SEMESTER III

17BTU301 PLANT PHYSIOLOGY 4H - 4C

Total hours/week: L:4 T:0 P:0 Marks: Internal: 40 External: 60 Total: 100

Scope: This will enable to learning the physiological conditions of the plants and metabolism.
Objective: This paper aims at introducing students to the basic and applied aspects of plant physiology.

UNIT-I
Anatomy: The shoot and root apical meristem and its histological organization, simple & complex permanent tissues, primary structure of shoot & root, secondary growth, growth rings, leaf anatomy (dorsi-ventral and isobilateral leaf)

UNIT-II
Plant water relations and micro & macro nutrients : Plant water relations: Importance of water to plant life, diffusion, osmosis, plasmolysis, imbibition, guttation, transpiration, stomata & their mechanism of opening & closing. Micro & macro nutrients: criteria for identification of essentiality of nutrients, roles and deficiency systems of nutrients, mechanism of uptake of nutrients, mechanism of food transport.

UNIT-III
Carbon and nitrogen metabolism: Photosynthesis- Photosynthesis pigments, concept of two photo systems, photphosphorylation, calvin cycle, CAM plants, photorespiration, compensation point. Nitrogen metabolism- inorganic & molecular nitrogen fixation, nitrate reduction and ammonium assimilation in plants.

UNIT-IV
Growth and development: Growth and development: Definitions, phases of growth, growth curve, growth hormones (auxins, gibberlins, cytokinins, abscisic acid, ethylene). Physiological role and mode of action, seed dormancy and seed germination, concept of photoperiodism and vernalization.

UNIT-V
Plant adaptation: Stress adaptation mechanism: Definitions, Indicators of stress response - morphological, physiological, biochemical and molecular level. Stress adaptation and tolerance mechanism – biotic and abiotic stress, Effect of stress on crop productivity, Global warming - physiological effects on crop productivity

References

1. Hopkins,W.G., & Huner, P.A. (2008). *Introduction to Plant Physiology*. John Wiley & Sons.
2. Nelson, D.L., & Cox, M.M. (2004). *Lehninger Principles of Biochemistry* (4th ed.). New York: USA, W.H. Freeman & Company.
3. Dickinson, W.C. (2000). *Integrative Plant Anatomy*. USA: Harcourt Academic Press.
4. Taiz, L., & Zeiger, E. (2006). *Plant Physiology* (4th ed.). MA: USA, Sinauer Associates Inc.
5. Esau, K. (1977) *Anatomy of Seed Plants.* Wiley Publishers.
6. Salisbury, F.B, & Ross, C.W. (1991). *Plant Physiology*. Wadsworth Publishing Co. Ltd.

KARPAGAM ACADEMY OF HIGHER EDUCATION

DEPARTMENT OF BIOTECHNOLOGY

II B.Sc., BIOTECHNOLOGY – SEMESTER 3

LECTURE PLAN –PLANT PHYSIOLOGY 17BTU301

S.No	Lecture Duration (hr)	Topic to be covered	Support materials
UNIT I			
1	1	Introduction to plant structure, its parts and regulation	T1 Pg 81-83
2	1	The shoot and root apical meristem and its introduction	T2 Pg 279-285
3	1	Histological organization of shoot apical meristem	W1 Pg 1-5
4	1	Histological organization of root apical meristem	T3 Pg 148-149
5	1	Simple & complex permanent tissues	T2 Pg 279-280
6	1	Structure of shoot & root	W2 Pg 1-10
7	1	Secondary growth and growth rings	T3 Pg 194-196
8	1	Leaf anatomy (Dorsi- ventral and isobilateral leaf)	T3 Pg 132-134
9	1	Revision	
UNIT II			
10	1	Plant water relations: Importance of water to plant life	T1 Pg 80-90
11	1	Diffusion and osmosis	T1 Pg 57-62
12	1	Plasmolysis and imbibition	T2 Pg 90-93
13	1	Guttation and transpiration	T1 Pg 98-110
14	1	Stomata & their mechanism of opening and closing.	T1 Pg 101-105
15	1	Criteria for identification of essentiality of nutrients	T1 Pg 125-139
16	1	Roles and deficiency system of nutrients	T1 Pg 125-139
17	1	Mechanism of uptake of nutrients	T1 Pg 125-139
18	1	Mechanism of food transport	T1 Pg 139-140
19	1	Revision	
UNIT III			
20	1	Photosynthesis- Photosynthesis pigments	T1 Pg 240-245
21	1	Concepts of two photosystems	T1 Pg 112-114

22	1	Photophosphorylation	T1 Pg 245-247
23	1	Calvin cycle and CAM plants	T1 Pg 247-251
24	1	Photorespiration and compensation points.	T1 Pg 255-260
25	1	Nitrogen metabolism- Introduction	T1 Pg 323-333
26	1	Inorganic & molecular nitrogen fixation	T1 Pg 323-333
27	1	Nitrate reduction	T1 Pg 201-204
28	1	Ammonium assimilation in plants	T2 Pg 201-204
29	1	Revision	
UNIT IV			
30	1	Growth and Development: Definition, phases of growth	T1 Pg 439-445
31	1	Growth curve, growth hormones	T1 Pg 439-445
32	1	Auxin, gibberellins, cytokinins	T2 Pg 306-308
33	1	Abscisic acid, ethylene	T2 Pg 344-350
34	1	Physiological role and mode of action	T2 Pg 362-365
35	1	Seed dormancy and seed germination	T2 Pg 480-485
36	1	Concepts of photoperiodism	T2 Pg 453-454
37	1	Vernalisation	T1 Pg 493-497
38	1	Revision	
UNIT V			
39	1	Stress adaptation mechanism: Definitions	T1 Pg 538-539
40	1	Indicators of stress response- Introduction	T1 Pg 538-544
41	1	Morphological, physiological response	T2 Pg 226-225
42	1	Biochemical and molecular level	T2 Pg 226-230
43	1	Stress adaptation and tolerance mechanism	T2 Pg 230-235
44	1	Biotic and abiotic stress	T2 Pg 238-245
45	1	Effect of stress on crop productivity	J1 Pg 253-266
46	1	Global warning- Introduction	T2 Pg 245-246
47	1	Physiological effects on crop productivity.	J1 Pg 253-266
48	1	Revision	

Reference Books

1. T1. S. N. Pandey, B.K. Sinha (2006), Plant Physiology, (4th Edition), Vikas publication Pvt. Ltd.
2. T2: Hopkins. W.G., Hunger, P.A., (2008), Introduction to Plant Physiology, John Wiley and Sons Publications.
3. T3: Dickson, W.C (2000), Intergrative Plant Anatomy, Harcourt academic press.
4. W1: http:/ learning.unobi.ac.ke
5. W2:www.biologydiscussion.com
6. J1: Donald L. Smith, Juan J Humaraz (2004), Climatic change and crop productivity: Contributions, impacts and adaptation, Canadian Journal of Plant Path., 26(3), 253-266.

UNIT-I

SYLLABUS

Anatomy: The shoot and root apical meristem and its histological organization, simple & complex permanent tissues, primary structure of shoot & root, secondary growth, growth rings, leaf anatomy (Dorsi- ventral and isobilateral leaf).

Anatomy of plants

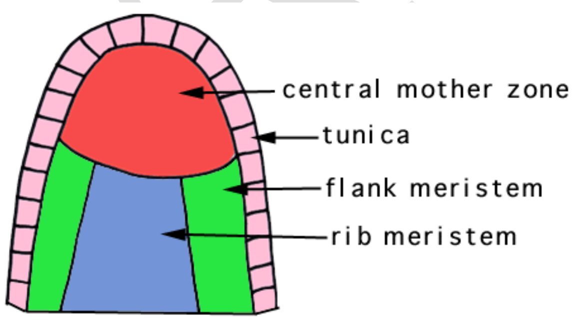
Shoot and root apical meristem

A **meristem** is the tissue in most plants containing undifferentiated cells (**meristematic cells**), found in zones of the plant where growth can take place. Meristematic cells give rise to various organs of the plant and keep the plant growing. There are two types of meristematic tissues 1) Apical Meristem 2) Lateral Meristem. The Apical Meristem is of two types they are *shoot apical meristem* (SAM) gives rise to organs like the leaves and flowers, while the *root apical meristem* (RAM) provides the meristematic cells for the future root growth. SAM and RAM cells divide rapidly and are considered indeterminate, in that they do not possess any defined end status. In that sense, the meristematic cells are frequently compared to the stem cells in animals, which have an analogous behavior and function. The term *meristem* was first used in 1858 by Karl Wilhelm von Nägeli (1817–1891) in his book *Beiträge zur Wissenschaft lichen Botanik* ("Contributions to Scientific Botany"). It is derived from the Greek word *merizein* (μερίζειν), meaning to divide, in recognition of its inherent function.

In general, differentiated plant cells cannot divide or produce cells of a different type. Therefore, cell division in the meristem is required to provide new cells for expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body. Meristematic cells are incompletely or not at all differentiated, and are capable of continued cellular division (youthful). Furthermore, the cells are small and protoplasm fills the cell completely. The vacuoles are extremely small. The cytoplasmdoes not contain differentiated plastids (chloroplasts or chromoplasts), although they are present in rudimentary form (proplastids). Meristematic cells are packed closely together without intercellular cavities. The cell wall is a very thin *primary cell wall*. Maintenance of the cells requires a balance between two antagonistic processes: organ initiation and stem cell population renewal. Apical meristems are the completely undifferentiated (indeterminate) meristems in a plant. These differentiate into three kinds of primary meristems. The primary meristems in turn produce the two secondary meristem types. These secondary meristems are also known as lateral meristems because they are involved in lateral growth. At the meristem summit, there is a small group of slowly dividing cells, which is commonly called the central zone. Cells of this zone have a stem cell function and are essential for meristem maintenance. The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery. It is also helps in the growth of the plant. Meristems also are induced in the roots of legumes such as soybean, *Lotus japonicus*, pea, and *Medicago truncatula* after infection with soil bacteria commonly called Rhizobium. Cells of the inner or outer cortex in the so-called "window of nodulation" just behind the developing root tip are induced to divide. The critical signal substance is the lipo-oligosaccharide Nod-factor, decorated with side groups to allow specificity of interaction.

Shoot apical meristems

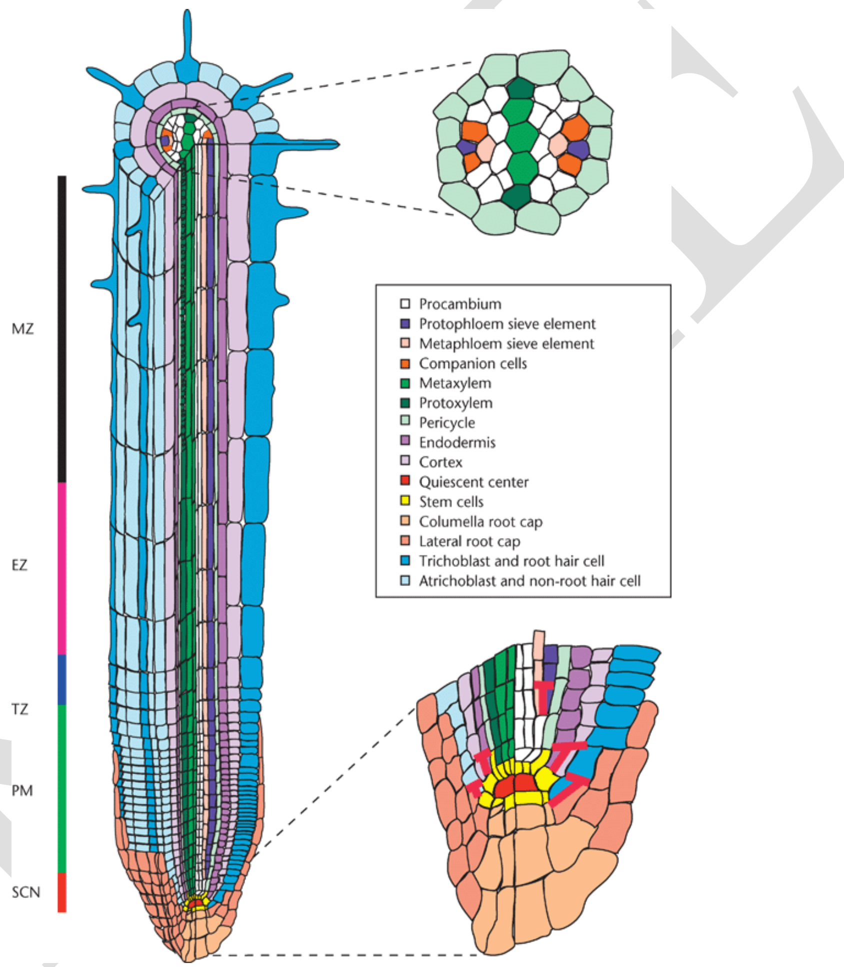
The source of all above-ground organs. Cells at the shoot apical meristem summit serve as stem cells to the surrounding peripheral region, where they proliferate rapidly and are incorporated into differentiating leaf or flower primordia. The shoot apical meristem is the site of most of the embryogenesis in flowering plants. Primordia of leaves, sepals, petals, stamens and ovaries are initiated here at the rate of one every time interval, called a plastochron. It is where the first indications that flower development has been evoked are manifested. One of these indications might be the loss of apical dominance and the release of otherwise dormant cells to develop as auxiliary shoot meristems, in some species in axils of primordia as close as two or three away from the apical dome. The shoot apical meristem consists of 4 distinct cell groups:



TYPICAL ANGIOSPERM SAM

Root apical meristem

Unlike the shoot apical meristem, the root apical meristem produces cells in two dimensions. It harbors two pools of stem cells around an organizing center called the quiescent center (QC) cells and together produce most of the cells in an adult root. At its apex, the root meristem is covered by the root cap, which protects and guides its growth trajectory. Cells are continuously sloughed off the outer surface of the root cap. The QC cells are characterized by their low mitotic activity. Evidence suggests that the QC maintains the surrounding stem cells by preventing their differentiation, via signal(s) that are yet to be discovered. This allows a constant supply of new cells in the meristem required for continuous root growth. Recent findings indicate that QC can also act as a reservoir of stem cells to replenish whatever is lost or damaged. Root apical meristem and tissue patterns become established in the embryo in the case of the primary root, and in the new lateral root primordium in the case of secondary roots.



Plant tissues

Plant tissues are categorized broadly into three tissue systems: the epidermis, the ground tissue, and the vascular tissue.

- Epidermis - Cells forming the outer surface of the leaves and of the young plant body.

- Vascular tissue - The primary components of vascular tissue are the xylem and phloem. These transport fluid and nutrients internally.
- Ground tissue - Ground tissue is less differentiated than other tissues. Ground tissue manufactures nutrients by photosynthesis and stores reserve nutrients.

Plant tissues can also be divided differently into two types:

1. Meristematic tissues
2. Permanent tissues.

Meristematic tissues

Meristematic tissue consists of actively dividing cells, and leads to increase in length and thickness of the plant. The primary growth of a plant occurs only in certain, specific regions, such as in the tips of stems or roots. It is in these regions that meristematic tissue is present. Cells in these tissues are roughly spherical or polyhedral, to rectangular in shape, and have thin cell walls. New cells produced by meristem are initially those of meristem itself, but as the new cells grow and mature, their characteristics slowly change and they become differentiated as components of the region of occurrence of meristematic tissues, they are classified as:

- **Apical Meristem** - It is present at the growing tips of stems and roots and increases the length of the stem and root. They form growing parts at the apices of roots and stems and are responsible for increase in length, also called primary growth. This meristem is responsible for the linear growth of an organ.
- **Lateral Meristem** - This meristem consist of cells which mainly divide in one plane and cause the organ to increase in diameter and growth. Lateral meristem usually occurs beneath the bark of the tree in the form of Cork Cambium and in vascular bundles of dicots in the form of vascular cambium. The activity of this cambium results in the formation of secondary growth.
- **Intercalary Meristem** - This meristem is located in between permanent tissues. It is usually present at the base of node, inter node and on leaf base. They are responsible for growth in length of the plant and increasing the size of the internode, they result in branch formation and growth.

The cells of meristematic tissues are similar in structure and have thin and elastic primary cell wall made up of cellulose. They are compactly arranged without inter-cellular spaces between them. Each cell contains a dense cytoplasm and a prominent nucleus. Dense protoplasm of meristematic cells contains very few vacuoles. Normally the meristematic cells are oval, polygonal or rectangular in shape.

Meristemetic tissue cells have a large nucleus with small or no vacuoles, they have no inter cellular spaces.

Permanent tissues

The meristematic tissues that take up a specific role lose the ability to divide. This process of taking up a permanent shape, size and a function is called cellular differentiation. Cells of meristematic tissue differentiate to form different types of permanent tissue. There are 3 types of permanent tissues:

1. simple permanent tissues
2. complex permanent tissues
3. special or secretory tissues (glandular).

Simple tissues

A group of cells which are similar in origin; similar in structure and similar in function are called simple permanent tissue. They are of four types:

1. Parenchyma
2. Collenchyma
3. Sclerenchyma
4. Epidermis (botany)

Parenchyma

Parenchyma (*para* - 'beside'; *chyma* - 'in filling, loose, unpacked') is the bulk of a substance. In plants, it consists of relatively unspecialised living cells with thin cell walls that are usually loosely packed so that intercellular spaces are found between cells of this tissue. This tissue provides support to plants and also stores food. In some situations, a parenchyma contains chlorophyll and performs photosynthesis, in which case it is called a chlorenchyma. In aquatic plants, large air cavities are present in parenchyma to give support to them to float on water. Such a parenchyma type is called aerenchyma.

Collenchyma

Collenchyma is Greek word where "Collen" means gum and "chyma" means infusion. It is a living tissue of primary body like Parenchyma. Cells are thin-walled but possess thickening of cellulose, water and pectin substances (pectocellulose) at the corners where number of cells join together. This tissue gives a tensile strength to the plant and the cells are compactly arranged and have very little inter-cellular spaces. It occurs chiefly in hypodermis of stems and leaves. It is absent in monocotsand in roots.

Collenchymatous tissue acts as a supporting tissue in stems of young plants. It provides mechanical support, elasticity, and tensile strength to the plant body. It helps in manufacturing sugar and storing it as starch. It is present in the margin of leaves and resist tearing effect of the wind.

Sclerenchyma

Sclerenchyma is Greek word where "Sclrenes" means hard and "chyma" means infusion. This tissue consists of thick-walled, dead cells. These cells have hard and extremely thick secondary walls due to uniform distribution of lignin. Lignin deposition is so thick that the cell walls become strong, rigid and impermeable to water.

