotton, sunflower, cucumber, peas and certain varieties of tobacco.

During recent years, intermediate categories of plants such as long short day plants and short long day plants have also been recognized.

i. Long short day plants

These are short day plants but must be exposed to long days during early periods of growth for subsequent flowering. E.g. Bryophyllum.

ii. Short -long day plants

These are long day plants but must be exposed to short day during early periods of growth for subsequent flowering. E.g. certain varieties of wheat and rye.

Differences between short day and long day plants

	Short day plant	Long day plant
1	Plants flower when photoperiod is less than the critical day length	Plants flower when photoperiod is more than the critical day length
2	Interruption during light period with darkness does not inhibit flowering	Interruption during light period with darkness inhibit flowering

3	Flowering is inhibited if the long dark period is interrupted by a flash of light	Flowering occurs if the long dark period is interrupted by a flash of light
4	Long continuous and uninterrupted dark period is critical for flowering	Dark period is not critical for flowering
5	Flowering does not occur under alternating cycles of short day and short light period.	Flowering occurs under alternating cycles of short day followed by still shorter dark periods

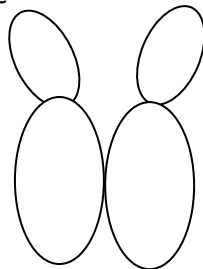
Phytochrome

It is observed that a brief exposure with red light during critical dark period inhibits flowering in a short day plant and this inhibitory effect can be reversed by a subsequent exposure with far-red light. Similarly, prolongation of the critical light period or the interruption of the dark period stimulates flowering in long-day plants.

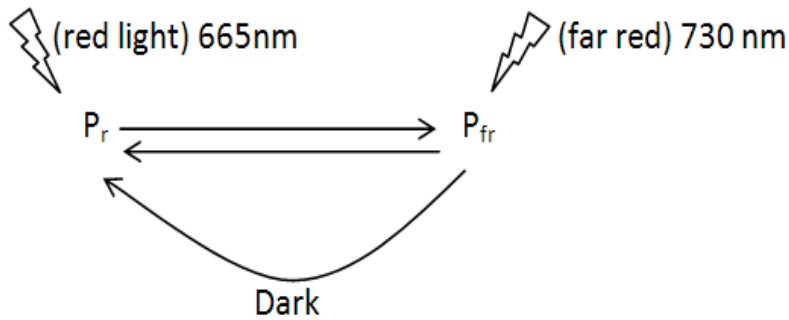
This inhibition of flowering in short day plant and stimulation of flowering in long day plants involves the operation of a proteinaceous pigment called phytochrome. It is present in the plasma membrane of cells and it has two components, chromophore and protein. Phytochrome is present in roots, coleoptiles, stems, hypocotyls, cotyledons, petioles, leaf blades, vegetative buds, flower tissues, seeds and developing fruits of higher plants.

chromophore

Polypeptide



The pigment, phytochrome exists in two different forms i.e., red light absorbing form which is designated as Pr and far red light absorbing form which is designated as Pfr. These two forms of the pigment are photo chemically inter convertible. When Pr form of the pigment absorbs red light (660-665 nm), it is converted into Pfr form. When Pfr form of the pigment absorbs far red light (730-735 nm), it is converted into Pr form. The Pfr form of pigment gradually changes into Pr form in dark.



It is considered that during day time, the Pfr form of the pigment is accumulated in the plants which are inhibitory to flowering in short day plants but is stimulatory in long day plants. During critical dark period in short day plants, this form gradually changes into Pr form resulting in flowering. A brief exposure with red light will convert this form again into Pfr form thus inhibiting flowering. Reversal of the inhibitory effect of red light during critical dark period in SDP by subsequent far-red light exposure is because, the Pfr form after absorbing far-red light (730-735 nm) will again be converted back into Pr form. Prolongation of critical light period or the interruption of the dark period by red- light in long day plants will result in further accumulation of the Pfr form of the pigment, thus stimulating flowering in long-day plants.

Differences between Pr and Pfr forms of phytochrome

	Pr form	Pfr form
1	It is blue green in colour	It is light green in colour
2	It is an inactive form of phytochrome and it does not show phytochrome mediated responses	It is an active form of phytochrome and hence shows phytochrome mediated responses
3	It has maximum absorption in red region (about 680nm)	It has maximum absorption in far-red region (about 730nm)
4	It can be converted into Pfr form in red region (660-665nm)	It can be converted into Pr form in far red region (730-735nm)
5	It is found diffused throughout the cytosol	It is found in discrete areas of cytosol
6	The Pr form contains many double bonds in	The Pfr form contains rearranged double

	pyrrole rings	bonds in all pyrrole rings
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Significance of photoperiodism

Photoperiodism is an example for physiological preconditioning. The stimulus is given at one time and the response is observed after months. Exposure to longer photoperiods hastens flowering (E.g). In wheat, the earing is hastened. During long light exposure, Pr form is converted into Pfr form and flowering is initiated. If dark period is greater, Pfr is converted into Pr form that inhibits flowering.

The important phytochrome mediated photo responses in plants include photoperiodism, seed germination, sex expression, bud dormancy, rhizome formation, leaf abscission, epinasty, flower induction, protein synthesis, pigment synthesis, auxin catabolism, respiration and stomatal differentiation.

THEORIES OF FLOWERING

Photoperiodic Induction

The influence of the length of day and night on the initiation of flowering is called photoperiodic induction or photo induction. Plants may require one or more inductive cycle for flowering. An appropriate photoperiod in 24 hours cycle constitutes one inductive cycle. If a plant which has received sufficient inductive cycle is subsequently placed under unfavourable photoperiod, it will still flower.

Flowering will also occur if a plant receives inductive cycles after intervals of unfavourable photoperiods (i.e. discontinuous inductive cycle). This persistence of photoperiodic after effect is called as photoperiodic induction.

- An increase in the number of inductive cycles results in early flowering of the plant. For instance, xanthium (a short day plant) requires only one inductive cycle and normally flowers after about 64 days. It can be made to flower even after 13 days if it has received 4-8 inductive cycle. In such case number of flowers is also increased.
- Continuous inductive cycles promote early flowering than discontinuous inductive cycle.

Perception of photoperiodic stimulus and presence of a floral hormone

- Photoperiodic stimulus is perceived by the leaves and a floral hormone is produced in the leaves which are then translocated to the apical tip, subsequently causing initiation of floral primordia.
- Photoperiodic stimulus perceived by the leaves can be shown by a simple experiment on cocklebur (xanthium), a short day plant. Cocklebur plant will flower if it has previously

been kept under short day conditions. If the plant is defoliated and kept under short day condition, it will not flower. Flowering will also occur if all the leaves of the plant except one leaf have been removed.

- If the cocklebur plant whether intact or defoliated is kept under long day condition it will not flower. But if even one of its leaves is exposed to short day condition and the rest are under long day condition, flowering will occur.
- The photoperiodic stimulus is transmitted from one branch of the plant to another branch. For example, if in a two branched cocklebur plant one branch is exposed to short day and the other to long day photoperiod, flowering occurs on both the branches.
- Flowering also occurs if one branch is kept under long day conditions and other branch from which all the leaves except one have been removed is exposed to short day condition. However, if one branch is exposed to long photoperiod and the other has been defoliated, under short day conditions, flowering will not occur in any of the branches.

Flowering stimulus: Florigen

The flowering stimulus is produced in leaves and translocated to apical and lateral meristems where flower formation is initiated. Chailakhyan (1937) called the flowering stimulus or flowering hormone as Florigen. Flowering stimulus is similar in long day plants and short day plants. This can be proved by a grafting experiment and can be translocated from one plant to another.

Maryland mammoth tobacco, a short day plant and *Hyoscyamus niger*, a long day plant, are grafted so that the leafy shoots of both the species are available for experiment. If the grafted plants are exposed to either long day or short day conditions, both partners flower. If grafting union is not formed, the flowering stimulus is not translocated from one partner to another partner.

Theories of Flowering

1. Bunning's hypothesis
2. Chailakhyan's hypothesis

Bunning's hypothesis:

Bunning (1958) assumes the presence of endogenous rhythms (Oscillator which consist of two half cycles. The first half cycle occurs in day and is called photophilous phase. During this, anabolic process predominates including flowering in plants. The other half cycle is dark, sensitive and is called skotophilous phase. In this, catabolic process (dehydration of starch) predominates.

