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# Syllabus

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## PAPER – I

### **Ecology, Utilization of Plants and Physiology (SC-137)**

#### UNIT – I

History and aspects of ecology; structure of ecosystem; its abiotic and biotic components; food chain; food web; ecological pyramids; energy flow; biogeochemical cycles of carbon,-nitrogen and phosphorus; ecological factors; ecological succession; ecological concept of species.

#### UNIT – II

Plant water relations; mineral nutrition.

#### UNIT – III

Photosynthesis; respiration; growth hormones and plant movements.

# UNIT-I

## ECOLOGY

History and Basic Aspects of  
Ecology

### 1

## HISTORY AND BASIC ASPECTS OF ECOLOGY

### STRUCTURE

- Introduction
- Some Definitions of Ecology
- Divisions of Ecology
- Branches of Ecology
- Ecology and Its Applications
- Summary
- Test Yourself
- Answers

### LEARNING OBJECTIVES

By learning this chapter you will be able to know about ecology, its definition, branches and applications.

#### 1.0. INTRODUCTION

In the primitive society, every individual for survival needed to have some knowledge of his environment *i.e.* of the forces of nature and of the plants and animals around him. The writings of **Hippocrates**, **Aristotle**, and other Greek philosophers contain material which may be considered of ecological nature. **Theophrastus** (370-285 B.C.) may well be regarded as the **first ecologist** in history because he spoke of plant communities and the relation of the plants to each other and to their physical environment. **Linnaeus** (1707-1778) and **Buffon** in his book **Natural History** in 1756 made notable contributions to ecology.

In 1859, **G.S. Hilaire** used the term 'ethology' to refer to the study of relationships between the organisms and the environment. Later in 1868, the German Zoologist, **Reiter** introduced the term **oekologie**, derived from the Greek words *oikos* (house) and *logos* (knowledge). **E. Haeckel** (1869) is often credited with the derivation of the term because he defined it in the literature. The term has since been rendered in English form to **Ecology**. He also gave a precise definition of ecology as "**the science treating of reciprocal relations of organisms and the external world**". In 1895, **Warming** employed it in the study of plants and defined ecology as the study of organisms in relation to their environment.

**Lecoq Sendtner** and **Kerner** introduced community aspects for plants in ecology. **Karl Mobius** (1877) elaborated this view for animals. **S. A. Forbes** (1887), **Cowles** (1899), **Warming** (1909), **Clements** (1916) etc. made notable contributions to plants and animal communities.

**Odum** (1963, 1970) defined ecology as the "study of structure and function of nature". The structural and functional aspects of communities along with their environment is called "**Ecological System or Ecosystem**". The term "**ecosystem**" was first proposed by **Tansley** (1935) and this started the era of ecosystem approach to ecology.

The Indian work on various aspects of the ecology was started in the beginning of the 20th century. **Dudgeon** (1921), **Misra** (1936), **Champion** (1938), **Bharucha** (1940) are some of the pioneer workers of ecology in India. **G. S. Puri** (1948–54) did a considerable amount of work on the distribution of forest trees in relation to the edaphic forests.

The autecological studies of a number of plants were carried out by **R. Misra, L. P. Mall, D.K. Tiwari, P.S. Ramakrishnan, H.R. Sant, D.N. Sen** and **R.S. Ambasht** and their coworkers. **R. Misra, S. C. Pandey, and K. P. Singh** have worked on production ecology, especially for forests and green lands. Now-a-days the work is being done in a number of centers such as Banaras Hindu University, Saurashtra University, Vikram University, Punjab University and some other centers. India is also one of the active participants in the International Biological Programme (I.B.P.).

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### 1.1. SOME DEFINITIONS OF ECOLOGY

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**Haeckel's Definition** : "Oekologie is the science of reciprocal relations of organisms and the external world" (**Haeckel**, 1869).

**Warming's Definition** : "Ecology is the science treating of community" (**Clements**, 1916).

**Elton's Definition** : "Ecology may be defined as the scientific natural history dealing with the sociology and economics of animals" (**Elton**, 1927).

**Taylor's Definition** : "Ecology is the science of all the relations of all organisms to all their environments" (**Taylor**, 1936).

**Woodbury's Definition** : "Ecology as a science which investigates organisms in relation to their environment, a philosophy in which the world of life is interpreted in terms of natural processes." (**Woodbury**, 1955).

**Odum's Definition** : Ecology may be defined as the study of structure and function of nature (**Odum**, 1973).

**Kreb's Definition** : "It is the scientific approach to the study of environmental interactions which control the welfare of living things, regulating their distribution, abundance, production and evolution" (**Krebs**, 1972).

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### 1.2. DIVISIONS OF ECOLOGY

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There are two main divisions of ecology on the basis of studies of plants and animals *i.e.*, Plant ecology and Animal ecology.

Plant ecology may be divided into :

(i) **Habitat ecology** : Study of habitats and their effects on the organisms living there.

(ii) **Autecology** : Study of inter-relationship between individual species of organisms (Autoecology of species) or individuals of the same species (Population ecology) and its environment.

(iii) **Synecology** : Study of the groups or communities in relation to their environment. It is further divisible into two sub-divisions :

(a) **Community ecology** : Units of study are individual communities.

(b) **Ecosystem approach** : Units of study are groups of communities together with their non-living environment interacting together so as to function as a system.

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### 1.3. BRANCHES OF ECOLOGY

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There may be various specific or general branches in ecology, of them the important ones are undermentioned :

(a) **Palaeoecology** : Study of organisms of a past geological eras and their environment.

(b) **Genecology** : Genetic make up of a species of population in relation to environment.

(c) **Conservation ecology** : Proper management of natural resources for the benefit of the human beings.

(d) **Production ecology** : The gross and net production of different ecosystem so that the proper land management may be achieved.

(e) **Ecological energetics** : The energy conservation and flow in the organisms within the ecosystem.

(f) **Population ecology** : Population dynamics in pure or mix stands.

(g) **Human ecology** : The environment with man as the central theme.

(h) **Pollution ecology** : Undesirable change in the biological, physical or chemical characteristics of the air, water and land, affecting the plant, animal and human lives.

(i) **Applied ecology** : To solve problems of agriculturists and forests as soil erosion, environment pollution, wildlife management etc.

(j) **Microbial ecology** : The studies of various principles that governs the distribution of microorganisms in nature.

**Ecology and other Branches of Science** : Ecology, a synthetic branch of biological science, is inherently related to morphology, taxonomy, physiology, biochemistry, cytology, genetics etc. Besides these topics a knowledge of chemistry, physics, mathematics, statistics, geography and geology is also essential in the study of complicated problems of ecology.

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#### 1.4. ECOLOGY AND ITS APPLICATIONS

(i) The knowledge of ecology is of great help in the conservation of nature and natural resources, soil erosion, reforestation, restoration of wild animals as well as grassland vegetation and food control.

(ii) Knowledge of ecology is applied in agriculture, food production, horticulture and silviculture.

(iii) In agronomy the soil conservation practices are in use these days.

(iv) It also helps in the development of antipollution measures.

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#### 1.5. SUMMARY

Hilaire, 1859 coined the term 'ethnology' where as Reiter, 1868 proposed the term 'Okologie' for this branch of botany. The latter was preferred which thereafter became ecology. Haeckel, 1869 defined it as the science treating the reciprocal relations of the organism with the external world. Warming, 1895, on the other hand, defined it as the study of organisms in relation to their environment. Clement, 1916 calls it as The Science of Community whereas Odum, 1971 defines it as the study of the structure and function of nature. The science is divided into animal ecology and plant ecology. It's important branches are habitat ecology, autecology, synecology, taxonomic ecology, space ecology, palaeoecology, genecology, production ecology, conservation ecology and so on. Applications of ecology are very vast. It is of great help in conservation of soil, natural resources, reforestation, food production and development of antipollution measures.

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#### 1.6. TEST YOURSELF

1. Who coined the term ethology ?
2. Name the term for the study of interaction between the living organisms and the environment.

3. Name the ecologist who defined ecology as the "study of structure and function of nature".
4. Who introduced the term 'Oekologie' ?
5. What is synecology ?

**ANSWERS**

1. G. S. Hilaire (1959)
2. Ecology
3. Odum
4. Reiter
5. Study of group or communities in relation to their environment.

□□□

## UNIT-I

## 2

## ECOSYSTEM

## STRUCTURE

- Introduction
- Divisions of Ecosystem
- Structure of Ecosystem
- Food Chains and Food Web
- Ecological Pyramids
- Pond ecosystem
- Energy Flow
- Biogeochemical Cycles
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know ecosystem from structural and functional point of view.

## 2.0. INTRODUCTION

“The structural and functional system of communities and their environment” is called **ecosystem**, a term first proposed by **Tansley** (1953), and since then a great deal has been written on the subject. The ecosystem in words of **Odum** (1965) is “The basic fundamental unit with which we must deal since it includes both the organisms and the non-living environment, each influencing the properties of the others and both necessary for maintenance of life as we have it on earth.”

Climate controls the development and the distribution of plants, animals and soil. On the other hand climate itself is also profoundly governed or affected by the nature of vegetation. Furthermore, vegetation also controls the distribution of animals. In turn the fauna also exerts some effects on vegetation. Similarly there are reciprocal relationships between soil and vegetation and between soil and fauna (Fig. 1).

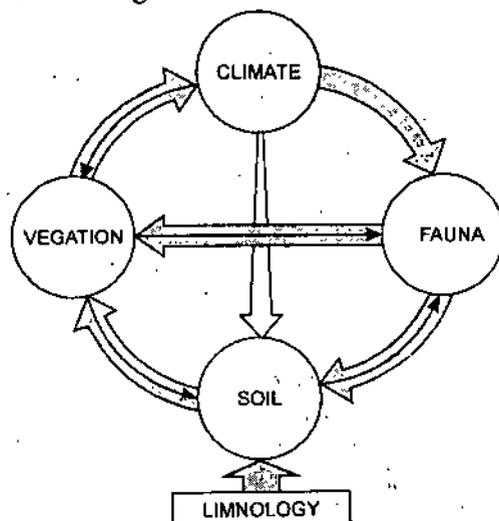


Fig. 1. Diagram showing reciprocal relationship among climate, vegetation, fauna and soil.

This complex of interacting phenomenon has been given the name **biotic complex** or **ecosystem**. A square meter of a grassland or forest, the edge of a pond, a tide pool or any large area of nature that has living organisms and non-living substances interacting and exchanging materials between them is called an **ecological system** or **ecosystem**. The term ecosystem refers to the sum total of physical and biological factors operating in any area. Keeping this in view the earth itself can be considered a giant ecosystem (Fig. 2). This vast ecosystem is known as **biosphere**.

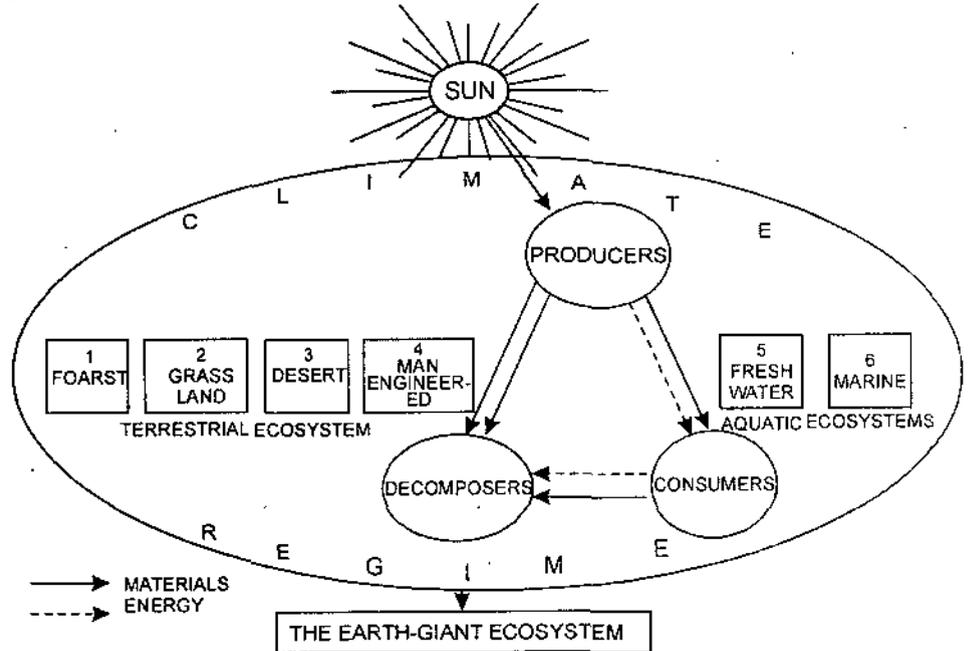
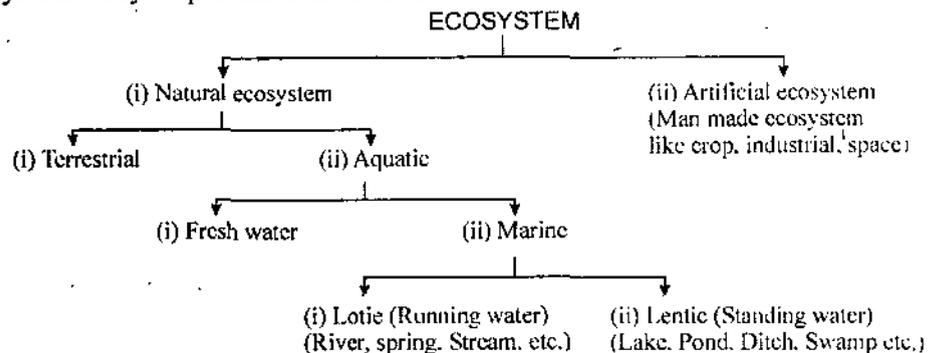


Fig. 2. Diagram showing the earth as a giant ecosystem.

### 2.1. DIVISIONS OF ECOSYSTEM

It is difficult for an individual or even a group of researchers to study the entire biosphere. Therefore, for the sake of convenience, many sub-divisions have been made and smaller ecosystems have been created. Some of the broad classification of these ecosystems may be presented as follows :



There are two basic processes in an ecosystem. The plants synthesize complex organic materials from the raw materials. The organic materials after decomposition are turned into inorganic form and ultimately returned to environment. This process is called **'cycling of materials'**. The energy for the above process comes from the sun. Not all organisms are able to utilize the energy. The plants are able to convert radiant energy of sun into chemical energy. Other organisms derive their nutrition and energy from the plants. The energy taken by these organisms is passed on to other organisms. The whole process is called **'flow of energy'**. During the process there is always loss of energy in each transfer. The energy has a unidirectional flow and does not circulate like

the nutrients. So, there is continuous flow of energy and cycling of materials through the non-living and living components of ecosystem.

## 2.2. STRUCTURE OF ECOSYSTEM

From a structural point of view the ecosystem is divided into :

(A) **Biotic Components** comprising of all the living organisms and

(B) **Abiotic Components** which include the physical (non-living) environment.

(A) **Biotic Components** : The biotic components in an ecosystem are distinguished into three major categories *i.e.*, producers, consumers and decomposers as under :

(i) **Producers or Autotrophs** : Solar energy is trapped by the chloroplast of green plants and used in synthesis of organic materials. Green plants take simple organic matter like salts, water and carbon-dioxide etc. and produce their own food and hence are called **autotrophs**. Since these organisms produce food for all the other organisms, they are also known as **producers**.

(ii) **Consumers** : Those organisms that feed directly on other organisms are known as consumers. *Directly or indirectly all animals live at the expense of green plants.* A community without green plants cannot exist whereas a community without animals can. The consumers are again divided into following four categories :

(a) **Consumers of the first order** : Herbivores which eat to the green plants (*i.e.*, producers) *e.g.*, Goat, Cow, Grass hopper, Deer, Rabbit etc.

(b) **Consumers of the second order** : Carnivores which eat the herbivores *e.g.*, Frog eats grass-hopper.

(c) **Consumers of the third order** : *Organisms which eat other carnivores e.g.*, snakes eat frogs or a bird eats all type of fishes including carnivores etc.

(d) **Top carnivores** : Carnivores which are not killed and eaten by other animals *e.g.*, Lion, Vulture, Leopard etc.

The consumer animals take plants or other inorganic materials as food, break them in their digestion process and produce new types of organic materials like animals tissue, proteins etc. Therefore, animals are also busy in the process of organic production. *Based on the above concept the green plants are called primary producers and heterotrophic organisms may also be considered as secondary producers.*

(iii) **Decomposers** : The primary and secondary producers complete their life cycles and new generations of populations develop while old one dies and decay. If the materials locked in the body of the organisms are not returned to soil and atmosphere after their death, the cycling of materials will stop and the earth will be full of organic matter. Certain microorganisms like bacteria, actinomycetes and fungi constantly decompose the dead organic matter into simple inorganic substances and thus, derive their food and energy from them.

Thus, biotic components in an ecosystem is essentially a producer—consumer—decomposer relationship in which food level at different stages is known as the trophic level. The amount of living material in different trophic levels is known as the **standing crop**. The standing crop in any ecosystem is expressed in terms of (a) number of organisms per unit area or (b) biomass *i.e.*, organisms mass which can be measured as living or dry weight, ash free dry weight, carbon weight or calories.

(B) **Abiotic Components** : The abiotic components can be classified into following three groups :

(i) **Physical environment** : *See environmental factors.*

(ii) **Nutrients (materials cycling)** : They include certain basic inorganic and organic elements or compounds *e.g.*, water, oxygen, carbon-dioxide, nitrogen, calcium, sulphur, phosphorus and certain organic acids. They continually keep on cycling *i.e.*, entering into the living system and through death and decay return to soil and

atmosphere. This process is called **mineral circulation** or **biogeochemical cycle**. The amount of inorganic substances, present at any given time in an ecosystem, is designated as the **standing state** or **standing quality**.

(iii) **Energy** : Energy circuit in an ecosystem includes the solar energy, heat energy and stored energy in form of chemical bonds (ATP). While the materials keep on cycling fresh energy is continuously trapped from the sun by the green plants on the one hand and lost in space through respiration and lost of heat by all types of organisms on the other (See also **Energy flow** for details).

Ans-3(i)

**2.3. FOOD CHAINS AND FOOD WEB**

**Food chains**

In any ecosystem mostly the green plants serve as producers of food energy. The food manufactured by the green plants is utilized by themselves and also by herbivores (consumers of the first order), which in turn form the food for carnivores (consumers of the second order) and finally the microbes (decomposers) feed upon all the dead plants and animals. Thus, food from one trophic level reaches to the other trophic level and in this way a chain is established. This is known as **food chain** (Fig. 3). A food chain may be defined as "the transfer of energy and nutrients through a succession of organisms through repeated process of eating and being eaten". A food chain in a grassland ecosystem comprises grasses → grasshopper → frog → snake → owl. Similarly, a fresh water ecosystem has algae → water-fleas → small fish → large fish → fish eating birds. Food chain can be of three types :

1. **The predator or grazing food chain** : It starts from plants and goes from smaller to larger animals.
2. **The parasitic food chain** : It goes from large to smaller organisms.
3. **The saprophytic chain or detritus food chain** : It goes from dead organic matter to microorganisms.

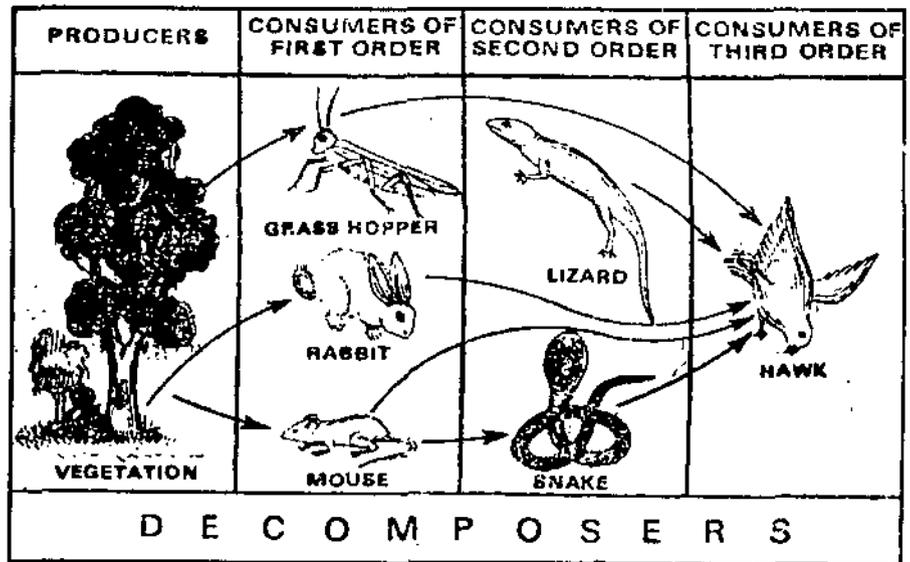


Fig. 3. Food chain in terrestrial ecosystem.

**Food Web**

In every ecosystem there is a inter-relationship among various organisms and they are linked through different food chains (Fig. 4). For example, in a grassland ecosystem if there are no rabbits the grasses may be eaten by mouse and if there are no snakes in the vicinity the mouse may be eaten by owl. Similarly, in a pond ecosystem, the small fish, instead of being eaten by big fish may be directly eaten by man. In this way food chains become inter-linked. A complex of inter-related food chains make a **food web**.

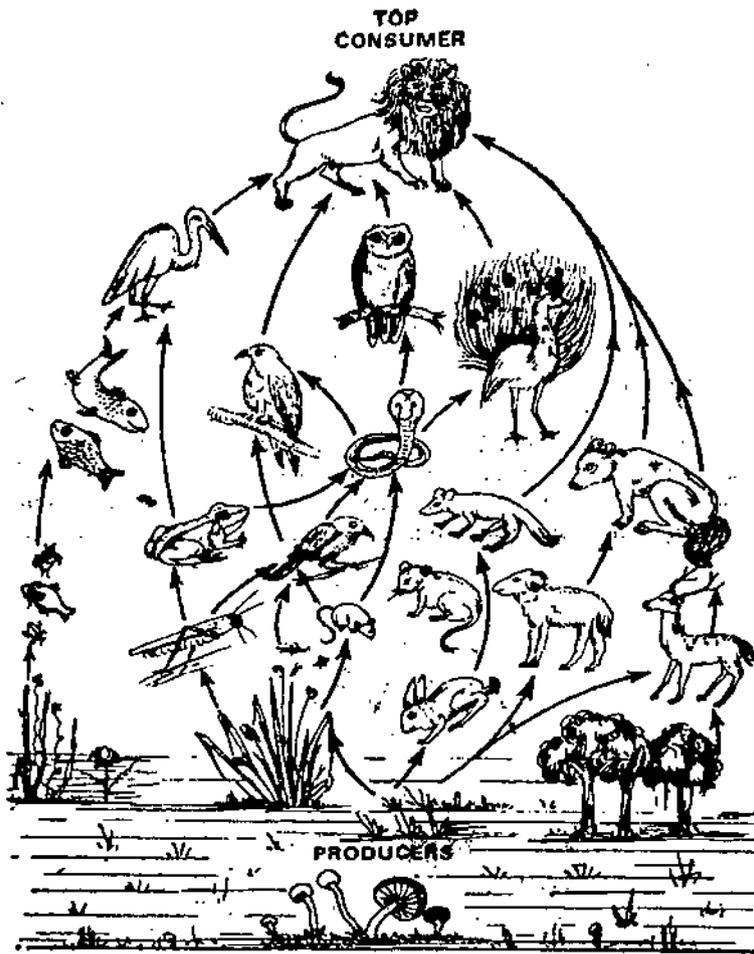


Fig. 4. Food web in forest ecosystem.

## 2.4. ECOLOGICAL PYRAMIDS

There is some sort of relationship between the numbers, biomass and energy of the primary producers, consumers of the first order, consumers of second order, consumers of third order and top carnivores in any ecosystem. All these three kinds of relationships can be shown graphically in the form of triangular pyramids which are called as **ecological pyramids**. In the triangular pyramid, the first producer level constitute the base of pyramid, and the successive levels, the tiers making the apex. The pyramids are of three kinds :

1. Pyramids of numbers.
2. Pyramids of biomass.
3. Pyramids of energy.

**1. Pyramids of numbers :** This type of pyramid shows the number of individual organisms at successive trophic levels. The pyramid is upright in grass land ecosystem, pond ecosystem, partly upright in forest ecosystem and inverted in parasitic food chain (Figs. 5 to 8). In a grassland and pond ecosystem the producers are the mainly grasses and algae and are always maximum in number. The primary consumers (herbivores) which are rabbit, mice, grass hoppers smaller fish, rotifers etc., are lesser in number than the producers. The secondary consumers (e.g., snakes, lizards, small fish, water beetles) are lesser in number than the herbivores. The tertiary consumers (e.g., hawks, birds, bigger fishes) are least in number (Fig. 5, 6). Thus, pyramids become upright. In a forest ecosystem, the producers are mainly large sized trees. They are lesser in number and form the base of pyramid. The herbivores are more in number than the

producers. Then, there is a gradual decrease in number of successive carnivores thus making the pyramid partly upright (Fig. 7).

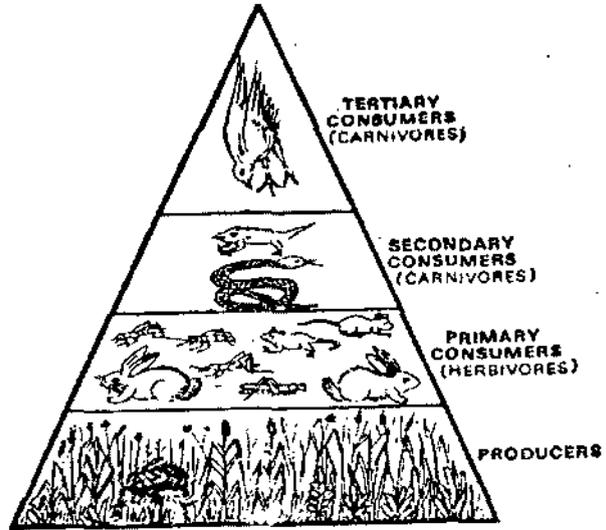


Fig. 5. Pyramid of numbers in grassland ecosystem.

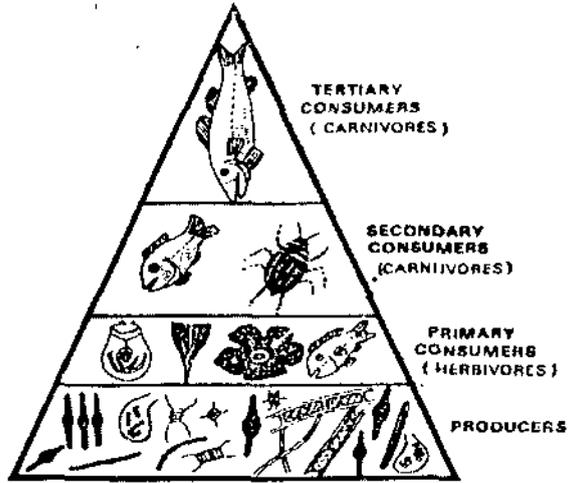


Fig. 6. Pyramid of numbers in pond ecosystem.

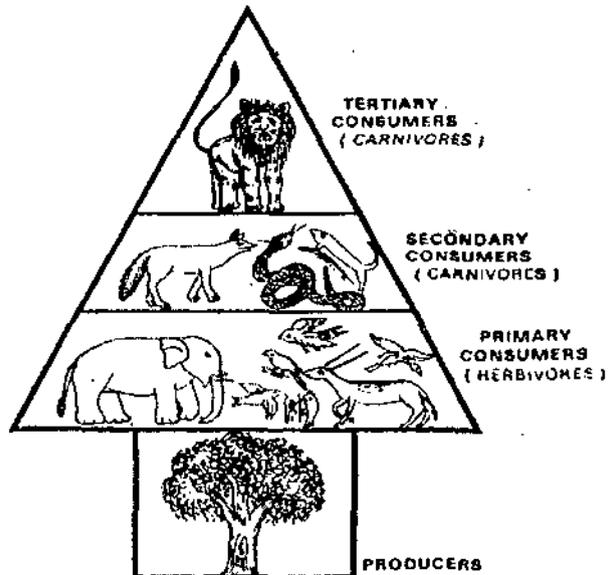


Fig. 7. Pyramid of numbers in forest ecosystem.

In detritus food chain a single tree (primary producer) supports a large number of fruit eating herbivore birds (primary consumers), which in turn supports a still higher number of hyperparasites like bugs and lice (secondary consumers). This relationship of increasing members from producers to consumers of different order constitutes an inverted pyramid (Fig. 8).

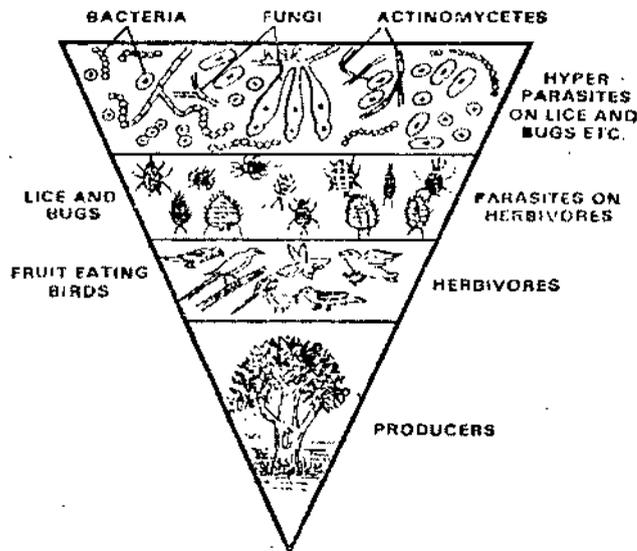


Fig. 8. Pyramid of numbers in parasitic food chain.

**2. Pyramids of biomass :** This type of pyramid shows the mass of living organisms at successive trophic levels. The pyramid of biomass may be upright in terrestrial ecosystem (grassland and forest ecosystem) or inverted in aquatic ecosystem (Fig 9A-C). In grassland and forest ecosystem, there is gradual decrease in biomass of organisms at successive trophic levels from producers to carnivores. Thus, pyramids are upright (Fig. 9A, B). However, in aquatic ecosystem, the situation is entirely reverse. The biomass of diatoms and phytoplanktons (primary producers) is very little as compared to herbivores that feed on them, and gradually shows an increase in biomass at successive trophic levels, making the pyramid inverted one (Fig. 9 C).

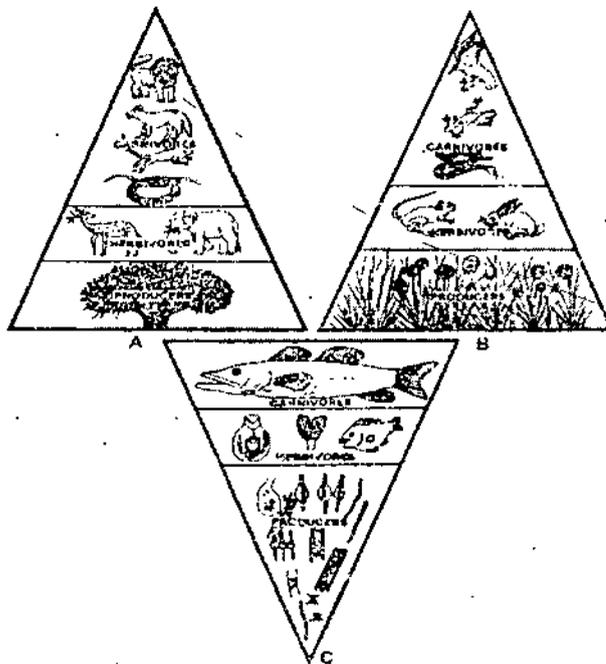


Fig. 9. A-C : Pyramids of biomass — A. Forest ecosystem, B. Grassland ecosystem, C. Pond ecosystem.

**3. Pyramids of energy :** This type of pyramid shows the amount of total energy utilized by the organisms at each trophic level and the actual role of various organisms in the transfer of energy. The pyramid of energy for all ecosystems is an upright one (Fig. 10) because there is always a gradual decrease in the energy content at successive trophic levels from the producers to various consumers. The amount of energy content in plants is measured by **bomb calorimeter**.

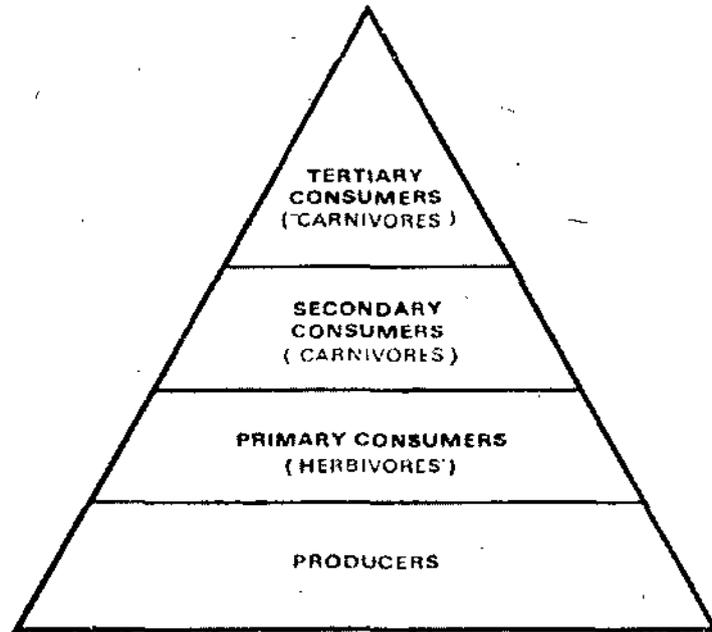


Fig. 10. Pyramid of energy.

## 2.5. POND ECOSYSTEM

The fresh water pond may be cited as a good example of small ecosystem that represents as a recognizable unit, both in structure and function. In pond ecosystem, there are two main components *i.e.*, biotic and abiotic.

**1. Biotic components :** Biotic components include the following :

**(A) Producers :** The producers organisms are of two types :

**(a) Macrophytes :** They are mainly large rooted plants and can be further classified into submerged, free floating and amphibians plants (Fig. 11). *Hydrilla, Vallisneria, Nelumbo, Nymphaea, Lemna, Azolla, Eichhornia, Eleocharis, Sagittaria, Potamogeton, Utricularia, Salvinia, Pistia, Trapa, Typha, Marsilea, Ceratophyllum* etc. are the common macrophytes which occur in the pond.

**(b) Microphytes :** These are minute floating plants and are also called as **phytoplanktons**. *Spirogyra, Ulothrix, Zygnema, Pandorina, Cladophora, Chlamydomonas, Volvox, Odeogonium, Eudorina, Pediastrum, Diatoms, Anabaena, Oscillatoria, Spirulina, Scendesmus* are some of the common microphytes of a fresh water pond.

**(B) Consumers :** The consumer organisms are of three types :

**(i) Primary consumers (herbivores) :**

**(a) Zooplankton :** They feed upon phytoplanktons. They are usually rotifers (*Lecane, Asplanchna* etc.), protozoans (*Euglena, Dileptus*, etc.) and crustaceans (*Cyclops, Stenocypris* etc.).

**(b) Benthos (Bottom forms) :** These are the larvae of mites, insects, mollusks, crustaceans and fishes etc. They also feed upon the plant remains lying at the bottom of pond.

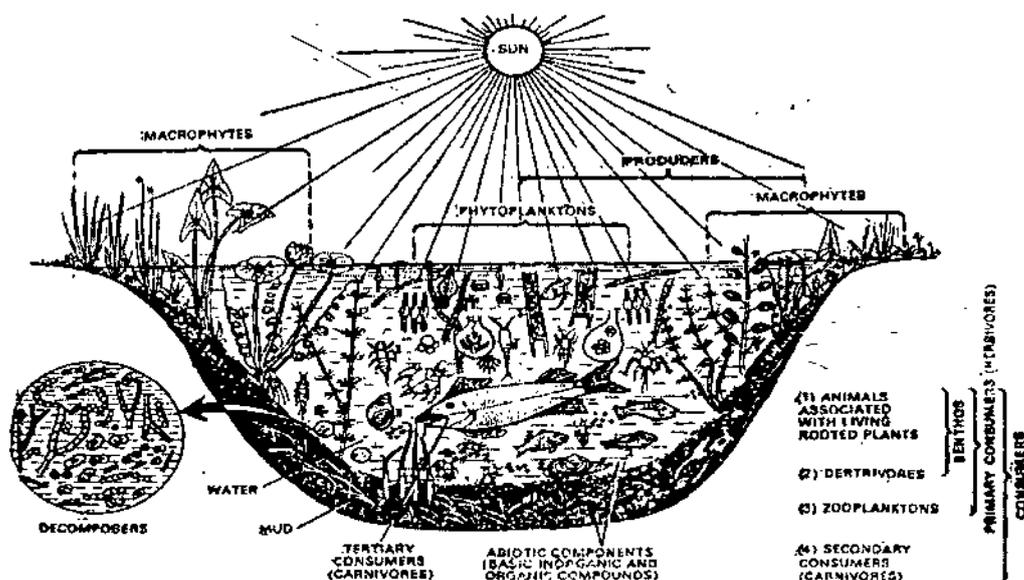


Fig. 11. Diagram showing the biotic and abiotic components of pond ecosystem.

Besides zooplanktons and benthos, sometimes some mammals and birds visit the pond and feed on marginal rooted hydrophytes and some animals.

(ii) **Secondary consumers (carnivores)** : Water beetles, small fishes, insects etc. feed on zooplanktons (Fig. 11).

(iii) **Tertiary consumers** : Large fishes feed on the small fishes.

(C) **Decomposers** : Several groups of bacteria, actinomycetes and fungi (*Aspergillus*, *Alternaria*, *Cladosporium*, *Pythium*, *Rhizopus*, *Fusarium*, *Saprolegnia*, *Curvularia* etc.) represent this group (Fig. 11). These organisms are especially abundant in the mud water along the bottom where bodies of animals accumulate. They bring about the decomposition of complex dead organic matter of plants and animals to simpler forms. Thus, they play an important role in the return of mineral elements again to the medium of the pond.

**2. Abiotic components** : Abiotic component of pond consists heat, light, pH value of water, inorganic and organic compounds such as water,  $\text{CO}_2$ ,  $\text{O}_2$ , nitrogen, calcium, phosphorus, salts, aminoacids etc. A small portion of nutrients present in solution, while a large part is stored in reserve in the bottom sediment as well as in the organisms themselves.

## CROPLAND ECOSYSTEM

This is artificial ecosystem aimed primary to grow simple species like sugarcane, vegetables, wheat, paddy, maize etc. In it, there are also two main components, *i.e.*, biotic and abiotic.

**1. Biotic components** : (i) **Producers** : The main producer is the dominant species, *i.e.*, the crop in a particular field. In addition to it a number of grasses weeds (*Cyperus*, *Fumaria*, *Euphorbia*, *Digitaria*, *Croton*, *Phyllanthus* etc.) also grow along with the crop and contribute to primary production of the field.

(ii) **Consumers** : (a) **Primary consumers (Herbivores)**. These are the insects like thrips, aphids, tinned buds, ants etc. and animals as rabbits, rats, birds and man etc.

(b) **Secondary consumers (carnivores)** : These are frog and birds etc.

(c) **Tertiary consumers** : These are snakes and hawks which can eat frogs and small birds respectively.

(iii) **Decomposers** : These are the microbes such as actinomycetes, fungi (*Helminthosporium*, *Coprinus*, *Agaricus*, *Mucor*, *Aspergillus*, *Fusarium*, *Alternaria* etc.) and bacteria (*Bacillus*, *Clostridium*, *Pseudomonas* etc.) found in soil and climate.

They decompose dead organic matter of plants and animals and help in circulation of minerals making available to producers again.

**2. Abiotic components :** These components are almost the same present in pond ecosystem. Chemicals, fertilizers, insecticides and proper irrigation are added into the soil to bring out higher yield of crop.

## 2.6. ENERGY FLOW

Green plants trap solar radiation in the form of complex chemical bonds. This energy is utilized by other organisms which pass it on to still other organisms (*i.e.*, from producers to consumers, decomposers and parasites). During this process a good energy is lost out of the living system. This process is called **flow of energy or energy flow**. This unidirectional flow of energy is the result of two laws of thermodynamics.

The chief source of energy are (1) radiant energy (2) heat energy (3) chemical energy and (4) mechanical energy. The different forms of energy interchange their forms under certain set rules.

Solar energy travelling in the form of radiation is called radiation energy. The radiant energy produced in the sun travels through the space in form of waves ranging in wavelength from  $0.03\text{\AA}$  to several kilometers. While most of the radiations are lost in space, those of the wavelengths from  $300\text{ m}\mu$  to  $10\text{ m}\mu$  and above  $1\text{ cm}$ . (radiowaves) enter the earth's outer atmosphere. Some of the ultra-violet, ( $300\text{ m}\mu$  to  $390\text{ m}\mu$ ) are absorbed by the ozone layer in the outer stratosphere. The energy reaching the earth's surface consists largely of the light ( $390\text{--}760\text{ m}\mu$ , light energy) and the heat radiations (infra-red). The dust and water vapours in the atmosphere also causes great changes in the amount of energy reaching the earth as some of it is absorbed or reflected back to the space.

According to the first law of thermodynamics "*Energy cannot be created or destroyed but may be converted from one form to another*". Thus, all the energy entering the earth's atmosphere can be accounted for. Some light (light energy) is used in photosynthesis. The light energy entering the chloroplast machinery of the plant body is taken by the electrons of the chlorophyll molecules and passed on through a series of stages into chemical energy in the form of organic compounds. The rest of the energy is reflected back to outer space as heat (heat energy) and used in converting the water into vapours or heating the soil and air. Mechanical energy may be of two forms : potential energy or the stored energy which remains in reserve and which can be used only on conversion into free form and kinetic energy or useful energy.

During the digestion of the food (organic compounds which are produced by the plants) by animals, the complex organic molecules are broken down to simpler molecules and new compounds are resynthesized. As a result a large part of the energy is again lost as a heat and a small fraction is stored in the animal tissues. Here the energy follows the second law of thermodynamics. According to this law "*Processes involving energy transformations will not occur spontaneously unless there is a degradation of energy from a non-random to a random form.*" In other words no energy transformation can be 100% efficient. This can be illustrated with the help of simple energy flow diagrams (Figs. 12 and 13).

Fig. 12 shows that out of the  $118,872\text{ g cal/cm}^2/\text{yr}$  total coming solar radiation, only  $111\text{ g cal/cm}^2/\text{yr}$  is used by the plants in gross production (net production plus respiration). Thus,  $118,761\text{ g cal/cm}^2/\text{yr}$  remain unutilized. Out of the  $111\text{ g cal/cm}^2/\text{yr}$  energy only  $15\text{ g cal/cm}^2/\text{yr}$  (13.6%) is utilized by herbivores, while  $23\text{ g cal/cm}^2/\text{yr}$  (20.7%) and  $3\text{ g cal/cm}^2/\text{yr}$  (2.7%) energy is consumed in respiration and decomposition respectively. However,  $70\text{ g cal/cm}^2/\text{yr}$  (63%) energy is not utilized at all. Thus, herbivores consume less energy (only  $15\text{ g cal/cm}^2/\text{yr}$  while much more energy is available to them. At herbivores level, out of the  $15\text{ g cal/cm}^2/\text{yr}$  energy  $4.5\text{ g cal/cm}^2/\text{yr}$  (30%) and  $0.5\text{ g cal/cm}^2/\text{yr}$  (3%) energy is lost in respiration and

decomposition respectively while 7 g cal/cm<sup>2</sup>/yr (46%) energy remains unutilized. Only 3.0 g cal/cm<sup>2</sup>/yr energy passes into carnivores. At the carnivores level 1.2 g cal/cm<sup>2</sup>/yr (40%) energy is not utilized while 1.8 g cal/cm<sup>2</sup>/yr (60%) energy is consumed in respiration. Thus, this is evident from the figure that there is **unidirectional flow of energy** and there is always **loss of energy at each successive trophic levels**.

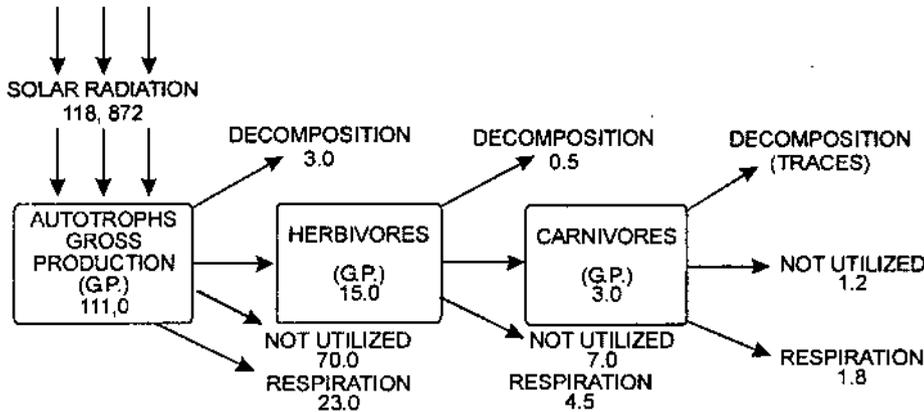


Fig. 12. Energy flow diagram for fresh water ecosystem in g cal/cm<sup>2</sup>/yr

In the Fig. 13 boxes represent the biomass or population mass (*i.e.*, standing crop) and the pipes represent the flow of energy between the organisms (*i.e.*, through the biotic community). Only half of the total sunlight is absorbed by the plants and only a small portion of absorbed light *i.e.*, 1% to 5% is converted into food energy. It is the gross production or primary productivity (PG or A). The 10% energy of the gross production is lost in respiration. The food which is potentially available to heterotrophs is 90% of the gross production and is depicted by PN (net production). The loss of energy in the form of heat due to respiration is denoted by R. The total light is represented by L and the absorption light by LA.

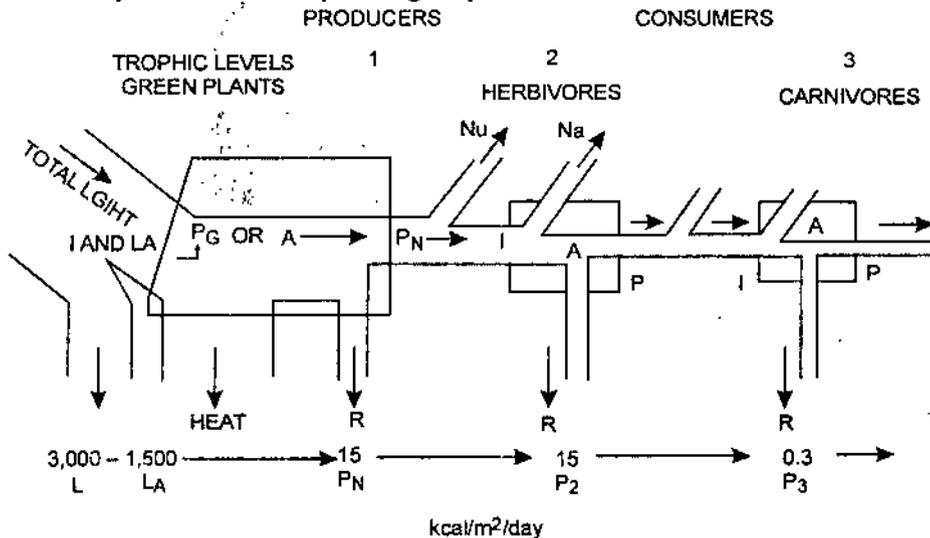


Fig. 13. Energy flow diagram.

Thus, Fig. 13 clearly shows a **reduction in energy flow**. 3000 k cal of energy per square meter of total light falling upon the green plants, approximately 50% (1500 k cal) is absorbed, of which 1% (15 k cal) is converted at first trophic level. Thus, net primary productivity is merely 15 k cal. Secondary productivity (denoted by P<sub>2</sub> and P<sub>3</sub> in diagram) tends to be 10% at successive consumer trophic level, *i.e.*, herbivores (1.5 k cal) and carnivores (0.3 k cal).

Here in the ecosystem radiant energy of sun is transformed into potential energy of food by the primary producers through the process of photosynthesis. At each stage

some energy is always dispersed into unavailable heat energy. No spontaneous transformation can be 100% efficient. Thus, both the laws of thermodynamics are confirmed.

According to Kozlovsky (1968) the amount of energy which is available to one trophic level from its predecessor amounts approximately 10% of the energy it receives. According to Philipson (1966) the study of the process of energy transfer between trophic levels is sometimes known as bioenergetics.

## 2.7. BIOGEOCHEMICAL CYCLES

Cycling of matter is a continuous process of absorption of materials for the purpose of production by the organisms and the release and the conversion of the organic matter into inorganic form. Materials flow from the non-living to living and back to non-living again in a perpetual cycle through elements passing back and forth in living and non-living environment are known as Biogeochemical cycle. The biogeochemical cycles are of two types :

1. **The gaseous cycle** : Represented by carbon, nitrogen and oxygen cycles. Air is the greatest reservoir in all gaseous cycles.

2. **The sedimentary cycles** : Represented by phosphorous, sulphur and calcium cycles. Reservoir in it is the earth crust. The sedimentary cycle involves two phases : Salt solutions and rocks.

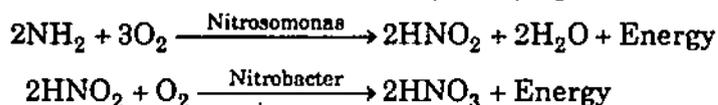
Some important biogeochemical cycles are as follows :

### NITROGEN CYCLE

Nitrogen is very important for plants and animals being an essential constituent of chlorophyll and all proteins. It is present in abundance (79%) in the atmosphere but it is never taken directly by any organism unless it is converted to a reduced ( $\text{NH}_4^+$ ) or oxidized ( $\text{NO}_3^-$ ) water soluble form.

Only a few bacteria and blue green algae are able to convert the gaseous nitrogen into nitrates and make it available for other organisms. The conversion of gaseous nitrogen into nitrates is termed nitrogen fixation. The atmospheric nitrogen is fixed symbiotically (bacteria living symbiotically with leguminous plant roots e.g., *Rhizobium*) as well as asymbiotically (independently living bacteria e.g., *Azotobacter*, *Beijerinckia*, *Clostridium*, *Aerobacter*, blue green algae e.g., *Nostoc*, *Anabaena* etc.) The lightning process also fix some proportion of atmospheric nitrogen.

These nitrates are absorbed by the plants for the manufacture of complex nitrogenous compounds. Plants in turn are eaten by animals. When the plants or animals die, certain bacteria, fungi and other microbes start acting on them and decompose the protein of dead organisms into ammonia. Such bacteria are called ammonifying bacteria. Ammonia is converted into soluble ammonium compounds which are released in the soil or water. Ammonia or the ammonium compounds are converted into nitric acid and then into nitrate by nitrifying bacteria.



In reverse reaction, some bacteria break of nitrates, nitrites and ammonium compounds to molecular nitrogen ( $\text{N}_2$ ) which is returned to atmosphere. Such bacteria are called denitrifying bacteria (e.g., *Pseudomonas denitrificans*, *Thiobacillus denitrificans*, *Micrococcus* and *Bacillus licheniformis*). This inorganic nitrogen is again recycled into the organic system upon absorption by the plants (Fig. 14).



### HYDROLOGIC OR WATER CYCLE

Water covers about 73% of the earth surface in form of sea, lakes and rivers. From each of these water sources, water is consistently evaporated by the heat of sun. In atmosphere it condenses into clouds and finally returns to the surface of earth as rain, snow or hail. Water falling in this way runs into streams and rivers and ultimately returns back to the ocean. Some amount of water during rainfall percolates into the deeper layers of earth. This water is picked up by the roots of plants and returned to the atmosphere through transpiration. Animal that eat plants have some of the plant water into their bodies. Animals return the water back into atmosphere either by excretion or by evaporation (Fig. 16).

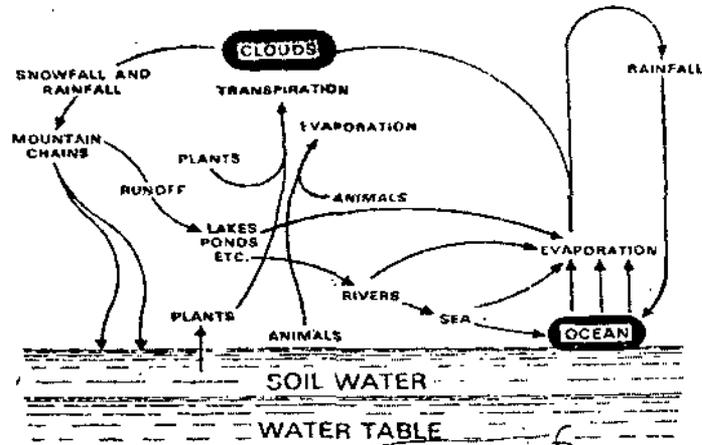


Fig. 16. Water cycle.

### SEDIMENTARY CYCLE

**Phosphorus cycle :** The major source of phosphorus are rock deposits. Through erosion and weathering inorganic phosphate becomes available to plants in dissolved condition. A good proportion of the available phosphate is washed into the sea. But from sea only a small fraction is returned to land system through man and certain sea birds. Phosphates from the soil taken by the producers, consumers and then to decomposers and made finally available for recycling through mineralisation and decomposition (Fig. 17).

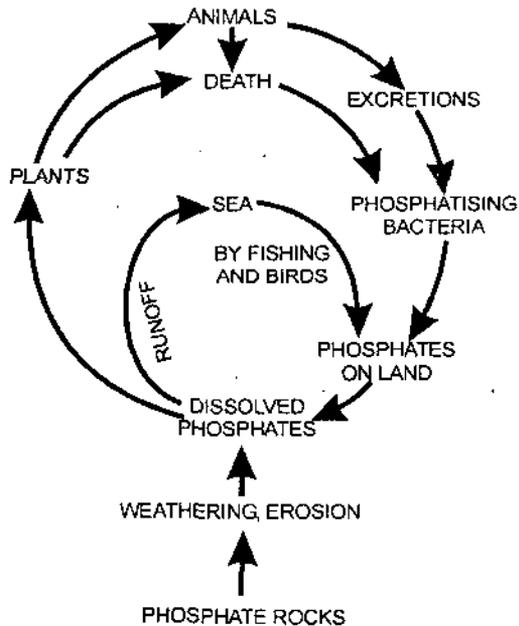


Fig. 17. Phosphorus cycle.

## 2.8. SUMMARY

Tansley (1935) proposed the term ecosystem and defined it as a system resulting from the interaction of all the living and non-living components of the environment. (Synonyms-geobiocoenosis, phytocoenosis, biocoenosis, biosystem, ecosom, microcosm, holocene). Our planet, the earth is a giant exosystem called biosphere. Since it is difficult to handle, it has been sub-divided into natural and artificial ecosystem. The natural ecosystems are divided into aquatic and terrestrial and the former into fresh water (lotic and lentic) and marine (shallow water, deep sea and estuarine). The artificial ecosystems are man made such as crop land.

The ecosystem comprises abiotic (non-living) and biotic (living) components. The abiotic components are inorganic substances, chemicals and the climatic regime. The amount of mineral matter present in an ecosystem at any given time is called as standing state or standing quality. The biotic components may be autotrophic or heterotrophic. The autotrophic components are called as producers and the heterotrophic as consumers. The consumers may be macroconsumers (e.g., herbivores, carnivores, omnivores) or microconsumers (decomposers).

The sole source of energy in an ecosystem is the light received from the sun. The sequence of biotic components in an ecosystem is : producers → consumers → decomposers. The food level of a component population in an ecosystem is called as trophic level. The producers constitute the first trophic level, herbivores second, carnivores third, top carnivores fourth and decomposers fifth. The trophic levels get reduced from producer to herbivore, herbivore to carnivore and carnivore to top carnivore. The amount of living material present in a component population of a specific trophic level is called as standing crop. The flow of food energy through a series of population in an ecosystem by eating and being eaten by another forms a food chains. They are of three types : grazing, parasitic and detritus. The grazing food chain starts from green living matter and proceeds to herbivore, carnivore and top carnivore. The parasitic chain however, proceeds from herbivore to parasite and hyperparasite. The detritus food chain starts from dead organic matter and proceeds to detritivore, carnivore and then to top carnivore. In nature, the food chains are not straight. Due to ample choice of food, these chains are interlinked and thus form a food web.

When various biotic components of an ecosystem are linearly arranged in interacting manner with reference to size metabolism, ecological or eltonian pyramids are formed. They are of three types, pyramids of number, biomass and energy. The pyramid of number in grassland and pond ecosystems are upright, that of forest ecosystem is rhomboidal and of parasitic ecosystem is inverted. The pyramid of biomass in grassland, forest and parasitic ecosystems are upright. For a shallow pond too, it is upright but inverted for deep pond and sea. The pyramid of energy is always upright in all ecosystems.

In each ecosystem several types of cycles operate simultaneously such as hydrological cycles, biogeochemical cycles and sedimentary cycles. In hydrological cycle, water is added to atmosphere by way of evaporation and transpiration through different sources. It is returned to soil by way of precipitation in different forms. The CO<sub>2</sub> of atmosphere and water is used by producers in photosynthesis and returned by respiration of all biotic components. The soil carbon is added in atmosphere by combustion, volcanic activity etc. and re-produced by all biotic components. The phosphates are taken by the plants from the soil. They join the food chain and then returned by decomposers. They leach to ocean basin, form phosphate rocks in due course of time which weather subsequently.

## 2.9. TEST YOURSELF

1. Who coined the term ecosystem ?
2. Our planet, the earth represents a giant ecosystem. What it is called ?

3. Briefly define the ecosystem.
4. Name the term for the ecosystem of running water.
5. From structural point of view the ecosystem is divided into how many components?
6. Name the term for the amount of living material in different trophic levels.
7. What that food chain is called which goes from dead organic matter to micro-organisms ?
8. What is the source of energy in an ecosystem ?
9. Who first of all designed the ecological pyramids ?
10. Which ecological cycle is directly driven by sunlight ?

**ANSWERS**

1. Tansley
2. Biosphere
3. Functional unit for ecological studies.
4. Lotic.
5. Biotic and abiotic.
6. Standing crop
7. Detritus food chain
8. Light received from the sun
9. Elton
10. Hydrologic.

□□□

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## ECOLOGICAL FACTORS

### STRUCTURE

- Introduction
- Climatic factors
- Topographic factors
- Edaphic factors
- Biotic factors
- Summary
- Test Yourself
- Answers

### LEARNING OBJECTIVES

By learning this chapter you will be able to know about ecological factors that influence the life of the organisms in one or more ways.

#### 3.0. INTRODUCTION

All organisms, including plants, are surrounded by the environment. The environment literally means the surroundings, and a factor may be defined as **any part or condition of the environment that influences the life of one or more organisms in one or more ways**. The environment is a complex of many factors *viz.* light, temperature, water and soil etc. These factors may be living (biotic) or non-living (abiotic or physio-chemical). All the factors are inter-related and variation in one may affect the other. All the ecological factors may be classified into two types :

- (a) **Direct factors** : Light, temperature, humidity, soil air, soil water and soil solutes.
- (b) **Indirect Factors** : Altitude, slope, wind, precipitation, soil structure, soil fauna and flora.

For convenience, we can divide the ecological factors into four major categories :

- (1) Climatic
- (2) Edaphic
- (3) Topographic
- (4) Biotic.

#### 3.1. CLIMATIC FACTORS

The atmospheric factors which affect the plants are called climatic factors. The climate word is of **Greek origin** and means inclination, *i.e.* the angle at which the sun's rays strike the earth. The climatic factors can be further sub-divided into :

- (1) Light factor
- (2) Temperature factor
- (3) Water factor
- (4) Wind factor.

A brief discussion of all these factors is undermentioned :

##### LIGHT FACTOR

Light is a factor of great physiological importance. It is a form of radiant energy. Light is composed of seven colours and wavelength ranges between 390  $m\mu$  to 760  $m\mu$ . The radiation with a wavelength below 390  $m\mu$  is termed **ultra-violet** and longer

than 760 m $\mu$  is infra-red. The ultra-violet rays have a damaging effect and most of them are absorbed in the upper layer of atmosphere.

### Effects of Light on Plants :

As described in the discussion of ecosystem only 2-3 percent of the solar energy is used in primary productivity. However, in deep shade under trees or under water light becomes limiting, below which photosynthesis is not sufficient or effective for growth. Compensation point is that intensity of light at which the rate of photosynthesis is just sufficient to meet the requirements of respiration. Based on their relative presence for natural growth in bright or diffused light the plants are classified into **heliophytes** (sun loving) and **sciophytes** (shade loving). Light affects plants in many ways, *i.e.*, by its intensity, quality and by duration as described below :

(i) **Effect of Light Intensity** : Light intensity falling at a particular place is normally enough for the plants. Very low light intensities, however, reduce the rate of photosynthesis and sometimes may even result in the closing of stomata. Very high light intensities are harmful to plants. It increases the rate of respiration and thus disturb the compensation point. It also causes rapid increase in transpiration which often results in the closure of stomata. The most harmful effect of the high light intensity is the phenomenon of **solarization** in which all the cell contents are oxidized by atmospheric oxygen. This oxidation is different from respiration and is termed **photo-oxidation**.

(ii) **Quality of Light** : Ultra-violet light kills bacteria and many fungi. It checks elongation of stem by inactivating the growth hormones. Infra-red radiation causes heating of plants and also affects germination and growth of plants.