Epidermis

The entire surface of the plant consists of a single layer of cells called epidermis or surface tissue. The entire surface of the plant has this outer layer of epidermis. Hence it is also called surface tissue. Most of the epidermal cells are relatively flat. The outer and lateral walls of the cell are often thicker than the inner walls. The cells forms a continuous sheet without inter cellular spaces. It protects all parts of the plant.

Xylem

Xylem tissue is organized in a tube-like fashion along the main axes of stems and roots. It consists of a combination of parenchyma cells, fibers, vessels, tracheids, and ray cells. Longer tubes made up of individual cells are vessels (tracheae), while vessel members are open at each end. Internally, there may be bars of wall material extending across the open space. These cells are joined end to end to form long tubes. Vessel members and tracheids are dead at maturity. Tracheids have thick secondary cell walls and are tapered at the ends. They do not have end openings such as the vessels. The tracheids ends overlap with each other, with pairs of pits present. The pit pairs allow water to pass from cell to cell. Though most conduction in xylem tissue is vertical, lateral conduction along the diameter of a stem is facilitated via rays. [1]. Rays are horizontal rows of long-living parenchyma cells that arise out of the vascular cambium. In trees and other woody plants, rays radiate out from the center of stems and roots, and appear like spokes on a wheel in cross section. Rays, unlike vessel members and tracheids, are alive at functional maturity.

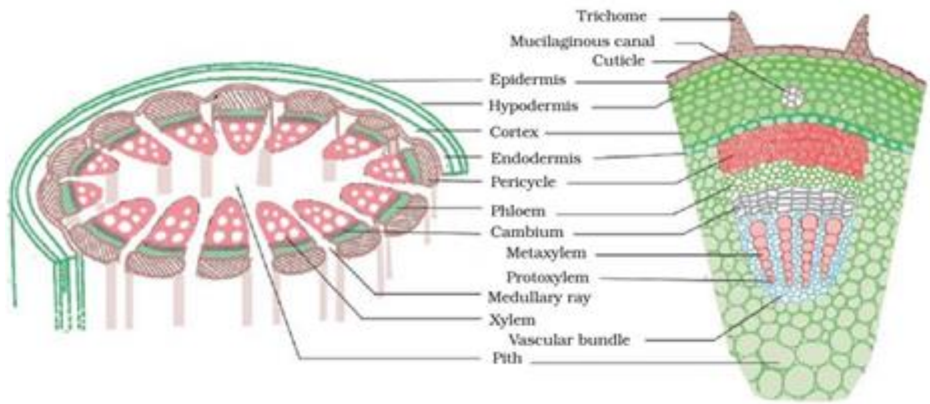
Phloem

Phloem consists of

- Sieve tube
- Companion cell
- Phloem fiber
- Phloem parenchyma.

Phloem is an equally important plant tissue as it also is part of the 'plumbing system' of a plant. Primarily, phloem carries dissolved food substances throughout the plant. This conduction system is composed of sieve-tube member and companion cells that are without secondary walls. The parent cells of the vascular cambium produce both xylem and phloem. This usually also includes fibers, parenchyma and ray cells. Sieve tubes are formed from sieve-tube members laid end to end. The end walls, unlike vessel members in xylem, do not have openings.

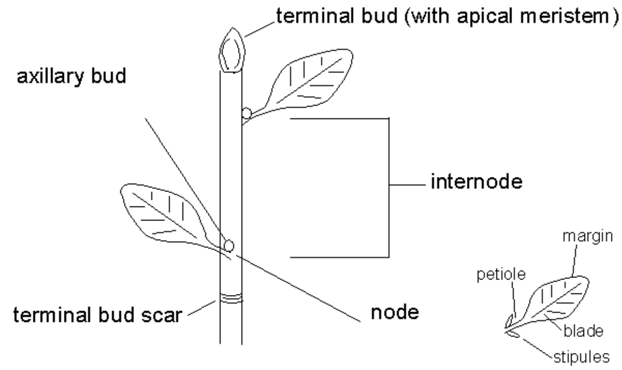
The end walls, however, are full of small pores where cytoplasm extends from cell to cell. These porous connections are called sieve plates. In spite of the fact that their cytoplasm is actively involved in the conduction of food materials, sieve-tube members do not have nuclei at maturity. It is the companion cells that are nestled between sieve-tube members that function in some manner bringing about the conduction of food. Sieve-tube members that are alive contain a polymer called callose, a carbohydrate polymer, forming the callus pad/callus, the colourless substance that covers the sieve plate. Callose stays in solution as long as the cell contents are under pressure. Phloem transports food and materials in plants upwards and downwards as required.



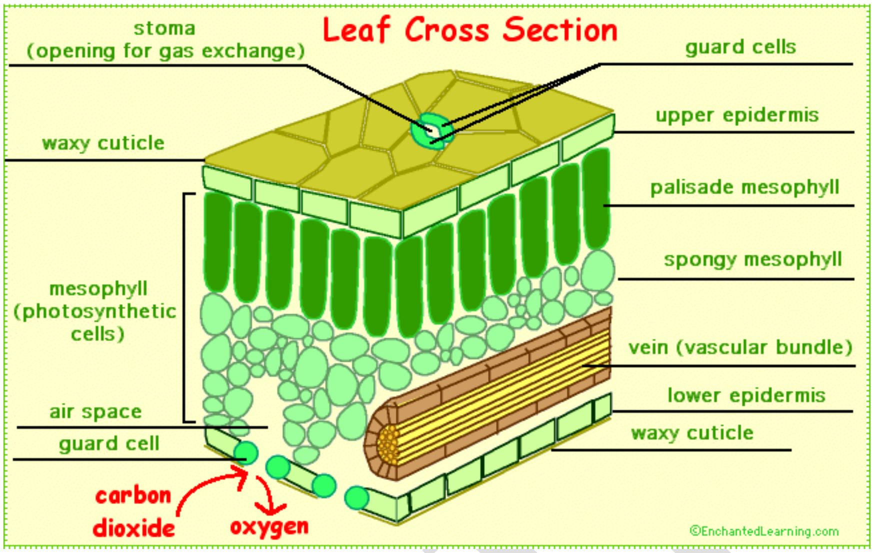
Section of Stem

Leaf anatomy

Leaf Structure:



A leaf is made of many layers that are sandwiched between two layers of tough skin cells (called the epidermis). The epidermis also secretes a waxy substance called the cuticle. These layers protect the leaf from insects, bacteria, and other pests. Among the epidermal cells are pairs of sausage-shaped guard cells. Each pair of guard cells forms a pore (called stoma; the plural is stomata). Gases enter and exit the leaf through the stomata. Most food production takes place in elongated cells called palisade mesophyll. Gas exchange occurs in the air spaces between the oddly-shaped cells of the spongy mesophyll. Veins support the leaf and are filled with vessels that transport food, water, and minerals to the plant.



Dorsiventral Leaf	Isobilateral Leaf
1. The number of stomata is more on the abaxial epidermis than the adaxial epidermis.	1. Almost equal number of stomata is present on the abaxial and adaxial surfaces.
2. Mesophyll is differentiated into spongy and palisade parenchyma.	2. Mesophyll layer is not differentiated into spongy and palisade parenchyma.
3. Vascular bundles are large and vary in size as per the size of veins.	3. Vascular bundles are similar in size, only the bundles near the mid vein are large.
4. Bulliform cells are absent.	4. Bulliform cells are present.

Vascular tissue

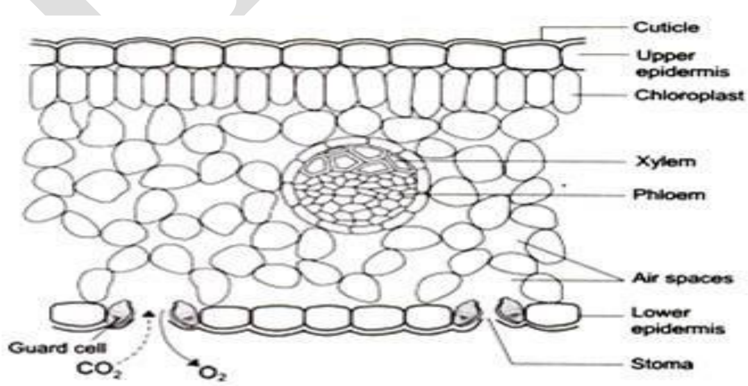
The **veins** are the vascular tissue of the leaf and are located in the spongy layer of the mesophyll. The pattern of the veins is called venation. In angiosperms the venation is typically parallel in monocotyledons and forms an interconnecting network in broad-leaved plants. They were once thought to be typical examples of pattern formation through ramification, but they may instead exemplify a pattern formed in a stress tensor field. A vein is made up of a vascular bundle. At the core of each bundle are clusters of two distinct types of conducting cells:

- Xylem: cells that bring water and minerals from the roots into the leaf.
- Phloem: cells that usually move sap, with dissolved sucrose (glucose to sucrose) produced by photosynthesis in the leaf, out of the leaf.

The xylem typically lies on the adaxial side of the vascular bundle and the phloem typically lies on the abaxial side. Both are embedded in a dense parenchyma tissue, called the sheath, which usually includes some structural collenchyma tissue.

Secondary growth

In botany, secondary growth is the growth that results from cell division in the cambia or lateral meristems and that causes the stems and roots to thicken, while primary growth is growth that occurs as a result of cell division at the tips of stems and roots, causing them to elongate, and gives rise to primary tissue. Secondary growth occurs in most seed plants, but monocots usually lack secondary growth. If they do have secondary growth, it differs from the typical pattern of other seed plants.



Anatomy of a leaf. Note how plants obtain CO_2 through stomata.

Abnormal secondary growth

Abnormal secondary growth does not follow the pattern of a single vascular cambium producing xylem to the inside and phloem to the outside as in ancestral lignophytes. Some dicots have anomalous secondary growth, e.g. in Bougainvillea a series of cambia arise outside the oldest phloem. Ancestral monocots lost their secondary growth and their stele has changed in a way it could not be recovered without major changes that are very unlikely to occur. Monocots either have no secondary growth, as is the ancestral case, or they have an "anomalous secondary growth" of some type, or, in the case of palms, they enlarge their diameter in what is called a sort of secondary growth or not depending on the definition given to the term.

Palm trees increase their trunk diameter due to division and enlargement of parenchyma cells, which is termed "primary gigantism" because there is no production of secondary xylem and phloem tissues, or sometimes "diffuse secondary growth".In some other monocot stems with anomalous secondary growth, a cambium forms, but it produces vascular bundles and parenchyma internally and just parenchyma externally. Some monocot stems increase in diameter due to the activity of a primary thickening meristem, which is derived from the apical meristem.

Possible Questions

Short questions

1. What is Shoot apical meristem
2. What is meristem
3. What is root apical meristem
4. What is quiescent center?
5. Write short note on meristematic tissues?
6. Define permanent tissues.
7. What is a Parenchyma tissues?
8. What is a sclerenchyma tissues?
9. What is a Collenchyma tissues?
10. What is aeranchyma?
11. What are xylem and phloem tissues?
12. What is leaf anatomy?

Essay type questions

1. Explain the meristematic tissues in detail.
2. Give in detail about the shoot and root apical meristem with neat diagram.
3. Explain in detail about complex and permenant tissues
4. Explain in detail about the different types of tissues.
5. Write in detail about the dorsi ventral and isobilateral leaf anatomy.
6. Discuss the leaf structure in detail.

UNIT-II

SYLLABUS

Plant water relation and Micro & Macro nutrient: Plant water relations: Importance of water to plant life, diffusion, osmosis, plasmolysis, imbibition, guttation, transpiration, stomata & their mechanism of opening and closing. Micro & micro nutrient: Criteria for identification of essentiality of nutrients, roles and deficiency system of nutrients, mechanism of uptake of nutrients, mechanism of food transport.

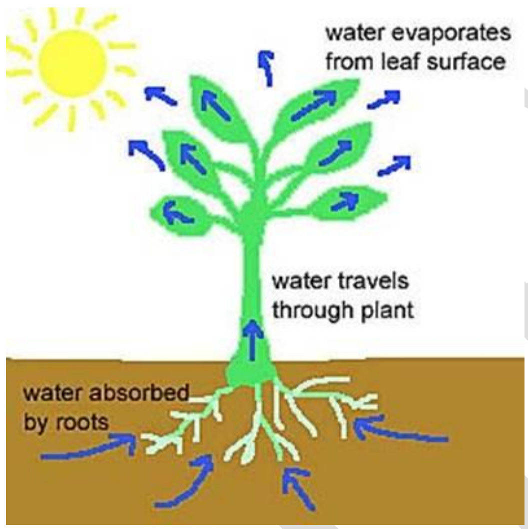
Plant water relations

Water being considered as universal solvent, occupies 75% of our planet in the form of oceans. Added to this water is also found in the atmosphere in the form of Hydrospheric mantle. The evaporation of water from the surface of ocean, formation clouds and raining, is a natural cycle evolved during course of Evolution of this planet. Nearly 3.8 billion years ago, life took its origin as a speck of protoplasm in the churning oceanic water which was not salty as it is today. In the course of Chemical Evolution, the birth of life has chosen H_2O as the medium of biochemical activities. Thus water has become mother of life or "Solvent of Life". Cells of all organisms are made up 90% or more of water. And all other components are either dissolved or suspended in water to form protoplasm, which is often referred to as physical basis of life. In this context one is tempted to know why water is so important and how water is useful to life forms.

Importance of water:

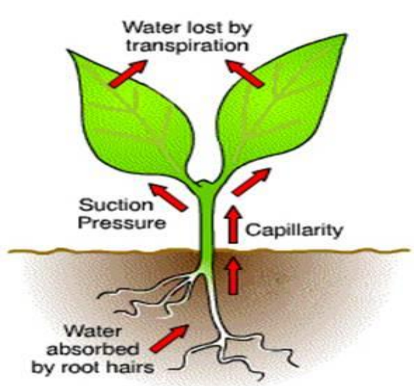
Water is the major component of living cells and constitutes more than 90% of protoplasm by volume and weight. In acts as medium for all biochemical reaction that takes place in the cell, and also acts a medium of transportation from one region to another region. Water is a remarkable compounded made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

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



Diffusion

Plant cells, like all other living cells, are surrounded by a semipermeable membrane, and any particle moving into or out of the cell must cross this membrane. There are three basic processes by which particles move across plant cell membranes: diffusion, facilitated diffusion, and active transport. The process of active transport requires the direct input of energy to move particles across the cell membrane. Diffusion and facilitated diffusion can occur without the direct expenditure of cellular energy.



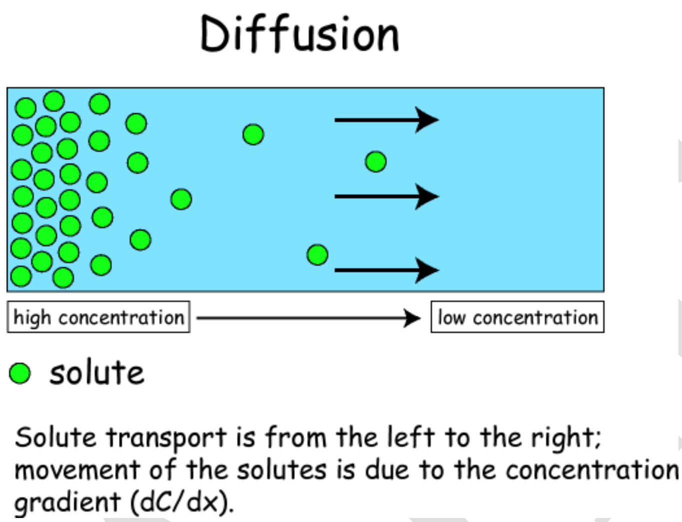
Drop a sugar cube into glass of water and immediately use a straw to sip a little water from the top of the glass, the water would not have a sweet taste. However, after a few hours, reason for the change in the taste of the water is diffusion, the net movement of particles down a concentration gradient (that is, from an area of higher concentration to an area of lower concentration). Concentration is the number of particles or amount of substance per unit volume, and a gradient occurs when some factor such as concentration changes from one volume of space to another.

Hence, the sugar molecules move more frequently from around the cube where they were highly concentrated to other parts of the glass where they were less concentrated. There is always some movement in both directions, but the net movement is down the concentration gradient.

Diffusion is possible because molecules in a liquid or gaseous phase are not static; they are in constant motion as a result of kinetic energy, which exists at temperatures above absolute zero. As the concentration of a substance increases, its free energy also increases. When molecules move, they collide with one another and exchange kinetic energy, and there is a random but progressive movement from regions of high free energy (high concentration) to regions of low free energy conservation. Diffusion can occur quite rapidly over short distances but can be extremely slow over long distances. For example, a molecule of glucose can diffuse across a typical 50-micrometer diameter cell in 2.5 seconds, but it takes thirty-two years for it to diffuse a distance of 1 meter.

Role in Plants

Diffusion is an important process in the lives of plants. Water is an important component of all cells, and water moves into plant cells by the process of osmosis. Osmosis is the diffusion of water across a semipermeable membrane. Many plant nutrients reach the root surface via diffusion through soil solution. Some nutrient molecules diffuse across root cell membranes into the cytosol (cell sap or cytoplasm) or from the cytosol of the endodermal cells into the xylem tissue. Carbon dioxide diffuses from the atmosphere through the stomata and into the air spaces of leaves. Water vapor evaporates from the surface of a leaf by diffusion through the open stomata. Diffusion also plays a role in the movement of photosynthetic products such as sugars into the phloem for transport throughout the plant. Because cellular membranes are composed of a lipid bilayer, lipid-soluble materials use simple diffusion to cross the membrane surface. Substances with low lipid solubility can move across membranes via facilitated diffusion. In this process, the substance binds to a transporter molecule, generally called an ionophore, which transports the substance across the membrane and down its concentration gradient.



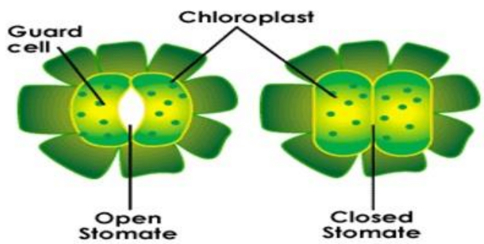
Osmosis

By definition, osmosis is the spontaneous movement of a solvent (water) through a cellular membrane. This is a special kind of diffusion that moves water molecules from a place of higher concentration to a place of lower concentration to create a stable and equal cellular environment. The process of osmosis is kind of like squeezing the middle of a water balloon. When you squeeze right in the middle the water displaces to either side equally. If you squeeze on one end all of the water (and weight) goes to one side or the other. Osmosis seeks to create a balance between the two sides of the water balloon like if you were to squeeze it in the center. Osmosis continues until there is an equal pressure of fluid on either side of the membrane.

