Chapter-5
PLANT GROWTH & MOVEMENTS

GROWTH

Definition : Growth is an important characteristic of living beings. It is a very complex process and cannot be easily defined. One important aspect of growth is the permanent change in size. The change in sizes is mostly an increase in length or volume. In some, cases, however, there is actually a decrease in the size of the growing structure. Increase in the size of a plant or plant organ due to growth need not be confused with temporary increase in the size of certain structures, e.g., water soaked seeds.

Another aspect of growth is visualized in the form of an increase in the dry weight. It is well known that a good amount of food synthesized by a plant is utilised in the building up of new tissues. This adds to the substances of the plant and, therefore, to the dry weight. During the early phase of the growth, however, the dry weight is decreased, e.g. in the sprouting potato tubers.

Growth may thus be broadly defined as a permanent and irreversible change in size or volume of a living structure which is very often accompanied with increase in dry weight.

PHASES OF GROWTH

Growth in a plant is generally limited to regions of growing points known as meristems. The two important growing points present in the root apex and stem apex are called **apical meristems** and growth due to them is known as **primary growth**. The formation of tissues of a plant, the increase in the length of the plant, and the differentiation of various appendages are due to the primary growth. In certain kinds of plants, e.g., bamboo, mint, etc. increase in length is due to **intercalary meristems**. These are actually a part of apical meristems, which get separated from the apex by the intervening permanent tissues. These meristems are of a temporary nature. A third type of growing point is known as the **lateral meristem**, which is responsible for the growth of the plant in thickness. This type of growth is called the **secondary growth**.

In growing plants, during the process of growth, the meristematic cells have to pass through three phases. The three phases of growth are the phase of cell division, the phase of cell enlargement and the phase of cell maturation.

The meristematic cells in the growth tips are thin walled. They have very dense protoplasm with very small vacuoles. The cells are isodiametric and do not have intercellular spaces. They have large nuclei which are centrally located. Cell divisions are of frequent occurrence in this region. Some elongation of the cells takes place during cell division but is very small compared to that of the phase of cell enlargement.

The second phase of growth, the phase of cell enlargement, now follows. The rich amount of solutes present within these cells cause absorption of water. As water diffuses into cell certain solutes are also absorbed. This further increases the growing cell's osmotic pressure, which is essential for maintaining a high turgor pressure. The turgor pressure stretches the walls of the growing cell. Two explanations have been given regarding the thickening of the cell walls which have been stretched out. According to one explanation new particles of cellulose are deposited between particles of the old wall. The process is known as **intussusception**. According to the second explanation new cell wall particles are deposited on the inner surface of the old wall by a process known as **apposition**.

During enlargement of the cell a large vacuole appears in the centre and the protoplasm occupies the peripheral region of the cell.

In the last phase of growth the cells are matured and differentiated into various shapes and sizes.

THE COURSE OF GROWTH

If the rate of growth of a plant or a part of it is measured and is plotted against time, a typical S-shaped curve is obtained. If the curve for the growth of a cell is examined it will be found that the rate of growth is slow in the phase of cell-division, but increases at a very rapid rate to a maximum during the phase of cell enlargement and then decreases slowly during the phase of cell maturation. The growth curve for the entire life of an annual plant, as measured in terms of dry weight has also got the same pattern. The early fall in the dry weight during germination is due to the utilisation of stored foods of the seed. Then ensues a **grand period of growth** for weeks together. It is followed by the **stationary phase**. In the old age of the plant (**senescent stage**) there is a gradual decline in the rate of growth, most probably because of catabolic processes being in excess of anabolic processes. A typical growth curve of an annual plant is given in the growth curve is usually divisible into four parts : (1) a **lag phase**, (2) a **logarithmic** or **exponential phase** (3) a **plateaue phase** and (4) **a phase of scencence** (Fig.). In certain populations the sigmoid growth curve is replaced by a J-shaped curve due to sudden disappearance of the organisms.