SD plants have a critical day length of 9 hours. This period falls within the photophilous phase. Light during scotophil phase will inhibit photo process initiated during photophase. The L.D. plants have a critical day length of 15 hours and some light falls in the skoto philous phase. Under these

conditions in L.D. plants will flower. In S.D. plants oscillator is present close to skoto philous phase, while in L.D. plants it is close to photo philous phase.

Chilakhyan's hypothesis:

This hypothesis assumes that flowering hormone - florigen is a complex of two types of substances - gibberellin and anthesins. Gibberellin is essential for growth of the plant stems and anthesins are required for flower formation. According to him, flowering in all annual seed plants requires two phases: (i) Floral stem formation phase (ii) Flower formation phase. First phase involves increased carbohydrate metabolism and respiration with increased content of GA in leaves. Second phase requires intensive nitrogen metabolism, higher content of anthesins in leaves and nucleic acid metabolites in stem buds. Long day conditions favour the first phase while short day conditions favour second phase. In long day plants gibberellins are critical, while anthesins are critical in short day plants. However, anthesin is hypothetical; it has not been isolated as yet.

VERNALISATION

The cold treatment given to plant buds, seeds or seedlings for promoting early flowering is known as vernalisation. In short, the chilling treatment for induction of early flowering is called Vernalisation. Besides an appropriate photoperiod, certain plants require a low temperature treatment during their early stages of the life for subsequent flowering in the later stages. This low temperature treatment requirement was termed as vernalization by Lysenko (1928). Due to vernalization, the vegetative period of the plant is reduced resulting in an early flowering. In nature, vernalisation takes place in the seed stage in annuals like winter rye (*Secale cereale*). The biennials and many perennials respond to cold treatment at a very late stage. E.g. Henbane, apples etc.

Perception of cold stimulus and presence of floral hormone

The cold stimulus is perceived by the apical meristems. The perception of the cold stimulus results in the formation of a floral hormone which is transmitted to other parts of the plant. In certain cases, the cold stimulus may even be transmitted to another plant across a graft union. For instance, if a vernalized henbane plant is grafted to an unvernallized henbane plant, the later also flowers. This is due to the induction of the plant to produce a hormone named as *Vernalin* by Melchers (1939).

Conditions necessary for vernalization

1. Age of the plant

The age of the plant is an important factor in determining the responsiveness of the plant to the cold stimulus and it differs in different species. In cereals like winter wheat, the vernalization is effective only if the germinating seeds have received cold temperature treatment for sufficient time. While in the case of biennial variety of henbane (*Hyoscyamus niger*), the plant will respond to the cold treatment, only if they are at rosette stage and completed at least 10 days of growth.

2. Appropriate low temperature and duration of the exposure

Most suitable temperature for vernalizing the plants ranges between 1-6°C. The effectiveness of low temperature treatment decreases from 0 to 4°C. Low temperature at about -6°C is completely ineffective. Similarly at high temperatures from 7°C onwards, the response of the plants is decreased. Besides an appropriate low temperature, a suitable duration of the cold treatment is essential for vernalization. Depending upon the degree of temperature and in different species this period may vary, but usually the duration of the chilling treatment is about one and half months or more.

3. Oxygen

The vernalization is an aerobic process and requires metabolic energy. In the absence of O₂, cold treatment becomes completely ineffective.

4. Water

Sufficient amount of water is also essential for vernalization. Vernalization of the dry seed is not possible.

Mechanism of Vernalization

There are two main theories to explain the mechanism of vernalisation.

1. Phasic developmental theory

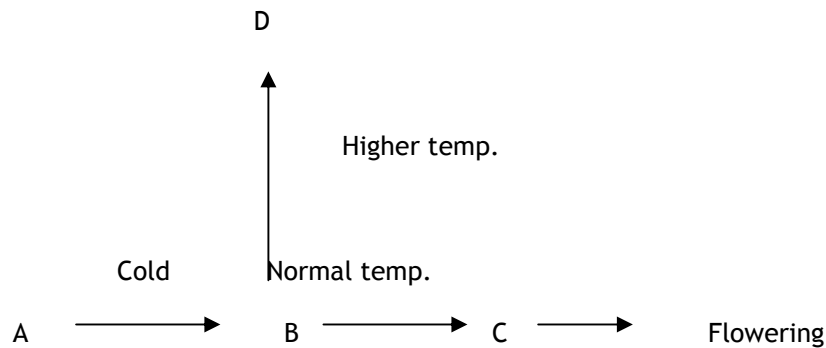
This theory was proposed by Lysenko (1934) as follows.

1. The growth (increase in size) and development (i.e. progressive change in the characteristic of the new organs) are two distinct phenomena.
2. According to this theory, the process of the development of an annual seed plant consists of a series of phases which must occur in some predetermined sequence.
3. Commencement of any of these phases will take place only when the preceding phase has been completed.
4. The phases require different external conditions for the completion such as light and temperature.
5. Vernalization accelerates the thermo phase i.e. that phase of development which is dependent upon temperature.

Thus, in winter wheat, low temperature is required for the completion of first thermo phase. After this, the next phase that is dependent upon light (photo phase) starts. Vernalization of winter wheat accelerates the first thermo phase so that there is an early swing from vegetative to reproductive phase or flowering.

2. Hormonal theories

It has already been described that vernalization probably involves the formation of a floral hormone called as *vernalin*. Based on this fact, many hypothetical schemes have been proposed by different workers from time to time. The first hormonal theory proposed by Long and Melchers (1947) is schematically shown below.



According to this scheme, the precursor A is converted into a thermo labile compound B during cold treatment. Under normal conditions B changes into C which ultimately causes flowering. But at higher temperature B is converted into D and flowering does not take place (devernalization).

Devernalization

The positive effect of the low temperature treatment on the vernalization of the plant can be counteracted by subsequent high temperature. This is called devernalization. The devernalized plant can again be vernalized by subsequent low temperature treatment.

Vernalization and Gibberellins

The gibberellins are known to replace the low temperature requirement in certain biennial plants such as henbane, where the plant normally remains vegetative and retains its rosette habit during the first growing season and after passing through the winter period flowers in the next season. The gibberellins cause such plants to flower even during the first year.

Significance of vernalization

1. Vernalization shortens the vegetative period of the plant
2. It increases cold resistance of the plants
3. Vernalization increases the resistance of plants to fungal diseases.
4. It is a physiological process that substitutes or compensates the effect of thermo phase. In biennials, vernalisation induces early flowering and early fruit setting. A non vernalised shoot apex can be induced to flower by grafting the plant with a vernalised plant.

PLANT GROWTH REGULATORS

Plant growth regulators or phytohormones are organic substances produced naturally in higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in lower concentration. Thimmann (1948) proposed the term Phyto hormone as these hormones are synthesized in plants. *Plant growth regulators* include auxins, gibberellins, cytokinins, ethylene, growth retardants and growth inhibitors. Auxins are the hormones first discovered in plants and later gibberellins and cytokinins were also discovered.

Hormone

An endogenous compound, which is synthesized at one site and transported to another site where it exerts a physiological effect in very low concentration. But ethylene (gaseous nature), exert a physiological effect only at a near a site where it is synthesized. Classified definition of a hormone does not apply to ethylene.

Plant growth regulators

- Defined as organic compounds other than nutrients, that affects the physiological processes of growth and development in plants when applied in low concentrations.
- Defined as either natural or synthetic compounds that are applied directly to a target plant to alter its life processes or its structure to improve quality, increase yields, or facilitate harvesting.

Plant Hormone

When correctly used, is restricted to naturally occurring plant substances, there fall into five classes. Auxin, Gibberellins, Cytokinin, ABA and ethylene. Plant growth regulator includes synthetic compounds as well as naturally occurring hormones.