The water creates a pressure that makes the balloon expand. In plants this pressure is called *turgor pressure*, or the pressure that pushes the cell membrane against the plasma wall to maintain the cell's shape. Turgor pressure is effected by *osmotic pressure*, or the pressure differentials that cause osmosis to occur. If one side of the membrane has a higher pressure, it will cause the other side of the cell to have low pressure which equals a not-well-supported plant structure. This difference in concentration is an osmotic pressure differential. The fuller the *vacuoles*, cellular sacs that hold fluid like water, the healthier the plant is and the more alive the plant looks. This also indicates successful and ongoing osmosis to make sure all of the cells have equal volume and pressure.

Osmosis in Plants

Osmosis is a vital function to the growth and stability of plant life. Without osmosis, photosynthesis would never occur and plants would wilt and die. A wilted plant looks wilted because the vacuoles of the cells do not have proper amounts of water. Although osmosis is still occurring, the lack of volume of water in the plant causes all of the cell walls to lose their turgor, and thus the plant loses its upright and healthy state. Osmosis distributes water through selectively permeable membranes to maintain this proper volume and pressure of all plant cells. Plant cell walls are incredibly tough and rigid which is necessary to uphold the integrity of the cell. It's when there is adequate water that the pressure from the water can become too high in some places and through osmosis the water moves to a place of lower pressure and concentration.



Photosynthesis

Osmosis is especially crucial to photosynthesis. Photosynthesis is the process of converting solar energy into chemical energy. Basically, the plant uses the sun to create proteins, sugars and lipids that in turn become energy for the plant's survival. Photosynthesis primarily occurs on plant leaves and requires a combination of carbon dioxide, sunlight and water to be successful. On every plant leaf there are many *guard cells* that literally "guard" the *stomata*. A stomata is a plant pore that lives on the plant leaf surface. Stomata are responsible for plant gas exchange which enables the process of photosynthesis. The guard cells have vacuoles that fill up with water and other fluids.

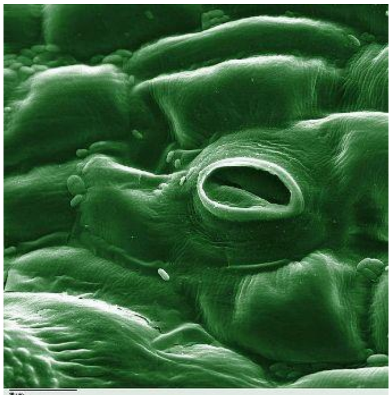
During osmosis, the guard cells swell with water and the pressure triggers the stomata to open. When the stomata open they suck in carbon dioxide from the air which is then used in combination with the water from the roots and the sunlight absorbed in chlorophyll to produce plant energy. Plant energy is then used to feed and nurture the plant. The by-product of this process is oxygen which is recirculated into the air that we breathe. This is why plants are fundamental to human survival! They eat up carbon dioxide which in high amounts is dangerous and produce more oxygen which we need.

Roots and Osmosis

The roots of a plant are the plants lifeline. They reach out into the soil to establish an avenue for the transport of nutrients and water to the rest of the plant. The roots absorb water through osmosis. If the water concentration outside of the plant roots is greater than that of the water concentration in the roots osmosis occurs. The difference in pressure triggers the plant to bring in water through the root cell walls to create a pressure balance and thus providing necessary water to the plant. When a plant has adequate water uptake, it will flourish and grow.

Stomata: Definition

Plants 'breathe' too, but they do it through tiny openings in leaves called **stomata** (singular: **stoma**). Stomata open and close to allow the intake of carbon dioxide and the release of oxygen.



Stoma of a plant: Function

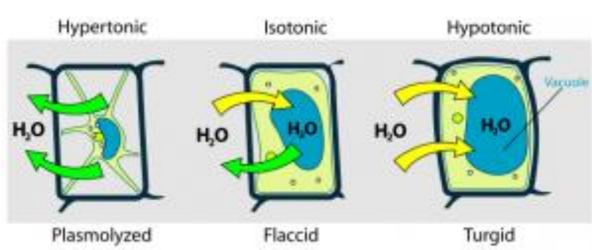
The gas exchange that occurs when stomata are open facilitates **photosynthesis**. Photosynthesis is the process by which plants convert sunlight into usable energy. During photosynthesis, carbon dioxide is taken in from the atmosphere through the stomata and oxygen is released as a waste product. Both photosynthesis and the gas exchange that powers it are essential to the plant's survival.

An unfortunate side effect of the stomata opening is that it allows for water loss. Unlike us, the plants do not need to sweat to cool off and prefer to keep their water inside; however, because the gas exchange of photosynthesis is so vital, some water loss through stomata is necessary. This process of plant water loss is called **transpiration**.

Although transpiration cannot be avoided, plants can minimize their water loss by controlling how wide their stomata are open, as well as what time of day they are open. Opening stomata when the surrounding air is more humid means that less water will evaporate from the plant leaves, but opening them when temperatures are warmer means more evaporation will occur. Likewise, if a plant is already dehydrated, it may close its stomata to prevent further water loss.

Plasmolysis Definition

Plasmolysis is when plant cells lose water after being placed in a solution that has a higher concentration of solutes than the cell does. This is known as a hypertonic solution. Water flows out of the cells and into the surrounding fluid due to osmosis. This causes the protoplasm, all the material on the inside of the cell, to shrink away from the cell wall. Severe water loss that leads to the collapse of the cell wall can result in cell death. Since osmosis is a process that requires no energy on the part of the cell and cannot be controlled, cells cannot stop plasmolysis from taking place.



Plasmolysis and Osmosis

Osmosis is responsible for the occurrence of plasmolysis. Osmosis is a special type of diffusion that occurs when water flows into or out of a membrane such as a cell's plasma membrane. It occurs based on the type of solution that a cell is in. A solution is a mixture that contains a fluid, or solvent (usually water), and a solute that is dissolved in the solvent. When a cell is placed into a hypertonic solution, there is a higher concentration of solutes outside the cell, so water flows out of the cell to balance the concentration on both sides of the membrane. Since plasmolysis is the loss of water from a cell, it occurs when a cell is in a hypertonic solution. Conversely, when a cell is placed into a hypotonic solution, there is a lower solute concentration outside the cell than inside, and water rushes into the cell. In an isotonic solution, solute concentrations are the same on both sides, so there is no net gain or loss of water.

Types of Plasmolysis

Concave Plasmolysis

Concave plasmolysis is a process that can usually be reversed. During concave plasmolysis, the protoplasm and the plasma membrane shrink away from the cell wall in places due to the loss of water; the protoplasm is then called protoplast once it has started to detach from the cell wall. Half-moon-shaped "pockets" form in the cell as the protoplast peels from the surface of the cell wall. This can be reversed if the cell is placed in a hypotonic solution, which will cause water to rush back into the cell.

Convex Plasmolysis

Convex plasmolysis is more severe than concave plasmolysis. When a cell undergoes complex plasmolysis, the plasma membrane and protoplast lose so much water that they completely detach from the cell wall. The cell wall collapses in a process called cytorrhysis. Convex plasmolysis cannot be reversed, and results in the destruction of the cell. Essentially, this is what happens when a plant wilts and dies from lack of water.

Guttation

Guttation is the exudation of drops of xylem sap on the tips or edges of leaves of some vascular plants, such as grasses. Guttation is not to be confused with dew, which condenses from the atmosphere onto the plant surface. At night, transpiration usually does not occur because most plants have their stomata closed. When there is a high soil moisture level, water will enter plant roots, because the water potential of the roots is lower than in the soil solution. The water will accumulate in the plant, creating a slight root pressure. The root pressure forces some water to exude through special leaftip or edge structures, hydathodes or water glands, forming drops. Root pressure provides the impetus for this flow, rather than transpirational pull. Guttation is most noticeable when transpiration is suppressed and the relative humidity is high, such as during the night. Guttation fluid may contain a variety of organic and inorganic compounds, mainly sugars, and potassium.On drying, a white crust remains on the leaf surface.

Girolami et al. (2005) found that guttation drops from corn plants germinated from neonicotinoid-coated seeds could contain amounts of insecticide consistently higher than 10 mg/l, and up to 200 mg/l for the neonicotinoid imidacloprid. Concentrations this high are near those of active ingredients applied in field sprays for pest control and sometimes even higher. It was found that when bees consume guttation drops collected from plants grown from neonicotinoid-coated seeds, they die within a few minutes. This phenomenon may be a factor in deaths and, consequently, colony collapse disorder (CCD).

Plant nutrition

Plant nutrition is the study of the chemical elements and compounds necessary for plant growth, plant metabolism and their external supply. In 1972, Emanuel Epstein defined two criteria for an element to be essential for plant growth:

1. In its absence the plant is unable to complete a normal life cycle.
2. The element is part of some essential plant constituent or metabolite.

This is in accordance with Justus von Liebig's law of the minimum. The essential plant nutrients include carbon, oxygen and hydrogen which are absorbed from the air, whereas other nutrients including nitrogen are typically obtained from the soil (exceptions include some parasitic or carnivorous plants).

There are 16 most important nutrients for plants. Plants must obtain the following mineral nutrients from their growing medium

- Macronutrients: nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), sulfur (S), magnesium (Mg), carbon (C), oxygen(O), hydrogen (H)
- Micronutrients: iron (Fe), boron (B), chlorine (Cl), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo)

These elements stay beneath soil as salt. So plants consume these elements as ion. The macronutrients are consumed in larger quantities; hydrogen, oxygen, nitrogen and carbon contribute to over 95% of a plants' entire biomass on a dry matter weight basis. Micronutrients are present in plant tissue in quantities measured in parts per million, ranging from 0.1 to 200 ppm, or less than 0.02% dry weight.

Most soil conditions across the world can provide plants adapted to that climate and soil with sufficient nutrition for a complete life cycle, without the addition of nutrients as fertilizer. However, if the soil is cropped it is necessary to artificially modify soil fertility through the addition of fertilizer to promote vigorous growth and increase or sustain yield. This is done because, even with adequate water and light, nutrient deficiency can limit growth and crop yield.

PRIMARY (MACRO) NUTRIENTS

Primary (macro) nutrients are nitrogen, phosphorus, and potassium. They are the most frequently required in a crop fertilization program. Also, they are need in the greatest total quantity by plants as fertilizer.

NITROGEN

- Necessary for formation of amino acids, the building blocks of protein
- Essential for plant cell division, vital for plant growth
- Directly involved in photosynthesis
- Necessary component of vitamins

- Aids in production and use of carbohydrates
- Affects energy reactions in the plant

PHOSPHORUS

- Involved in photosynthesis, respiration, energy storage and transfer, cell division, and enlargement
- Promotes early root formation and growth
- Improves quality of fruits, vegetables, and grains
- Vital to seed formation
- Helps plants survive harsh winter conditions
- Increases water-use efficiency
- Hastens maturity

POTASSIUM

- Carbohydrate metabolism and the break down and translocation of starches
- Increases photosynthesis
- Increases water-use efficiency
- Essential to protein synthesis
- Important in fruit formation
- Activates enzymes and controls their reaction rates
- Improves quality of seeds and fruit
- Improves winter hardiness
- Increases disease resistance

SECONDARY NUTRIENTS

The secondary nutrients are calcium, magnesium, and sulphur. For most crops, these three are needed in lesser amounts that the primary nutrients. They are growing in importance in crop fertilization programs due to more stringent clean air standards and efforts to improve the environment.

CALCIUM

- Utilized for Continuous cell division and formation
- Involved in nitrogen metabolism
- Reduces plant respiration
- Aids translocation of photosynthesis from leaves to fruiting organs
- Increases fruit set
- Essential for nut development in peanuts
- Stimulates microbial activity

MAGNESIUM

- Key element of chlorophyll production
- Improves utilization and mobility of phosphorus
- Activator and component of many plant enzymes
- Directly related to grass tetany
- Increases iron utilization in plants
- Influences earliness and uniformity of maturity

SULPHUR

- Integral part of amino acids
- Helps develop enzymes and vitamins
- Promotes nodule formation on legumes
- Aids in seed production
- Necessary in chlorophyll formation (though it isn't one of the constituents)

MICRONUTRIENTS

The micronutrients are boron, chlorine, cooper, iron, manganese, molybdenum, and zinc. These plant food elements are used in very small amounts, but they are just as important to plant development and profitable crop production as the major nutrients. Especially, they work "behind the scene" as activators of many plant functions.

BORON

- Essential of germination of pollon grains and growth of pollen tubes
- Essential for seed and cell wall formation
- Promotes maturity
- Necessary for sugar translocation
- Affects nitrogen and carbohydrate

CHLORINE

- Not much information about its functions
- Interferes with P uptake
- Enhances maturity of small grains on some soils

COPPER

- Catalyzes several plant processes
- Major function in photosynthesis
- Major function in reproductive stages
- Indirect role in chlorophyll production
- Increases sugar content
- Intensifies color
- Improves flavor of fruits and vegetables

IRON

- Promotes formation of chlorophyll
- Acts as an oxygen carrier
- Reactions involving cell division and growth

MANGANESE

- Functions as a part of certain enzyme systems
- Aids in chlorophyll synthesis
- Increases the availability of P and CA

MOLYBDENUM

- Required to form the enzyme "nitrate reductas" which reduces nitrates to ammonium in plant
- Aids in the formation of legume nodules
- Needed to convert inorganic phosphates to organic forms in the plant

ZINC

- Aids plant growth hormones and enzyme system
- Necessary for chlorophyll production
- Necessary for carbohydrate formation
- Necessary for starch formation
- Aids in seed formation

Possible Questions

Short questions

1. What is osmosis?
2. What is transpiration?
3. What is guttation?
4. What is nutrient?
5. Write short note on stomata?
6. Define structure of stomata.
7. What is a diffusion?
8. What is a plasmolysis?
9. What is a macronutrient?
10. What is micronutrient?

Essay type questions

1. Explain the plant relation to water in detail.
2. What are micro and macro nutrients and their importance in plant growth?
3. What is the mechanism of stomata opening and closing & their role in water relation in plant?
4. What are the deficiency systems of nutrients in plants?
5. Describe the mechanism of nutrient and food transport in plant.
6. Explain in detail about guttation process.
7. Explain about the transpiration and osmosis in detail.

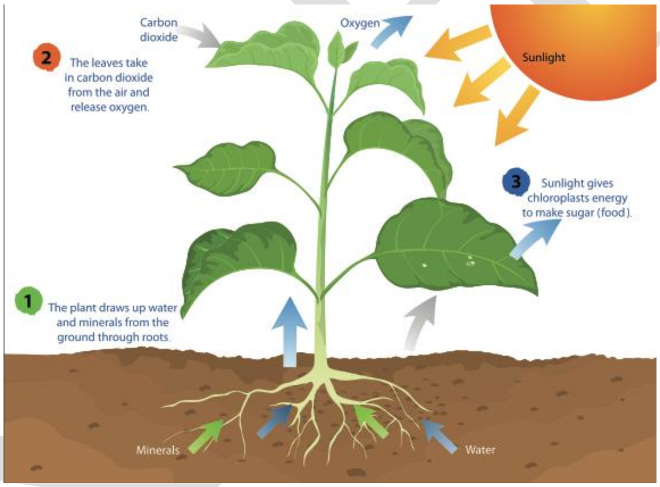
UNIT-III

SYLLABUS

Carbon and Nitrogen metabolism: Photosynthesis- Photosynthesis pigments, concepts of two photosystems, photophosphorylation, Calvin cycle, CAM plants, photorespiration, compensation points. Nitrogen metabolism- inorganic & molecular nitrogen fixation, nitrate reduction and ammonium assimilation in plants.

Photosynthesis

Photosynthesis is a process used by plants and other organisms to convert light energy into chemical energy that can later be released to fuel the organisms' activities (energy transformation). This chemical energy is stored in carbohydrate molecules, such as sugars, which are synthesized from carbon dioxide and water – hence the name *photosynthesis*, from the Greek φῶς, *phōs*, "light", and σύνθεσις, *synthesis*, "putting together". In most cases, oxygen is also released as a waste product. Most plants, most algae, and cyanobacteria perform photosynthesis; such organisms are called photoautotrophs. Photosynthesis is largely responsible for producing and maintaining the oxygen content of the Earth's atmosphere, and supplies all of the organic compounds and most of the energy necessary for life on Earth.



Although photosynthesis is performed differently by different species, the process always begins when energy from light is absorbed by proteins called reaction centres that contain green chlorophyll pigments. In plants, these proteins are held inside organelles called chloroplasts, which are most abundant in leaf cells, while in bacteria they are embedded in the plasma membrane. In these light-dependent reactions, some energy is used to strip electrons from suitable substances, such as water, producing oxygen gas. The hydrogen freed by the splitting of water is used in the creation of two further compounds that act as an immediate energy storage means: reduced nicotinamide adenine dinucleotide phosphate (NADPH) and adenosine triphosphate (ATP), the "energy currency" of cells.

In plants, algae and cyanobacteria, long-term energy storage in the form of sugars is produced by a subsequent sequence of light-independent reactions called the Calvin cycle; some bacteria use different mechanisms, such as the reverse Krebs cycle, to achieve the same end. In the Calvin cycle, atmospheric carbon dioxide is incorporated into already existing organic carbon compounds, such as ribulose bisphosphate (RuBP). Using the ATP and NADPH produced by the light-dependent reactions, the resulting compounds are then reduced and removed to form further carbohydrates, such as glucose.

The first photosynthetic organisms probably evolved early in the evolutionary history of life and most likely used reducing agents such as hydrogen or hydrogen sulfide, rather than water, as sources of electrons. Cyanobacteria appeared later; the excess oxygen they produced contributed directly to the oxygenation of the Earth, which rendered the evolution of complex lifepossible. Today, the average rate of energy capture by photosynthesis globally is approximately 130 terawatts, which is about three times the current power consumption of human civilization. Photosynthetic organisms also convert around 100–115 thousand million metric tonnes of carbon into biomass per year.

Photosynthesis is the process by which plants, some bacteria, and some protistans use the energy from sunlight to produce sugar, which cellular respiration converts into ATP, the "fuel" used by all living things. The conversion of unusable sunlight energy into usable chemical energy, is associated with the actions of the green pigment chlorophyll. Most of the time, the photosynthetic process uses water and releases the oxygen that we absolutely must have to stay alive.