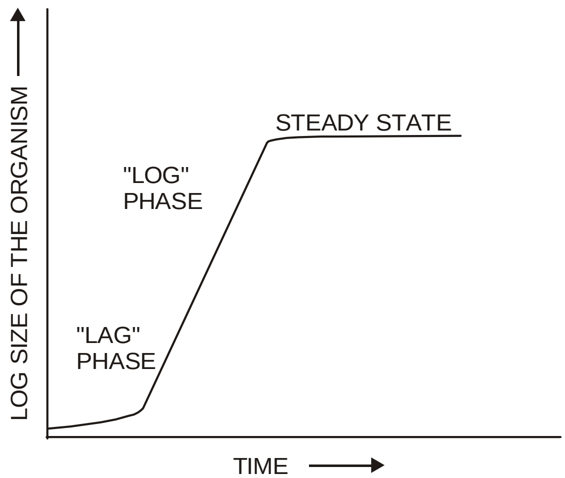

Fig. Sigmoid growth curve.

FACTORS AFFECTING GROWTH

Two important climatic factors of growth are discussed below :

LIGHT :

The effect of the light on growth can be studied under three headings (a) light intensity (b) light quality and (c) duration of light. Growth is generally favoured by darkness, none the less, light is indispensable because of its role in the manufacture of food. Young plants growing in absence of light develop elongated but thin stems with narrow leaves and poorly developed root system. Such plants are known as **etiolated**.

(a) **Light intensity :** In weak intensity of light the internodes are long and the leaves are expanded. In strong intensity of light the plant assumes a normal height (short and stocky). Very high light intensity reduces the rate of growth indirectly by increasing the rate of the loss of water from the growing cells. Very low light intensity also reduces the rate of overall growth of the plant, presumably by lowering the rate of photosynthesis.

(b) **Quality of Light :** The overall growth of an entire plant in the full spectrum of visible light has been found to be better then the growth in any one of the different colours of light. Red colour seems to be most favourable for growth. The internode elongates most in blue-violet and least in complete spectrum of visible light, while the expansion of leaves is maximum in the latter and least in the green light. Shorter rays below the violet and longer rays beyond the red are definitely detimental to growth.

(c) **Duration of Light :** The duration of light has pronounced effect on the growth of vegetative as well as reproductive structures. The influence of duration of light is most marked and spectacular in inducing or suppressing flowering. The phenomenon is termed photoperiodism and is described in detail in the topic on physiology of flowering. There are, however, many important effects of duration of light on the vegetative growth of a plant.

Most of the plants, whether they are short day, long-day or indeterminates, show very luxuriant vegetative growth under long days. Long-day plants form only a compact rosette of leaves when grown in short days. It has been found that the amount of vegetative growth is proportional to the duration of day light. The onset of winter dormancy and the autumnal shedding of leaves in deciduous trees are, in part, responses to length of day. Short day conditions cause decreased root growth as well as shoot growth. Morphological features like the formation of bulb, tuber and other storage organs are affected by length of the day.

Although suggestions have been put forward to account for various effects of duration of light on plants, nothing is known definitely about the underlying casual mechanism.

Seed Germination : Light is not indispensable for the germination of seed. Seeds can germinate well even in total darkness. There are, however, a number of examples of seeds, which germinate better when they are exposed to light. **Kinzel** (1926) divided the plants into three groups on the basis of influence of light on the germination of seed.

(a) Seeds stimulated to germinate by exposure to light (light sensitive, photoblastic)

(b) Seeds stimulated to germinate by exposure to darkness

(c) Seeds "indifferent" to illumination

Temperature

Temperature has a pronounced effect on the growth of a plant. Like photosynthesis the minimum, optimum and maximum temperatures for growth vary from plant to plant and habitat to habitat. The minimum, optimum, and maximum temperature for growth of plants of the temperate zone are generally 5ºC, 25ºC-30ºC and 35ºC respectively. These values for plants of arctic will be lower and of tropical zone greater than those of the temperate zone. It is interesting to note that optimum temperature for growth of a plant depends very much upon the stage of its development.

If temperature is low in night so as to reduce respiration and high in daytime so as to increase photosynthesis, there will be a high gain of photosynthetic product, which will result in increased rate of growth. This is why tubers of potato and other vegetables and fruits growing on hills are much larger than those of the plains.

GROWTH HORMONES

Growth of a plant was for long believed to be due to the minerals (absorbed from the soil) and the food material (synthesized by the plant). It is now certain that the growth of the plant is very much regulated by certain chemical substances. They are synthesized by the plant in very small quantities. These substances are formed in one tissue or organ of the plant and are then transported to other sites where they produce specific effects on growth and development. They are often referred to as plant hormones. The plant hormones are also known as growth factors, growth hormones, growth substances, growth regulators, and phytochormones, etc. The three major growth promoting hormones have been chemically designated as auxins, gibberellins and cytokinins.