(iii) **Light Duration** : The plants depend not only upon the intensity but also upon duration of light to which they are exposed. Some plants like *Abies*, *Picea*, *Taxus* etc can survive, grow and develop in shade and are termed "**tolerant species**". On the other hand the plants which demand light are known as "**intolerant species**" *e.g.* sunflower etc. The duration of total light period in a year and the duration of daily light period (photoperiod) at a peculiar place have pronounced effects on the vegetative as well as reproductive structures. The areas having many sunny days produce better vegetation than areas having cloudy days. On the basis of their photoperiod, the plants may be classified as : (a) **Short day plants**, that develop normally only when the photoperiod is less than a critical (between 12-14 hours) maximum (b) **Long day plants**, those demanding a photoperiod in excess of certain critical minimum and (c) **Day neutral plants**, indifferent to above conditions. These are also called **photoneutrals** or **indeterminate plants**.

Most of the plants belong to the first category, which requires a relatively long period of uninterrupted darkness for flowering. The photoperiod also plays an important role in the geographical distribution of plants in time and space. Morphological features like the formation of bulb, tuber and other storage organs are also affected by the length of the day.

### TEMPERATURE FACTOR

Temperature regulates all the chemical processes of plant metabolism. It also regulates the activity of enzymes which in turn regulates several physical processes. Each vital activity of plants require three degree of temperature—minimum, optimum and maximum. The three temperature limits are also called **cardinal temperature**.

**1. Minimum Temperature** : The lowest temperature at which any plant can survive indefinitely in an active state is termed minimum effective temperature.

(ii) **Optimum Temperature** : The range of temperature at which the physiological activities of plants are at the maximum is termed optimum temperature.

(iii) **Maximum Temperature** : The greatest intensity of heat at which a species live indefinitely in the active state is said to be the maximum temperature.

The temperature of a place is largely determined by its distance from the equator, i.e., on the latitude of the place. The temperature is maximum at the equator and decreases gradually one goes to the north or to the south. The vegetation of the earth can be grouped under different temperature zones, e.g. equatorial forests, tropical forests, coniferous forest, alpine vegetation etc. On mountains, a decrease in temperature and increasing altitude results a similar pattern of vegetation (Fig. 1).

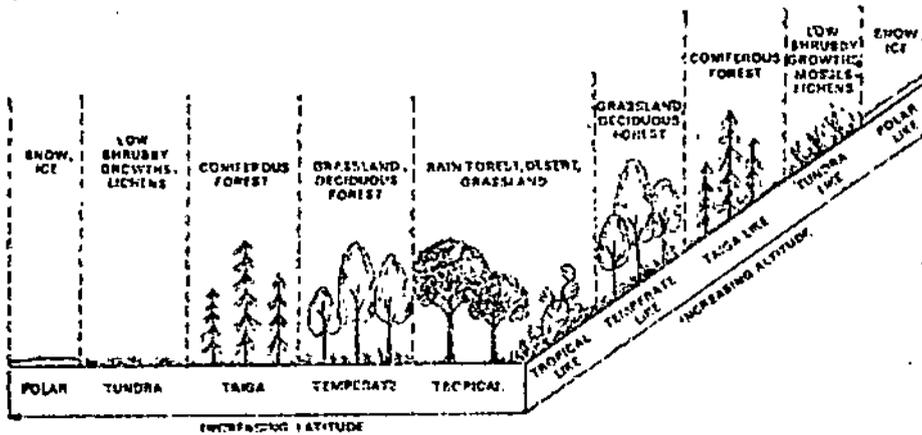


Fig. 1. Diagram showing different temperature zones.

The world vegetation can be divided into megatherms (plants of warm habitat), microtherms (plants of cold habitat), mesotherms (plants of habitat which is neither very hot nor very cold) and heskiotherms (plants of very cold habitat).

Many plants are resistant to very low temperature (below  $0^{\circ}\text{C}$ ) and are called cold resistant or frost resistant, and those able to survive under high temperature are known as heat resistant plants.

**Effects :** The low temperature damages the plants by making the water not available, reduced cell wall permeability, freezing of cell sap which leads to the rupture of cell walls, freezing of water in intercellular spaces and precipitation of proteins. Higher temperature during day increase the rate of photosynthesis and transpiration. In night, high temperature also increases the rate of cuticular transpiration even if the stomata are closed. High temperature also causes injury in the plants by desiccation and disintegration of the chlorophyll. The protein component of the protoplasm is coagulated at high temperature and the protoplasm is killed.

There are rhythmic variations in several important environmental factors due to certain geological phenomenon. As sun rises, light and temperature increases. Due to this, the temperature of any place changes constantly from hour to hour in a diurnal cycle. Variation in temperature during a day, season or months has a close relationship with phenology (phenology is the study of the periodic phenomenon of animal and plant life and their relation to the weather and climate e.g. time of flowering). Many plants, in course of time, got adjusted to the rhythmic diurnal cycle in temperature for several phenological events (germination of seed, elongation of shoot, pollination, secondary growth and leaf fall etc.) This regulation of phenology in periodic thermal changes is called thermoperiodism.

### WATER FACTOR

Water is the most important ecological factor in the life of an organism. All the physiological processes take place in the medium of water. It is the universal solvent and nutrients enter into the plant body in a dissolved condition. Thus, water helps in nutrient absorption. As an essential constituent of photosynthesis water itself is needed in the manufacture of carbohydrates. Protoplasm, the very basis of life is made up mostly of water.

**Sources of Water :** Water (marine and freshwater) covers about 75% of the earth's surface. It is also present below the land surface in the form of permanent

**water table** which is used by the deep roots of big trees and by crop plants through artificial means of irrigation from wells and tube wells. It is also present in the form of ice on large scale on south and north poles and on the tops of high mountains.

In nature, water is found in three principal forms—(a) Atmospheric moisture (b) Precipitation and (c) Soil moisture, of which precipitation is the chief source. Atmospheric moisture is found in two forms (i) invisible vapour forms and (ii) visible cloud or fog.

**(a) Atmospheric Moisture :** The moisture in the air in the form of water vapour is called **humidity**. The amount of water present in the air is called **absolute humidity**. The amount of moisture in the air as a percentage of the amount, which the air could hold at saturation at the existing temperature is called **relative humidity**.

Humidity in the air has a more significant influence on plant life than light and temperature because it effects the water relations of the plant. Low water humidity increases water loss through transpiration and affects growth. The roots of most land species do not grow either into the saturated soils or into the soils devoid of available water. Under these conditions plants are shallow rooted.

**(b) Precipitation :** At saturation point, if the temperature is lowered, the water holding capacity of atmosphere is reduced which causes the condensation of water vapours in the form of rainfall, dew, frost, sleet, snow and hail etc. This is **precipitation**. Of these, rainfall is most important, as most plant absorb water from the soil. The number of rainy days play a very important role in determining the vegetation of a place. In the warm tropics heavy rainfall distributed throughout the whole year results in **evergreen forests**. Heavy rainfall, confined to a few months in a year, results in **deciduous forests**. In regions of high winter rainfall **sclerophyllous** type of forest is developed. **Grassland** are found in regions of high summer rainfall and low winter rainfall. **Deserts** are found in regions of very low summer and winter rainfall.

The interaction of **rainfall** with temperature also has a very profound effect on the vegetation of a place. Very heavy rainfall and high temperature in the equatorial and tropical zone causes the formation of most highly developed vegetation of the world "**the tropical rain forests**". If the precipitation is abundant but the temperature is low, the vegetation consists of lichens, small conifers and scattered hardy shrubs and herbs. Conversely, if the rainfall is low but temperature is very high, the vegetation consists of small scattered trees, shrubs and cacti etc. of deserts. Extremely low rainfall or complete absence of rainfall accompanied with very high temperature results in drought, which very often results in outright killing of the plants of the weaker types.

**Snow** is injurious as well as beneficial to plants. It breaks off tree branches, flowers and fruits and may cause bending of slender stems, while some sedges prefer to grow in snow patches. Hails (balls or lumps of ice) and sleet (pellets of ice) may cause serious injuries specially to young crops. On the basis of their water requirements the plants are grouped into three ecological groups :

- (i) **Hydrophytes**—Plant adapted to aquatic environment.
- (ii) **Xerophytes**—Plants adapted to grow in dry lands where water content is low.
- (iii) **Mesophytes**—Plants living in the habitat that usually show neither an excess nor a deficiency of water.

**(c) Soil Moisture :** It is a chief source of water for plants, which mainly comes from rainfall.

(For detail see, **Edaphic factors**)

### WIND FACTOR

When air of large areas warms up, it starts moving and then it is called **wind**. The speed at which it moves is called wind velocity. Wind has both direct and indirect effects on plant life. The direct effect of strong wind is mechanical and it consists of **uprooting of trees**, breaking of branches and twigs etc. The indirect effect of wind is physiological. **Transpiration** makes the air surrounding the plant moist. Wind removes the moist air, bring in dry air and thus increases transpiration.

The wind is useful to the plants for the dispersal of pollen grains, for wind pollination (**anemophily**). It also transports many micro organisms, fungal spores and bacteria. Dispersal of seeds and fruits and other propagules in many plants depends upon wind for their movement from one place to another. Dispersal and migration are very important aspects of ecology.

Plants developing under the influence of drying winds never attains a degree of hydration. This leads to less expansion of cell walls and as a result all organs are dwarfed. When wind blows regularly from one direction, the form and position of the shoot may become permanently altered. This is called **deformation** (wind training). It inhibits the development of branches on trees on the side facing the wind, and thus trees with branching on only one side are produced. Such trees are called flag trees. Plants like wheat, maize, sugarcane etc., fall flat on the ground due to injury caused by strong winds. The phenomenon is called **lodging**. Wind also carry the soil or ice particles which serve as slow abrasive force and due to which buds, brak etc, are eroded. This process is called **abrasion**.

High velocity of wind causes constant **soil erodin**. The upper surface of the soil is blown away by wind in thickly vegetated area and renders it unfertile. In deserts, large sand masses (**dunes**) are blown by wind and deposited at another place when it loses its speed. No plant can be expected to grow on such unstable soil.

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### 3.2. TOPOGRAPHIC FACTORS

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The earth surface is not even at all places but show several irregularities in the form of depressions and elevations. The depressions and elevations may be a few millimeters or a few meters deep or high or may be several thousand meters as mountains and oceans. The unevenness or irregular factors of the earth's surface are known as **topographic** or **physiographic** factors. They include (A) Altitude, (B) Slope and (C) Direction of mountain chains and valleys.

**(A) Altitude** : The large scale altitudinal differences greatly affect the distribution of both plants and the animals. With the rise in the altitude the temperature decreases, rainfall increases and the wind velocity also increases. It has been found that the temperature decreases 6-7°C per 1000 meters.

(Also see Temperature and Fig. 1).

**(B) Slope** : The steep slopes allows rapid run-off and hence the soil is thin, ill developed, dry and sometimes completely eroded. Therefore, its surface is unstable on which plants are unable to establish themselves firmly.

The direction of the slope also affects the vegetation because it influences the availability of moisture, light and wind velocity. The eastern slopes of the Himalayas receives more rains than the western slopes. The slope facing north are affected by chilly winds while the southern slopes are warmer.

**(C) Direction of Mountain Chains** : Mountains affect climate. They steer wind into definite directions and capture moisture from wind on certain sides. Consequently water vapour accumulates in preferred directions in the form of clouds which come down as rain. Therefore, on certain sides and at a particular height luxuriant forests are developed. In the Himalayan mountain range, the outer Himalayas are covered with luxuriant forests and the middle and inner Himlayas are dry because the moisture in the winds is condensed and deposited before the interior is reached.

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### 3.3. EDAPHIC FACTORS (SOIL FACTORS)

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Soil is the medium in which plants grow. From the soil the plants derive their water and nutrients. It also acts as a reservoir for all water plants, rooted or submerged plants. The soil can be defined as "**the weathered (or broken particles) surface of the earth's crust which is mixed with organic material and in which plant grow**".

The factors which related to the structure and composition of the soil are called edaphic factors. Soil factors can be described under following sub-headings :

### MINERAL MATTER

**(a) Soil Formation :** The Soil is originated from the rocks by the various weathering processes. The weathering of the solid rocks may be brought about by mechanical means (e.g. strong winds, extreme temperature variations, shearing effect of the ice sheets and running water etc.), by chemical means (e.g. hydrolysis, oxidation, carbonation and hydration etc.) and as well as by biological means (action of various organisms particularly lower plants as lichens and mosses which secrete various organic acid and produce humic acid after death and decay. These acids help in the weathering process).

The mineral particles thus formed may remain over the parent rock or may be transported by different agencies to distant places. The former is called **residual soil** while the other is **transported**. Depending upon the agencies of transport the soils are called **alluvial** (by river, running water), **colluvial** (by gravity), **glacial** (by glaciers), and **eolian** (by wind) etc.

The weathered material undergo a number of changes, known as **pedogenesis** or soil development. To these is added the huus (the dead and decaying organic substances) in due course of time and thus soil is produced. Continuous addition of organic matter and its decomposition improves the properties of the soil which effects the growth of different types of plant on it. This process is called **maturation**. The structure of the soil can be better studied by cutting a section (vertical) of the soil.

**Soil-profile :** In a vertical section we can see a number of layers (horizon) super-imposed one above the other and all of them collectively called as soil-profile. In a typical soil profile (Fig. 2) following layers can be recognized.

**'A' horizon :** It is the top fertile soil richly mixed with organic material in different stages of disintegration. It can be further divided into several layers:

$A_{00}$  — Top layer of fallen leaves and twigs still intact or only slightly broken.

$A_0$  — Layer of partly decomposed organic matter where decomposing organs have lost their identity.

$A_1$  — Fully decomposed organic matter, *i.e.* humus, dark in colour.

$A_2$  — Decreasing quantity of humus and are less dark than  $A_1$  layer.

**'B' horizon :** It has iron and aluminium compound along with clay and humus and light brown in colour. The A and B horizons of soil together form the **true soil**.

**'C' horizon :** It represents a stage of weathered parent material. It is also called as the **sub-soil**.

**'D' horizon :** It is the lowest region of soil-profile components, air and water containing dissolved substances. On an average soil has the following composition :  
40% mineral matter, 10% organic matter, 25% soil water and 25% soil air.

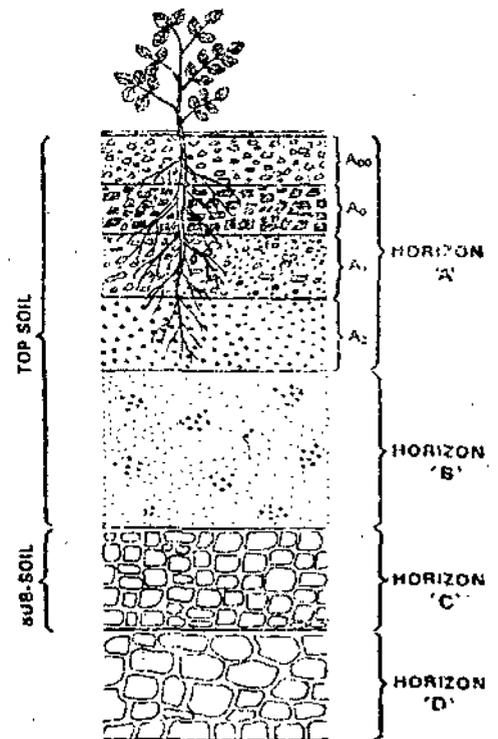


Fig. 2. Diagrammatic representation of soil-profile.

(b) **Size of the Mineral Particles** : The mineral contents of the soil consists of different sized particles which are produced by weathering of rocks. According to the size, the different soil particles have been named differently by **International Society of Soil Sciences** as under :

S.N.	Name of Particles	Diameter
1.	Gravel	More than 5.0 mm
2.	Fine gravel	5.0 mm to 2.0 mm
3.	Coarse sand	2.0 mm to 0.2 mm
4.	Fine sand	0.2 mm to 0.02 mm
5.	Silt	0.02 mm to 0.002 mm
6.	Clay	Less than 0.002 mm

(c) **Soil texture** : The relative proportion of rock particles of different sizes determines the texture of the soil and affects the plants which grow on it. On the basis of texture soils are usually classified into following types :

S.No.	Soil type	Percentage of various types of particles		
		Sand	Silt	Clay
1.	Sand	85—100	0—15	0—10
2.	Loamy sand	70—90	0—30	0—15
3.	Sandy loam	43—80	0—50	0—20
4.	Loam	23—52	28—50	7—21
5.	Silt loam	0—50	50—88	0—27
6.	Silt	0—20	80—100	0—12
7.	Sandy clay loam	45—80	0—28	20—35
8.	Clay loam	20—45	15—53	27—40
9.	Clay	0—45	0—40	40—100

Sandy soils are composed of coarse particles and are termed as **light textured**. In sandy soils, the spaces are large and the amount of water that can be held in the spaces between these particles is very little. Thus, the sandy soil cannot support a good vegetation. Clayey soils are composed of fine colloidal particles and are normally termed as **heavy textured**. The clay particles are colloidal in nature and being small in size, leave very thin capillary spaces between the particles. Clay swells up when moist and shrinks when dry. This shrinkage is accompanied by soil cracking which often causes great damage to plant roots. Due to presence of small interspaces between them neither water nor air can move freely. Such soils readily become water logged and not suitable for plant growth. A soil in which the sand, silt and clay particles are present in more or less equal proportion is called **loam** and is most suitable for plant growth. A loamy soil in which sand particles predominate is called **sandy loam** and the one in which clay is predominant is called **clayey loam**.

#### SOIL HUMUS

The organic matter added to soil is hardly 10 percent of its dry weight and has a marked effect on the vegetation of the place. The organic matter largely comes from (i) dead and decaying roots of plants and living organism present inside the soil and (ii) dry leaves, dead plant parts and animals. The dead materials are acted upon by a series of microorganisms which convert them into humus and the process is called **humification**. The humus is further converted to simpler substances such as  $\text{CO}_2$ , water and minerals by a process known as **mineralization**. In the forests, in each season raw humus occurs in three distinct stages of decomposition. All dead, fresh organic matter fallen recently to the ground is called **litter**. Beneath it is a layer of partially decomposed organic matter called **duff**. Still deeper, the decomposition of

organic matter has progressed further so that it has lost its original form altogether. This deeper layer is called leafmould. In cold climate, the organic matter and humus accumulate in large amounts because the rate of decomposition is very slow and this results in the formation of peat.

Humus is of two types :

(a) **Mor humus** (raw humus) : It is in the form of a thick carpet of undecomposed organic matter with low percentage of minerals. Earthworms do not occur in it.

(b) **Mull humus** : It support a large number of bacterial, fungal populations and earthworm fauna. It is loose, porous, friable mass with a crumby structure and consists of an intimate mixture with mineral soil.

Soil humus is the main source of nutrients for plants. It also has important physical effects upon the soil. It improves the soil structure, provides better aeration, has a binding effect upon the soil particles and increase the water holding capacity of the soil.

### SOIL WATER

The chief source of soil water is rain. The soil water is not only important in connection with direct requirements of plants, but it also acts as the medium through which mineral salts, essential for plant nutrition, enter the plants. All the water present in the soil is not available to plants. After a heavy rainfall some of the water drains away along the slopes. This is called run-away water. Some of the water flows downward under the influence of gravity. This is called the gravitational water. Some of this water is absorbed by the soil and is being hold tightly by them. The water thus absorbed by them is called hygroscopic water. The remainder of the water remains in the soil spaces due to the force of capillary tension. This is the capillary water and is of greatest importance to the plant because it is this water that is readily absorbed by the roots.

The total water present in the soil is called holard. The amount of water (gravitational and capillary water) that plants can absorb out of holard is called chresard. The hygroscopic and combined water which plant cannot absorb is termed echart. The percentage of water, that is left in the soil at the time when the plants first wilt permanently and is unable to recover, is termed permanent wilting point or wilting coefficient.

### SOIL AIR

Soil is a porous structure and about 30-60% of the soil has porous spaces, partly filled by moisture and partly by air. The soil acration is essential for the proper functioning of the roots of the plant. The absorption rate is rapid in the well aerated soil and the rates gets reduced in the oxygen deficient soils. The oxygen present in the soil air is an important factor in soil fertility. Oxygen is necessary for the breaking down of insoluble minerals into soluble salts, for bacterial nitrification, nitrogen fixation, seed germination, root growth, development of root hairs, absorption and for respiration of earthworm and other soil organisms. In the deficiency of oxygen these activities are slowed down and ultimately ceases. In the poorly aerated soils the carbon-dioxide release during respiration of organisms and roots get accumulated in the soil which is detrimental for the water absorption of the plants. Soil air also increases the fertility of soil.

### SOIL TEMPERATURE

Besides the physical and chemical processes taking place in the soil, rate of absorption of water and solutes, the germination of seeds and growth rate of underground parts of the plants, are also affected by temperature. The optimum temperature for maximum water absorption and metabolic activities generally varies from 20°C to 30°C. Plants cannot tolerate extremes of temperature. The main source of soil temperature is the heat of sun light absorbed by soil particles. Soil temperature

plays important role in determining the geographical distribution of plants on earth. It also effects the activities of microorganisms. The useful bacteria, such as those concerned in the decomposition of organic matter, nitrification and nitrogen fixation, all require favourable temperature conditions.

### SOIL COVER

The soil cover may be living or non-living *e.g.*, dead plant leaves, snow and plants. It protects the soil from loss of water and rapid temperature changes. In alpine regions snow-cover protects the soil and small plants growing there. The living cover vegetation protects the moisture, temperature and soil erosion. It checks movement of water over the surface of soil by means of stems and leaves and directs the water in soil along the roots or old root channels or opening left by earthworms and other organisms.

### SOIL ORGANISMS

The important soil organisms are bacteria, algae, fungi, actinomycetes, roots, rhizoids, rhizomes, protozoa, rotifers, nematodes, mites, insects and earthworm etc. It has been estimated that each gram of surface soil contains fifty to one hundred thousand fungi and several millions bacteria. The large number of microorganisms present in the soil brings about the decomposition of dead organic matter of plants and animals to simpler substances. These simpler forms of this matter are again utilized by plants. The bacteria and blue green algae (*Azotobacter*, *Clostridium*, *Rhizobium*, and *Anabaena* etc) increase soil fertility by fixing the atmospheric nitrogen. Some fungi form **mycorrhizal-association** with root system of higher plants and help them in absorption of water and minerals. Some bacteria and fungi and pathogenic and cause diseases of plants. Some bacteria and blue green algae produce mucilaginous substances which help in binding of soil particles and larger aggregates. The microorganisms also produce toxic substances and cause diseases and injury to the plants.

The large organisms like earthworms improve the aeration and fertility of the soil by burrowing and mixing of the organic matter to the soil.

### SOIL REACTION (pH Value)

The pH of the soil solution, *i.e.* the soil reaction directly affects the plant growth by controlling the availability of nutrients in balanced amounts. The negative logarithm of hydrogen ion concentration is denoted as pH. The neutral solution has a pH value of 7. The lower values denote acidity and higher denote the alkalinity of the medium.

The soils may be neutral, acidic or alkaline depending upon the presence of basic and acidic salts in the soils. Neutral or slightly acidic soils are best for the growth of the majority of the plants. The acidity of the soil beyond a particular limit is injurious to plant growth. Certain plants like *Rumex* sps. can tolerate acid conditions while a few others would grow only in acidic soils. *Rhododendron* grows best in acidic soil. Acid soils are usually deficient in calcium and plants growing on them are called **calciphobous** (lime fearing). Soil acidity beyond a particular limit is injurious to plant growth. It checks the nitrifying and nitrogen fixing bacteria. In acidic soils normal decay of humus is prevented and carbon-dioxide and other toxic substances accumulate. Acidity of soil adversely affects the solubility of salts and minerals like phosphate, magnesium, calcium etc. and thus greatly reduces their availability. It also destroys the crumbly structure of the soil and diminish its air and water contents.

Soils which contain high concentrations of soluble salts are described as **alkali soils**. The alkaline soils are usually devoid of plant life because under such conditions the root cells may even loose water on account of the high concentration of solution. Some species like *Salsola foetide* and *Salicornia* can grow best on alkali soils.

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## 3.4. BIOTIC FACTORS

The biotic factors include the influence of living organisms, both plants and animals, upon vegetation. Plants live together in a community and influence one

another. In a forest there are many plant communities such as trees, herbs, shrubs, mosses, lichens etc which interact with one another and adjust according to environmental conditions. They may effect directly or indirectly what may be beneficial to one community, may be harmful to the other. Similarly animals associated with the plants also effect the plant life in one or several ways. Many animals use plants as their food (herbivores), some utilize them for their shelter (birds and others). Among the animals man is also modifying the vegetation, according to his wish. This whole phenomenon is called **biological inter-relationship**. The biotic factors can be discussed into following three sub-headings :

- (A) Effects of Plants
- (B) Effects of Animals
- (C) Effects of Man.

#### **EFFECTS OF PLANTS**

(i) **Competition** : An organism competes with members of its own species as well as with representatives of other species for space, light, food or other necessities. Competition increases with increase in population. The nature of the competition between species differs because of the variation in precise needs and adaptation of different species. As a result of competition the height, size, vigour of the plant, branching, number of flowers etc, are reduced. There are two types of competition among living organisms :

(1) **Intra-specific Competition** : The competition among the individuals of the same species is generally for a common resource and is more severe among plants.

(2) **Inter-specific Competition** : The competition between two different species occurring together affects both of them in smaller or larger degree.

The success of a species in competition depends upon the rate of growth and reproduction. Among the plants, the difference in the time of seed germination and seedling establishment also affects the result of competition.

(ii) **Relationship Among Organisms** : All the biological interrelationships among the organisms have been called symbiosis by McDougall (1918). DeBary (1879) defined symbiosis as "*the living together of the dissimilar organisms*". The term is derived from the Greek words *Sym* (= together) and *bios* (= life). Among animals there is some slightly different association where the benefit derived by weaker partner is less clear. It is called **commensalism**, while specialized association like that of algae and fungi in lichens is called **mutualism**. McDougall (1918) divided symbiosis into two major groups :

(1) **Disjunctive Symbiosis** (Associated organisms are not in constant contact) :

(A) **Social** (No direct nutritional relationships) : It includes the effect of one plant on another with respect to shade, air movement, soil moisture etc., and also the substrate relation of saprophytic organisms.

(B) **Nutritive** : (a) **Antagonistic** : Herbivores animals and their food plants, carnivores plants and their prey.

(b) **Reciprocal** (Reciprocal does not imply that the two symbionts are mutually helpful but it shows a condition of reciprocal parasitism in which the advantage of the relationship exceed the disadvantages of both organisms). Animals effecting pollination or dissemination incidental to their activities in obtaining food from plants, fungi cultured and disseminated by insects that use them for food.

(2) **Conjunctive Symbiosis** : (Dissimilar organisms living in contact with each other) :

(A) **Social** : Lianas and other plants for support, algae inhabiting hollow interiors of *Azolla* leaves the roots of cycads, the ventral cavities of the thallus of *Anthoceros*.

(B) **Nutritive** : (a) **Antagonistic** : Parasitism of plants by bacteria, fungi, protozoa, nematodes, insects etc.; parasitism of animals by bacteria and fungi.

(b) **Reciprocal** : Lichens, mycorrhiza, nitrogen fixing bacteria in roots, stem and leaves, algae inhabiting protozoa.

An account of some of the most important examples of symbiotic relationship of one organism with another is given below :

(1) **Lichens** : These plants are more common in tropical rain forests where light at ground level is scarce because of the dense and multistoried growth of vegetation. They are woody plants rooted in the ground but climb up with the support of other trees and reach almost to the top of forest canopy e.g. *Bauhinia vauhili*.

(2) **Lichens** : Some peculiar type of algae and fungi associate together to give rise to a peculiar type of life form called lichens. (e.g. *Graphis scripta* and *Haematomma puniceum* etc.). The algae manufacture food which the fungal component also uses. Fungus on the other hand protects the algae from drying up and so these are able to colonize dry rocks and tree barks. This type of association is also termed **mutualism**.

(3) **Epiphytes** : Epiphytism is another type of biotic association where the plants grow on other plants but do not derive their food from the supporting plant: Epiphytes derive their supply of moisture and nutrient from the frequent rains and debris accumulation in bark cervices. Roots of epiphytes also store water in a special tissue called **velamen**. Epiphytes include a wide range of plants e.g. algae, lichens, liverworts mosses and a number of vascular plants (ferns, orchids etc.).

(4) **Parasites** : Parasitic relationship between plants and animals or plants and plants are of very wide spread occurrence. Parasites obtain nutrition from living plants or animals, which are called host. In angiosperms parasitism is less frequent in comparison to fungi and bacteria. Some common examples of root and stem parasites in the plants are as follows :

Total stem parasite—*Cuscuta*; Partial stem parasite—*Loranthus*, *Viscum*; Total root parasite—*Orobanche*; Partial root parasite—*Santalum*.

*Puccinia graminis* is a parasitic fungus causing rust disease in wheat. Mildews, smut, white rust, damping off and blight diseases are caused generally by parasitic fungi. The common example of parastic algae is *Cephaleuros*, which is found on a number of organisms.

(5) **Mycorrhizal association** : Sometimes fungi grow on the surface or inside the roots of the higher plants. They are called **mycorrhiza**. It is of two types : (a) **Ectotrophic** (fungus lives on the surface) and (b) **Endotrophic** (fungus penetrates the deeper tissues of roots).

The roots with mycorrhizae are unbranched and without root caps and root hairs. Fungal hyphae in this association act like root hairs, absorb water and minerals from the soil and supply them to the roots. The roots in return provide food and shelter to these mycorrhizae. It is also believed that the fungus regulates the acidity and sugar content in the root tissue and enable the roots to grow vigorously. It has been estimated that some species of plants in about 80% families of seed plants have mycorrhizal association. Orchid seedling do not develop properly unless they become infected with mycorrhizae.

(6) **Insectivorous plants or carnivorous plants** : A number of highly specialized plants like *Utricularia*, *Nepenthes*, *Drosera* etc. are dependent for part of their nitrogen requirements upon small animals like insects. The soil in which they grow is waterlogged and swampy. The plants growing in such habitats have poorly developed roots. These plants have some specialized structure and mechanism to trap insects and thus secrete enzymes to 'digest' the protein contents of the insect body.

(7) **Root Nodules** : *Rhizobium* forms nodules in the roots of leguminous plants and live symbiotically with the host. Plant provides food materials to bacteria and in turn fix gaseous nitrogen, making available to plant (mutualism).

### EFFECT OF ANIMALS

(i) **Pollination** : Bees, moths, butterflies etc., derive food from the nectar or other plant products and in turn bring about pollination (mutualism). Pollination caused by the animals is known as zoophily. Zoophilous flowers are of following type :

- (a) Entomophilous (pollinated by insect)
- (b) Orthophilous (pollinated by bird)
- (c) Chiropterophilous (pollinated by bat)
- (d) Malacophilous (pollinated by slug and snail).

(ii) **Dissemination** : Seeds and fruits are commonly transported by animals. The fruits are eaten by birds, mammals etc., and seed contained in them are dispersed through excreta, often for many miles from the original place.

(iii) **Soil organisms** : (See edaphic factor).

(iv) **Grazing** : (See soil erosion and soil conservation).

### EFFECT OF MAN

The influence of man on vegetation is one of the most important biotic factors. With the advances of civilization and growing population man is becoming more and more dependent on plants and animals. Man kills animals for his food, clothing, self protection, entertainment etc. The influence of man upon vegetation can be studied under following headings :

(a) **Domesticated and wild animals** : Domesticated animals damage most of the forest vegetation by grazing and browsing. Heavy grazing reduces the photosynthetic parts so much that many plants succumb. The unpalatable species avoided by grazing animals multiply and increase in number in absence of competition. Excessive browsing by goats and sheep has laid bare areas and made them susceptible to erosion. Thus, natural forest equilibrium is greatly disturbed which results in the disturbance in successional processes.

(b) **Excessive felling** : Excessive and indiscriminate felling of the trees for the purpose of timber and for cultivation purposes has completely changed the vegetation of different places. Excessive felling of forests has a serious effect on the development of soils. It is believed that the creating of *usar*, *reh* and *kallar* soils in some parts of Indo-Gangetic plain is due to excessive felling of indigenous vegetation.

(c) **Cultivation** : Besides the old methods man has adopted certain advanced methods e.g. cutting, budding and grafting etc. for the cultivation of the plants. In cultivation, the destruction of weeds by man eliminates the competition among plants. Proper spacing of plants during cultivation also checks the competition among them for food.

(d) **Forest fire** : Fire is a biological factor rather than a physical factor because it is mostly caused by man's activity. Fire may be caused by lightning or volcanic activity or man himself may set fire to vegetation for several reasons. Sometimes forest fire also develop due to mutual friction between tree (bamboo etc.) surfaces. Various kinds of fire are known to occur in nature :

(i) **Ground fire** : The kind of fire which are flameless and subterranean and occurs in the area having thick accumulation of organic matter.

(ii) **Surface fire** : The fire which often sweeps on the ground surface rapidly, the flames consuming litter, living herbs and shrubs and scorching the bases of any trees it may encounter.

(iii) **Crown fire** : A type of fire which extends from dense woody vegetation and travels from the canopy of one plant to another.

### EFFECTS OF FIRE

Fire injure plants directly by subjecting the tissues to lethal temperatures but it also affects them indirectly. Some scars which are formed on trees due to fire injury serves as suitable avenues of parasitic fungi and insects. The high temperature

promotes germination of several legumes and grasses as *Cassia*, *Indigofera*, *Andropogon* etc. The primary production has also been found to increase in certain cases. In *Pinus* and *Eucalyptus* the axillary buds sprout and grow rapidly after fire. Fire also brings about marked alternation of environmental factors such as light, rainfall, nutrient cycles, fertility of soil, litter and humus contents of soil, pH and soil fauna. The fire under control can be used for elimination of competitors, harmful animals and release of nutrients. Litter accumulation physically prevent the healthy production and growth of some plant species in grassland. Fire not only removes the choking litter accumulation but also referred the organic debris to ashes.

The branch of ecology which deals with the effects of the fire on ecosystem is called 'fire ecology' or 'Ecophysiology'. Plants having ability to withstand fire with little or no damage are referred pyrophytes.

**Adaptation to fire :** In areas where fires are very common the plants have developed some adaptations for their survival, e.g. in *Rhus ceanothus* the seed coats are very hard and the breakage of seed coat depends on fire. Fire cracks the seed coats and then seedlings develop in great numbers. Some plants as *Pinus* and *Larix* are fire resistant due to poor compounds as resin or oil and thus may check surface fires. They also develop thick bark which often escapes fire injury. The cones of various conifers (*Pinus*, *Picea*) are serotinous i.e. cones remaining on trees with viable seeds for several years (even upto 75 years). Fire cause the prompt opening of these cones by burning surface coatings of resins.

**(e) Pollution :** It can be defined as "an undesirable change in the physical, chemical or biological characteristic of our land and water that may or will waste or deteriorate our raw material resources". It is mainly due to activity of man.

### 3.5. SUMMARY

The word environment literally means the surrounding. It is the aggregate of all external and internal conditions affecting the existence, growth and metabolism of any living being. Hence, those conditions which affect the very existence, organization and metabolic processes of an organism in the slightest manner may be referred to as **environmental or ecological factors**. The ecological factors are generally classified into four major categories :

**(A) Climatic :** They refer to temperature, water and wind.

**(B) Edaphic :** It relates to soil.

**(C) Topographic or physiographic :** They include altitude, steepness of the slope, direction of mountain chains.

**(D) Biotic :** They include the influence of other living beings.

The source of light for our planet is sun. Only 2-3 percent of light is utilised by the plants. On the basis of light requirements, plants have been divided into heliophytes and sciophytes. Light intensity affects the various physiological processes for e.g., photosynthetic, respiration etc. On the basis of light duration plants have been divided into three categories namely long day plants, short day plants and day neutral plants.

Temperature regulates all the chemical processes of plant metabolism. The cardinal of temperature vary considerably for different physiological processes. As many as five temperature based altitudinal and latitudinal zones are differentiated namely tropical, temperate, taiga, tundra and polar vegetation is also differentiated into four temperature based groups namely megatherms, mesotherms, microtherms and hekiotherms. Temperature is also related with phenology. The regulation of phenology in periodic thermal changes is called thermoperiodism.

In nature water occurs in several forms such as salt water, fresh water, snow, ice and vapours. The chief source of soil water is atmospheric precipitation occurring in the form of snow, rain, hail, sleet, frost dew, fog and mist. On the basis of water requirements plants are grouped into three ecological groups namely hydrophytes,

xerophytes and mesophytes. The effect of the wind on the plants may be useful or harmful. It brings about dispersal of pollen grains, spores seeds, fruits and also causes injuries in plants through dust or snow storms. The plants may be totally or partly flattened or deformed. Wind velocity in one direction is also responsible for the formation of flag trees. The unevenness of the earth's surface or irregular factors of in earth's surface are known as topographic or physiographic factors. They include mainly altitude, slope and direction of mountain chains.

The factors which relate to the structure and composition of the soil are called edaphic factors. The soil formation occurs in two stages, weathering and pedogenesis. The weathering of rocks may occur by chemical, physical or biological methods. Soil is of two types : residual and transported. The latter type is further divided into four categories on the basis of means of transport as alluvial, colluvial, eolian and glacial. The soil layers distinguished on the basis of colours etc. are called horizons. As many as two horizons are differentiated namely A horizon (further subdivided into four layers.  $A_{00}$ ,  $A_0$ ,  $A_1$  and  $A_2$ ) and B horizon.

On the basis of size, the six soil particles are named. These are : gravel, fine gravel, coarse sand, fine sand and clay. The relative proportions of these particles determines the texture of soil. Humus is of two types namely mor and mull humus. It is main source of nutrients for plants. Capillary water is of great importance because plants can readily absorb by the roots. Soil air is needed for root respiration, seed germination and development of root hairs. Soil temperature plays important role in geographical distribution of plants on earth. Soil cover protects the soil from loss of water and rapid temperature changes. Soil organisms perform several important role in the soil. Soil reaction may be acidic, alkaline or neutral. Depending upon the nature of soil solution we have the vegetation. The biotic factors include the influence of living organisms, both plants and animals upon vegetation. Human beings are the most powerful biotic components. They are responsible for excessing felling of trees, soil erosion, overgrazing, forest fire and pollution.

**3.6. TEST YOURSELF**

1. Name the term for any part or condition of the environment that influence the life of the organisms in one or more ways.
2. What is humus?
3. Define ehard.
4. Name the plants growing on sand and gravel.
5. What is the important character shown by serotinous cones?
6. What is study of the soil is called?
7. Name the agents which are mainly responsible for physical weathering of the rocks.
8. Name the soil which is transported by air .
9. Name the soil water which is available to plants.
10. Name the plants which grow extremely in cold soils.

**ANSWERS**

- |                      |  |
|----------------------|--|
| 1. Factor            | 2. Minerals and fully decomposed organic matter. |
| 3. Unavailable water | 4. Psammophytes                                  |
| 6. Pedology          | 5. Longer viability                              |
| 9. Capillary water.  | 7. Rain, heat                                    |
|                      | 8. Eolian  |
|                      | 10. Psychrophytes.                               |



## ECOLOGICAL SUCCESSION AND ECOLOGICAL CONCEPT OF SPECIES

### STRUCTURE

- Introduction
- Basic types of succession
- Trends in succession
- Time factor in succession
- Causes of succession
- Process of succession
- Concept of climax
- Kinds of succession
- Hydrosere
- Xerosere
- Ecological concept of species
- Summary
- Test Yourself
- Answers

### LEARNING OBJECTIVES

By learning this chapter you will be able to know about trends, causes and process of succession. You will also know about the ecological concept of species.

#### 1.0. INTRODUCTION

Succession from the ecological point of view may be defined as “**an orderly sequence of communities of organisms over a period of time at the same place**”. At any place the existing communities modify the environment due to its presence and biological activities so as to make less suitable to this environment, replace it in the same order of sequence. New community replaces the old one, after modifying the environment, till there sets up a relatively stable climax community.

**Odum (1971)** defined ecological succession in terms of the following three parameters :

1. It is the orderly process of community changes. These are directional and therefore predictable.
2. It results from the modification of the physical environment by the community.
3. It culminates in the stable climax in which maximum biomass and symbiotic function between organism are maintained per unit of available energy flow.

The series of different stages during succession is called **sere**. The relatively transitory community are variously called **seral stages** or **pioneer stages**, while the terminal stabilised system is known as **climax**. Ecological succession is community controlled and is a biological process, but not physical as the physical environment determines the pattern of succession but does not cause it.

#### 1.1. BASIC TYPES OF SUCCESSION

Succession always start on bare area. The various types of succession have been grouped in different ways on the basis of different aspects. Some basic types of succession, however, are as follows :

**1. Primary succession :** Succession that begins on a sterile area where conditions of existence are not at first favourable for e.g., a newly exposed sand dune or a recently lava flow.

**2. Secondary succession :** The community development on sites which are previously occupied by well developed communities or succession on sites. The nutrients and condition of existence are already favourable such as ploughed grass land, cut over forest or new ponds.

**3. Autotrophic succession :** It is characterized by early and continued dominance of autotrophic organisms like green plants and begins in a predominantly inorganic environment.

**4. Heterotrophic succession :** It is characterized by early dominance of heterotrophs viz., fungi, bacteria and animals and begins in a predominantly organic environment.

**5. Autogenic succession :** Sometimes succession community themselves modify the environment, suitable for another community and thus causing its own replacement by new communities. Such a successional process is termed as **autogenic succession**.

**6. Allogenic succession :** In some cases one community replaces the other largely due to the forces other than the effects of communities on the environment and then the succession is called **allogenic**.

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## 1.2. TRENDS IN SUCCESSION

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Ecological succession is such a continuous process where one community replaces the other. The term in this process include species structure, organic structure and energy flow. To explain major trends of succession the following four aspects are more significant :

- (i) The kinds of plant and animal changes continuously with succession.
- (ii) Biomass and standing crop of organic matter increases with succession.
- (iii) Diversity of species tends to increase with succession.
- (iv) A decrease in net community production and a corresponding increase in community respiration are two important trends in successions.

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## 1.3. TIME FACTOR IN SUCCESSION

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Trends of succession in all ecosystems and geographical locations are the same. The community structure and physical environment affects. (i) the time required for completion of succession i.e., weeks, months or years, (ii) the relative stability of climax.

As in cultures, in open water systems community modify the physical environment to a small extent only and succession completes only in few weeks. In a typical marine pond, it takes a season while on sites as sand dunes or recent lava flow is atleast 1000 years. Thus succession at different sites requires different time periods.

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## 1.4. CAUSES OF SUCCESSION

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As mentioned earlier, sere always starts on bare area. The bare area may be caused by a number of factors :

- 1. Topographic processes :** Producing mostly primary bare areas :
  - (a) **Erosion :** by wind, water, gravity or glaciers.
  - (b) **Deposition :** by wind, water, gravity, glaciers or volcanoes etc.
  - (c) Emergence of barren land surfaces.
- 2. Climatic processes :** Producing mostly secondary bare areas :
  - (a) wind eliminating the previous vegetation,
  - (b) drought, drying and killing the weaker species.
  - (c) lightning causing fire in forests,
  - (d) by hails and storm.

**3. Biotic agents :** Producing mostly secondary bare areas :

- (a) man destroying natural vegetation,
- (b) animals overgrazing etc.
- (c) bacteria, fungi and insects eliminating species by disease.

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### 1.5. PROCESS OF SUCCESSION

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The whole process of succession completed through a number of sequential steps which follow one another. These steps are as follows :

**1. Nudation :** The development of a bare area without any form of life is called **nudation**. This is brought about by several topographic, climatic and biotic factors.

**2. Invasion :** Once a bare area is formed, it is soon invaded by organisms and their establishment in the new area is called **invasion**. Plants are the first invaders (pioneers) in any area because the animals depends on them for food. The invasion is completed in three steps :

- (a) **Migration :** When a seed, spore or vegetative propagules reach the new area, the process is called **migration**.
- (b) **Ecesis :** Ecesis means that the propagule makes the new area at its home. It includes germination, growth and reproduction. If the propagule fails to germinate or to reach the reproductive stage after germination, it cannot be said to have ecised.
- (c) **Aggregation :** The organism is able to multiply and aggregate in a large population in the area.

**3. Competition :** The aggregation of individuals in an area leads to interspecific and intraspecific competition. Competition is usually for water, nutrients, heat, light, carbon di-oxide, oxygen and spaces.

**4. Reaction :** The mechanism of the modification of the environment through the influence of living organism is known as **reaction**. It is one of the most important factor in the process of succession. The modification of environment is such that it becomes less favorable to the species and yields to new invaders.

**5. Stabilization and climax :** The whole process of succession results in stabilization. Of the vegetation and the final stage which is in equilibrium with the climate of the area is called climax.

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### 1.6. CONCEPT OF CLIMAX

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The end product of succession after several serial communities is the climax community. It reaches after hundreds or thousand of years at a place. It is generally believed that once the climax is attained the community does not change at all, but this is not exactly so. Climax communities also change due to what may be said as 'aging'. In this process it is likely that the community and the environment in course of time get 'aged'. Storms and disease could hasten the aging and death of a climax and its replacement by a young, perhaps, different community.

On the margins of climaxes a stable community is developed, known as **pro-climax**. This can easily undergo changes in appearance on disturbance. Sometimes a strip of vegetation of higher life forms is found within a climax, this higher type of vegetation is called **post-climax**. For example, a forest along a stream in a grassland constitutes post climax stage. If climax is in localized regions or margins in which plants of lower order than climax, the strip of formation is **sub-climax** or **pre-climax**.

#### Theories of Climax

(a) **Monoclimax theory :** This theory was advanced by an American plant ecologist, **Clements (1916)**. According to him the climax formation is only controlled by the climatic factors. Such a climax is, therefore, **climatic climax**. It is not affected

by soil or topography. There is only one true climax community in a climatic region or in a geographical area. Other communities which are present in the area in addition to climax community are regarded as sub-ordinate communities. Terms **pro-climax**, **sub-climax**, **pre-climax** and **post-climax** are used to define sub-ordinate communities.

(b) **Poly-climax theory** : This theory was advanced by Tansley (1935). According to him, a climax reflects not only the climatic factors but also other factors of the environmental complex viz., edaphic, biotic etc. The climax can be of several other kinds which are different from the climatic climax of the area. They can be edaphic climax (soil factors are dominant), physiographic climax (physiographic factors dominant), fire climax (fire tolerant species only) and zootic climax (when retrogressive succession caused by the grazing of the herbivore animals leads to community in equilibrium with herbivore pressure).

### 1.7. KINDS OF SUCCESSION (SERES)

The succession of plants can be classified into two kinds on the basis of the nature of the habitat :

(A) **Hydrarch** : Succession takes place in water area *i.e.*, from hydric to mesic conditions. It is of two types :

- (a) **Hydrosere** : Succession starts in ponds, pools, lakes and marshes.
- (b) **Halosere** : Succession starts in saline water.

(B) **Xerarch** : Succession takes place in drier area *i.e.*, from xeric to mesic conditions. This can be of two types :

- (a) **Lithosere** : It takes place on bare rocks.
- (b) **Psammosere** : It takes place in a primary sandy area.

### 1.8. HYDROSERE OR HYDRARCH

Ecological succession which begins in ponds, lakes, marshes or elsewhere in water are termed **hydrarch**, and different stages are called **hydrosere**. The various stages and the process which results in the development of climax community are shown in Fig. 1 and may be described as follows :

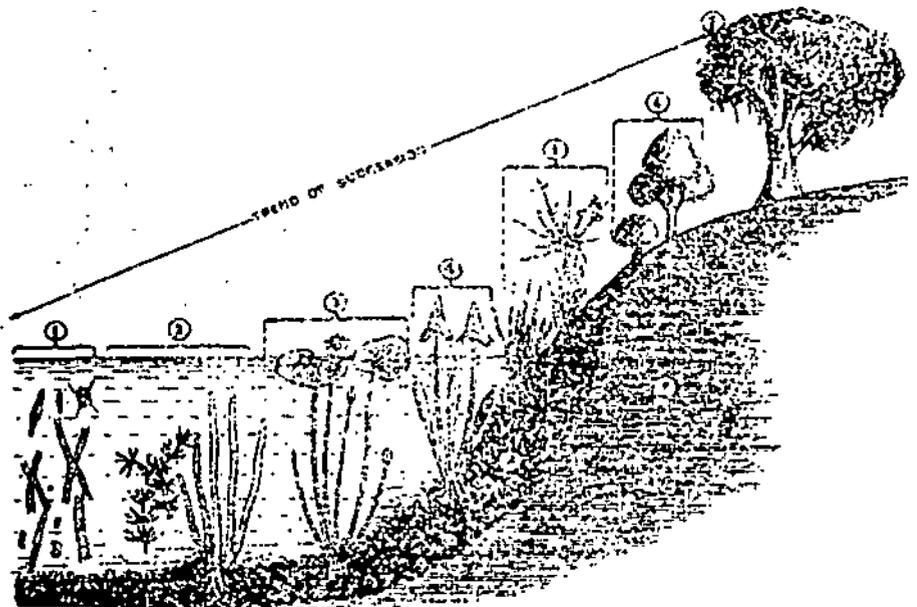


Fig. 1. Diagrammatic representation of different plant communities in hydrosere.

1. **Photoplankton stage** : In the initial stage the water is poor in nutrients and devoid of much life. The water is incapable of supporting larger life forms. The

unicellular and colonial planktonic forms (some blue green algae, diatoms, bacteria, animals like *Paramecium*, *Amoeba* etc.) are the first invaders and hence it may be called the **phytoplanktonic stage**. These algae add larger quantities of the organic matter and nutrients are brought with the dust blown by wind. With the death of phytoplanktons and animals depending upon them the population of decomposing organisms like bacteria and fungi increases in the pond mud. Decomposition results the release of nutrients and enrichment of aquatic habitat. The rich mud now supports the growth of some rooted hydrophytes.

**2. Rooted submerged hydrophytes :** The rooted submerged hydrophytes are *Vallisneria*, *Ceratophyllum*, *Potamogeton*, *Utricularia*, *Myriophyllum*, *Hydrilla* etc. After the death and decay of these plants, their remains sink to the bottom where they form humus. This humus binds the soft muddy soil. They also help in depositing soil particles at the bottom. As a result of these reactions the water becomes shallow and the habitat become unsuitable for submerged plants. This new habitat now replaces these plants giving way to another types of plants which are of "floating types".

**3. Rooted floating plants :** These plants are rooted hydrophytes with their large leaves, floating on water surface. *Nymphaea*, *Nelumbo*, *Trapa*, *Monochoria*, etc. are the common examples of this type. Gradually, with evaporation of water the concentration of nutrients increases and becomes sufficient to support free floating genera like *Azolla*, *Lemna*, *Wolffia*, *Pistia*, *Spirodella*, *Eichhornia*, *Salvinia* etc. They gradually cover the water surface. The submerged plants therefore, cannot get direct sunlight and these must migrate into deeper water for their survival. The decomposing mass of the dead plants of these species and the water-borne soil are deposited together to build up the substratum at the bottom. In few years the rapid solid building process reduce the water depth to such an extent that it becomes too shallow for the survival of the floating species. The floating species disappear, giving way to the reed-swamp plants particularly on the shore ward margin of the floating plant zone.

**4. Reed-swamp stage :** It is also called the **amphibious stage**. The important plants constituting this stage *Typha*, *Scirpus*, *Phragmites*, *Sagittaria*, *Pontederia*, *Rumex* etc. These plants cut off the light from the floating plants, in this way make the habitat still more unsuitable for them. These plants have large much branched rhizomes. The vegetation is very dense and therefore, it helps in accumulating sedimentary materials and plant remains. The water depth is further decreased and the habitat becomes unfavourable for the amphibious species.

**5. Sedge-meadow stage (Marginal mats) :** This stage includes hydrophytes or water loving plants. The substratum at this stage is hardly covered by 1-2 feet deep water so to say the soil becomes marshy. Numerous species of sedges as *Juncus*, *Carex*, *Eleocharis*, *Polygonum* etc. colonise the area. They form a mat like vegetation towards the centre of the pond with the help of their much branched rhizomes and slender copious roots. Many species of herbs like *Mentha*, *Caltha*, *Campanula* etc. are also found intermixed with sedges. As a result of high rates of transpiration, the sedge-meadow becomes too dry for these water loving plants to thrive. Under these circumstances, they are gradually replaced by species of another community.

**6. Woodland stage :** If the climate is dry then the former stage produces a grass-land but under moist climate woodland is formed containing certain shrubs (*Salix*,

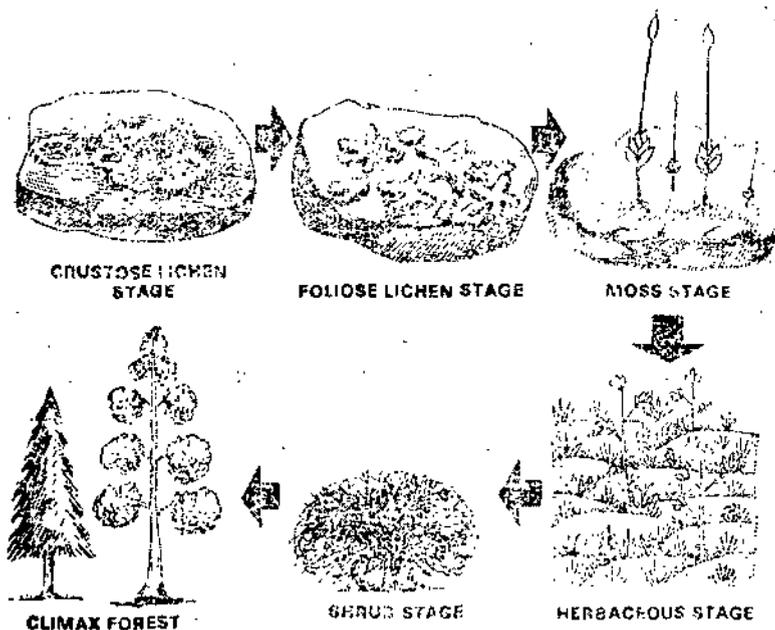
*Cornus* etc.) and small trees (*Populus, Alnus* etc.) These plants by their reactions make the soil unsuitable for them. With this large amount of humus, bacteria, fungi and organisms accumulate in the soil. All this favours the arrival of new tree species in the area and leading to the climax stage.

**7. Climax stage or forest stage :** The nature of the climax is dependent upon the climate of the region. In tropical regions where rainfall is high dense rain forests develop. In temperate regions mixed forests of *Quercus, Hicoria, Ulmus* etc. or coniferous forests are formed. In regions of moderate rainfall, deciduous forests or monsoon forests are formed.

### 1.9. XEROSERE OR XERARCH

Succession initiated on bare rocks, sand dunes, rocky slopes etc., where there is extreme deficiency of water are termed xerarch and different stages of development are collectively called xeroseres. In this type of succession following sequential sages are met within (Fig. 2).

**1. Crustose lichen stage (Pioneer stage) :** The pioneers on a primary bare area on the land are usually simple organisms which can live on bare rocks. Due to great exposure of the sun and extreme deficiency of water and nutrients on the bare rock, only a few plants are able to grow. The most successful to these are lichens (*Rhizocarpon, Rinodnia, Lecidea* and *Lcanora* etc.). The carbonic acid produced by the metabolic activities of these lichens help to corrode and decompose the rock supplementing the other forces of weathering. The dead organic matter of lichens becomes mixed with the dust and small particles of rocks and provide space for foot hold and growth conditions for higher life forms like foliose lichens and mosses.



**Fig. 2. Diagrammatic representation of different plant communities in xerosera.**

**2. Foliose lichen stage :** This community includes species of *Parmelia, Dermatocarpon, Umbilicaria* and others. These lichens have large leaf like thalli which overlap the crustose lichens. The latter are thus cut off from direct light. This result in death and decay of crustose lichens. Foliose lichens retains more moisture and produce

more organic matter which helps in the further build up of substratum. The rocks are also eaten up by the acids secreted by the living and the decaying plants. The weathering of the rocks and the rapid addition of humus to it result in the formation of a thin layer of soil above the rough surface of the rocks and thus, this change in habitat opens up avenues for the growth of xerophytic mosses.

**3. Moss stage :** These are commonly the species of *Tortula*, *Bryum*, *Barbula*, *Funaria*, *Polytrichum*, *Hypnum* etc. The rhizoids of mosses and foliose lichens compete for water and nutrients, and the stems of the former attain greater height than the latter. The mosses increase the amount of soil. By their death and decay a mat may be formed on the rock surface. The thick mat of humus and mineral particles not only provide the rooting medium for higher plants but also make available plenty of nutrients and water.

**4. Herb stage :** The soil formed in the moss stage favours the growth of various xerophytic herbs, specially short lived annuals. These annuals are replaced by biennials and perennial forbs and later xerophytic herbs make their appearance. It consists of plants like *Poa*, *Sporobolus*, *Lindenbergia*, *Adiantum*, *Asplenium*, *Cheilanthes*, *Actiniopteris*, *Justicia* and *Tridax* etc. The number of roots increases and the weathering of the rocks continues. The humus and nutrients accumulates in the soil. The soil is shaded and the xeric conditions like high temperature extremes and high evaporation rate are decreased and the humidity is increased. The arrival of animals (insects, nematodes and larger animals) also modifies the environment. Thus, habitat shows a gradual change and favours the next stage.

**5. Shrub stage :** The common shrubs (*Zizyphus*, *Capparis*, *Zygophyllum*, *Rhus* etc.) may start from seeds or invade from adjacent areas by rhizomes. The soil is further enriched by the dense shrubs growth. The shade of shrub also check evaporation of water from soil. The roots may penetrate into the rocks and their cervices; more organic matter is produced, soil becomes mature and the species diversity of both flora and fauna increase. The temperature extremes are no more noted and the humidity is maintained under the shrubs and in the soil. All these favour the growth of seedlings of trees which starts invading the area.

**6. Climax forest :** This stage is to be determined again by the climate. In dry climates, the weathering is slow and only a small layer of soil formed. Further, the dense growth of trees requires sufficiently high rainfall, and therefore, the climax may comprise small trees those of *Acacia*, *Prosopis*, *Boswellia* etc. In moist and wet climates dense forest develop as climax communities. In temperate regions the same forest community will develop but different species would occur as conifers, oaks and maples etc.

The above account indicates clearly that the one time barren area of rocks which had only crustose lichens in the early stages, has now changed into a fully developed thick forest of big trees which represent the climax stage of the plant succession in xeric conditions.

## 1.10. ECOLOGICAL CONCEPT OF SPECIES

The species is the smallest unit of taxonomic classification, referring for the most part to a group of individuals capable of breeding themselves. The genetic setup in the species itself is dynamic as by small predictable changes by mutation and hybridization

at produces very large number of variants. During the early part of nineteenth century it became clear that a species commonly includes genetically distinct races. **Turreson (1922)** made extensive cultural work on a number of species collected from different parts of their distributional geographical area. He made a series of population samples (20 or more individuals) from various path of the species area and grew them in uniform conditions in his experimental garden at Akarp in Sweden. He noted the reactions of the plants in cultivation over the years in terms of habit, height, flowering time etc. and found that in some cases the differences noted between populations in the field disappeared, in other cases show integradation, but in most cases persisted. On the basis of such studies he could put forward a new concept of **gene ecology**. On the basis of his experimental studies **Turreson (1922)** proposed the following classification of plants :

**1. Ecads :** (*Syn.* Ecophenes, habitat forms, environmentally reduced variations)

These are the plants which show variation in the size of vegetative parts (number of leaves, stems, flowers and growth habit etc.) but belong to the same genetic stock *i.e.*, they all are genetically similar. These variations are temporary, somatic and reversible. When different ecads are transplanted into the same-habitat, all would become similar in appearance *e.g.*, *Euphorbia hirta*. There are present two ecads of this species, one growing in dry hard soils (prostrate type) and the other along the foot paths under trampling (prostrate compact type). But both the ecads show no variation when grown in the same habitat.

**2. Ecotypes :** (*Syn.* Ecological races or physiological races):

According to **Turreson (1922)** an ecotype is “the product arising as a result of genotypical response of an ecospecies to a particular habitat.” Thus, the ecotypes are the ecological races in which the variations associated to certain factor of environment are genetically fixed *i.e.*, if we grow such races under the same environment, the variation will remain as such.

One of the earlier studies in India showed that the two closely related species of *Lindenbergia* namely *L. polyantha* and *L. urticaefolia* were not two distinct species but only two ecotypes of the same species (**Misra and Sivarao, 1948**). An another study **Rama Krishnan (1958)** showed that the two populations, red and green in colour, of *Euphorbia thymifolia* were two ecotypes which had their distribution related to the exchangeable calcium content of the soil. The red ecotype is a facultative calcicole *i.e.*, it grows in calcium rich soil but may also occur in calcium deficient soil. On the other hand, the green ecotype is an obligate calcifuge and cannot grow in calcium rich soil. All the combinations of green and red colour could be observed in hybrids. In the earlier studies on *Potentilla* and *Achillea*, ecotypes in relation to altitude are described (**Clausen, 1948**).

**3. Ecospecies :** It is an unit of classification which contains one or more ecotypes, which although interfertile but do not cross or atleast do not produce viable offsprings, if crossed with ecotypes of other ecospecies.