We can write the overall reaction of this process as:

$6H_2O + 6CO_2$ ----------> $C_6H_{12}O_6 + 6O_2$

Six molecules of water plus six molecules of carbon dioxide produce one molecule of sugar plus six molecules of oxygen

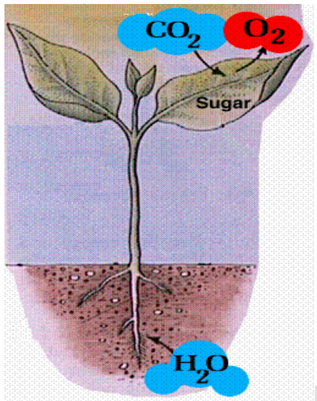
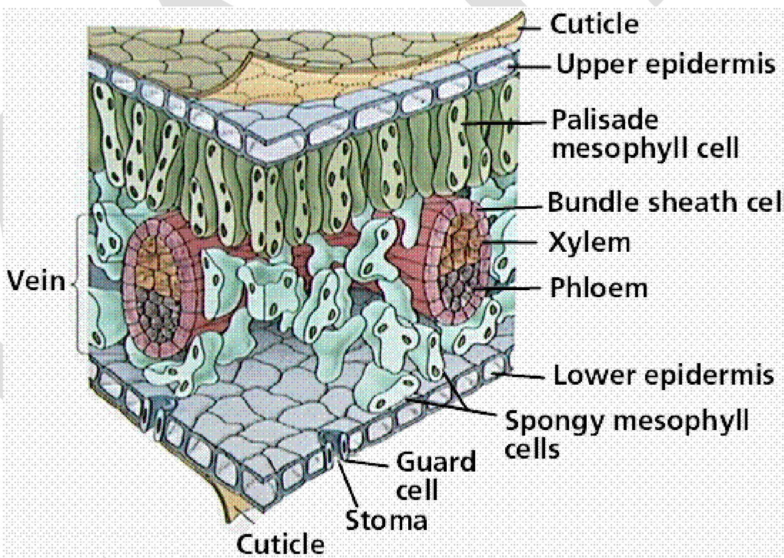


Diagram of a typical plant, showing the inputs and outputs of the photosynthetic process

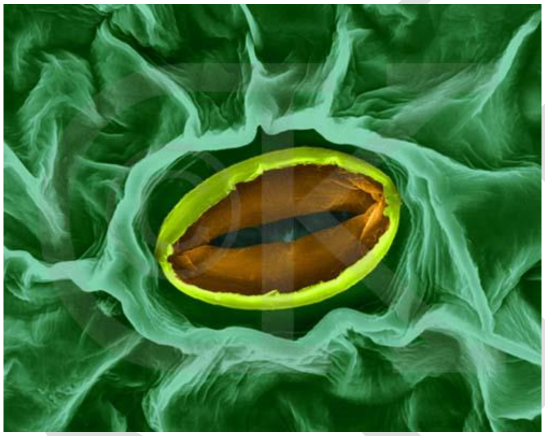
Leaves and Leaf Structure

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

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

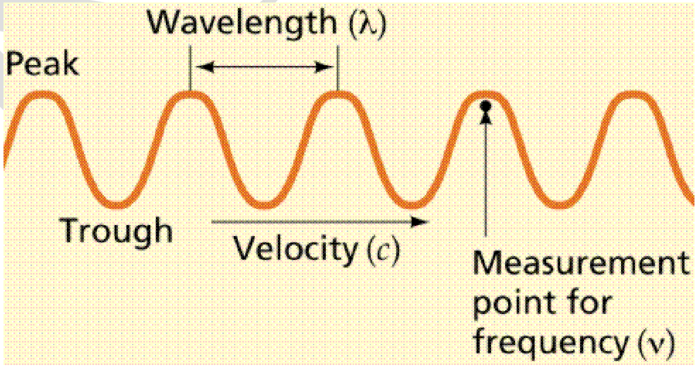


Cross section of a leaf, showing the anatomical features important to the study of photosynthesis: stoma, guard cell, mesophyll cells, and vein. Water enters the root and is transported up to the leaves through specialized plant cells known as xylem (pronounces zigh-lem). Land plants must guard against drying out (desiccation) and so have evolved specialized structures known as stomata to allow gas to enter and leave the leaf. Carbon dioxide cannot pass through the protective waxy layer covering the leaf (cuticle), but it can enter the leaf through an opening (the stoma; plural = stomata; Greek for hole) flanked by two guard cells. Likewise, oxygen produced during photosynthesis can only pass out of the leaf through the opened stomata. Unfortunately for the plant, while these gases are moving between the inside and outside of the leaf, a great deal water is also lost. Cottonwood trees, for example, will lose 100 gallons of water per hour during hot desert days. Carbon dioxide enters single-celled and aquatic autotrophs through no specialized structures.

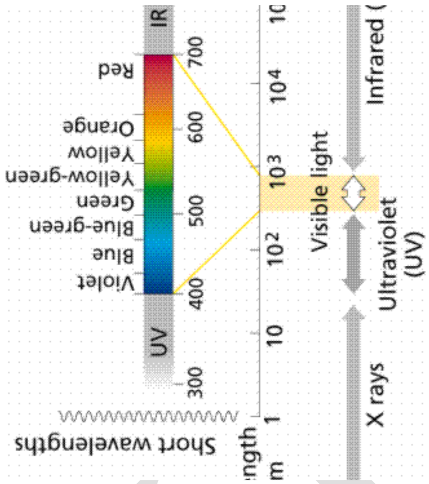


The Nature of Light

White light is separated into the different colors (=wavelengths) of light by passing it through a prism. Wavelength is defined as the distance from peak to peak (or trough to trough). The energy of is inversely proportional to the wavelength: longer wavelengths have less energy than do shorter ones.



The order of colors is determined by the wavelength of light. Visible light is one small part of the electromagnetic spectrum. The longer the wavelength of visible light, the more red the color. Likewise the shorter wavelengths are towards the violet side of the spectrum. Wavelengths longer than red are referred to as infrared, while those shorter than violet are ultraviolet.

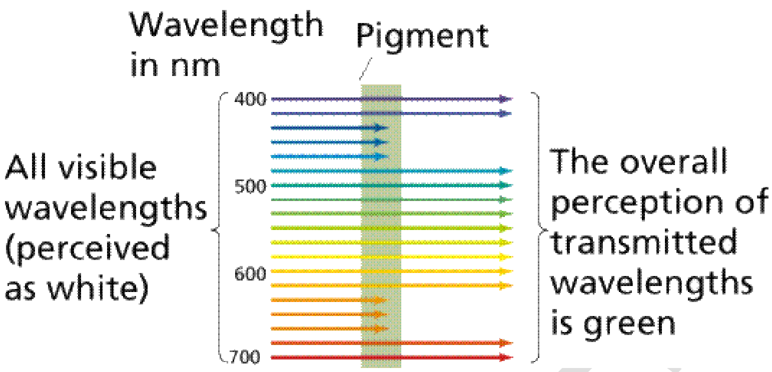


The electromagnetic spectrum.

Light behaves both as a wave and a particle. Wave properties of light include the bending of the wave path when passing from one material (medium) into another (i.e. the prism, rainbows, pencil in a glass-of-water, etc.). The particle properties are demonstrated by the photoelectric effect. Zinc exposed to ultraviolet light becomes positively charged because light energy forces electrons from the zinc. These electrons can create an electrical current. Sodium, potassium and selenium have critical wavelengths in the visible light range. The critical wavelength is the maximum wavelength of light (visible or invisible) that creates a photoelectric effect.

Chlorophyll and Accessory Pigments

A pigment is any substance that absorbs light. The color of the pigment comes from the wavelengths of light reflected (in other words, those not absorbed). Chlorophyll, the green pigment common to all photosynthetic cells, absorbs all wavelengths of visible light except green, which it reflects to be detected by our eyes. Black pigments absorb all of the wavelengths that strike them. White pigments/lighter colors reflect all or almost all of the energy striking them. Pigments have their own characteristic absorption spectra, the absorption pattern of a given pigment.



Photophosphorylation

In the process of photosynthesis, the phosphorylation of ADP to form ATP using the energy of sunlight is called photophosphorylation. Only two sources of energy are available to living organisms: sunlight and reduction-oxidation (redox) reactions. All organisms produce ATP, which is the universal energy currency of life. Commonly in photosynthesis this involves photolysis of water and a continuous unidirectional flow of electrons from water to PS In photophosphorylation, light energy is used to create a high-energy electron donor and a lower-energy electron acceptor. Electrons then move spontaneously from donor to acceptor through an electron transport chain.

ATP is made by an enzyme called ATP synthase. Both the structure of this enzyme and its underlying gene are remarkably similar in all known forms of life.

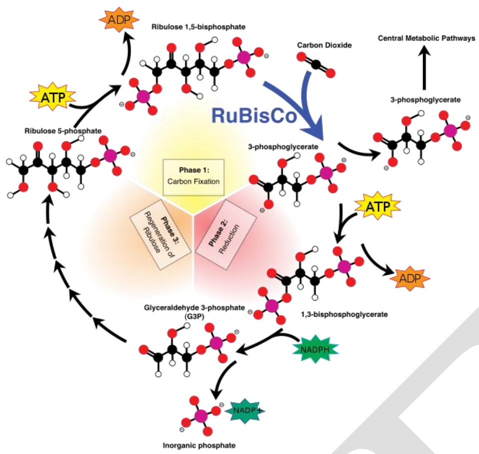
ATP synthase is powered by a transmembrane electrochemical potential gradient, usually in the form of a proton gradient. The function of the electron transport chain is to produce this gradient. In all living organisms, a series of redox reactions is used to produce a transmembrane electrochemical potential gradient, or a so-called proton motive force (pmf).

Redox reactions are chemical reactions in which electrons are transferred from a donor molecule to an acceptor molecule. The underlying force driving these reactions is the Gibbs free energy of the reactants and products. The Gibbs free energy is the energy available ("free") to do work. Any reaction that decreases the overall Gibbs free energy of a system will proceed spontaneously (given that the system is isobaric and also adiabatic), although the reaction may proceed slowly if it is kinetically inhibited. The transfer of electrons from a high-energy molecule (the donor) to a lower-energy molecule (the acceptor) can be *spatially* separated into a series of intermediate redox reactions. This is an electron transport chain. The fact that a reaction is thermodynamically possible does not mean that it will actually occur. A mixture of hydrogen gas and oxygen gas does not spontaneously ignite. It is necessary either to supply an activation energy or to lower the intrinsic activation energy of the system, in order to make most biochemical reactions proceed at a useful rate. Living systems use complex macromolecular structures to lower the activation energies of biochemical reactions.

It is possible to couple a thermodynamically favorable reaction (a transition from a high-energy state to a lower-energy state) to a thermodynamically unfavorable reaction (such as a separation of charges, or the creation of an osmotic gradient), in such a way that the overall free energy of the system decreases (making it thermodynamically possible), while useful work is done at the same time. The principle that biological macromolecules catalyze a thermodynamically unfavorable reaction *if and only if* a thermodynamically favorable reaction occurs simultaneously, underlies all known forms of life. Electron transport chains (most known as ETC) produce energy in the form of a transmembrane electrochemical potential gradient. This energy is used to do useful work. The gradient can be used to transport molecules across membranes. It can be used to do mechanical work, such as rotating bacterial flagella. It can be used to produce ATP and NADPH, high-energy molecules that are necessary for growth.

Calvin cycle

The **Calvin cycle** (also known as the Calvin–Benson cycle) is the set of chemical reactions that take place in chloroplasts during photosynthesis. The cycle is light-independent because it takes place after the energy has been captured from sunlight. The Calvin cycle is named after Melvin Calvin, who won a Nobel Prize in Chemistry for finding it in 1961. Calvin and his colleagues did the work at the University of California, Berkeley. Using the radioactive carbon-14 isotope as a tracer, Calvin, Andrew Benson and their team mapped the complete route that carbon travels through a plant during photosynthesis. They traced the carbon-14 from its absorption as atmospheric carbon dioxide to its conversion into carbohydrates and other organic compounds. The single-celled algae *Chlorella* was used to trace the carbon-14.[5] The Calvin group showed that sunlight acts on the chlorophyll in a plant to fuel the manufacture of organic compounds, not directly on carbon dioxide as previously believed.



Steps

The steps in the cycle are as follows:

1. Grab: A five-carbon carbon catcher catches one molecule of carbon dioxide and forms a six-carbon molecule.

2. Split: the enzyme RuBisCO (with the energy of ATP and NADPH molecules) breaks the six-carbon molecule into two equal parts.

3. Leave: A trio of three carbons leave and become sugar. The other trio moves on to the next step.

4. Switch: Using ATP and NADPH, the three carbon molecule is changed into a five carbon molecule.

5. The cycle starts over again

Crassulacean acid metabolism

Crassulacean acid metabolism, also known as CAM photosynthesis, is a carbon fixation pathway that evolved in some plants as an adaptation to arid conditions. In a plant using full CAM, the stomata in the leaves remain shut during the day to reduce evapotranspiration, but open at night to collect carbon dioxide (CO_2). The CO_2 is stored as the four-carbon acid malatein vacuoles at night, and then in the daytime, the malate is transported to chloroplasts where it is converted back to CO_2, which is then used during photosynthesis. The pre-collected CO_2 is concentrated around the enzyme RuBisCO, increasing photosynthetic efficiency. This metabolism was first studied in plants of the family Crassulaceae. These mainly include succulents. The first time it was studied, *Crassula* was used as a model organism. The word "crassulacean" is from the Latin word *crassus*, meaning “thick;” succulent plants have leaves that are thick and full of moisture, and they often have a waxy or hairy coating to help prevent evaporation. CAM was first suspected by de Saussure in 1804 in his *RecherchesChimiques sur la Vegetation*, confirmed and refined by Aubert, E. in 1892 in his *Recherchesphysiologiques sur les plantes grasses* and expounded upon by Richards, H. M. 1915 in *Acidity and Gas Interchange in Cacti*, Carnegie Institution.

The term CAM may have been coined by Ranson and Thomas in 1940, but they were not the first to discover this cycle. It was observed by the botanists Ranson and Thomas, in the succulent family Crassulaceae (which includes jade plants and *Sedum*). Its name refers to acid metabolism in Crassulaceae, not the metabolism of "crassulacean acid".

CAM photosynthesis is also found in aquatic species in at least 4 genera, including: Isoetes, Crassula, Littorella, Sagittaria, and possibly Vallisneria, being found in a variety of species e.g. Isoeteshowellii, *Crassulaaquatica*. These plants follow the same nocturnal acid accumulation and daytime deacidification as terrestrial CAM species. However, the reason for CAM in aquatic plants is not due to a lack of available water, but a limited supply of CO2. CO2 is limited due to slow diffusion in water, 10000x slower than in air. The problem is especially acute under acid pH, where the only inorganic carbon species present is CO2, with no available bicarbonate or carbonate supply.

Aquatic CAM plants capture carbon at night when it is abundant due to a lack of competition from other photosynthetic organisms. This also results in lowered photorespiration due to less photosynthetically generated oxygen. Aquatic CAM is most marked in the summer months when there is increased competition for CO2, compared to the winter months. However, in the winter months CAM still has a significant role.

Photorespiration

Photorespiration is a wasteful pathway that competes with the Calvin cycle. It begins when rubisco acts on oxygen instead of carbon dioxide. At mid-day, when temperature and CO_2 content are high, the affinity of RuBP carboxylase increases for O_2 but decreases for CO_2. Thus,

it converts RuBP to 3-carbon compound (PGA) and a 2-carbon compound (phosphoglycolate). The phosphoglycolate is converted rapidly to glycolate in the peroxisomes.
Glycolate is further converted to glycine, serine, CO_2 and NH_3 without the generation of ATP or NADPH. Thus net result is oxidation of organic food synthesized during photosynthesis. This process is called photorespiration or glycolate pathway as it occurs at high rate in the presence of light. As already mentioned that photorespiration is a loss to the net productivity of green plants having Calvin cycle.

The green plants having Calvin cycle are C_3 plants. Overcoming photo-respiratory loss poses a challenge to plants growing in the tropics. Photorespiration occurs due to fact that the active site of enzyme Rubisco (ribulose bisphosphate carboxylase oxygenase) is same for both carboxylation and oxygenation.

The oxygenation of RuBP (ribulose bisphosphate) in the presence of O_2 is first reaction of photorespiration that leads to the formation of one molecule of phosphoglycolate, a two-carbon compound and one molecule of PGA. Where PGA is used in Calvin cycle, and phosphoglycolate is dephosphorylated to form glycolate in the chloroplast.

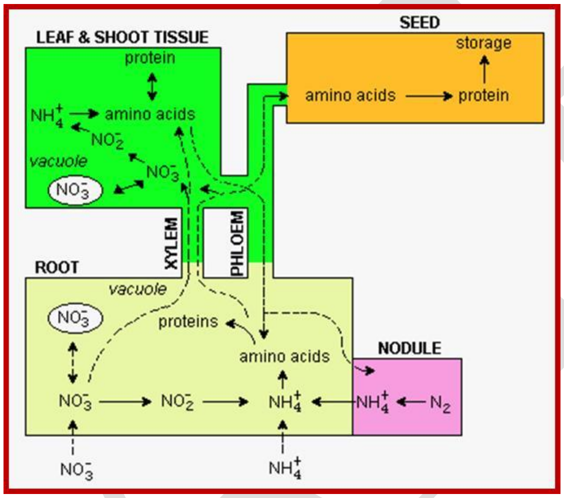
From chloroplast, glycolate is diffused to peroxisome where it is oxidised to in glyoxylate. Here glyoxylate is used to form amino acid, glycine. Now, glycine enters mitochondria where two glycine molecules (4 carbons) give rise to one molecule of serine (3 carbons) and one molecule of CO_2 (one carbon). Now, serene is taken up by peroxisome, and through a series of reactions is being converted into glycerate.

This glycerate leaves the peroxisome and enters the chloroplast, where it is phosphorylated to form PGA. Now PGA molecule enters the Calvin cycle to make carbohydrates, but one CO_2 molecule released in mitochondria during photorespiration has to be re-fixed. This means, 75 per cent of the carbon lost by the oxygenation of RuBP is recovered and 25 per cent is lost as release of one molecule of CO_2.Photorespiration is also known as photosynthetic carbon oxidation cycle.

Nitrogen Metabolism

Nitrogen is a very important constituent of cellular components. Alkaloids, amides, amino acids, proteins, DNA, RNA, enzymes, vitamins, hormones and many other cellular compounds contain nitrogen as one of the elements. It is not exaggerating to say that

Nitrogen is the key element for it is the most important constituent of proteins and nucleic acids. Thus N2 plays a significant role in the formation of the above said compounds which in turn control cellular activities. Without nitrogen, no living organism can survive. Paradoxically all the living organisms are virtually submerged in a sea of atmospheric nitrogen (i.e. 78%), but unfortunately not all organisms are endowed with the potentiality to utilize this abundantly available molecular N2 directly. Only some organisms like certain bacteria, blue green algae and few fungi, have the potentiality to utilize molecular N2 directly and fix it. However, most of the plants are capable of utilizing other forms of nitrogen with ease and facility.