Important groups of growth hormones in plant system are:

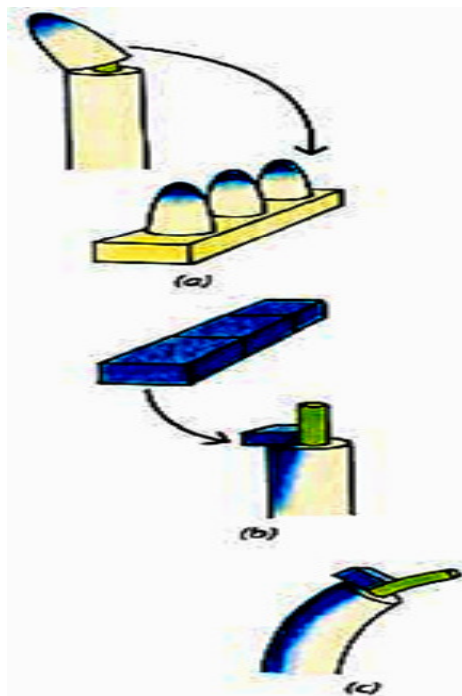
1. Auxins
2. Gibberellins
3. Cytokinins
4. Abscisic acid
5. Ethylene

Auxins

Auxins are a group of phytohormones produced in the shoot and root apices and they migrate from the apex to the zone of elongation. Auxins promote the growth along the longitudinal axis of the

plant and hence the name (auxein : to grow). The term, auxin was introduced by Kogl and Haagen-Smit (1931). Went (1928) isolated auxin from the Avena coleoptile tips by a method called Avena coleoptile or curvature test and concluded that no growth can occur without auxin. Auxins are widely distributed throughout the plant however, abundant in the growing tips such as coleoptile tip, buds, root tips and leaves. Indole Acetic Acid (IAA) is the only naturally occurring auxin in plants. The synthetic auxins include,

Avena Curvature Test



Cut off the tips of Avena coleoptile

Placed on agar block

Auxin diffuses into agar block

**Placed the agar block
Asymmetrically On cut coleoptile
stump**

**Coleoptile showed typical
curvature**

IBA : Indole Butyric Acid

NAA : Naphthalene Acetic acid

MCPA: 2 Methyl 4 chloro phenoxy acetic acid

2, 4-D : 2, 4 dichloro phenoxy acetic acid

2, 4, 5-T: 2, 4, 5 - Trichloro phenoxy acetic acid

Natural auxins may occur in the form of either free auxins- which freely move or diffuse out of the plant tissues readily or bound auxins- which are released from plant tissues only after hydrolysis, autolysis or enzymolysis.

Physiological effects of auxin

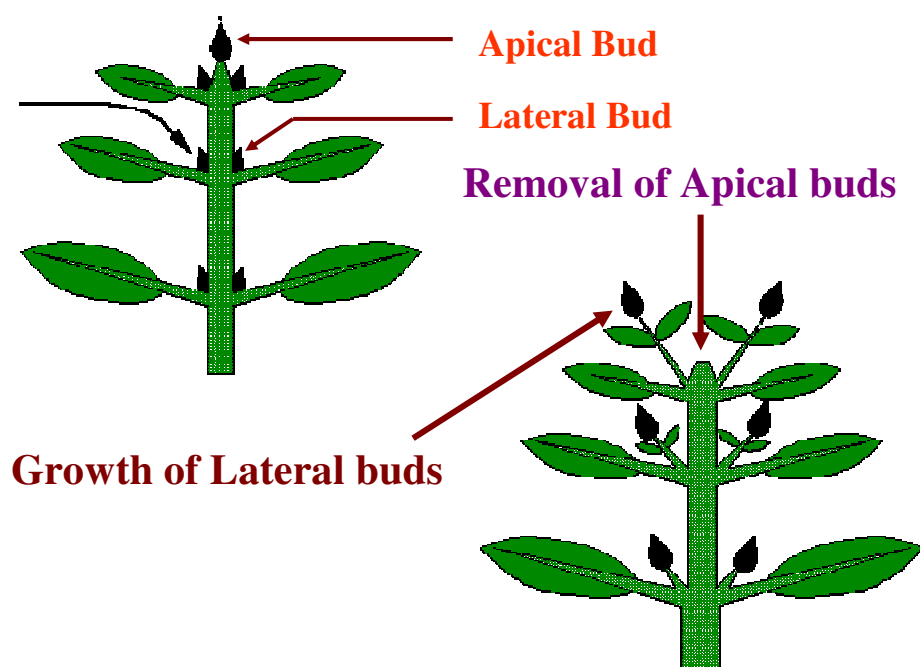
1. Cell division and elongation

The primary physiological effects of auxin are cell division and cell elongation in the shoots. It is important in the secondary growth of stem and differentiation of xylem and phloem tissues.

2. Apical dominance

In many plants, if the terminal bud is intact and growing, the growth of lateral buds just below it remains suppressed. Removal of the apical bud results in the rapid growth of lateral buds. This phenomenon in which the apical bud dominates over the lateral buds and does not allow the lateral buds to grow is known as *apical dominance*.

Skoog and Thimmann (1948) pointed out that the apical dominance might be under the control of auxin produced at the terminal bud and which is transported downward through the stem to the lateral buds and hinders the growth. They removed the apical bud and replaced it with *agar* block. This resulted in rapid growth of lateral buds. But when they replaced the apical bud with agar block containing auxin, the lateral buds remained suppressed and did not grow.



3. Root initiation

In contrast to stem, the higher concentration of auxin inhibits the elongation of roots but the number of lateral roots is considerably increased i.e., higher concentration of auxin induces more lateral branch roots. Application of IAA in lanolin paste (lanolin is a soft fat prepared from wool and

is good solvent for auxin) to the cut end of a young stem results in an early and extensive rooting. This fact is of great practical importance and has been widely utilized to promote root formation in economically useful plants which are propagated by cuttings.

4. Prevention of abscission

Natural auxins prevent the formation of abscission layer which may otherwise result in the fall of leaves, flowers and fruits.

5. Parthenocarpy

Auxin can induce the formation of parthenocarpic fruits (fruit formation without pollination and fertilization). In parthenocarpic fruits, the concentration of auxin in the ovaries is higher than in the ovaries of plants which produce fruits only after fertilization. In the later cases, the concentration of the auxin in ovaries increases after pollination and fertilization.

6. Respiration

Auxin stimulates respiration and there is a correlation between auxin induced growth and respiration. Auxin may increase the rate of respiration indirectly through increased supply of ADP by rapidly utilizing ATP in the expanding cells.

7. Callus formation

Besides cell elongation, auxin may also be active in cell division. In many tissue cultures, where the callus growth is quite normal, the continued growth of such callus takes place only after the addition of auxin.

8. Eradication of weeds

Some synthetic auxins especially 2, 4- D and 2, 4, 5-T are useful in eradication of weeds at higher concentrations.

9. Flowering and sex expression

Auxins generally inhibit flowering but in pine apple and lettuce it promotes uniform flowering.

Distribution of auxin in plants

In plants, auxin (IAA) is synthesized in growing tips or meristematic regions from where; it is transported to other plant parts. Hence, the highest concentration of IAA is found in growing shoot tips, young leaves and developing auxiliary shoots. In monocot seedling, the highest concentration of auxin is found in coleoptile tip which decreases progressively towards its base.

In dicot seedlings, the highest concentration is found in growing regions of shoot, young leaves and developing auxiliary shoots. Within the plants, auxin may present in two forms. i.e., *free auxins* and *bound auxins*. Free auxins are those which are easily extracted by various organic

solvents such as diethyl ether. Bound auxins on the other hand, need more drastic methods such as hydrolysis, autolysis, enzymolysis etc. for extraction of auxin. Bound auxins occur in plants as complexes with carbohydrates such as glucose, arabinose or sugar alcohols or proteins or amino acids such as aspartate, glutamate or with inositol.

Biosynthesis of auxin (IAA) in plants

Thimann (1935) found that an amino acid, tryptophan is converted into Indole 3 acetic acid. Tryptophan is the primary precursor of IAA in plants. IAA can be formed from tryptophan by two different pathways.

1. By deamination of tryptophan to form indole-3-pyruvic acid followed by decarboxylation to form indole-3-acetaldehyde. The enzymes involved are tryptophan deamination and indole pyruvate decarboxylase respectively.
2. By decarboxylation of tryptophan to form tryptamine followed by deamination to form indole-3-acetaldehyde and the enzymes involved are tryptophan decarboxylase and tryptamine oxidase respectively. Indole 3-acetaldehyde can readily be oxidized to indole 3-acetic acid (IAA) in the presence of indole 3-acetaldehyde dehydrogenase.

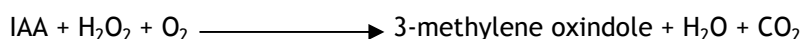
Transport of auxin in plant

The transport of auxin is predominantly polar. In stems, polar transport of auxin is basipetal i.e., it takes place from apex towards base. Polar transport of auxin is inhibited by 2, 3, 5 Triiodobenzoic acid (TIBA) and Naphthyl thalamic acid (NPA). The substances are called as antiauxins.