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### 1.11. SUMMARY

Succession may be defined as, “an orderly sequence of communities of organisms over a period of time at the same place”. Odum, 1971 calls it as an

orderly process of community development. The succession is of several types. It may be primary, secondary, autotrophic, heterotrophic or autogenic or allogenic. The succession may be initiated due to physiographic factors such as erosion, deposition, submergence or emergence, due to the climatic factors such as wind, water, snow, hail, fire or drought or due to biotic factors such as animals, human beings or microorganisms. The processes for succession are migration, ecesis, aggregation, competition, and reaction. The stabilization occurs when the community is best adjusted with the climate. The plant succession, therefore occurs through several stages such as nudation, migration, ecesis, aggregation, competition, reaction and stabilization. The nudation occurs due to erosion, deposition, wind, water, gravity, slipping of glaciers, fire, lightening, volcanic activity, grazing or human activities. The migration occurs by the act of dispersal of seed or spores. The establishment of species through the act of germination is called as ecesis. They multiply as a result of reproduction (aggregation), and thus new species invade. The competition may be interspecific or intraspecific. The effect of individuals of species on each other is called as coaction. The organisms, thus modify the environment (reaction). The sequence of communities in a locality is called as sere. The final seral community which has best adjustment with the climate stabilizes. This is called as climax community and the stage as climax stage.

According to Clement's, 1916 monoclimax hypothesis, the succession is an orderly process whose direction can be predicted. The climate causes stabilization. Tansley, 1935 proposed the polyclimax hypothesis and identifies topographic, edaphic and biotic climax separately.

The plant succession in a lake or pond (hydrosere) occurs through several stages namely phytoplankton stage, submerged stage, floating stage, reed-swamp stage, sedge-meadow stage, woodland stage and forest stage. The phytoplanktons (algal forms) are the pioneers in a hydrosere. This is followed by the appearance of submerged plants like *Hydrilla*, *Ceratophyllum* etc. When some humus is collected, floating plants (*Nymphaea*, *Lemna* etc.) are introduced. Further reduction in pond depth causes appearance of amphibious plants (*Scirpus*, *Typha* etc.). Increased transpiration causes further shallowing of the pond and plants like *Carex*, *Cyperus* etc. appear (sedges). The drying of the soil invites a community of rhizomatous woody plants (*Salix*, *Populus* etc.). The woodland stage is replaced by a mesophytic forest representing the climax stage. The plant succession on bare rock (lithosere) occurs through the stages like crustose lichen stage, foliose lichen stage, moss stage, herb stage, shrub stage and forest stage. The crustose lichens (*Rhizocarpon* etc.) are the pioneers in a lithosere. They corrode the rock by acid action and form the soil. They are replaced by foliose lichens like *Parmelia* etc. Further corrosion or rock builds up more soil. The foliose lichens are replaced by xerophytic mosses like *Polytrichum*, *Grimmia* etc. When better substratum has been built by mosses, the herbs invade and plants like *Poa*, *Aristida*, *Tridax* etc. appear. The herb stage is replaced by shrubs like *Zizyphus*, *Capparis* etc. when more organic matter decays, the xerophytic trees invade. They are replaced by mesophytic trees which constitute the climax vegetation comprising plants like *Acer*, *Abies*, *Acacia*, *Prosopis* etc.

On the basis of experimental studies Turreson (1922) classified the plants into ecads, ecotypes and ecospecies. Ecads show variation in the size of vegetative parts but belong to same genetic stock. These variations are temporary and reversible. Ecotypes are the ecological races in which variations are genetically fixed. Ecospecies is unit of classification which contains one or more ecotypes.

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### 1.12. TEST YOURSELF

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1. Write the correct sequence of events occurring during ecological succession.
2. In hydrosere which stage is the pioneer stage ?
3. Who advanced the monoclimal theory ?
4. Name the succession which takes place in a primary sandy area.
5. What is nudation ?
6. Write the topographic processes which cause succession.
7. What that succession is called in which succession community themselves modify the environment, suitable for another community.
8. What those plants are called which show variation in their vegetative parts but belongs to the same genetic stock ?

### ANSWERS

1. Nudation → migration → ecesis → aggregation
2. Phytoplankton stage
3. Clements (1916)
4. Psammosere
5. Development of a bare area without any form of life.
6. Erosion, deposition
7. Autogenic succession
8. Ecads.



# UNIT - II

## PLANT PHYSIOLOGY

### PLANT-WATER RELATIONS

#### STRUCTURE

- Introduction
- Permeability
- Diffusion
- Osmosis
- Plasmolysis
- Osmotic relations of plant cell
- Concept of water potential
- Imbibition
- Student activity
- Summary
- Test Yourself
- Answers

#### LEARNING OBJECTIVES

By learning this chapter you will be able to know about permeability, diffusion, osmosis, imbibition, osmotic relations of plant cell and about concept of water potential.

#### 1.0. INTRODUCTION

Water is essential for all the physiological activities of the plant and plays a very important role in all living organism *e.g.*,

- Major portion of the plant body is water.
- Framework of the colloidal structure of protoplasm.
- It is the most useful solvent. It can keep many organic and inorganic compounds in solution, and enables such substances to be transported within the plant.
- Terrestrial plants evaporate water in the air through the process transpiration.
- Maintains the turgidity and shape of plant organs.
- Necessary in photosynthesis and respiration.
- Important in seed and spore germination and cell growth.

To comprehend plant-water relations an understanding of certain standard terms is necessary. These are :

#### 1.1. PERMEABILITY

In osmotic relations of plant cell we take ectoplast to be semipermeable membrane, but the presence of mineral salts in the plant cells clearly show that the substances pass through it. This ability of protoplasm to allow the diffusion of dissolved substances through it is known as **permeability**.

Plasma membrane is permeable to some solutes and impermeable to others, so it acts as a **selectively or differentially permeable membrane**. Mostly it is impermeable to organic substances and permeable to inorganic ones. The permeability of protoplasm

changes from time to time. It may be permeable to some substances at one time and may be impermeable at other time.

It is seen that the substances that enter the protoplasm, sometimes do not reach the vacuole. It is due to the difference in the permeability of the ectoplast and tonoplast (a substance permeable to ectoplast may be impermeable to tonoplast). The contents of vacuoles of the same cell are also found to be different. This is also due to the difference in the permeability of their respective tonoplasts.

### Theories of permeability

Various theories from time to time have been put forward to account for the differential permeability of the cell membranes :

**1. Sieve or ultrafiltration theory of Traube (1867) :** According to this theory the plasma membrane is like a sieve or ultra-screen allowing the molecules below a certain size to pass through it and checking the passage of bigger particles.

This theory has to face a great objection that the plasma membranes are permeable to the large molecules of alkaloids while they are impermeable to smaller molecules of amino acids.

**Solutions of Lipoid theory :** Proposed by Overton in 1895. The lipoids form a constituent of the plasma membrane together with protein. According to Overton only the substances soluble in lipoid can pass through the membrane.

Objection to this theory is that a large number of inorganic substances insoluble in lipoid pass easily through the membrane.

**2. Chemical combination theory :** According to this theory the membrane is made up of those substances to which it is permeable. The reaction is taken to be reversible so that the diffusing substance be freed on the other side from its combination with the membrane.

**3. Colloidal theory :** The protoplast is regarded as polyphase, emulsoid, colloidal system. Its permeability has been explained by Lloyd in 1915 and Free 1918, on the basis of changes in viscosity, phase inversion or electrical reactions which are common phenomenon in colloidal system.

Sphaeth (1916), Clowes (1916) and Kaho (1921) also supported this theory with certain modifications.

**4. Mosaic theory :** by Nuthansohn (1904). The plasma membrane is a Mosaic consisting of — (1) an aqueous phase, which allows the passage of water soluble substances, (2) a lipoid phase through which fat soluble matters can pass.

No single theory can adequately explain the behaviour of protoplasmic membranes but as protoplasm changes its properties rapidly with environmental changes, any one theory may explain its behaviour for one particular conditions.

### Factors affecting permeability

**1. Light :** Permeability increases with the increase in light.

**2. Concentration of external solution :** More concentrated solution decrease the permeability.

**3. Accumulation of proteins in the cytoplasm increases the permeability.**

**4. Temperature :** The permeability is at its optimum at 35°C. Above or below it the permeability decreases.

**5. Nature of solutes :** The permeability of a membrane also depends upon the nature of solutes passing through it.

### 1.2. DIFFUSION

The movement of molecules of substances from higher concentration to low concentration is called as **diffusion**. This process is involved in the movement of

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(b)

substances into or out of the plants and also in the movement from one place to the other within the plant. It can be studied under two main heads.

**1. Diffusion of Gases :** If a bottle of ammonia, peppermint oil or any volatile substance with characteristic odour is opened in one corner, the odour can be detected in all parts of the room within a short time. This dispersal of gas molecule is due to diffusion, though also assisted by air current.

The rate of diffusion of a substance is influenced by the presence of molecules of other substances. If we open one vial of bromine under a bell jar full of air and the other, under the evacuated bell jar, we find that bromine fills in the later one earlier than the former one. If we increase the pressure of air in the bell jar, the rate of diffusion will be further decreased.

The particles remain in constant motion because of their kinetic energy. They move in straight lines, if remain uninterrupted. Since numerous molecules are moving, they collide with one another and as such the direction of movement is changed. Thus, due to these collisions and the change in the direction of movements of the particles, the diffusion takes place in all the directions, from a region of higher concentration to that of lower concentration. Even when the concentration throughout the area becomes equal, the movement of particles continues, but now equal number of particles are moving in both the directions. To such condition we call as **dynamic equilibrium** and not diffusion.

The process of diffusion results in the development of a pressure called **diffusion pressure**. The temperature remaining constant the diffusion of a gas is directly proportional to its concentration or the diffusion of molecules of a gas depends upon the differences in the **partial pressure** or the diffusion pressure exerted by that gas in different directions. Thus, the diffusion of gases is the net movement of molecules from a region of their greater diffusion pressure to the region of their lesser diffusion pressure. It may be further recalled that the direction of movement of a gas is controlled mainly by its own difference in diffusion pressures and is not influenced by either the direction or the rate of diffusion of other substances.

#### Factors influencing the rate of Diffusion of Gases

**(A) Density of the Gas :** The relative speeds of diffusion of gases are inversely proportional to the square roots of their relative densities ('Graham's law of diffusion'). The relative density means the weight of a given volume of gas as compared with the weight of some volume of hydrogen. The density of hydrogen being one, that of oxygen is 16. Thus, the rate of diffusion for hydrogen is  $1/\sqrt{1}$  and for oxygen  $1/\sqrt{16}$ . Hydrogen will diffuse as rapidly than four times oxygen under the same temperature and pressure.

**(B) Temperature :** The speed of diffusion increases with the rise in temperature. It is because of the increase in the kinetic energy of the molecules.

**(C) Diffusion pressure gradient :** The rate of diffusion is directly proportional to the difference in the diffusion pressures, but is inversely proportional to the length of the diffusion path. These two factors are the components of what may be called is **diffusion pressure gradient** which is equivalent to the difference between the diffusion pressures between the delivering and receiving ends of the diffusion system divided by the length of the distance between the two.

**(D) Concentration of the medium through which diffusion occurs :** The rate of diffusion becomes slower, if we increase the concentration (no. of molecules per unit area) of the medium through which the diffusing molecules must pass.



Fig. 1. Diffusion of a solid in water.

**2. Diffusion of solutes :** Introduce a crystal of potassium permanganate, or some other compound which is coloured, when in solution, into the bottom of a large beaker filled with water. This beaker is kept at constant temperature. The gradual change in the colour of the solution, indicate the diffusion of molecules or ions in the water. This is because of the fact that the molecules or ions of a solute possess sufficient kinetic energy to move from one place to the other within the limits of solution.

The direction of the diffusion of any solute occurs in accordance with its own difference in diffusion pressures, regardless of the direction or rate of diffusion of other substances in the same system.

The rate of diffusion of solutes together with temperature and diffusion pressure gradient, is also influenced by :

**(A) Size and Mass of diffusing particles :** Smaller molecules or ions diffuse more rapidly than larger ones. Similarly ions with less of water bound to them diffuse more rapidly than highly hydrated molecules.

**(B) Solubility :** The diffusion of a substance is directly proportionate to its solubility in the liquid.

6 (b)

### 1.3. OSMOSIS

When a solution and its solvent\* or two solvents of different concentrations are separated by a semipermeable membrane, the diffusion of solvent or water to the solution of higher concentration is called osmosis.

Membranes usually are of three types : (1) **Impermeable membranes**, are those through which neither the solute nor the solvent pass through e.g., rubber piece, (2) **Permeable membrane** allow the passage of both the solvent and the solute particles dissolved in it e.g., filter paper or cellulose cell wall and (3) **Semipermeable membrane** allow only the solvent particles to pass through it. The solute particles are not allowed to diffuse e.g. sheep's bladder, cell membrane etc. Truly semipermeable membranes are rare and usually some diffusion of the solute also takes place. Such membranes are, therefore preferably called as **differentially or selectively permeable membranes**.

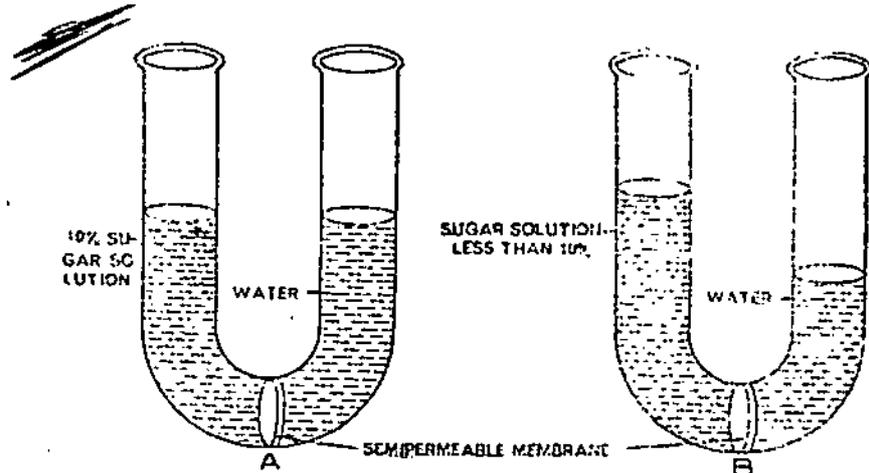


Fig. 2. Diagram showing Osmosis—(A) Initial stage, (B) Final stage.

Fix a semipermeable membrane in the centre of a U-shaped tube. The left limb of the tube is partly filled with water and the right limb is filled with equal volume of 10% sugar solution. After some time the level in the right limb rises and in the left limb falls down. It is because the membrane is freely permeable to water molecules, and is almost impermeable to sugar molecules. In this case actually the diffusion of the water

\* In plants movement usually takes place of water or substances dissolved in it, so in our discussion water is taken as the solvent.

molecules takes place both — ways across the membrane but the diffusion is more from the water to the sugar solution. The water in the left limb is 100% while in the right limb it is 90% water. Thus, it is the diffusion of water (solvent) from the region of its higher concentration to the region of its lower concentration. This diffusion of water (solvent) through a semipermeable membrane is called osmosis.

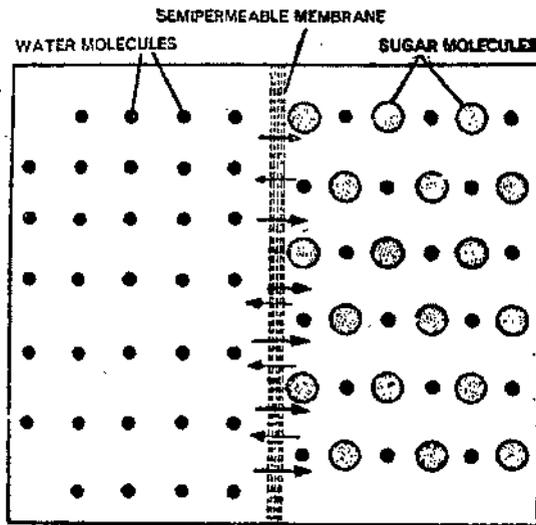


Fig. 3. Diagram showing osmosis. The wider arrows indicate faster diffusion of water molecules.

The diffusion of solvent particles into a living cell or structure because of the latter's higher concentration (hypertonic solution) is called endosmosis. Conversely, the diffusion of the solvent out of a living cell or structure because of lower concentration (*hypotonic solution*) is called *exosmosis*. The three terms hypotonic, hypertonic and isotonic are not absolute values but are relative terms as depicted in Fig. 4.

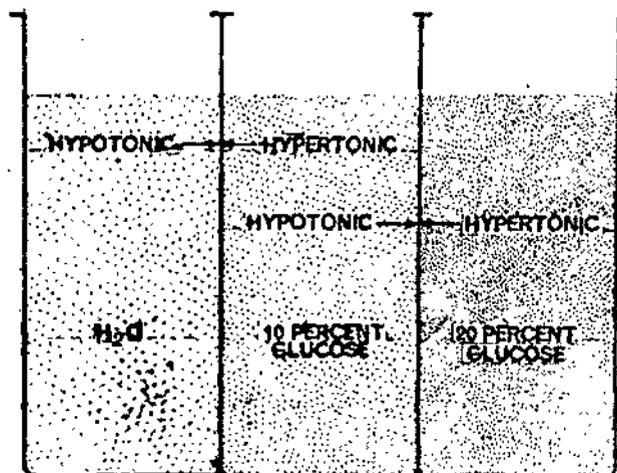


Fig. 4. The diagram showing the relationship of a hypotonic and a hypertonic solution.

Osmotic quantities are measured in terms of atmospheric pressures or in bars (a unit of metric system : 1 atm. = 1.01 bars). Vant's Hoff's equation relating the osmotic pressure to the concentration of the solution is expressed as :

$$\pi V = n_s RT$$

When  $\pi$  is osmotic pressure in bars or atmospheres,  $V$  is the volume of solvent,  $n_s$  the moles of solute,  $R$  is the gas constant (0.0820 litre atm/degree mole), and  $T$  is the absolute temperature. One mole of solute in 1 litre of solvent at 273°C gives a volume of  $\pi$  of 22.4 atm. or 22.7 bars. This equation is applicable only to nonelectrolytes.

**Table 1 : Osmotic potentials (bars of solutions of given molar and molal concentrations at 20°C**

Conc.	Molar Sucrose	Molal Sucrose	Molar NaCl	Molal KCl
0.1	-2.7	-2.6	-4.4	-4.7
0.2	-5.4	-5.2	-8.5	-8.9
0.3	-8.2	-7.7	-12.6	-12.8
0.4	-11.2	-10.2	-16.8	-16.9
0.5	-14.5	-13.0	-21.2	-20.8
0.6	-18.0	-15.6	-26.0	-24.4
0.7	-21.7	-18.3	-30.1	-28.7
0.8	-25.8	-21.1	-34.7	-32.6
0.9	-30.1	-24.0	-39.1	-36.4
1.0	-35.1	-26.9	-43.8	-39.7

A molar solution contains 1 g molecular wt. 1 litre of solution.

A molal solution is 1 g molecular weight + 1000 g of water.

**Role of Osmosis :** Osmosis has some very important roles to play in plant metabolism such as :

1. Plants absorb large amount of water from the soil through the root hairs by the process of osmosis.
2. It also helps in the movement and distribution of water across the cells of the plant.
3. The osmotic diffusion of water helps in maintaining the turgidity of plant cells and thus, helps in maintaining the shape of various plant organs.
4. It also helps in maintaining the turgidity of guard cells which regulates the opening of stomata.
5. Growth of the young cells is brought about by the osmotic pressure and turgor pressure of these cells.
6. High osmotic concentration increases the resistance of the plant to freezing temperature and desiccation.

**Osmotic pressure :** The term was originally employed to designate the maximum pressure which develops in a solution enclosed within an osmometer under certain ideal conditions. These being, (i) membrane be permeable to solvent only, (ii) that it be immersed in pure solvent and (iii) pressure equilibrium be attained without any appreciable dilution of the enclosed solution. The osmotic pressure may also be called as the rating of the potential maximum pressure which can be developed in the solution as a result of osmosis or it may also be recalled as an index of the diffusion pressure deficit of the water in a solution in so far as this results from the presence of solutes. It may be defined as "the pressure which is developed in a solution, when it is separated from its pure solvent by a semipermeable membrane and enclosed in a rigid vessel."

**Turgor Pressure (T. P.) :** Turgor pressure is the actual pressure which develops in a closed osmometer or plant cell as a result of osmotic diffusion of water or imbibition. During endosmosis the turgor pressure increases and when it has reached its maximum, it is equal to osmotic pressure.

**Wall Pressure (W. P.) :** Due to turgor pressure rigid cell wall offer resistance. This resistance which works in a direction opposite to the turgor pressure but is equal in strength to turgor pressure is called as **wall pressure**.

$$W. P. = T. P.$$

**Diffusion Pressure Deficit (D. P. D.) or Suction Pressure (S. P.) :** Every liquid has a diffusion pressure. The diffusion pressure of pure solvent is always more than that of its solution *i.e.*, if a solution of sugar or NaCl is prepared in water the diffusion pressure of water will be more than that of solution. The amount by which the diffusion pressure of a solution is lower than that of its solvent is called **Diffusion Pressure Deficit**. DPD is the index of absorbing power of a solution. It is also called **suction Pressure**.

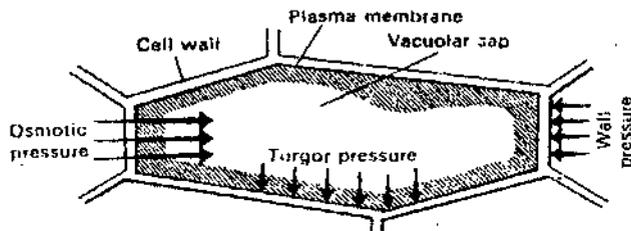


Fig. 5. A cell showing turgor pressure, wall pressure and osmotic pressure.

#### PLASMOLYSIS

When a cell is kept in a hypertonic solution, water begins to pass out of the cell due to exosmosis. The volume of vacuole gradually decreases and also the pressure exerted by the cytoplasm on the wall decreases, the cytoplasm leaves the cell wall and starts shrinking. Gradually it comes to lie in the centre. The vacuole is further reduced and finally be broken into smaller vacuoles. This **shrinking of cytoplasm due to exosmosis is called plasmolysis**.

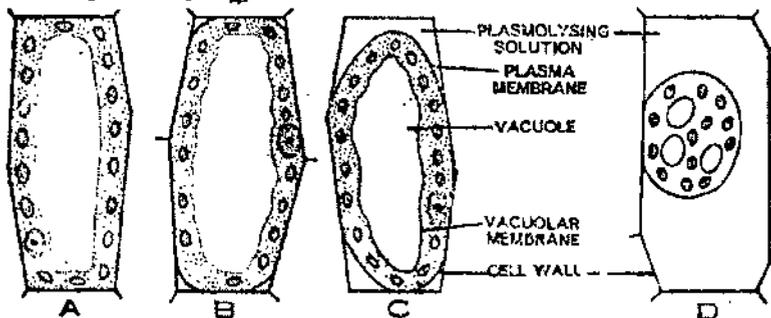


Fig. 6. Plasmolysis. A. turgid cell B-D, cell placed in hypertonic solution of cane sugar.

The space between the cytoplasm and the cell wall is filled with the hypertonic solution. The process of plasmolysis continues till the equilibrium is reached between the cell sap and the outer hypertonic solution.

Due to plasmolysis metabolic activities of the cells, are retarded and may result in permanent wilting of plant parts. This is what happens when the soil in which the plant is growing, is irrigated with a concentrated solution of common salt. Plants affected by plasmolysis turn brownish-black and are called as 'burnt'. Burning may also be caused by the application of excessive chemical fertilizers or fungicides or insecticides. The advantage of plasmolysis is that the salting of meat and fish and the addition of sugar to jams and jellies plasmolyses bacteria and fungus spores which could spoil them. Weeds and other unwanted plants are also killed by salting the soil.

The plasmolytic method is made use to find out the approximate osmotic pressure of the cell and also to know whether the cell is living or not.

#### Plant cell as an osmotic system

Each plant cell has a sap contained in the vacuole. It is the aqueous solution of salts, sugars and organic acids with a fairly high osmotic pressure. It is enclosed in a plasma membrane which acts as the semipermeable membrane. Both ectoplast and tonoplast are the semipermeable membranes. The cellulose cell wall however, is a

permeable membrane. A plant cell is in contact with either the watery environment or with other cells containing water. It may therefore, absorb or loose water by osmosis.

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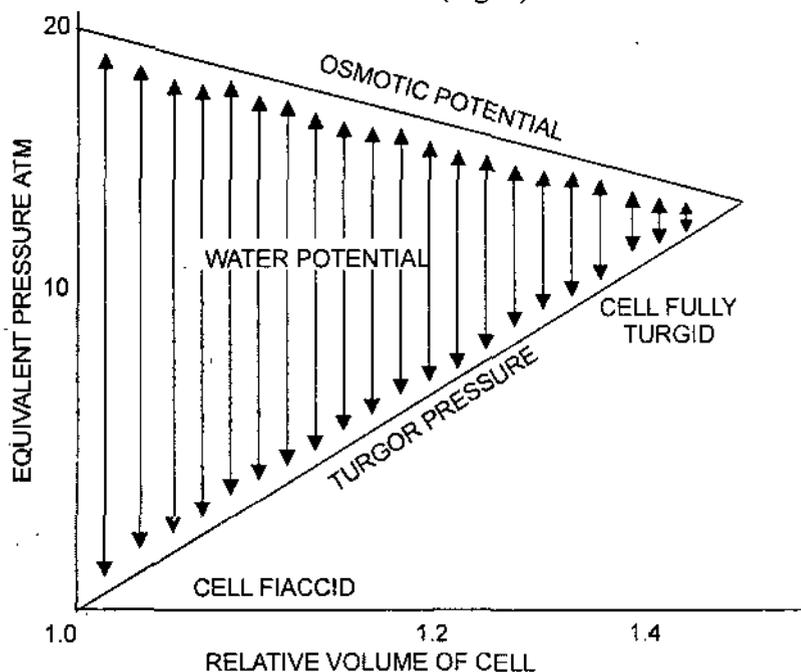
**1.5. INTERRELATIONSHIP OF OP, TP (WP) AND DPD (SP) Or OSMOTIC RELATIONS OF PLANT CELL**

When a plasmolysed cell is placed in water, inward diffusion of water takes place due to endosmosis and the size of vacuole gradually increases. The cell finally attains normal distended position. This phenomenon is called **deplasmolysis**. The force with which water is drawn inwards is equal to the osmotic pressure of the cell sap. The entrance of water into the cell sap increases the volume of the cell sap which stretches the cytoplasm which presses the cell wall and the cell becomes **turgid**. The hydrostatic pressure with which the cytoplasm presses the wall is called **turgor pressure**. The cell now can be compared with an inflated football. The turgor pressure is often so great that it would burst the cytoplasm if it were not for the cell wall. The cell wall, being elastic, tends to turn to its original position and thus exert counter pressure on cytoplasm called **wall pressure**. The value of the wall pressure at any moment in a turgid cell is equal to turgor pressure and it tends to throw the water out of the cell.

The net force with which water is drawn into the cell, **suction pressure** or **diffusion pressure deficit** is the difference between the osmotic pressure of the cell sap and the wall pressure. The wall pressure is equal to turgor pressure in a turgid cell. The relation between suction pressure (SP), osmotic pressure (OP), wall pressure (WP) and turgor pressure (TP) will thus be :

$$\begin{aligned} \text{As } & \text{SP} = \text{OP} - \text{WP} \\ & \text{WP} = \text{TP} \\ & \text{SP} = \text{OP} - \text{TP} \end{aligned}$$

The decreasing effect of increasing turgor pressure on the suction pressure or diffusion pressure deficit of the cell is shown in (Fig. 7).



**Fig. 7. Diagrammatic interrelationships of osmotic pressure, turgor pressure, diffusion pressure deficit and volume of the cell.**

In plasmolysed cell the value of TP being zero, suction pressure equals to osmotic pressure and at turgid condition the suction pressure becomes zero as the turgor pressure becomes equal to osmotic pressure.

The entry of water from one cell to the other depends upon the suction pressure of the cell and not on the osmotic pressure, is clear from Fig. 8. Where the entry of water takes place from cell A to B though the OP is more in cell A.

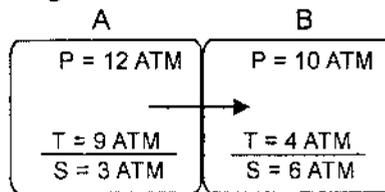


Fig. 8. Diagram showing the movement of water from one cell to the other.

## 1.6. THE CONCEPT OF WATER POTENTIAL

According to principles of thermodynamics every component of a system possess **free energy**\* which is available for conversion to work under constant temperature conditions. In fact **the basic driving force in osmosis is difference in the free energy of the water on the two sides of the membrane.**

To understand water movement in plants we are concerned with free energy present in a specified number of molecules in one condition compared to their free energy after undergoing some change. The free energy per mole of any particular chemical species in a multicomponent system is defined as the chemical potential of that species. The larger the chemical potential of a substance, the greater will be its tendency to undergo chemical reactions, and other processes such as diffusion. The chemical potential of water is a property of considerable importance to our understanding of water and its movement in the plant and the soil. Chemical potential of water is also called water potential and is given value of zero at the prevailing temperature and atmospheric pressure. If water potential differs in various parts of a system, water will tend to move from point of higher potential (less negative) to regions of lower water potential (more negative).

If two arms of a tube, are separated with the help of a semipermeable membrane in one arm of which is placed pure water and in the other a sugar solution, water will diffuse into the arm with solution because of a difference in water potential across the membrane. This difference in water potential is due to interaction of water molecules with the solute particles in such a way that the **free energy of water molecules is decreased**. Within a wide range of concentration of solute molecules or ions the diminution in the water potential is closely proportional to the ratio of solute particles to that of solvent molecules. As water accumulates in the sugar solution it becomes more and more diluted, the rate of water movement into the solution slows down accordingly. There is less difference between the chemical potential of pure water and that of solution as the process proceeds.

**The components of water potential :** A typical plant cell consists of a cell wall, a vacuole filled with an aqueous solution and a layer of cytoplasm between the vacuole and cell wall. When such a cell is subjected to the movement of water many factors begin to operate which ultimately determine the water potential of cell sap. For solution such as contents of cells, water potential is determined by three major sets of internal

\* Free energy may be defined by the following equations

$$G = E + PV - TS$$

where  $G$  is free energy,  $E$  is internal energy,  $PV$  is pressure volume product,  $T$  is absolute,  $S$  is entropy (extent of randomness of disorder).

**Internal energy :** Every substance is associated with a definite amount of energy which depends upon its chemical nature, pressure and volume. The chemical nature includes the manner in which molecules are put together, the nature of individual atoms and arrangement and number of electrons and the energy possessed by the nucleus.

factors viz., matric potential ( $\psi_m$ ), solute potential ( $\psi_s$ ) and pressure potential ( $\psi_p$ ). The water potential ( $\psi_w$ ) in a plant cell or tissue can be written as the sum of matric potential (due to binding of water to cell wall and cytoplasm), the solute potential (due to concentration of dissolved solutes, which by its effect on the entropy components reduces the water potential) and the pressure potential (due to hydrostatic pressure, which by its effect on energy components increases the water potential).

$$\psi_w = \psi_s + \psi_m + \psi_p$$

Water component and its components are discussed below as follows :

**Matric potential :** ( $\psi_m$ ) is the term used for the surface (e.g., soil particles, cell wall, cell cytoplasm) to which water molecules are adsorbed. In this case of plant cells and tissues it is usually disregarded because it is not significant in osmosis. Hence the above given equation is written as follows :

$$\psi_w = \psi_s + \psi_p$$

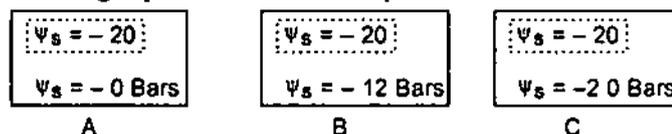
**Solute potential :** ( $\psi_s$ ) Also known as osmotic potential. It is defined as the amount by which the water potential is reduced as a result of the presence of solute. Solute potential is always negative number.

**Pressure potential :** ( $\psi_p$ ) Plant cell is elastic and it exerts a pressure on the cellular contents. As a result of inward wall pressure hydrostatic pressure is developed in the vacuole termed as turgor pressure. The pressure potential is usually positive and operates in plant cell as wall pressure.

**Relationship of Osmotic quantities :** We take three cells A, B and C with zero turgor potential (pressure potential) and with osmotic potential of - 20 bars. Initial water potential will be equal to osmotic potential of - 20 bars as there is no turgor pressure in cell sap. If cell A is kept in water the water potential of cell sap is - 20 bars and that of the water in petridish is zero, the osmosis of water will take place from the petridish into the cell (from higher to lower osmotic water potential). The entrance of water into the cell will increase turgor potential of cell sap. When the value of pressure potential reaches 20 bar its water potential will increase to zero. This is the water potential of pure water present in the dish. Hence an equilibrium is reached when turgor potential of cell sap reaches 20 bars.

Cell B is immersed in a dish with a solution of - 12 bars osmotic potential instead of pure water. The water potential of cell sap of cell B is - 20 bars and that of the solution in the dish -12 bars. There will be a net movement of water into the cell. The cell will develop a maximum turgor pressure of 8 bars. Because the initial water potential of cell sap was - 20 bars the imposition of a turgor pressure of 8 bars reduces this to -12 bars which is the water potential of the surrounding solution. Hence an equilibrium will be reached when turgor pressure is 8 bars.

Cell C is immersed in a solution with an osmotic potential of - 20 bars. The water potential of cell sap is equal to that of the surrounding solution in the dish. Since their osmotic potentials are equal and neither is under any pressure. Hence an equilibrium is attained as soon as the cell is immersed in petridish since there is no net movement of water into the cell, no turgor pressure will develop.



Below given diagram represents the interrelationship amongst Osmotic potential, Turgor potential and Water potential of a plant cell.

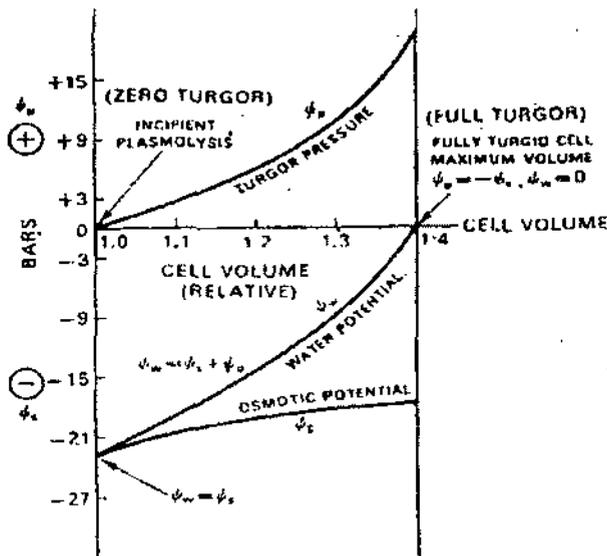


Fig. 9. Diagrammatic relationship of  $\psi_w$ ,  $\psi_s$  and  $\psi_p$  in a cell (Two extreme conditions, plotted on the horizontal axis are zero turgor, (1.0) and full turgor (1.4).

The two extreme conditions plotted on the horizontal axis are zero turgor (1.0) and full turgor (1.4). Zero turgor can be induced experimentally by bringing the cell to a state of plasmolysis and full turgor by keeping the cell in distilled water. Pressure in bars is plotted on the vertical axis. The uppermost curve indicates pressure potential (positive bars) and the lowermost curve osmotic potential (negative bars). The middle curve is water potential of the cell (at any cell volume the value of middle curve may be obtained by adding the value of upper and lower curves).

This figure shows that a cell at zero turgor (*i.e.*, a flaccid cell has a solute potential equal to the water potential). On the other hand a cell at full turgor has a water potential equal to zero bar, its solute and pressure potential are equal but opposite in sign.

Under natural conditions a cell is usually at a state between zero turgor and full turgor. Zero turgor is approached under natural conditions when a tissue is severely wilted. On the other hand the cells of a young leaf of a young vigorous plant growing in well watered soils will approach full turgor when the leaf reaches maximum water content during the early morning hours.

**Osmotic movement of water in adjoining cells :** Let us imagine two cells *A* and *B* in contact with one another. Suppose cell *A* has an osmotic potential of -20 bars and turgor potential of 12 bars and cell *B* has an osmotic potential of -16 bars and turgor potential of 6 bars.

$\psi_s = -20$ bars	$\psi_s = 16$ bars
$\psi_p = 12$ bars	$\psi_p = 6$ bars
$\psi_w = -8$ bars	$\psi_w = -10$ bars
A	B

The water potential of cell *A* would be ( $\psi_w = \psi_s + \psi_p$ ) -20+12 = -8 bars. The turgor potential of 12 bars raises the water potential of cell sap to -8 bars. Similarly the water potential of cell *B* is more negative (-10) than that of cell *A* and therefore osmosis of water molecules will take place from *A* to *B* (osmosis takes place from less negative to more negative water potential). The movement of water will continue until the water potential of two cells are equal. **Thus in the cell to cell movement of water it is the gradient of water potential and not the osmotic potential which governs entry of water molecules into a cell.**

## 1.7. IMBIBITION

Like colloids many other substances such as agar, cellulose, gelatin etc. take large amount of water from the surroundings and swell up. This taking of water and swelling of colloidal and other substances is called **imbibition**. Water is not imbibed in liquid form only, but vapours are also imbibed e.g., swelling of doors, window and other woodwork in rains.

Imbibition is basically a diffusion process as it takes place because of the difference in the diffusion pressures of one liquid in the imbibant and outside. It is believed that phenomenon like capillary, surface tension are also involved in it. There seems to be some **specific force of attraction** between the water (or solution) of imbibant molecules. Dry seeds imbibe water when placed in water or some aqueous solution, but do not do so when placed in ether or other organic substances. A piece of rubber, on the other hand, imbibes ether and not the water.

### Volume changes and energy relations in imbibition

The volume of the imbibant always increases after the imbibition has taken place, but this increased volume is less than the value of the imbibant and the volume of solution imbibed. This is probably because, adsorption is involved in imbibition, because of which the molecules are placed closer due to force of attraction.

Similarly the adsorbed particles loose a sufficient amount of kinetic energy in the system, which can be read as rise in temperature of the system with the help of thermometer.

The rise in temperature increases the rate of imbibition. It is because of the increase in the kinetic energy of molecules. The increase in the osmotic pressure of the liquid decreases the rate of imbibition.

**Imbibition pressure** : It can be observed by keeping some seeds with water in a tightly corked bottle. The bottle bursts within some time due to force of imbibition. This force is so high that it is made use in the splitting of rocks and also in surgical operations.

Imbibition pressure now is not used for the actual pressure that develop during imbibition, but as an index of (1) the potential maximum pressure which can develop in an imbibant as a result of imbibition, (2) the diffusion pressure deficit of the water in an imbibant as long as its free expansion is not impeded in any way.

### Quantitative aspect of imbibition

The diffusion pressure deficit in an imbibant is equal to the imbibition pressure minus the turgor pressure,  $D.P.D. = IP - TP$ .

Since in an unconfined imbibant no turgor pressure develops,

$$D.P.D. = I.P.$$

If an imbibant having 100 atm. imbibition pressure is immersed in pure water, its D.P.D. will be 100 atm. When equilibrium is attained the D.P.D. and I.P. both become zero. If this imbibant now is immersed in a solution with 20 atm. osmotic pressure, both the D.P.D. and I.P. in the imbibant will become 20 atm.

## 1.8. STUDENT ACTIVITY

1. Define OP, TP, WP and DPD. What is their relationship in a plant cell ?

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2. Write short notes on osmosis, imbibition and plasmolysis.

**1.9. SUMMARY**

Water is the main constituent of plants and is essential for the maintenance of life, growth and development. A membrane that allows the free movement of solute and solvent particles through it, is said to be permeable. No movement is allowed through impermeable membrane. Such a membrane which permits the solvent and not the solute to pass through it is called as semipermeable. Some quantity of solute is allowed to pass through a differentially or selectively permeable membrane. **Diffusion** is the movement of molecules of gases, liquids and solutes from the region of their higher concentration to the region of their lower concentration. The rate and direction of diffusion are influenced by temperature and pressure. The force responsible for carrying out the diffusion of molecules is their **kinetic energy** (also referred as **chemical potential**). Diffusion pressure is the pressure exerted by the diffusing particles. The process of diffusion is involved in the exchange of gases through stomata, transpiration, absorption of ions and the translocation of food materials.

**Osmosis** is defined as the movement of solvent molecules (water in cells) from a region of its high free energy (high concentration/high diffusion pressure) to a region of its low free energy when the two are separated by a semipermeable membrane till a state of equilibrium is reached. The value of water potential of pure water at normal temperature and pressure is zero. It is expressed in **bars**. Osmosis is of two types : **endosmosis** is the osmotic inflow of water into a cell when it is placed in a solution whose solute concentration is lower than that of the cell sap. **Exosmosis** is the osmotic outflow of water from a cell when it is placed in a solution whose solute concentration is higher than that of the cell sap. **Plasmolysis** is the contraction and separation of protoplasm from the cell walls due to exosmosis, when a plant cell is placed in a highly concentrated sugar or salt solution. A plasmolysed cell is flaccid. Plasmolysis leads to the wilting of leaves. **Deplasmolysis** is the phenomenon of absorption of water by a plasmolysed cell through endosmosis. It occurs when a plasmolysed cell is placed in pure water or in a hypotonic solution. A deplasmolysed cell become turgid. Deplasmolysis recovers the wilting of leaves. The phenomenon of plasmolysis is utilized in the daily life in the preservation of meat, jellies and food stuffs, in killing of weeds from tennis courts and in preventing the growth of plants in the cracks of walls. **Hypertonic** solution is a solution with such a solute concentration that it gains water or solvent by osmosis across a semipermeable membrane from some other specified solution. **Hypotonic** solution is a solution with such a solute concentration that it loses water or solvent by osmosis across a semipermeable membrane to some other specified solution. **Isotonic** solution is a solution having such a solute concentration that it neither gains nor loses water or solvent by osmosis when separated by a semipermeable membrane from a specified solution.

**Osmotic pressure (OP)** is defined as the **pressure** which is developed in a solutin when it is separated from its pure solvent by a semipermeable membrane. It is due to the net movement of water (or solvent) molecules into a closed system like the cell. Osmotic pressure depends upon the number of solute and solvent molecules in a solution. Besides, temperature and pressure also influence the osmotic movement of water (or the solvent) and thereby affect osmotic pressure. Osmotic pressure is expressed in terms of atmospheres. The value of OP is always positive since it increases gradually from zero as the solute concentration increases. **Turgor pressure**

(TP) is the hydrostatic pressure with which the protoplasm is pressed against the cell wall. It occurs due to the osmotic entry of water into the cell by endosmosis. **Wall pressure (WP)** is the pressure exerted by the cell wall to counter the turgor pressure. It is equal (in magnitude) and opposite (in direction) to the turgor pressure. Turgor pressure keeps the cell and their organelles fully stretched, provides strength to the non-woody tissues, and keeps the leaves fully expanded and properly oriented to light. Besides, it helps in the opening and closing of stomata, causes the movements in plants and prevents the wilting of plants.

**Diffusion pressure deficit (DPD)** is the amount by which the diffusion pressure of a solution is lower than that of its pure solvent. In modern terminology, it is referred as water potential ( $\psi$ ). DPD of a cell denotes the net pressure that causes water to enter the cell. The difference between the free energy of water molecules in pure water and the energy of water in any other system (e.g., water in a solution or in a plant cell) is called as water potential. It is represented by a Greek letter psi ( $\psi$ ). In solutions, water potential is determined by three major sets of internal factors such as matric potential ( $\psi_m$ ), solute potential ( $\psi_s$ ) and pressure potential ( $\psi_p$ ). A plant cell functions as an osmotic system. The osmotic relations of a cell vary under different physical states of the cell i.e., in a fully turgid cell, a fully flaccid cell or a plasmolysed cell. Osmosis plays an important role in the absorption of water by the root-hairs, cell to cell movement of water, induction of turgidity, providing mechanical strength, penetration of roots in the soil. Besides, it helps the plants in developing resistance to drought injury, movement of plant parts and opening and closing of stomata. **Imbibition** is the process of absorption of water by the particles of solid substances without forming a solution. The imbibing substance is called imbibant. The imbibants are rich in hydrophilic colloids. The imbibition results in an increase in volume, production of heat and the development of an imbibition pressure. Imbibition helps in the germination of seeds, movement of water from cell to cell in the plant body, and the ripening of seeds. Besides, it carries out the wasping of wooden frames in rainy season.

### 1.10. TEST YOURSELF

1. When a cell is fully turgid which of the following will be zero ?
2. What is osmosis ?
3. A cell is reduced in size on placing in a solution of sugar. What type of solution it is ?
4. A thin slice of sugarbeet is placed in a concentrated solution of sodium chloride. What will happen ?
5. A man supplied excess fertilizer and watered the grass well. After some time the leaves turned brown. Why ?
6. What is the main real force responsible for the movement of water from one cell to another cell ?
7. Why the dry seeds swell when placed in water ?
8. What occupies the space between cell wall and plasma membrane in a plasmolysed cell ?
9. What is the water potential of an aqueous solution ?
10. Name the osmosis measuring device.

### ANSWERS

1. Diffusion pressure deficit
2. Diffusion of solvent through semipermeable membrane
3. Hypertonic
4. loose water from its cells
5. Exosmosis occur in roots and plant die
6. DPD
7. Due to imbibition
8. Plasmolysing solution
9. Less than one
10. Osmometer.

□□□

## 2

## ABSORPTION OF WATER

## STRUCTURE

- Introduction
- Roots as water absorbing system of plants
- Mechanism of water absorption
- Factors affecting the rate of absorption of water
- Other methods of water absorption
- Student activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know the mechanism of absorption of water by plants.

## 1.0. INTRODUCTION

Water is one of the most important constituents of plant as it forms the greater part of the plant weight. It is essential to bring about a number of plant activities. To fulfil the need of water, plants absorb water. Although water may be absorbed through almost any surface of plant, only negligible amount is absorbed through organs other than roots in terrestrial plants. The roots remain in soil and absorb water from there.

## 1.1. ROOTS AS WATER ABSORBING SYSTEM OF PLANTS

The roots remaining in the soil perform the function of absorption of water. The main root, together with its branches, constitute the root system and often exceeds in area, the aerial parts of the plant. The total lengths of roots is very large, so much so that in one wheat plant it measured 40 miles. Though, species decide the depth to which the root of a plant is to penetrate in the soil, still it is affected by various factors such as water, temperature, oxygen and minerals of the soil. In some species roots penetrate deeper in the soil (deep feeders) while in others they are distributed just beneath the soil surface (surface feeders). In deep feeders the roots remain in touch with the permanent supply of water while in surface feeders they remain in touch with water after every irrigation or rain. Plants having both type of roots are best with regards to obtaining water from the soil.

The entire surface of the root does not take part in the absorption of water. The absorption is done mainly in the apices of roots. Out of the four zones (Fig. 1) the maximum absorption takes place in root hair zone which is situated 1-10 cms behind the root tip. **Kramer** (1956, 1959) has explained that maximum absorption takes place in root hair zone as in this zone the xylem is not mature and the epidermis as well as the endodermis are still permeable. In the apical most part, the absorption is restricted due to dense cytoplasm in cells and lack of xylem. In the lower parts suberization and lignification of cells checks the water absorption. The roots hairs always remain in touch with water as in growing roots new roots hairs are formed regularly with the death of older ones.

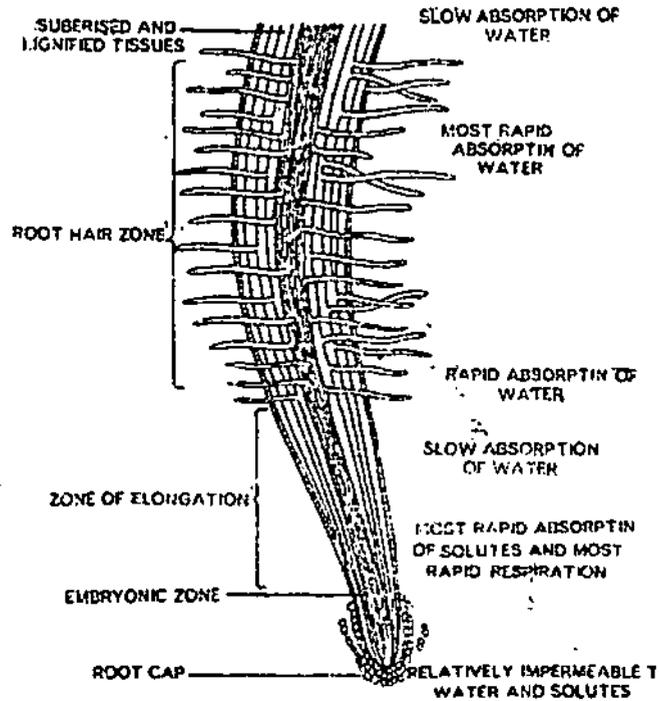


Fig. 1. Tip of a young root showing various zones and the regions of absorption of water and solutes.

A root hair is a delicate tabular outgrowth of the outer wall of epiblema. It projects almost at right angles to the long axis of epiblema cell. Usually they vary from 0.7 mm to 1 cm in length with an average diameter of  $10 \mu$ . The cell wall of the root hair is very thin and delicate. It has two layers, the outer one of pectic material and the inner one of cellulose. The outer layer due to its imbibitional properties helps the root hair to cling firmly to the soil particles. The number of root hairs in plants are very large being in millions or billions and thus greatly increase the absorptive surface. A winter rye plant has been reported to have 14 billion root hairs with an area of 4,321 sqs. fit. In conifers the root hairs are either absent or poorly developed and the function of absorption of water there is done by mycorrhiza.

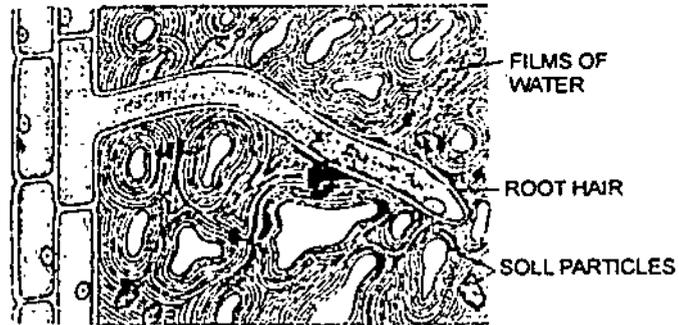


Fig. 2. Diagrammatic representation of the relation of a root hair to the soil.

## 1.2. MECHANISM OF WATER ABSORPTION

Two types of theories have been suggested to explain the mechanism of absorption of water. These are (1) Active absorption and (2) Passive absorption.

**1. Active Absorption of Water :** In slowly transpiring and well watered plants it is believed that the forces for the intake of water develop within the roots. It has been explained in the following ways :

(a) **Osmotic explanation of active absorption :** According to this theory the roots behave as osmometers in which water moves from the dilute solution of the soil to the xylem of the cells along a gradient of diffusion pressure deficit. The roots hairs are in contact with the water films of the soil. The value of osmotic pressure of the cells sap of root hairs is generally 2 atmos. and in some cases may be upto 3 to 8 atmos. as

against less than 1 atmos. osmotic pressure that of the soil solution. The water is first imbibed by the pectic wall layer of the root hair and then is taken in to the root hairs due to endosmosis through the semipermeable cytoplasmic membranes. The water in the soil capillary then is drawn from the nearby area due to cohesive power of water molecules.

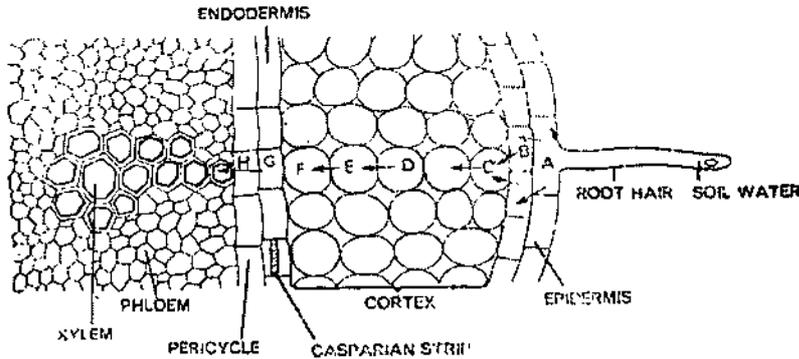


Fig. 3. Diagram showing the path of water from the soil into the root upto the xylem.

As the root hairs are the outgrowths of the epiblema, these remain in contact with cortical cells. Due to the absorption of water the root hair and the epiblema cells become turgid and their diffusion pressure deficit becomes lower than that of the adjacent cortical cell *b*. Thus, water will move from epiblema cell to cortical cell *b* which also becomes turgid and the D.P.D. of this cell also falls and becomes lower than the adjacent cell *c*. The water thus, moves from cell *b* to *c*. In the same manner the water will pass from cell *c* to *d* and gradually to the innermost cortical cell which is in contact with the endodermal cells. The endodermal cells outside the protoxylem usually are thin walled and are called as **passage cells**. Thus, the water enters from cortical cell *f* to the endodermal cell and then to the pericycle cell inside it which does not exert any pressure and readily give up water to xylem cells in its contact. The wall of xylem cell being inelastic, do not exert any turgor pressure and whole of the osmotic pressure of the xylem sap is the D.P.D. This is higher than the reduced D.P.D. of pericycle cell, water is thus, drawn into the xylem vessel. A good number of workers have shown that D.P.D. of xylem increases due to accumulation of salts in it.

In the above mechanism the water is forced into the xylem vessels by the surrounding cortical cells with a certain force. This force induces a pressure which can raise the water to many feet in the xylem and is called root pressure. The existence of root pressure can be demonstrated by a simple experiment. Cut the stem of a well watered plant just above the soil level, water starts exuding out of the stump. This may be called as bleeding. Guttation is another example of the existence of root pressure in the plants. Root pressure is generally observed in plants growing in well aerated, well watered and warm soil and humid air. The magnitude of root pressure under normal conditions is 1 to 2 atmos. but higher root pressure have also been observed in certain plants e.g., 6.4 atmos. in *Juglans regia* by Molish and 10 atoms. in plants grown under water culture by White.

For measurement of root pressure the shoot in a well watered potted plant is cut few centimeters above the soil level and a manometer is fixed on the stump is shown in Fig. 4. The rise in mercury level in the free limb of manometer gives the value of root

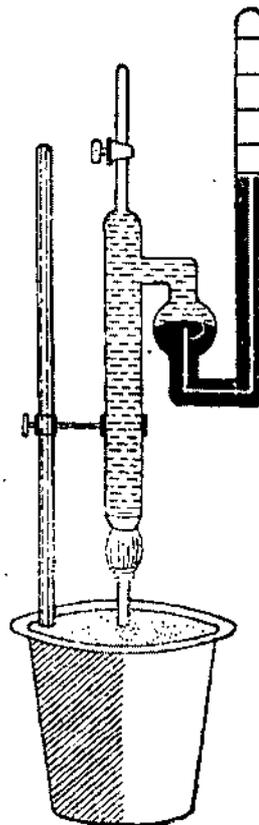


Fig. 4. An apparatus for the measurement of root pressure.

pressure. It is a vital phenomenon and depends upon the living activity of cortical cells of root. It ceases when cells are killed by the addition of poisonous substances.

**(b) Non-osmotic Theory of Active Absorption :** It has been reported that in some cases the osmotic concentration of the soil solution is slightly higher than that of the cell sap. It indicates that water is absorbed against a concentration gradient also. This 'active intake' of water obviously requires an expenditure of energy which comes mainly from the respiration of roots. A good number of evidences are given in support of the correlation between respiration and water intake by plants. These are :

- (i) Poor oxygen supply, low temperature and respiratory inhibitors which check respiration, also reduce intake of water.
- (ii) Auxins and other chemicals which increase, the metabolic activity of plants also increase the water intake.
- (iii) Temperature coefficient for water absorption is 2 to 3 while for a purely physical phenomenon, it would be 1.2 to 1.3.
- (iv) There exists a direct correlation between respiratory rate and the water intake.

**Kramer (1969)** has said that accumulation of salts which is essential for water intake is dependent on expenditure of metabolic energy. Reduction in respiration reduces the active absorption of solutes. The intake of solutes requires much more energy than needed for the intake of water. Thus, it can be said that the relation between respiration and intake of water is indirect. The energy of respiration affects the membrane permeability and the absorption and accumulation of salts and thus, to the intake of water.

**2. Passive Absorption of Water :** In rapidly transpiring plants the absorption of water is caused by forces which originate in the leaves and are then transmitted to the roots. The roots play a passive role and work only as reservoirs through which water is taken in. It is called '*passive absorption*' by Renner.

Water is transpired from the mesophyll cells of the leaves. The diffusion pressure deficit of the water of these cells increases and in turn they take water from the xylem of the leaves. Thus, a tension is developed on the water column of xylem. During active transpiration the tension is even more. This tension from xylem elements of the leaf is transferred lower down to the xylem of stem and finally to that of the root. It increases the diffusion pressure deficit in the inner layer of root cells and a gradient of diffusion pressure deficit is created from xylem to the epiblema of the root cells. The higher osmotic pressure of epiblema or root hair cells causes endosmosis of soil water. The passive absorption theory is supported by the fact that the rate of absorption is almost equal to the rate of transpiration.

Both for active and passive absorption mechanism there are experiments for their support. These experiments supporting one view refute the possibility of other. For example, root pressure experiment support active absorption. In this case the water continued to be absorbed even when the entire upper part of the plant is removed and as such there is no question for transpiration to act upon it. Similarly in a twig removed from a plant and kept in beaker of water, the transpiration and absorption both continue showing thereby the importance of passive absorption. As the water is being absorbed here even in the absence of roots, the active absorption mechanism is completely ruled out. Thus, it may be concluded that under different environmental conditions both active and passive absorption mechanism are operative in the absorption of water in plants.

### **1.3. FACTORS AFFECTING THE RATE OF ABSORPTION OF WATER**

The rate of absorption is mainly influenced by the factors of the soil which are as follows :

**1. Concentration of minerals in soil solution :** The osmotic pressure of soil solution depends upon the quantity of minerals dissolved in it. High concentration of minerals increase the osmotic pressure of soil solution and thus, check water absorption. Even exosmosis might take place. Such soils are called physiologically dry. e.g., salt marshes, alkaline soils. High concentrations of artificial fertilizers are therefore, harmful for the plants and must always be followed by adequate supply of water.

2. **Available soil water** : The water is best absorbed when it is present in field capacity. The decrease in amount of water below permanent wilting percentage greatly reduces its absorption. Increase in water beyond field capacity may check absorption due to decrease in the aeration of water.

3. **Soil air** : The absorption of water is a vital phenomenon involving the expenditure of cell energy released in the process of respiration. Thus, the rate of absorption of water is more in well aerated soils and is retarded in soils deficient of oxygen. In water logged soils the roots are asphyxiated, water absorption is retarded and the plants wilt. This also is a type of physiological dryness. In soils lacking oxygen anaerobic bacteria develop and gradually atmosphere becomes rich in carbon dioxide which decreases the permeability of the cells.

4. **Soil temperature** : The rate of water absorption is at its best between 20–35°C. Rather increase in temperature retards the rate of absorption. The decrease in temperature below 20°C retards the rate of absorption appreciably so much so that it becomes almost negligible at 0°C. The cold soils are physiologically dry, because lowering the temperature (a) increases the viscosity of water (b) decreases the elongation of root (c) reduces the metabolic activity of cells (d) decreases the permeability of cell membranes and (e) reduces the rate of diffusion of water to the roots.

#### 1.4. OTHER METHODS OF WATER ABSORPTION

The aerial parts of plants specially leaves when present in moist atmosphere may absorb a little amount of water directly due to the suction pressure of its epidermal cells. A special method of absorption of water is met with in epiphytic angiosperms e.g., orchids. These plants normally grow under moist conditions and have aerial roots. On the outside of epiblemma on these roots is present a special tissues called *velamen* (Fig. 5). The velamen cells absorb water from the atmosphere and pass on to the xylem. Some epiphytes absorb water through the hygroscopic hairs present on their aerial parts.

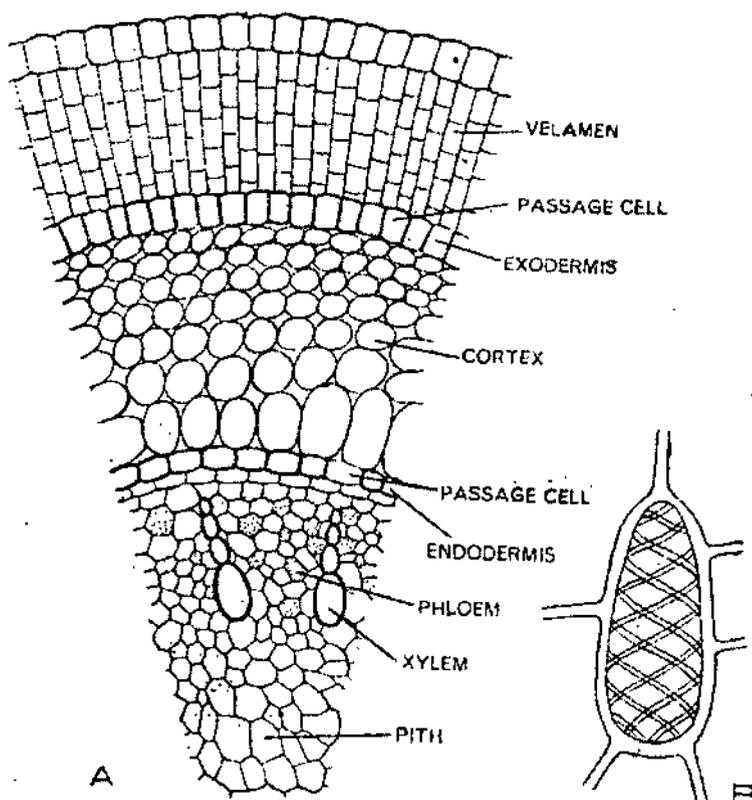


Fig. 5. (A) T. S. of aerial root of orchid showing velamen, (B) a velamen cell.