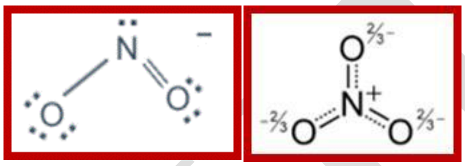
Elemental Nitrogen, Ammonical and organic form of Nitrogen:

Ammonical form of N2 is available in soil in the form of urea or NH4 in free-state. Urea, if present, is first split into NH4 and CO2, and NH4 is then utilized directly by metabolic pathways by higher plants. But recent studies indicate that urea can be directly used up by metabolic pathways in certain plants. It should be remembered here, that free ammonia is the only utilizable form of N2 that can be directly incorporated into amino acids. Whatever may be the source of nitrogen, first it has to be converted to NH3 and fixed into amino acid. It can be converted or transferred to other forms by various pathways that operate in living systems.

The decay of dead plants and animals also releases different kinds of nitrogen compounds of which amino acids, nucleotides and other such Nitrate compounds constitute organic form of N2. The same are absorbed by the root system and utilized directly. Thus the decaying organic matter acts as the rich source of organic nitrogen that can be utilized by not only higher plants but also by micro-organisms.

Nitrate / nitrite form

Invariably the N2 that is available in the soil is in the form of nitrates. And nitrites are also found but in small quantities. These forms are available as ions and the same are easily absorbed by the roots or cellular surfaces from its surrounding soil solution. The absorption of NO3 or NO2 ions is not by just diffusion process, but it is facilitated by specific carriers.



Once the nitrate or nitrite ions enter into cellular milieu they have to be converted to NH4, before the same can be incorporated into cellular components. Under normal conditions, nitrite is never accumulated in the soil in sufficient quantities and it is toxic to plants and to other microbes.

The mechanism of conversion of NO3 and NO2 to NH4

Plant structures like roots as well as leaves can utilize nitrates and the same can be converted to NH4. But more of nitrate reductive activity is found in leaves than in roots. However, the mechanism of nitrate and nitrite reduction is performed by different enzymes while NO3 is reduced by nitrate reductase enzymes and the NO2 is reduced by nitrite reductases.

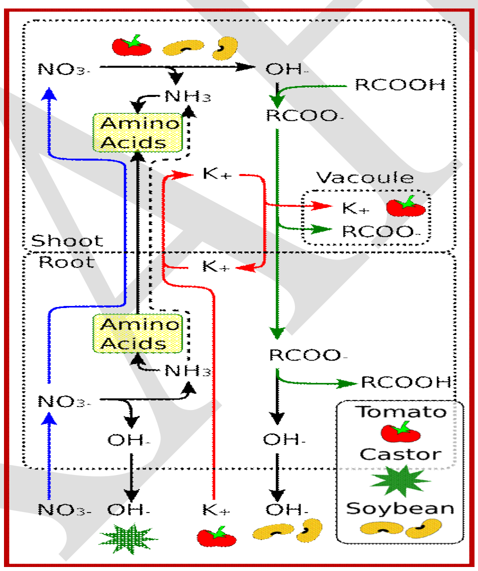
Nitrate reduction

Nitrate reduction to NH4 is not a single step process, but it is a series of reactions in which the first step is performed by nitrate reductase. This enzyme has been isolated and purified from various sources like Aspergillus, bacteria, chlorella, blue green algae, alfa alfa and other higher plants. The mol. Wt. of it is about 3.5 x 10^5 daltons. The enzyme is associated with 2 cofactors i.e. FAD and two molybdenum ions. The enzyme also requires reducing power supplied by NADH+H or NADPH+H. The former is available in non chlorophyllous tissues and the latter is found in chloroplast containing leaves.

Nitrate reductase is an inducible enzyme

In the absence of NO3 the amount of this enzyme present in the tissues is very low. With the addition of NO3 as the substrate, the amount of this enzyme increases many fold. However, the induction requires light without which the enzyme induction is not possible to the fullest extent. The nitrate induced enzyme synthesis can be inhibited by the inhibitors of transcription and translation like actinomycin D and cycloheximide respectively, which indicates that NO3 acts as an inducer of nitrate reductase gene expression. How light modulates the gene expression is not yet clear.

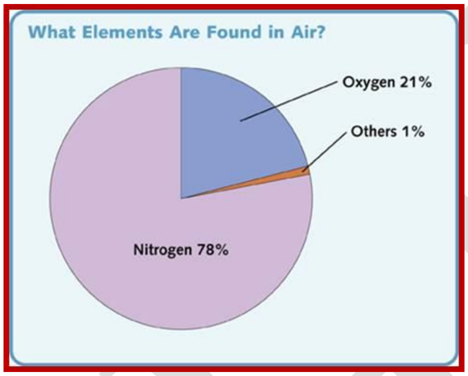
Furthermore, phytohormones, particularly cytokinin also induces nitrate reductase synthesis denovo even in the absence of light and NO3. Cytokinin induced NO3 reductase activity can be inhibited with actinomycin or CHI. The mechanism of denovo synthesis of nitrate reductase, though not clear, it is fully accepted that the nitrate reductase is an inducible enzyme.

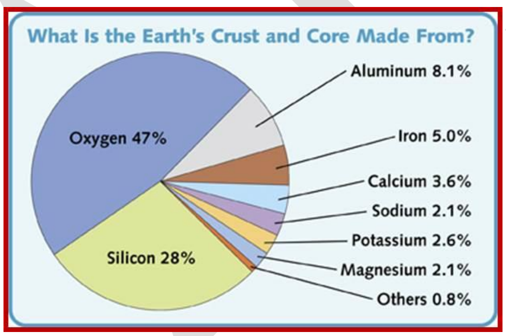


Different plants use different pathways to different levels. Tomatoes take in a lot of K^+ and accumulate salts in their vacuoles, castor reduces nitrate in the roots to a large extent and excretes the resulting alkali. Soy bean plants moves a large amount of malate to the roots where they convert it to alkali while the potassium recirculates

Molecular nitrogen

Abundantly available molecular N2 is more or less inert. With the exception of some bacteria, fungi and blue green algae none of the higher plants are capable of utilizing molecular N2 directly. However, nature has devised mechanisms to fix this type of N2 into utilizable form of N2 i.e. NH4 by non biological and biological methods.





Fixation of Inorganic N2:

Atmospheric N2 is converted into Ammonia by Haber's process; then ammonia is converted into different forms of nitrates, which is used by bacteria and plants.

N2 + 8H+ + 8e- + 16ATP = 2NH3 + H2 + 16ADP = 16 Pi

NITROGEN FIXATION

Non biological Method:

Electrical discharges in atmosphere due to lightening leads to the formation of various oxides and reductants of N2. In the presence of water vapors they dissolve and produce nitrous and nitric acids. These inturn, come down to earth along with rain water. Later they get converted to nitrates. Annually many billion tons of atmospheric N2 is fixed by this non biological process.

Biological method – asymbiotic process

Among the living plant world, some free living bacteria, fungi and blue green algae are capable of fixing molecular nitrogen into utilizable form of N2 i.e. NH4. Ex. *Azatobactorveinlandi, Clostridium pasteurianum, Rhodospirullum rubrum, Chromatium, Nostoc, Anabaena, Rivularia,* etc. When the above said organisms are allowed to multiply in the soil, under favourable conditions they easily fix 15-40 kgs. of N2 per acre per year. In recent years, the above said organisms are made available to farmers as bio-fertilizers.

When the cultures of them are spread in the fields and allowed to grow, they enrich the soil with a lot of nitrogen as a natural fertilizer. The mechanism by which molecular N2 is converted to NH4 is described elsewhere. One important aspect of it is to maintain moisture in the soil. This living fertilizer renewable and enriches the soil all the time.

Symbiotic process

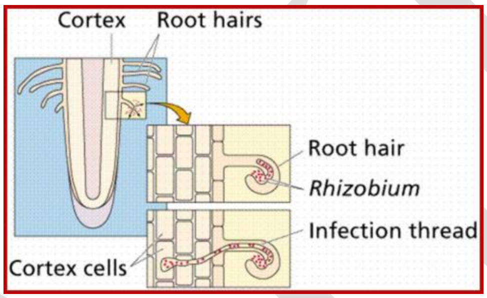
None of the known crop plants, or any other angiosperms are capable of utilizing molecular N2 directly, but some have developed a method by which they obtain nitrogen through symbiotic association with bacteria. It is widely known that many species of bacteria and also some blue green algal colonies live in association with higher plants, either in the roots, leaves, lichens, liverworts and coralloid roots. But the roots of leguminous plants possess characteristic root nodules in which nitrogen fixing bacteria called Rhizobium are present.

These bacteria, on infecting host roots induce the development of characteristic pink colored root nodules. In their symbiotic association, bacteria obtain carbohydrates and other minerals from host cells and host cells in return obtain nitrogen fixed by bacteria. So by growing leguminous plants in the fields the soil will be enriched with nitrogen fertilizers up to the tune of 40-80 kg./acre./year.

Development of root nodules

Specificity of bacteria and host association

The symbiotic association between bacteria and the host is highly specific. For example, Rhizobium phaseolin infects phaseolus species only but not others. Similarly, Rhizobium trifoli infects *Trifoliumrepens* but not others. The host bacterial specificity is due to the presence of glycoproteins as receptors in host root cell surface which recognizes some proteins found on the bacteria cell wall. These recognize each and other as in the case of enzyme recognizing its specific substrate.



Legumes have the unique ability to undergo symbiotic associations with bacteria belonging to the *Rhizobiaceae*family. These Rhizobacteria secrete signaling molecules (Nodule Factors) that trigger physiological and morphological plant responses. In the course of this interaction, rhizobia invade the host root leading to the formation of a novel symbiotic plant organ: the root nodule. Rhizobia remain surrounded by a plant-derived plasma membrane from the very first moment of host invasion until age-dependent degradation of the symbiotically active bacteroids. This membrane serves as an essential interface for plant-microbe signal transduction and is certainly one of the key determinants for the success of the association. Using DNA microarrays, a remorin gene (SYMREM1) that is strongly induced in root nodules of *Lotus japonicus* and *Medicagotruncatula.*

Possible Questions

Short questions

1. What is Photosynthesis?
2. What is photosynthetic pigments?
3. What is meant by chlorophyll?
4. What isphotophosphorylation?
5. Write short note on CAM plants?
6. Define photorespiration.
7. What is the outcome of photosynthesis?
8. What is the outcome of Calvin cycle?
9. What is the nitrogen metabolism?
10. What is nitrate reduction?
11. How symbiosis process takes place?

Essay type questions

1. Explain in detail about photosynthesis.
2. What are pigments involved in photosynthesis in plant growth?
3. What is the mechanism of two photosystem in plant?
4. What is Calvin cycle? How it is performed in plants?
5. Describe the mechanism of photorespiration in plant.
6. Explain in detail about photophosphorylation.
7. What is Nitrogen? How it is metabolized and obtained by the plants?
8. Describe the mechanism of biological and non-biological nitrogen fixation.

UNIT-IV

SYLLABUS

Growth and Development: Definition, phases of growth, growth curve, growth hormones (Auxin, gibberellins, cytokinins, abscisic acid, ethylene). Physiological role and mode of action, seed dormancy and seed germination, concepts of photoperiodism and vernalisation.

Growth and Development

"Development" and "growth" are sometimes used interchangeably in conversation, but in a botanical sense they describe separate events in the organization of the mature plant body. **Development** is the progression from earlier to later stages in maturation, e.g. a fertilized egg *develops* into a mature tree. It is the process whereby tissues, organs, and whole plants are produced. It involves: growth, morphogenesis (the acquisition of form and structure), and differentiation. The interactions of the environment and the genetic instructions inherited by the cells determine how the plant develops.

Growth is the irreversible change in size of cells and plant organs due to both cell division *and* enlargement. Enlargement necessitates a change in the elasticity of the cell walls together with an increase in the size and water content of the vacuole. Growth can be determinate—when an organ or part or whole organism reaches a certain size and then stops growing or indeterminate—when cells continue to divide indefinitely. Plants in general have indeterminate growth.

Differentiation is the process in which generalized cells specialize into the morphologically and physiologically different cells. Since all of the cells produced by division in the meristems have the same genetic make-up, differentiation is a function of which particular genes are either expressed or repressed. The kind of cell that ultimately develops also is a result of its location: Root cells don't form in developing flowers, for example, nor do petals form on roots.

Mature plant cells can be stimulated under certain conditions to divide and differentiate again, i.e. to dedifferentiate. This happens when tissues are wounded, as when branches break or leaves are damaged by insects. The plant repairs itself by *dedifferentiating* parenchyma cells in the vicinity of the wound, making cells like those injured or else physiologically similar cells.

Plants differ from animals in their manner of growth. As young animals mature, all parts of their bodies grow until they reach a genetically determined size for each species. Plant growth, on the other hand, continues throughout the life span of the plant and is restricted to certain meristematic tissue regions only. This continuous growth results in:

- Two general groups of tissues, primary and secondary.
- Two body types, primary and secondary.

- Apical and lateral meristems.

Apical meristems, or zones of cell division, occur in the tips of both roots and stems of all plants and are responsible for increases in the length of the primary plant body as the primary tissues differentiate from the meristems. As the vacuoles of the primary tissue cells enlarge, the stems and roots increase in girth until a maximum size (determined by the elasticity of their cell walls) is reached. The plant may continue to grow in length, but no longer does it grow in girth. Herbaceous plants with only primary tissues are thus limited to a relatively small size.

Woody plants, on the other hand, can grow to enormous size because of the strengthening and protective secondary tissues produced by lateral meristems, which develop around the periphery of their roots and stems. These tissues constitute the secondary plant body.

Plant growth hormone

Plant hormones (also known as phytohormones) are chemicals that regulate plant growth. In the United Kingdom, these are termed 'plant growth substances'. Plant hormones are signal molecules produced within the plant, and occur in extremely low concentrations. Hormones regulate cellular processes in targeted cells locally and, moved to other locations, in other functional parts of the plant. Hormones also determine the formation of flowers, stems, leaves, the shedding of leaves, and the development and ripening of fruit. Plants, unlike animals, lack glandsthat produce and secrete hormones. Instead, each cell is capable of producing hormones.

Plant hormones shape the plant, affecting seed growth, time of flowering, the sex of flowers, senescence of leaves, and fruits. They affect which tissues grow upward and which grow downward, leaf formation and stem growth, fruit development and ripening, plant longevity, and even plant death. Hormones are vital to plant growth, and, lacking them, plants would be mostly a mass of undifferentiated cells. So they are also known as growth factors or growth hormones. The term 'Phytohormone' was coined by Thimann in 1948. Phytohormones are found not only in higher plants but in algae, showing similar functions,[1] and in microorganisms, such as unicellular fungi and bacteria, but in these cases they play no hormonal or other immediate physiological role in the producing organism and can, thus, be regarded as secondary metabolites.

Classes of plant hormones

In general, it is accepted that there are five major classes of plant hormones, some of which are made up of many different chemicals that can vary in structure from one plant to the next. The chemicals are each grouped together into one of these classes based on their structural similarities and on their effects on plant physiology. Other plant hormones and growth regulators are not easily grouped into these classes; they exist naturally or are synthesized by humans or other organisms, including chemicals that inhibit plant growth or interrupt the physiological processes within plants. Each class has positive as well as inhibitory functions, and most often work in tandem with each other, with varying ratios of one or more interplaying to affect growth regulation.

Abscisic acid

Abscisic acid (also called ABA) is one of the most important plant growth regulators. It was discovered and researched under two different names before its chemical properties were fully known, it was called *dormin* and *abscicin II*. Once it was determined that the two compounds are the same, it was named abscisic acid. The name "abscisic acid" was given because it was found in high concentrations in newly abscissed or freshly fallen leaves. This class of PGR is composed of one chemical compound normally produced in the leaves of plants, originating from chloroplasts, especially when plants are under stress. In general, it acts as an inhibitory chemical compound that affects bud growth, and seed and bud dormancy. It mediates changes within the apical meristem, causing bud dormancy and the alteration of the last set of leaves into protective bud covers. Since it was found in freshly abscissed leaves, it was thought to play a role in the processes of natural leaf drop, but further research has disproven this.

In plant species from temperate parts of the world, it plays a role in leaf and seed dormancy by inhibiting growth, but, as it is dissipated from seeds or buds, growth begins. In other plants, as ABA levels decrease, growth then commences as gibberellin levels increase. Without ABA, buds and seeds would start to grow during warm periods in winter and be killed when it froze again. Since ABA dissipates slowly from the tissues and its effects take time to be offset by other plant hormones, there is a delay in physiological pathways that provide some protection from premature growth. It accumulates within seeds during fruit maturation, preventing seed germination within the fruit, or seed germination before winter. Abscisic acid's effects are degraded within plant tissues during cold temperatures or by its removal by water washing in out of the tissues, releasing the seeds and buds from dormancy.

Auxins

Auxins are compounds that positively influence cell enlargement, bud formation and root initiation. They also promote the production of other hormones and in conjunction with cytokinins, they control the growth of stems, roots, and fruits, and convert stems into flowers. Auxins were the first class of growth regulators discovered. They affect cell elongation by altering cell wall plasticity. They stimulate cambium, a subtype of meristem cells, to divide and in stems cause secondary xylem to differentiate. Auxins act to inhibit the growth of buds lower down the stems (apical dominance), and also to promote lateral and adventitious root development and growth. Leaf abscission is initiated by the growing point of a plant ceasing to produce auxins. Auxins in seeds regulate specific protein synthesis, as they develop within the flower after pollination, causing the flower to develop a fruit to contain the developing seeds. Auxins are toxic to plants in large concentrations; they are most toxic to dicots and less so to monocots. Because of this property, synthetic auxin herbicides including 2,4-D and 2,4,5-T have been developed and used for weed control. Auxins, especially 1-Naphthaleneacetic acid (NAA) and Indole-3-butyric acid (IBA), are also commonly applied to stimulate root growth when taking cuttings of plants. The most common auxin found in plants is indole-3-acetic acid or IAA. The correlation of auxins and cytokinins in the plants is a constant (A/C = const.)

Cytokinins

Cytokinins or CKs are a group of chemicals that influence cell division and shoot formation. They were called kinins in the past when the first cytokinins were isolated from yeast cells. They also help delay senescence of tissues, are responsible for mediating auxin transport throughout the plant, and affect internodal length and leaf growth. Cytokinins and auxins often work together, and the ratios of these two groups of plant hormones affect most major growth periods during a plant's lifetime. Cytokinins counter the apical dominance induced by auxins; they in conjunction with ethylene promote abscission of leaves, flower parts, and fruits.[16] The correlation of auxins and cytokinins in the plants is a constant (A/C = const.).