Destruction / Inactivation of auxin in plants

Auxin is destroyed by the enzyme IAA oxidase in the presence of O₂ by oxidation.

IAA Oxidase



Rapid inactivation may also occur by irradiation with x-rays and gamma rays. UV light also reduces auxin levels in plants. Inactivation or decomposition of IAA by light has been called as photo oxidation.

Mechanism of Action

IAA increases the plasticity of cell walls so that the cells stretch easily in response to turgor pressure. It has been suggested that IAA acts upon DNA to influence the production of mRNA. The mRNA codes for specific enzymes responsible for expansion of cell walls. Recent evidences indicate that IAA increases oxidative phosphorylation in respiration and enhanced oxygen uptake. The growth stimulation might be due to increased energy supply and it is also demonstrated that auxin induces production of ethylene in plants.

Gibberellins

A Japanese scientist Kurosawa found that the rice seedlings infected by the fungus *Gibberella fujikuroi* grow taller and turned very thin and pale. An active substance was isolated from the infected seedlings and named as Gibberellin.

Biosynthesis of gibberellins in plants

The primary precursor for the formation of gibberellins is acetate.

Acetate + COA → Acetyl COA → Mevalonic acid → MA pyrophosphate → Isopentanyl pyrophosphate → Geranyl pyrophosphate → GGPP → Kaurene → Gibberellins.

Physiological effects of gibberellins

1. Seed germination

Certain light sensitive seeds eg. Lettuce and tobacco show poor germination in dark. Germination starts vigorously if these seeds are exposed to light or red light. This requirement of light is overcome if the seeds are treated with gibberellic acid in dark.

2. Dormancy of buds

In temperate regions the buds formed in autumn remain dormant until next spring due to severe cold. This dormancy of buds can be broken by gibberellin treatments. In potato also, there is a dormant period after harvest, but the application of gibberellin sprouts the tuber vigorously.

3. Root growth

Gibberellins have little or no effect on root growth. At higher concentration, some inhibition of root growth may occur. The initiation of roots is markedly inhibited by gibberellins in isolated cuttings.

4. Elongation of internodes

The most pronounced effect of gibberellins on the plant growth is the elongation of the internodes. Therefore in many plants such as dwarf pea, dwarf maize etc gibberellins overcome the genetic dwarfism.

5. Bolting and flowering

In many herbaceous plants, the early period of growth shows rosette habit with short stem and small leaves. Under short days, the rosette habit is retained while under long days bolting occurs i.e. the stem elongates rapidly and is converted into polar axis bearing flower primordia. This

bolting can also be induced in such plants by the application of gibberellins even under non-inductive short days.

In *Hyoscyamus niger* (a long day plant) gibberellin treatment causes bolting and flowering under non-inductive short days. While in long day plants the gibberellin treatment usually results in early flowering. In short day plants, its effects are quite variable. It may either have no effect or inhibit or may activate flowering.

6. Parthenocarpy

Germination of the pollen grains is stimulated by gibberellins; likewise, the growth of the fruit and the formation of parthenocarpic fruits can be induced by gibberellin treatment. In many cases, eg. pome and stone fruits where auxins have failed to induce parthenocarpy, the gibberellins have proven to be successful. Seedless and fleshy tomatoes and large sized seedless grapes are produced by gibberellin treatments on commercial scale.

7. Synthesis of the enzyme α - amylase

One important function of gibberellins is to cause the synthesis of the enzyme α - amylase in the aleurone layer of the endosperm of cereal grains during germination. This enzyme brings about hydrolysis of starch to form simple sugars which are then translocated to growing embryo to provide energy source.

Distribution of gibberellins in plant

Gibberellins are found in all parts of higher plants including shoots, roots, leaves, flower, petals, anthers and seeds. In general, reproductive parts contain much higher concentrations of gibberellins than the vegetative parts. Immature seeds are especially rich in gibberellins (10-100 mg per g fresh weight). In plants, gibberellins occur in two forms free gibberellins and bound gibberellins. Bound gibberellins usually occur as gibberellin - glycosides.

CYTOKININS (Kinetin)

Kinetin was discovered by Skoog and Miller (1950) from the tobacco pith callus and the chemical substance was identified as 6-furfuryl aminopurine. Because of its specific effect on *cytokinesis* (cell division), it was called as cytokinins or kinetin. The term, cytokinin was proposed by Letham (1963). Fairley and Kingour (1966) used the term, phytokinins for cytokinins because of their plant origin. Chemically cytokinins are kinins and they are purine derivatives. Cytokinins, besides their main effect on cell division, also regulate growth and hence they are considered as natural plant growth hormones. Some of the very important and commonly known naturally occurring cytokinins are Coconut milk factor and Zeatin. It was also identified that cytokinin as a constituent of t-RNA.

Naturally occurring cytokinins

Cytokinins can be extracted from coconut milk (liquid endosperm of coconut), tomato juice, flowers and fruits of *Pyrus malus*; fruits of *Pyrus communis* (Pear), *Prunus cerasiferae* (plum) and *Lycopersicum esculentum* (bhendi); Cambial tissues of *Pinus radiata*, *Eucalyptus regnans* and *Nicotiana tabacum*; immature fruits of *Zea mays*, *Juglans* sp. and *Musa* sp; female gametophytes of *Ginkgo biloba*; fruitlets, embryo and endosperms of *Prunus persica*; seedling of *Pisum sativum*; root exudates of *Helianthus annuus* and tumour tissues of tobacco. According to Skoog and Armstrong (1970), at least seven well established types of cytokinins have been reported from the plants.

Biosynthesis

It is assumed that cytokinins are synthesised as in the case of purines in plants (nucleic acid synthesis). Root tip is an important site of its synthesis. However, developing seeds and cambial tissues are also the site of cytokinin biosynthesis. Kende (1965) reported that cytokinins move upwards perhaps in the xylem stream. However, basipetal movement in petiole and isolated stems are also observed. Seth *et al* (1966) found that auxin enhances kinetin movement (translocation) in bean stems.

Physiological effects of cytokinins

1. Cell division

The most important biological effect of kinetin on plants is to induce cell division especially in tobacco pith callus, carrot root tissue, soybean cotyledon, pea callus etc.

2. Cell enlargement

Like auxins and gibberellins, the kinetin may also induce cell enlargement. Significant cell enlargement has been observed in the leaves of *Phaseolus vulgaris*, pumpkin cotyledons, tobacco pith culture, cortical cells of tobacco roots etc.

3. Concentration of apical dominance

External application of cytokinin promotes the growth of lateral buds and hence counteracts the effect of apical dominance

4. Dormancy of seeds

Like gibberellins, the dormancy of certain light sensitive seeds such as lettuce and tobacco can also be broken by kinetin treatment.

5. Delay of senescence (Richmand - Lang effect)

The senescence of leaves usually accompanies with loss of chlorophyll and rapid breakdown of proteins. Senescence can be postponed to several days by kinetin treatment by improving RNA

synthesis followed by protein synthesis. Richmand and Lang (1957) while working on detached leaves of *Xanthium* found that kinetin was able to postpone the senescence for a number of days.

6. Flower induction

Cytokinins can be employed successfully to induce flowering in short day plants.

7. Morphogenesis

It has been shown that high auxin and low kinetin produced only roots whereas high kinetin and low auxin could promote formation of shoot buds.

8. Accumulation and translocation of solutes

Plants accumulate solutes very actively with the help of Cytokinin and also help in solute translocation in phloem.

9. Protein synthesis

Osborne (1962) demonstrated the increased rate of protein synthesis due to translocation by kinetin treatment.

10. Other effects

Cytokinins provide resistance to high temperature, cold and diseases in some plants. They also help in flowering by substituting the photoperiodic requirements. In some cases, they stimulate synthesis of several enzymes involved in photosynthesis.

11. Commercial applications

Cytokinins have been used for increasing shelf life of fruits, quickening of root induction and producing efficient root system, increasing yield and oil contents of oil seeds like ground nut.

ETHYLENE

Ethylene is the only natural plant growth hormone exists in gaseous form.

Important physiological elects

1. The main role of ethylene is it hastens the ripening of fleshy fruits eg. Banana, apples, pears, tomatoes, citrus etc.
2. It stimulates senescence and abscission of leaves
3. It is effective in inducing flowering in pine apple
4. It causes inhibition of root growth
5. It stimulates the formation of adventitious roots
6. It stimulates fading of flowers

7. It stimulates epinasty of leaves.

ABSCISIC ACID

Addicott (1963) isolated a substance strongly antagonistic to growth from young cotton fruits and named Abscissin II. Later on this name was changed to Abscisic acid. This substance also induces dormancy of buds therefore it also named as Dormin. Abscisic acid is a naturally occurring growth inhibitor.