**1.5. STUDENT ACTIVITY**

1. How the soil water reaches the xylem ?

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2. Describe the various factors affecting the process of water absorption.

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**1.6. SUMMARY**

A plant root is distinguishable into five regions. Maximum absorption of water occurs through the region of root hair. Internally, a root is distinguishable into epidermis, cortex and endodermis enclosing the stele. Unthickened passage cells are present in endodermis opposite to protoxylem groups. The soil complex comprises inorganic matter, organic matter, soil solution soil air, soil moisture and soil organisms. The sources of soil water is atmospheric precipitation. The soil contains water in four different forms namely capillary water, hygroscopic water, combined water and water vapour. Of these, only capillary water is available to plants. A plant may absorb water from the soil actively under no tension condition or passively under the influence of high rate of transpiration. Increased rate of transpiration increases DPD of mesophyll cells. As a result, water is drawn from neighbouring cells. The deficiency of water is then conveyed from leaf xylem to stem xylem and then to the root xylem. The root xylem takes water from pericycle and the deficiency is conveyed finally to the root hair. The root hair absorbs water due to increased suction tension, endosmotically from the soil. The active osmotic absorption of water occurs by simple endosmosis through the root hair. It passes across the cortex along a gradient of DPD. A high concentration in xylem is maintained by the addition of salts or sugars. The active non-osmotic absorption of water takes place by the expenditure of metabolic energy. A correlation has been observed in the rates of respiration and absorption. The absorption of water is affected by many soil components such as soil water, soil solution, soil temperature, soil aeration and soil CO<sub>2</sub>.

**1.7. TEST YOURSELF**

1. When water will be absorbed by the root hair ?
2. Name the rapid water absorption.
3. How the absorption of minerals and water in submerged hydrophytes takes place ?
4. Name the region of the root which is responsible for maximum absorption of water?
5. Why the water logged soils show slow absorption rate ?

**ANSWERS**

1. Concentration of the solutes in the cell sap is high
2. Passive absorption
3. Outer surface of the plant body
4. Root hair region
5. Due to absence of soil air and accumulation of CO<sub>2</sub>.



## 3

## TRANSPIRATION AND GUTTATION

## STRUCTURE

- Introduction
- Kinds of transpiration
- Stomatal transpiration
- Mechanism of stomatal movement
- Measurement of transpiration
- Factors affecting transpiration
- Significance of transpiration
- Guttation
- Water economy of plants
- Student activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know that what is transpiration? You will also know the mechanism of opening and closing of stomata, guttation and significance of transpiration.

## 1.0. INTRODUCTION

In most species of plants very large percentage of the water absorbed by the roots is lost by the aerial parts in the form of invisible water vapour. Only a very small fraction of it is used for metabolic activities of the plants. **The loss of water in the form of vapours from the surface of aerial parts of plants is called as transpiration.** It is not purely a physical phenomenon but is a vital function of plants.

The amount of water lost in transpiration by the plants is surprisingly high. It may exceed the final weight of the plant by several times. In the course of a summer day a beech tree may lose an amount of water nearly five times the fresh weight of its leaves. An acre of beech trees may lose 3000 gallons of water per day. Egyptian cotton plants may transpire 50 tons of water per acre per day. It has also been estimated that about 20-50 lbs of water is transpired for the addition of one ounce of dry matter in the plants.

## 1.1. KINDS OF TRANSPIRATION

Loss of water vapour may take place from any part of a plant which is exposed to air. Generally leaves are the principal organs of transpiration. Most of the transpiration of the leaves takes place through stomata and is termed **stomatal transpiration**. Some amount of water is also lost by the general surface through the cuticle and is termed **cuticular transpiration**. The loss of water vapour also takes place through the lenticles of fruits and woody stems and is termed **lenticular transpiration**. Since more than 90% of the water usually is transpired through the stomata, it forms the most important of the 3 types and will be discussed in details.

## 1.2. STOMATAL TRANSPIRATION

The leaf in general has loosely packed spongy cells enclosed on either side by an epidermal layer. The air spaces of parenchyma communicate with the outside

atmosphere by means of minute breathing pores or stomata situated in leaf epidermis. The mesophyll cells of leaf get water from the xylem of the leaf vein by osmotic diffusion, and become turgid and saturated with water. The water then evaporates from their moist walls into the intercellular spaces of mesophyll, which become saturated with water vapour. This water vapour then diffuses through the stomata into outer atmosphere which is unsaturated. More water then is taken in the intercellular spaces from the xylem through the mesophyll cells. Thus, the process of transpiration through the stomata continues. If stomata are closed, the water evaporating from the mesophyll cell wall will saturate the entire intercellular space area with water vapour, which will diffuse out when stomata open.

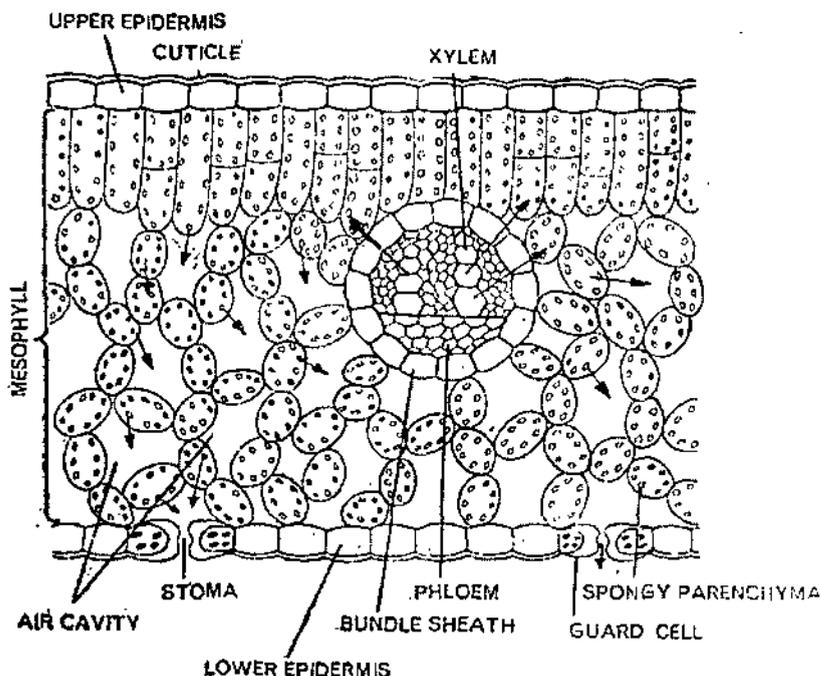


Fig. 1. Vertical section of a typical dicot leaf showing the movement of water during transpiration. The bigger arrows indicate liquid water and the smaller arrows water vapour.

**Structure of stomata :** The stomata (singular, stomata) are minute pores which occur in the epidermis of plants. They are surrounded by two kidney shaped epidermal cells called the **guard cells**. Unlike other epidermal cells, the guard cells have chloroplast and large proportion of cytoplasm. These also have a nucleus. The wall of guard cells is thick towards the pore while the outer wall is thin. In some cases the epidermal cells surrounding the guard cells are of different nature and are named as **subsidiary cells** or **accessory cells**.

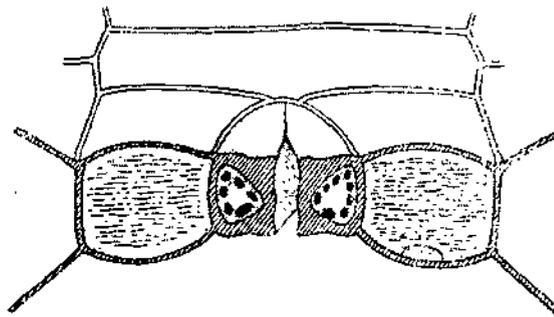


Fig. 2. Perspective view of a stomata and adjacent cells.

**Size and distribution of stomata**

The size of stomatal pore is different not only in different species but even in leaves growing on different twigs of the plants. The size of the pore is too small and is

represented in microns, however the size is too large when compared with the molecules of water or gas passing through it. Thousands of such molecules can pass through the pore at a time, the diameter of water molecule being  $0.000454 \mu$  as against that of the pore being more than  $1 \mu$ .

The number of stomata per unit area depends upon the environmental conditions and varies with the species also. It may vary from a few thousand to several hundred thousand per square centimeter. The number of stomata may be different in different parts of the same plant (one part growing in shade and the other in light or one developing earlier and the other later).

The position of stomata on the two surfaces of the leaf is quite variable and may be divided into five types :

(a) **Apple or Mulberry type** : The stomata are present on the lower surface of the leaf e.g., peach, nasturtium, *Oxallis* etc.

(b) **Potato type** : The stomata are present mainly on the lower surface of the leaf. Some stomata are present on the upper surface also e.g., tomato, cabbage, pea etc.

(c) **Oat type** : The stomata in this case are almost equally distributed on the two surfaces of the leaf. Most of the monocotyledons belong to this group.

(d) **Water lily type** : The stomata are present only on the upper surface of the leaf. Aquatic plants with floating leaves are the examples of this type.

(e) **Potamogeton type** : The stomata in this type are either absent or are rudimentary or functionless. Most of the submerged plants form examples of this type.

There is a direct correlation between the size and number of stomata and the rate of transpiration. Distribution of stomata in various types of leaves is given in table 1.

**Table 1 : Distribution of stomata on the leaves of various types of plants.**

Species	Average number of stomata per $\text{cm}^2$	
	Upper epidermis	Lower epidermis
Apple ( <i>Pyrus malus</i> )	0	29,400
Bean ( <i>Phaseolus vulgaris</i> )	0	22,900
Begonia ( <i>Begonia coccinea</i> )	0	4,000
Black Oak ( <i>Quercus velutina</i> )	0	58,000
Castor bean ( <i>Ricinus communis</i> )	6,400	17,000
Geranium ( <i>Pelargonium domesticum</i> )	1,900	5,900
Jimson weed ( <i>Datura stramonium</i> )	11,400	18,900
Maize, ( <i>Zea mays</i> )	5,200	6,800
Mulberry ( <i>Morus alba</i> )	0	48,000
Oat ( <i>Avena sativa</i> )	2,500	2,300
Potato ( <i>Solanum tuberosum</i> )	5,100	16,100
Tomato ( <i>Lycopersicum escutentum</i> )	1,200	13,000
Wheat ( <i>Triticum sativum</i> )	3,300	1,400

### 1.3. MECHANISM OF STOMATAL MOVEMENT

Mohl (1856) had shown that the opening and closing of stomata is operated by changes in the turgidity of the guard cells. Later Schwandener (1881, 1889) told that with the increase in the turgor, the thinner walls of the guard cells are stretched more than the thicker ones. The thicker walls then take a concave shape, thus making a gap — the opening of the stomata. When turgor of guard cells decreases, the reverse takes place and the stomata close (Fig. 3). In graminaceous stomata, the central part of each guard cell is narrow and very heavily thickened, only the dialated ends being

sufficiently than walled to be capable of expansion. These swell under increased turgor and cause the rodlike central part to separate and open the stomata.

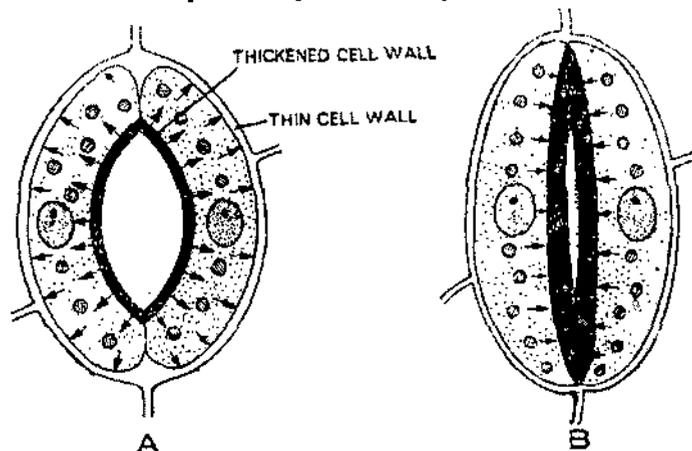


Fig. 3. Stomatal movement — A. Open stomata , B. Closed stomata.

In sunken stomata the opening is caused by the change in shape of guard cells as a result of turgor.

The turgor differences in the guard cells and subsidiary cells are controlled by various factors. These are :

**1. Light associated with CO<sub>2</sub> concentration :** The stomata mostly open in light and close in darkness. **Mohl** (1856) suggested that chloroplasts in guard cells produced osmotically active substances under the influence of light which increased their turgor and caused opening. Recently it has been shown that the chloroplasts of the guard cells are either totally incapable or can do only very little of photosynthesis.

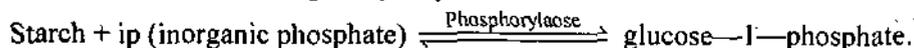
**Lloyd** (1908) put forward starch  $\rightleftharpoons$  sugar hypothesis. In light an enzyme is secreted in the guard cells which hydrolyzes the starch to sugar thus raising the osmotic pressure and also the turgidity of the guard cells. The stomatal opening is thus negatively correlated with the starch of guard cells. He found an increase in the amount of starch in the noon and also a simultaneous partial closure of stomata was observed.

**Loftfield** (1921) shown the presence of a starch/sugar balance in the guard cells.

It has also been shown that opening of stomata does not depend upon the photosynthetically production of carbohydrates but is dependent upon the removal of carbon dioxide by photosynthesis. **Mansfield** (1965) has shown that stomata remain open even in dark if CO<sub>2</sub> is removed and are closed in light if carbon dioxide concentration increases.

**Sayre** (1926) has shown that the light increases the pH of guard cells which favours the hydrolysis of starch to sugar by diastase resulting in increased osmotic pressure and stomatal opening.

**Yin and Tung** (1948) have shown the presence of an enzyme phosphorylase in the guard cells, which catalyzes the reversible transformation of starch to glucose, 1-phosphate in the presence of inorganic phosphates.



From the foregoing it seems that the carbon dioxide released in respiration is utilized in photosynthesis in light and results in the lowering of H<sup>+</sup> ion concentration or acidity of the guard cells. The pH of these cells become high and enzymatic conversion of starch to sugar is favoured. In the dark carbon dioxide released in respiration accumulates in the intercellular spaces of mesophyll. This increases the acidity and decreases the pH of the guard cells which favours the enzymatic conversion of sugar to starch.

The mechanism may thus be summarized as under :

Table 2 : Mechanism of stomatal movement

Illuminated guard cells	Dark guard cells
(a) CO <sub>2</sub> of the intercellular spaces used in photosynthesis by mesophyll.	(a) CO <sub>2</sub> released in respiration accumulates in intercellular spaces.
(b) pH of guard cells increases.	(b) pH of guard cells decreases.
(c) The decrease in acidity brings about hydrolysis of starch to sugar.	(c) The increase in acidity converts sugar to starch.
(d) The O. P. of the cell sap of guard cells increases.	(d) The O. P. of cell sap of guard cells decreases.
(e) Water enters the guard cells due to endosmosis which becomes turgid and swollen.	(e) Water goes out of guard cells due to exosmosis, which become flaccid.
(f) Stomatal aperture open.	(f) Stomatal aperture closes.

Steward (1964) has suggested that glucose-1-phosphate should be further converted into glucose and inorganic phosphate so as to increase the osmotic pressure of guard cells. The scheme is shown as under :

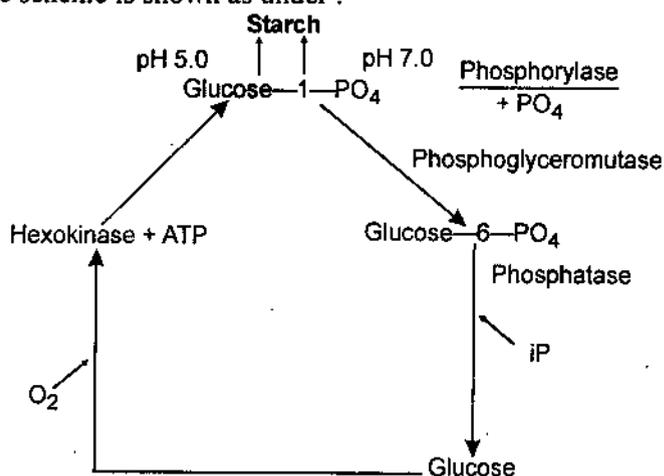


Fig. 4. Scheme of Steward for interconversion of glucose and starch.

Recently it has been shown that the opening of stomata in carbon dioxide free atmosphere and light requires the presence of K<sup>+</sup> ions (Fischer and Hsiao 1968). Fusino (1967) and Hamble and Raschke (1971) have shown that this stomatal movement is the result of an active transport of potassium into the guard cells and out of them.

Raschke (1975) reviewing the whole situation has shown that stomatal opening could be caused due to any of the following :

- Disappearance of starch from the guard cells
- Production of organic acids, particularly malic acid
- Excretion of H<sup>+</sup> from the guard cells.
- Uptake of K<sup>+</sup> into the guard cells and
- Uptake of it into the guard cells.

An increase in the amount of organic acids during the opening of stomata has been shown by Allaway (1973) and Pallas and Wright (1973). Wilmer *et. al.* (1973) have even shown the conversion of starch to organic acids by the enzyme phosphoenol pyruvic carboxylase in the guard cells.

It has also been shown that uptake of K<sup>+</sup> or Cl<sup>-</sup> or the expulsion of H<sup>+</sup> are active processes and require the utilization of energy of respiration.

A new concept called "The proton transport concept of photoactive opening" is given by Levitt (1974). According to him a light induced proton is transported from cytoplasm to the chloroplast of the guard cells. To replace it a K<sup>+</sup> enters into the cytoplasm and pH of cytoplasm is raised which favours the conversion of CO<sub>2</sub> to

HCO<sub>3</sub>. The latter then is converted to organic acid utilizing the starch of the guard cells and make the stomata open.

**2. Effect of water supply evaporating power of the air and changing leaf water content :** Milthrope and Spencer (1957) have shown that the rate and direction of change in local water contents is more important than the water deficit of the leaf as a whole in affecting stomatal movement. In clear warm days the water content of the leaf cell decreases. The turgor of guard cells also decreases due to the movement of their water to neighbouring cells and partial to complete closure of stomata takes place. The decrease in water contents of the guard cells bring about decrease in pH of cell sap which helps in the conversion of sugar to starch and the osmotic pressure of the guard cells decreases. Thus, stomata could close even in favourable light conditions if there is an internal water deficit.

When the leaves are subjected to dry air or to moving air, in the first case the closure and in the later case the opening is accelerated.

**3. Responses to temperature :** Under constant and favourable light and other environmental conditions the opening of stomata increases in a good number of plants e.g., cotton, tobacco with a rise in temperature upto 25°–30°C. Above and below it the stomata close. The high temperature, 35°–30°C in some cases causes opening in the dark.

In a representative summer day, when other conditions are normal the stomata open in the morning, the maximum aperture is obtained within an hour and then during mid-day they close partially or completely and again open in the after-noon before a final closure in the evening.

This mid-day closing of stomata has been attributed by Sayre and Lofffield to the loss of water. But Nutman (1937) has shown the mid-day closure in *Coffea* even in absence of water strain. Heath has shown that the minimum intercellular space carbon-dioxide concentration (T) of leaf increases with temperature, particularly between 30°–35°C and causes closing of stomata. This is proved by the fact that if carbondioxide free air is swept in leaf, the closure does not take place. The value of T varies in different plants. He also found that if excessive accumulation of carbondioxide in the intercellular spaces does not occur, raising the temperature causes opening. This may be due to the lower solubility of carbondioxide in the guard cell sap or might be independent of Carbondioxide.

Together with these there are some other factors also which determine the stomatal mechanism.

### Autonomous Diurnal Rhythms

In some plants like *Prunus* (Maskell, 1928) and wheat (Heath and Russell, 1954), a 24-hour cycle of stomatal movement is observed even under constant conditions.

Heath suggested that periodic changes in starch  $\rightleftharpoons$  sugar balance might provide the turgor changes for such autonomous diurnal rhythms.

### Effects of Shocks, Narcotics and other Factors

The stomatal movements are affected negligibly by wounds. Mechanical pressure however, brings sudden closure of stomata followed by a gradual opening. The burning shock also brings a little of closure of the stomata. Electric shocks if light bring opening and if strong the closing of stomata.

The narcotics like chloroform and ether and poisons bring closure of stomata. If the dose is not high, they may reopen also.

Thus, it seems that the stomata provides us a single system which is operated by a number of mechanisms which interact in an elaborate way to provide a sensitive control well adapted to the conditions normally encountered.

## Daily Movement of Stomata

Loftfield has classified stomata into 3 main groups with regards to their daily movement.

1. **Alfalfa type** : Stomata remain open throughout day and close at night. These are found in thin leaved mesophytes e.g., pea, mustard, bean etc.

2. **Potato type** : Stomata remain open for 24 hours except for few hours in the evening e.g., cabbage, onion, pumpkin etc.

3. **Barley type** : Stomata open only for few hours during the day. It is found in most of the cereals like wheat.

## 1.4. MEASUREMENT OF TRANSPIRATION

Transpiration can be measured by the following methods :

1. **Gravimetric Method** : This method can be used for potted plants. The pot is enclosed in an oil cloth so as to avoid evaporation of water from the soil surface. The potted plant now is weighed at regular intervals. The increase in weight gives the amount of water transpired. The changes in weight due to photosynthesis or respiration are negligible.

2. **Potometer Method** : The principle employed in this method is amount of water transpired = amount of water absorbed. In this case we actually measure the amount of water absorbed by the plant. Potometers are of different types :

(a) **Simple potometer = Students potometer** : Designed by F. Darwin as shown in Fig. 5. It consists of a glass tube with a side limb in which a twig is fixed through the hole of the cork. The upper end of the straight tube is closed by a cork and in the lower end is fixed a glass capillary about 20–30 cms in size. The apparatus is filled with water and all joints are made air tight. The potometer is placed in sunlight. During transpiration water is absorbed from the potometer and level of water in the capillary rises. As soon as a bubble of air enters the capillary tube, dip its end in a beaker of water. The rate of ascent of bubble gives us the rate of transpiration and can be measured by fixing a scale on the capillary.

(b) **Farmer's Potometer** : Used by Farmer (Fig. 6). It consists of a wide mouth bottle with a three holed cork. A twig is placed in the central hole, while in the rest of the two holes are fixed a reservoir and a bent tube. A graduated scale is attached on the bent tube. The apparatus is filled with water and is made air tight. As the water transpires the air enters in open end of the bent tube. The movement of air column in this tube in one minute is noted. The air column is then thrown out of the tube by opening the stopper of the reservoir. Again the readings are taken in the same manner.

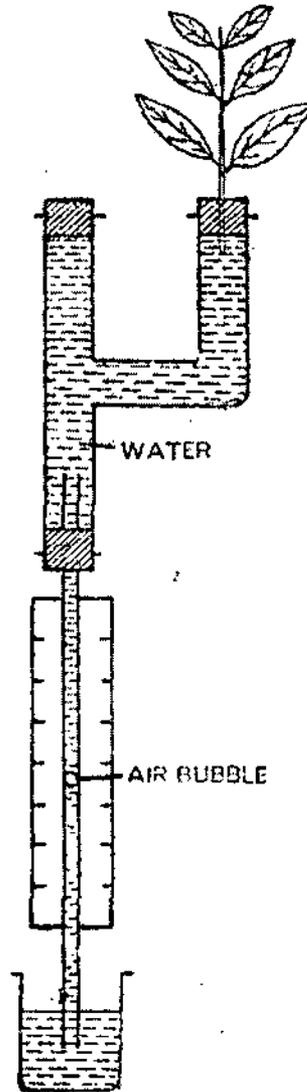


Fig. 5. A simple potometer.

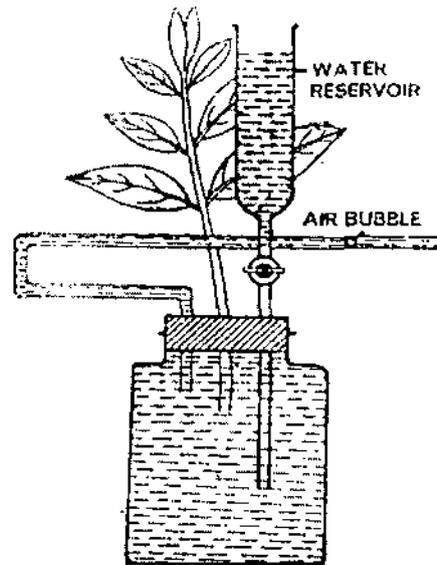


Fig. 6. Farmer's potometer.

(c) **Ganong's Potometer's** : Designed by Ganong (Fig. 7). The apparatus consists of a graduated capillary tube with one end bent to the underside and a wide vertical end on the other end. A reservoir is fixed on it near the vertical tube in which the plant twig is fixed. As the transpiration takes place, the air bubble enters through the hole of the bent tube, which now is kept in a beaker of water. The movement of the air bubble on the graduated scale can be noted against time. As the air bubble reaches near the reservoir, its stopper is opened and the air bubble is brought back to the bent tube. The stopper then is closed and next reading is taken for the movement of the air bubble.

In all the potometers the rate of transpiration is taken as the mean of several readings taken. The rate of transpiration can be studied under varying conditions like sunlight or under fan etc.

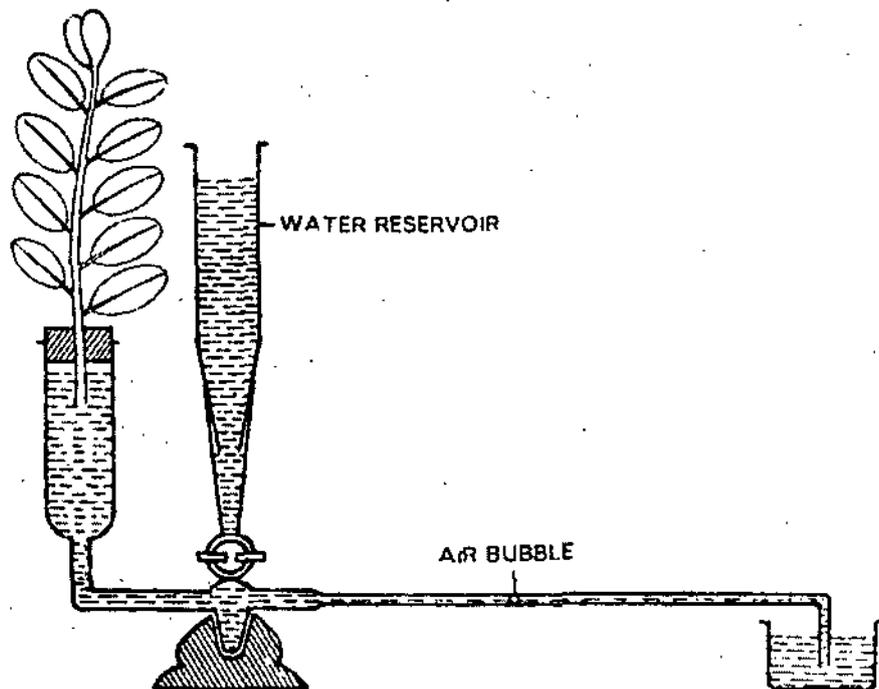


Fig. 7. Ganong's potometer.

**3. Cobalt chloride method** : This method is made use to compare the rate of transpiration from two surfaces of the leaf.

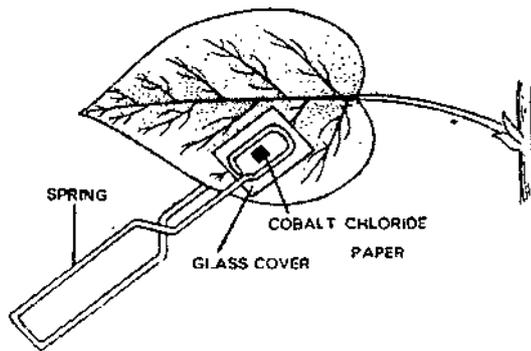


Fig. 8. Cobalt chloride experiment to show transpiration from two surfaces of leaf.

This is a qualitative method. The cobalt chloride is blue when anhydrous and becomes pink when wet. Filter papers are soaked in 3% solution of cobalt chloride and dried in an oven. One filter paper is placed on either side of the leaf of a potted plant and covered by Ganong's leaf clip as shown in Fig. 8. Due to transpiration the colour of filter paper gradually changes to pink. The side changing the colour earlier indicates faster transpiration.

This method now is used to find out the **index of transpiration**. It is the ratio of time taken for the change of colour of the cobalt chloride papers in contact with water and the leaf. For instance, if the time-interval for cobalt chloride paper in contact with a leaf to turn pink is 50 seconds and for a similar change over a moist blotting paper is 10 seconds, then the index of transpiration of that leaf is 5.

**4. Calcium chloride method :** This method also is meant to compare the rate of transpiration from the two surfaces of leaf. It is a quantitative method. Two narrow belljars are fixed on the two sides of a leaf as shown in Fig. 9. The contact between the belljar and the leaf is made air tight by the use of vaseline. In each belljar is placed a small tube containing weighed amount of anhydrous calcium chloride. On the top of each belljar a U-tube filled with glycerine or mercury is attached so as to disconnect the inner air from the outer atmosphere. After two hours the two tubes are weighed again. The gain in weight of these tubes gives the amount of water transpired from each surface of the leaf.

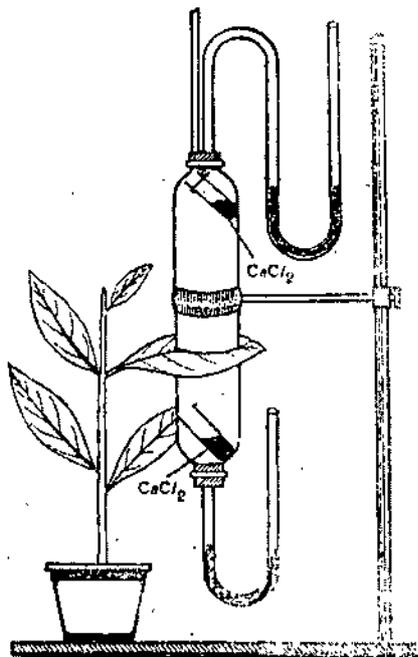


Fig. 9. Calcium chloride method to measure the rate of transpiration.

## Factors Affecting Transpiration

The rate of transpiration is influenced by the following factors :

**1. Humidity of the Air :** The diffusion of water vapour from the leaves to the outer atmosphere follows the simple law of diffusion and will take place only if the vapour pressure in the outer atmosphere is less than that of the leaf. If the atmosphere is saturated with water vapour, the loss of water from leaves becomes negligible. The rate of transpiration is more if the air is dry and is the least on a rainy day. It thus, depends upon the capacity of the atmosphere to take up more moisture, which depends upon the difference between the amount of water vapour actually present in the air and the amount necessary to completely saturate it or the **saturation deficit**. Absolute humidity expressed as percentage of the amount necessary for saturation at a particular temperature is called **relative humidity**. At lower relative humidity the rate of transpiration is more.

**2. Temperature :** With the increase in temperature the vapour pressure of the intercellular spaces increases very much. There is a rise in the vapour pressure of the outer atmosphere also, but because of the corresponding expansion of the atmosphere, it becomes insignificant. The increase in temperature also brings about decrease in relative humidity. Thus, the rate of transpiration increases with the rise in temperature. High temperature also increases transpiration by causing the opening of stomata even in the dark. At low temperature the rate of transpiration falls.

**3. Light :** Light affects the rate of transpiration by controlling the stomatal movement. In light the stomata open and the transpiration takes place. The rate of transpiration increases even in diffused light and is more in intermittent light. It also changes with the change in wavelengths of light, being maximum in blue light.

The light also influences the rate of transpiration by raising the temperature of the leaves and by increasing the permeability of cytoplasmic membranes. -

**4. Wind :** It influences the atmospheric humidity. The blowing dry wind removes the accumulated humidity and brings fresh air near the leaves. The rate of transpiration thus, increases. Humid air, on the other hand, lowers the rate of transpiration. Very fast winds may also lower the rate of transpiration due to its effect in lowering the temperature, though there might be an initial increase in the rate.

**5. Atmospheric Pressure :** The rate of transpiration increases with the lowering of atmospheric pressure. At high altitudes the atmospheric pressure is low, but the rate of transpiration does not increase due to low temperature prevailing there.

**6. Available soil water :** Availability of capillary water is a direct factor in maintaining the rate of transpiration. With the decrease in the availability of soil water, the rate of transpiration goes down. The factors like high concentration of minerals or low temperature etc. that influence the rate of absorption will also influence the rate of transpiration.

**7. Internal Factors :** The role of stomata and cuticle in regulating the rate of transpiration has already been discussed. Various adaptations in the xerophytes *i.e.* the reduction in the size of leaves, falling of leaves, thick cuticle, sunken stomata etc. are meant to reduce the rate of transpiration. Water relation of the mesophyll cells also influence the rate of transpiration and has already been discussed.

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## 1.6. SIGNIFICANCE OF TRANSPIRATION

Transpiration in plants has been described as a **necessary evil** by Curtis (1926). The greatest disadvantage is that the huge amount of water which is of vital importance to the plants is lost in the process. This loss of water becomes a serious problem when there is a deficient water supply. Deciduous trees have to shed their leaves in unfavourable conditions (excessive transpiration) to conserve their water supply, though it costs them the cutting of their food forming photosynthetic activity. Due to

high rate of transpiration and inadequate water supply the turgour of the cells is lost and plant organs may fall. Growth of the plants is stunted and the yield is reduced very much. The question naturally arises as to what is the use of this loss of water? Some people assign it to the fact that the leaf structure with water saturated, thin walled mesophyll cells, intercellular spaces and the stomata, is built to suit the exchange of gases ( $\text{CO}_2$  and  $\text{O}_2$ ) from the atmosphere. This structure also suitable for evaporation of water which becomes inevitable.

Some workers have assigned some **advantages** to the process of transpiration :

**1. Absorption of water :** According to passive absorption theory, the water is taken in through the roots due to the diffusion pressure deficit created by the transpiration. What role does it play in herbs growing in well watered soil can not be explained properly.

**2. Circulation of water in plants :** The water absorbed by the roots is taken to the topmost parts of the tree due to the force developed in transpiration. It has been said that this water in the upper part is needed only to fulfill the need of transpiration. Still it may be said that whatever small amount of water is needed in the leaves for metabolic processes must reach them by some means and transpiration provides that force.

**3. Absorption and Translocation of Minerals :** It was said earlier that the minerals are absorbed and translocated together with the water current which is dependent on transpiration. It has now been made clear that the mechanism of absorption of minerals is independent of the absorption of water. It is now believed to be an 'active' process brought about by metabolic energy, though workers like **Kramer** (1957) have shown a 'passive' uptake of ions under the influence of transpiration.

Once the salts have entered the roots, their further distribution through the xylem is greatly helped by transpiration. Some workers have shown that increased transpiration resulted in an increase in the ash content of the plants. An important argument against this concept is that lack of transpiration has not been found to create any appreciable mineral deficiency in the various organs of the plant. These people thus believe that transpiration is not useful in mineral translocation also.

**4. Regulating the temperature of the plant body :** Transpiration is supposed to prevent the leaves from heating due to radiant energy. The radiant energy is soon converted to heat energy and could raise the temperature of the leaf in very short period to a point which may be injurious to the cytoplasm. This energy used in removing the water vapour from the leaf surface and keeps the leaf cool.

This so called advantage is a fallacy as it is now well known that transpiration by itself is insufficient to cause the total dissipation of the absorbed radiant energy. When transpiration was checked in some plants by plugging the stomata by Vaseline, no appreciable increase in their temperature was observed. Xerophytic plants are adopted to reduce the rate of transpiration, yet their body temperature does not remain high. Thus, it may be said that transpiration may account for the loss of some heat from the leaves and does not regulate the body temperature of the leaves.

**5. Other Advantages :** High rates of transpiration may increase the osmotic concentration of sugar in fruits. It may favour the development of mechanical tissues in the plants.

## 1.7 GUTTATION

The release of water from the uninjured parts of plants in the form of drops is called **Guttation** (Fig. 10). It takes place in plants growing in conditions where absorption of water exceeds transpiration. It takes place through special structures called **hydathodes** or **water stomata** present at the apex of main veins of leaves. Usually it takes place in the morning and the drops of water found on the tips of leaves in some plants in the morning, which are commonly regarded as dew, may be gutted

water also. This water normally contains variety of dissolved inorganic and organic substances. After the evaporation of water, the solutes are left behind on the leaf. These are found in garden nasturtium, potato, tomato, oat, grasses and colocacia etc.

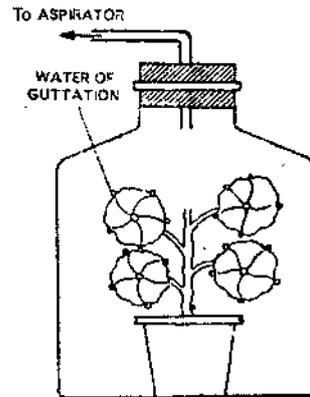


Fig. 10. Demonstration of guttation.

Each hydathode consists of large pore which remains always open and has thin walled cells. Beneath the pore is a loose parenchyma called **epithem**. The cells of epithem do not have chloroplast and are situated over the open vein endings (Fig. 11). The liquid from the tracheids is forced into the epithem and then to the outside due to root pressure.

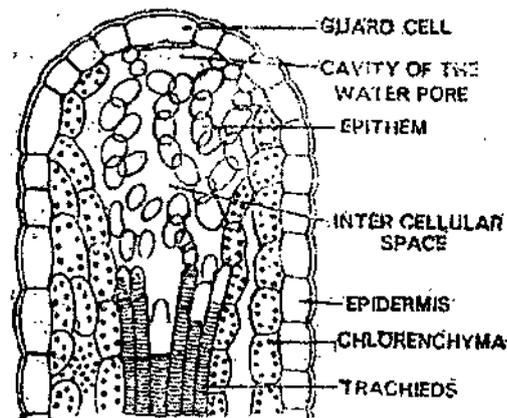


Fig. 11. Vertical section through the leaf tip *Primula sinensis* showing hydathode.

### 1.8. WATER ECONOMY OF PLANTS

Plants normally maintain turgidity of their cells when there is normal absorption of water and transpiration. In bright warm days mesophyll cells of the leaves loose some turgidity due to rate of transpiration exceeding the rate of absorption. This partial loss of turgidity does not arise visible wilting and is called **incipient wilting** and is soon recovered.

In very hot summer days when there is excessive transpiration, the leaves and young twigs of plants are wilted due to complete loss of turgor. This is called **temporary wilting** and the wilted parts regain turgidity during night.

When the soil becomes deficient of water and excessive transpiration takes lace, not only the leaf cells but other parts of plants including root hairs also loose turgidity. It is called **permanent wilting** and recovery from this effect can be when the soil is quickly watered. The recovery in this case is very slow. It is most harmful to the plants.



**ANSWERS**

1. Increase in both osmotic and turgor pressure.
2. There is high humidity in the atmosphere
4. Oat
3. Levitt
5. at night.

□□□

## 4

## ASCENT OF SAP

## STRUCTURE

- Introduction
- Xylem structure and ascent of sap
- Theories of mechanism of ascent of sap
- Vital theories
- Root pressure theory
- Physical force theories
- Student activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know the path and various theories of mechanism of ascent of sap.

## 1.0. INTRODUCTION

Most of the water absorbed by the roots of land plants is either lost in transpiration or guttation or is used in photosynthesis in the leaves. Water must, therefore, move through the intervening tissues and organs from the roots to the leaves. This process of movement of water is called **transport or translocation or conduction of water or ascent of sap**. The problem becomes more striking in large trees some of which attain a height of more than 100 meters e.g., *Sequoia sempervirens*, of California and *Eucalyptus spp.* of Australia. The deeply penetrating roots of these trees make the distance for the water to travel even longer.

## Path of water in the plant

Xylem is the principal tissue through which translocation of water takes place. When a leafy twig of balsam plant is placed in a weak eosine solution (red). After few hours the veins of leaves become red. When transverse sections of leaves are cut the red colour is seen only in the xylem, showing that the eosine solution was moving up through the xylem. The **ringing or girdling experiment of Malpighi (1971)** confirmed the above fact. Take three twigs placed in a beaker. In twig A girdle the stem so that a narrow band of all the tissues outside the xylem are removed. In twig B the xylem tissue is removed from a band leaving the outer tissues intact. The twig C is left as such. In twig A and C the leaves remain fresh and do not show any sign of wilting while in twig B wilting takes place. Fig. 1 shows the condition of A. The water rises upward through the lumen and not through the walls can be shown by plugging the lumen of xylem of a twig with wax. The water ceases to rise up.

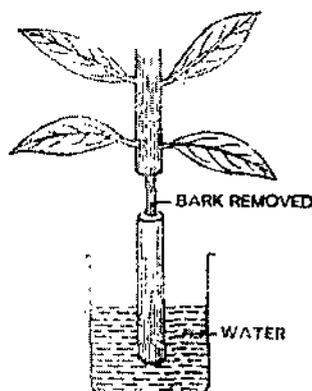


Fig. 1. Ringing experiment.

## 1.1. XYLEM STRUCTURE AND ASCENT OF SAP

The structure of xylem is well suited to the translocation of water. It is continuous from just back of the tips of roots through the roots, into and through the stems, the petioles of the leaves and ultimately, usually after much branching, terminates in the mesophyll of the leaf. Most of the cells of leaf are only a few cell distant from vein or vein ending. Thus, the xylem tissue is a continuous unit system within the body of the plant for the movement of water. The xylem tissue of the wood of angiosperms are composed of vessels, tracheids, fibers, xylem parenchyma and ray cells which vary in the proportional distribution and arrangement in different species. Vessels form the most characteristic element of xylem of angiosperms. These are long tube like structures made by the union of several cells, each one of them originating from cambium, and attaining a length of several meters. The cross walls may or may not be perforated. The vessels are contiguous with others through the pit pairs present in their walls. The walls of vessels are lignified and these are nonliving. Thus, the structure is very much suited to the translocation of water.

Tracheids, from another important element of xylem and are usually spindle shaped cells with thick angular walls. Mature tracheids lack cytoplasm, and the largest tracheid are about 5 mm long and 30  $\mu$  in diameter. These also are water conducting tissues with pitted walls. These form more important conducting tissue in Gymnosperms where vessels are absent.

The xylem parenchyma is the living tissue of the xylem. The cells die only when its wood is converted into heartwood. These cells remain in contact with vessels and tracheids throughout their length.

Along with the vertically oriented cells, there are present a transverse, radiating system of living cells called as vascular rays. These extend from outer extremity of phloem through the cambium upto the xylem. Their height and diameter varies in different plants. The xylem rays probably serve as routes for lateral movement of water from xylem to the phloem.

## 1.2. THEORIES OF THE MECHANISM OF ASCENT OF SAP

Various theories suggested for the mechanism of ascent of sap are placed in three groups :

1. Vital force theories
2. Root pressure theory
3. Physical force theories.

## 1.3. VITAL FORCE THEORIES

These theories suggested that living cells are responsible for the upward movement of water. Godlewski (1884) was the first to advocate for the activity of living cells being responsible for the ascent of sap. In this 'relay pump' theory he suggested that rhythmic change in osmotic pressure of xylem parenchyma and vascular ray cells brought about a pumping action of water. The water first enters from the bordering vessels into the parenchyma cell with high osmotic pressure. The absorbed water lowers its osmotic pressure and the water is pumped back into the xylem vessel situated higher to the parenchyma cell.

Sir J. C. Bose (1923) was another strong advocate for vital force theory. According to him the pulsatory activity of the innermost layer of cortical cells of root is responsible for upward translocation of water. He has shown the presence of pulsatory activity in these cells with the help of an apparatus called electric probe (Fig. 2) which consists of galvanometer, an electric needle, a circuit and a plant. The deflection of galvanometer needle when electric needle is touched to innermost layer of cortical cells indicates the presence of pulsation.

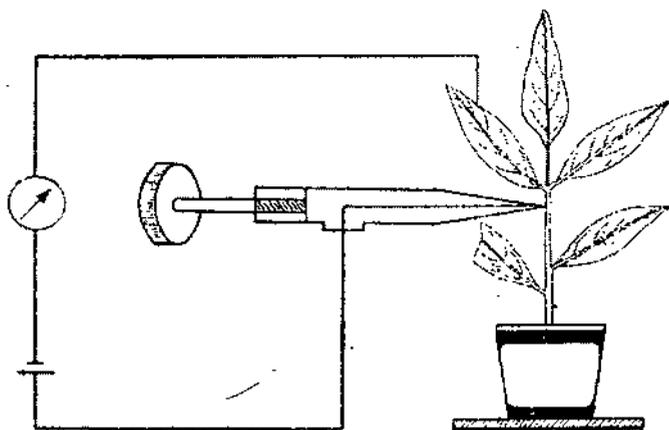


Fig. 2. Bose's electric probe.

#### 1.4. ROOT PRESSURE THEORY

Exudation of xylem sap takes place from the freshly cut stump of a potted plant or from the borings made in the stem of a plant. These exudations usually are the results of the pressure developed in the sap of xylem as a result of **root pressure** developed in the cortical cells of roots. Usually a maximum of 2 atmos. pressure is developed in the roots and in some trees *e.g.*, birch with increasing height in the tree, the magnitude of root pressure decreases at the rate of about 0.1 atmos. per meter of height.

Though under certain conditions root pressure explains the upward movement of water satisfactorily but there are some objections to it :

(1) The root pressure of 2 atmos. can hardly raise the water to about 20 meters or so and for raising the level of water in tall trees a pressure of about 15–20 atmos. is needed.

(2) In some plants root pressure does not develop *e.g.*, gymnosperms.

(3) Root pressure is lower or even negative in summers when rate of transpiration is maximum.

(4) Water continues to rise even in the complete absence of root pressure (cut twig placed in beaker of water), and

(5) The rate of flow of sap in exudation is not adequate to compensate for the known rate of transpiration.

#### 1.5. PHYSICAL FORCE THEORIES

(a) **Capillary Force Theory : Boehm (1809)** proposed that the ascent of sap takes place due to the force of capillary existing in xylem ducts.

The objections to this theory are :

(1) The force of capillary could hardly raise the water to few centimeters.

(2) The septa present specially in gymnosperms make the rise of water due to capillary force difficult as it requires free surface.

(3) Usually in taller trees the bore of xylem duct is rather wider than being narrower.

(b) **Imbibition Force Theory : Sachs (1878)** suggested that the water rise up in the xylem ducts due to the force of imbibition. It has already been discussed earlier in this chapter that the water rises up through the lumen and not through the walls of xylem ducts.

(c) **Jamin's Chain Theory : Jamin** believed that water and air were arranged alternately inside the xylem duct. When air expanded, it moved up carrying along with

it the water column present above it. The theory is not accepted as it can not explain the rapid unidirectional flow of sap.

(d) **Transpiration Pull and Cohesion of Water Theory** : The theory initially was put forward by **Dixon and Joly (1894)** and was later modified by **Dixon (1924)**. During recent years it was supported by **Curtis and Clark (1951)**, **Bonner and Gulston (1952)** and **Kramer and Kozlowski (1966)**. The theory could be compared with a man sitting on the edge of a well and pulling out water from the well. The force of man and the chain that brings the bucket out are the two important aspects of it and can be compared with the two important aspects of this theory viz., transpiration pull and cohesive force of water respectively.

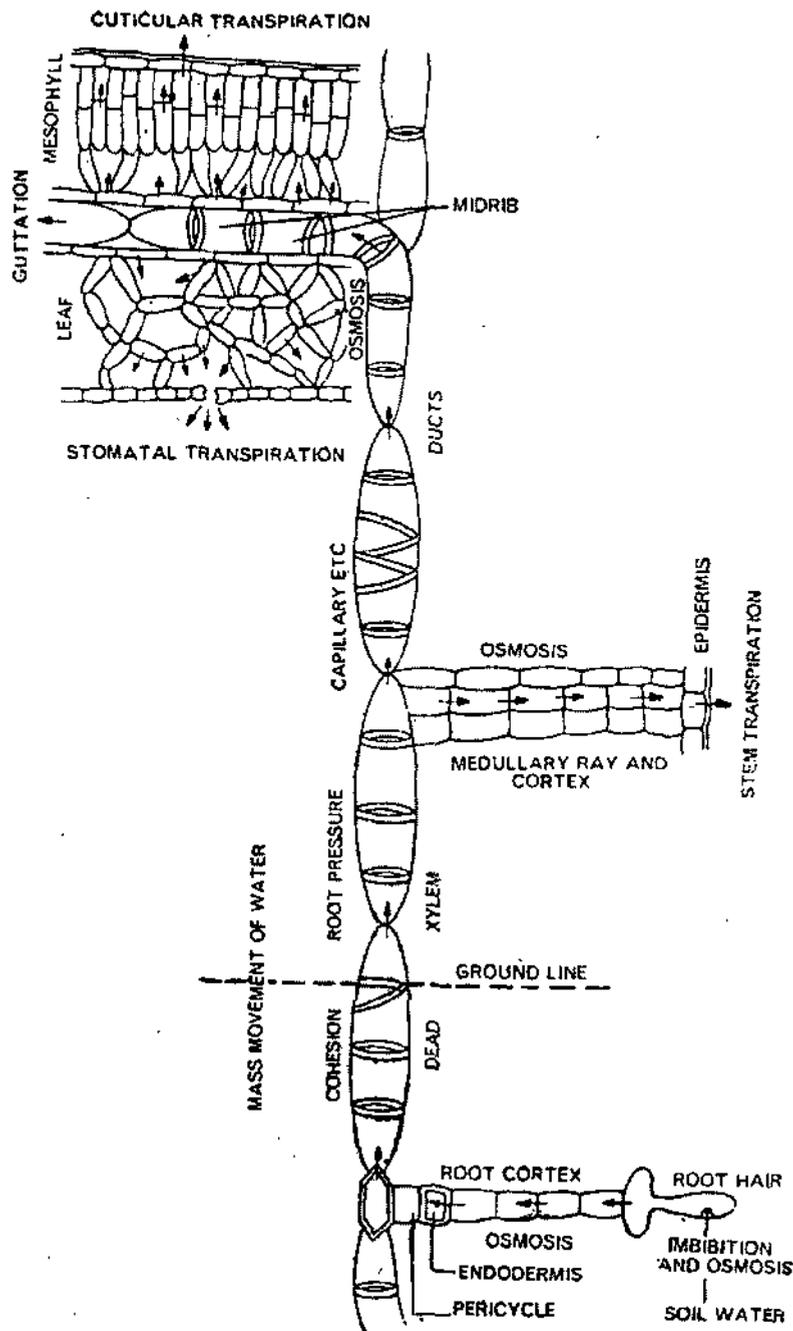


Fig. 3. Diagrammatic representation of the path of water through the plant. Various forces concerned are also shown.

(1) **Transpiration pull** : Water evaporates from the mesophyll cells to the intercellular spaces of the leaves and then finally diffuses out through the stomata. The diffusion pressure deficit for water in the mesophyll cells increases and they absorb water from the neighbouring cells and finally from the xylem of the nearby vein. These veins then get water from the midrib of the leaf (Fig. 3). Which in turn pull water from the stem. Thus, with the increase in the rate of transpiration the water in the xylem element remains under tension and the water through the stem is taken up from the roots. This tension developed due to transpiration is called the **transpiration pull** and has been found to reach a value of 10 to 15 atmos. in some cases. Since 1 atmos. can raise the level of water to about 10 meters, it requires a maximum pressure of about 12 atmosphere to raise the water in tallest trees which measure about 120 meters.

The existence of transpiration pull in plants can be shown by a simple experiment. A vertical glass tube is filled with water. On its upper end is fitted the cut end of a branch and the lower end is dipped in a vessel containing mercury (Fig. 4). As the water is transpired mercury is drawn in the tube. Rise in the level of mercury gives us the pressure developed due to transpiration. During the hot dry summer month, when transpiration is most active, if a hole is made in the tree trunk and is connected air tightly to a vessel of water through a bent tube, the water from the vessel is taken into the stem and not forced out of it. It indicates that there is present more pull on the water from above than the pressure from below.

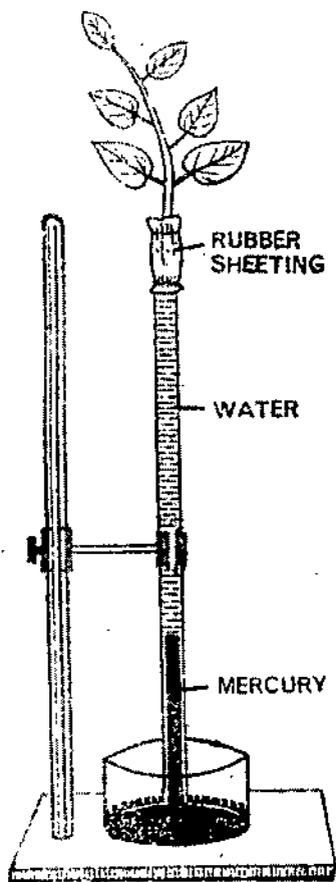


Fig. 4. Demonstration of force of transpiration pull.

(2) **Cohesive Force of Water** : Water molecules are firmly attached with each other due to pressure of the mutual attraction force or cohesive force between them. There also exists some attraction between the wall of the xylem element and the water





4. When wilting of plant occurs ?
5. According to relay pump hypothesis, water rises in stem due to activity of which cells ?

**ANSWERS**

1. Transpiration
2. Transpiration is very low and absorption is very high
3. Transpiration-cohesion theory of Dixon
4. Xylem is blocked
5. Medullary rays.

□□□

## 5

## ABSORPTION OF MINERAL SALTS

## STRUCTURE

- Introduction
- Elements found in plants
- Soil as source of mineral elements
- Mechanism of mineral salt absorption
- Passive absorption of minerals
- Active absorption of minerals
- Student activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know that how the plants absorb mineral salts ?

## 1.0. INTRODUCTION

When a plant or its part is kept at 100°C for some time, its water content evaporates and the dry matter is left which though ranges from 90 percent (in dormant structures like seeds) to about 5 percent or even less in succulent plants. This dry matter fraction when heated at about 600°C in a muffle furnace, a small greyish residue is left and is called the ash. Almost all of the dry matter is oxidized and the decomposition products pass off in the form of gases. Nitrogen also is released together with hydrogen, oxygen and carbon. It shows that the dry matter mainly consists of organic substances. The ash content on the other hand corresponds to the mineral elements which occur mainly as oxides. The total ash content of plant tissues and organs usually varies from a fraction of 1 to 15 percent of the dry weight of the plant material.

## 1.1. ELEMENTS FOUND IN PLANTS

On chemical analysis the plant ash is found to have almost upto sixty of the known mineral elements. The composition of ash varies both with the species and the environmental conditions under which the plant is growing. The commonly present minerals are K, Ca, Mg, Fe, Mn, Al, Si, P, S and Cl. Besides the plant also contain C, H, O and N which go out as carbon dioxide, water and ammonia during combustion. Carbon is obtained in the plants from air as carbon dioxide, hydrogen as water from soil and oxygen is derived both from water and carbon dioxide. All other elements are absorbed from the soil.

## 1.2. SOIL AS SOURCE OF MINERAL ELEMENTS

Most clay particles or micelles of the soil have negatively charged surface (anions). These charges are usually balanced by the binding of positively charged ions (cations), taken from the soil. Of the cations present in the soil aluminium ion,  $Al^{+++}$ , is the most strongly absorbed. Other ions commonly found in the soil can be represented in order of decreasing affinity for negatively charged surface, are  $H^+ > Ca^{++} > Mg^{++} > K^+ > NH_4^+ > Na^+$ . The situation in which one species of cation trades position or displaces a sound species of cation at an absorption site on any negatively

charged surface is referred to as cation exchange. Addition of cations to the soil may decrease its pH. Due to the negative charge on clay micelles, anions such as  $\text{NO}_3^-$  are usually not retained in the surface layers of soil. It is therefore, suggested that nitrate containing fertilizers be applied fairly frequently to the soil. The principal anions of the soil are  $\text{NO}_3^-$ ,  $\text{SO}_4^{--}$ ,  $\text{HCO}_3^{--}$ ,  $\text{H}_2\text{PO}_4^-$  and  $\text{OH}^-$ .

### 1.3. MECHANISM OF MINERAL SALT ABSORPTION

For long it was believed that the inorganic salts are passively carried away into the plant with the absorption of water or diffuse into the roots by the process of osmosis. Recent studies have however clearly shown that inorganic salt absorption is an active process. Various views regarding mineral salt absorption are studied under two main heads : (1) Passive absorption and (2) Active absorption.

### 1.4. PASSIVE ABSORPTION OF MINERALS

The absorption of ions by diffusion or other purely physical process, in which metabolic energy of living cells is not used, is called **passive absorption**. It may take place in various ways :

(1) **Diffusion** : When the concentration of mineral elements is more in the soil solution than that of the root cells, the absorption of these elements by the roots is done by simple physical process called diffusion. It may continue only till its concentration inside the cells is lower than its concentration outside. It has however, been found that ions accumulate against a concentration gradient also.

(2) **Mass Flow** : Many workers like **Kramer** (1956) and **Russel and Balber** (1960) believe that ions are taken up by the roots with the mass flow of water, taking place under the influence of transpiration. Increase in the rate of transpiration could increase the rate of salt absorption, where ion concentration bathing the roots is high. However, transpiration rate seems to have little or no effect on the rate of salt absorption if the ion concentration around the roots is low. Thus, the entry of ions into the roots is more dependent upon the maintenance of a steep concentration gradient between the root cells and the soil, rather than on transpiration current.

(3) **Mechanism of ionic Exchange** : In this case exchange of anions or cations from within the cells for ions of the same sign and equivalent charge in the outer solution. In excised barley roots which have absorbed radioactive  $\text{K}^+$  ions, these ions are replaced by non radioactive  $\text{K}^+$  ions when these roots are placed in a solution of non radioactive  $\text{KBr}$ , but the ions do not come out when the roots are placed in distilled water. This ionic exchange is not affected by the rate of respiration and has been explained by two theories : (a) the **contact exchange theory** and (b) the **carbonic acid exchange theory**. In the case of contact exchange theory an ion may be absorbed by the root of plant without being first dissolved in soil solution. An ion adsorbed electrostatically to a solid particle, such as a clay micelle or plant root, is not held too tightly and oscillates within a certain small volume of space. An exchange of ions takes place when the oscillation volume of one ion overlaps the oscillation volume of another ion (Fig. 1A). In carbonic acid exchange theory, the soil solution provides the medium for the exchange of ions between the root and the clay micelles. Carbon dioxide released in respiration combines with water to form carbonic acid in the soil solution. The carbonic acid dissociates into  $\text{H}^+$  and  $\text{HCO}_3^-$  ions. A cation adsorbed to the clay surface may be exchanged with  $\text{H}^+$  ion of the soil solution. This cation may then diffuse to the root surface in exchange for  $\text{H}^+$  ion. The cation may also be absorbed as ion pairs with bicarbonate. The ion exchange mechanism, thus, would allow for a greater absorption of ions from the external medium than expected by simple diffusion.

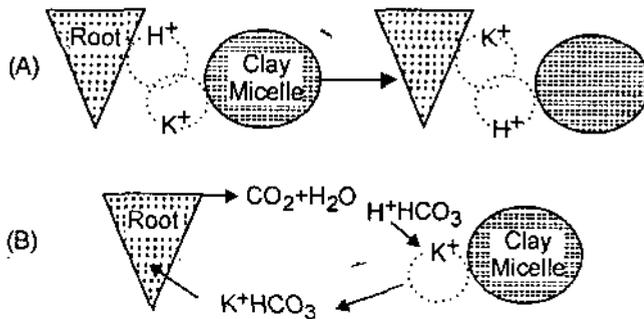


Fig. 1. Diagrammatic representation of (A) The contact exchange theory and (B) The carbonic acid exchange theory.

(4) **Donnan Equilibrium Theory** : It takes into account the effect of fixed or indiffusible ions. Suppose the membrane separating the cell from the external medium is permeable to some ions and not to others. On the inner side of this membrane there is a concentration of anions to which the membrane is impermeable (fixed anions). If this membrane is permeable to the cations and anions present in the external solution, equal number of cations and anions from the external solution will diffuse across the membrane until the equilibrium is established. This equilibrium normally is balanced electrically also. To balance the negative charge of fixed 'anions' present on the inner side, additional cations are absorbed. The cation concentration therefore, would be greater in the internal solution than in the external solution and the anion concentration would be less in internal solution.

$R^-$  are the fixed anions in Fig. 2, and are balanced by the entry of  $K^+$  ions from outside. The external anion ( $Cl^-$ ) enter into the cell due to diffusion gradient. Together with each anion a cation of equal charge also enters in. As such the entry of  $K^+$  will be against its concentration gradient and their concentration inside the cell becomes greater than that on the outside. This equilibrium which is controlled both by electrical as well as diffusion phenomenon is called **Donnan equilibrium**.

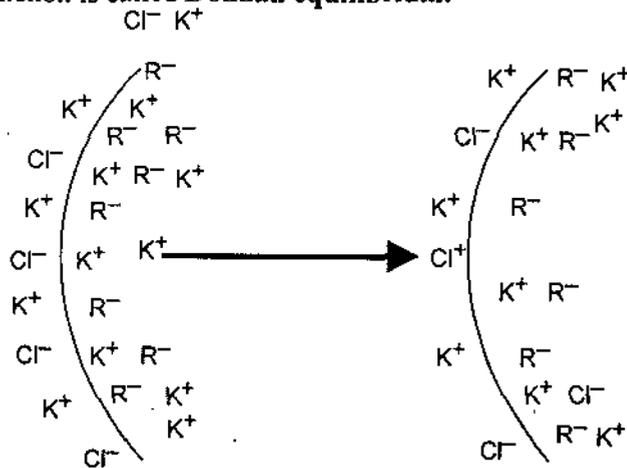


Fig. 2. Donnan equilibrium. At equilibrium the ratio of  $Cl^-$  concentration outside to that inside the cell

$$\frac{(Cl^-)^0}{(Cl^-)^I} \text{ equals the ratio of } K^+ \text{ concentration inside to that outside the cell. } \frac{(K^+)^I}{(K^+)^0}$$

Thus, the Donnan equilibrium results in an accumulation of ions in a cell against their concentration gradient without using the metabolic energy.