I. THE AUXINS

Auxins are one of the most important groups of plant hormones because of their many-sided roles in plants. These substances were also the first growth factors identified as plant hormones.

Discovery : The first important worker, who suspected the presence of a growth substance in the tips of the plants, was the famous biologist, **Charles Darwin** (1880). Working on canary grass (*Phalaris canariansis*) Darwin demonstrated that the effects of light and gravity on the bending (tropic movement) of both roots and shoots were mediated by the tip. He found that if a unilateral source of light was given, the coleoptile would bend towards the source of light. He believed that the tip contained a substance which was transmitted to the lower portion, where it caused the curve. He also demonstrated that a decapitated coleoptile or a coleptile which was covered with a tinfoil cap failed to respond to unilateral light (Fig.).

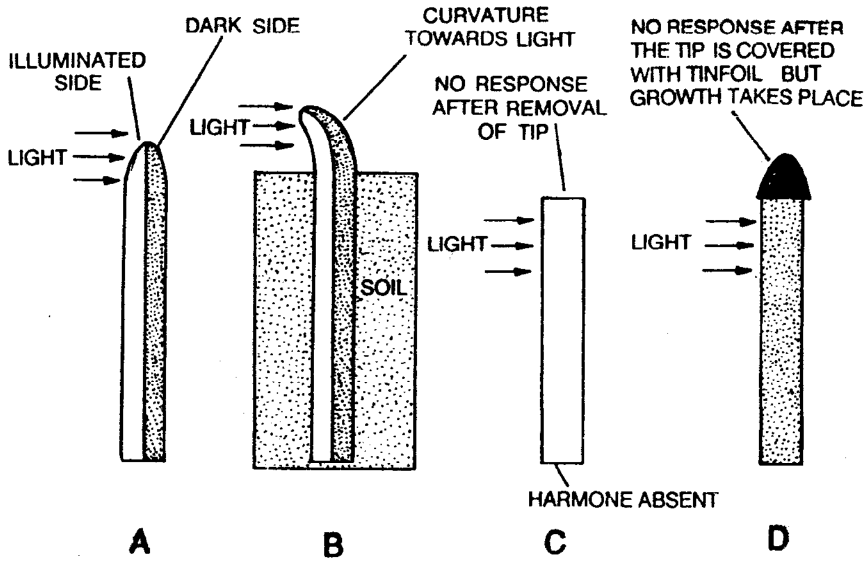

Fig. Darwin's experiments of canary grass.

The experiments and the observations, made by Darwin, were confirmed and extended by **Boysen-Jensen** and **Paal**.

Boysen-Jensen (1910-1913) of Denmark found that whereas the ability to make a phototropic response was lost by decapitation of the tip, it could be recovered if the tip was replaced on the stump. The phototropic response could also be recovered even by placing a piece of gelatin in between the stump and the decpitated tip. He further demonstrated that if a transverse slit was caused in the coleoptile on the dark side and a piece of mica was inserted into the slit, no phototropic response took place. On the other hand there was a phototropic response if the slit and the piece of mica were on the illuminated side (Fig.).

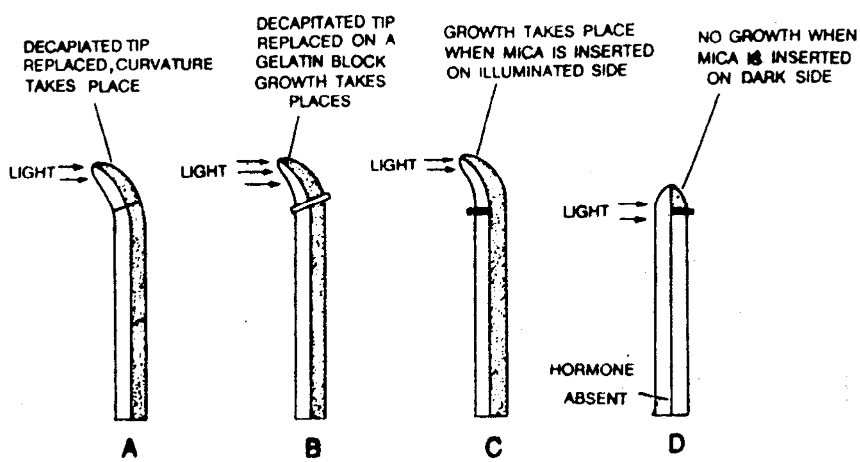

Fig. Boysen–Jensen's experiment on *Avena sativa*.