Physiological effects

1. Geotropism in roots

Geotropic curvature of root is mainly due to translocation of ABA in basipetal direction towards the root tip.

2. Stomatal closing

ABA is synthesized and stored in mesophyll chloroplast. In response to water stress, the permeability of chloroplast membrane is lost which results in diffusion of ABA out of chloroplast into the cytoplasm of the mesophyll cells. From mesophyll cells it diffuses into guard cells where it causes closing of stomata.

3. Other effects

- i. Including bud dormancy and seed dormancy
- ii. Includes tuberisation
- iii. Induces senescence of leaves fruit ripening, abscission of leaves, flowers and fruits
- iv. Increasing the resistance of temperate zone plants to frost injury.

Growth retardants

Synthetic compounds which prevent the gibberellins from exhibiting their usual responses in plants such as cell enlargement or stem elongation. So they are called as anti gibberellins or growth retardants. They are

1. Cycocel (2- chloroethyl trimethyl ammonium chloride (CCC))
2. Phosphon D - (2, 4 - dichlorobenzyl - tributyl phosphonium chloride)
3. AMO - 1618
4. Morphactins
5. Maleic hydrazide

Commercial uses of growth regulators

Rooting and plant propagation

- Auxin compound like IBA NAA, 2,4-D, 2, 4,5-T
- IBA produces strong fibrous root system

Germination and dormancy

- Gibberellin is a potent germination promoter
- Abscissic acid - germination inhibitor (Anti - Gibberellin)
- Induce Dormancy - ABA
- Breaking of dormancy - Auxins and Gibberellin

Fruit set and Development

- Fruit setting-2, 4, 5 - T
- Fruit size increment in grapes - Gibberellic acid
- Shelf life increment in fruits and flowers-Cytokinin
- Good fruit shape-Gibberellic acid + Cytokinin
- Parthenocarpic fruit - Gibberellins, IAA and PAA

Sex expression

- Production of male flowers- Gibberellins (cucumber)
- Production of female flowers- Auxins for cucumber and Gibberellins for maize

Abscission

- Control of abscission-NAA and IAA
- Induce Abscission-Ethrel

Morphogenesis

- Auxin and Cytokinin

Weed control

- 2, 4-D and 2, 4, 5-T

Plant organ size

- Increases plant height- GA

- Shorten the plant height-TIBA
- Antitranspirants -ABA and PMA (Phenyl mercury acetate)
- Papaya Later flow-Ethephon
- Rubber latex flow-2, 4 - D and 2, 4,5 - T
- Fruit ripening-Ethrel
- Sugarcane ripeners-Glyphosphate and CCC

SEED GERMINATION

The process of seed germination starts with the imbibition of water by seed coat and emergence of growing root tip of embryo. The process ends with the development of embryo into a seedling.

Physiological and biochemical changes during seed germination

1. Water uptake

Seed germination starts with the imbibition of water by dry seed coat. Due to imbibition of water, the seed coats become 1) More permeable to O₂ and water and 2) less resistant to outward growth of embryo.

2. Respiration

Rapid increase in respiration rate of embryo occurs. Sucrose is probably the respiratory substrate at this stage which is provided by endosperm.

3. Mobilization of reserve materials

As germination progresses, there is mobilization of reserve materials to provide.

1. building blocks for the development of embryo
2. energy for the biosynthetic process and
3. nucleic acids for control of protein synthesis and embryonic development

Changes in these components are as follows

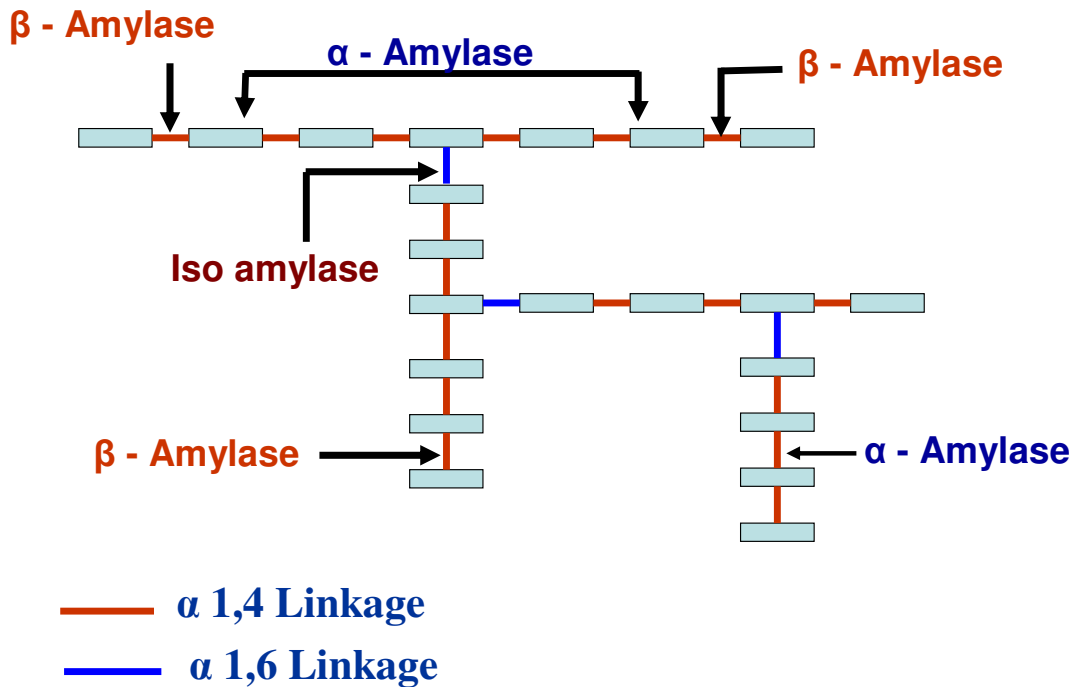
i) Nucleic acids

In monocots, during imbibition, there is a rapid decrease of DNA and RNA content in the endosperm with a simultaneous increase in the embryonic axis probably due to their transportation as such. High concentration of RNA in the embryonic axis precedes cell division. Due to more cell division, DNA content is increased.

ii) Carbohydrates

Insoluble carbohydrates like starch are the important reserve food of cereals in the endosperm. During germination, starch is hydrolyzed first into maltose in the presence of α -amylase and β -amylase and then maltose is converted into glucose by maltase. The glucose is further converted into soluble sucrose and transported to growing embryonic axis. During germination, the embryonic axis secretes gibberellic acid into the aleurone layer which causes synthesis of α -amylase.

ENZYME ACTION ON STARCH



3. Lipids

Plants like castor bean, peanut etc., store large amount of neutral lipids or fats as reserve food in their seeds. During germination, the fats are hydrolyzed into fatty acids and glycerol by lipase enzyme. Fatty acids are further converted into acetyl - CoA by the process, β - oxidation. The acetyl CoA is further converted into sucrose via glyoxylate cycle and is transported to the growing embryonic axis.

4. Proteins

Some plants store proteins as reserve food in their seeds in the form of aleurone grains. Proteins are hydrolyzed into amino acids by peptidase enzyme. The amino acids may either provide energy by oxidation after deamination (removal of amino group) or may be utilized in the synthesis of new proteins.

5. Inorganic materials

A number of inorganic materials such as phosphate, calcium, magnesium and potassium are also stored in seeds in the form of phytin. These stored materials are liberated during germination due to the activity of various phosphatases including phytase.

Emergence of seedling out of the seed coat

All the changes described above gradually result in splitting of seed coat and emergence of the growing seedling. The radical comes out first and grows downward, and then plumule comes out and grows upward. Due to the continued growth of this seedling, the plumule comes out of the soil, exposed to light and develops its own photosynthetic apparatus.

Splitting of seed coat may take place either by imbibition pressure or by internal pressure created by the growing primary root or by hydrolytic enzymes which act on cell wall contents of seed coat and digest it (e.g. cellulose and pectinase). Sometimes the seed coat may be extensively rotted by the activity of micro-organisms in the soil.

DORMANCY OF SEEDS

All the viable seeds have capacity to germinate if placed under suitable conditions necessary for germination. But, some seeds fail to germinate sometimes even if placed under the condition favourable for germination. This may be due to some internal factors or due to specific requirement for some environmental factors. During this period, the growth of the seed remains suspended and they are said to be in rest stage or dormant stage and this phenomenon is called as dormancy of seeds.