### 1.5. ACTIVE ABSORPTION OF MINERALS

The absorption of ions at the expense of metabolic energy of living cells is known as **active absorption**. **Hogland** (1944) demonstrated that both cations and anions are accumulated by plants against concentration gradients. The concentration of these salts is invariably higher in the cell sap than on the outside.

There are two main evidences supporting the active uptake of ions :

(a) Rate of absorption of ions is too rapid to be explained by passive absorption.

(b) Rate and amount of mineral absorption is directly related to the expenditure of metabolic energy.

Various mechanisms suggested to explain ion transport generally accept the presence of a **carrier compound** which mediates the transport of ions across an impermeable membrane.

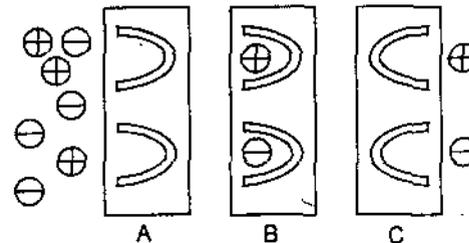


Fig. 3. Model explaining the carrier concept (a) membrane is semipermeable to ions (b) carrier ion complex is formed and (c) ions are released into inner space.

**The Carrier Concept**

The plasma membrane does not allow the free movement of ions from outside to the inside. It is believed that the carrier compounds present in the membrane, form **carrier ion complex** which moves across the membrane. Ions are released from the complex on the inside and can not move out and thus, are accumulated. The carrier compound brings in more ions (Fig. 3).

Two mechanisms have been described for salt absorption by carrier concept :

(1) **Carrier mechanism involving ATP : Bennel Clark (1956)** suggested a mechanism using ATP for active salt absorption. According to him the phospholipids may be important in the transport of ions across the membranes. In this transport **lecithin**, a phospholipid, is synthesized and hydrolyzed in a cyclic manner picking up ions on the outer surface and releasing them on hydrolysis into inner space. The synthesis of at least one of the components of this **phosphatide cycle** requires ATP (Fig. 4).

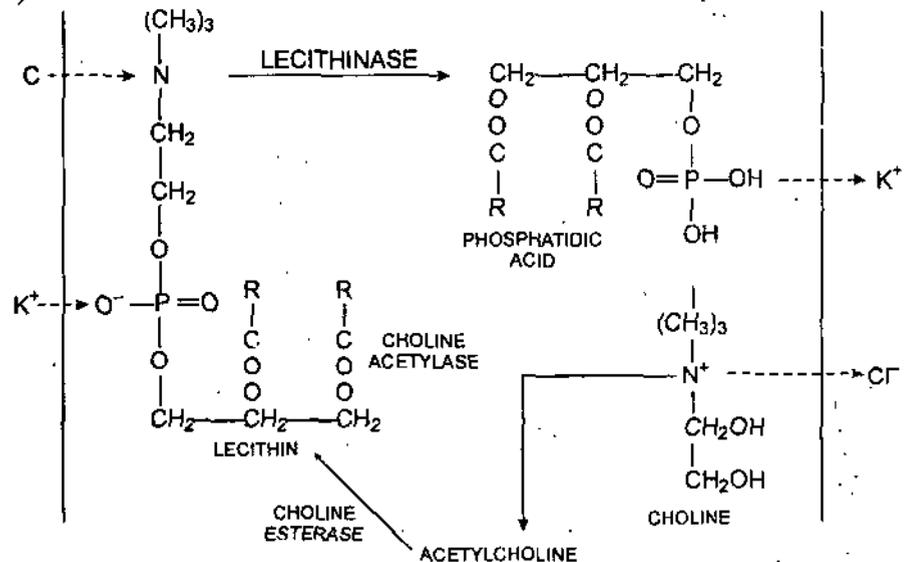


Fig. 4. Diagrammatic representation of phosphate cycle. At left ions from outerspace are picked up by lecithin. Hydrolysis of lecithin-ion complex release ion to inner space. Lecithin is then resynthesized (After Bennet-Clark 1956).

(2) **Cytochrome Pump Hypothesis : Lundegarh and Burstrom (1933)** have shown increase in the rate of respiration in a plant when it is transferred from water to salt. This increase in rate of respiration they called as **salt respiration**. **Lundegarh (1950,**

1954), observed a quantitative correlation between anion absorption and salt respiration. Such correlation does not exist with cations and therefore, he believed that only anions are transported actively. The salt respiration and anion absorption are both inhibited by cyanides or carbon monoxide. **Lundegarth**, therefore, believed that transport of anions is mediated through cytochrome oxidase and that cytochromes may be the ion carriers. (Fig. 5).

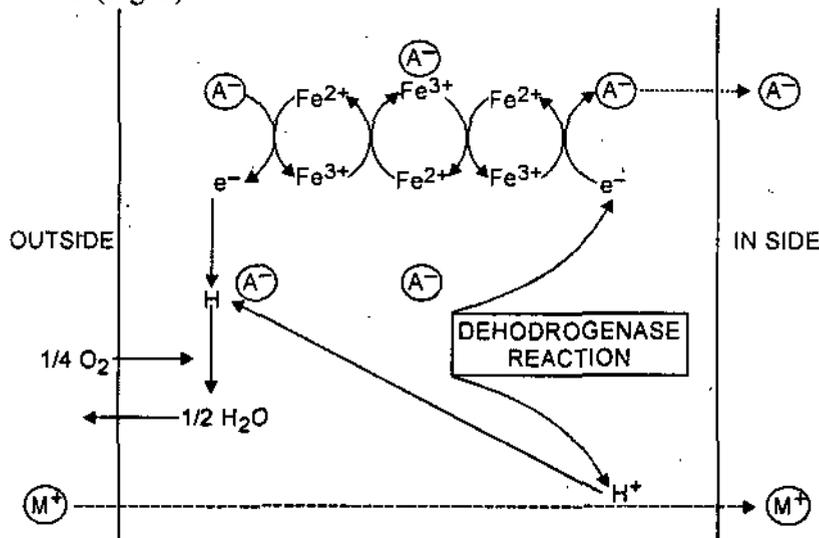


Fig. 5. A diagrammatic representation of Lundegardh's cytochrome pump theory on salt absorption. The anions ( $A^-$ ) are actively absorbed via 'cytochrome pump'. The cations ( $M^+$ ) are absorbed passively (After Lundegardh 1950).

According to **Lundegarth**, of the protons ( $H^+$ ) and electrons ( $e^-$ ) produced by on the inner surface by dehydrogenase reaction, the electrons move outward via a cytochrome chain, while anions move inward. At the outer surface of the membrane, the reduced ion of the cytochrome is oxidized, losing an electron and picking up an anion. The electron units with a proton and oxygen to form water. At the inner surface the oxidizing ion of the cytochrome becomes reduced by the addition of an electron released in dehydrogenase reaction. The anion is released on the inside. The cations ( $M^+$ ) are absorbed passively to balance the potential difference caused by the accumulation of anions on the inner surface.

The cytochrome transport theory, though, gives a good account of the utilization of metabolic energy in ionic absorption, yet it has been criticized by several workers. For example **Robertson et al.** (1957) found that 2, 4-dinitrophenol (DNP) increases respiration but decreases salt absorption. **Overstreet** (1955) has shown that not only anions but also cations like potassium and sodium stimulated respiration. Lastly as assumed in this theory, the presence of one carrier for all anions, a competition be set up for binding sites of anions, but it is now well known fact that anions like sulphate, nitrate, and phosphate etc. do not compete with one another.

**Absorption of Mineral Salts by Aerial organs :** Minerals can also be absorbed by the stem and leaves in the plants by spraying methods. This method has usually been found satisfactory in case of micronutrients and not for macronutrients, though, nitrogen in the form of urea has been supplied successfully in pine apple. The minerals can also be lost from the leaves to a little extent by leaching during rains.

## 1.6. STUDENT ACTIVITY

1. Give active absorption of mineral salts by higher plants.

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2. Give a concise account of the mechanism of absorption of mineral salts by the plants.

### 1.7. SUMMARY

Plants absorb the essential (mineral) elements from the soil through roots by passive or active absorption. An absorption (or transport) of ions and molecules into the cells propelled by the physical driving forces *i.e.*, without the use of metabolically produced energy is called **passive absorption**. Passive absorption of minerals in plants is carried out by diffusion, facilitated diffusion, ion exchange mechanism, Donnan equilibrium and by **mass flow hypothesis**. In free diffusion and facilitated diffusion, the ions and molecules move from a region of their higher chemical potential (concentration) to lower chemical potential along the concentration gradient. The ion exchange mechanism provides a greater opportunity for absorption of ions from the external medium. It can be explained by the two widely accepted theories namely, the contact exchange theory and the carbonic acid exchange theory. The Donnan equilibrium theory describes the effect of fixed or non-diffusible anions which mostly accumulate on the inner surface of the outer (cell) membrane. Donnan equilibrium refers to the maintenance of electrical balance of the cations and anions within the cells. Mass flow hypothesis of the mineral transport proposes that the ions move through the roots alongwith the stream of water under the influence of transpiration. The Donnan equilibrium theory and the mass flow hypothesis explain, very well, the accumulation of ions against a concentration gradient without the participation of metabolic energy.

The absorption (or transport) of mineral ions by the plants against the concentration gradient, involving the expenditure of metabolically produced energy is called **active absorption**. The energy utilized in active transport of minerals is derived from respiration and is supplied through ATP. The mechanism of active absorption of mineral is explained on the basis of carrier concept (Honert 1937). According to this, certain specific carrier compounds (*i.e.*, cytochromes or ATP) present in the plasma-membrane are believed to help in the transport of ions. Experimental evidences indicate that there is a sudden fall in active absorption of mineral ions when the roots are deprived of oxygen (*i.e.*, no respiration and no release of energy).

### 1.8. TEST YOURSELF

1. By what method, ions are absorbed by plants ?
2. Who proposed the mass flow hypothesis for ionic absorption ?
3. Which hypothesis best explains the passive absorption of ions against concentration gradient ?
4. According to **Lundegarth** which enzyme facilitates the ion transport ?
5. According to **cytochrome pump hypothesis**, how the anions and cations are transported ?

### ANSWERS

1. By carriers and pumps.
2. **Hylmo**
3. Donnan-equilibrium hypothesis
4. Cytochrome oxidase
5. by active and passive mechanism respectively.

□□□

## 6

## MINERAL NUTRITION OF PLANTS

## STRUCTURE

- General role of the mineral elements in plants
- Essential and non-essential elements
- Specific role of essential elements in plants : Macronutrients
- Micronutrients
- Soilless growth or hydroponics
- Student activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know the deficiency system of the mineral elements and their role in plants.

## 1.0. GENERAL ROLES OF THE MINERAL ELEMENTS IN PLANTS

Minerals influence the physiological processes in plants only when present in ionic form or as constituent of organic molecules. They perform following functions in the plant cells :

**1. Constituent of Plant Body :** Elements like carbon, hydrogen and oxygen become constituents of structural molecules *e.g.*, carbohydrates, which enter into the composition of protoplasm and cell wall. These are called **framework elements**. Elements like sulphur, nitrogen and phosphorus form constituent of proteins and nucleotides and are called **protoplasmic elements**. Magnesium enters in chlorophyll while calcium in calcium pectate of the cell wall.

**2. Catalytic functions :** Elements like, zinc, copper and iron work as prosthetic groups of certain enzymes. Iron is a constituent of cytochromes also. Some elements like magnesium, manganese, potassium, cobalt, molybdenum and boron act as activator or inhibitor in some enzymatic systems.

**3. Regulation of Osmotic Potential :** Osmotic potential of the cell sap of any cell together with organic compounds is also determined by the dissolved minerals it contains.

**4. Influence on the pH :** The minerals absorbed from the soil also affect the pH of the cell sap. Potassium, calcium, sodium and magnesium form important cations of the two important buffer systems found in plants – the phosphate and the carbonate systems.

**5. Toxic effect on protoplasm :** Elements like aluminium, arsenic, boron, copper, fluorine, lead, magnesium, mercury, molybdenum, silver and zinc are highly toxic to the plants, at least under certain conditions. Some of these elements are essential for plant metabolism but become toxic beyond a certain required concentration.

**6. Influence on the Permeability :** Some of the ions present in contact with the cytoplasmic membranes increase their permeability, while others decrease it.

**7. Antagonistic or Balancing function :** Some elements counteract the toxic effect of other minerals by maintaining the ionic balance. Calcium, magnesium and potassium are some of such elements.

## 1.1. ESSENTIAL AND NON-ESSENTIAL ELEMENTS

Of the large number of elements found in the plants only some are needed for their healthy growth. These are called **essential elements**. The rest of the elements were considered as **non-essential elements**. In the beginning only ten essential elements were known, carbon, hydrogen and oxygen obtained from water or air and N, P, S, Ca, Mg, K and Fe obtained from the soil. Recently by refined techniques six more elements have been added to this list — B, Mn, Zn, Mo, Cl and Cu. Of these sixteen elements, the first ten are required by the plants in large quantities and are known as **macronutrients** or **macrometabolic elements** or **major elements**, while the last six are needed in traces and are called **macronutrients** or **macrometabolic elements** or **minor elements** or **trace elements**. There is every possibility that in near future further addition might take place in the list of essential elements.

The essentiality or the role of a particular mineral is studied with the help of **culture experiments** which may be of two types — **water culture** (Fig. 1) and **sand culture**. In this method the plants are grown in an artificially provided nutritive culture having all essential elements except the one for which the role is to be determined. The change from the normal structure of plant is ascribed to the absence of that element. Several workers like Sachs, Knop, Shive and Hoagland have given some standard culture solutions in which plants could be grown in healthy manner. The composition of these solutions are given in table 1.

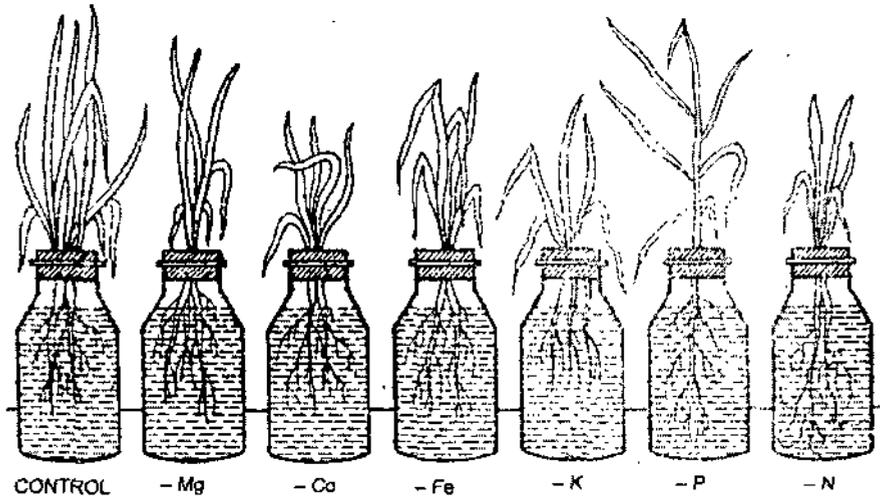


Fig. 1. Solution culture experiment.

Table 1 : The composition of some nutrient solutions

Salt	Sach's solution (1860) g/litre	Knop's solution (865) g/litre	Shive's solution (1915) g/litre	Hoagland's solution (1920) g/litre
$\text{KNO}_3$	1.0	0.2	—	0.51
$\text{Ca}_3(\text{PO}_4)_2$	0.5	—	—	—
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.5	0.2	0.55	0.49
$\text{CaSO}_4$	0.5	—	—	—
$\text{NaCl}$	0.25	—	—	—
$\text{FeSO}_4$	Trace	Trace ( $\text{FePO}_4$ )	0.005	—
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	—	0.8	1.06	1.18
$\text{KH}_2\text{PO}_4$	—	0.2	0.31	0.14
Minor elements	—	—	trace	0.005 (ferric tartarate)

## 1.2. SPECIFIC ROLE OF ESSENTIAL ELEMENTS IN PLANTS : MACRONUTRIENTS

**Carbon, Hydrogen and oxygen.** These elements, though are not minerals but are included here because the existence of plant body is not possible without these elements. These are absorbed as carbon dioxide and water from air and water respectively.

### Nitrogen

It is absorbed from the soil in the form of nitrates, nitrites and ammonium salts. Though it can be given to the plants as nitrates of sodium, potassium or calcium but the best form is ammonium nitrate. Some bacteria fix the atmospheric nitrogen and make it available to the plants.

**(a) Physiological role :** Nitrogen forms an important constituent of proteins, amino acids, nucleic acids etc. It also forms a component of certain enzymes, coenzymes, chlorophyll, and many hormones.

**(b) Deficiency symptoms :** The most typical symptom of nitrogen deficiency is the development of chlorosis in the leaves which gradually changes to general yellowing of the plant. As nitrogen is readily translocated in the upper parts, the younger leaves are affected later. Due to lack of chlorophylls the carotenoid pigments mask the leaves. The rate of formation of anthocyanins, is increased and the leaves turn purplish. In nitrogen deficient plants, the leaves become smaller, early defoliation takes place, shoot growth is suppressed, shoot becomes thin and weak and the flowering is delayed or completely suppressed.

### Sulphur

It is absorbed from the soil as sulphate ion.

**(a) Physiological role :** Sulphur is used in the formation of certain amino acids *e.g.*, cystine, cysteine and methionine which form a part of certain proteins and enzymes. The vitamins thiamin and biotin also contain sulphur. In addition, it also forms a component of coenzymes A of Kreb's cycle. Sulphur also helps in the formation of oils and provides typical odour to the mustard, garlic and onion. It also promotes cell division, fruit formation and the formation of chlorophyll.

**(b) Deficiency symptoms :** In sulphur deficient plants the leaves become reduced, growth is stunted, and chlorosis also takes place. As it is immobile, the young leaves are affected by chlorosis earlier. Other symptoms developing on the plants are — rapid leaf fall, leaf margins and tips rolled inward, root system becomes extensive, sclerenchyma increases in stems and the growth of the terminal bud is inhibited, while premature development of lateral buds takes place.

### Phosphorus

It is absorbed from the soil in the form of phosphate ions,  $H_2PO_4^-$  and  $HPO_4^{2-}$ .

**(a) Physiological role :** Phosphorus forms an important constituent of the nucleic acids nucleoproteins, phospholipids, sugar phosphates, ATP, NADP and numerous phosphorylated compounds which are used in cell metabolism. It is relatively more abundant in the growing and storage regions.

**(b) Deficiency symptoms :** Due to phosphorus deficiency rate of protein synthesis decreases, and carbohydrates and nitrogenous compounds accumulate. It may result in premature leaf and fruit fall and the anthocyanin pigments are developed. The leaves become dark green and brown necrotic patches develop on the leaves and petioles. Root growth is checked, flowering is delayed and branching is sparse.

## Calcium

It is absorbed from the soil as  $\text{Ca}^+$  ions from calcium carbonate or calcium oxide.

**(a) Physiological role :** Most of calcium is found in the leaves of plants. It is present more in older leaves. It forms the middle lamella of cell wall in the form of calcium pectate. In some cases it is present as crystals of calcium oxalate. It is essential for continued growth of apical meristem, and for nitrogen assimilation. In the absence of calcium, urea serves as the source of nitrogen to the plants. It serves as an activator for certain enzymes *e.g.*, amylase, and pollen tube germination. It stimulates the development of root hairs and promotes the activity of chloroplasts. It favours the movement and utilization of carbohydrates and amino acids in the plants. Stability of chromosome depends on the presence of calcium (Hewitt, 1963). It reduces the toxicity of inorganic elements like magnesium and sodium.

**(b) Deficiency symptoms :** In calcium deficient plants, chlorosis usually occurs along the margins of young leaves, the root and shoot tips are disintegrated and become disfigured, flowers fall prematurely in legumes and the seed formation is hindered.

## Potassium

It is taken from the soil as  $\text{K}^+$  ion.

**(a) Physiological role :** Potassium occurs in plants mainly as soluble inorganic salts, though some salts of organic acids are also found. It is found in large amounts in actively growing regions of plants like buds, young leaves, root and shoot tips. Its fundamental roles in plant metabolism are largely catalytic and regulatory. It also plays a role, probably osmotic, in the opening of stomata. It acts as an activator of over forty enzymes including the ones needed for protein synthesis and phosphorylations. It is also essential for the formation and translocation of sugars in the plants. Plants like sugar-beets, potatoes and others which store large quantities of carbohydrates are quite responsive to the supply of potassium. It is also needed for cell division, reduction of nitrates, maintaining the cellular organization, permeability and hydration.

**(b) Deficiency symptoms :** In potassium deficient plants scorching of older leaves is the most typical symptom. The leaf tip and margins show chlorosis, the growth of internodes is retarded. Sometimes the dominance of apical bud is diminished resulting in a bushy appearance due to lateral buds becoming active. The grain weight decreases. Growth in the apical regions is checked. Other effects of potassium deficiency are the loss of vigour, disease resistance is reduced, and the mechanical tissues are poorly developed.

## Magnesium

It is taken from the soil.

**(a) Physiological role :** Magnesium forms the mineral constituent of chlorophyll molecule. It is also present in the seeds. Magnesium ion works as activator for a number of enzymes like certain transphosphorylases, dehydrogenases and carboxylases. The integrity of the ribosomes is also maintained by the presence of magnesium. It also helps in the absorption and movement of phosphorus in the plant and thus, influences the nucleoprotein synthesis and also the process of respiration.

**(b) Deficiency symptoms :** Magnesium deficiency causes extensive chlorosis in the leaves. The older stages Leaves are affected earlier than the younger ones. In later stages anthocyanin pigments and necrotic patches are developed on the leaves.

## Iron

It is absorbed from the soil in ferrous forms, though some ferric ions are also absorbed, which are changed to ferrous stage in the cells. In alkaline soil it remains in insoluble state.

(a) **Physiological role** : Iron is essential for the formation of chlorophyll. It also forms a constituent of ferredoxin, flavoproteins, iron-porphyrin-proteins including cytochromes, peroxidases, and catalysis and therefore, plays an important role in respiration.

(b) **Deficiency symptoms** : Iron deficient plants develop chlorosis. The young leaves may become yellow or white with prominent green veins. The chlorosis may be general or local (due to immobility). Sometimes the chlorosis may be found in the leaves containing as much iron as green leaves. It is because the iron there is present in unavailable form.

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### 1.3. MICRONUTRIENTS OR TRACE ELEMENTS

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#### Manganese

It is taken in very small amounts from the soil.

(a) **Physiological role** : Manganese is most abundant in physiologically active parts e.g., leaves. It acts primarily as an additional catalyst in oxidation reduction phenomenon and also as an activator for certain enzymes. It also seems to be related in some way with the synthesis of chlorophyll and the transfer of electrons from water to photooxidized chlorophyll in photosynthesis (Homann, 1967).

(b) **Deficiency symptoms** : Manganese deficient plants also show chlorosis but slightly different than those developed due to N or Mg deficiencies. It results in a mottled appearance of the leaf, with dead brown or gray spots. Some common diseases developed in plants due to Mn deficiency are 'gray speck of oats' 'spackled yellows of sugar beet' and the 'frenching of tung'.

#### Boron

It is absorbed from the soil as borate ions.

(a) **Physiological role** : Boron reaches its greatest concentration in the leaves and is believed to be useful for the translocation of sugars. It has been seen that places of high metabolic activity in a plant, requiring high quantities of sugar, are the first to be affected by boron deficiency. It is also believed to influence cell division, active salt absorption, photosynthesis, flowering and fruiting in the plants.

(b) **Deficiency symptoms** : Deficiency of boron causes death of the shoot tips and the root tips. The shoot growth is stunted, and the flower formation is checked. The formation of nodules in the leguminous roots is checked. The formation of new leaves is stopped which ultimately leads to the death of the plant. At the end of twigs the branches may form rosettes, probably due to degeneration of terminal bud. Some common physiological diseases caused by the boron deficiency are 'leaf roll of potato', heart rot of sugar beet, browning of cauliflower and brown heart of turnip.

#### Zinc

The element is highly toxic to the plants except in very low concentrations.

(a) **Physiological role** : Zinc is a constituent of the enzymes carbonic anhydrase and glutamic dehydrogenase. It also works as an activator for certain enzymes. Its presence is essential for the synthesis of indole acetic acid, and some amino acids and therefore might influence protein synthesis.

(b) **Deficiency symptoms** : The zinc deficient plants show aberrancies in the root tips, the dwarfing of vegetative growth and the failure of seed formation. Some of the

common diseases caused due to zinc deficiency are — rosettes of pecan, white bud of maize, 'mottle leaf' diseases of apple and walnut, etc. Intraveinal chlorosis may develop in the leaves.

Large tracts of land in U. P., Punjab, Gujrat, Maharastra and South Indian states are deficient in zinc. It could be cured by foliar spray of zinc sulphate.

### Molybdenum

It is taken as molybdate ion from the soil and is required in smallest quantities in the plants (0.1 ppm).

(a) **Physiological rôle** : Molybdenum works as an activator for the enzyme nitrate reductase in nitrogen metabolism. It might be helpful in the synthesis of ascorbic acid also.

(b) **Deficiency symptoms** : Molybdenum deficient plants develop chlorotic interveinal mottling of the lower leaves and flower formation is inhibited on them. In cauliflower 'whiptail' disease has been assigned to molybdenum deficiency.

### Chlorine

Recently chlorine ion ( $Cl^-$ ) has been shown to be essential micrometabolic element in plants. **Vernon and Ke (1966)** believe that it is essential in the transfer of electrons from water to photooxidized chlorophyll in photosynthesis. It appears to act as an enzyme activator in the water — splitting reactions.

Apart from these sixteen so far described essential elements some more elements like sodium, cobalt, silicon, vanadium, aluminium and selenium play an important role in plant growth in some cases. For example **sodium** regulates the transport of amino acids to the nucleus and therefore, controls the synthesis of nucleoproteins and thus, is quite important for the growth of some plants. **Cobalt** ions are known to activate some enzymes like carboxylases and peptidases. It is a constituent of vitamin  $B_{12}$  and is supposed to be essential for some blue green algae.

## 1.4. SOILLESS GROWTH OR HYDROPONICS

The growing of plant in large shallow tanks constructed of concrete or sheet metal and filled with nutrient solutions with or without sand or soil is called **soilless growth** or **hydroponics** or **tank forming**. The ponds are covered with wire netting for the support of the plants. The aeration to these ponds is supplied with an inlet tube (Fig. 2). Some vegetables or ornamental plants like, tomatoes carrots and roses are grown by this method.

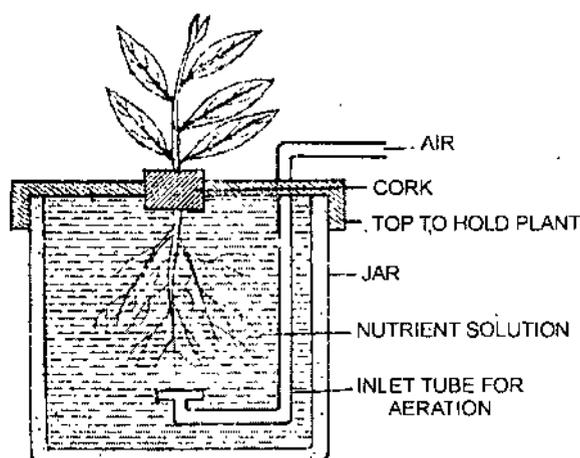


Fig. 2. Modern solution culture or pond culture.

### 1.5. STUDENT ACTIVITY

1. Write short note on trace elements.

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2. List the elements essential for plants. Mention the physiological role of nitrogen and iron.

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### 1.7. SUMMARY

The process of involving the absorption and utilization of various mineral ions by the plants for their growth and development is called **mineral nutrition**. Studies have revealed that as many as 60 different elements are present as constituents of plants. All of them are, however, not essential for plant growth. A mineral element is said to be **essential**, when it is absolutely necessary for normal growth and reproduction, when its requirement is specific and not replaceable by another element, and further the element is a part of the structural molecule and takes part in the biochemical process. Plants require some essential elements in relatively large quantities (**macronutrients**) and others in small amounts (**micronutrients**). The technique of cultivating or culturing plants (vegetable and ornamental) in nutrient solution (or water cultures) is known as **hydroponics**. An element is said to be **essential** if in its absence a plant does not grow normally and shows certain deficiency symptoms (hunger signs). Arnon and Hoagland (1940)'s nutrient solution is widely used in water culture experiments because it contains all the macro - and-micronutrients which are needed for the growth of a normal plant. Plants obtain all the elements from the atmosphere, water and soil. Carbon of a plant is derived from that of the carbon dioxide of the atmosphere. Hydrogen enters the plant mainly through water. Oxygen of a plant is obtained from the air, or from that of the water and often in the form of inorganic ions. Heterotrophic organisms obtain their nitrogen supply through the plants. All the inorganic essential elements which are obtained by the plants from the soil are called as **mineral elements**. On the other hand, the essential elements (C, H, O) which are obtained from the air or water are known as **non-mineral elements**. Nitrogen is considered a unique element as it is derived from both mineral and non-mineral resources. Mineral elements contribute towards the body make-up, affect the osmotic potential, pH of the cells, influence the permeability of the cell membranes and serve as catalysts in many reactions besides producing toxic, balancing and antagonistic effects in the plants. Deficiency of essential elements leads to symptoms such as chlorosis, stunting, necrosis, molting, abscission, heart rot and poor reproductive development etc.

### 1.7. TEST YOURSELF

1. Name the technique of growing plants in water or solution culture.
2. What is the major role of the phosphorous in plant metabolism?
3. Write the framework elements of the plants.

4. Name the process of involving the absorption and utilization of various mineral ions by the plants for their growth and development.
5. Write the sources from which plants obtain all the elements.

**ANSWERS**

- |                                |                                 |
|--------------------------------|---------------------------------|
| 1. Hydroponics                 | 2. To generate metabolic energy |
| 3. Carbon, hydrogen and oxygen | 4. Mineral nutrition            |
| 5. Atmosphere, water and soil. |                                 |

□□□

## 1

## PHOTOSYNTHESIS

## STRUCTURE

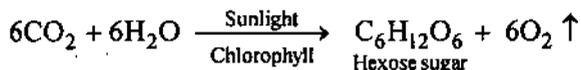
- Introduction
- Significance of photosynthesis
- Landmarks in studies of photosynthesis
- Chloroplast : The site of photosynthesis
- The chloroplast pigments
- Absorption spectrum and action spectrum
- Mechanism of photosynthesis
- Light reaction
- Dark reaction
- Photorespiration
- Hatch and slack cycle or C<sub>4</sub> cycle
- Factors affecting photosynthesis
- Student Activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

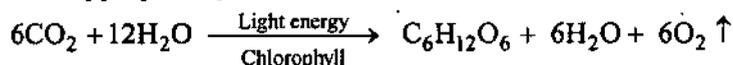
By learning this chapter you will be able to know the mechanism and significance of photosynthesis.

## 1.0. INTRODUCTION

*Ans-1* Green plants capture solar energy and convert it into chemical energy by the process **photosynthesis**. In simpler terms it is the conversion of the **light energy** into **chemical energy**. It is essentially the only mechanism of energy input into the living world. Photosynthesis literally means 'synthesis with the help of light'. It is an **anabolic, endothermic and reductional** process. The process of photosynthesis may be defined as "**the synthesis of simple carbohydrates from carbon dioxide and water in the presence of sunlight inside the chlorophyll containing cells**".



This definition consists only that simple carbohydrates are formed from photosynthesis. It is also proved that many other organic compounds are formed from intermediates of photosynthesis. In photosynthetic process water acts as reactant and provides hydrogen and electrons but in some micro-organisms such as bacteria hydrogen is obtained from other source than water. Therefore, some authors defined photosynthesis as "**the production of carbon containing compounds from carbon dioxide and a hydrogen donor by illuminated green cells**". In recent years this equation has been appropriately modified as follows :



About 170 million tones of dry matter is produced by the process photosynthesis annually. Globally 85-90% of the total photosynthesis is carried out by the algae of the oceans *i.e.*, **phytoplanktons** (Rabinowitch, 1951) but according to **Pyther** (1970), **Woodfall** (1970) only one third of the total photosynthesis can be attributed to the marine plants.

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### 1.1. SIGNIFICANCE OF PHOTOSYNTHESIS

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Photosynthesis is the most fundamental process, which is essential for the continued existence of life on earth. The significance of photosynthesis is as follows :

1. In any ecosystem plants are primary producers. Plants (autotrophs) trap the solar energy and form the carbohydrates with the help of inorganic raw materials. These carbohydrates provide food directly or indirectly to all consumers (heterotrophs). The light energy stored in the photosynthesis is released in the process of respiration and it is utilised in carrying out all the vital functions of life. So, we can say that **all the life is bottled sunshine**.

Plants without animals can survive but animals without plants cannot. So, it is true to say that "**all flesh is grass**".

2. Photosynthesis is the only natural process by which oxygen is liberated for the use of the other organisms. Thus, it creates and maintains the oxygenic atmosphere on the planet earth. Cyanobacteria (blue green algae) were the organisms which first began to release oxygen as a byproduct of photosynthesis.

3. It maintains the carbon oxide and oxygen ratio in the atmosphere.

4. Human beings use plants for fodder, timber, firewood, fibres etc. which are photosynthetic products.

5. Fossil fuels such as coal, petroleum, and natural gas are also the products of photosynthetic organism which lived million of years ago.

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### 1.2. LANDMARKS IN STUDIES OF PHOTOSYNTHESIS

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Manufacturing of food material by plants has attracted the attention of earlier philosophers. The modern knowledge of the process of photosynthesis is based on the experiments and discoveries of a number of scientists. Some important events in the history of process of photosynthesis are described there in chronological order :

**Ancient Indians** : They believed that plants fed from their feet. The Word **Padapa** means that which drinks from the feet. It is used in Sanskrit for a plant.

**320 B.C. — ARISTOTLE and THEOPHRASTUS** : They were great philosophers. They proclaimed that plants obtain all materials, inorganic and organic directly from soil. Plants obtain their food in pure form from soil humus. This idea become famous as **humus theory** and this theory reigned supreme for over seventeen centuries.

**1648 — VAN HELMONT** : Aristotle's idea was over thrown by a simple experiment performed by Flemish physician **J.B. Van Helmont**. He grew a small willow plant weighing 5 pound, in a barrel containing preweighed, oven dried 200 pounds of soil. The pot was carefully covered and was supplied by rainwater as and when needed. He watered it for five years. The small plant grew into young tree, which he carefully removed and weighed. It has gained 164 pounds and three ounces. He then redried the soil and weighed. It has lost only 2 ounces of the original weight. He, therefore concluded that all vegetation is only water.<sup>1</sup>

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1. It is an erroneous conclusion. Today, by the experiments it is confirmed that water is one of the essential raw materials contributing to dry matter. Hence, Van Helmont's view was only partially correct

1671 — **MARCELLO MALPIGHI** : In his book *Anatome Plantarum*, he had indicated that the green cells are the organs which prepare food for the plants.

1772 — **JOSEPH PRIESTLEY** : On the basis of his experiments he concluded that **Vegetation purifies the air which had been injured by burning of candle**. He called the air product by burning of the candle as "**phlogiston**" which is noxious for a mouse and said that plants convert it into "**dephlogiston**" which keeps the atmosphere pure.

1779 — **JAN INGEN-HOUSZ** : He demonstrated the role of light and green parts of the plants in purifying noxious air. He said that in dark, green leaves and stalks give out phlogisticated air (air rich in carbon dioxide) and light these green parts give out dephlogisticated air (air rich in oxygen) and make the air pure.

1782 — **JENE SENEBIER** : He showed that as the concentration of carbon dioxide is increased, the rate of oxygen evolution also increases.

1783 — **LAVOISIER** : He identified the purifying principle produced by green plants in sun light as oxygen (dephlogiston) and noxious air produced by the burning of candle as carbon dioxide (phlogiston).

1804 — **N. T. de SAUSSURE** : He recognised the importance of water in photosynthesis.

1818 — **PELLETIER and CLAVENTON** : They named the green coloured substance as **chlorophyll**.

1837 — **DUTROCHET** : He recognized the importance of chlorophyll in photosynthesis.

1840 — **LEIBIG** : He pointed out that organic matter was derived from carbon dioxide of the air.

1845 — **ROBERT MAYER** : He stated that ultimate source of energy utilised in both plants and animals is the sun and this light energy when absorbed by the plants is converted into chemical energy.

1862 — **SACHS** : He determined that starch was the end product of photosynthesis.

1870 — **VAN BAEYER** : He was a German scientist. He suggested that formaldehyde ( $\text{CH}_2\text{O}$ ) would be formed during photosynthesis as an intermediate and it would be converted into proteins.

1888 — **ENGLEMANN** : He plotted the action spectrum of photosynthesis.

1905 — **F.F. BLACKMAN** : He enunciated the law of limiting factors. He observed that the process of photosynthesis has two steps-**photochemical reaction** which proceeds only in the presence of light and a **dark reaction** for which light is not necessary.

1920 — **WARBURG** : He introduced the unicellular green algae *Chlorella* as a suitable experimental material to study photosynthesis.

1932 — **EMERSON and ARNOLD** : They carried out flashing light experiments and showed the existence of light and dark reactions.

1937 — **ROBERT HILL** : He demonstrated that isolated chloroplasts evolved oxygen when they were illuminated in the presence of suitable electron acceptor.

1941 — **RUBEN and KAMEN** : They used the radioactive oxygen ( $\text{O}^{18}$ ) to prove that the source of oxygen in photosynthesis is water.

1954 — **MELVIN CALVIN and Coworkers** : They traced the **path of carbon**. Calvin discovered various reactions involved in the conversion of carbon dioxide into carbohydrates using  $\text{C}^{14}\text{O}_2$ . These reactions are collectively known as  **$\text{C}_3$  cycle** or **Calvin cycle**. He was awarded the Nobel prize for this work in 1961.

1965 — **M. D. HATCH and C.R. SLACK** : They reported the  $\text{C}_4$  pathway for carbon dioxide fixation in certain tropical grasses.

1973 — **ROUHANI** : He proposed photosynthetic pathway in **CAM** (Crassulacean Acid Metabolism) plants.

1985 — HUBER, MICHEL and DISSENHOFER : They crystallized the photosynthetic centre of the bacterium, *Rhodobacter*. They analysed the structure of photosynthetic centre by X-ray diffraction technique. The Nobel prize in chemistry for 1988 was awarded to them for their work.

### 1.3. CHLOROPLAST : THE SITE OF PHOTOSYNTHESIS

In plants, photosynthetic apparatus are the chloroplasts. Schimper (1883) called the green plastids 'Chloroplasts'. Chloroplasts are present in all the green coloured eukaryotic cells. In higher plants they are present in peripheral cytoplasm of the palisade tissue and spongy parenchyma and cortical cells of the young stem. In prokaryotic cells such as cyanobacteria (blue green algae) and bacteria organized chloroplasts are absent. Fungi lack chloroplasts and are therefore, heterotrophs.

The chloroplasts in green plants constitute the photosynthetic apparatus. Typically, the chloroplasts of higher plants are discoidal or ellipsoidal in shape, 4-6 $\mu$  thick. The chloroplast is bounded by two unit membranes each approximately 50  $\text{A}^{\circ}$  thick and consisting of lipids and proteins. The thickness of the two membranes including the space enclosed by them is approximately 300  $\text{A}^{\circ}$ . Internally the chloroplast is filled with a hydrophilic matrix called stroma in which grana are embedded. Each granum has a diameter of 0.25-0.8 $\mu$  and consists of 5-25 disk shaped grana lamellae placed one above the other like the stack of coins (Fig. 1A). In cross section these lamellae are paired to form sac like structures and have been called as thylakoids. Each grana lamella or thylakoid encloses a space, the *loculus*. The ends of disk-shaped thylakoids are called as margins (which are fused to form sac like structure) while the contiguous membranes between two thylakoids form the partition. The grana lamellae or thylakoids consist of alternating layers of lipids and proteins.

Some of the grana-lamellae or thylakoids of a granum are connected with thylakoids of the grana by somewhat thinner stroma-lamellae or fret membranes. These also enclose spaces which are called as fret-channels (Fig. 1B).

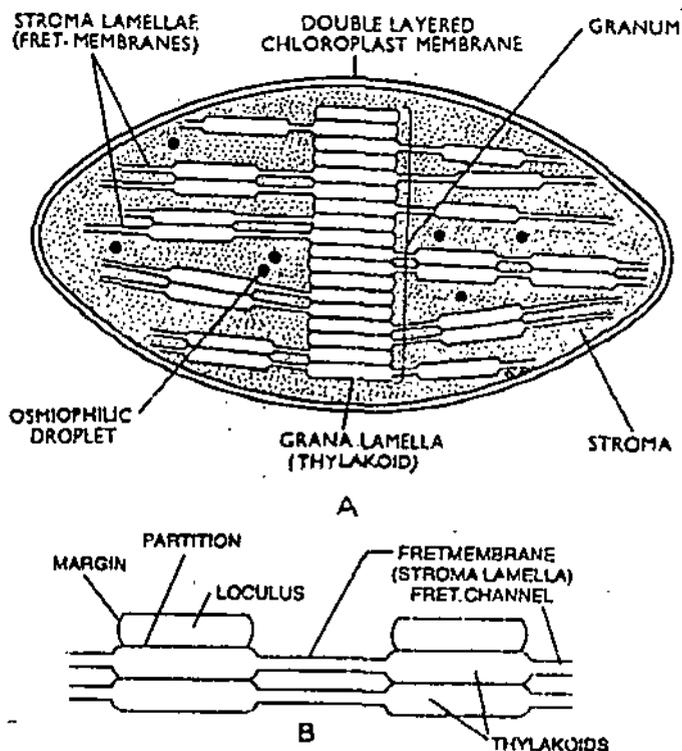


Fig. 1. A. Internal structure of a chloroplast. B. Few enlarged thylakoids from two grana.

Chlorophylls and other photosynthetic pigments are confined to grana. The latter are the sites of **primary photochemical reaction**. Besides necessary enzymes, some ribosomes and DNA have also been found in chloroplasts which give them (chloroplasts) a **partial genetic autonomy**.

#### 1.4. THE CHLOROPLAST PIGMENTS

The light is absorbed through the agency of certain molecules called **pigments**. Pigments are located on the thylakoid membranes and constitute about 5-8% of the total dry weight of the chloroplast. The role of pigment is to convert absorbed solar energy into chemical energy. Different colours of pigments are due to the visible spectrum which they reflect or transmit. There are mainly three types of pigments : **A. Chlorophylls**, **B. Carotenoids** and **C. Phycobilins**. The carotenoids and phycobilins are associated with chlorophylls and are known as **accessory pigments**.

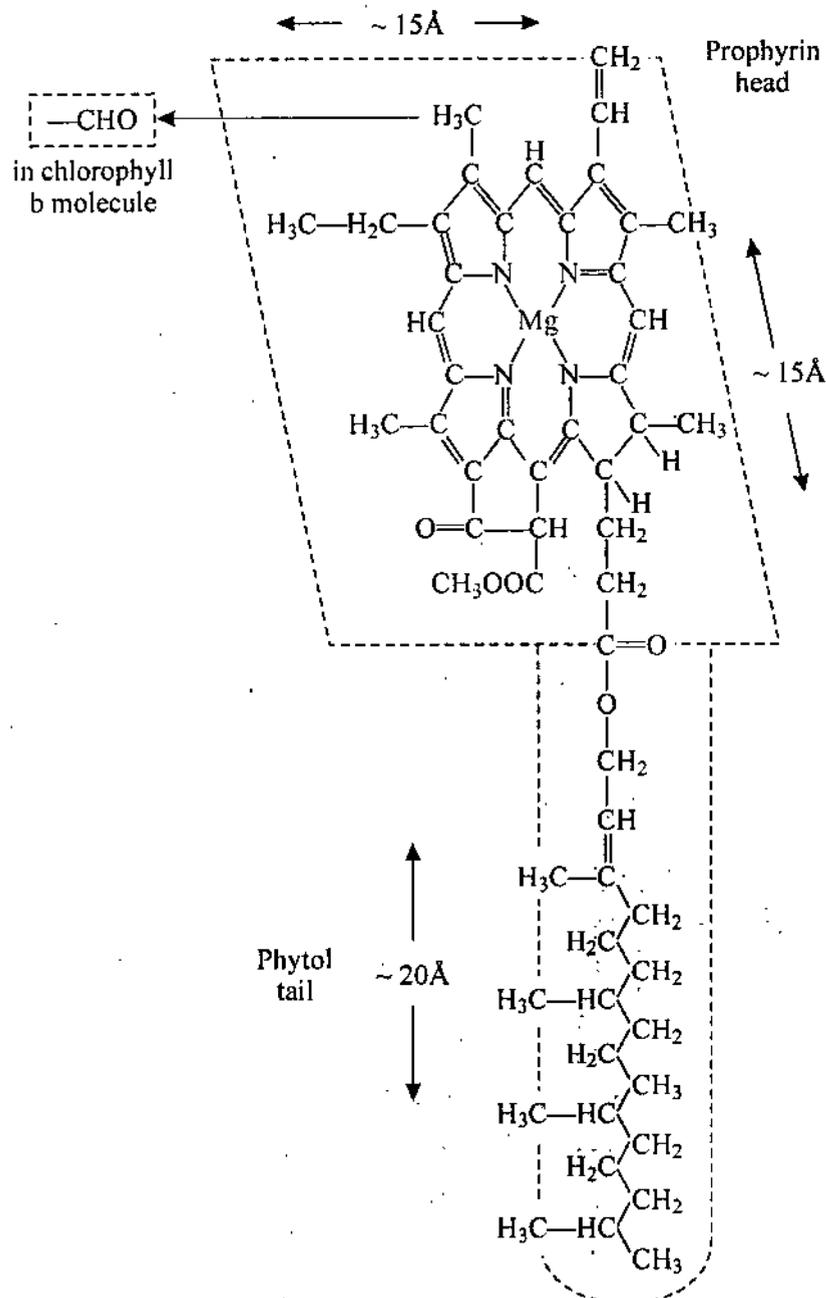
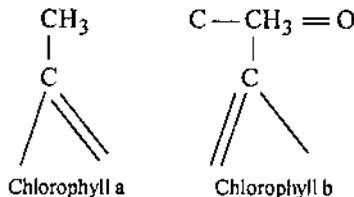


Fig. 2. The chlorophyll a molecule

**A. Chlorophylls :** Chlorophylls (Gr. **Chlor** = green, **phyll** = leaf) are the main pigments which plants used in photosynthesis. The name chlorophyll was given to the green pigment by **Pelletier** and **Caventou** (1817). As many as eight major types of chlorophylls known to exist in the plant kingdom, e.g., chlorophylls *a, b, c, d, e*, bacteriochlorophyll *a, b* and chlorobium chlorophyll (**Allen**, 1966). Chlorophyll *a* and *b* are two main pigments which occur in higher plants in the ratio of 3 : 1.

**1. Chlorophyll a :** It is basically the chelate salt of the magnesium with an empirical formula  $C_{55}H_{72}O_5 N_4 Mg$  and a molecular weight of 893. It was synthesized in the laboratory by the **Woodward** (1960) and studied in detail. The molecule is distinguished into a head of size  $15 \times 15 \text{ \AA}$  and a tail of  $20 \text{ \AA}$  length. The head is made up of **porphyrin**, a tetrapyrrole closed ring derivative and tail is made up of **phytol** ( $C_{20}H_{39}O$  carbon alcohol). There is a fifth isocyclic ring of **cyclopentanone** (fig. 2). A non ionic Mg atom is held in the center by nitrogen atoms of four pyrrole (tetrapyrrole) rings by two covalent and two co-ordinate bonds ( $-C=C-C=C-$ ), i.e., alternate single and double bonds (fig. 2). The four pyrrole rings are held by methane bridges. The pyrrole ring contains 5 atoms – 4 carbon and one nitrogen. In chlorophyll *a* the external carbon atoms of the tetrapyrrole ring have been numbered 1 to 8. The phytol tail is attached to carbon 7 position of pyrrole ring IV with a propionic ester bond. The phytol tail extends into the interior of the chloroplast's membrane and interacts with other hydrophobic lipid molecules. It is useful in orientation and anchoring of the chlorophyll molecules in the chloroplast lamellae. It is a blue green pigment (reflect most of the blue green, green and yellow light, that is why leaves appear green in colour), most soluble in petroleum ether and present in all photosynthetic organisms and bacteria.

**2. Chlorophyll b :** Its empirical formula is  $C_{55}H_{72}O_6 N_4 Mg$  and molecular weight of 907. It is an olive green pigment. It has a structure similar to chlorophyll *a*, except in having a formyl or aldehyde group ( $-CHO$ ) instead of methyl group ( $-CH_3$ ) at third carbon atom of the second pyrrole ring.



It absorbs blue and orange wavelengths giving peaks at 430, 595 and 644 nm. It is best soluble in methyl alcohol and is present in all green plants except diatoms, red, blue green algae and bacteria.

**3. Chlorophyll c :** It has empirical formula  $C_{35}H_{32}O_5 NuMg$  and molecular weight 712. It absorbs blue and orange wavelength of the spectrum giving peaks of 447 and 579 nm. It is found in the brown algae, diatoms and also in pyrophyta and cyanophyta.

**4. Chlorophyll d :** Its empirical formula is  $C_{54}H_{70}O_6 N_4 Mg$  and the molecular weight 895. It absorbs blue, yellow and red wavelengths of light giving peaks at 447, 548 and 688 respectively. It is reported in some red algae on the basis of *in vitro* studies.

**5. Chlorophyll e :** Its empirical formula is unknown. It is found in *Vaucheria* and *Tribonema* (members of Xanthophyceae). It absorbs blue and red wave-lengths giving peaks at 415 and 654.

**6. Bacteriochlorophylls.** It is of two types-bacteriochlorophyll *a* and *b*. The empirical formula of bacteriochlorophyll *a* is similar to chlorophyll *a*. It has acetyl instead of vinyl group at carbon 2-position. II & IV Pyrrole rings are reduced. It absorb ultra-violet, violet, yellow and red wavelengths, giving peaks at 358, 391, 577 and 773

nm. It is found in photosynthetic bacteria. The empirical formula and structure of bacteriochlorophyll b is not known. It is found in bacteria *Rhodospseudomonas*.

**7. Chlorobium chlorophylls.** It was earlier known as **bacteriovirdin**. The empirical formula is unknown. It has hydroxy-methyl group ( $\text{CH}_3\text{CHOH}$ ) at carbon 2 position in the tetrapyrrole ring. There is normal propyl chain at carbon 5 position. There is no carboxy methyl group at carbon 10. Farnesal ( $\text{C}_{15}\text{H}_{24}\text{OH}$ ) is present in propionic acid chain at carbon 7. It is found in **green sulphur bacteria**.

**B. Carotenoids.** Carotenoids are very large group of pigments bound in chloroplasts and chromoplasts. They are lipid compound yellow to purple in colour and widely distributed in various concentrations in plants, animals and microorganisms e.g., red and green algae, photosynthetic bacteria and fungi. They are unsaturated hydrocarbons made of eight isoprene units containing conjugate, double bond ( $\text{CH}_2 = \text{C}(\text{CH}_3) - \text{CH} = \text{CH}_2$ ). They are **insoluble in water but soluble in fats and other organic compounds**. Light is not necessary for their biosynthesis. This is the reason that plant seedlings grown in darkness develop only yellowing colour of carotenoids. The autumnal yellow brown colour of leaves is a result of degeneration of chlorophylls and unmasking of carotenoids. They absorb light in blue and green part of the spectrum. **Godwin (1965)** suggested that the chlorophylls and the carotenoids may be attached to the same protein, forming a complex known as '**photosynthin**'. Carotenoids are of two types :

**1. Carotenes.** Carotenoids that consists exclusively of hydrogen and carbon are termed **carotenes** (named after carrot in which is was abundant). These are orange coloured pigments having empirical formula  $\text{C}_{40}\text{H}_{56}$  and molecular weight 536. Some of the common carotenoids are  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$  carotene, phytotene lycopene, neurosporene etc. The lycopene is a red coloured pigment bound in red tomatoes and red pepper.  $\beta$  carotene is most common carotene and known as **provitamin A**. On hydrolysis yields **vitamin A**.

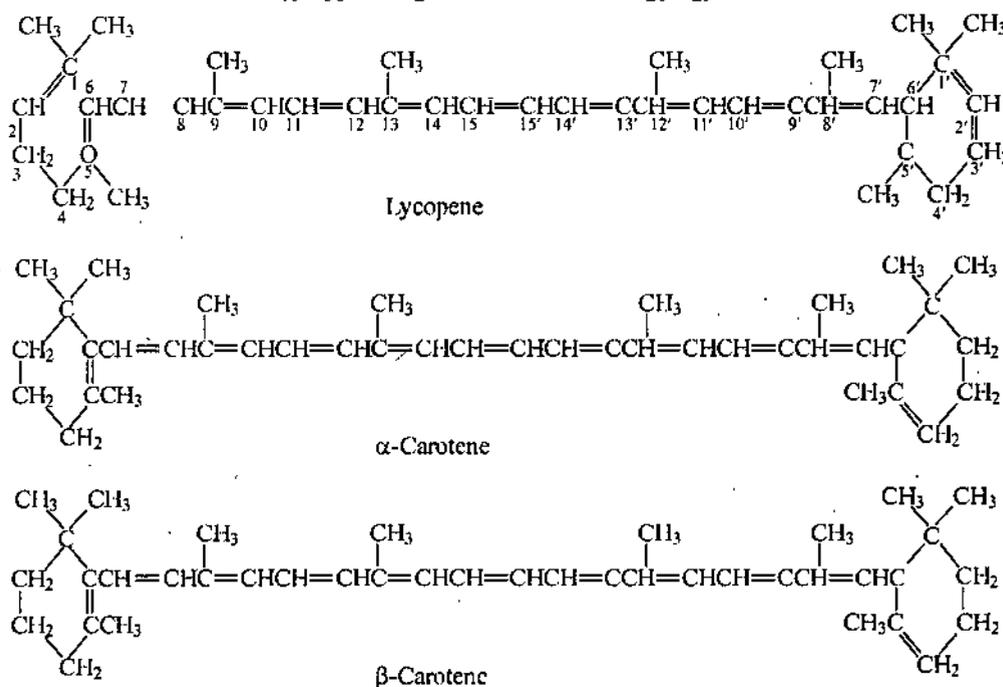
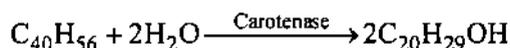


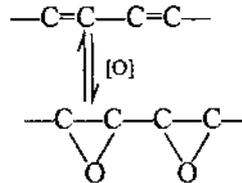
Fig. 3. Carotenes

**2. Xanthophylls :** Carotenoids containing oxygen are called **xanthophylls**. The xanthophylls are yellow coloured and more abundant in nature than the carotenes.

Their formation takes place in dark under aerobic conditions. The most common xanthophyll in green plants is **leutein**. Its empirical formula is  $C_{40}H_{56}O_2$ . In brown algae, the brown pigment is **fucoxanthin** with empirical formula  $C_{40}H_{60}O_2$ . The yellow autumn colouration of leaves is due to **zeaxanthin** (isomer of leutein). Other common xanthophylls are cryptoxanthin, violaxanthin, neoxanthin etc. The maximum absorption occurs in blue region. Both carotenes and xanthophylls are soluble in organic solvents. Carotenes are more soluble in carbon disulphide than xanthophylls.

### Role of Carotenoids

1. **Wolken** (1968) is of the opinion that due to the presence of the double bonds. Carotenoids can help in taking up oxygen during photolysis of water by forming epoxide. They may thus help in **photolysis of water**. Oxygen is then released in a dark reaction by an enzyme depoxidase.



2. On account of their affinity for oxygen, they prevent **photo-oxidation of chlorophyll**. It has been observed that in carotenoid deficient mutant of *Rhodospirillum rubrum*, bacteriochlorophyll decomposes on illumination in presence of oxygen.

3. They help in converting elementary oxygen to molecular form.

4. Carotenoids absorb light energy and transfer it to chlorophyll for a use in photosynthesis and thus function as **accessory photosynthetic pigments**.

5.  $\beta$ -carotene produces vitamin A in animals.

6. Carotenoids make the flowers and fruits conspicuous to animals for pollination and dispersal.

3. **Phycobilins (Biliproteins)** : These are photosynthetically active pigments of some algal groups which are structurally related to bile pigments. All the pigments are conjugated with proteins, therefore, the pigments are conjugated with proteins, therefore, the pigments are also known as **phycobiliproteins** or simply **biliproteins**. They are open chain tetrapyrroles which lack phytol and magnesium. Phycobilins are water soluble and are of three types-phycoerythrin, phycocyanin and allophycocyanin.

## 1.5. ABSORPTION SPECTRUM AND ACTION SPECTRUM

Chlorophylls absorb light. A visible spectrum is obtained when a ray of light is passed through a prism. However, spectrum shows dark coloured absorption bands when the light is transmitted through leaf is passed through a prism. All the wavelengths are not absorbed at the same rate. We can measure the rate of absorption by an instrument called **spectrophotometer**. A curve obtained by plotting the amount of absorption of different wavelength of light by a particular pigment is called **absorption spectrum** of that pigment. Absorption spectra of different pigments are different. Chlorophyll a and b show strong absorption band in blue and red region of the spectrum. However, the exact position of the peaks of absorption depends upon the solvent in which the pigments are dissolved (fig. 4).

Depending upon the maximum absorption peaks, there are several spectrally different forms of chlorophyll a, e.g., Chl a 670-673, chl a 680-683, chl a 690-705 etc. In addition, there are some chlorophyll a molecules e.g., Chl a 680 (P680), Chl a 700 (P700) which functions a trap centres in Photosystem II and Photosystem I.

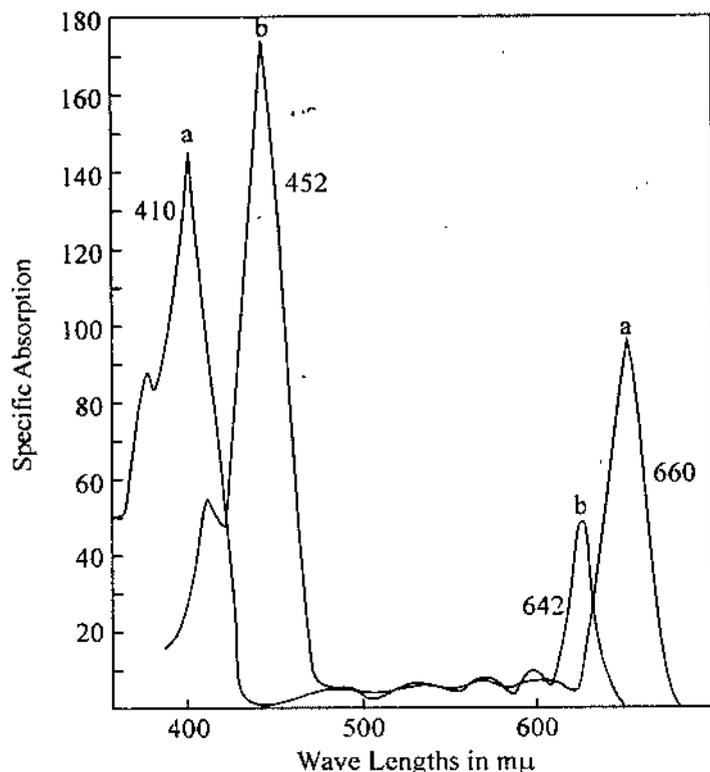


Fig. 4. Absorption spectra of chlorophyll-a and b in ether solution.

### Action spectrum

Photosynthesis occurs in visible light spectrum ranging from 390 nm to 760 nm. However, this process does not occur at the same rate in the different wavelengths of light. **Curve showing the rate of photosynthesis at different wavelengths of light is called action spectrum.** The effectiveness of different wavelengths can be measured by the quantum yield (oxygen production) or the amount of action (carbon dioxide fixation, NADP<sup>+</sup> reduction). Comparison between the action spectrum and absorption spectrum shows that it is closely related to absorption spectrum in photosynthetic plants. In higher plants it almost runs parallel to the absorption spectrum of chlorophylls. The maximum photosynthesis occurs in blue and red region of the spectrum and it is almost that region of spectrum where the chlorophyll absorbs maximum amount of light.

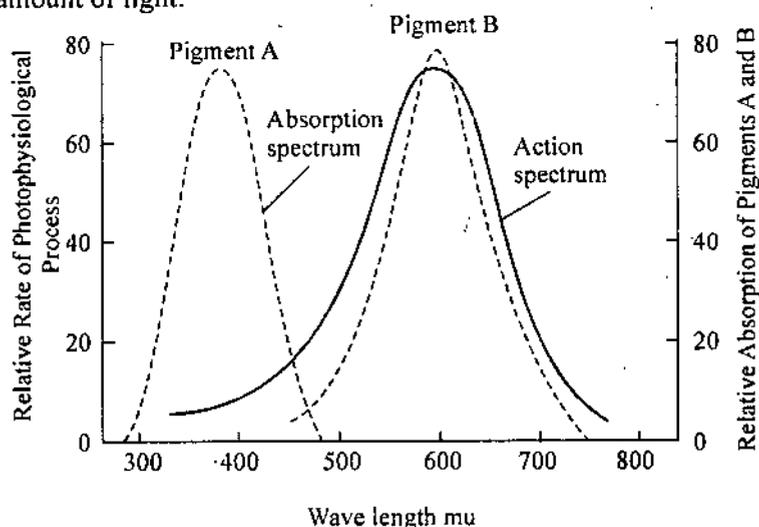


Fig. 5. Action spectrum of a hypothetical photophysiological process and absorption spectra of two pigments a and b isolated from the plant.