Paal (1914-1919) of Hungary found that the phototropic response did not occur if cocoa butter, mica, or platinum foil was used instead of gelatin. He concluded that the stimulus was produced at the tip and that it was water soluble (fat-soluble substance can pass through cocoa butter and electrical substance can pass through platinum). He also demonstrated that even in the dark growth substance travelled downwards to cause growth as was shown by the bending away of the coleoptile from the side on which the decapitated tip was replaced eccentrically (Fig.). Paal suggested three possible mechanisms to explain the unequal distribution of the growth substance :

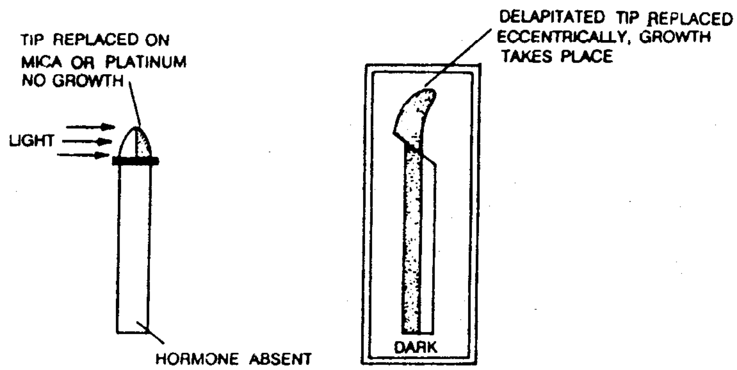

Fig. Paal's experiment performed in total darkness.

(a) Inhibition of the production of the growth substance on the illuminated side.
(b) Photochemical inactivation of the substance on the illuminated side.
(c) Inhibition of downward movement on the illuminated side.

The great advances that have been made in our knowledge of auxin, both chemically and physiologically, are due to the brilliant work of Dutch investigators, viz., **F.W. Went**, **Kogl**, **Dolk** and others.

F.W.Went (1928) finally succeeded in isolating the growth substance, about the presence of which the workers had already given sufficient evidence. He placed several freshly cut coleoptile tips on an 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 coleoptile tips and placed the agar cubes eccentrically on decapitated coleoptile stumps for 2 hours in the dark. The effect of the agar cube in causing curvature was similar to that of the stem tip (Fig.). He named the substance auxin.

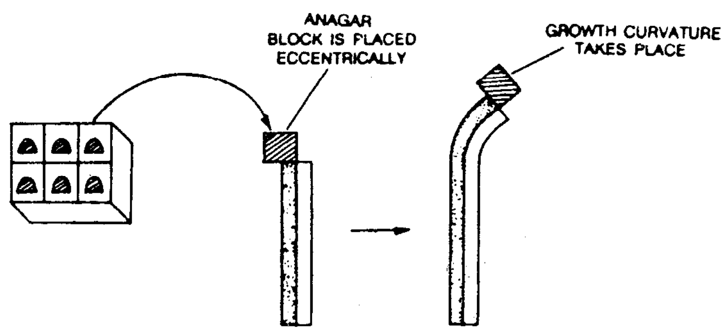

Fig. F.W. Went's experiment on auxins using agar block.

To measure quantitatively the amount of auxin in an unknown organ, the extract is taken, the curvature caused by it is measured and is compared with curvatures produced by known quantities of auxin in another experimental series. The curvature in the stem apex is known as the bioassay for auxin. Because of the use of Avena plant for the bioassay by Went it subsequently became known as the Avena curvature test.

Practical Applications of Auxins

In addition to its role in promoting cell elongation, auxin plays a host of important roles in many order physiological activities of the plants. They are discussed below :

1. Cell Division and Cell Enlargement

Auxin has been found to be responsible for initiating as well as promoting cell division in certain tissues, e.g., cambium. Wherever wound is caused in the plant a swelling (wound tissue) called callus is developed because of the proliferation of the parenchyma cells. The callus formation is linked with the cambial activity which is believed to stimulated by auxin and a chemical substance, traumatic acid, formed by the damaged tissue. This can be put to practical use in grafting, where the callus plays an important role in strengthening the union between stock and scion.