Factors causing dormancy of seeds

1. Seed coats impermeable to water

The seeds of certain plants especially those belonging to the family's leguminaceae, solanaceae, malvaceae, etc. have very hard seed coats which are impermeable to water. The seeds remain dormant until the impermeable layer decay by the action of soil micro-organisms.

2. Seeds coats impermeable to oxygen

In many plants such as cocklebur and many grasses, the seed dormancy is due to the impermeability of the seed coat to oxygen. However, during the period of dormancy, the seed coat gradually becomes more permeable to oxygen so that they may germinate.

3. Immaturity of the Embryo

In certain orchids, the seed dormancy is due to the immaturity of the embryos which fail to develop fully by the time the seeds are shed. In such cases, the seeds germinate only after a period or rest during which the development of embryo inside the seed is completed.

4. Germination Inhibitors

In certain seeds, the dormancy of the seeds is due to the presence of certain germination inhibitors like coumarin, ferulic acid, abscissic acid, etc. These may be present in endosperm, embryo, testa or juice or pulp of fruit.

5. Chilling or low temperature requirement

In certain plants such as apple, rose, peach etc, the seeds remain dormant after harvest in the autumn as they have a low temperature or chilling requirement for germination. In nature, this requirement is fulfilled by the winter temperatures. In such case the seeds remain dormant throughout the winter season and germinate only in the following spring.

6. Light sensitive seeds

In many species, the germination of the seeds is affected by light resulting in seed dormancy. Such light sensitive seeds are called *photo blastic*. Seeds of lettuce, tomato and tobacco are positively photo blastic and germinate only after they have been exposed to light. On the other hand, the seeds of certain plants are negatively photo blastic and their germination is inhibited by light.

Advantages of dormancy

1. In temperature zones, the dormancy of seeds helps the plants to tide over the severe colds which may be injurious for their vegetative and reproductive growth.
2. In tropical regions, the dormancy of seeds resulting from their impermeable seed coats ensures good chances of survival.
3. Dormancy of seeds in many cereals is of utmost importance to mankind. If these seeds germinate immediately after harvest in the field, they will become useless to man for consumption as food.

RIPENING

Ripening is a process in fruits that causes them to become more edible. In general, a fruit becomes sweeter, less green, and softer as it ripens. However the acidity as well as sweetness rises during ripening, but the fruit still tastes sweeter regardless. The reason for this is the Brix-Acid Ratio. Depending upon plucking, fruits are classified as climacteric (ripening happens after plucking of fruits from tree) and nonclimacteric fruits (which ripen in the tree itself).

Physiological and biochemical changes during fruit ripening.

1. An organic compound involved with ripening is ethylene, a gas created by plants from the amino acid methionine.
2. Ethylene increases the intracellular levels of certain enzymes in fruit and fresh-cut products, which includes Amylase, which hydrolyzes starch to produce simple sugars, and Pectinase, which hydrolyzes pectin, a substance that keeps fruit hard.
3. Other enzymes break down the green pigment chlorophyll, which is replaced by blue, yellow, or red pigments.

SENESCENCE AND ABSCISSION

Like human beings, plants also grow old and undergo aging and then they die. Aging is the sum total of changes in the total plant or its organs. During aging, the plants undergo chemical and structural changes. Aging leads to senescence and later phase of development that ultimately terminates to death.

Senescence

The deteriorative process which naturally terminates the functional life of an organ, organism or other life unit is collectively called senescence. Senescence is a phase of the aging process. The major characteristic of senescence is that the metabolic processes are catabolic and eventually become irreversible and terminate to death.

Senescence is not confined only to whole plant. It may be limited to a particular plant organ such as leaf and flowers or cells or cell, organelles. Senescence is closely associated with the phenomenon of aging. Aging leads to senescence. Wheat plant dies after the development of fruit. This is the senescence of an entire plant. Leaf fall in a coconut tree is an example of senescence.

Types of senescence

Leopold (1961) has proposed types of senescence patterns in plants which are as follows.

(a) Overall Senescence

This type of senescence occurs in annuals where whole plant is affected. It is also called whole plant senescence. The entire plant dies after the development of fruit and seeds. E.g. Paddy, wheat, soybean etc.

(b) Top Senescence

In top senescence, the parts remaining above the ground or (shoot system) may die, but the root system and underground system remain viable. It is also called shoot senescence. E.g. Dock, perennial herbs.

(c) Deciduous Senescence

In deciduous woody plants, all the leaves die but the bulk of the stem and root system remains viable. It is called deciduous senescence or simultaneous or synchronous senescence. E.g. Leaf fall in deciduous trees.

(d) Progressive Senescence

It is a gradual death of old leaves from the base to the top of the plants. It may occur at any time. It is also called sequential senescence. E.g. Leaf fall in a coconut tree.

Causes of Senescence

1. Leaf senescence is accompanied by early loss in chlorophyll, RNA and enzymes.
2. Cellular constituents are decreased due to slower synthesis or faster break down.
3. Competition between vegetative and reproductive organs for nutrients.
4. A senescence factor (a hormone) is produced in soybean fruits that move to leaves where it causes senescence.
5. Short-day and long-night conditions induce flowering and leaf senescence.
6. Degradation of food reserves and loss of integrity in food storage cells of seeds.
7. Senescence is also hormonally controlled.

Physiology of Senescence

The following physiological changes occur during senescence.

1. Photosynthesis stops.
2. Chlorophyll degradation: The colour of leaf changes from green to yellow.
3. Anthocyanin pigments accumulation in the leaves causing reddening in leaves.
4. The vacuoles function as lysosomes and digest the cellular materials.
5. The starch content decreased.
6. RNA and proteins are decreased.
7. DNA molecules are degraded by the enzyme DNase.
8. Growth promoting hormones such as cytokinin decrease.
9. The deteriorative hormones such as ethylene and abscisic acid (ABA) content are increased.

Senescence Promoters

Senescence is promoted by hormones such as abscisic acid and ethylene. The senescence accelerating ability of abscisic acid is well documented. The function of ABA as a promoter of flower tissue senescence including initiation of colour fading or blueing has been established. The ABA content of aging leaves increases markedly as senescence is initiated. Ethylene plays a very important role in the senescence of certain plant parts, particularly fruit and petals and in the abscission process. It is an inducer in the senescence of flower tissue.

Senescence Retardants

The primary plant hormones involved here are auxin, gibberellin and cytokinin.

Significance of Senescence

1. The whole plant senescence occurs in monocarpic plants coinciding the seed setting and seed dispersal.
2. Due to the formation of abscission layer, the older leaves tend to fall down so that the nutrients will be diverted to the next young leaf.
3. The senescence process helps the mobilization of nutrients and of the vegetative parts of the plant into the fruits.
4. Plants escape the influence of seasonal adversity by undergoing senescence of its organs. Leaf fall in deciduous trees reduces the rate of transpiration to survive under adverse conditions.

Abscission

Shedding of leaves, flowers and fruits is called abscission. Abscission is distinct in deciduous trees and shrubs. In autumn, all the leaves of deciduous plants fall, at about the same time giving the plants a naked appearance. In evergreen plants there is gradual abscission of leaves. The older leaves fall while new leaves are developed continuously throughout the year. In most of the herbaceous species, however the leaves are not shed even after they die. In many cases leaves are retained in withered dry condition even after the whole shoot is dead. Abscission is a complex physiological process. During abscission, the colour of the leaves, flowers and fruits changes due to degradation of chlorophyll and the synthesis of anthocyanin pigment.

Leaf abscission takes place at the base of the petiole. The site of abscission is internally marked by a distinct zone called abscission zone. This zone is made up of one or more layers of cells arranged transversely across the petiole base. This is called abscission layer. The abscission zone is pale or brown in colour. The cells of the abscission layer separate from each other due to the dissolution of middle lamellae and the primary cellulose walls under the influence of the activity of enzymes, pectinase and cellulase.

At this stage, the petiole remains attached to the stem by vascular elements only. But due to its own weight and the wind force, the leaf is detached from the stem. The broken vascular elements are soon plugged with tyloses or gums. Wound healing in cells proximal to the breaking point involves formation of a corky layer that protects the plant from pathogen invasion and excess water loss. Suberin and lignin are synthesized during healing.