## 1.6. MECHANISM OF PHOTOSYNTHESIS

According to modern concept photosynthesis is fundamentally an **oxidation-reduction process** in which water is oxidised to  $O_2$  and  $CO_2$  is reduced to carbohydrates. The process photosynthesis involves two distinct phases :

1. **Photochemical phase or light reaction or Hill reaction**
2. **Biosynthetic phase or dark reaction**

### Photochemical phase or light reaction

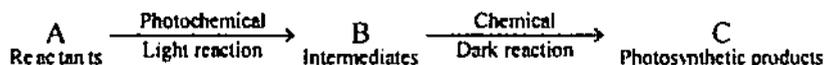
In the light reaction solar energy is trapped by chlorophyll and stored in the form of ATP and reducing power  $NADPH_2$  is generated at the same time. Both ATP and  $NADH_2$  are called assimilatory power of the plant. Oxygen is also evolved by splitting of water in light reaction.

### Dark reaction

Light is not required in this phase. The reducing power of the NADP and the energy of ATP are utilized in the conversion of carbon dioxide to carbohydrates.

### Evidences for existing light and dark reactions in photosynthesis

(1) **Intermittent light experiment** : Warburg (1919) obtained higher rate of photosynthesis in *Chlorella* when its cell were exposed to rapid and alternate periods of light and darkness instead of continuous illumination. This observation shows that an essential phase of photosynthesis goes on independently in the presence of light. In intermittent light this phase will proceed not only in the light periods but also in dark periods thereby enhancing the rate of photosynthesis per unit time of illumination. It is also possible that when light is given continuously, the rate of photosynthesis is limited by the slow rate of dark reaction. It can explained in the term of the following reaction sequence.

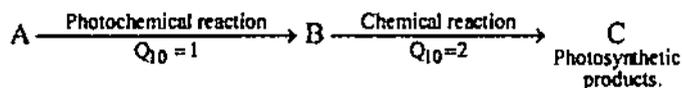


The reactants A are first being converted to intermediates B and then to end product C. Since photosynthesis never begins in absence of light, the first reaction *i.e.*, conversion of A into B is a light dependent reaction, a **photochemical reaction**. If the conversion of B into C was also light dependent reaction, the yield ought to have been the same in the two experiments. Since, it is not so, the conversion of B into C is a light independent reaction, a **chemical reaction**.

Higher photosynthetic yield can also be explained by the reaction sequence. In the continuous light experiment A changed into B quickly and B into C rather slowly. The amount of C formed depends upon the conversion of B into C. But in intermittent light experiment more B was converted into C during introducing dark phase and hence the yield was more.

(2) **Temperature Coefficient ( $Q_{10}$ )** : The presence of two distinct phases in photosynthesis can be proved by the measurement of temperature coefficient of photosynthesis. The temperature coefficient is defined as the rate of the velocity of a reaction at a particular temperature to that at a temperature  $10^\circ C$  lower. For a physical process the value of  $Q_{10}$  is one. However, in case of chemical reaction the value of  $Q_{10}$  is two or more *i.e.*, with the rise of  $10^\circ C$ , temperature the rate of chemical reaction is doubled. Blackman could get an increase in the rate of photosynthesis upon a certain stage beyond which the photosynthesis either remained static or declined until the temperature was raised. Subsequent workers have obtained  $Q_{10} = 2$  under alternating high and low light intensities. From this it becomes clear that in photosynthesis at least two stages occur. In the first stage there is a photo-chemical

reaction. It is followed by dark phase consisting chemical reaction. The dark phase is also called **Blackman's reaction** :



(3) **Induction Phase** : Induction phase is a period of change from one state to another *i.e.*, the time lag between illumination and carbon dioxide reaction. The increase in the rate of intake of carbon dioxide is greater in strong light than in weaker light at a constant temperature. But the rate of evolution of oxygen is not affected by the intensity of light. It indicates carbon dioxide fixation and oxygen liberation are two separate processes.

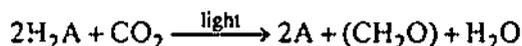
(4) **Dark pick of  $^{14}\text{CO}_2$**  : The most accepted evidence in support of the existence of two phases in photosynthesis comes from **tracer experiments**. The  $^{14}\text{CO}_2$  has been found to be reduced by the green cells in the dark after **pre-illumination**.

(5) **Inhibitors** : **Warburg** (1920) when applied low concentration of cyanide to photosynthetic regions, it inhibited photosynthesis to a greater extent under high intensity than at low intensity.

### 1.7. THE LIGHT REACTION (Photochemical Reaction or Hill Reaction)

Evidences in support of light reaction :

1. **Experiments to demonstrate the origin of oxygen** : **Van Niel** observed that photosynthetic bacteria fixed carbon dioxide in the presence of Hydrogen sulphide (not water) and no oxygen was evolved and instead globules of sulphur were formed). He prepared a general formula for photosynthesis by substituting  $\text{H}_2\text{O}$  and  $\text{H}_2\text{S}$  as  $\text{H}_2\text{A}$ .

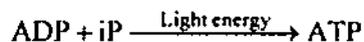


where A stands for sulphur or oxygen.

2. **Hill's work with isolated chloroplasts** : Hill observed evolution of oxygen from water by isolated chloroplast in sunlight in presence of ferricyanides or benzoquinones. He attributed the production of oxygen reduction of reagents and the splitting of water into oxygen and hydrogen to light. In the early 1940's **Warburg** found that chloride ions has a stimulating effect on the Hill's reaction probably by facilitating the release of oxygen from  $\text{OH}^-$  ions.

3. **By using non radioactive heavy isotope  $\text{O}^{18}$**  : **Ruben, Hassid and Kamen** (1941) using non radioactive heavy isotope in water supplied to the plant found that oxygen released in photosynthesis came from water molecule and not from  $\text{CO}_2$ .

4. **Arnon's work with isolated chloroplasts** : **Arnon** (1951) discovered that hydrogen acceptor is coenzyme II (TPN<sup>+</sup> now called  $\text{NADP}^+$ ). In an experiment with isolated chloroplasts, he found great increase in the rate of oxygen production with presence of  $\text{NADP}^+$ . He also observed that chloroplast could also synthesize ATP in the light from ADP and inorganic phosphate (iP). It is called **photosynthetic phosphorylation** and may be represented as :



**Arnon** (1959) showed that isolated chloroplasts could even reduce carbon dioxide in presence of light and this would result in the synthesis of carbohydrates. According to him conversion of carbon dioxide to sugar (dark reaction) occurs in stroma and light reaction occurs in grana.

#### 5. Emerson effect and two pigment system

(a) **Red drop** (Emerson's first experiment) : Emerson and co-workers measured the efficiency of *Chlorella* cells in monochromatic light (*i.e.*, only one wavelength of light at a time). They observed that the quantum yield of photosynthesis decreased at a

wavelength greater than 680 nm in the red zone. The fall in the photosynthetic yield beyond red light of spectrum is called **red drop** or **Emerson's first effect** (Fig. 6). –

(b) **Enhancement effect** : (Emerson's second experiment). In another experiment **Emerson** and coworkers (1957) observed that photosynthetic efficiency of light of 680 nm (or lower) is enhanced, if light of shorter wavelength (less than 680 nm) is supplied simultaneously. They also observed that when both wavelengths were given together, the quantum yield of photosynthesis was greater than the sum effect when both these wavelengths given separately. The enhancement of photosynthetic yield by combined effect of short and long wavelength of light is known as enhancement effect or **Emerson's second effect** (fig. 6).

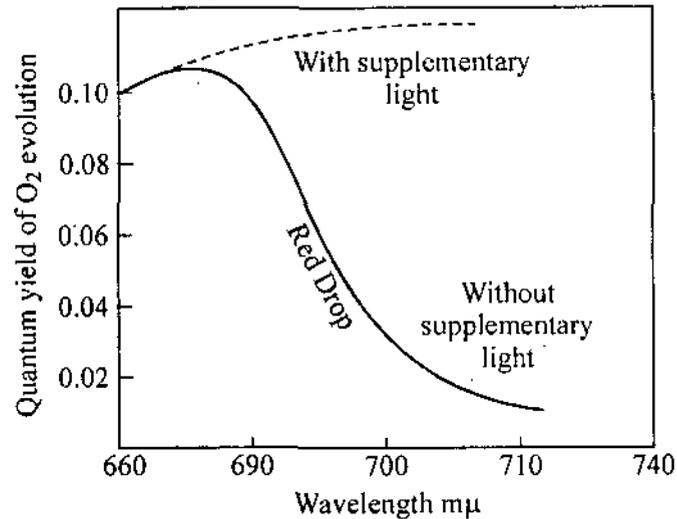


Fig. 6. Red drop and the Emerson's effect in *Chlorella*.

**Emerson** (1957) proposed that two pigment system or photochemical reactions are involved in light phase which act synergistically.

The complete light reaction can be discussed under the following sub-headings :

- (i) Photoexcitation of chlorophyll molecule.
- (ii) Two pigments system or light trapping system.
- (iii) Electron transport system or cyclic and non-cyclic photophosphorylation.
- (iv) Photolysis of water and evolution of oxygen.

(i) **Photoexcitation of chlorophyll molecule** : The first step in the light reaction is the photoexcitation of chlorophyll molecule. According to Grothus-Draper law a quantum used in the photochemical reaction must be absorbed. When a visible light photon strikes a chlorophyll molecule, it is absorbed by the pigment molecule. It releases an electron in the other molecular orbit. It comes in the outer larger orbit and finally leaves it creating a 'hole' or 'gap'. This state of the chlorophyll molecule is called **excited** or **second singlet** state as opposed to the ground state when the electron is in its normal position. This is unstable and has a half-life of  $10^{-12}$  seconds. From here the electron moves downhill, losing energy in the form of heat, to excited first singlet state having half life  $10^{-9}$  seconds, which is also unstable. From first singlet state the excited electron may return to the ground state in two ways : (i) either losing its remaining extra energy in the form of heat or (ii) by losing energy in the form of radiation energy. The latter process is called **fluorescence**. The substances which show this property of fluorescence emit fluorescent light only during the period when they are exposed to incident light. Secondly, the fluorescent light is of higher wavelength than the incident light. From first excited singlet state the electron may be placed in the triplet state by internal conversion. The triplet state is met a stable having half life  $10^{-3}$  seconds.

From triplet state the electron may return to ground state in three ways :

- (a) By losing its remaining extra energy in the form of heat.
- (b) By losing the extra energy in the form of radiations.

This process is called as **phosphorescence**. The substances which show the property of phosphorescence emit phosphorescent light even after the radiation light is cut off. Secondly, the phosphorescent light is of higher wavelength than the incident light and also fluorescent light. The two phenomenon *i.e.*, fluorescence and phosphorescence jointly constitute a large phenomenon called **phospholuminescence**.

(c) The electron may be ejected from the molecules and used in some chemical reactions. The excited state of the pigment molecule say chlorophyll a lasts for about  $5 \times 10^{-9}$  seconds.

As a result of photoexcitation the pigment molecule is oxidized due to loss of electron. It moves uphill and reduces an acceptor say *z* and then it moves downhill (oxidation-reduction reaction). This movement of electron may be compared to up and down movement of a rubber ball thrown in a stair case. The downhill movement of electron occurs through various acceptors say *y*, *x*, involving the phenomenon of oxidation and reduction. It finally returns to the original donor say *w*. During downhill course, when the electron is transferred between two such carriers having significant differences in their redox potentials, it dissipates considerable amount of energy. This energy is used in performing some chemical reactions such as conversion of ADP to ATP.

If the same electron comes to original donor, the transport of electron is said to be the **cyclic**. If the original electron is consumed in some chemical reaction, the gap of the original donor is filled by some other donor and it is called **non-cyclic electron transport**.

(ii) **Two pigment systems or light trapping system.** Pigment systems are concerned with the trapping of the sunlight. They are also called **light trapping centers** or **photosystems**. The discovery of Emerson effect clearly indicates that two groups of pigments are involved in photosynthesis. Two photochemical processes are believed to be associated with these two different group of pigments called **Pigment system I (PSI)** and **Pigment System II (PSII)**. These two pigment systems after treating with detergents, can be separated by the ultracentrifugation of chloroplast due to different densities. The heavier fraction largely comprises the PSII and lighter fraction the PSI.

**Pigment System I (PSI).** It is located both in grana and stroma lamellae. It has more of chlorophyll a molecule, which is known as  $P_{700}$  because of its absorption band at 700 nm (The letter P stands for pigment and the figures for the wavelength of light which these molecules absorb). **Govindjee and Govindjee (1974)** and many other workers suggested that PSI comprises chlorophyll a molecules (Chlorophyll a 705-735, chl a 690-700, chl a 678-687, chl a 670-680, chl a 660-670) Chlorophyll b and carotenoids.

PSI carry on cyclic photophosphorylation (synthesis of ATP in presence of light). It derives an electron from PSII (through plastocyanin) to  $NADP^+$  so that latter may combine with  $H^+$  ions.

**Pigment system II (PSII) :** It is predominantly located in grana. The components of PSII are chl a ( $P_{680}$ ), Chlb,  $\beta$  Carotene, pheophytin (chlorophyll without  $Mg^{++}$ ) bound to Mn proteins. The trap or reaction centre is a special molecule of chl a called  $P_{680}$  (Fig. 4.28). It is surrounded by chl a 685-695, chl a. 678-787; chl a 670-680, chl a 660-670, chl. b and Carotenoids (**Govindjee and Govindjee, 1974**). It is concerned with photolysis of water and evolution of oxygen. Photosystem II carry the non cyclic photophosphorylation.

$P_{700}$ ,  $P_{680}$  forms the **photocentre** or **reaction centre** of the PSI and PSII respectively. The accessory pigments and other chlorophyll molecules harvest solar energy and pass it on to reaction centre. The energy trapped by the chlorophyll molecule is not enough to start the first chemical reaction that could occur in light. Chlorophyll and other accessory pigments help to capture light over larger areas and pass it on to the photocentres. Thus, a photon absorbed anywhere in the harvesting zone of a  $P_{680}$  can pass its energy to  $P_{680}$  molecules. The cluster of pigment molecules which transfer the energy to  $P_{680}$  absorb at or below the wavelength of 680 nm. Together with  $P_{680}$  they form the PSII and similarly  $P_{700}$  forms the PSI along with pigment molecules which absorb light at or below 700 nm (fig. 7).

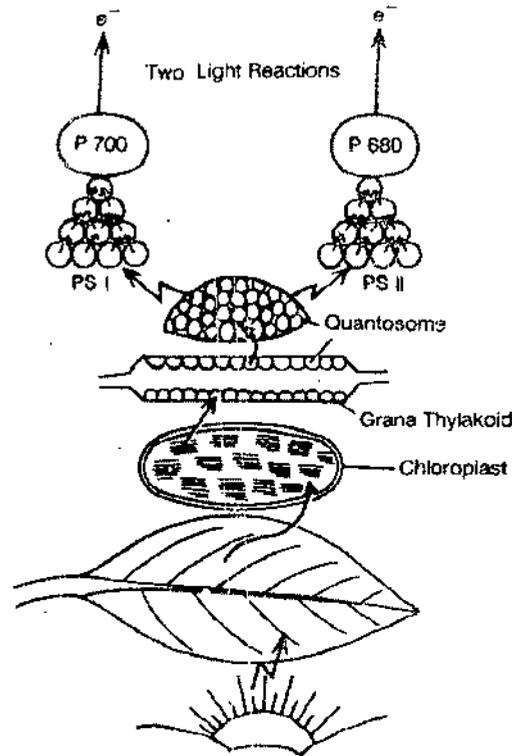


Fig. 7. The two light reactions.

As the light energy is captured by the components of PSI it is funneled to  $P_{700}$  by inductive resonance and  $P_{700}$  release an electron. The energy collected on behalf of PSII is transferred to  $P_{680}$  by inductive resonance and releases another electron and thus two light reactions start simultaneously (fig. 7).

**(iii) Electron transport system or cyclic and noncyclic photophosphorylation:**

The electron transport system (E.T.S.) can be explained by the **Z-scheme** (so named because of its shape See fig. 8).

*Ans-1*

**Non Cyclic electron transport or photophosphorylation.**

The electron ejected on behalf of PSI by  $P_{700}$  is passed on to an unknown primary electron acceptor, believed to be iron sulphur protein [A (FeS)]. From here it moves downhill to Ferradoxin and ultimately to  $NADP^+$  which is reduced to  $NADPH + H^+$ . The transfer of electron (to  $NADP^+$ ) creates an electron debit (commonly referred as 'hole') in photosystem I. This deficit is make up by the excitation of  $P_{680}$  of photo system II. The electron released by  $P_{680}$  also moves up and reduces the  $Q$  (unknown product). From  $Q$  the electron moves downhill through  $B$  (unknown product), plastoquinone ( $PQH_2$ ), cytochrome  $f$  (Cyt $f$ ), plastocyanin (Pc) and then to  $P_{700}$ . The hole created in PSII is filled by electron that are derived from the splitting of water and oxygen is evolved.

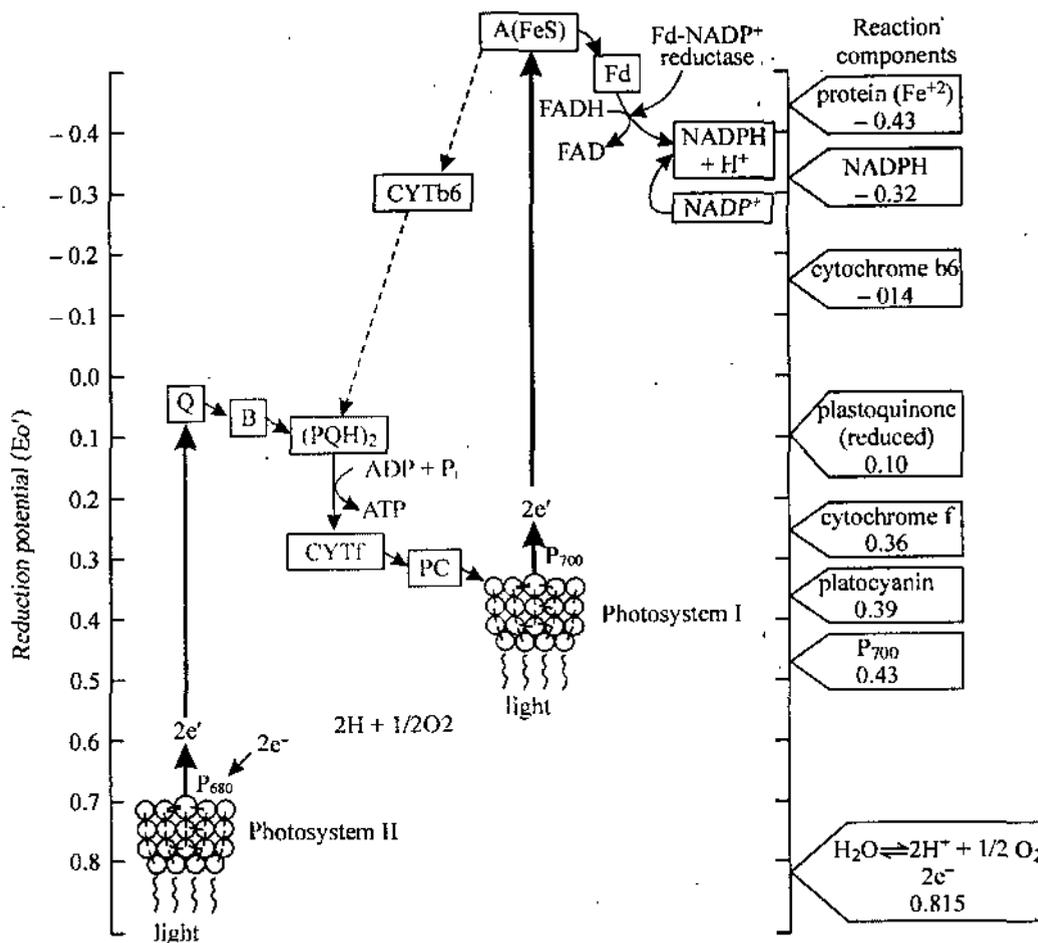


Fig. 8. Photoinduced electron transport (Z-scheme) in photosynthesis showing cyclic and non-cyclic photophosphorylation. Abbreviations are : plastoquinone (PQ), cytochrome  $b_6$  (CYT  $b_6$ ), cytochrome  $f$  (CYT  $f$ ), plastocyanin (PC), iron-sulfur protein acceptor (A[FeS]), ferredoxin (Fe), flavine adenine dinucleotide (FAD) and FAD reduced (FADH).

In this electron transport  $Mn^{+2}$  is oxidized to  $Mn^{+3}$  and then reduced to  $Mn^{+2}$ . Since the gap of  $P_{700}$  is filled by electron from other source, the transport is said to be non-cyclic. During transport of electron from plastoquinone to cytochrome  $b_6$  on ATP molecule is generated (fig. 8) due to significant difference of redox potential of the two carriers. This is non-cyclic photophosphorylation.

Non-cyclic photophosphorylation generates ATP and  $NADPH_2$ —The assimilatory power, used to fix and reduce carbon dioxide in Calvin cycle during dark reaction of photosynthesis.

### Cyclic electron transport or cyclic photophosphorylation.

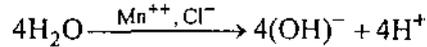
The electron ejected by  $P_{700}$  moves uphill and reduces [A (FeS)]. From here it moves downhill to ferredoxin (Fd) to plastoquinone (PQ) and then to cytochrome  $b_6$  (Cy  $b_6$ ). It passes electron back to  $P_{700}$  via cytochrome  $f$  (CYT  $f$ ) and plastocyanine (PC). There is some evidence that plastoquinone (PQ) instead of cytochrome  $b_6$  may act as primary acceptor of electron from A (FeS). Since the gap to  $P_{700}$  is filled by the same electron, the transport is said to be cyclic (fig. 8). ATP molecules are generated in cyclic photophosphorylation at two steps :

- (i) From ferredoxin to cytochrome  $b_6$ .
- (ii) From cytochrome  $b_6$  to plastoquinone.

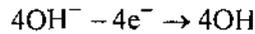
**Photolysis of water and evolution of oxygen.**

The flow of electrons from PSII (P<sub>700</sub>) to PSI (P<sub>700</sub>) and finally to NADP leaves a hole in the PSII. The positively charged P<sub>680</sub> molecules exert a strong pull on the water molecules splitting it into H<sup>+</sup> and OH<sup>-</sup> ions. This is called **photolysis of water**. It requires the Mn<sup>++</sup> and Cl<sup>-</sup> ions as catalyst according to Warburg chloride ions stimulate quick release of electrons from water. This process occurs in the following steps :

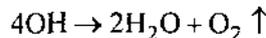
**(i) Photolysis of water**



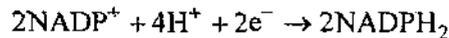
(ii) The OH<sup>-</sup> ions donate their electrons to oxidized P<sub>680</sub> (PSII) so that 'hole' is filled up and it becomes functional again.



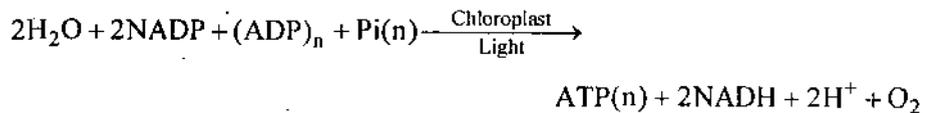
(iii) The OH radicals form water and release oxygen as a byproduct.



(iv) **Formation of NADPH<sub>2</sub>** : Hydrogen ions formed as a result of photolysis of water (Step I) are directly accepted by NADP and form NADPH<sub>2</sub>.



The light reaction phase of photosynthesis can be summarized by the following equation :



The number of ATP molecules produce per oxygen molecules is not clear. Some scientists claim 2 molecules of ATP are produced for every oxygen molecule liberated, while others claimed four. It has been estimated 8-12 quanta (photons) appear to be necessary to produce NADPH and ATP sufficient for carbon dioxide fixation. Approximately 2NADPH and 3ATP molecules are required to fix one molecule of carbon dioxide into a sugar phosphate. 6 molecules of NADPH and 9 molecules of ATP are required of fix 3 molecules of carbon dioxide.

**Differences between cyclic and non-cyclic photophosphorylation or electron transport**

Cyclic		Non-cyclic	
1.	Pathway of electrons is cyclic. Electrons expelled from PSI (P <sub>700</sub> ) returns to it.	1.	Pathway of electrons is non cyclic. Electron expelled from PSII is not returned to it.
2.	It involves only PSI.	2.	It involves both PSI and PSII.
3.	Only ATP is formed.	3.	Both reduced NADP and ATP are formed.
4.	Oxygen is not liberated	4.	Oxygen is liberated.
5.	Water is not consumed in this process.	5.	Water is consumed in this process.
6.	End product is only ATP.	6.	End products are ATP, NADPH <sub>2</sub> and oxygen.
7.	Insensitive to DCMU.	7.	Dichloro phenyl methyl urea (DCMU) stops it because it checks the flow of electrons from water to

			NADP <sup>+</sup> .
8.	The system is dominant in bacteria.	8.	This system is dominant in green plants.
9.	It operates under anaerobic conditions, low light intensity and lower availability of carbon dioxide.	9.	It takes place under aerobic conditions, optimum light and presence of different quantum of carbon dioxide.

#### Differences between Photosystem (PSI) and Photosystem II (PSII)

PSI		PSII	
1.	It is located in stroma.	1.	It is predominantly located in grana lamellae.
2.	It consists of pigment molecules absorbing both shorter and longer wavelength of light.	2.	It consists of pigment molecules which absorb only shorter wavelength of light.
3.	The reaction centre is P <sub>700</sub> .	3.	The reaction centre is P <sub>680</sub> .
4.	PSI have molecules of chl. a, chl. b and Carotenoids are comparatively less.	4.	It posses Chl. a, Chl. b and carotenoids. Chlorophyll carotenoid rate is 3.7 : 1.
5.	It lies on the surface of thylakoids.	5.	It occurs on the inner surface of thylakoids.
6.	It participates in both cyclic as well as non-cyclic flow of electrons.	6.	It is evolved only in noncyclic flow of electrons.
7.	In this system molecular oxygen is not released.	7.	In this system molecular oxygen is released.
8.	Cyclic photophosphorylation occurs.	8.	Non-cyclic photophosphorylation occurs.

### 1.8. BIOSYNTHETIC PHASE OR DARK REACTION OR BLACKMAN'S REACTION

Dark reaction involved **fixation and reduction of carbon dioxide** resulting in the formation of carbohydrates. It occurs in the stroma of chloroplast where all the enzymes are located. It is independent of light (does not require light energy) and can occur either in presence or absence of light. However, it depends upon the products of light reaction or photochemical phase. It utilizes ATP and reduced NADP (assimilatory power) obtained as a result of light reaction for the reduction and fixation of carbon dioxide. Dark reaction is also known as Blackman's reaction, named after the scientist who reported it for the first time.

The exact path of carbon dioxide fixation and its conversion to sugar etc. could not be known as 1930's because of the fact that the laboratory techniques were not well developed. The development of the radioactive isotopes of carbon gave the impetus to study in intermediates. Initial studies were made by **Ruben et. al.** (1939) using C<sup>14</sup> to trace the path of the carbon in dark reaction but then carbon isotope had very short half life (C<sup>14</sup>-22 minutes). **Ruben and Kaman** (1940) used C<sup>14</sup> which is a stable isotope with half-life of 5200 years. The isotope C<sup>14</sup> was used by many workers like **Benson, Calvin, Bessham** etc., and three modes of carbon dioxide fixation was observed :

- (i) Calvin cycle or Calvin and Benson cycle or Reductive pentose phosphate cycle.
- (ii) C<sub>4</sub> or dicarboxylic acid cycle.

(iii) Crassulacean acid metabolism (CAM).

The plants exhibiting these pathways are respectively known as  $C_3$  plants,  $C_4$  plants and CAM plants.

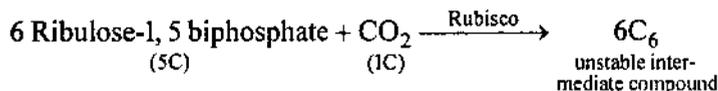
### C<sub>3</sub> cycle or Calvin cycle

The whole sequence of chemical reactions by which carbon dioxide gas is assimilated and reduced to form sugar and other carbohydrates were extensively investigated and discovered by American scientist **Melvin Calvin** and co-workers (1954-57) using a radio isotope  $C^{14}$  ( $C_{14}O_2$ ) in *Chlorella pyrenoidosa* and *Scenedesmus obliquus* (green algae). For this work M. Calvin was awarded nobel prize in 1961. These reactions are variously known as **Path of CO<sub>2</sub> fixation**, **C<sub>3</sub> cycle**, **Calvin cycle**, **Calvin-Benson-Bassham Cycle**.

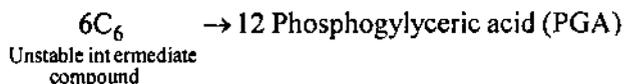
Calvin Cycle can be divided into three phases :

- (i) Carboxylation of pentose sugar.
- (ii) Glycolytic reversal.
- (iii) Regeneration of RuBP (ribulose-1, 5 biphosphate).

**Phase I : Carboxylation of pentose sugar :** Addition of carbon dioxide to a compound is called **carboxylation**. The carbon dioxide acceptor in Calvin cycle is a 5 carbon sugar Ribulose-1, 5 biphosphate (also known as Ribulose-1, 5 diphosphate). It is synthesized in the chloroplasts and already present in the cells. Ribulose -1, 5 biphosphate combines with the carbon dioxide and this reaction takes place in the presence of enzyme **ribulose biphosphate carboxylase oxygenase** abbreviated as **rubisco** (also called carboxydismutase). It is located on the stromal surface of thylakoid membrane. It is a large protein molecule, constitutes about 16% of chloroplast protein and one of the most abundant protein on the earth. Six molecules of RuBP combines with 6 molecules of carbondioxide to produce short lived six carbon intermediate compound called 2-carboxy 3 keto-ribitol-1, 5 biphosphate.



This six-carbon compound is unstable and breaks down immediately 2 molecules of 3-C compound-phosphoglyceric acid. Thus, 6 molecules of the unstable intermediate ( $6C_6$ ) compound form 12 molecules of phosphoglyceric acid.

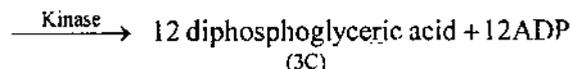


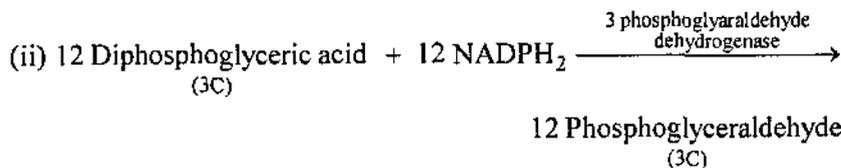
Since the first product of a Calvin cycle is 3-C compound, this cycle is called as **C<sub>3</sub> cycle** and the plants in which the cycle is found are called **C<sub>3</sub> plants**.

**Phase II : Glycolytic reversal.** In this phase of dark reaction formation of hexose sugar takes place (the reducing power is obtained from  $NADPH_2$  rather than  $NADH$ ). The following are the major steps :

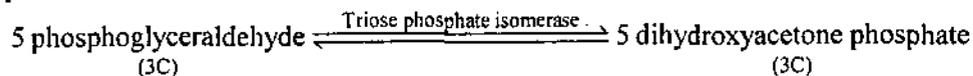
**Step I : Synthesis of phosphoglyceraldehyde.** Twelve molecules of 3-phosphoglyceric acid (3-PCA) are phosphorylated and reduced to 12 molecules of phosphoglyceraldehyde by utilizing 12 molecules each of ATP and  $NADPH_2$  (The assimilatory power produced in light reaction).

- (i) 12 Phosphoglyceric acid + 12 ATP  
(3C)

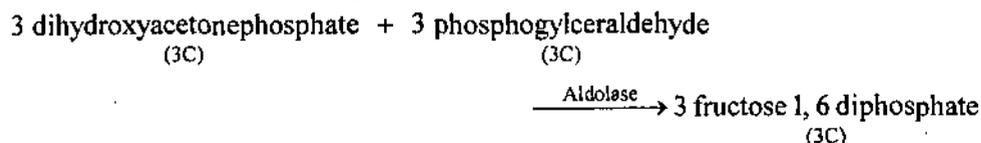




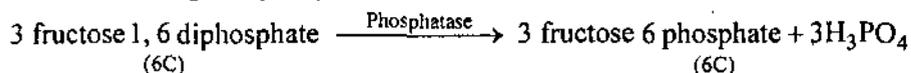
**Step II : Synthesis of dihydroxy acetone phosphate :** 3-Phosphoglyceraldehyde is a key product and used in the synthesis of carbohydrates of the 12 molecules of 3-phosphoglyceraldehyde, 5 molecules are transformed into its isomer dihydroxy acetone phosphate.



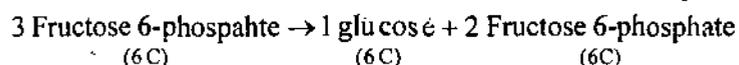
**Step III : Synthesis of fructose 1, 6 diphosphate :** 3 molecules of dihydroxy acetone phosphate combines with the 3 molecules of phosphoglyceraldehyde to form the 3 molecules of fructose 1, 6 diphosphate.



**Step IV : Synthesis of fructose 6 phosphate.** Three molecules of fructose 1, 6 diphosphate are converted into 3 molecules of fructose 6 phosphate by giving out of three molecules of inorganic phosphate (PI) as  $\text{H}_3\text{PO}_4$ .

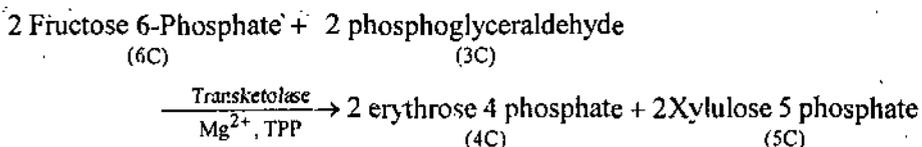


**Step V : Production of Hexose Dugar.** Fructose 6 phosphate is converted into glucose 6 phosphate by the activity of the enzyme phosphohexose isomerase. Glucose 6 phosphate is converted into glucose +  $\text{H}_3\text{PO}_4$ . Enzyme involved in the reaction is glucose 6-phosphatase. This glucose is used in the plants to form other carbohydrates such as starch and sugars and variety of other organic compounds required for the structure and function of plant body. As glucose is a six carbon compound, six turns of Calvin cycle are required to synthesize one molecule of glucose. It is the net gain from the Calvin cycle. The remaining two molecules of fructose 6 phosphate are used in regeneration of the carbon dioxide acceptor ribulose 1, 5-biphosphate (fig. 9).



**Phase III : Regeneration of RuBP (Ribulose 1, 5-biphosphate).** Ribulose 1, 5 biphosphate is needed to initiate the Calvin Cycle because it is the primary acceptor of carbon dioxide (or carboxylation). ATP,  $\text{NADPH}_2$ , 3-phosphoglyceraldehyde, dihydroxyacetone phosphate, fructose 6-phosphate actively participate in the synthesis of RuBP. The sequence of reactions is as follows :

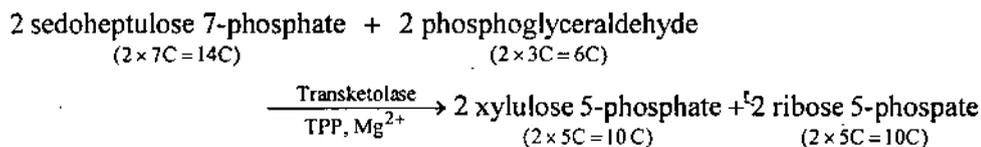
**Step I :** Two molecules of fructose 6-phosphate (6C) reacts with 2 molecules of 3 phosphoglyceraldehyde (3C) to give rise to 3 molecules of erythrose 4 phosphate (4C) and 2 molecules of xylulose 5 phosphate (5C). The enzyme requires thiamine pyrophosphate (TPP) and  $\text{Mg}^{2+}$  as cofactors.



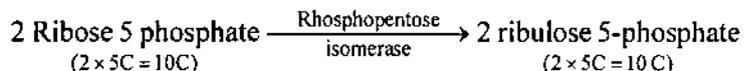
**Step II :** Two molecules of dihydroxy acetone phosphate react with 2 molecules of erythrose 4 phosphate to produce two molecules of sedoheptulose 1, 7- diphosphate.



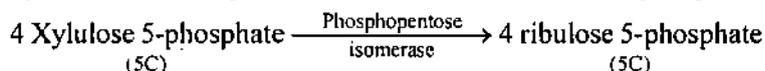
**Step IV :** Two molecules of sedoheptulose 7-phosphate combines with the remaining two molecules of 3-phosphoglyceraldehyde to produce two molecules of Xylulose 5-phosphate (5C) and 2 molecules of ribose 5-phosphate.



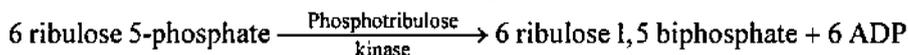
**Step V :** Both the molecules of ribose 5-phosphate are isomerised to ribulose 5-phosphate.



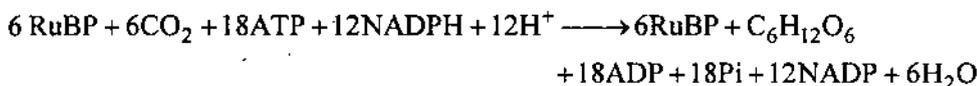
**Step VI :** All the four molecules of Xylulose 5-phosphate (two molecules generated in step I and two in step IV) are isomerized to ribulose 5-phosphate.



**Step VII :** Six molecules of ribulose 5-phosphate (two molecules generated in step V and four in step VI) react with 6 molecules of ATP (get phosphorylated) and regenerate 6 molecules of ribulose 1-5 biphosphate.



The regeneration of Ribulose 1, 5-biphosphate completes the Calvin cycle. The net reaction  $C_3$  cycle of carbon dioxide fixation in dark is :



It is already proved that overall rate of photosynthesis is higher in intermittent light as compared to continuous light. It is due to fact that in intermittent light ADP and NADP are regenerated. However, in continuous light, the dark reaction is slow and sufficient amount of ATP and NADP are not regenerated to utilize additional light energy. Thus, the dark reaction of photosynthesis is rate limiting step, it is slower than the light reaction and determines the rate of photosynthesis. In photosynthesis 264 gms of carbon dioxide and 216 gms of water give raise to 108 gms of water, 192 gms of oxygen and 180 gms of glucose.

### 1.9. PHOTORESPIRATION OR GLYCOLATE METABOLISM ( $C_2$ CYCLE)

**Warburg (1920)**, a German scientist first of all observed that photosynthesis in green algae was inhibited by high level of oxygen in the atmosphere. This was termed as **Warburg effect**. **Decker (1959)** observed that intake of oxygen and evolution of carbon dioxide has stimulated in Tobacco and *Mimulus* under illumination. **The light independent uptake of oxygen and release of carbon dioxide in the photosynthetic system is called as photorespiration.** It takes place in all the photosynthesizing organs under aerobic conditions with particularly exception of plants belonging the deserts and tropics. The process occurs in three cell organelle—chloroplast, peroxysomes and mitochondria.

#### In chloroplast

Photorespiration usually occurs in  $C_3$  plants when there is higher concentration of oxygen, high temperature and low carbon dioxide. **RuBP carboxylase** enzyme, in the presence of higher concentration of oxygen acts as **RuBP oxygenase**. It converts one molecule of **Ru BP (5C)** to one molecule of three carbon compound **phosphoglyceric acid (3PGA)** and one molecule of two carbon compound **phosphoglycolic acid**, which

is soon dephosphorylated into **glycolate**. Glycolate forms the substrate from photorespiration.

**In peroxisomes**

The glycolate diffuses out of the chloroplast and enters into the peroxisomes. Here it is oxidised (photorespired) to **glyoxylate** and **hydrogen peroxide** by the enzyme **glycolic acid oxidase**. Glyoxylate is converted into amino acid **glycine** by a **glutamate**; **glyoxylate amino-transferase**. The hydrogen peroxide is completely destroyed by **catalase**. Glycine moves out of peroxisomes.

**In chloroplast**

In mitochondria or cytoplasm, two molecules of glycine (2C) combine (one molecule formed from serine, fig. 10) and decarboxylated to produce another amino acid called **serine**. This reaction takes place in the presence of enzymes **glycine decarboxylase** and **hydroxy methyl transferase**. It releases carbon dioxide and **ammonia**. The liberation of this carbon dioxide is recorded as photorespiration and was named as such by **Decker**.

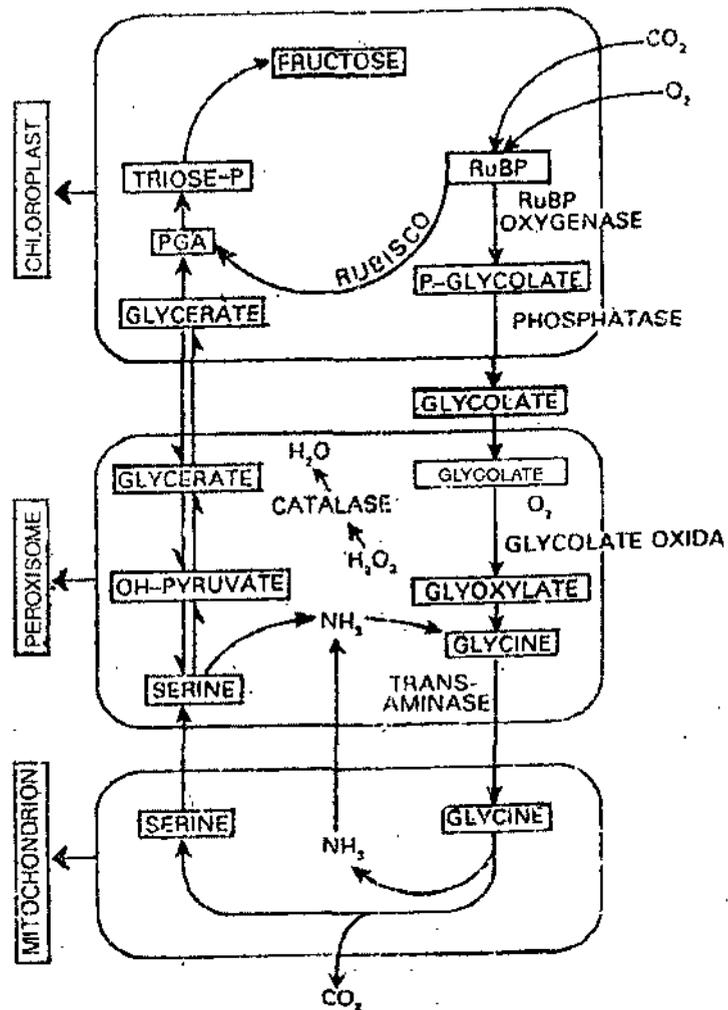


Fig. 10. Glycolate metabolism

The serine returns to the **peroxisomes** where it is converted to **hydroxy pyruvate** by an enzyme **amino transferase**. Hydroxy pyruvate is reduced to glycerate by the **NADH** enzyme **hydroxy pyruvate reductase**. The glycerate is then converted into phosphoglycerate which enters in the **C<sub>3</sub>** cycle in the chloroplasts.

## Importance of Photorespiration

As temperature rises, more and more photosynthetically fixed carbon is lost by photorespiration. As much as half the photosynthetically fixed carbon dioxide may be lost by photorespiration. It acts to undo the work of photosynthesis as no energy rich compound is produced in photorespiration.

However, it is not always harmful to the plants. It appears to have some useful functions in the plants such as :

(i) Amino acids (glycine, serine) synthesized during photorespiration metabolisms are precursors of many important metabolites like chlorophyll, proteins, nucleotides etc.

(ii) NADPH generated in the light reaction is consumed in the conversion of glycolate to glyxylate. Thus, photorespiration is involved in dissipating excess reducing power.

(iii) Glycolate protects against the destructive action of photo-oxidation and aerobic oxidation.

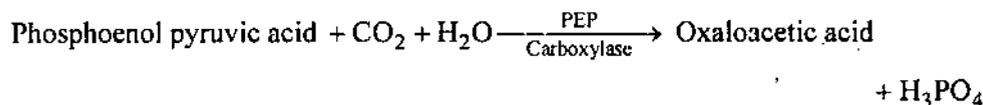
Since, photorespiration involves synthesis of 2C compounds—glycolate, glyoxylate and glycine, it is also called **C<sub>2</sub> cycle**.

## 1.10. C<sub>4</sub> CYCLE OR HATCH AND SLACK CYCLE

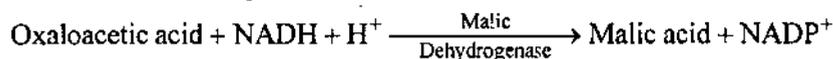
**Kortschak, Hart and Burr (1965)** found that during the photosynthesis of sugarcane leaves, the labelled carbon (C<sup>14</sup>O<sub>2</sub>) appeared first in a 4-carbon compound (dicarboxylic acid) rather than the 3-carbon compound (Phosphoglyceric acid). In 1967, two Australian scientists **M.D. Hatch** and **C. R. Slack** discovered another pathway of carbon dioxide. In this pathway the carbon dioxide acceptor is phosphoenol pyruvic acid (PEP) and the first stable product is oxaloacetic acid (OAA) – a 4 carbon compound. Hence, it is called as **C<sub>4</sub> cycle**, or **dicarboxylic acid cycle** or **β carboxylation pathway** and the plants in which this cycle is found are called as **C<sub>4</sub> plants**. A number of tropical plants, both monocots and dicots are C<sub>4</sub> plants for e.g., members of family Poaceae (Maize, Sugarcane, Sorghum, Panicum, Pennisetum etc.), Cyperaceae (Cyperus), Chenopodiaceae (*Chenopodium*) Amaranthaceae, Asteraceae, Euphorbiaceae (*Euphorbia*), Portulacaceae, Nyctaginaceae etc.

The C<sub>4</sub> plants have a peculiar type of Anatomy called 'Kranz' anatomy (German, *Kranz* = Wreath) (The chloroplasts of C<sub>4</sub> plants are dimorphic i.e., the chloroplasts of the mesophylls cells are of normal type but back Ribulose biphosphate carboxylase (RuBP carboxylase) enzymes activity. The chloreplasts of bundle sheath cells are large, agranal, without PSII, arranged centripetally and at maturity accumulate starch. These chloroplasts show ribulose biphosphate carboxylase activity. In C<sub>4</sub> plants mesophyll cells form a ring (Kranz) around the bundle sheath cells and viens of the leaves.

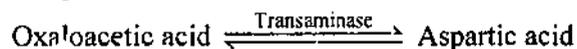
In C<sub>4</sub> plants initial reaction takes place in the mesophyll cells where the primary carbon dioxide acceptor is **phosphoenol pyruvate carboxylase enzyme**. This enzyme catalyses the formation of **oxaloacetic acid** from phosphoenol pyruvate and carbon dioxide.

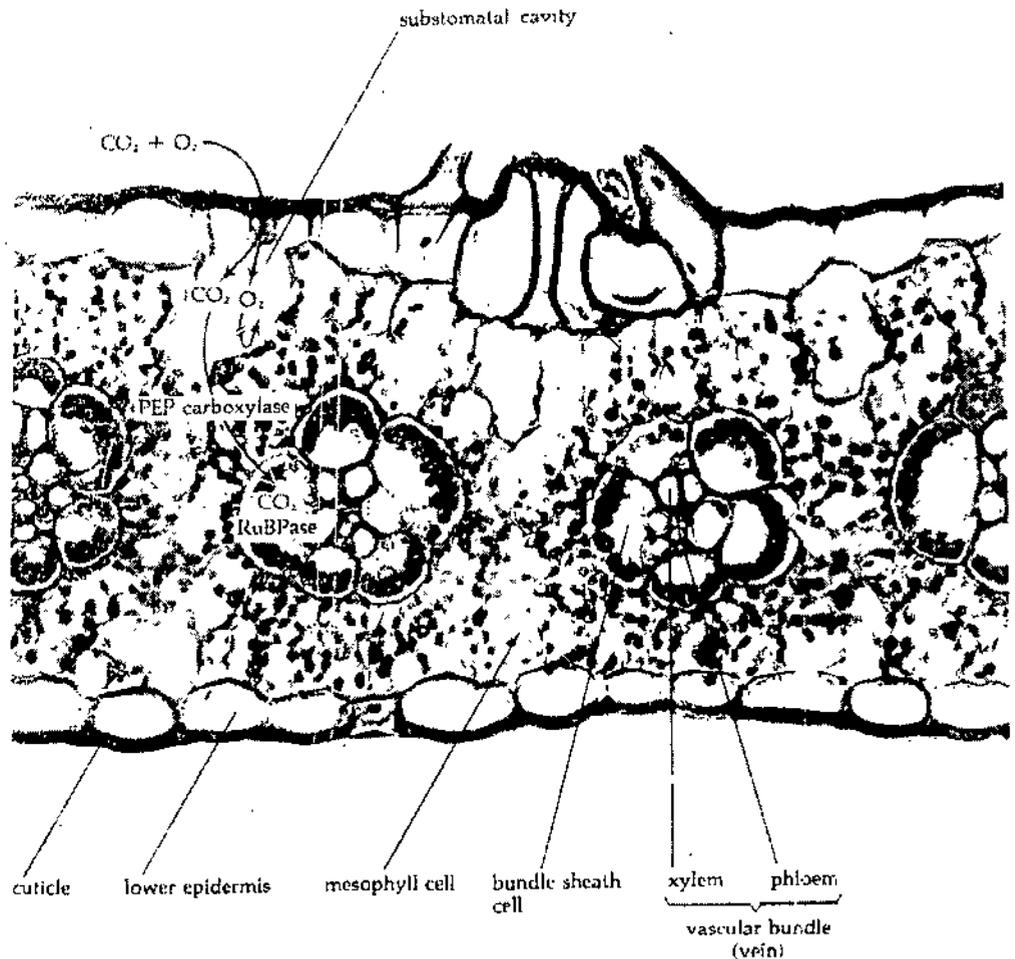


Oxaloacetic acid is quite unstable and in converted into malic acid.



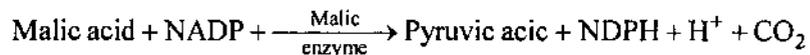
However, in some C<sub>4</sub> plants oxaloacetic acid is transminated to aspartic acid.





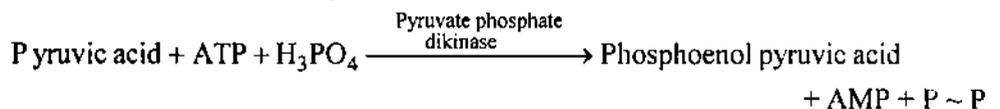
**Fig. 11. Cross section of monocot leaf illustrating typical Kranz anatomy.**

These C<sub>4</sub> acids (aspartic acid, malic acid, oxaloacetic acid) are transported to the cells of the bundle sheath. The malic acid in the bundle sheath cells undergoes oxidative carboxylation to yield pyruvic acid and carbon dioxide. It increases the carbon dioxide concentration in the bundle sheath cells of cuplants.



The carbon dioxide and  $\text{NADPH}^+ + \text{H}$  enters into the Calvin cycle. The RUBP is called the secondary or final acceptor in C<sub>4</sub> plants.

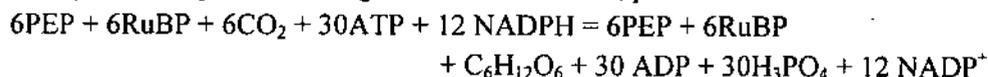
The pyruvic acid is transported back to the mesophyll cells where it is phosphorylated to phosphoenol pyruvic acid.



This conversion requires energy in the form of ATP (2ATP) or two phosphate bonds. Thus, instead of 3 ATP required for fixation of one molecule of carbon dioxide in C<sub>3</sub> plants by Calvin cycle, C<sub>4</sub> plants require 5ATP for the fixation of one molecule of carbon dioxide.

So, the total requirement of ATP for the synthesis of one molecule of glucose in C<sub>3</sub> plants are 18 molecules ( $3 \times 6 \text{ ATP} = 18 \text{ ATP}$ ), whereas, in C<sub>4</sub> plants it is 30 ATP molecules ( $5 \times 6 \text{ ATP} = 30 \text{ ATP} - 18 \text{ ATP in Calvin Cycle} + 12 \text{ additional ATP molecules}$ ).

The  $C_4$  cycle is more energy expansive than  $C_3$  cycle, but realizing that many tropical plants lose more than half of the photosynthetic carbon in photorespiration, the  $C_4$  pathway is an adaptive advantage. Net reactions in  $C_4$  plants is :



**Significance of  $C_4$  pathway :**  $C_4$  plants are better adapted to the tropical climate and can tolerate the halophytic conditions because of presence of organic acids. Closely packed mesophyll cells reduce the intensity of the solar radiations and have better utilization of available water.  $C_4$  plants can perform the photosynthesis even when the stomata are closed (from  $\text{CO}_2$  produced in respiration).  $C_4$  cycle in plants increases their adaptability to high temperature high light intensities and rate of carbon dioxide fixation at 25 to 30°C as compared to  $C_3$  plants. Therefore, these plants are well adapted to high temperature and intense radiations of tropics.  $C_4$  plants have the **low compensation point** because photorespiration is absent (PEP carboxylase is insensitive to oxygen) in these plants.

#### Differences between the $C_3$ and $C_4$ plants

$C_3$ Plants		$C_4$ plants	
1.	Calvin cycle ( $C_3$ cycle) is present in all the green cells of the leaf.	1.	Hatch-slack cycle ( $C_4$ cycle) is present in the mesophyll cells and Calvin cycle is present in the bundle sheath.
2.	First stable product of photosynthesis is a 3-carbon compound PGA (Phosphoglyceric acid).	2.	First stable product of photosynthesis is a 4-carbon compound OAA (oxaloacetic acid).
3.	Ribulose 1, 5-biphosphate (RuBP) is carbon dioxide acceptor.	3.	There are two carbon dioxide acceptors in $C_4$ plants-phosphoenol pyruvic acid (PEP) in mesophyll chloroplasts and RuBP in the bundle sheath chloroplasts.
4.	Kranz anatomy absent.	4.	Kranz anatomy present.
5.	Ribulose biphosphate carboxylase oxygenase enzyme (Rubisco) is present in the chloroplast of mesophyll cells.	5.	Ribulose biphosphate carboxylase oxygenase enzyme is present in the chloroplast of bundle sheath while phosphoenol pyruvate carboxylase (PEP carboxylase) enzyme is present in the chloroplasts of mesophyll cells.
6.	The optimum temperature for $C_3$ cycle is 10-25°C.	6.	It is 30-45°C for $C_4$ cycle.
7.	Enzyme Rubisco shows lesser affinity for carbon dioxide.	7.	These plants are much more efficient because of stronger affinity of the carbondioxide and the enzyme PEP carboxylase.
8.	Carbon dioxide compensation point is high (40-60 PPM $\text{CO}_2$ ).	8.	Carbon dioxide compensation point is low (0 – 19 PPM, $\text{CO}_2$ ).
9.	In each chloroplast PSI and PSII are present.	9.	In chloroplast of bundle sheath cells PSII is absent. Therefore, these are dependant to mesophyll chloroplast for $\text{NADH} + \text{H}^+$ .

10.	Photorespiration occurs in those plants which reduces the photosynthetic yield.	10.	Photorespiration is absent. It present (in bundle sheath chloroplasts), it is negligible.
11.	They show oxygen inhibition of photosynthesis.	11.	They do not show oxygen inhibition of photosynthesis.
12.	These plants require 1000-4000 foot candles light intensity to reach solution.	12.	It is difficult to reach saturation even in full sun light.
13.	C <sub>3</sub> plants are usually adapted to cool and moist climate.	13.	They are well adapted to tropical climate.
14.	C <sub>3</sub> cycle is quite common in photosynthetic plants.	14.	C <sub>4</sub> cycle is found in certain tropical grasses, subtropical grasses, monocots and dicots.
15.	C <sub>3</sub> cycle is independent.	15.	C <sub>4</sub> cycle is closely associated with C <sub>3</sub> cycle.

### 1.11. FACTORS AFFECTING PHOTOSYNTHESIS

**The principle of limit factors :** Sachs (1860) introduced the concept of 'three cardinal points'-minimum, optimum and maximum for each factor for e.g. with any given species, there may be a given temperature below which no photosynthesis takes place, at optimum temperature the rate of photosynthesis will be highest and a maximum temperature above which no photosynthesis will take place. All factors of a physiological process, particularly the smallest one affected the total rate of process was realised first realised by Liebig (1843) when he gave the law of minimum. F. F. Blackman (1905) elaborated Liebig's statement and enunciated the 'Principle of limiting factors. According to him 'When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest factor'.

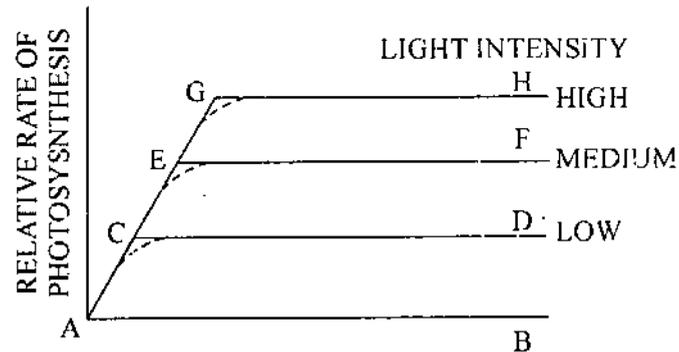


Fig. 12. Graphic representation of the principle of limiting factors.

The Blackman's Law of limiting factors can be explained by the fig. 12. Point a shows no photosynthesis in the absence of carbon dioxide. Carbon dioxide concentration is raised from 0 to 5 mg per hour and the rate of photosynthesis increases along the line AC. However, at this stage the rate of photosynthesis does not increase further and it becomes constant at line CD because the light intensity is now limiting factor. Increase in carbon dioxide concentration will have no effect on the rate of photosynthesis. If the light increased further to the medium level, the rate of photosynthesis increases upto CE level provided that there is further increase in carbon dioxide concentration. So, C, E and G are the points where the rate of photosynthesis

stops because of limiting nature of light. Like light and carbon dioxide, other factors of photosynthesis become limiting under certain conditions.

### External Factors

**1. Light :** The photosynthesis is affected by the intensity, quality and duration of light.

**Light intensity.** No photosynthesis occurs in a very low light intensity perhaps due to non opening of stomata and very low rate of light diffusion. The intensity of light beyond which a further increase fails to accelerate the rate of photosynthesis is called the 'light saturation intensity'. Optimum light intensity (saturation point) is 10% of full sunlight for shaded plants and 50-70% full summer sunlight for  $C_3$  plants. In  $C_4$  plants saturation point is not reached even in full sunlight. At very high light intensities there is decrease in the photosynthesis due to **photoinhibition** (reduction in hydration and closure of stomata) and **photooxidation** (oxidation of photosynthetic pigments, intermediates and enzymes—also called **solarization**).

During peak hour the maximum P/R ratio attained is 20 : 1 *i.e.*, the rate of photosynthesis is about 20 times faster than that of respiration. However in the morning as well as in the evening the rate of photosynthesis equals the rate of respiration. It is called **CO<sub>2</sub> compensation point** or **light compensation point**. During compensation point there is no evolution of gas. It is higher in  $C_3$  plants than  $C_4$  plants.

**Light quality :** Photosynthesis is successfully accomplished only in the visible light ( $39000\text{Å}$  to  $76000\text{Å}$  – Wavelength of spectrum. Rate of photosynthesis is maximum in red light (655 nm), average in blue (440 nm) and minimum in green light. Carbohydrates synthesis is favoured by red light, whereas blue stimulates the protein synthesis. However, maximum synthesis occurs in full sunlight.

**Light duration.** The duration of light has little effect on the rate of photosynthesis. Plants getting an average duration of 10-12 hours light per day show higher rate of photosynthesis than those which receives continuous light.

**Carbon dioxide.** The concentration of carbon dioxide in the atmosphere is 0.03% by volume. As carbon dioxide concentration increases, the rate of photosynthesis also increases, if no other factors are limiting. High concentration of carbon dioxide become toxic and further increase fails to accelerate the rate of photosynthesis. It is **CO<sub>2</sub> saturation point**.

**Oxygen :** The oxygen concentration in the atmosphere is 21% by volume. Optimal concentration of oxygen for photosynthesis is 2-5% in  $C_3$  plants. The higher concentration of oxygen has an inhibitory effect on photosynthesis (Warburg effect). It is due to photorespiration because no such effect is observed in  $C_4$  plants.

**Water.** A plant utilizes just 1% of water from its total amount and rest is transpired. Even a slight deficiency of water reduce the photosynthesis by decreasing the diffusing capacity (CO<sub>2</sub> in water) of stomata. Water is substrate in photosynthesis. An actual dehydration restricts the Hill reaction, activity of photosynthetic enzymes, photosynthetic electron transport and ultimately NADP reduction. The effect of water is more indirect than direct.