Ethylene

Ethylene is a gas that forms through the breakdown of methionine, which is in all cells. Ethylene has very limited solubility in water and does not accumulate within the cell but diffuses out of the cell and escapes out of the plant. Its effectiveness as a plant hormone is dependent on its rate of production versus its rate of escaping into the atmosphere. Ethylene is produced at a faster rate in rapidly growing and dividing cells, especially in darkness. New growth and newly germinated seedlings produce more ethylene than can escape the plant, which leads to elevated amounts of ethylene, inhibiting leaf expansion (see Hyponastic response). As the new shoot is exposed to light, reactions by phytochrome in the plant's cells produce a signal for ethylene production to decrease, allowing leaf expansion.

Ethylene affects cell growth and cell shape; when a growing shoot hits an obstacle while underground, ethylene production greatly increases, preventing cell elongation and causing the stem to swell. The resulting thicker stem can exert more pressure against the object impeding its path to the surface. If the shoot does not reach the surface and the ethylene stimulus becomes prolonged, it affects the stem's natural geotropic response, which is to grow upright, allowing it to grow around an object. Studies seem to indicate that ethylene affects stem diameter and height: When stems of trees are subjected to wind, causing lateral stress, greater ethylene production occurs, resulting in thicker, more study tree trunks and branches. Ethylene affects fruit-ripening: Normally, when the seeds are mature, ethylene production increases and builds-up within the fruit, resulting in a climacteric event just before seed dispersal. The nuclear protein Ethylene Insensitive2 (EIN2) is regulated by ethylene production, and, in turn, regulates other hormones including ABA and stress hormones

Gibberellins

Main function: initiate mobilization of storage materials in seeds during germination, cause elongation of stems, stimulate bolting in biennials, stimulate pollen tube growth. Gibberellins, or GAs, include a large range of chemicals that are produced naturally within plants and by fungi. They were first discovered when Japanese researchers, including Eiichi Kurosawa, noticed a chemical produced by a fungus called *Gibberellafujikuroi* that produced abnormal growth in rice plants. Gibberellins are important in seed germination, affecting enzyme production that mobilizes food production used for growth of new cells. This is done by modulating chromosomal transcription. In grain (rice, wheat, corn, etc.) seeds, a layer of cells called the aleurone layer wraps around the endosperm tissue. Absorption of water by the seed causes production of GA. The GA is transported to the aleurone layer, which responds by producing enzymes that break down stored food reserves within the endosperm, which are utilized by the growing seedling. GAs produce bolting of rosette-forming plants, increasing internodal length. They promote flowering, cellular division, and in seeds growth after germination. Gibberellins also reverse the inhibition of shoot growth and dormancy induced by ABA.

Seed dormancy

A dormant seed is one that is unable to germinate in a specified period of time under a combination of environmental factors that are normally suitable for the germination of the non-dormant seed. Dormancy is a mechanism to prevent germination during unsuitable ecological conditions, when the probability of seedling survival is low.

One important function of most seeds is delayed germination, which allows time for dispersal and prevents germination of all the seeds at the same time. The staggering of germination safeguards some seeds and seedlings from suffering damage or death from short periods of bad weather or from transient herbivores; it also allows some seeds to germinate when competition from other plants for light and water might be less intense.

Another form of delayed seed germination is seed quiescence, which is different from true seed dormancy and occurs when a seed fails to germinate because the external environmental conditions are too dry or warm or cold for germination. Many species of plants have seeds that delay germination for many months or years, and some seeds can remain in the soil seed bank for more than 50 years before germination. Some seeds have a very long viability period, and the oldest documented germinating seed was nearly 2000 years old based on radiocarbon dating.

True dormancy or innate dormancy is caused by conditions within the seed that prevent germination under normally ideal conditions. Often seed dormancy is divided into two major categories based on what part of the seed produces dormancy: exogenous and endogenous. There are three types of dormancy based on their mode of action: physical, physiological and morphological.

There have been a number of classification schemes developed to group different dormant seeds, but none have gained universal usage. Dormancy occurs because of a wide range of reasons that often overlap, producing conditions in which definitive categorization is not clear. Compounding this problem is that the same seed that is dormant for one reason at a given point may be dormant for another reason at a later point. Some seeds fluctuate from periods of dormancy to non dormancy, and despite the fact that a dormant seed appears to be static or inert, in reality they are still receiving and responding to environmental cues.

Photoperiodism is the physiological reaction of organisms to the length of day or night. It occurs in plants and animals. Photoperiodism can also be defined as the developmental responses of plants to the relative lengths of light and dark periods.Manyflowering plants (angiosperms) use a photoreceptor protein, such as phytochrome or cryptochrome, to sense seasonal changes in night length, or photoperiod, which they take as signals to flower. In a further subdivision, *obligate* photoperiodic plants absolutely require a long or short enough night before flowering, whereas *facultative* photoperiodic plants are more likely to flower under one condition.

Phytochrome comes in two forms: pr and pfr. Red light (which is present during the day) converts phytochrome to its active form (pfr). This then triggers the plant to grow. In turn, far-red light is present in the shade or in the dark and this converts phytochrome from pfr to pr. Pr is the inactive form of phytochrome and will not allow for plant growth. This system of pfr to pr conversion allows the plant to sense when it is night and when it is day.[2]Pfr can also be convereted back to Pr by a process known as dark reversion, where long periods of darkness trigger the conversion of Pfr. This is important in regards to plant flowering. Experiments by Halliday et al. showed that manipulations of the red-to far-red ratio in Arabidopsis can alter flowering. They discovered that plants tend to flower later when exposed to more red light, proving that red light is inhibitory to flowering. Other experiments have proven this by exposing plants to extra red-light in the middle of the night. A short-day plant will not flower if light is turned on for a few minutes in the middle of the night and a long-day plant can flower if exposed to more red-light in the middle of the night.

Cryptochromes are another type of photoreceptor that is important in photoperiodism. Cryptochromes absorb blue light and UV-A. Cryptochromes entrain the circadian clock to light.[6] It has been found that both cryptochrome and phytochrome abundance relies on light and the amount of cryptochrome can change depending on day-length. This shows how important both of the photoreceptors are in regards to determining day-length.

In 1920, W. W. Garner and H. A. Allard published their discoveries on photoperiodism and felt it was the length of daylight that was critical,[1][8] but it was later discovered that the length of the night was the controlling factor.[9][10] Photoperiodic flowering plants are classified as *long-day plants* or *short-day plants* even though night is the critical factor because of the initial misunderstanding about daylight being the controlling factor. Along with long-day plants and short-day plants, there are plants that fall into a "dual-day length category". These plants are either long-short-day plants (LSDP) or short-long-day plants (SLDP). LSDPs flower after a series of long days followed by short days whereas SLDPs flower after a series of short days followed by long days. Each plant has a different length critical photoperiod, or critical night length.

Modern biologists believe that it is the coincidence of the active forms of phytochrome or cryptochrome, created by light during the daytime, with the rhythms of the circadian clock that allows plants to measure the length of the night. Other than flowering, photoperiodism in plants includes the growth of stems or roots during certain seasons and the loss of leaves. Artificial lighting can be used to induce extra-long days.

Long-day plants

Long-day plants flower when the night length falls below their critical photoperiod. These plants typically flower in the northern hemisphere during late spring or early summer as days are getting longer. In the northern hemisphere, the longest day of the year (summer solstice) is on or about 21 June. After that date, days grow shorter (i.e. nights grow longer) until 21 December (the winter solstice). This situation is reversed in the southern hemisphere (i.e., longest day is 21 December and shortest day is 21 June).

Some long-day obligate plants are:

- Carnation (*Dianthus*)
- Henbane (*Hyoscyamus*)
- Oat (*Avena*)

Some long-day facultative plants are:

- Pea (*Pisumsativum)*
- Barley (*Hordeum vulgare*)
- Lettuce (*Lactuca sativa*)
- Wheat (*Triticumaestivum*)

Short-day plants

Short-day plants flower when the night lengths exceed their critical photoperiod. They cannot flower under short nights or if a pulse of artificial light is shone on the plant for several minutes during the night; they require a continuous period of darkness before floral development can begin. Natural nighttime light, such as moonlight or lightning, is not of sufficient brightness or duration to interrupt flowering.

In general, short-day (i.e.long-night) plants flower as days grow shorter (and nights grow longer) after 21 June in the northern hemisphere, which is during summer or fall. The length of the dark period required to induce flowering differs among species and varieties of a species. Photoperiodism affects flowering by inducing the shoot to produce floral buds instead of leaves and lateral buds.

Some short-day facultative plants are:

- Kenaf (*Hibiscus cannabinus*)
- Marijuana (*Cannabis*)
- Cotton (*Gossypium*)
- Rice (*Oryza*)
- Jowar (*Sorghum bicolor*)
- Green Gram (Mung bean, *Vignaradiata*)
- Soybeans (*Glycine max*)

Day-neutral plants

Day-neutral plants, such as cucumbers, roses, and tomatoes, do not initiate flowering based on photoperiodism. Instead, they may initiate flowering after attaining a certain overall developmental stage or age, or in response to alternative environmental stimuli, such as vernalisation (a period of low temperature).

Vernalization (from Latin*vernus*, "of the spring") is the induction of a plant's flowering process by exposure to the prolonged cold of winter, or by an artificial equivalent. After vernalization, plants have acquired the ability to flower, but they may require additional seasonal cues or weeks of growth before they will actually flower. Vernalization is sometimes used to refer to herbal (non-woody) plants requiring a cold dormancy to produce new shoots and leaves but this usage is discouraged.

Many plants grown in temperate climates require vernalization and must experience a period of low winter temperature to initiate or accelerate the flowering process. This ensures that reproductive development and seed production occurs in spring and winters, rather than in autumn. The needed cold is often expressed in chill hours. Typical vernalization temperatures are between 5 and 10 degrees Celsius (40 and 50 degrees Fahrenheit).

For many perennial plants, such as fruit tree species, a period of cold is needed first to induce dormancy and then later, after the requisite period of time, re-emerge from that dormancy prior to flowering. Many monocarpic winter annuals and biennials, including some ecotypes of *Arabidopsis thaliana*and winter cereals such as wheat, must go through a prolonged period of cold before flowering occurs.

History of vernalization research

In the history of agriculture, farmers observed a traditional distinction between "winter cereals", whose seeds require chilling (to trigger their subsequent emergence and growth), and "spring cereals", whose seeds can be sown in spring, and germinate, and then flower soon thereafter. Scientists in the early 19th century had discussed how some plants needed cold temperatures to flower. In 1857 an American agriculturist John Hancock Klippart, Secretary of the Ohio Board of Agriculture, reported the importance and effect of winter temperature on the germination of wheat.

One of the most significant works was by a German plant physiologist Gustav Gassner who made a detailed discussion in his 1918 paper. Gassner was the first to systematically differentiate the specific requirements of winter plants from those of summer plants, and also that early swollen germinating seeds of winter cereals are sensitive to cold.[5] In 1928 a Russian geneticist Trofim Lysenko published his works on the effects of cold on cereal seeds, and coined the term "яровизация" ("jarovization") to describe a chilling process he used to make the seeds of winter cereals behave like spring cereals (*Jarovoe* in Russian, originally from *jar* meaning fire or the god of spring).

Lysenko himself translated the term into "vernalization" (from the Latin *vernum* meaning Spring). After Lysenko the term was used to explain the ability of flowering in some plants after a period of chilling due to physiological changes and external factors. The formal definition was given in 1960 by a French botanist P. Chouard, as "the acquisition or acceleration of the ability to flower by a chilling treatment".

Lysenko's 1928 paper on vernalization and plant physiology drew wide attention due to its practical consequences for Russian agriculture. Severe cold and lack of winter snow had destroyed many early winter wheat seedlings. By treating wheat seeds with moisture as well as cold, Lysenko induced them to bear a crop when planted in spring. Later however, Lysenko inaccurately asserted that the vernalized state could be inherited, i.e. the offspring of a vernalized plant would behave as if they themselves had also been vernalized and would not require vernalization in order to flower quickly.

Early research on vernalization focused on plant physiology; the increasing availability of molecular biology has made it possible to unravel its underlying mechanisms. For example, a lengthening daylight period (longer days), *as well as* cold temperatures are required for winter wheat plants to go from the vegetative to the reproductive state. Due to plant flowering requiring the successful co-operation of several metabolic pathways, computer models that incorporate vernalization have also been made.

Possible Questions

Short questions

1. What is growth of plant means?
2. What is growth curve?
3. What is meant by growth hormones?
4. What is auxin?
5. Write short note on gibberellins.
6. Define cytokinins.
7. What is the seed dormany?
8. Photoperiodism – Define.
9. What is vernalisation?

Essay type questions

1. Explain in detail about Growth and development.
2. What are growth hormones and its uses?
3. What is the mechanism of seed dormancy in plant?
4. Explain in detail about photoperiodism and discuss the short and long day plants.
5. Highlight the important points of vernalisation and its history behind it.

UNIT-V

SYLLABUS

Stress physiology: Stress adaptation mechanism: Definitions, Indicators of stress response-morphological, physiological, biochemical and molecular level. Stress adaptation and tolerance mechanism – biotic and abiotic stress, Effect of stress on crop productivity. Global warning-Physiological effects on crop productivity.

The basic concepts of plant stress, acclimation, and adaptation

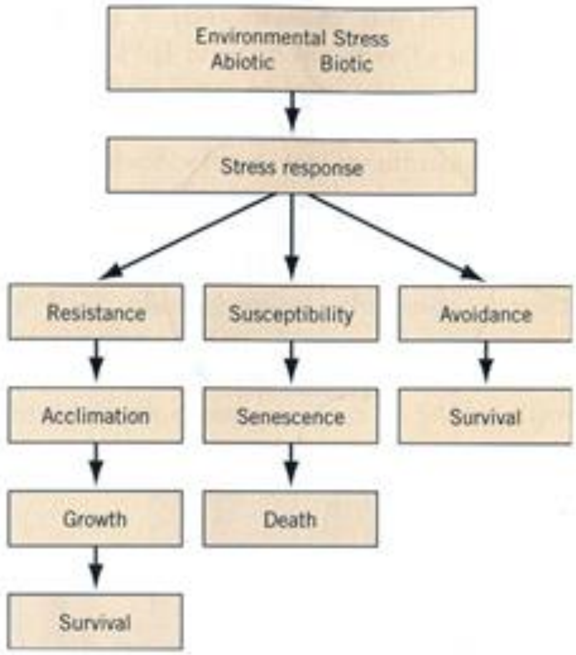
Energy is an absolute requirement for the maintenance of structural organization over the lifetime of the organism. The maintenance of such complex order over time requires a constant through put of energy. The results in a constant flow of energy through all biological organisms, which provides the dynamic driving force for the performance of important maintenance processes such as cellular biosynthesis and transport to maintain its characteristic structure and organization as well as the capacity to replicate and grow. The maintenance of a steady-state results in a meta-stable condition called **homeostasis**.

Environmental modulation of homeostasis defined as biological stress

Any change in the surrounding environment may disrupt homeostasis. Environmental modulation of homeostasis may be defined as **biological stress**. Thus, it follows that **plant stress** implies some adverse effect on the physiology of a plant induced upon a sudden transition from some optimal environmental condition where homeostasis is maintained to some suboptimal condition which disrupts this initial homeostatic state. Thus, plant stress is a relative term since the experimental design to assess the impact of a stress always involves the measurement of a physiological phenomenon in a plant species under a suboptimal, stress condition compared to the measurement of the same physiological phenomenon in the same plant species under optimal conditions.

Plants respond to stress in several different ways

Plant stress can be divided into two primary categories. **Abiotic stress** is a physical (e.g., light, temperature) or chemical insult that the environment may impose on a plant. **Biotic stress** is a biological insult, (e.g., insects, disease) to which a plant may be exposed during its lifetime. Some plants may be injured by a stress, which means that they exhibit one or more metabolic dysfunctions. If the stress is moderate and short term, the injury may be temporary and the plant may recover when the stress is removed. If the stress is severe enough, it may prevent flowering, seed formation, and induce senescence that leads to plant death. Such plants are considered to be **susceptible**. Some plants escape the stress altogether, such as ephemeral, or short-lived, desert plants.



The effect of environmental stress on plant survival

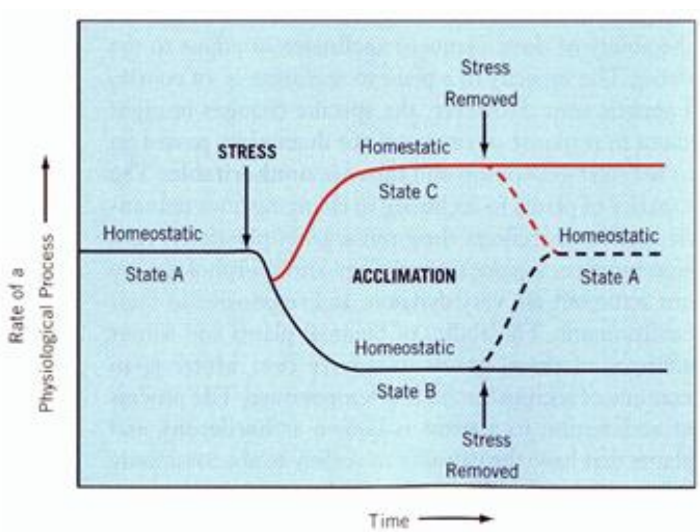
Ephemeral plants germinate, grow, and flower very quickly following seasonal rains. They thus complete their life cycle during a period of adequate moisture and form dormant seeds before the onset of the dry season. In a similar manner, many arctic annuals rapidly complete their life cycle during the short arctic summer and survive over winter in the form of seeds. Because ephemeral plants never really experience the stress of drought or low temperature, these plants survive the environmental stress by **stress avoidance**. Avoidance mechanisms reduce the impact of a stress, even though the stress is present in the environment. Many plants have the capacity to tolerate a particular stress and hence are considered to be **stress resistant**. Stress resistance requires that the organism exhibit the capacity to adjust or to acclimate to the stress.

Stress resistance requires that the organism exhibit the capacity to adjust or to acclimate to the stress

A plant stress usually reflects some sudden change in environmental condition. However, in stress-tolerant plant species, exposure to a particular stress leads to **acclimation** to that specific stress in a time-dependent manner. Thus, plant stress and plant acclimation are intimately linked with each other. The stress-induced modulation of homeostasis can be considered as the signal for the plant to initiate processes required for the establishment of a new homeostasis associated with the acclimated state. Plants exhibit stress resistance or stress tolerance because of their genetic capacity to adjust or to acclimate to the stress and establish a new homeostatic state over time. Furthermore, the acclimation process in stress-resistant species is usually reversible upon removal of the external stress.