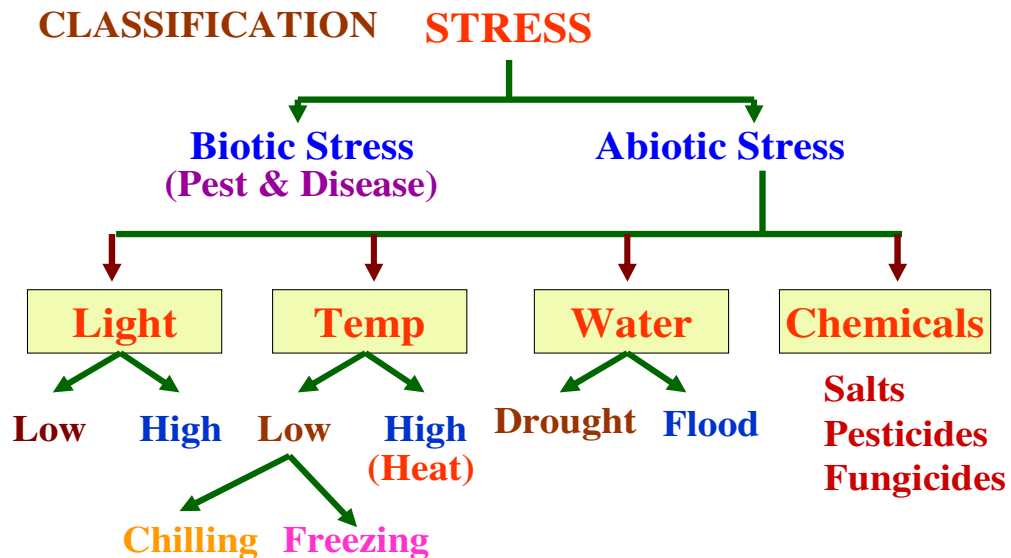
Several environmental factors such as drought and N deficiency promote abscission. Auxin is synthesized in growing leaf blades and it strongly retards senescence and abscission. Abscission starts when the amount of auxin begins to decrease. Cytokinins and gibberellins arriving from the roots also delay senescence and abscission. Abscission is caused by the formation of cell wall degrading enzymes in the abscission zone, due to ethylene production.

Significance of Abscission

1. It helps in diverting water and nutrients to the young leaves
2. It is a self pruning process through which fruits and injured organs are shed from the parent plant.
3. It helps in disseminating fruits and vegetative propagates.
4. Abscission serves as function in removing plant parts containing waste materials.

UNIT V: STRESS PHYSIOLOGY

In both natural and agricultural conditions, plants are frequently exposed to environmental stresses. **Stress** is usually defined as an external factor that exerts a disadvantageous influence on the plant. The concept of stress is intimately associated with that of **stress tolerance**, which is the plant's fitness to cope with an unfavorable environment.



DROUGHT (Water stress)

Drought is defined as the deficiency of water severe enough to reduce the plant growth. Drought has been classified into two broad categories viz., soil drought and atmospheric drought. Soil drought leads to atmospheric drought. Atmospheric drought occurs due to low atmospheric humidity, high wind velocity and high temperature which cause a plant to lose most of its water.

Drought resistance

- The ability of the plant to grow satisfactorily when exposed to periods of water stress is called drought resistance (May & Miltthrope, 1962)
- The ability of plants to withstand drought and to overcome easily prolonged wilting with the slightest damage both to the plant and the yield.

Drought resistance can be classified into three types.

I. Drought escape: The ability of the plant to complete its life cycle before soil and plant water deficits develop. Developmental plasticity and rapid phenological development comes under this.

II. Drought Avoidance: The ability of the plant to bear the periods of drought by maintaining a high plant water status either by saving the water or getting more water. Having less transpiration by waxiness or by deep roots

III. Drought tolerance :The ability of a plant to survive under low water potential or ability of the plant to function all metabolic activity under low water potential.

Physiological changes occur due to drought

1. Functioning of stomata

In general, stomata lose their function and may die, because wilting after certain limit denatures the starch in the guard cells and also in the mesophyll cells.

2. Carbohydrates metabolism in green leaves

The very first effect of drought on carbohydrates metabolism is that starch disappears from the wilted leaves and sugar accumulates simultaneously.

3. Photosynthetic activity

CO₂ diffusion into the leaf is prevented due to decrease in stomatal opening and there by reduces photosynthetic activity in green cells.

4. Osmotic pressure

The reduced amount of water during drought causes an increase in the osmotic pressure of plant cell. This increase in osmotic pressure permits the plant to utilize better soil moisture.

5. Permeability

The permeability to water and urea increases during drought.

6. Biochemical effects

Water shortage alters the chemical composition. For example, starch is converted to sugar, besides this, there is a considerable increase in nitrate nitrogen and protein synthesis is adversely affected.

Adaptation to drought

1. Ephemerals

These are short lived plants and they complete their life cycle within a short favourable period during rainy season. They pass dry periods in the form of seeds. They are called as *drought escaping plants*.

2. Succulent plants

These plants accumulate large quantities of water and use it slowly during dry period. Thus, they pass dry periods or drought without facing it. Such plants develop several morphological adaptations for reducing transpiration such as thick cuticle, reduced leaf area, sunken stomata etc.

3. Non succulent plants

These plants are in fact the real drought enduring (tolerant) plants. They tolerate drought without adapting any mechanism to ensure continuous supply of water. They develop many morphological adaptations which are collectively called *xeromorphy*. They develop, in general, greyish colour, reflecting surfaces, smaller leaves, extensive root system, leaf fall during dry season, sunken stomata and thick cuticle etc. They develop an elaborated conducting system. The stomata remain closed mostly in dry periods.

Methods to overcome drought

- Selection of drought tolerant species
- Adjusting the time of sowing in such a way that the crop completes its lifecycle before the onset of drought
- Seed hardening with KCl, KH_2PO_4 , CaCl_2 or Thiourea
- Thinning of poorly established plants
- Mulching to minimize the evaporative loss
- Foliar spray of antitranspirants such as Kaolin, PMA, Waxes and Silicone oils
- Foliar spray of KCl
- Foliar spray of growth retardants such as CCC and MC

TEMPERATURE STRESS

Temperature stress includes both high temperature stress and low temperature stress. Low temperature stress causes chilling injury and freezing injury.

1. Chilling injury

The tropical origin plants are injured when the temperature drops to some point close to 0°C. The injury which occurs due to low temperature but above zero degree centigrade is called chilling injury.

2. Freezing injury

Freezing injury occurs when the temperature is 0°C or below.

Effect of freezing and chilling injury plants

- The lipid molecules in cell membrane get solidified i.e. changed from liquid state to solid state. Hence, the semi-permeable nature of the membrane is changed and the membrane becomes leaky.
- Inactivation of mitochondria
- Streaming of protoplasm is stopped
- Accumulation of respiratory metabolites which become highly toxic
- Ice formation inside the cell occurs.

Prevention of cold injury

- Some plants change the pattern of growth.
- The growth is completely arrested during this period.
- In cell membrane, unsaturated fatty acid content is increased.
- Intracellular ice formation is reduced.
- The quantity of free enzymes, sugars and proteins increases.

High temperature stress

The effect of high temperature is heat injury. Heat injury occurs when plant temperature is higher than that of environment (exceeds 35°C).

General effects of high temperature

1. Seedling growth and vigour
2. Water and nutrient uptake
3. Solute transport
4. Photosynthetic activity is more sensitive than respiration to higher temps
5. Fertilization and maturation

6. at warmer temps, lipids are too fluid and can lead to ion leakage
7. Warmer temps also tend to denature/inactivate proteins

Resistance mechanisms

- Plants that are adapted to warmer temps tend to have higher concentration of saturated lipids in the membranes
- Reflecting infrared radiation (cuticle, trichomes reflect more)
- Convection cooling by cooler air around the leaf
- Evaporative cooling by transpiration (evaporation of water absorbs heat)
- Acute heat stress induces the synthesis of heat shock proteins (HSPs)
- HSPs preserve protein structure and assembly at higher temperatures

ALLEVIATING HIGH TEMPERATURE STRESS

1. **Shade:** It may used for high cash crops (Ornamentals), typically a cloth or lathe house. Shading decreases leaf temperature, not air temperatures.
2. **Green house:** It should be whitewash, provide fans, evaporative coolers (Where humidity allows)
3. **Overhead Irrigation:** As water evaporates heat is absorbed. Cools plant body, but encourages disease.
4. **GA₃ and proline** application exhibit positive effects on stress alleviation through the stimulation of α - amylase expression
5. **Zeatin Riboside** is the most effective in slowing leaf senescence and alleviating heat induced lipid peroxidation of cell membranes.
6. The inhibitory effect of high temperature on seed germination can be overcome by exogenous application of **ethylene**.
7. Application of **Glycine Betaine** under heat stress appreciably reduced the leakage of all these ions, particularly Ca^{2+} , K^+ and NO_3 .
8. Exogenous application of **salicylic acid** enhanced the thermo tolerance ability of both roots and hypocotyls in intact seedlings

Low light stress

Major constraint in low productivity in second season is lowlight situation. About 40% of normal light only received.