**Temperature.** The normal temperature at which plants start photosynthesis is 0-5%. Photosynthesis occurs in a wide range of temperature (lichens at  $-20^\circ\text{C}$ , conifers at  $35^\circ\text{C}$ , blue green algae at  $75^\circ\text{C}$ , Xerophytic plants like *Opuntia* at  $75^\circ\text{C}$ ). The optimum temperature for photosynthesis lies between 15-35°C for  $C_3$  plants and 35-45°C for  $C_4$

plants. Under the optimum value the rate of photosynthesis increases with the rise in temperature. It follows Von Hoff's rule that  $Q_{10} = 2$ . (i.e., temperature quotient-with every 10°C rise the rate of reaction is doubled). Above the 37°C the rate of photosynthesis show initial increase but it declines with time. The decline with time is described, as 'time factor'. The possible contents of time factor may be less availability of enzymes, destructive effects on other protoplasmic constituents. failure of carbon dioxide to diffuse, oxygen to come out and accumulation of end products.

**Mineral nutrients.** A number of mineral are required for photosynthesis. Mg is a constituent of Chlorophyll. Fe, Cu, Mn are essential for the formation of Chlorophyll. Mn and Cl take part in evolution of oxygen and transfer of electrons. P as  $H_3-PO_4$  is required for production of ATP. S, P and some other minerals take part in photosynthesis as constituent or activators of enzymes.

**Pollutants :** Several air pollutants reduce photosynthetic efficiency directly or indirectly. Dust particles and smoke reduces the intensity of light falling on the photosynthesizing organs. Smoke contains sulphur dioxide, which affects all the membrane system of plants. Thus, reducing the photosynthesis. Photochemical smog blocks the Hill reaction.

**Internal factors:**

**Chlorophyll.** Chlorophyll is essential for photosynthesis. The amount of carbon dioxide fixed by a gram of chlorophyll in an hour is called **photosynthetic number** or **assimilation number**, a term introduced by Willstatter and Stoll (1918) in order to determine reaction between photosynthesis and chlorophyll. They observed that assimilation number varies from species to species. However, the number decreases with increasing age of the leaf. Carotenoids are essential to prevent photo-oxidation which reduce photosynthesis.

**Internal structure of leaf.** The anatomical structures influencing photosynthesis are : thickness of epidermis, cuticle, size, structure, position and frequency of stomata. distribution of vascular tissues, intercellular spaces, position and number of chlorenchymatous cells and their chloroplast. These anatomical structures reduce the amount of carbon dioxide diffusion and rate of translocation of end products of photosynthesis.

**Accumulation of end products.** Slow rate of translocation results in accumulation of end products during afternoon. It reduces the rate of photosynthesis. If the end products are removed from the cells, the rate of photosynthesis increases.

**Protoplasmic factor.** Photosynthesis does not start immediately after the exposure of the plant to light and immediately after the development of the chlorophyll. The reason for this is not known. Hence, it is called the protoplasmic factor (unknown factor).

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**1.12. STUDENT ACTIVITY**

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1. Write down the significance of light reaction in photosynthesis.

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2. What is Blackman's law of limiting factor ? Describe the brief in factors affecting photosynthesis.

### 1.13. SUMMARY

Green plants make their own food by photosynthesis. During this process carbon dioxide from the atmosphere is taken in by leaves through stomata and used for making carbohydrates, principally glucose and starch. Photosynthesis takes place only in the green parts of the plants, mainly the leaves. Within the leaves, the mesophyll cells have a large number of chloroplasts that are responsible for CO<sub>2</sub> fixation. Within the chloroplasts, the membranes are sites for the light reaction, while the chemosynthetic pathway occurs in the stroma. Photosynthesis has two stages : the light reaction and the carbon fixing reactions. In the light reaction the light energy is absorbed by the pigments, and funnelled to special chlorophyll a molecules called reaction center chlorophylls. There are two photosystems, PSI and PSII. PSI has a 700 nm absorbing chlorophyll a P700 molecule at its reaction centre, while PS II has a P680 reaction centre that absorbs red light at 680 nm. After absorbing light, electrons are excited and transferred through PS II and PS I and finally to NAD forming NADH. During this process a proton gradient is created across the membrane of the thylakoid. The breakdown of the protons gradient due to movement through the F<sub>0</sub> part of the ATPase enzyme releases enough energy for synthesis of ATP. Splitting of water molecules is associated with PS II resulting in the release of O<sub>2</sub>, protons and transfer of electrons to PS II.

In the carbon fixation cycle, CO<sub>2</sub> is added by the enzyme, RuBisCO, to a 5-carbon compound RuBP that is converted to 2 molecules of 3-carbon PGA. This is then converted to sugar by the Calvin cycle, and the RuBP is regenerated. During this process ATP and NADPH synthesized in the light reaction are utilized. RuBisCO also catalyses a wasteful oxygenation reaction in C<sub>3</sub> plants; photorespiration.

Some tropical plants show a special type of photosynthesis called C<sub>4</sub> pathway. In these plants the first product of CO<sub>2</sub> fixation that takes place in the mesophyll, is a 4-carbon compound. In the bundle sheath cells the Calvin pathway is carried out for the synthesis of carbohydrates.

### 1.14. TEST YOURSELF

1. What is the correct molecular formula of chlorophyll a ?
2. Why light is necessary in the process of photosynthesis ?
3. Write the equation which most adequately sums up the photosynthetic reaction.
4. What is NADP ?
5. Who discovered the process of photophosphorylation ?
6. What is the source of oxygen liberated in process photosynthesis ?
7. Name the single most abundant protein on earth.
8. Who discovered C<sub>4</sub> cycle ?
9. In which light the rate of photosynthesis is maximum ?
10. Who proposed the law of limiting factors ?

**ANSWERS**

1.  $C_{55}H_{72}O_5N_4Mg$ .
2. To produce ATP and a reducing substance.
3.  $6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$ .
4. A co-enzyme
5. Arnon
6. Water
7. Ribulose 1-5 bi-phosphate carboxylase
8. Hatch and Slack
9. Red
10. Blackman.



## RESPIRATION

## STRUCTURE

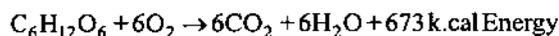
- Introduction
- Types of respiration
- Mechanism of respiration
- Glycolysis
- Aerobic respiration
- Krebs Cycle
- Electron transport system
- ATP
- Pentose phosphate pathway
- Anaerobic respiration
- Respiratory enzymes
- Fermentation
- Respiratory quotient (R.Q.)
- Respiration and photosynthesis
- Factors affecting the rate of respiration
- Student Activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know the aerobic respiration, anaerobic respiration, factor affecting respiration and respiratory quotient.

## 1.0. INTRODUCTION

ANS-2  
Respiration may be defined as the enzymes mediated process of biological oxidation of food material such as carbohydrates, fatty acids, amino acids and other organic acids. In this process there is generally intake of oxygen and release of  $\text{CO}_2$ . However in some cases only either process may occur *i.e.*, intake of oxygen without corresponding release of  $\text{CO}_2$  or release of  $\text{CO}_2$  without any intake of oxygen. The complete combustion of glucose which produces  $\text{CO}_2$  and  $\text{H}_2\text{O}$  as end products, yields energy most of which is given out as heat. The complete process can be summarized as:



The compounds that are oxidized during this process are known as respiratory substrates.

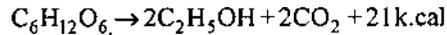
## 1.1. TYPES OF RESPIRATION

In normal respiratory process oxidation of organic substances takes place with the help of oxygen. This type of respiration which requires oxygen is called **aerobic respiration**. Animal respiration is essentially aerobic respiration and ceases altogether if oxygen is not available.



Many plants on the other hand continue to respire and give off carbon dioxide for some time even in the complete absence of oxygen. This kind of respiration is called **anaerobic respiration**.

In anaerobic respiration the food material is incompletely oxidised, forming ethyl alcohol and carbon dioxide.

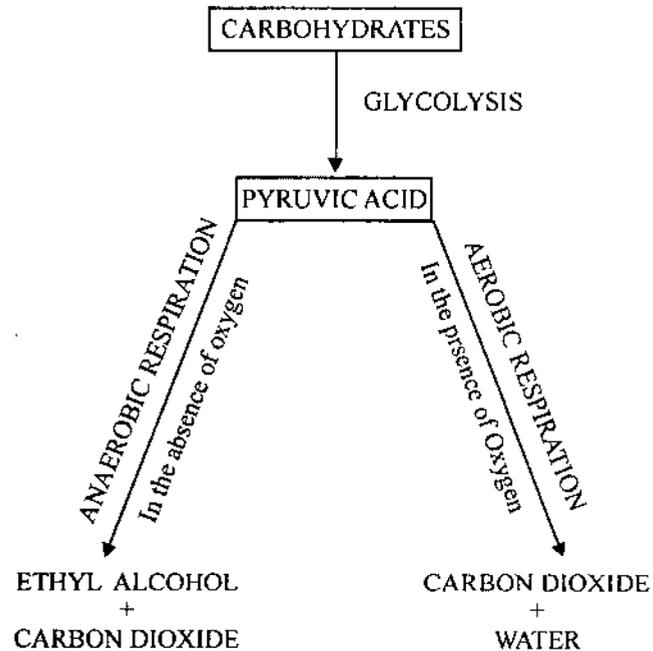


Fermentation is the form of anaerobic respiration which is carried on by some fungi and bacteria.

The plants that normally respire using oxygen can respire for sometime anaerobically if the oxygen supply is checked. Such plants are called **facultative anaerobes**. To these plants when oxygen is again supplied, the rate of sugar consumption is reduced and that of carbon dioxide evolution is increased. This process by which oxygen checks the anaerobic respiration and initiates aerobic one is named **Pasteur effect** after the name of scientist who first studied it. Plants living completely in absence of oxygen are called **obligate anaerobes**.

### 1.2. MECHANISOM OF RESPIRATION

The mechanism of respiration is not so simple as shown in the equation. The breakdown of carbohydrates in aerobic and anaerobic respiration follow the same course up to a certain stage. The fate of the intermediate products at this stage depends on the presence or absence of oxygen. The final products are carbon dioxide and water in the presence of oxygen and ethyl alcohol and carbon dioxide in its absence. Glycolysis is common to both aerobic and anaerobic respiration.



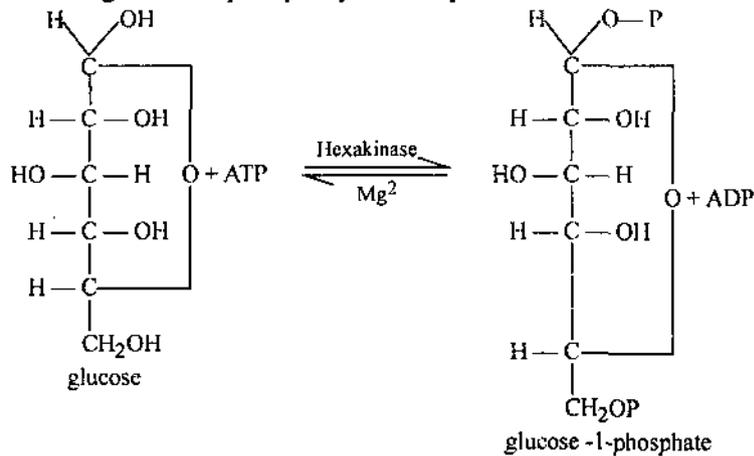
### 1.3. GLYCOLYSIS OR TRIOSIS OR EMBDEN-MEYERHOF-PARANA'S PATHWAY

The glycolytic pathway, also called **Embden-Meyerhof-Parana's pathway** named after the person who discovered it's various intermediates and enzymes, involving conversion of a hexose molecule to pyruvic acid, a three carbon compound (hence called triosis). The pyruvic acid is the end product of glycolysis. It operates in the cytoplasm and do not require oxygen. The EMP pathway can be divided into two phases :

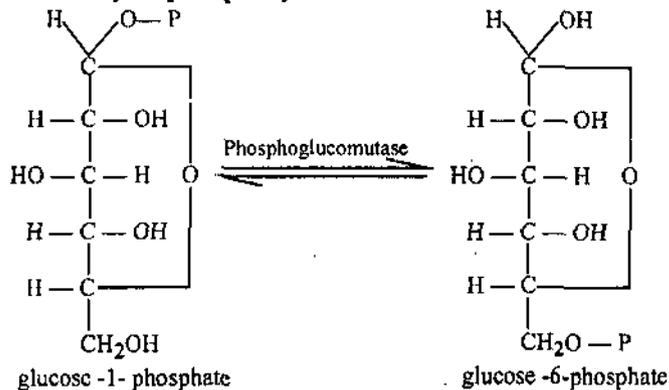
- (1) **Phosphorylation of hexose molecule** : Convesion of hexose molecule into fructose 1, 6 diphospnate.
- (2) Breaking of Fructose 1, 6 diphosphate into two pyruvic acid molecules (3 carbon compound).

1. **Phosphorylation of hexose molecule** : Glycolysis starts with the phosphorylation of hexose sugar (Fig. 1). In most of the cases it is done by the transfer of phosphate group from ATP, but sometimes directly from phosphoric acid.

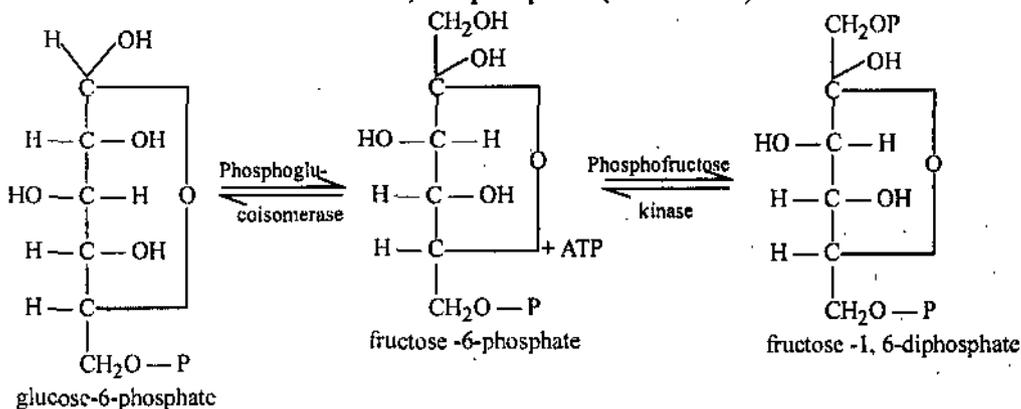
In reaction I D glucose is phosphorylated at position 1.



In II reaction the phosphate group of glucose-1-phosphate is shifted to position 6. Most of the glucose-1-phosphate in plant cells is formed by the phosphorylation of starch in presence of enzyme *phosphorylase*.



In reaction III glucose-6-phosphate is converted to fructose-6-phosphate which reacts with ATP to form fructose 1, 6-diphosphate (reaction IV)



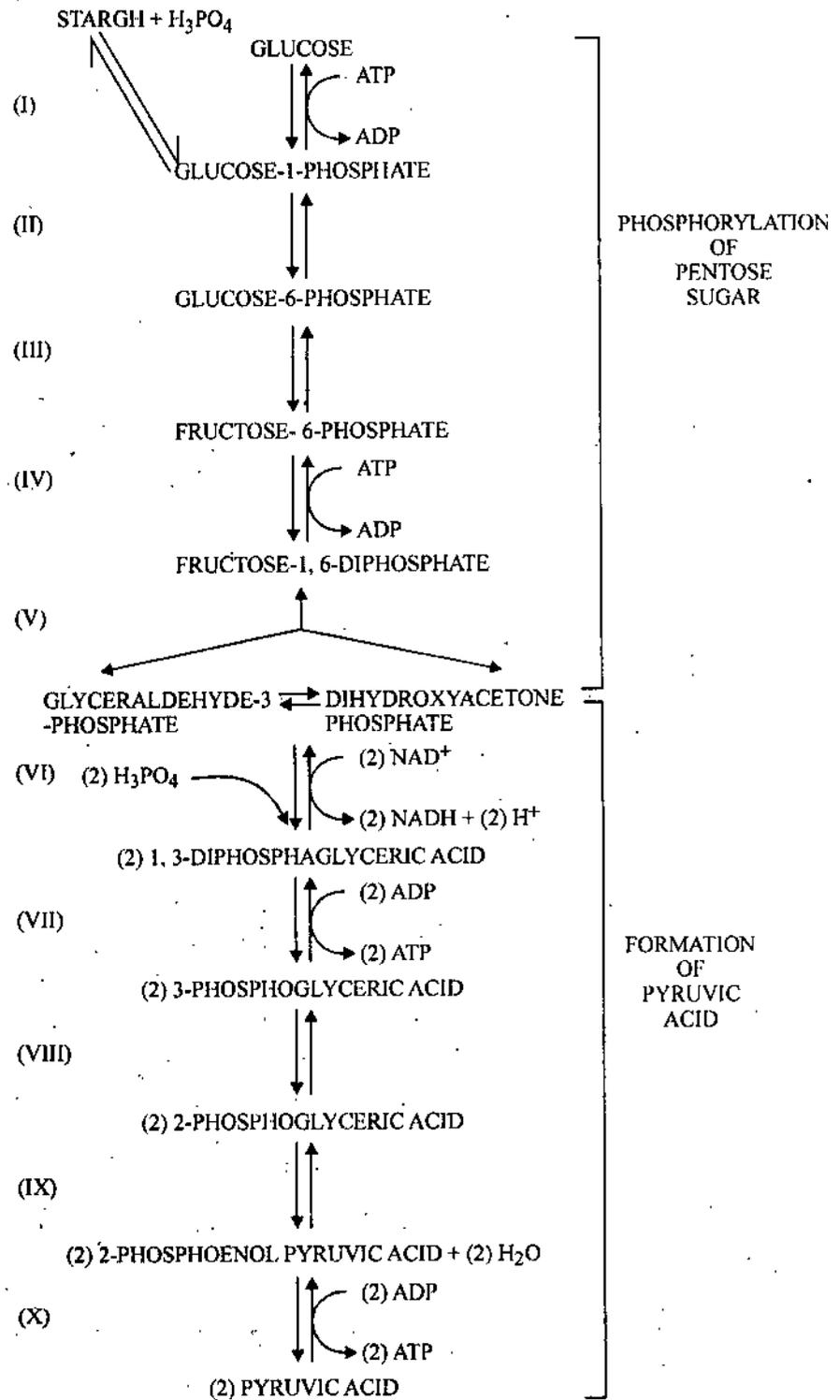
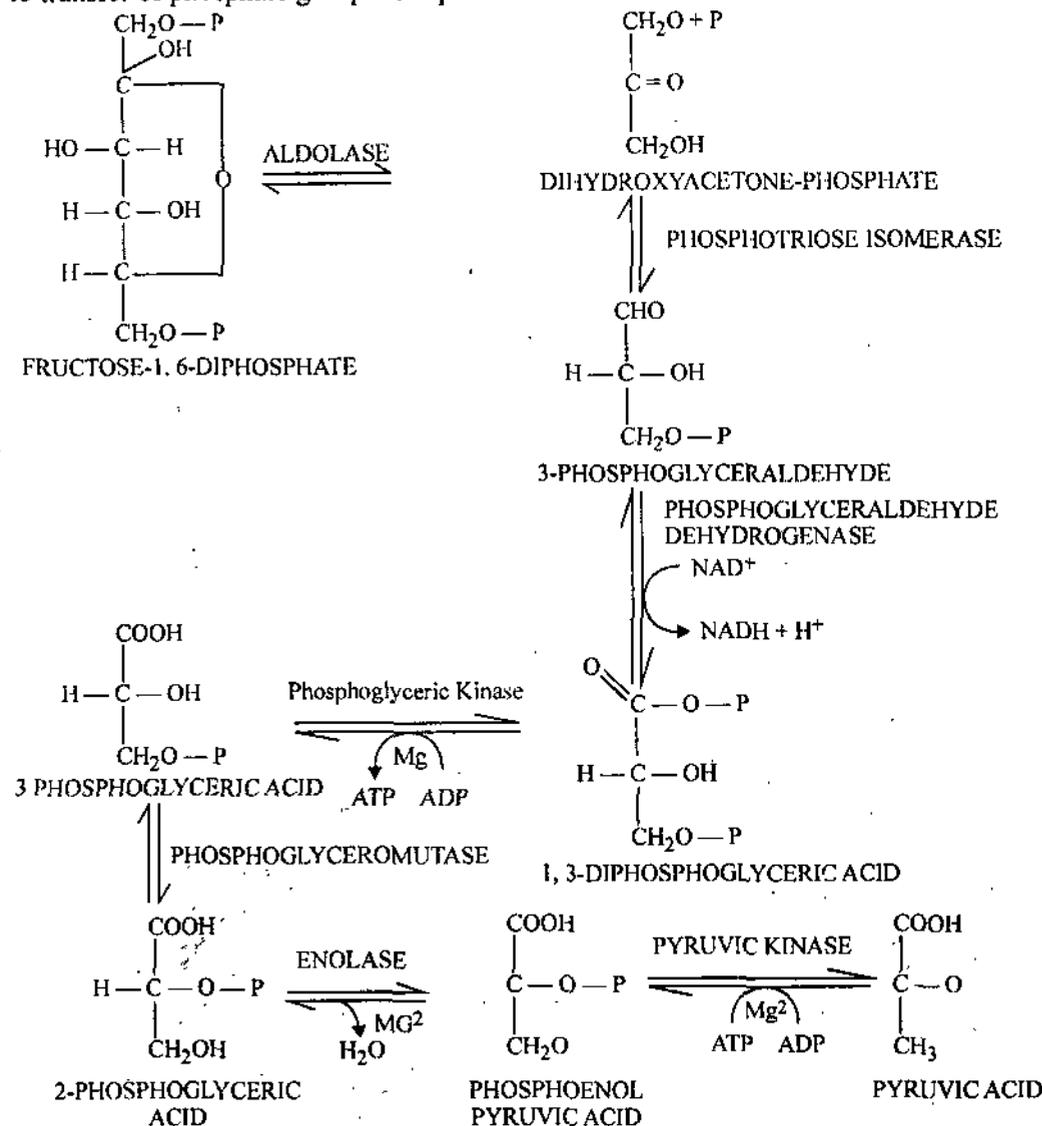


Fig. 1. E.M.P. Pathway for glycolysis.

**2. Breaking down of Fructose 1, 6 diphosphate into pyruvic acid :** In reaction V fructose-1, 6-diphosphate is split into two trioses, glyceraldehyde-3-phosphate and dihydroxyacetone-phosphate in equal amounts. Of these the former is used in further reactions and therefore, dihydroxyacetone-phosphate is regularly converted to glyceraldehyde-3-phosphate. Thus, for each glucose molecules two molecules of glyceraldehyde-3-phosphate are available for further reactions.

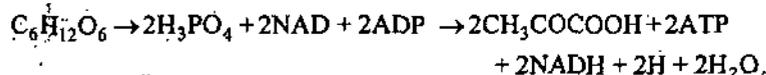
In reaction VI the glyceraldehyde-3-phosphate is both oxidized (by the loss of 2H's to NAD<sup>+</sup>) and phosphorylated by a reaction with phosphoric acid to form 1, 3-diphosphoglyceric acid.

In reaction VII, 1, 3-diphosphoglyceric acid reacts with ADP to form ATP and 3-phosphoglyceric acid which in reaction VIII is changed to 2-phosphoglyceric acid due to transfer of phosphate group from position 3 to 2.



In reaction IX, 2 phosphoglyceric acid is dehydrated forming phosphoenol pyruvic acid which then reacts with ADP to form ATP and pyruvic acid in reaction X,

A summary equation of glycolysis based on fig. 1 can thus, be written as :



In glycolysis thus, net gain of two moles of ATP (of the 4 ATP formed, two are used in converting the hexose to hexose-diphosphate) and two moles of NADH + H<sup>+</sup>, takes place in the breaking of one hexose molecule. As it will be discussed later, in the oxidation of each NADH + H<sup>+</sup>, 3 moles of ATP are formed. Thus from 2 moles of NADH + H<sup>+</sup>, six moles of ATP are formed only under aerobic conditions through ETS and the overall gain of ATP in glycolysis of aerobic respiration comes to be 8 moles of

**HEXOSE MOLECULE.** This ATP is used as energy source in other metabolic reactions.

**Salient features of glycolysis**

- (a) A hexose molecule is converted into two molecules of pyruvic acid.
- (b) No oxygen is used in the process and there is no evolution of  $\text{CO}_2$ .
- (c) There is gain of two ATP molecules per hexose molecule.

**Energetic after glycolysis**

Total production =  $2\text{NADH} + \text{H}^+ + 4\text{ATP}$

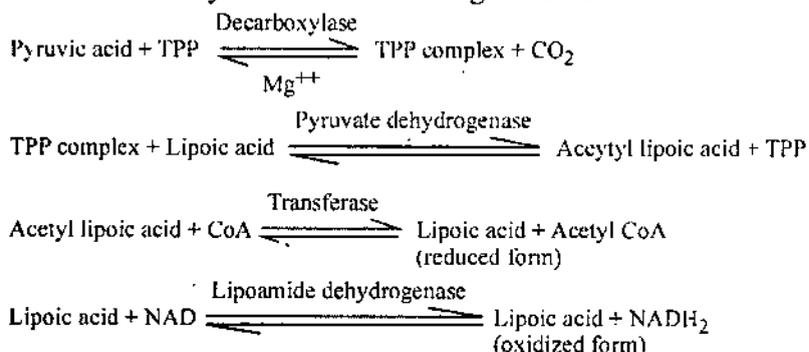
Loss in phosphorylation =  $2\text{ATP}$

Net gain =  $2\text{NADH} + \text{H}^+$  and  $2\text{ATP}$ .

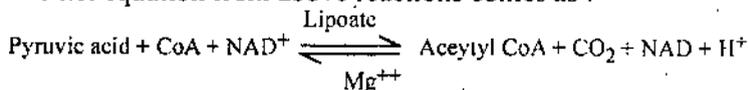
#### 1.4. AEROBIC RESPIRATION

For aerobic respiration or aerobic oxidation (in presence of oxygen), the pyruvic acid enters the mitochondria, where it is first converted into acetyl coenzyme A. The conversion of pyruvic acid to acetyl CoA probably occurs in the perimitochondrial space.

**Formation of acetyl co-enzyme A :** When sufficient oxygen is present, oxidative decarboxylation of pyruvic acid takes place to form acetyl co-enzyme A. This is a complex reaction and requires the presence of at least five cofactors, and a complex of enzymes called pyruvic acid dehydrogenase. The cofactors are thiamine pyrophosphate (TPP), Mg ions,  $\text{NAD}^+$ , coenzyme A (CoA) and lipoic acid. The substrate is dehydrogenated and the free hydrogen is passed on to  $\text{NAD}^+$ . TPP acts as the decarboxylating agent and lipoic acid as a carrier of the acetyl group from TPP to CoA. The reactions for acetyl CoA formation are given below.



The net equation from above reactions comes as :

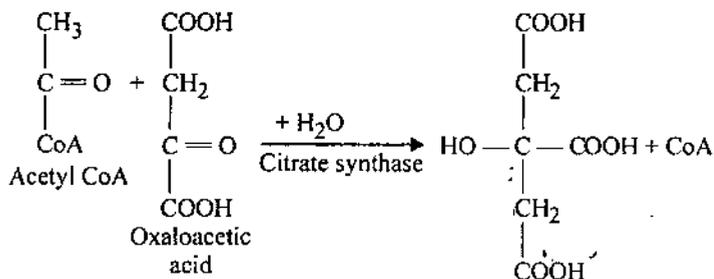


Acetyl CoA is the connecting link between glycolysis and Krebs's cycle.

#### 1.5. THE TRICARBOXYLIC ACID (TCA) CYCLE OR KREBS' CYCLE

The end product of the glycolysis is pyruvic acid. During aerobic respiration it enters the Krebs's cycle. The connecting line between glycolysis and Krebs cycle is Acetyl CoA. The cycle is named after **H. A. Krebs's** who discovered it. It is also called **tricarboxylic acid cycle (TCA)** or **Citric acid cycle** because of the cyclic manner in which the starting compound oxaloacetic acid is regenerated. All the enzymes of Krebs's cycle are present within the mitochondrion and therefore, the chain reactions are completed within it.

The first reaction of Krebs's cycle is the condensation of acetyl CoA with **oxaloacetic acid**, a 4-C dicarboxylic acid, to form **citric acid** (6-C acid). The CoA is released and a molecule of water is used up.



This oxaloacetic acid is regenerated back through a cycle of reactions as shown in Fig. 2. Citric acid first loses a water molecule back to form **isocitric acid**. The enzyme **aconitase** catalyses these both the reactions. The isocitric acid is then oxidized to **oxalosuccinic acid** using  $\text{NAD}^+$  in presence of enzyme isocitric acid dehydrogenase.  **$\alpha$ -Ketoglutaric acid** (5-C compound) in presence of a **carboxylase** enzyme. One molecule of  $\text{CO}_2$  is released. The  $\alpha$ -Ketoglutaric acid then reacts similar to pyruvic acid. Its *oxidative decarboxylation* results in the formation of **succinyl CoA**. The reaction is mediated by a complex of enzymes called  **$\alpha$ -ketoglutaric dehydrogenase**. Coenzyme A is then released from succinyl CoA under the influence of the enzyme **succinic thiokinase**. In this reaction **guanosine diphosphate (GDP)** is converted to **guanosine triphosphate (GTP)**. **Succinic acid** is formed and a water molecule is also used in this reaction.

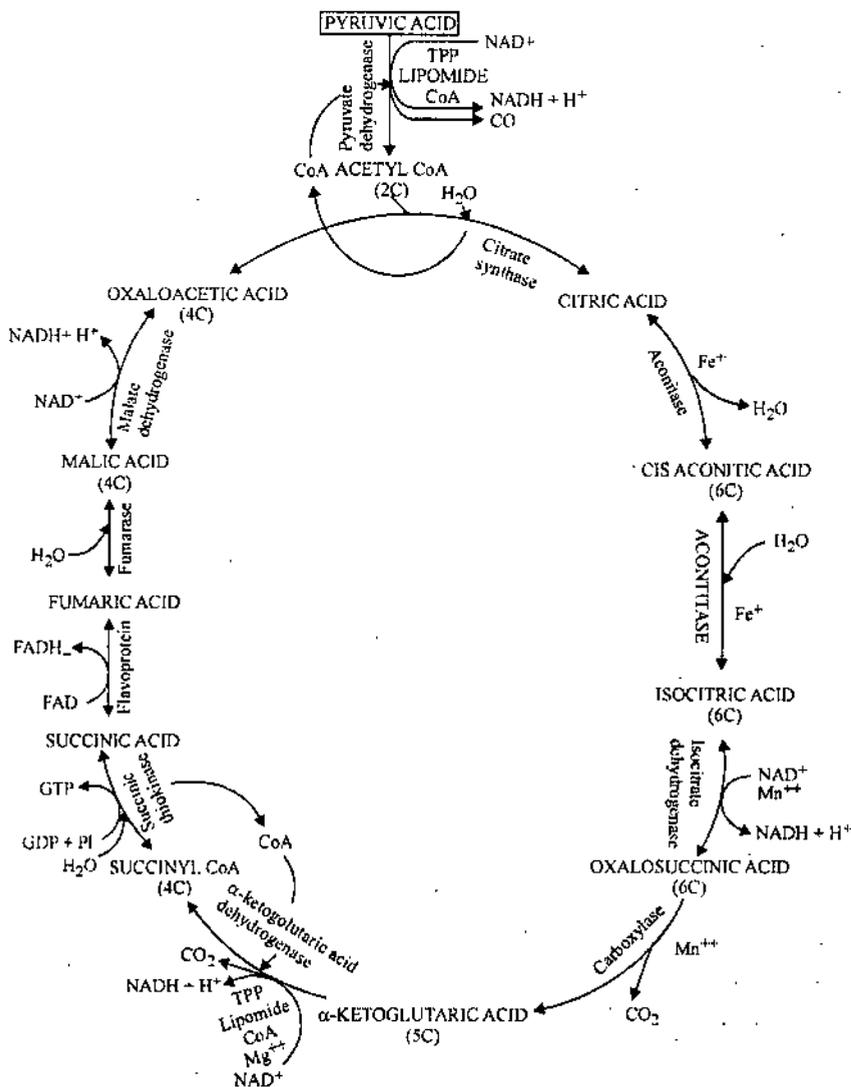


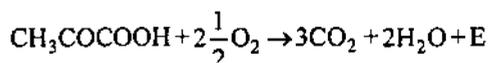
Fig. 2. Kreb's (Tricarboxylic acid) cycle.

In the next reaction succinic acid is oxidized to **fumaric acid** under the influence of the enzyme **succinic dehydrogenase**. This reaction is interesting in the sense that instead of NAD or NADP, the flavin prosthetic group, **flavine adenine denucleotide (FAD)** is used for oxidation and to receive two H<sup>+</sup> ions and two electrons from succinic acid. The fumaric acid then is hydrated by a molecule of H<sub>2</sub>O in the presence of **fumarse** to form **malic acid**.

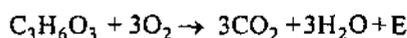
In the last oxidation reaction of the cycle, malic acid is converted to oxaloacetic acid in the presence of malic dehydrogenase. In this process NAD is converted to NADH<sub>2</sub>.

The regeneration of oxaloacetic acid, thus, completes the cycle. In the four oxidation steps four pairs of H ions and four pairs of electrons are removed from the intermediate products of the cycle. Of these three pairs are used in the reduction of NAD or NADP while the fourth pair reduces the FAD.

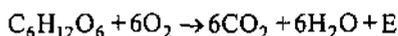
The total amount of oxygen consumed in the five oxidation steps of pyruvic acid is  $2\frac{1}{2}$  molecules, with release of carbondioxide at three steps. Water is released at six steps but is used up at 4 places, thus, only two molecules of water is the net gain of the cycle. The summary equation for the oxidation of pyruvic acid thus, is :



If we add  $\frac{1}{2}\text{O}_2$  required to oxidize NADH<sub>2</sub> formed in glycolysis on the left and a molecule of H<sub>2</sub>O so formed on the right hand side of the equation, it would read as :



Since each glucose molecule entering the glycolysis forms 2 molecules of pyruvic acid, both of which pass through glycolysis and the Kreb's cycle, the above equation is to be doubled and will read as :



The localization of complete process of respiration is shown in Fig. 3.

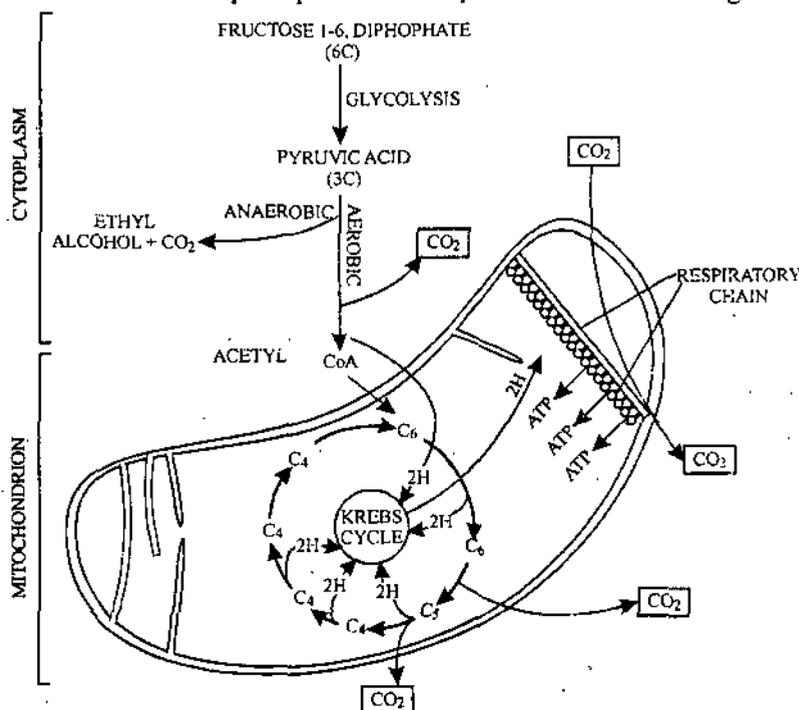


Fig. 3. Schematic representation of the localization of the mechanism of respiration.

### 1.6. ELECTRON TRANSPORT SYSTEM

In the process of glycolysis and the respiratory cycle at several places oxidation reaction takes place. In these reactions the  $H^+$  ions taken out do not combine directly with oxygen but are received by pyridine nucleotides (NAD, NADP) and FAD. These compounds are then oxidized through the electron transport system and the energy released in this process is used in the synthesis of ATP.

The electron transport system consists of a sequential series of cytochrome enzymes which pass on electrons from one to another. The electrons received by the hydrogen acceptors (NAD, NADP, FAD) are transferred to this system and are then passed 'down' the chain of these cytochrome enzymes. In each step of this series the energy level of electrons is lowered and is used in the change of ADP to ATP. Fig. 4 represents the schematic electron transport system.

It can also be seen from the figure that 3 ATP are formed from every pair of electrons passed through this system. The ATP synthesis takes place in the oxidation of  $NADH^+$ , 2 cytochrome b, and 2 cytochrome a. The electrons from cytochrome  $a_3$  are passed to oxygen at their lowest energy level. The oxygen so activated the  $H^+$  ions to form water. The overall production of ATP in the process of respiration is shown in fig. 4.

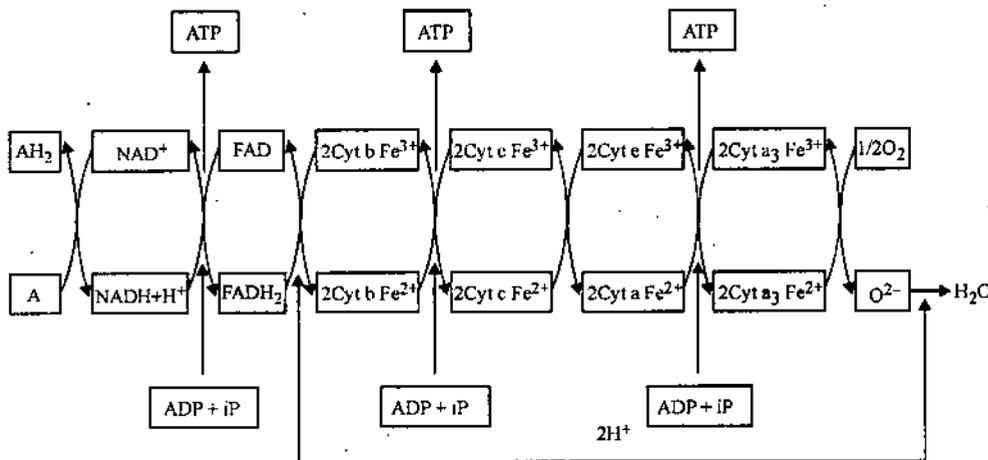
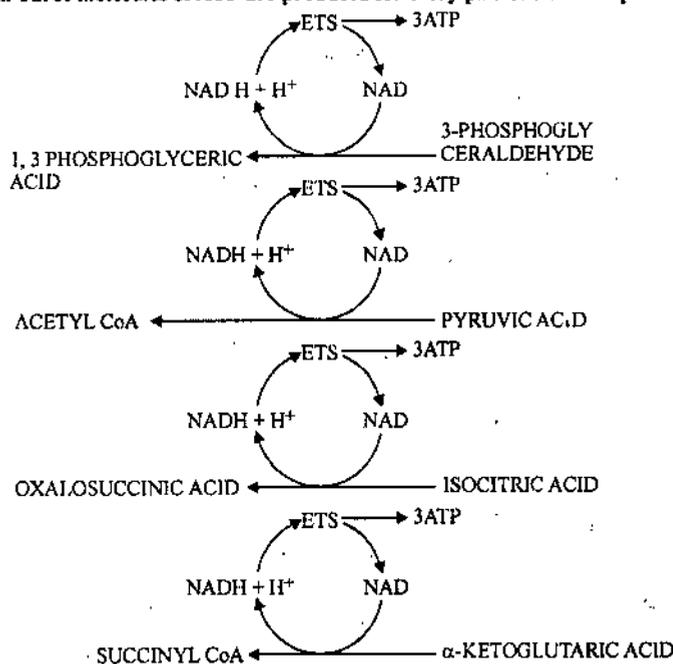
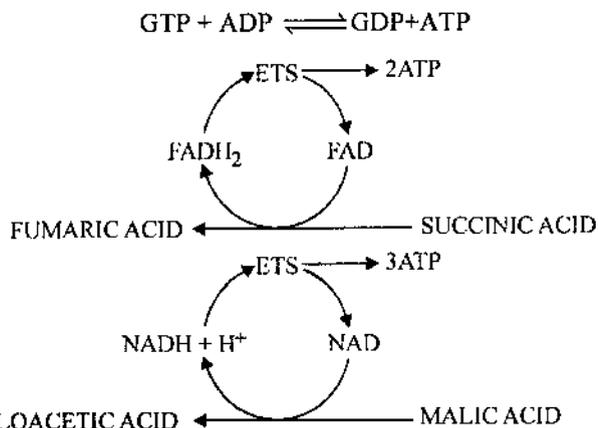


Fig. 4. The electron transport system. A Krebs cycle intermediate is oxidized releasing two hydrogen atoms in the process. The two electrons possessed by the hydrogen atoms are passed along a sequential series of cytochrome enzymes to oxygen. Three molecules of ATP are produced for every pair of electrons passed along this system.



In the conversion of succinyl CoA to succinic acid one molecule of GTP is formed. This GTP is converted to ATP.



Thus from the oxidation of one triose sugar 15 ATP are formed after glycolysis and 4 ATP are formed during glycolysis (3 in the oxidation of NAD and 1 ATP formed otherwise). From each hexose 2 triose sugars are formed. Thus, the net gain from the oxidation of hexose molecules will be 30 ATP after glycolysis in Krebs's cycle, 2 during glycolysis and 6 partly during glycolysis, and partly later by the oxidation of NAD, thus, totalling to 38 ATP.

### 1.7. ADENOSINE TRIPHOSPHATE (ATP)

ATPs are the temporary energy store houses of the cells. The energy released in the oxidation of carbohydrates, lipids or proteins is used up in the formation of ATP from ADP taking iP. The bond joining the last phosphate group of ATP is referred to as a **high energy bond** (~). It probably means that this energy is readily transferred to other compounds.

The terminal phosphate group of ATP contains about 7,600 calories of energy. From 38 ATP the total usable energy available will be  $7,600 \times 38 = 288,800$  calories. It has been mentioned earlier that from one hexose molecule 686,000 calories are obtained. Thus, the respiratory process is efficient only by  $686,000/288,800$  i.e. forty percent.

It has been shown that within the mitochondrion the ATP synthesis takes place in the head pieces of the F<sub>1</sub> particles.

### 1.8. PENTOSE PHOSPHATE PATHWAYS (PPP)

Other than the normal pathway for the aerobic respiration (as discussed earlier in this chapter), in some organisms there exists an alternative pathway for the oxidation of glucose. This pathway which requires the presence of oxygen and involves as number of pentose sugars, a 7-C sugar and a 4-C sugar is called **pentose phosphate pathway** (PPP) or **hexose monophosphate shunt** (Fig. 5).

As can be seen from the figure, NADPH + H<sup>+</sup> is formed in the reactions forming 6-phosphogluconic acid and ribulose-5-phosphate. One glucose molecule on oxidation forms 1 molecule of carbon dioxide. Thus, for the formation of 6CO<sub>2</sub>, six moles of glucose monophosphate are broken, of which 5 moles of fructose monophosphate are regenerated and 12NADPH<sub>2</sub> are formed. These are oxidized to 12NADP and 36ATP are formed. Thus, the energy outcome in the oxidation of glucose via this pathway is almost as efficient as that of the glycolytic Krebs's cycle pathway.

The PPP has an advantage over Krebs's cycle that its intermediate compound ribose-5-phosphate is used in the synthesis of nucleic acid.



**phosphorylation.** Some of the reactions of glycolysis are catalysed by these enzymes. Some of the enzymes of this group and the reactions catalysed by them are given in table. 1.

**Table 1**  
**Transphosphorylase Enzymes**

	Enzyme	Substrate	End Products
1.	Hexokinase	Glucose or Fructose + ATP	Glucose or Fructose -1-phosphate + ADP
2.	Phosphorylase	Starch + phosphate	Glucose-1-phosphate
3.	Phosphohexokinases	Glucose -6-phosphate + ATP	Glucose-1, 6-diphosphate + ADP
4.	Phosphoglucomutase	Glucose -1-phosphate	Glucose-6-phosphate
5.	Phosphoglycerokinase	1, 3, diphosphoglyceric acid + ADP	3-phosphoglyceric acid + ATP
6.	Phosphopyruvate kinase	2-Phosphopyruvic acid + ADP	Pyruvic acid + ATP

(2) **Desmolases.** These enzymes catalyse reactions where carbon chains are broken or lengthened. **Aldolase** which splits up fructose-1, 6-diphosphate into 3-phosphoglyceraldehyde and dihydroxyacetone phosphate form a typical example.

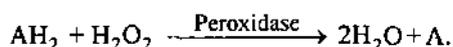
(3) **Hydrases.** These enzymes catalyse reactions where water molecule is added to or removed from a molecule without causing its splitting. **Enolase** enzyme removes water from 2-phosphoglyceric acid to form 2-phosphopyruvic acid. It is a reversible reaction. Other examples of this group are **aconitase** and **fumarase**.

(4) **Carboxylases.** These enzymes catalyse reactions where carbon dioxide is added or removed from a molecule. For example oxalosuccinic acid is decarboxylated by enzyme **carboxylase**.

(5) **Oxidases.** These enzymes bring about oxidation with the help of atmospheric oxygen which works as hydrogen acceptor. The **cytochrome** pigments, form one example of this group. These are proteins containing iron in their prosthetic group. The iron atom is oxidized by the atmospheric oxygen from ferrous to ferric state. **Cytochrome a<sub>3</sub>** also contains copper.

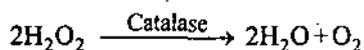
Other important oxidases are (a) **phenolases** which bring about oxidation of phenolic compounds and (b) **tyrosinases** which bring about the oxidation of tyrosine, an amino acid phenol, which is converted first into a red pigment and then into a black pigment called **melanin**.

(6) **Peroxidases.** These enzymes are of universal occurrence in higher plants and bring about the oxidation in presence of hydrogen peroxide or some organic peroxide which receiving the hydrogen atom and the electron gets converted to water.

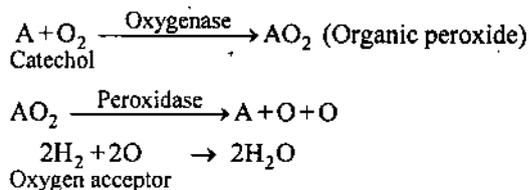


The organic compounds reacted upon are pyrogallol, catechol and amines etc.

**Catalase** enzyme of this group brings about the decomposition of  $\text{H}_2\text{O}_2$  into water and  $\text{O}_2$ .

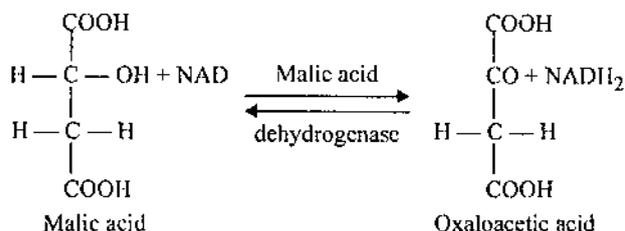


(7) **Oxygenases.** These enzymes are themselves oxidized to form peroxide or oxidise substrates like catechol with the help of atmospheric oxygen. The peroxide is then split by peroxidase enzyme to give active oxygen.



Oxygenases are active only in presence of peroxidases and are not present universally in plants.

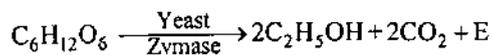
(8) **Dehydrogenases.** These enzymes have an organic coenzyme as hydrogen acceptor. The hydrogen atoms or the electrons are taken up by these acceptors which get reduced. **Dehydrogenases catalyse** these reactions. NAD or NADH usually acts as coenzyme. Flavoprotein form another group of such enzymes whose prosthetic group FMN or FAD is reduced.



## 1.11. FERMENTATION

Fermentation is a process quite similar to anaerobic respiration and is often carried out by fungi and bacteria. The peculiar feature of the process is that the substrate is present outside the cell as a solution.

**Alcoholic fermentation** of sugar brought about by yeast is the oldest and best known example of fermentation. A reference to it is found even in Vedas (about, 5000 years old). In this process also the hexose sugar is decomposed by yeast to form ethyl alcohol and carbon-dioxide. Certain mould fungi and bacteria also can bring about alcoholic fermentation.

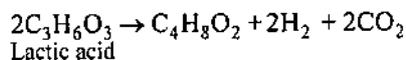


The enzyme system, *Zymase* secreted by the yeast cells brings about fermentation. The enzyme taken out from the yeast cells after grinding and crushing them could also bring about alcoholic fermentation in presence of some phosphates. Enzymes *sucrase* and *maltase* are also secreted by the yeast cells which hydrolyse the sucrose or maltose to *hexoses*. *Starch* can not be fermented by yeast cells as yeast does not produce *amylase*.

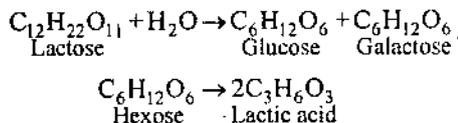
Yeast cells are killed by ethyl alcohol when its concentration reaches 10-15%. This property of yeast is used in brewing to produce alcohol and in baking to produce carbon dioxide which lightens the dough.

**Butyric acid fermentation** is brought about by a number of bacteria like *Clostridium butyricum*, *C. pasteurianum* and *Bacillus butyricus* etc. which are obligate anaerobes. The rancid butter forms the common example of butyric acid fermentation.





**Lactic acid fermentation** occurs during souring of milk and is brought about by several bacteria. Of these *Bacterium Acidi lacti* is an aerobic while *Bacterium Lactis acidi* is anaerobe. The former is abundant in the upper layers and the latter in the deeper layers of milk. Lactose of the milk is fermented and lactic acid is formed.



**Acetic acid fermentation** is brought about by the acetic acid bacteria like *Acetobacter aceti*, *A. xylinum*, and *A. rancens*. The ethyl alcohol is broken down to acetic acid.



It is slightly different than true fermentation as oxygen is used in breaking down of alcohol.

Other examples of fermentation are 'ripening' of cheese, 'retting' of flax, hemp and jute, 'Tanning' of leather and 'Curing' of tea and tobacco etc.

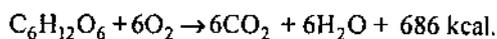
## 1.12. RESPIRATORY QUOTIENT (R.Q.)

The ratio of the volume of carbon dioxide released to the volume of oxygen taken in the respiration is called the **respiratory quotient** or R.Q.

$$\text{R.Q.} = \text{CO}_2/\text{O}_2$$

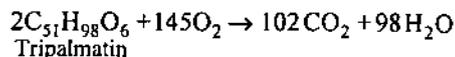
The value of R.Q. in a plant tissue depends upon the type of substrate it is utilising for respiration as is shown below.

**(a) R.Q. is unity.** Carbohydrates form the most common respirable material. In hexoses the amount of carbon dioxide released is equal to the amount of oxygen taken in.

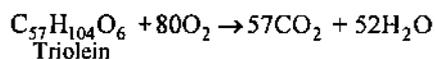


$$\text{R.Q.} = \text{CO}_2/\text{O}_2 = 6/6 = 1$$

**(b) R.Q. less than unity.** When substrates poor in oxygen like **fats** and **oils** are used as respirable material, the value of R.Q. is less than unity e.g. germinating fatty seeds of castor, mustard, cotton etc.



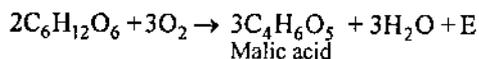
$$\text{R.Q.} = \text{CO}_2/\text{O}_2 = 102/145 = 0.7$$



$$\text{R.Q.} = \text{CO}_2/\text{O}_2 = 57/80 = 0.7$$

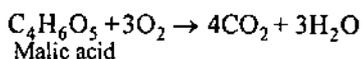
Fats before being oxidized are hydrolyzed to fatty acids and glycerol and utilize some oxygen without liberation of carbon dioxide. In the case of **proteins** also the value of R.Q. is less than one (about 0.8 or 0.9).

In some **succulents** like *Opuntia*, incomplete oxidation of carbohydrates takes place to form organic acids without the release of carbon dioxide.



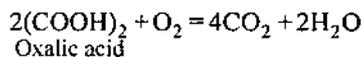
$$R.Q. = \text{CO}_2 / \text{O}_2 = 0/3 = 0$$

During the day the malic acid is oxidized to give carbon dioxide which is used in photosynthesis

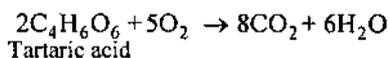


In succulents like *Bryophyllum*, the leaves directly use carbon dioxide released for the synthesis of organic acids in the dark. Thus the value of R.Q. becomes less than unity.

(c) **R.Q. more than unity.** When substances rich in oxygen (organic acids) are used as respirable materials, the value of R.Q. becomes more than unity.



$$R.Q. = \text{CO}_2 / \text{O}_2 = 4/1 = 4$$



$$R.Q. = 8/5 = 1.6$$

In **anaerobic respiration** also where carbon dioxide is released without the utilization of oxygen, the value of R.Q. is more than unity.

In **maturing fatty seeds** carbohydrates are converted to fats with the release of oxygen. This internal oxygen is used in respiration. Thus, carbon dioxide is released without oxygen being taken from outside. The value of R.Q. thus, is more than unity.

#### Measurement of R.Q.

The R.Q. is measured with the help of **Ganong's Respirometer**. The tube is filled with mercury or with strong sodium chloride solution. Use of water is avoided because carbon dioxide dissolves in it.

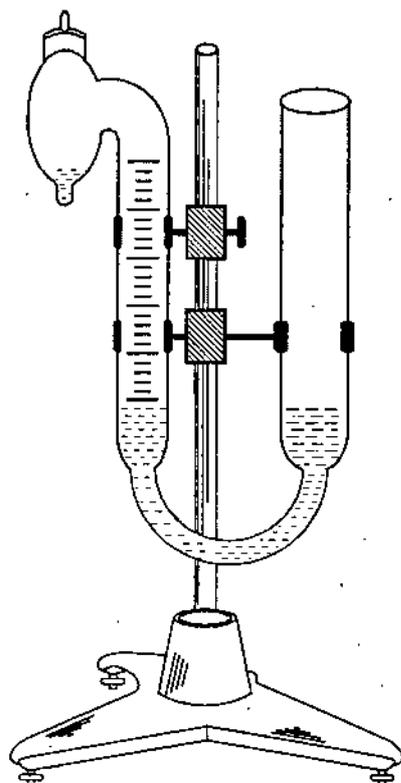


Fig. 6. Ganong's respirometer

It is an apparatus by which together with the amount of carbon dioxide released we can also measure the amount of oxygen taken in. The apparatus as shown in Fig. 6, consists of a bulb with a graduated side tube. The total volume of these both is about 102 ml (2 ml for respirable material). There is present a hole each in the neck of the bulb and its stopper at same height. The graduated tube is connected with a levelling tube with the help of a rubber tubing and solution is filled in the apparatus.

The plant material is placed in the bulb (If green, cover the bulb with black cloth) and the 2 holes in the neck are brought opposite to each other so that the air in the bulb communicates with the air outside and is at atmospheric pressure. The level of the caustic potash solution is adjusted at 100 ml mark. Now rotate the stopper so that the 2 holes separate and the connection of the bulb from outside is cut.

Carbon dioxide produced in respiration is absorbed by caustic potash due to which solution in the graduated tube rises say upto 75 ml mark. It indicates that 25 ml of carbon dioxide is released or 25 ml of oxygen is taken in.

In case of carbohydrates the level of mercury in the tube remains unchanged indicating that carbon dioxide released in respiration is equal to oxygen taken in. The amount of carbon dioxide released can be measured by adding caustic potash in the tube. The rise in the mercury level in the graduated tube will give the carbon dioxide released in respiration.

In fatty seeds when R.Q. is less than one, the level of mercury rises up in the tube because less of carbon dioxide is released than oxygen absorbed. Suppose the rise is  $V_1$  ml (excess  $O_2$  taken). By adding caustic potash, further rise in the mercury level takes place by  $V_2$  ml and indicates the carbon dioxide released. The total volume of oxygen taken thus will be equal to  $V_1 + V_2$  ml. The R.Q. in this case will be equal to

$$\frac{V_2}{V_1 + V_2}$$

In case of organic acids, where less of oxygen is taken than carbon dioxide released the level in the tube falls. Suppose fall which indicates excess of carbon dioxide released is equal to  $V_1$  ml. Add caustic potash to the tube. There will be a rise in the level of mercury. Suppose this rise is equal to  $V_2$  ml and represents the total amount of carbon dioxide released. Thus, the amount of oxygen taken will be equal to

$$V_2 - V_1 \text{ and the value of R.Q.} = \frac{V_2}{V_2 - V_1}$$

### 1.13. RESPIRTION AND PHOTOSYNTHESIS

The two processes are just the reverse of each other as is shown in table 2.

**Table 2. Comparison between Respiration and Photosynthesis**

Respiration		Photosynthesis	
1.	It is a catabolic process,	1.	It is an anabolic process.
2.	Organic food is used up.	2.	Organic food is formed.
3.	Dry weight decreases.	3.	Dry weight increases.
4.	Chemical energy is changed into kinetic energy.	4.	Radiant energy is changed to chemical energy.
5.	Raw materials used are generally hexoses.	5.	Raw materials used generally are carbon dioxide and water.

6.	The end products are CO <sub>2</sub> and H <sub>2</sub> O.	6.	The end products are hexoses and O <sub>2</sub> .
7.	It takes place in all the plants.	7.	It takes place only in green plants.
8.	It takes place in all the parts of the plants.	8.	It takes place only in the green parts of the plants.
9.	It is independent of light and therefore, takes place for 24 hours.	9.	It is light dependent and therefore, takes place only during the day.
10.	In gaseous exchange, CO <sub>2</sub> is given out and O <sub>2</sub> is taken in.	10.	In gaseous exchange O <sub>2</sub> is given out and CO <sub>2</sub> is taken in.

### 1.14. FACTORS AFFECTING THE RATE OF RESPIRATION

#### External Factors

(1) **Temperature.** It is one of the most important external factor affecting the rate of respiration. The rate of respiration rises with the rise of temperature between 0°C—45°C. Within this range the temperature co-efficient of respiration ( $Q_{10}$ ) varies between two to three. The optimum temperature however, varies between 30°C—40°C. Above the optimal level of temperature, the rate of respiration rises but soon declines. Higher the rise in temperature more rapid is the fall in the rate. This decline is due to the 'Time factor' *i.e.* the enzymes become inactive at high temperatures. The denaturation of enzymes is not sudden but starts after some time and is accompanied with the fall in the rate of respiration.

The rate of respiration declines at lower temperatures. The lowest limit for the respiration varies in different plants. Normally it may continue even at —20°C at a very slow rate, and the dormant seeds retain their viability even at —50°C. For this reason the fruits and vegetables are stored at very low temperatures. Due to decrease in the rate of respiration, low night temperatures are advantageous for the development of large storage organs *e.g.* potato tubers etc. At high night temperature the tubers are not formed properly due to utilization of food during higher rate of respiration.

(2) **Oxygen.** The presence and absence of oxygen determines the type of respiration. As there is a very high percentage of oxygen in the atmosphere, fluctuations in its concentration do not show significant change in the rate of respiration. However, if the oxygen concentration is reduced to a level of about 2% the rate of carbon dioxide evolution is also reduced.

(3) **Light.** It is not a direct factor as the respiration continues even in the dark. However, increase in the light intensity increases the rate of respiration. It is probably through the rise in temperature, opening the stomata and accumulation of respirable material in photosynthesis, that influences the rate of respiration.

(4) **Carbon-dioxide.** Normally the percentage of carbon dioxide in the atmosphere remains unchanged, while it changes significantly in the soil. Increase in the carbon-dioxide concentration reduces the rate of respiration. It causes the inhibition of germination in some seeds. This quality is used in the storaton of fruits. The fruits kept in high carbon dioxide concentration respire at a very low rate and thus, do not deteriorate soon.

(5) **Water.** For respiration the presence of water is essential. It is evident from the fact that the respiration is very slow in dry seeds and increases rapidly when seeds are soaked in water. The seed viability can be preserved with a minimum deterioration by removing their water to a level where the rate of respiration is minimum.



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### 1.16. SUMMARY

Plants unlike animals have no special systems for breathing or gaseous exchange. Stomata and lenticels allow gaseous exchange by diffusion. Almost all living cells in a plant have their surfaces exposed to air.