The establishment of homeostasis associated with the new acclimated state is not the result of a single physiological process but rather the result of many physiological processes that the plant integrates over time, that is, integrates over the acclimation period. Plants usually integrate these physiological processes over a short-term as well as a long-term basis. The *short-term processes* involved in acclimation can be initiated within seconds or minutes upon exposure to a stress but may be transient in nature. That means that although these processes can be detected very soon after the onset of a stress, their activities also disappear rather rapidly.

As a consequence, the lifetime of these processes is rather short. In contrast, *long-term processes* are less transient and thus usually exhibit a longer lifetime. However, the lifetimes of these processes overlap in time such that the short-term processes usually constitute the initial responses to a stress while the long-term processes are usually detected later in the acclimation process. Such a hierarchy of short- and long-term responses indicates that the attainment of the acclimated state can be considered a complex, time-nested response to a stress. Acclimation usually involves the differential expression of specific sets of genes associated with exposure to a particular stress. The remarkable capacity to *regulate gene expression* in response to environmental change in a time-nested manner is the basis of plant plasticity.



A schematic relationship between stress and acclimation

Adaptation and phenotypic plasticity

Plants have various mechanisms that allow them to survive and often prosper in the complex environments in which they live. **Adaptation** to the environment is characterized by genetic changes in the entire population that have been fixed by natural selection over many generations. In contrast, individual plants can also respond to changes in the environment, by directly altering their physiology or morphology to allow them to better survive the new environment. These responses require no new genetic modifications, and if the response of an individual improves with repeated exposure to the new environmental condition then the response is one of acclimation. Such responses are often referred to as **phenotypic plasticity**, and represent nonpermanent changes in the physiology or morphology of the individual that can be reversed if the prevailing environmental conditions change.

Individual plants may also show phenotypic plasticity that allows them to respond to environmental fluctuations

In addition to genetic changes in entire populations, individual plants may also show phenotypic plasticity; they may respond to fluctuations in the environment by directly altering their morphology and physiology. The changes associated with phenotypic plasticity require no new genetic modifications, and many are reversible. Both genetic adaptation and phenotypic plasticity can contribute to the plant's overall tolerance of extremes in their abiotic environment. As a consequence, a plant's physiology and morphology are not static but are very dynamic and responsive to their environment. The ability of biennial plants and winter cultivars of cereal grains to survive over winter is an example of acclimation to low temperature. The process of acclimation to a stress is known as **hardening** and plants that have the capacity to acclimate are commonly referred to as hardy species. In contrast, those plants that exhibit a minimal capacity to acclimate to a specific stress are referred to as no hardy species.

Imbalances of abiotic factors have primary and secondary effects on plants

Plants may experience physiological stress when an abiotic factor is deficient or in excess (referred to as an imbalance). The deficiency or excess may be chronic or intermittent. Abiotic conditions to which native plants are adapted may cause physiological stress to non-native plants. Most agricultural crops, for example, are cultivated in regions to which they are not highly adapted. Field crops are estimated to produce only 22% of their genetic potential for yield because of suboptimal climatic and soil conditions.

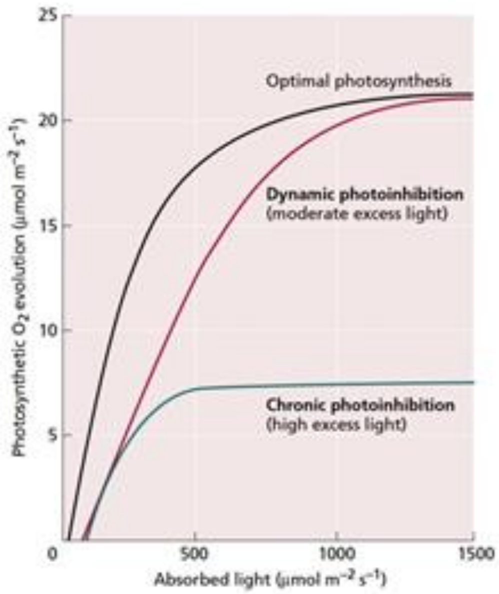
Imbalances of abiotic factors in the environment cause *primary and secondary effects* in plants. Primary effects such as reduced water potential and cellular dehydration directly alter the physical and biochemical properties of cells, which then lead to secondary effects. These secondary effects, such as reduced metabolic activity, ion cytotoxicity, and the production of reactive oxygen species, initiate and accelerate the disruption of cellular integrity, and may lead ultimately to cell death. Different abiotic factors may cause similar primary physiological effects because they affect the same cellular processes. This is the case for water deficit, salinity, and freezing, all of which cause reduction in hydrostatic pressure (turgor pressure, Ψp) and cellular dehydration. Secondary physiological effects caused by different abiotic imbalances may overlap substantially. It is evident that imbalances in many abiotic factors reduce cell proliferation, photosynthesis, membrane integrity, and protein stability, and induce production of *reactive oxygen species (ROS)*, oxidative damage, and cell death.

The light-dependent inhibition of photosynthesis

As photoautotrophs, plants are dependent upon – and exquisitely adapted to – visible light for the maintenance of a positive carbon balance through photosynthesis. Higher energy wavelengths of electromagnetic radiation, especially in the ultraviolet range, can inhibit cellular processes by damaging membranes, proteins, and nucleic acids. However, even in the visible range, irradiances far above the light saturation point of photosynthesis cause high light stress, which can disrupt chloroplast structure and reduce photosynthetic rates, a process known as **Photoinhibition**.

Photoinhibition *by high light leads to the production of destructive forms of oxygen* Excess light excitation arriving at the PSII reaction center can lead to its inactivation by the direct damage of the D1 protein. Excess absorption of light energy by photosynthetic pigments also produces excess electrons outpacing the availability of NADP+ to act as an electron sink at PSI. The excess electrons produced by PSI lead to the production of reactive oxygen species (ROS), notably superoxide (O2●-). Superoxide and other ROS are low-molecular-weight molecules that function in signaling and, in excess, cause oxidative damage to proteins, lipids, RNA, and DNA.

The oxidative stress generated by excessive ROS destroys cellular and metabolic functions and leads to cell death.



Changes in the light-response curves of photosynthesis caused by photoinhibition

Temperature stress

Mesophytic plants (terrestrial plants adapted to temperate environments that are neither excessively wet nor dry) have a relatively narrow temperature range of about 10°C for optimal growth and development. Outside of this range, varying amounts of damage occur, depending on the magnitude and duration of the temperature fluctuation. In this section we will discuss three types of temperature stress: high temperatures, low temperatures above freezing, and temperatures below freezing. Most actively growing tissues of higher plants are tillable to survive extended exposure to temperatures above 45°C or even short exposure to temperatures of 55°C or above. However, nongrowing cells or dehydrated tissues (e.g., seeds and pollen) remain viable at much higher temperatures. Pollen grains of some species can survive 70°C and some dry seeds can tolerate temperatures as high as 120°C.

Most plants with access to abundant water are able to maintain leaf temperatures below 45°C by evaporative cooling, even at elevated ambient temperatures. However, high leaf temperatures combined with minimal evaporative cooling causes heat stress. Leaf temperatures can rise to 4 to 5°C above ambient air temperature in bright sunlight near midday, when soil water

Deficit causes partial stomatal closure or when high relative humidity reduces the gradient driving evaporative cooling. Increases in leaf temperature during the day can be more pronounced in plants experiencing drought and high irradiance from direct sunlight.

Temperature stress can result in damaged membranes and enzymes

Plant membranes consist of a lipid bilayer interspersed with proteins and sterols, and any abiotic factor that alters membrane properties can disrupt cellular processes. The physical properties of the lipids greatly influence the activities of the integral membrane proteins, including H+-pumping ATPases, carriers, and channel-forming proteins that regulate the transport of ions and other solutes. High temperatures cause an increase in the fluidity of membrane lipids and a decrease in the strength of hydrogen bonds and electrostatic interactions between polar groups of proteins within the aqueous phase of the membrane. High temperatures thus modify membrane composition and structure, and can cause leakage of ions. High tempeatures can also lead to a loss of the three-dimensional structure required for correct function of enzymes or structural cellular components, thereby leading to loss of proper enzyme structure and activity. Misfolded proteins often aggregate and precipitate, creating serious problems within the cell.

Temperature stress can inhibit photosynthesis

Photosynthesis and respiration are both inhibited by temperature stress. Typically, photosynthetic rates are inhibited by high temperatures to a greater extent than respiratory rates. Although chloroplast enzymes such as rubisco, rubisco activase, NADP-G3P dehydrogenase, and PEP carboxylase become unstable at high temperatures, the temperatures at which these enzymes began to denature and lose activity are distinctly higher than the temperatures at which photosynthetic rates begin to decline. This would indicate that the early stages of heat injury to photosynthesis are more directly related to changes in membrane properties and to uncoupling of the energy transfer mechanisms in chloroplasts.

This imbalance between photosynthesis and respiration is one of the main reasons for the deleterious effects of high temperatures. On an individual plant, leaves growing in the shade have a lower temperature compensation point than leaves that are exposed to the sun (and heat). Reduced photosynthate production may also result from stress-induced stomatal closure, reduction in leaf canopy area, and regulation of assimilate partitioning.

Freezing temperatures cause ice crystal formation and dehydration

Freezing temperatures result in intra- and extracellular ice crystal formation. Intracellular ice formation physically shears membranes and organelles. Extracellular ice crystals, which usually form before the cell contents freeze, may not cause immediate physical damage to cells, but they do cause cellular dehydration. This is because ice formation substantially lowers the water potential (Ψw) in the apoplast, resulting in a gradient from high Ψw in the symplast to low Ψw in the apoplast. Consequently, water moves from the symplast to the apoplast, resulting in cellular dehydration. Cells that are already dehydrated, such as those in seeds and pollen, are relatively less affected by ice crystal formation. Ice usually forms first within the intercellular spaces and in the xylem vessels, along which the ice can quickly propagate. This ice formation is not lethal to hardy plants, and the tissue recovers fully if warmed. However, when plants are exposed to freezing temperatures for an extended period, the growth of extracellular ice crystals leads to physical destruction of membranes and excessive dehydration.

Imbalances in soil minerals

Imbalances in the mineral content of soils can affect plant fitness either indirectly, by affecting plant nutritional status or water uptake, or directly, through toxic effects on plant cells.

Soil mineral content can result in plant stress in various ways

Several anomalies associated with the elemental composition of soils can result in plant stress, including high concentrations of salts (e.g., Na^+ and Cl^-) and toxic ions (e.g., As and Cd), and low concentrations of essential mineral nutrients, such as Ca^{2+}, Mg^{2+}, N, and P. The term salinity is used to describe excessive accumulation of salt in the soil solution. **Salinity stress** has two components: nonspecific osmotic stress that causes water deficits, and specific ion effects resulting from the accumulation of toxic ions, which disturb nutrient acquisition and result in cytotoxicity. Salt-tolerant plants genetically adapted to salinity are termed *halophytes*, while less salt-tolerant plants that are not adapted to salinity are termed *glycophytes*.

Soil salinity occurs naturally and as the result of improper water management practices

In natural environments, there are many causes of salinity. Terrestrial plants encounter high salinity close to the seashore and in estuaries where seawater and freshwater mix or replace each other with the tides. The movement of seawater upstream into rivers can be substantial, depending on the strength of the tidal surge. Far inland, natural seepage from geologic marine deposits can wash salt into adjoining areas. Evaporation and transpiration remove pure water (as vapor) from the soil, concentrating the salts in the soil solution. Soil salinity is also increased when water droplets from the ocean disperse over land and evaporate.

Human activities also contribute to soil salinization. Improper water management practices associated with intensive agriculture can cause substantial salinization of croplands. In many areas of the world, salinity threatens the production of staple foods. Irrigation water in semiarid and arid regions is often saline. Only halophytes, the most salt-tolerant plants, can tolerate high levels of salts. Glycophytic crops cannot be grown with saline irrigation water.

Saline soils are often associated with high concentrations of NaCl, but in some areas Ca2+, Mg2+, and SO4- are also present in high concentrations in saline soils. High Na+ concentrations that occur in sodic soils (soils in which Na+ occupies ⩾10% of the cation exchange capacity) not only injure plants but also degrade the soil structure, decreasing porosity and water permeability. Salt incursion into the soil solution causes water deficits in leaves and inhibits plant growth and metabolism.

High cytosolic Na+ and Cl- denature proteins and destabilize membranes

The most widespread example of a specific ion effect is the cytotoxic accumulation of Na+ and Cl- ions under saline conditions. Under non-saline conditions, the cytosol of higher plant cells contains about 100 mM K+ and less than 10 mM Na+, an ionic environment in which enzymes are optimally functional. In saline environments, cytosolic Na+ and Cl- increase to more than 100 mM, and these ions become cytotoxic. High concentrations of salt cause protein denaturation and membrane destabilization by reducing the hydration of these macromolecules. However, Na+ is a more potent denaturant than K+.

At high concentrations, apoplastic Na+ also competes for sites on transport proteins that are necessary for high-affinity uptake of K+, an essential macronutrient. Further, Na+ displaces Ca2+ from sites on the cell wall, reducing Ca2+ activity in the apoplast and resulting in greater Na+ influx, presumably through nonselective cation channels. Reduced apoplastic Ca2+ concentrations caused by excess Na+ may also restrict the availability of Ca2+ in the cytosol. Since cytosolic Ca2+ is necessary to activate Na+ detoxification via efflux across the plasma membrane, elevated external Na+ has the ability to block its own detoxification.

Developmental and physiological mechanisms against environmental stress

Plants can modify their life cycles to avoid abiotic stress

One way plants can adapt to extreme environmental conditions is through modification of their life cycles. For example, annual desert plants have short life cycles: they complete them during the periods when water is available, and are dormant (as seeds) during dry periods. Deciduous trees of the temperate zone shed their leaves before the winter so that sensitive leaf tissue is not damaged by cold temperatures. During less predictable stressful events (e.g., a summer of significant but erratic rainfall) the growth habits of some species may confer a degree of tolerance to these conditions. For example, plants that can grow and flower over an extended period (*indeterminate growth*) are often more tolerant to erratic environmental extremes than plants that develop preset numbers of leaves and flower over only very short periods (*determinate growth*).

Phenotypic changes in leaf structure and behavior are important stress responses

Because of their roles in photosynthesis, leaves (or their equivalent) are crucial to the survival of a plant. To function, leaves must be exposed to sunlight and air, but this also makes them particularly vulnerable to environmental extremes. Plants have thus evolved various mechanisms that enable them to avoid or mitigate the effects of abiotic extremes to leaves. Such mechanisms include changes in leaf area, leaf orientation, trichomes, and the cuticle.

Turgor reduction is the earliest significant biophysical effect of water deficit. As a result, turgor-dependent processes such as *leaf expansion* and root elongation are the most sensitive to water deficits. When water deficit develops slowly enough to allow changes in developmental processes, it has several effects on growth, one of which is a limitation of leaf expansion. Because leaf expansion depends mostly on cell expansion, the principles that underlie the two processes are similar. Inhibition of cell expansion results in a slowing of leaf expansion early in the development of water deficits.

The resulting smaller leaf area transpires less water, effectively conserving a limited water supply in the soil over a longer period. Altering *leaf shape* is another way that plants can reduce leaf area. Under conditions of water, heat, or salinity extremes, leaves may be narrower or may develop deeper lobes during development. The result is a reduced leaf surface area and therefore, reduced water loss and heat load (defined as amount of heat loss [cooling] required to maintain a leaf temperature close to air temperature). For protection against overheating during water deficit, the leaves of some plants may orient themselves away from the sun. *Leaf orientation* may also change in response to low oxygen availability.

Altered leaf shape can occur in response to environmental changes: leaf from outside (left) and inside (right) of a tree canopy.

Plants can regulate stomatal aperture in response to dehydration stress

The ability to control stomatal aperture allows plants to respond quickly to a changing environment, for example to avoid excessive water loss or limit uptake of liquid or gaseous pollutants through stomata. Stomatal opening and closing is modulated by uptake and loss of water in guard cells, which changes their turgor pressure. Although guard cells can lose turgor as a result of a direct loss of water by evaporation to the atmosphere, stomatal closure in response to dehydration is almost always an active, energy-dependent process rather than a passive one. Abscisic acid (ABA) mediates the solute loss from guard cells that is triggered by a decrease in the water content of the leaf. Plants constantly modulate the concentration and cellular localization of ABA, and this allows them to respond quickly to environmental changes, such as fluctuations in water availability.

Plants adjust osmotically to drying soil by accumulating solutes

Osmotic adjustment is the capacity of plant cells to accumulate solutes and use them to lower Ψw during periods of osmotic stress. The adjustment involves a net increase in solute content per cell that is independent of the volume changes that result from loss of water. The decrease in

ΨS (= osmotic potential) is typically limited to about 0.2 to 0.8 MPa, except in plants adapted to extremely dry conditions.

There are two main ways by which **osmotic adjustment** can take place. A plant may *take up ions* from the soil, or *transport ions* from other plant organs to the root, so that the solute concentration of the root cells increases. For example, increased uptake and accumulation of K+ will lead to decreases in ΨS due to the effect of the potassium ions on the osmotic pressure within the cell. This is a common event in saline areas, where ions such as potassium and calcium are readily available to the plant. The accumulation of ions during osmotic adjustment is predominantly restricted to the vacuoles, where the ions are kept out of contact with cytosolic enzymes or organelles.

When ions are compartmentalized in the vacuole, other solutes must accumulate in the cytoplasm to maintain water potential equilibrium within the cell. These solutes are called *compatible solutes* (or *compatible osmolytes*). Compatible solutes are organic compounds that are osmotically active in the cell, but do not destabilize the membrane or interfere with enzyme function, as high concentrations of ions can. Plant cells can hold large concentrations of these compounds without detrimental effects on metabolism. Common compatible solutes include amino acids such as proline, sugar alcohols such as mannitol, and quaternary ammonium compounds such as glycine betaine.

Many plants have the capacity to acclimate to cold temperature

The ability to tolerate freezing temperatures under natural conditions varies greatly among tissues. Seeds and other partially dehydrated tissues, as well as fungal spores, can be kept indefinitely at temperatures near absolute zero (0 K, or -273°C), indicating that these very low temperatures are not intrinsically harmful. Hydrated, vegetative cells can also retain viability at freezing temperatures, provided that ice crystal formation can be restricted to the intercellular spaces and cellular dehydration is not too extreme.