Physiological changes during lowlight

1. Photosynthetic activity reduced
2. Respiration is reduced
3. Leaf size is reduced
4. Leaf area index is reduced
5. Nutrient uptake is reduced
6. Chlorophyll content reduced
7. Spikelet sterility increased
8. Yield is reduced

Ultraviolet radiation stress

Ultraviolet (UV) radiation is an integral part of the sunlight that reaches the surface of the Earth. The UV region of the spectrum is by convention divided into three parts: UVA (320-400 nm), UVB (280-320 nm) and UVC (less than 280 nm). Of these, only UVA and longer-wavelength UVB have biological importance because the stratospheric ozone layer very effectively absorbs UV radiation that has wavelengths below 290 nm. UVB represents a small fraction of total solar radiation, yet exposure to UVB at ambient or enhanced levels is known to elicit a variety of responses and causes stress in all living organisms, including higher plants

UV radiation and plant response

1. UV radiation slows down the growth of plants
2. Damage the process of photosynthesis
3. Prevent maturation and ripening process
4. Accelerate genetic mutation.

SALT STRESS

Salt stress occurs due to excess salt accumulation in the soil. As a result, water potential of soil solution decreases and therefore exosmosis occurs. This leads to physiological drought causing wilting of plants.

Classification of saline soil: 1. Saline soil 2. Alkaline soil

1. Saline soil

In saline soils, the electrical conductivity is greater than 4 dS/m, exchangeable sodium percentage is less than 15% and pH is less than 8.5. These soils are dominated by Cl^- and SO_4^{2-} ions.

2. Alkaline soil

Alkaline soils are also termed as sodic soils wherein, the electrical conductivity is less than 4 dS/m, exchangeable sodium percentage is greater than 15% and pH of the soil is greater than 8.5. These soils are dominated by CO_3^{2-} and HCO_3^- ions.

Classification of plants

Plants are classified into two types based on the tolerance to salt stress. They are halophytes and glycophytes.

1. Halophytes

Halophytes are the plants that grow under high salt concentrations. They are again divided into two types based on extreme of tolerance.

Euhalophytes: can tolerate extreme salt stress

Oligohalophytes: can tolerate moderate salt stress

2. Glycophytes

Glycophytes are the plants that cannot grow under high salt concentration.

Effect of salt stress on plant growth and yield

1. Seed germination

Salt stress delays seed germination due to the reduced activity of the enzyme, α -amylase

2. Seedling growth

The early seedling growth is more sensitive. There is a significant reduction in root emergence, root growth and root length.

3. Vegetative growth

When plants attain vegetative stage, salt injury is more severe only at high temperature and low humidity. Because under these conditions, the transpiration rate will be very high as a result uptake of salt is also high.

4. Reproductive stage

Salinity affects panicle initiation, spikelet formation, fertilization and pollen grain germination.

5. Photosynthesis

Salinity drastically declines photosynthetic process. Thylakoid are damaged by high concentration of salt and chlorophyll *b* content is drastically reduced.

Mechanism of salt tolerance

1. Some plants are able to maintain high water potential by reducing the transpiration rate.
2. Salts are accumulated in stem and older leaves in which metabolic processes take place in a slower rate.
3. Na^+ (sodium ion) toxicity is avoided by accumulating high amount of K^+ ions.
4. Accumulation of toxic ions in the vacuole but not in the cytoplasm.
5. Accumulation of proline and abscissic acid which are associated with tolerance of the plants to salt.

Relative salt tolerant crops

Tolerant crops: Cotton, sugar cane, barley

Semi tolerant crops: Rice, maize, wheat, oats, sunflower, soybean

Sensitive crops: Cow pea, beans, groundnut and grams

Alleviation of salt stress

1. Leaching of salts with adequate water
2. Application gypsum to convert the highly injurious carbonates to less injurious sulphate
3. Selection of salt tolerant crops and Use of FYM and other organic manures

GLOBAL WARMING

Global warming is the observed increase in the average temperature of the Earth's atmosphere and oceans in recent decades. The Earth's average near-surface atmospheric temperature rose 0.6 ± 0.2 °Celsius (1.1 ± 0.4 °Fahrenheit) in the 20th century. The prevailing scientific opinion on climate change is that "most of the warming observed over the last 50 years is attributable to human activities".

The increased amounts of carbon dioxide (CO₂) and other greenhouse gases (GHGs) are the primary causes of the human-induced component of warming. They are released by the burning of fossil fuels, land clearing and agriculture, etc. and lead to an increase in the greenhouse effect. The first speculation that a greenhouse effect might occur was by the Swedish chemist Svante Arrhenius in 1897, although it did not become a topic of popular debate until some 90 years later.

An increase in global temperatures can in turn cause other changes, including a rising sea level and changes in the amount and pattern of precipitation. These changes may increase the frequency and intensity of extreme weather events, such as floods, droughts, heat waves, hurricanes, and tornados. Other consequences include higher or lower agricultural yields, glacial retreat, reduced summer streamflows, species extinctions and increases in the ranges of disease vectors. Warming is expected to affect the number and magnitude of these events; however, it is difficult to connect particular events to global warming. Although most studies focus on the period up to 2100, warming (and sea level rise due to thermal expansion) is expected to continue past then, since CO₂ has an estimated atmospheric lifetime of 50 to 200 years. Only a small minority of climate scientists discount the role that humanity's actions have played in recent warming. However, the uncertainty is more significant regarding how much climate change should be expected in the future, and there is a hotly contested political and public debate over what, if anything, should be done to reduce or reverse future warming, and how to deal with the predicted consequences.

Greenhouse effect

Greenhouse gases are absorbing infrared radiation from the sun and re emit these radiations making the earth's atmosphere temperature to increase. This phenomenon is called green house effect.

Global warming on crop productivity

1. Increase in temperature, speed up the development and hence reduction in days between sowing and harvesting and hence biomass reduces, so yield reduces.
2. Increase in carbon dioxide concentration has both positive and negative effect.
 - a) Increase in carbon dioxide concentration increases photosynthesis and hence yield increases. But this advantage is more for C₃ plants than C₄ plants.

b) Increase in concentration increases temperature and hence soil moisture depletion will be more and hence less availability moisture. So naturally development process gets hindered.

3. Increase in carbon dioxide concentration has effect on quality in negative side

4. Increase in carbon iodide concentration leads to reduced uptake of nitrogen and reduced uptake of zinc.

CARBON SEQUESTRATION

Atmospheric levels of CO₂ have risen from 280 parts per million (ppm) to 375 ppm. This rise in level is primarily due to use of fossil fuels for energy. Predictions of energy use in the next century suggest a continued increase in carbon emissions and rising concentrations of CO₂ in the atmosphere. The ways to manage the carbon emissions are

1. To use energy more efficiently to reduce our need for a major energy and carbon source—fossil fuel combustion.
2. To increase our use of low-carbon and carbon-free fuels and technologies (nuclear power and renewable sources such as solar energy, wind power, and biomass fuels).
3. The third and newest way to manage carbon is through **carbon sequestration**.

Carbon sequestration refers to the provision of long-term storage of carbon in the terrestrial biosphere, underground, or the oceans, so that the buildup of carbon dioxide (the principal greenhouse gas) concentration in the atmosphere will reduce or slow. The different ways of carbon sequestration are.

- Sequestering Carbon in Underground Geologic Repositories
- Enhancing the Natural Terrestrial Cycle: Identifying ways to enhance carbon sequestration of the terrestrial biosphere through CO₂ removal from the atmosphere by vegetation and storage in biomass and soils.
- Carbon Sequestration in the Oceans: Enhancing the net oceanic uptake from the atmosphere by fertilization of phytoplankton with nutrients, and injecting CO₂ to ocean depths greater than 1000 meters.