The breaking of C-C bonds of complex organic molecules by oxidation cells leading to the release of a lot of energy is called cellular respiration. Glucose is the favoured substrate for respiration. Fats and proteins can also be broken down to yield energy. The initial stage of cellular respiration takes place in the cytoplasm. Each glucose molecule is broken through a series of enzyme catalysed reactions into two molecules of pyruvic acid. This process is called glycolysis. The fate of the pyruvate depends on the availability of oxygen and the organism. Under anaerobic conditions either lactic acid fermentation or alcohol fermentation occurs. Fermentation takes place under anaerobic conditions in many prokaryotes, unicellular eukaryotes and in germinating seeds. In eukaryotic organisms aerobic respiration occurs in the presence of oxygen. Pyruvic acid is transported into the mitochondria where it is converted into acetyl CoA with the release of CO<sub>2</sub>. Acetyl CoA then enters the tricarboxylic acid pathway or Krebs' cycle operating in the matrix of the mitochondria. NADH + H<sup>+</sup> and FADH<sub>2</sub> are generated in the Krebs' cycle. The energy in these molecules as well as that in the NADH + H<sup>+</sup> synthesized during glycolysis are used to synthesise ATP. This is accomplished through a system of electron carriers called electron transport system (ETS) located on the inner membrane of the mitochondria. The electrons, as they move through the system, release enough energy that are trapped to synthesise ATP. This is called oxidative phosphorylation. In this process O<sub>2</sub> is the ultimate acceptor of electrons and it gets reduced to water.

The respiratory pathway is an amphibolic pathway as it involves both anabolism and catabolism. The respiratory quotient depends upon the type of respiratory substance used during respiration.

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### 1.17. TEST YOURSELF

1. What will happen to the plant if the rate of respiration becomes more than that of photosynthesis?
2. What is the importance of respiration in plants?
3. What is RQ?
4. What is the end product of glycolysis?
5. What is the site of oxidative phosphorylation?
6. What is ATP?
7. How many molecules of ATP are generated in one Krebs cycle?
8. What is fermentation?
9. What are the end products of fermentation when sugars are used as raw materials?
10. If CO<sub>2</sub> is given out in respiration, why does the amount of CO<sub>2</sub> in the atmosphere remains relatively constant?

**1.18. ANSWERS**

1. Plant will die due to starvation.
2. It liberates energy.
3. Ratio of  $O_2$  taken to  $CO_2$  liberated.
4. Pyruvic acid
5. Mitochondria.
6. A molecule which contains high energy phosphate bond.
7. 12.
8. An anaerobic respiration with few differences.
9. Alcohol and  $CO_2$ .
10.  $CO_2$  is converted to carbohydrate in the process photosynthesis.



## 3

## GROWTH HORMONES

## STRUCTURE

- Introduction
- Auxins
- Gibberellins
- Cytokinins
- Ethylene
- Abscisic acid
- Student Activity
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know different growth hormones and their physiological effects.

## 1.0. INTRODUCTION

The growth and differentiation of plants is controlled by special class of chemical compounds called **hormones**. The term hormone was derived from a Greek word "*hormao*" which means "**to urge on**" and was first used by **Starling** (1906) to refer to substances secreted in vertebrate bodies in ductless glands and capable of evoking responses in other regions. The presence of growth regulating substances in plants was first suggested by **Julius Van Sachs** (1882), when he suggested that there were organ forming substances in plants. According to **Thimann** (1934) a plant hormone or phytohormone can be defined as "**organic substances produced naturally in the higher plants, controlling growth or other physiological functions at the site remote from the place of production and active in small amounts.**" **Plant hormones** or **phytohormones** are also known as **growth regulators, growth substances, growth hormones** etc. As the above definition indicates all phytohormones are growth regulators but all growth regulators are not phytohormones. Growth regulators include all naturally occurring as well as synthetic substances.

Following five major types of phytohormones are recognised in plants :

1. **Auxins** (concerned with cell elongation, and cell division).
2. **Gibberellins** (concerned with cell enlargement and differentiation).
3. **Cytokinins** (concerned with cell division).
4. **Abcisic acid** (concerned with resting stages in the lateral buds).
5. **Ethylene** (concerned with senescence and ageing).

**F. W. Went** (1928) of Holland carried out a series of experiments and demonstrated that tip of coleoptile contain a substance which is capable of promoting cell enlargement. He placed several freshly cut coleoptile tips on agar block which was kept on a piece of inert material such as glass. After a particular period of time, he cut the agar block into small cubes. He discarded the tips and placed the agar cubes eccentrically on decapitated coleoptile stumps for nearly two hours in the dark (Fig. 1.) The effect of the agar cube was similar to the tip as was shown by the curvature of the

coleoptile. Coleoptiles grow and bent away from the sides on which the block was placed. The degree of the curvature of coleoptile was directly proportional to the concentration of the chemical influence in the agar block.

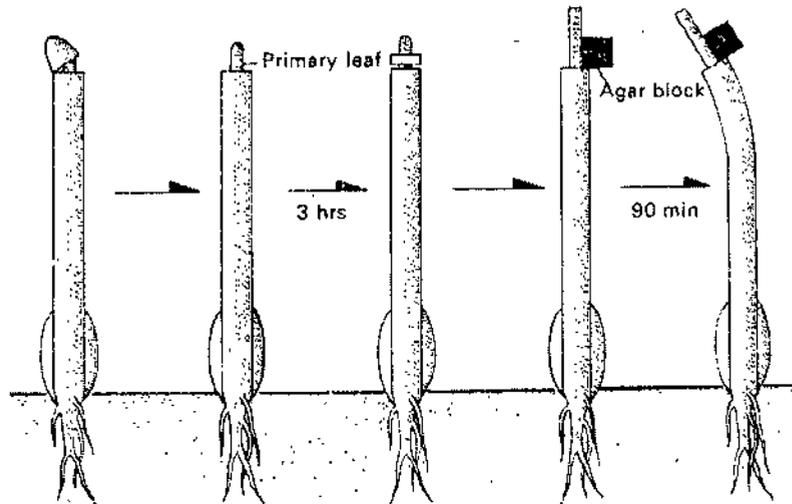


Fig. 1. Discovery of auxins-Experiments of F.W. Went *Avena* Curvature Test:

Because of the use of the *Avena* plant for this bioassay it subsequently become known as *Avena* curvature test. He named this substance as **auxin** (Greek, *auxein*, to grow). He further found that when unilateral light falls upon an excised *Avena* coleoptile tip placed in contact with two agar blocks separated by mica sheet; growth hormones is displaced towards the shaded side (65%) as compared to illuminated side (35%) (Fig. 2 A, B).

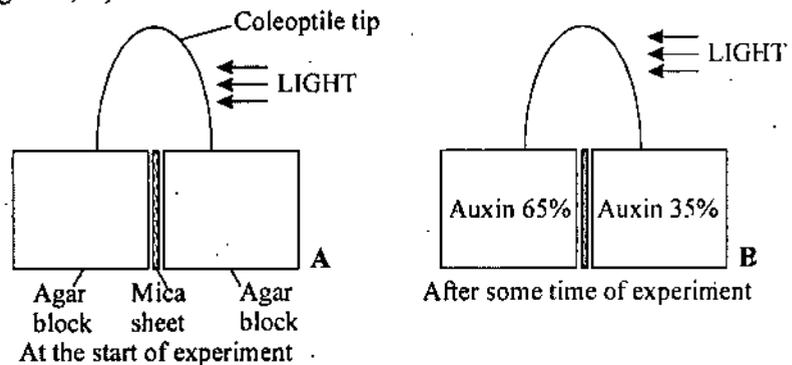


Fig. 2. Differential distribution of auxin in coleoptile tip under the influence of unilateral light.

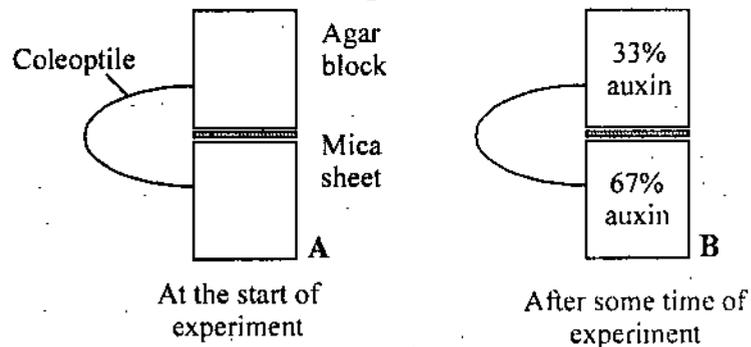


Fig. 3. Differential distribution of auxin from coleoptile under the influence of gravitational force.

Dolk (1920) demonstrated that when an excised coleoptiles tip is placed in a horizontal position in contact with the agar blocks, growth hormone is displaced towards the lower side (67%) as compared to upper side (33%) (Fig. 3A, B).

## 1.1. AUXINS

The auxins were the first hormones to be discovered in the plants. The first worker who suspected the presence of growth substance in the tips of the plant were **Charles Darwin** and his son **Francis Darwin** (1880), **Charles Darwin** demonstrated the effect of light and gravity on bending of both roots and shoots tip (tropic movement) were mediated by the tips. He exposed the tip of the **Canary grass** (*Phalaris Canariensis*) to unilateral light and observed it bends towards light. When the tip of coleoptile was removed, it gave no response to unilateral illumination (Fig. 4).

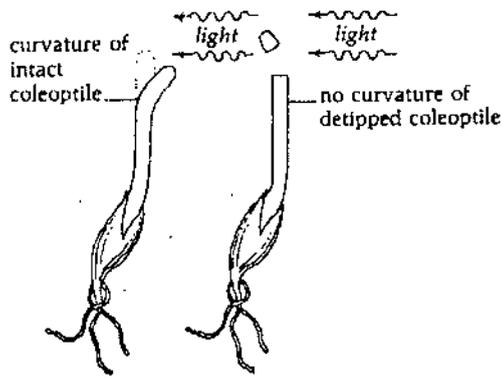
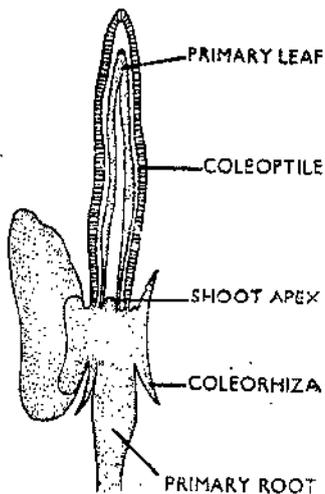


Fig. 4. Darwin Experiment

**Fitting** (1907, fig. 5), working in a room saturated with water vapours observed that lateral incisions either on one or both sides of the *Avena* coleoptile do not prevent it bending toward light given from one side. His observations suggested that cellular integrity was not essential for passing of internal stimulus. **Boysen-Jensen** (1910), found that phototropic response was lost by decapitation of the tip but it could be recovered if the tip was replaced on stump. He also concluded that curvature causing stimulus is active on the down side of the coleoptile **Stark** (1917) observed that the sap collected from *Avena* coleoptiles could be dispersed in agar blocks. When these blocks are placed asymmetrically to the stumps of detipped coleoptiles curvature resulted. **Paal** (1918, Fig. 5) demonstrated that even in dark the growth substance travelled downwards to cause growth. He also concluded that stimulus was reduced at the tip and it was water soluble.

### Coleoptiles



In the monocots *e.g.*, grasses, oats, maize etc., the plumule in the seed remains covered by a protective cap like structure called as **Coleoptile**. On germination of the seed, the coleoptile grow upward in the form of a tubular covering which surrounds the long narrow primary leaf during early stages of the development of seedling (see figure in box).

Charles Darwin observations are recorded in this famous book on "**The Power of movement in plants**" (1881).

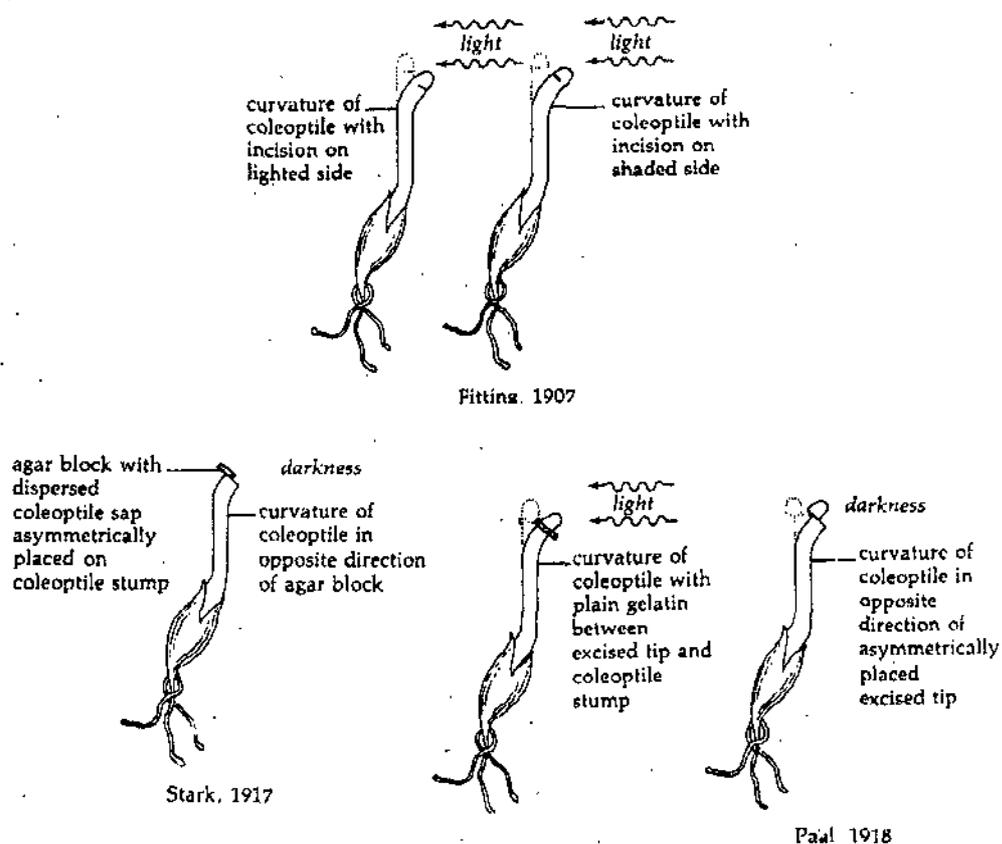


Fig. 5. L. S. of the oat (*Avena sativ*, Seedling and experiments of Fitting, Stark and Paal).

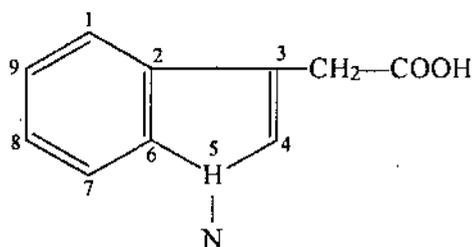
### Isolation of auxins

Kögl and Haagen-Smit (1931) isolated a pure crystalline substance from human urine (40 mg from 150 litres) and named it as **auxin-A** (auxentriolic acid- $C_{18}H_{33}O_5$ ). Kögl, Erxleben, and Haagen-Smit (1934) isolated a new crystalline substance from corn germ oil and named it as **auxin-B** (auxenolonic acid -  $C_{18}H_{30}O_4$ ). Finally in 1934 they isolated a third compound from human urine and named it as **heteroauxin**. It is now called as **indole-3-acetic acid** (IAA,  $C_{10}H_9O_2N$ ). It occurs in the human urine of persons suffering from **pellagra** (niacin or nicotinic acid deficiency). The role of IAA in humans is not known.

### Chemical Structure

**Natural auxins.** Auxin-A and auxin-B have never been isolated again. IAA is the principal natural auxin, has been found in all plants studied so far and fungi. Other naturally occurring auxins are **Indole-3-acetaldehyde**, **Indole-3-acetonitrile**, **Indole-3-pyruvic acid**, **Indole-3-ethanol** etc.

**Synthetic auxins.** Some synthetic chemical compounds show the similar physiological activities as that of auxins. These chemicals are called **synthetic auxins**. Some of them are : Indole-3-butyric acid, Indole-3-propionic acid (Indoles), 2, 3, 6-trichlorobenzoic acid, 2-methoxy 3, 6-dichloro-benzoic acid (Benzoic acids),  $\alpha$ -naphthalene acetic acid,  $\beta$ -naphthalene acetic acid (Naphthalene acids), 2, 4-dichlorophenoxy acetic acid (2, 4-D), 2, 4, 5-Trichlorophenoxyacetic acid (2, 4, 5-T-Chlorophenoxyacids),  $\alpha$ -naphthoxyacetic acid (Naphthoxy acid) etc.



Indole-3-acetic acid (IAA)

### Biosynthesis

**Thimann** (1935), observed that a fungus *Rhizopus Suinus* can convert the aminoacid **tryptophan** to IAA. **Wiedermann et. al.**, (1940) worked out the conversion of tryptophan into Indole-3-acetic acid. Tryptophan is first converted Indole acetaldehyde either through Indole pyruvicacid or through tryptamine. Indole acetaldehyde is then converted to Indole-3-acetic acid.

### Transport

The usual sites of auxin-synthesis are meristem and enlarging tissues. From these parts the auxins are transported to other plant parts. The transport of auxins in plants is predominantly polar. In stem is the **basipetal i.e.**, it takes place from apex towards base. In roots it is **acropetal i.e.**, from base to apex. **Jacobs** (1961) found that in *Coleus* stem sections the ratio the basipetal to acropetal (base to tip) transport of auxin is 3 : 1. Some of the auxin produced by the leaf is transported in the phloem tissues to other parts of plant (**Audus**, 1959), a type of transport that is definitely not polar.

### Physiological effects of Auxins

**1. Cell elongation.** The primary physiological effect of the auxins in the plants is to stimulate cell elongation in the stem of plants (inhibits cell elongation in roots) e.g., **phototropism** and **geotropism**. In **phototropism** unilateral light leads to displacement of auxin on the shaded side of the plant, thus causing more growth on the darker side and hence curvature of the shoot towards light takes place. In **geotropism** curvature is caused by displacement of the hormone on the lower side of the axis. The shoot curve upwards because its growth is promoted on the lower side and root curve downwards because its growth is inhibited by the auxins on the lower side (fig. 6).

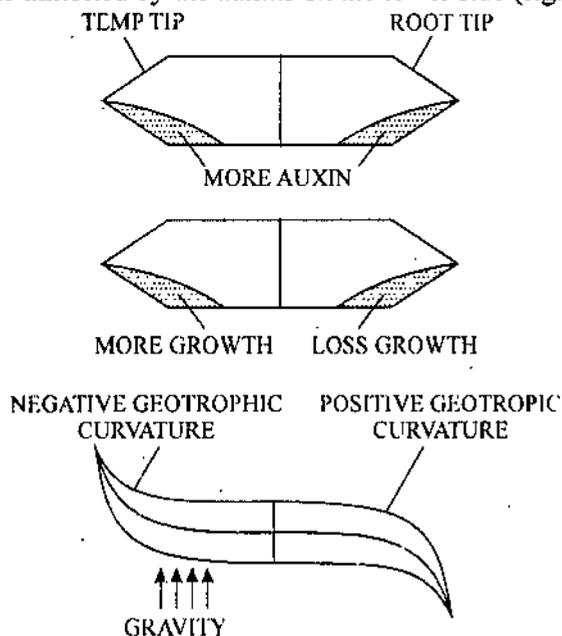


Fig. 6. Effect of auxins to stimulate cell elongation in the stem of the plants.

## 2. Cell division

Auxins induce cell division in **cambium**. The reactivation of the cambium in the growing season apparently triggered by IAA moving from the developing shoot apices. During injury it is also responsible for the formation of **wound tissue** (also called **callus**).

## 3. Development of callus

In tissue cultures, the continued callus growth is possible only in the presence of auxin. Tissue culture studies which has been so valuable for the study of morphogenesis depends on the action of auxins on cell division.

## 4. Differentiation of Xylem and phloem

Only when IAA is present in the medium for tissue culture, no phloem differentiation occurs. Xylem differentiation is more pronounced than the phloem.

## 5. Apical dominance

In most vascular plants if the apical bud is intact, the lateral buds formed immediately below the apex do not grow properly. However, if the apical bud is excised, the lateral buds grow vigorously. The influence of the apical bud in suppressing the growth of the lateral buds growing immediately below it is known as **apical dominance**. By applying of auxin paste to a decapitated stump inhibits the development of the lateral buds. It clearly indicate that the auxin of the terminal bud is responsible for apical dominance. (**Thimann and Skoog, 1934**).

## 6. Control of abscission layer

In some plants shedding of leaves, flowers, fruits takes place due to the formation of an abscission layer or separation layer at the base of the petiole or pedicels. If the dilute solution of the auxin is sprayed upon the plant the shedding of the fruits or leaf fall may be delayed.

## 7. Production of parthenocarpic fruits

Artificial application of auxins to unpollinated pistils can form seedless fruits which resemble the natural fruits except for the presence of seeds *e.g.*, **citrus, cucurbits, apples, grapes** etc.

## 8. Flower initiation

Auxins generally inhibits flowering but in pineapple (*Ananas sativus*) spray of NAA causes flowering.

## 9. Sex expression

The auxins cause femaleness in plants. The spray of auxins increase the number of female flowers in cucurbits.

## 10. Eradication of weeds

High concentration of synthetic auxin (2,4-D) kill weeds due to high concentration of auxin roots are distorted, sieve tubes get blocked and cell divisions are disturbed. 2, 4-D is most effective and very selective. It is toxic to dicotyledons for broad leaved plants (weeds) and nontoxic to narrow leaved plants (crops).

## 11. Dormancy

Treatment of potato tubers with indole-3-butyric acid, or  $\alpha$ - naphthalene acetic acid, or malic hydrazide (MH) inhibits the spraying of lateral buds. This treatment permits the storage upto three years.

## 12. Shortening of internodes

Apple and pear have two types of branches—long shoots and dwarf shoots. Fruits are formed only on dwarf shoots. If the terminal shoots are treated with the high concentration of  $\alpha$ -naphthalene acetic acid, their elongation is prevented and they become dwarf shoots which can also bear fruits.

## 13. Prevention of lodging

Plants such as oat, flax fall flat on the ground due to strong winds. These plants have excessively elongated stems which are weak at the base due to softening of the cells. Application of  $\alpha$ -naphthyl acetamide induces cell division in the cambium and increases amount of the xylem in the cell division in the cambium and increases amount of the xylem in the basal part of the stem and thus prevents lodging.

## 14. Root initiation.

Auxins have been found to increase the rate of formation and number of root initials.

## 15. Respiration

Auxins have been found to stimulate respiration. It is connected with the enhancement of metabolic activity on the application of auxins.

## Agricultural uses of synthetic auxins

A large number of synthetic auxins are presently being used in agriculture. Their important functions are :

1. **Eradication of weeds.** 2, 4-D and 2, 4, 5-T (2, 4, 5-trichlorophenoxy acetic acid) are used as **weedicide**.

2. **Root differentiation on stem cuttings.** Dilute solution of Naphthalene acetic acid (NAA) and Indole butyric acid (IBA) give very good results.

3. **Flower initiation in Pineapple.** Foliar spray of naphthalene acetic (NAA) and 2, 4-D on pineapple and a litchi plants causes flowering.

4. **Parthenocarpy.** Parthenocarpic development of fruits can be achieved by spraying the flowers with a dilute solution of NAA and IBA e.g., Banana, orange, grapes, apple etc.

5. **Premature fruit drop.** Application of NAA is useful in checking the fruit drop in tomato. Spraying of 2, 4-D in aqueous solution stops premature fruit drop in orange, apple, etc. It increases the yield.

6. **Sex expression.** Spraying of NAA on maize plants during the period of inflorescence differentiation can induce the formation of hermaphrodite or female flowers in a male inflorescence.

7. **Prevention of lodging.** During windy season lodging of crop plants can be prevented by spraying Naphthalene acetamide (NAAM).

8. **Dwarf shoots.** Spraying of NAA on apple trees increases the number of dwarf shoots as well as the number of fruits.

9. **Storage of potato tubers.** NAA prevents the sprouting of potato tubers kept in storage and potatoes can be stored for a longer time.

## 1.2. GIBBERELLINS

Sawada (1912), that the "Bakanae or foolish seedling disease" of rice plants might be caused by something secreted by fungus *Gibberella fujikuroi*. Kurosawa (1926), an Formosan scientist performed experiments to demonstrate that filtrates of the culture of the fungus produced characteristic symptoms when applied to the healthy seedlings of rice.

**Isolation.** In 1938, **Yabuta** and **Sumiki** finally succeeded in isolating a pure crystalline substance from the fungus, which they named as **gibberellin**. **Cross et. al.** (1961) isolated 6 gibberellins from the fungus *Gibberella* and they were termed as GA<sub>1</sub>, GA<sub>2</sub>, GA<sub>3</sub>, GA<sub>4</sub>, GA<sub>7</sub> and GA<sub>9</sub>. So far about 100 gibberellins have been isolated of which 15 have been isolated from the fungus *Gibberella*. The gibberellins have been present in all group of plants *i.e.*, from algae to angiosperms but rarely in fungi and bacteria.

### Chemical structure

Chemically gibberellins are represented by molecular formula such as C<sub>19</sub>H<sub>24</sub>O<sub>6</sub> (GA<sub>1</sub>), C<sub>19</sub>H<sub>26</sub>O<sub>6</sub> (GA<sub>2</sub>), C<sub>19</sub>H<sub>22</sub>O<sub>6</sub> (GA<sub>3</sub>), C<sub>19</sub>H<sub>24</sub>O<sub>5</sub> (GA<sub>4</sub>), C<sub>19</sub>H<sub>22</sub>O<sub>5</sub> (GA<sub>7</sub>), C<sub>19</sub>H<sub>24</sub>O<sub>4</sub> (GA<sub>9</sub>). All the gibberellins are various forms of gibberellic acid and contain "gibbane ring" skeleton (Fig. 7).

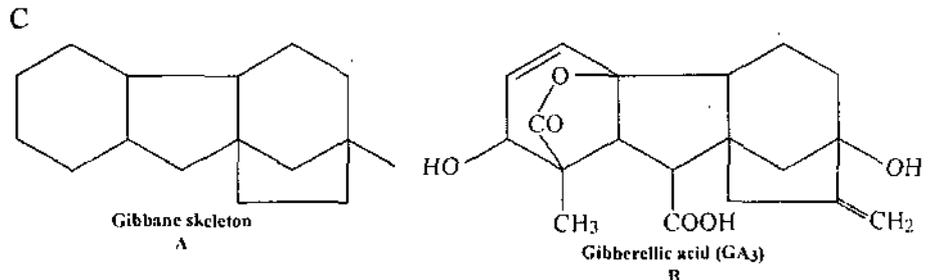


Fig. 7. A, B. Gibberellins. A. Gibbane ring or skeleton; B. Chemical structure of GA<sub>3</sub>.

### Biosynthesis

In a plant the concentration of gibberellins is higher in seeds and young leaves. The hormone is synthesized at the apical shoot buds and developing young leaves. **Acetyl CoA** acts as precursor. The biosynthesis of gibberellins is initiated by condensation of three molecules of acetates with acetylcoenzyme A via mevalonic acid pathway.

### Transport of gibberellins

This transport is non polar. The transport is done by diffusion through xylem as also through phloem.

### Bioassay

The two common methods of gibberellins bioassay are (a) (i) lettuce hypocotyl elongation and (ii) cereal endosperm digestion.

### Physiological effects

**1. Stem elongation.** The important effect of gibberellin is stem elongation *i.e.*, gibberellin induce cell elongation (no effect on roots and leaf expansion).

**2. Elongation of genetically dwarf plants.** Application of gibberellin cause elongation of genetically dwarf plants. It stimulates the elongation of internodes cells. In some varieties of Pea and maize in which internodes are very short, by gibberellin treatment the internodes become long and the whole plant becomes tall resembling the natural tall varieties.

**3. Bolting and Flowering.** In many biennials herbaceous plants (*Hyoscyamus niger*) early period of growth shows rosette habit with short stem and cauline leaves. Under short days the rosette habit is retained while under long day conditions bolting occurs. (The stem elongates readily and is converted into floral axis bearing flower primordia). In normal conditions the bolting effect is produced after the rosette plant has received a number of long days or after receiving cold treatment of winter *e.g.*, *Hyoscyamus niger*. By Gibberellin treatment bolting can be produced even in the first

year of growth. Thus gibberellins can induce flower in long day plants under unfavourable short day conditions.

**4. denovo synthesis of the enzyme amylase.** Gibberellins cause *denovo* synthesis of the enzyme **amylase** in the aleurone layer of endosperm of cereal grains during germination (an enzyme which brings about hydrolysis of starch to form simple sugars which are translocated to growing areas to provide energy source).

**5. Parthenocarp.** When gibberellins are applied at anthesis to emasculated flowers, parthenocarpic fruits develop *e.g.* Prunus, Cherry etc. (more affective than auxins). Application of gibberellins increases fruiting and fruit development. In tomato, application of GA<sub>3</sub> before flower initiation, increases fruit size.

**6. Breaking of dormancy.** Gibberellins effectively break the dormancy of potato tubers and winter buds of many trees. In potato, there is a dormant period after harvest, but application of gibberellins sprout the eyes vigorously.

**7. Substitute of cold treatment.** If biennials are treated with gibberellins, produce flowers in one growing season.

**8. Induction of flowering.** Applied gibberellins generally do not induce flowering in applied short day plants. Some examples of species where gibberellins have been found to induce flowering are *Bryophyllum* sps. *Xanthium* sps, etc. On the other hand gibberellins inhibit flowering in some woody angiosperms such as *Salix*, *Bougainvillea*, apple etc.

**9. Sex expression.** Gibberellins change sex expression of plants. In most species, it induce the formation of male flowers. Exogenous application of gibberellins induce male flowers formation on genetically female plants in *Cucumis*.

**10. Prevention of senescence.** Exogenous application of gibberellins can prevent senescence of leaves. (Fletcher and Osborne, 1965). The hormone has also been found to delay senescence of fruits besides that of leaves.

### Application of gibberellins in agriculture

Gibberellins was sprayed in vineyards to increase the number and size of grapes in clusters. GA<sub>3</sub> has been used to produce 'Thompson's seedless' grapes. Improvement in the size colour and quality of apples, pear and many other fruits is also achieved by spraying of gibberellins. Application of gibberollins promotes the elongation of sugarcane internodes without decreasing the sugar contents. They are used to increase  $\alpha$  amylase activity in germinating barley seeds which are used for malt production in beer industry. Gibberellins are also used for uniform bolting and increase seed production in lettuce, breaking dormancy in potato and to improve flower size and longevity in geraniums.

**Table 1. Differences between Auxins and Gibberellins.**

Physiological effects		Auxins	Gibberellins
1.	Chemical structure	A single or double unsaturated ring structure and a side chain.	A 'gibbane ring' structure.
2.	Precursor	Tryptophan	Acetyl CoA
3.	Apical dominance	Auxins promotes apical dominance	No effect
4.	Root growth	Higher concentration inhibits root growth but initiates formation of lateral roots	No effect

5.	Callus formation	Stimulated by the presence of auxins	No effect
6.	Lodging	Prevents lodging	No effect.
7.	Effect on intact plants	No effect on intact plants but cause growth in dwarf pea sections.	Cause growth of intact dwarf pea plant but has no effect on pea section.
8.	Genetically dwarf plants	No effect	Genetically dwarf plants often elongate.
9.	Bolting effect and flowering	No effect	Promotes bolting and flowering in long day plants and non vernalized plants.
10.	<i>denovo</i> synthesis of $\alpha$ -amylase enzyme	No effect	Causes <i>de novo</i> synthesis of $\alpha$ amylase enzyme in barley seeds.
11.	Sex expression	Auxins has feminising effect in some plants	Gibberellin has masculinising effect in some plants.
12.	Seed and bud dormancy	No effects	Promotes seeds germination and breaking of dormancy.

### 1.3. CYTOKININS

Australian plant physiologist **G. Haberlandt** discover that vascular tissues of various plants contain an unknown diffusible factor which stimulates cell division or cytokinesis. **J. Van Overbeek** (1940) observed that milky endosperm of immature coconut fruits also contain this factor. **Jablonski** and **Skoog** (1954) reported that a substance present in the vascular tissue was responsible for cell division in tobacco plants. **Carlos O. Miller** and co-workers initially observed that yeast extract in combination with IAA is as active as coconut milk in promoting continuous cell division of cultured tobacco pith segments. **Skoog** and co-workers show that herring sperm DNA that had aged on the shelf for sometime, were found to contain a very active substance of cell division in the tobacco stem. As a result **Miller** and co-workers (1955, 1956) isolated and purified in crystalline form, a purine from herring sperms DNA, which they later identified as **6-furfurylamino purine**. They named the compound **kinetin** because it induced cytokinesis of cultured tobacco cells.

In 1963, **Letham** obtained a crystalline substance from immature maize grains and named it as **Zeatin**. **Letham et.al.** (1964) identified it as 6-C-4 hydroxy 3 methyl trans-2 butenyl amino purine. Its synthesis was done by **Wilson** (1964). Some other naturally occurring Cytokinins are N<sup>6</sup>-methylamino purine, N<sup>6</sup>N<sup>5</sup>-dimethylallyl amino purine, N<sup>6</sup>- $\gamma$ ,  $\gamma$ -dimethylallyl) amino purine. The liquid endosperm is full of cytokinins. The most widely distributed cytokinin in plants is 2 iPA.

According to **Skoog et. al.** out of 18 cytokinin known till then, 13 alone occur in higher plants. They occur in root extract of sunflower, pea seedlings, flowers and fruits of apple, pear, plum, tomato, cambial tissues of *Eucalyptus* and tobacco. Cytokinins are synthesized at the meristematic region of shoot, leaf (expanding), root etc. Besides higher plants the cytokinins occur in diatoms, red and brown algae.

## Transport

Cytokinins synthesized in the root travel upward through in xylem sap because it has been invariably recovered in the xylem exudate (Kende, 1965). Movement by diffusion is also recorded.

## Physiological effects

1. **Cell division.** Cytokinins promote cell division by activating DNA synthesis (in the presence of auxins only).

2. **Cell enlargement.** Cytokinins induce cell enlargement. The cell enlargement is due to stimulated water uptake and partly due to increased plasticity of cell walls.

3. **Morphogenesis.** One of the most important effect of the cytokinins is the phenomenon of organ formation in the tissue culture. Cells of the tobacco pith form callus if supplied with nutrients and sugar (Skoog and Miller, 1957). However, by varying the balance between cytokinin and auxin it is possible selectively to initiate the development of either root or shoot.

(i) High auxin and low cytokinin ratio in the medium cause differentiation of root.

(ii) High cytokinin and low auxin ratio in the medium causes differentiation of shoot.

(iii) Intermediate cytokinin and auxin ratio in the medium causes formation of root as well as shoot.

(iv) Intermediate cytokinin and low auxin in the medium caused growth of large amount of callus.

4. **Initiation of intrafascicular cambium.** Cytokinins induce the formation of intrafascicular cambium.

5. **Delay of senescence : The Richmond-Lang effect.** Richmond and Lang (1957) showed that senescence (chlorophyll disappearance and protein degradation) could be postponed to several days in detached *Xanthium* leaves by kinetic treatment. This effect in delaying the senescence is called Richmond-Lang effect.

6. **Breaking of seed dormancy.** The dormancy of seeds of *Lactuca sativa*, tobacco and barley is broken by the application of cytokinins.

7. **Suppression of apical dominance.** The cytokinins counteract the phenomenon of apical dominance provided they are applied directly over the lateral buds.

8. **Resistance.** Death or injury to high temperature (upto 49.5°C) or cold (upto -20°C) and diseases can be prevented by cytokinins.

9. **Accumulation of solutes.** Cytokinins help plants to accumulate solutes very actively.

10. **Nutrient transport.** They regulate phloem transport. In the presence of cytokinins, the phloem carries more of nitrogen and other nutrients required during development.

**Application of cytokinins.** Cytokinins are essential for tissue cultures. In agriculture, they are used to prevent premature senescence in crop plants. By applying cytokinins we can also prevent senescence in leafy vegetables and keep them young for a longer period. They are also important in developing resistance to temperature changes and resistance.

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## 1.4. ETHYLENE

Since long it was known that a ripe or injured fruit in the basket hastens the ripening of the other fruits. Kerosene lamp and hay have been used by merchants to hasten colour development in fruits. It is only recently that scientist have learnt that these effects are due to ethylene.

A Russian scientist **Dimitry N. Neljow** (1901) demonstrated that ethylene effects plant growth. **R. Gano** (1934) provided chemical proof that ethylene was produced by ripe apples. **Galston and Devices** (1970) recognized it as a growth regulator. It is also released as pollutant by human activities such as combustion of natural gas and petroleum products.

Ethylene is unique in being the only gaseous natural plant regulator. It stimulates transverse or isodiametric growth but retards the longitudinal one.

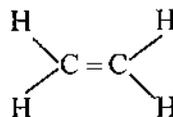
### Biosynthesis

There are no specific sites. All plant parts are capable to produce ethylene. Both meristematic and permanent regions can synthesize ethylene. It has usually high concentration in leaves, dormant buds and flowers undergoing senescence. Ethylene formation increases with the maturity and the ripening of fruits.

Roots are the main site of ethylene biosynthesis. The primary precursor of ethylene synthesis is amino acid **methionine**. Being a gas ethylene can easily diffuse in the plants through intercellular spaces.

### Chemical nature

It is unsaturated hydrocarbon. It is a colourless gas which is lighter in air and sparingly soluble in water.



### Physiological effects

**1. Ripening of Fruits.** It plays an important role in natural ripening of fruits. It hastens post harvest maturation (ripening) of fleshy fruits e.g., Banana, pear, apple, tomato, citrus fruit etc.

**2. Seed germination.** Ethylene break dormancy and include germination of lettuce, ground nut, wheat and cocklebur seeds.

**3. Growth inhibitor.** In most cases exogenous application of ethylene inhibits plant growth. In most dicots, the elongation, growth of stem, root and leaves is inhibited. However, the ethylene enhances the radial growth, as a result both stem and root swell in response to ethylene.

**4. Epinastic responses.** Exposure to ethylene causes epinastic movements in the petioles, as a result the leaves bend down. This is because of more growth on upper side than on lower side of the petiole.

**5. Flowering inhibition.** Ethylene inhibits flowering in most plants, although it is known to induce flowers in pineapple in off reason. In *Plumbago indica*, a short day plant, flowering can be induced by ethylene in long day conditions.

**6. Sex expression.** Ethylene changes sex in unisexual plants. It increases female flowers in several members of cucurbits.

**7. Senescence.** It governs the senescence and abscission of plant part both natural and induced. It accelerates senescence of leaves, flower and fruits. Endogenous ethylene increases during senescence.

**8. Abscission.** It is the most widely response of the ethylene. It includes abscission of leaves, fruits, petals and flowers. The abscission increases with ethylene concentration, saturating at about 10 P.P.M. Exposing fruiting cotton plants to 0.5 P.P.M. ethylene causes 100% abscission of young fruits and floral buds in two days. It is also believed that the initial effect of ethylene is to lower the auxin content.

**9. Fruit ripening and enzyme activity.** Some of the most important effects of ethylene are fruit ripening and abscission. These are due to the activation of gene expansion and protein synthesis. Several enzymes such **polygalacturonases** (a cell walls softening enzymes) increase due to their activated synthesis. These enzymes synthesize numerous phenolic compounds including **anthocyanidins**. The anthocyanidins impart bright colour to the fruits and their increased production is an important aspect of fruit ripening. Increased **cellulase** and some related enzymes activities may be the factor involved in softening of the fruits during ripening.

**10. Transport of auxins.** It inhibits basipetal, lateral and polar transport of auxins. A high concentration of auxin produce ethylene but ethylene lowers the level of auxin.

### Commercial application of ethylene.

Ethylene has been used for synchronized flowering and fruit ripening for centuries. Several chemicals which release ethylene e.g., etaphon (2 chloroethyl phosphoric acid,  $\text{Cl}-\text{CH}_2-\text{CH}_2-\text{PO}_3\text{H}_2$ ) is used now a days for promotion of flowering in pine-apple. Exogenous supply of small amount of ethylene increases the number of female flower (e.g. cucurbits) and hence the fruits.

## 1.5. ABSCISIC ACID

Abscisic acid (ABA) is an acidic growth hormone which functions as a general growth inhibitor by counteracting other hormones (auxins, gibberellins, cytokinins) or reactions mediated by them. It is also called 'stress hormone' because the production of hormone is stimulated by draught, water logging and other adverse environmental conditions. It acts as a growth inhibitor even at a very low concentration (1 PPM).

**Liu and Cairns** (1961) isolated a pure crystalline substance from mature cotton fruits and called it '**abscission I**'. **Ohkuma et. al.** (1963) isolated another substance from the young cotton fruits and named it **abscission II**. Almost at the same time **Eagles and Wareing** (1963) extracted an inhibitor of apical growth from birch leaves and called it as **dormin**. Later, **Ohkuma** and Coworkers (1965) proposed the chemical structure of abscisin II. **Conforth et. al.** (1965) isolated dormin in pure form methanolic extract of sycamore leaves and showed that the abscisin II and dormin were the same compounds. The terms abscisin I, abscisin II and dormin were dropped and the scientists termed the newly termed compound as **abscisic acid**, or ABA.

### Biosynthesis

It is mainly produced in nature leaves. It is of general occurrence in monocots, dicots, gymnosperms and ferns. Besides leaves, it is also synthesized in stem, fruits and seeds and then transported to the rest of the plant through vascular tissues, mainly the phloem. **Mevalonic acid** acts as precursor for the synthesis of ABA.

### Chemical nature

It is a sesquiterpens consisting of 15 carbon and characterised by six membered ring, with a chiral (asymmetrical) center and an unsaturated six carbon substituent.

### Physiological effects

**1. Inhibition of seed germination.** Exogenous application of ABA inhibits the germination of most non dormant seeds.

**2. Inhibition of seedling growth.** ABA inhibits the seedling growth in some cases for e.g., *Glycine max.*

**3. Inhibition of bud growth.** Exogenous application of ABA induces bud dormancy in woody plants. ABA also inhibit lateral and growth of tomato plants.

**4. Stomatal closing.** ABA controls the stomatal opening Exogenous application of ABA to epidermal strips causes stomatal closure. ABA inhibits potassium ions uptake and proton release. It also increase malate leakage from epidermal strips. All these factors will induce stomatal closure not only because of reduced turgidity but because of loss of source of protons.

**5. Geotropism.** ABA stimulates a positive geotropic response. The exogenous applied ABA induces positive geotropism although it inhibits root growth.

**6. Senescence and abscission.** It accelerates the senescence and abscission of the leaves. Exogenous application of ABA induces primary yellowing in leaf tissues in many plants.

**7. In drought resistance.** ABA plays an important role in drought resistance because it promotes stomatal closure and thus water loss due to transpiration.

**8. Antigibberellins.** It inhibits gibberellins induced growth.

### **Agricultural Application of abscisic acid**

Application of ABA to the leaves reduces the rate of transpiration. It acts as **antitranspirant** and serves to conserve the water. It is also used for inducing dormancy in buds and seeds.

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### **1.6. STUDENT ACTIVITY**

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1. Write the short notes on auxins and gibberellins.

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2. Write short notes on the physiological role of growth regulators in apical dominance, abscission, parthenocarpy and tissue culture.

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### 1.13. SUMMARY

The growth and differentiation of plants is controlled by special types of chemical compounds called phytohormones. Five major types of phytohormones are recognized in plants. Auxins, gibberellins, cytokinins, abscisic acid and ethylene.

Darwin performed experiments on canary grass (*Phalaris*) and concluded interaction between tip and light responsible for unilateral curvature. Boysen-Jensen's experiments concluded that the curvature causing stimulus is water soluble and active on dark side. Went extracted the substance from *Avena* coleoptiles tip and named it auxin. Biosynthesis of the auxins has been traced back from the amino acid tryptophan. Auxins induce cell division, cell elongation and callus formation. They are also responsible for the phenomenon of apical dominance. When they are applied on the stigma, parthenocarpy is induced. A spray of auxins prevents premature abscission. A concentration of 2, 4 D/2, 3, 5-T acts as strong weedicide.

Yabuta and Sumiki isolated the first gibberellin from the fungus *Gibberella fujikuroi*. Gibberellins induce stem elongation. Genetically dwarf plants become normally tall by the action of gibberellin. They induce flowering in long day plants. Endogenous application of gibberellins induce parthenocarpy.

Miller and co-workers isolated and purified an active substance from Herring sperms DNA which induced cell division and named it as kinetin. Later it was identified as 6-furfuryl aminopurine. The cytokinins induce cell division activity. Besides they also induce cell enlargement. A balanced application of cytokinin and auxin induces the buds in the callus. The dormancy of seeds can be broken by a spray of cytokinins. Suppression of the phenomenon of apical dominance has also caused due to cytokinins. They also delay senescence.

A Russian scientist Neljobow demonstrated that ethylene effects plant growth. Galston and Davies, later recognised it as growth regulator. It induces fruit ripening, causes petal discoloration, may stimulate germination and inhibit root and stem elongation. It also induces epinasty and leaf expansion.

ABA is an acidic growth hormone which functions as growth inhibitor. Liu and Cairns isolated abscission I, Ohkuma and co-workers abscission II and Wareing extracted dormin. It causes aging, abscission of leaves, closure of stomata, accelerates senescence, inhibits germination, regulates dormancy and inhibits gibberellins induced growth activities.

### 1.18. TEST YOURSELF

1. What do you mean by apical dominance ?
2. Name the growth hormone which is responsible for the bending of stems towards light due to uneven growth of the cells.
3. From which plant gibberellins were first extracted ?
4. Richmond-Lang effect is shown by which hormone ?
5. Who first of all demonstrated that the curvature causing stimulus is active on the dark side of the coleoptile tip ?
6. Who coined the term auxin ?
7. Which growth hormone is responsible for a cell division ?
8. Which phytohormone can convert biennials into annuals ?
9. Who was the first to isolate kinetin.
10. Which phytohormone regulates the dormancy of the seeds ?

**ANSWERS**

1. Suppression of growth of the axillary bud by the presence of apical bud.
2. Auxins.      3. Fungi      4. cytokinin      5. Boysen-Jensen
6. Went      7. Cytokinin      8. Gibberellins      9. Miller      10. ABA.

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## 4

## PLANT MOVEMENTS

## STRUCTURE

- Introduction
- Classification of plant movements
- Vital movements
- Movement of locomotion
- Movements of curvature
- Variation movements
- Physical movements
- Summary
- Test Yourself
- Answers

## LEARNING OBJECTIVES

By learning this chapter you will be able to know the different types of plant movements.

## 1.0. INTRODUCTION

Living plants have the characteristic of showing some characters due to changes in the environment or due to some endogenous causes. Such changes are called **movements**. These changes are due to **irritability** or **sensitivity** of the protoplasm. Irritability is the fundamental property of the protoplasm. Any specific environmental factor which gives irritability reaction is called **stimulus** and reaction due to stimulus is called **response**. According to the nature the stimulus may **paratonic** (induced) due to external stimuli or **autonomous** (spontaneous), due to internal stimuli. The stimulus is perceived by the specific region of the plant is called **perceptive region**. The region which exhibit response is called **responsive region**. The minimum duration of a time required for a stimulus to be applied continuously on the perceptive region to produce visible response is called **presentation time**.

## 1.1. CLASSIFICATION OF PLANT MOVEMENTS

These are divided into two types :

1. **Vital movements**—shown by living cells or plants.
2. **Physical movements**—shown by dead plant parts.

## 1.2. VITAL MOVEMENTS

- (i) **Movements of locomotion**—shown by free living organisms.
- (ii) **Movements of curvature**—shown by fixed plants.

## 1.3. MOVEMENTS OF LOCOMOTION

- (i) Movement of locomotion are further sub-divided into two types :
  - (A) **Autonomic movement**.
  - (B) **Paratonic movement**.
- (A) **Autonomic movement** of locomotion are of three types :

(a) **Ciliary** : Movements due to cilia or flagella e.g., *Volvox*, *Chlamydomonas*.

(b) **Amoeboid** : Like amoeba, pseudopodia are produced which helps in locomotion e.g., Plasmodia of Myxomycetes, Slime molds.

(c) **Cyclosis**. In living cells of many cells, cytoplasm including various cell organelle move around the vacuoles. If cytoplasm moves either a clockwise or anticlockwise around a central vacuole, it is called **rotation** e.g., *Chara*, *Hydrilla* and if it moves both in clockwise or anticlockwise it is called **circulation** e.g., Staminal hairs of *Tradescantia*.

(B) **Paratonic movements** of locomotion are of three types :

(a) **Phototactic or phototaxis** (Stimulus-light)-shown by gametes and zoospores of certain algae e.g., *Volvox*, *Ulothrix*, *Cladophora*, *Chlamydomonas* etc. Positive thermostatic movements are under diffused light and negative thermostatic movements case under intense light.

(b) **Chemotactic or chemotaxic movement** (Stimulus-chemical)- Shown by antherozoids of bryophytes and pteridophytes when archegonia secretes some chemicals and antherozoids attracted chemotactically.

(c) **Thermotactic or Thermotaxic movements** (Stimulus-Temperature). A test tube containing *Chlamydomonas* in cold water is warmed on the side, cells will move towards higher temperature zone—**positic thermotactic movement**, however, a **negative thermotactic movement** will occur, if the temperature becomes too high.

#### 1.4. MOVEMENTS OF CURVATURE

Movements are restricted to the bending or curvature of the plant parts.

These movements are of two types : **growth movement** and **variation movement**.

**Growth movement** are further sub-divided into

(i) Autonomic movement

(ii) Paratonic movement.

(i) **Autonomic movement** are of three types :

(a) **Nutational**. Shoot apex or seedling growth in zig-zig may because the two sides of the apex alternately growth more.

(b) **Circumutational**. Tendrils show encircling movement due to unequal growth e.g., twinners and climbers.

(c) **Nastic movements**. Movements due to the differences in the rate of the growth on two opposite sides. If the growth is more on the upper surface, the movement is called **epinasty** and if the growth is more on the lower surface the movement is called **hyponasty** e.g., Poppy-drooping condition of bud is due to epinastic growth movement, formation of upright sloth of flower-hyponastic growth of the floral axis.

(ii) **Paratonic movements**. The movements induced by certain external stimuli are called **tropic movements** and this phenomenon is called **tropism**. These are of following types :

(a) **Phototropism (stimulus-light)**. Stem grows towards light hence it is **positive phototropic** and root is **negative geotropic** (grows away from the source of light). Leaves are **diaphototropic** (at right angle to sun rays). In *Arachis hypogoea* ovary stalk is positive phototropic before fertilization. It becomes negative phototropic after fertilization; bends towards the soil and pushes the ovary into the soil where the development of the fruits takes place.

The phototropic movements are due to unequal distribution of auxins under the influence of light. More auxins accumulate on the shaded side and thus more growth occurs on the shaded side of the stem, as a result it curves towards the source of light. The concentration of auxins that induce growth in the stem retards the growth in the

roots. As a result the roots curve away from the source of light (fig. 1). In the laboratory phototropism can be demonstrated by growing a plant in the **heliotropic chamber**. After some time the stem bends towards the source of light. It confirms positive phototropic movement of stem.

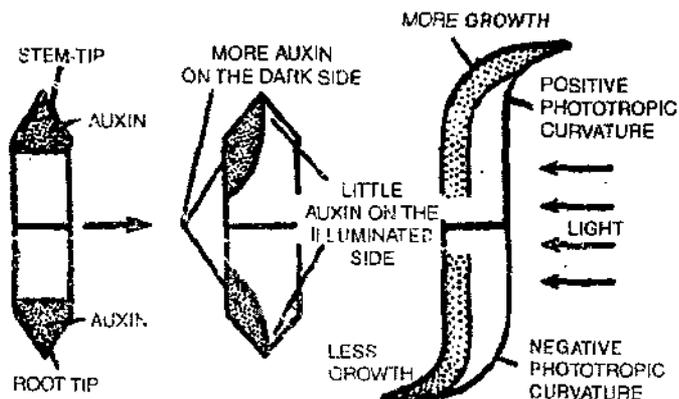


Fig. 1. The interaction of light and auxin on the growth of the stem and the root apex.

(b) **Geotropism (stimulus-gravity)**—The primary root always grows towards the direction of gravity and hence called the **positive geotropic**. On the contrary, the stem grows away from the force of gravity and hence called as **negatively geotropic**. **coralloid roots** and **pneumatophores** are also negative geotropic or ageotropic or apogeotropic. Primary root grows vertically downward exactly towards the force of gravitation (earth centre), hence, it is called **positively orthogeotropic**. The stem and root branches growing at an angle of 45° from vertical axis are called **diageotropic**.

The best explanation of geotropism and phototropism is the unequal distribution of auxins. Some earlier workers believed the gravitational stimulus is perceived by large starch grains called **statoliths**. The cells containing starch grains are called **statocysts** or **statocytes**. **Clinostat** is the apparatus which is used to neutralize the effect of light and gravity.

(c) **Hydrotropism (stimulus-water)**—Roots are positively hydrotropic as they bend towards the source of water.

(d) **Thigmotropism (Stimulus-contact)**. Twinners and climbers are very sensitive to contact and when they come in contact with any object they climb over (Fig. 2).

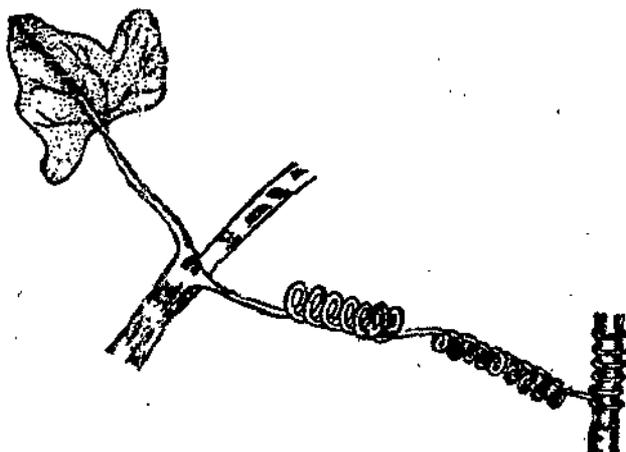


Fig. 2. Showing thigmotropic curvature.

(e) **Chemotropism (Stimulus-Chemical)**. Movement of pollen tube through the style towards ovary, movement of fungal hyphae towards the region of the medium where more nutrients are concentrating are the examples of chemotropism.

(f) **Aerotropism (Stimulus air particular oxygen)**. Roots are described as **positive aerotropic** whereas pollen tubes are described as **positive aerotropic** where

as pollen tubes are **negative aerotropic**. Pneumatophores grow against the gravity stimulus due to aerotropism.

### 1.5. VARIATION MOVEMENTS

Variation movements are further sub-divided into (i) Autonomic movement and (ii) Paratonic movement.

(i) **Autonomic movements.** This type of movement is seen in **Indian telegraph plants (*Desmodium gyrans*)**. In this plant the leaves are trifoliate compound. The terminal leaflet is fixed and the lateral leaflets change their angle at the petiole according to sunlight. The lateral leaflets perform to and fro movement (rotatory movement) to get the maximum amount of light (fig. 3).

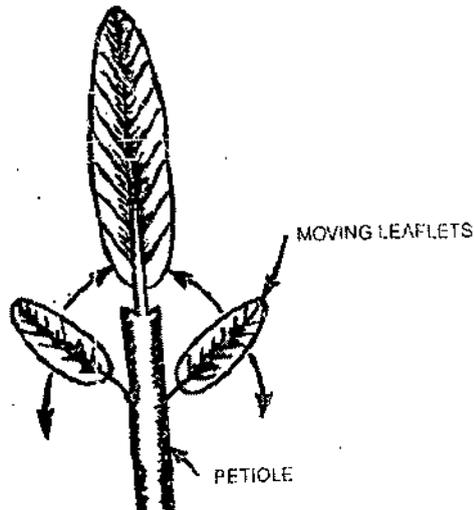


Fig. 3. A portion of the Telegraph plant.

(ii) **Paratonic or Nastic movement.** These are of following types :

(a) **Nyctinastic movement or sleep movements.** The diurnal variation in the position of flowers and leaves of many plants in day and night is called **nyctinastic movement**. If these movements are induced by light they are called **photonastic** (fig. 4) and when induced by temperature, they are called **thermonastic**. Photonastic movements are seen in several plants for e.g., *Oxalis*, *Marsilea*, *Impatiens* etc. The leaves are expanded horizontally during the day and droops at night. Flowers of many plants (e.g., *Nelumbo*) open during the day and close in the evening. Flower of *Crocus* and *Tulip* show thermonastic movements. These flowers open at high temperature and close at low temperature.

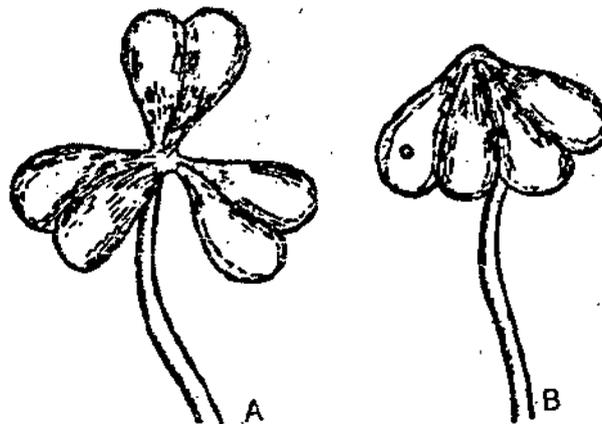


Fig. 4. *Oxalis* showing photonastic movement of the leaf A. Open leaves during day. B. Closed leaves during night.

(b) **Seismonastic movements (Stimulus-Touch or shock).** This movements is best seen in *Mimosa pudica* (Touch me not). By touching a single leaflet, whole leaf drops down. This movement occur due to change in the turgor pressure, hence, these movements are also called **turgor movement** (Fig. 5).

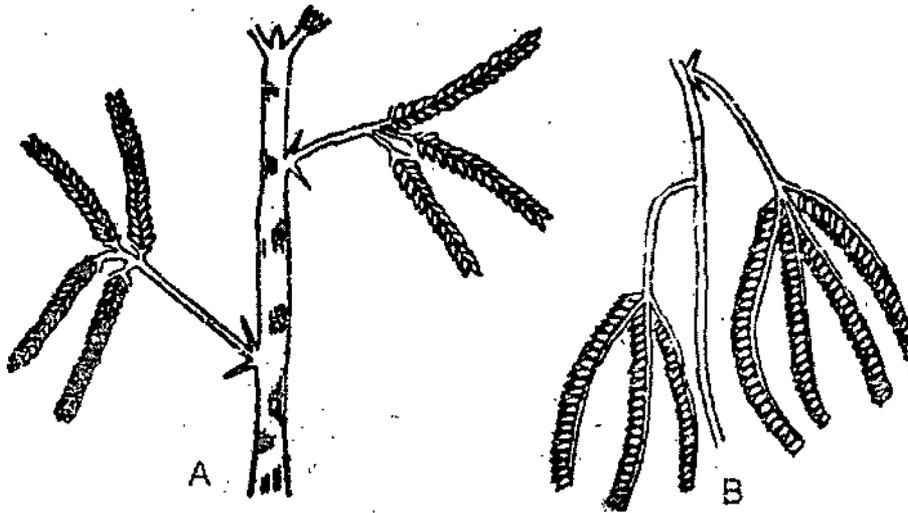


Fig. 5. *Mimosa pudica* showing seismonasty. A. Normal leaf ; B. Dropping leaf.

(c) **Thigmonastic movements (Stimulus – touch).** Tentacles of *Drosera* are very sensitive to touch of insects. The touch stimulus imported by the insect is permitted to the entire leaf and all the tentacles bend over the insect. Similarly *Dionaea* fold on coming in contact with insects.

### 1.6. PHYSICAL MOVEMENTS

These movements are performed during the dispersal of spores, pollengrains and seeds. These are of following types :

(a) **Hydrochasy.** The hygroscopic movements performed due imbibition of water is called hydrochasy movements e.g., movements in the peristome of moss, elaters in the *Equisetum* etc.

(b) **Xerocnasy.** The hygroscopic movements performed due to loss of water is called Xerocnasy for e.g., dehiscence of pods etc.

### 1.7. STUDENT ACTIVITY

1. Describe the movements of variation.

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2. Describe the movements of growth.

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**1.13. SUMMARY**

Living plants show some characters due to endogenous causes or changes in the environment. These changes are called movements. The plants movements may be vital or physical. For whatever purpose or in whatever response a movement occurs, it may be autonomous (spontaneous) or paratonic (induced). The autonomous locomotion movement may be ciliary, amoeboid or cyclosis. The paratonic locomotion movements may be phototactic, thigmotactic or chemotactic. The movements may be nastic or nutational. The former occur due to differential growth on the two sides whereas the latter occurs due to specific relay pattern of growth. The paratonic movements may be induced by light (phototropism), gravity (geotropism), water (hydrotropism), chemicals (chemotropism), touch (thigmotropism) and air (aerotropism). The variation movements may be autonomic, paratonic, or nastic. Autonomic variation movement is shown by the leaflets of Indian telegraphic plant. Nyctinastic movements may be due to diurnal variation. The physical or hygroscopic movements may be due to gain or loss of water.

**1.8. TEST YOURSELF**

1. Why the leaves of *Mimosa* drops down on touch ?
2. Name the movement shown by the opening of a flower and dropping of a bud.
3. Why the stem bends towards unilateral light ?
4. Two plants are fixed in two clinostats in a horizontal position. Clinostat A is rotated while clinostat B is stationary. What will happen ?
5. Name the movement in which tendrils of stems of climbing lines curl around the solid objects.
6. What is the form of chemotactic stimulus supplied to the antherozoids in bryophytes ?
7. Name the growth hormone whose unequal distribution is responsible for the growth of the cells that causes plant stems to bend towards light.
8. Name the hygroscopic movement performed due to imbibitions of water.

**ANSWERS**

1. Due to change in turgor pressure of leaf base.
2. Epinastic movement.
3. Cells on the shaded side elongate more
4. In A clinostat, roots and stems will grow horizontally; In B, roots will move down and stem upwards.
5. Thigmotropism
6. Sugars
7. Auxins
8. Hydrochasy.

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