Temperate plants have the capacity for *cold acclimation* – a process whereby exposure to low but nonlethal temperatures (typically above freezing) increases the capacity for low temperature survival. Cold acclimation in nature is induced in the early autumn by exposure to short days and nonfreezing, chilling temperatures, which combine to stop growth. A diffusible factor that promotes acclimation, most likely ABA, moves from leaves via the phloem to overwintering stems. ABA accumulates during cold acclimation and is necessary for this process.

Plants survive freezing temperatures by limiting ice formation

During rapid freezing, the protoplast, including the vacuole, may supercool; that is, the cellular water remains liquid because of its solute content, even at temperatures several degrees below its theoretical freezing point. Supercooling is common to many species of the hardwood forests. Cells can supercool to only about -40°C, the temperature at which ice forms spontaneously. Spontaneous ice formation sets the low-temperature limit at which many alpine and subarctic species that undergo deep supercooling can survive. It may also explain why the altitude of the timberline in mountain ranges is at or near the -40°C minimum isotherm. Several specialized plant proteins, termed **antifreeze proteins**, limit the growth of ice crystals through a mechanism independent of lowering of the freezing point of water. Synthesis of these antifreeze proteins is induced by cold temperatures. The proteins bind to the surfaces of ice crystals to prevent or slow further crystal growth.

Cold-resistant plants tend to have membranes with more unsaturated fatty acids

As temperatures drop, membranes may go through a phase transition from a flexible liquid-crystalline structure to a solid gel structure. The phase transition temperature varies with species (tropical species: 10-12°C; apples: 3-10°C) and the actual lipid composition of the membranes. Chilling-resistant plants tend to have membranes with more unsaturated fatty acids. Chilling-sensitive plants, on the other hand, have a high percentage of saturated fatty acid chains, and membranes with this composition tend to solidify into a semicrystalline state at a temperature well above 0°C. Prolonged exposure to extreme temperatures may result in an altered composition of membrane lipids, a form of acclimation. Certain transmembrane enzymes can alter lipid saturation, by introducing one or more double bonds into fatty acids. This modification lowers the temperature at which the membrane lipids begin a gradual phase change from fluid to semicrystalline form and allows membranes to remain fluid at lower temperatures, thus protecting the plant against damage from chilling.

A large variety of heat shock proteins can be induced by different environmental conditions

Under environmental extremes, protein structure is sensitive to disruption. Plants have several mechanisms to limit or avoid such problems, including osmotic adjustment for maintenance of hydration and chaperone proteins that physically interact with other proteins to facilitate protein folding, reduce misfolding and aggregation, and stabilize protein tertiary structure. In response to sudden 5 to 10°C increases in temperature, plants produce a unique set of chaperone proteins referred to as **heat shock proteins** (HSPs). Cells that have been induced to synthesize HSPs show improved thermal tolerance and can tolerate subsequent exposure to temperatures that otherwise would be lethal. Heat shock proteins are also induced by widely different environmental conditions, including water deficit, ABA treatment, wounding, low temperature, and salinity. Thus, cells that have previously experienced one condition may gain cross-protection against another.

During mild or short-term water shortage, photosynthesis is strongly inhibited, but phloem translocation is unaffected until the shortage becomes severe

Changes in the environment may stimulate shifts in metabolic pathways. When the supply of O2 is insufficient for aerobic respiration, roots first begin to ferment pyruvate to lactate through the action of lactate dehydrogenase; this recycles NADH to NAD+, allowing the maintenance of ATP production through glycolysis. Production of lactate (lactic acid) lowers the intracellular pH, inhibiting lactate dehydrogenase and activating pyruvate decarboxylase. These changes in enzyme activity quickly lead to a switch from lactate to ethanol production. The net yield of ATP in fermentation is only 2 moles of ATP per mole of hexose sugar catabolized (compared with 36 moles of ATP per mole of hexose respired in aerobic respiration). Thus, injury to root metabolism by O2 deficiency originates in part from a lack of ATP to drive essential metabolic processes such as root absorption of essential nutrients.

Water shortage decreases both photosynthesis and the consumption of assimilates in the expanding leaves. As a consequence, water shortage indirectly decreases the amount of photosynthate exported from leaves. Because phloem transport depends on pressure gradients, decreased water potential in the phloem during water deficit may inhibit the movement of assimilates. The ability to continue translocating assimilates is a key factor in almost all aspects of plant resistance to drought.

Global warming, and potential climate abnormalities associated with it, crops typically encounter an increased number of abiotic and biotic stress combinations, which severely affect their growth and yield. Concurrent occurrence of abiotic stresses such as drought and heat has been shown to be more destructive to crop production than these stresses occurring separately at different crop growth stages. Abiotic stress conditions such as drought, high and low temperature and salinity are known to influence the occurrence and spread of pathogens, insects, and weeds. They can also result in minor pests to become potential threats in future. These stress conditions also directly affect plant–pest interactions by altering plant physiology and defense responses. Additionally, abiotic stress conditions such as drought enhance competitive interactions of weeds on crops as several weeds exhibit enhanced water use efficiency than crops.

The effect of combined stress factors on crops is not always additive, because the outcome is typically dictated by the nature of interactions between the stress factors. Plants tailor their responses to combined stress factors and exhibit several unique responses, along with other common responses. Therefore, to fully recognize the impact of combined abiotic and biotic stresses on plants, it is important to understand the nature of such interactions. Mittler and colleagues developed a “stress matrix” to compile the interactions among various abiotic and biotic stresses on plant growth and productivity. This matrix illustrates that the stress combinations can have negative as well as positive effects on plants. Therefore, development of plants with enhanced tolerance to combined abiotic and biotic stresses involves identification of physio-morphological traits that are affected by combined stresses.

Based on the currently available studies on the effect of concurrent stresses on plants, this review attempts to improve and amend the current understanding of stress combinations by explaining some fundamental concepts pertaining to them, highlighting their global occurrence and assessing their influence on crop growth.

Examples of Different Stress Combinations Occurring in Nature

Based on the number of interacting factors, stresses can be grouped into three categories: single, multiple individual, and combined stresses. A single stress represents only one stress factor affecting plant growth and development, whereas multiple stress represents the impact of two or more stresses occurring at different time periods without any overlap (multiple individual) or occurring concurrently with at least some degree of overlap between them (combined). The co-occurrence of drought and heat stresses during summer is an example of a combined abiotic stress, whereas a bacterial and fungal pathogen attacking a plant at the same time represents a case of combined biotic stress. For example, brown apical necrosis of *Juglans Bregia* (walnut) is caused by fungal pathogens *Fusarium* spp., *Alternaria* spp., *Cladosporium* spp., *Colletotrichum* spp., and *Phomopsis* spp., and a bacterium, *Xanthomonas arboricola*.

A first stress factor preceded by another stress factor in sequence may either "endure" (due to priming) or "predispose" the plants to the subsequent stress. For example, drought predisposes *Sorghum bicolor* (sorghum) to *Macrophomina phaseolina*. There are also scenarios where plants are exposed to "repetitive" stresses, where a single or multiple stresses are intervened by short or long recovery periods. For instance, incidences of multiple spells of hot days or multiple occurrences of drought and high temperature at different phenological stages of plants represent repetitive stresses.

Some examples of different stress combinations that are expected to arise due to climate change and their impact on plants. Simultaneously occurring drought and heat stress stands as the most evident stress combination Likewise, plants growing in arid and semi-arid regions often face a combination of salinity and heat stress. High light stress also often accompanies heat stress. *Vitis vinifera* (grapes) growing in regions characterized by a continental climate, such as North China, face a combination of drought and cold stress which affects their productivity Plants growing in the Mediterranean region encounter combined cold and high light stress. *Triticum aestivum* (winter wheat) is also known to experience a combination of ozone and cold stress which reduces its frost hardiness (Barnes and Davison, 1988). Likewise, salinity combined with ozone stress reduces yields of *Cicer arietinum* (chickpea) and *Oryza sativa* (rice).

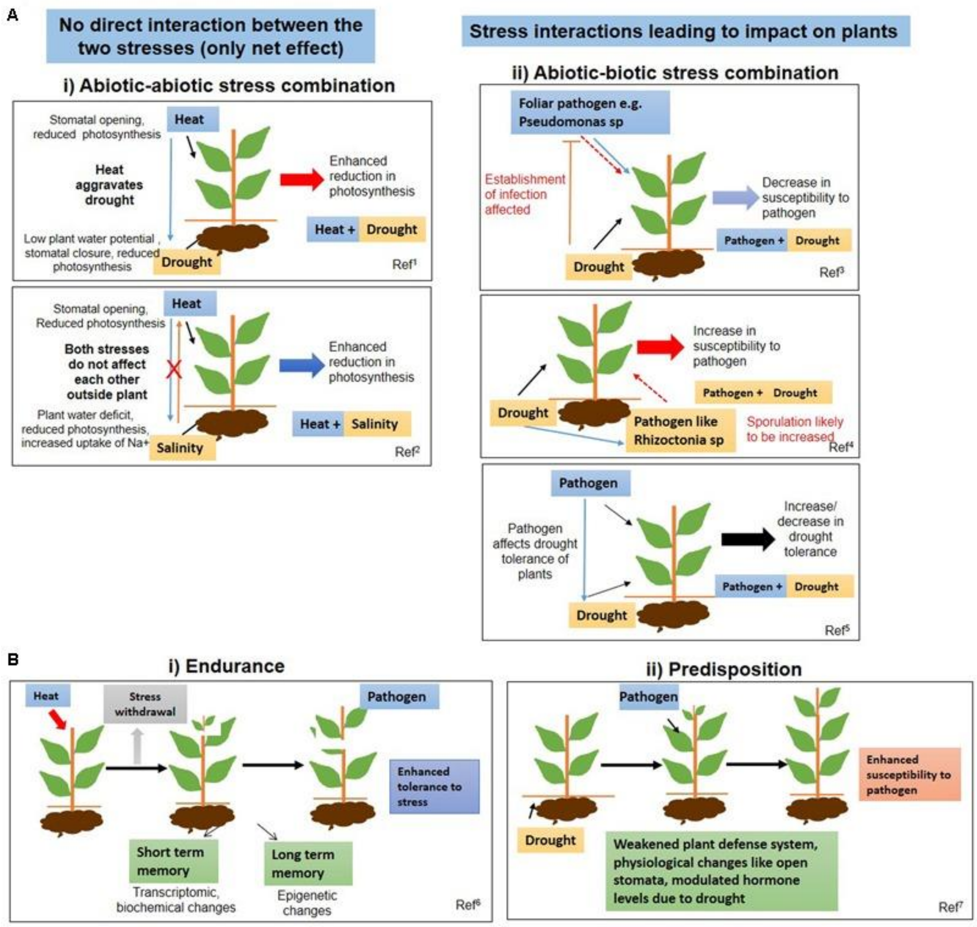
Similar to the different abiotic stress combinations, plants also encounter more than one biotic stresses simultaneously or sequentially. Infection by a combination of fungi, bacteria, and viruses are common and are known to cause severe disease symptoms, compared to infections by individual pathogens. Various biotic stress combinations and their impact on plants.

Plants also encounter biotic stressors simultaneously with abiotic stressors. The impact of environmental factors on plant diseases popularly known as the "disease triangle" has always been an important consideration for plant pathologists. Reports have documented the effect of drought or salinity leading to resistance or susceptibility of plants to *Puccinia* spp. (causal agent of rust), *Verticillium* spp. (causal agent of verticillium wilt), *Fusarium* spp. (causal agent of Fusarium wilt), *Pythium* spp. (causal agent of root rot), and *Erysiphe* spp. (causal agent of powdery mildew).The influence of co-occurring, high temperature, or cold stress on increased competitiveness of weeds over crops has also been documented.

Stress Interactions as an Important Aspect Governing the Impact of Stress Combinations on Plants crop productivity

Different types of stress interactions can have a range of effects on plants depending on the nature, severity, and duration of the stresses. In case of some abiotic–abiotic and majority of abiotic–biotic stress combinations, interactions not only occur between the plant and the stressors at the plant interface, but also directly between the stressors at or outside the plant interface. In fact, the nature of such interactions between the stressors governs the magnitude of their impact on crop response.

For example, a concurrent heat wave during a drought period may lead to more soil water evaporation resulting in aggravated drought conditions and increased crop yield loss. In addition to this, drought and heat stresses have synergistic effects on plant physiology, resulting in greater negative net impact manifested as drastic yield reduction. Likewise, concurrent drought and weed stress further reduces water availability to crops and subsequently increases the competitiveness of weeds on them.



Schematic representation of effect of stress combination on plants.

(A) Effect of combined stresses on plants is explained by representative examples of heat and drought (abiotic–abiotic stress) and drought and pathogen stress (abiotic–biotic stress) combination.

(i) Depending on the nature of stresses, the two stresses can either not interact physically, but individually affect the plant leading to a net negative impact on plant growth or interact at plant interface and cause a net effect on the plant. Generally, abiotic stress combinations are examples of "only net effects and no stress interactions". For example, simultaneous exposure to heat and salinity leads to enhanced retardation of physiological processes such as photosynthesis.

(ii) Stress interactions are conspicuous in abiotic and biotic stress combinations wherein one stress factor affects the other stress factor *per se*. For example, exposure to combined drought and pathogen stress may result in a complex scenario encompassing an interaction of the two stresses along with the impact of the two stresses on the plant. Depending on the plant patho-system, the interaction may lead to enhanced or reduced susceptibility to a particular pathogen. Some pathogens also modulate drought tolerance of the plant.

(B) Effect of multiple individual stresses (sequential stresses) on plants. Sequential stresses may either lead to priming or predisposition of plants to the subsequent stress as explained by examples of heat–pathogen and drought–pathogen stress combinations.

(i) Priming: Exposure of plants to moderate heat stress (indicated by red arrow) may prime the plants to the subsequent pathogen infection. Mild stress can evoke stress memory in the form of epigenetic changes or transcriptomic changes in plants which may last short or long-term, leading to enhanced tolerance of stress to subsequent more severe stresses (same or different stress).

(ii) Predisposition: A pre-occurring drought stress can pre-dispose plants to pathogen infection due to weakened plant defenses or any other metabolic changes occurring due to the drought stress.

In case of stress combinations involving heat and pathogen stress, high temperatures not only affect plants but also pathogens. Temperature is, in fact, one of the most important factors affecting the occurrence of bacterial diseases such as those caused by *Ralstonia solanacearum* (causal agent of wilt in tomato), *Acidovorax avenae* (causal agent of seedling blight and bacterial fruit blotch of cucurbits) and *Burkholderia glumae* (causal agent of bacterial panicle blight in rice) (Kudela, 2009). An increase in temperature modifies the growth rate and reproduction of pathogens (Ladanyi and Horvath, 2010). Temperature also affects the incidence of vector-borne diseases by altering the population development and spread of vectors. Similarly, the effect of salt stress on plant diseases might be the outcome of its modulation on the pathogen virulence, the host physiology and microbial activity in soils. For example, increased incidence of *Fusarium* wilt in *Solanum lycopersicum* (tomato) under salt stress was found to be caused by more sporulation of the fungi under saline conditions.

The combination of two stresses (abiotic–abiotic or abiotic–biotic) does not always lead to negative impact on plants. Some stress combinations negate the effect of each other, leading to a net neutral or positive impact on plants. One stress may also provide endurance to plants against another stress and hence yield is not always negatively impacted. For example, individual drought and ozone stresses are detrimental to the growth of *Medicago truncatula* (alfalfa), but the combination of drought and ozone results in increased tolerance of plants to the stress combination.

High CO_2 has been shown to ameliorate the effect of drought stress in *T. aestivum* and *Poa pratensis* (bluegrass). Likewise, an increase in CO_2 level from 350 to 675 ppm favored the competitiveness of the C_3 crop *Glycine max* (soybean) over the C_4 weed *Sorghum halepense* (johnsongrass),*S. lycopersicum* exposed to combined salinity and heat stress performs better than plants subjected to these stresses separately. Ozone treatment also provides enhanced resistance to *Puccinia* spp. in *T. aestivum, Pseudomonas glycinea* (causal agent of bacterial blight) in *G. max* and *Erysiphe polygoni* in *Pisum sativum* (pea).

Some stress combinations exhibit far more complex interactions and their effect on plants are variable. Heat–pathogen and drought–pathogen stress combinations are examples of such complex interactions. For example, with increased temperature, *T. aestivum* and *Avena sativa* (oats) become more susceptible to *Puccinia* spp., but some forage species such as *Cynodon dactylon* (Bermuda grass) become more resistant to rust disease. Heat–pathogen and drought–pathogen interactions can be regarded as two agriculturally important stress combinations.

Drought–Pathogen Stress Combination: A Model for Understanding Combined Abiotic–Biotic Stresses

Drought stress interacts with pathogen infection both additively and antagonistically. On the basis of the number of reports of plant diseases being affected by drought stress and the frequency of occurrence of drought stress, this combination can be considered as one of the most important stress combinations affecting crop yields worldwide. Drought stress is reported to enhance the susceptibility of *S. bicolor, T. aestivum, Senecio vulgaris* (groundsel), *Hordeum vulgare* (barley), *Gossypium* spp. (cotton), and *C. arietinum* to *M. phaseolina, Puccinia* sp., *Erysiphe graminis* f. sp. *hordei, Fusarium oxysporum* f. sp. *vasinfectum,* and *Rhizoctonia bataticola*, respectively. On the other hand, drought stress is reported to provide endurance to tomato, *Medicago sativa* and *Arabidopsis thaliana*against *Botrytis cinerea* (causal agent of gray mold), *Oidium neolycopersici* (causal agent of powdery mildew), *Verticillium albo-atrum* (causal agent of verticillium wilt), and *Pseudomonas syringae* (causal agent of bacterial speck disease), respectively. In some cases, concurrent pathogen infection helps plants to endure drought stress, resulting in increased yield. For example, infection with *Cucumber mosaic virus*(CMV) led to improved drought tolerance of *Capsicum annum* (pepper), *S. lycopersicum*, and *Nicotiana tabacum*.

Possible Questions

Short questions

1. What is plant stress?
2. What is acclimation?
3. What is stress adaptation means?
4. What is stress indicators?
5. What is biotic stress?
6. Write short note on abiotic stress.
7. Define global warming.
8. What is crop productivity?

Essay type questions

1. Explain in detail about stress adaptation of plants.
2. What are environmental stress and indicators revealed in plants?
3. What is the mechanism of plant in the stress conditions under global warming?
4. What is acclimation? How the plants respond to it?
5. Describe the mechanism of biotic and abiotic stress.
6. Explain in detail about crop productivity and discuss the physiological effects in plants.