In tissue culture, cell division is entirely dependent on the presence of auxin. In cultures, where the callus growth is quite normal its continued growth is possible only in the presence of auxin. It has been found that the amount of callus tissue formed is related to the concentration of IAA applied. The cambial activity is also promoted by auxin. Seasonal activity of the cambium in a plant has been observed to be closely paralleled by a similar variation in auxin synthesis by the developing seedlings. It has been demonstrated that for continued growth cytokinin is needed in addition to IAA. It is assumed that while IAA induces DNA synthesis and mitosis, the cytokinin is needed for karyokinesis. The cytokinin also takes part in mitosis.

2. **Shortening of Internodes :**

In apple and pear there are two types of branches. The fruits are borne by the dwarf 'spurs'. If the terminal shoots are treated with high concentration of α-naphtalene acetic acid, their elongation is prevented and they become dwarf shoots. These dwarf shoots can also bear fruits.

3. **Prevention of Lodging :**

Many crop plants, e.g., certain varieties of oats and flax tend to lodge, i.e., to fall down due to an excessive elongation and softening of the cells in the basal internodes. It has been found that α naphthyl-acetamide treatment on the base of such plants causes them to grow stiff, woody and erect.

4. **Root Initiation :**

In nature root formation by a plant has been shown to be possible only if there are developing buds or leaves on them. Dormant buds fail to induce rootings. Ringing the cuttings immediately below developing buds also prevents rootings. Evidently the rootings in all such cases depend on the presence of a hormone. **Thimann** and his collaborators have shown that root forming substance and auxin are identical. The auxin has been found to increase the rate of formation and final number of root initials. The polar transport of auxin is very clearly pronounced in cutting. The roots would be formed at the end which was originally farthest removed from the terminal bud. This property of auxin has been found to be advantageous in propagating plants by cuttings in nurseries.

Quick adventitious root formation in cuttings is absolutely essential for their successful development into new plants. A number of compounds have been applied to cuttings, particularly in 'hard to root' species, to initiate root formation. In fact, over forty substance have been found to be useful but phenyl acetic acid, α-nephthalene acetic acid, indole acetic acid, butyric acid, and 2, 4-D are the most commonly used.

5. **Apical Dominance And Dormancy :**

In many plants only the apical bud grows and the lower axillary buds are suppressed. Removal of the apical bud, however, results promptly in the growth of one or several of the lower buds. The auxin of the terminal bud is thus responsible for inhibiting the development of lateral buds by a phenomenon known as apical dominance. This is further confirmed by applying auxin paste to a decapitated stump which also inhibits the development of lateral buds.

This particular property of auxins has been put to some constructive use in agriculture. The sprouting of lateral buds ('eyes') of the potato tuber is checked (dormancy period is increased) by applying synthetic auxins. This treatment results in storing in the tuber for three years instead of one year. Substances like indole-butyric acid, α-naphthalene acetic acid and maleic hydrazide have proved to be very useful for the purpose.

Synthetic auxins are also useful in delaying the opening of bud on fruit trees to avoid the very bad effects of late frost, and in reducing the shoot growth in nursery trees and bushes during storage and transport.

6. **Prevention of Abscission Layer :**

The formation of abscission layer often results in the premature fall of leaves, flowers, and fruits. In these cases a separation layer is formed at the base of the petiole, pedicel or peduncle. Abscission is believed to be due to the dissolution of the middle lamella or of the middle lamella and the primary walls, or of the whole cell.

The premature drop of fruits such as apple, pear, and citrus can be prevented to a great extent by spraying the tree with a dilute solution of 2,4-dichlorophenoxyacetic acid, IAA, NAA or some related auxin. The cabbage and cauliflower that often occurs during harvesting. To remove the leaves of cotton plants for facilitating the picking of balls by machine, 'anti-auxins' are sprayed over the field several days before harvesting.

7. **Flower Initiation :**

Auxin generally inhibit flowering. In pineapple (***Annas sativus***), however, auxins have been found to promote flowering. In pineapple flowering and fruiting are so much erratic that the pickers have to visit the field again and again to collect fruits as they ripen. If substances like 2, 4-D, acetylene and NAA in dilute concentrations are sprayed over a field of pineapple the whole crop flowers with amazing uniformity.

8. **Production of Parthenocarpic Fruits :**

After pollination and fertilization the ovule is converted into seed and ovary into a fruit. The increase in the rate of growth (cell enlargement) of the ovary wall leading to the formation of a fruit is believed to be due to the activity of auxin. The pollen tube is believed to release some stimulus for the increased growth in the ovary wall. It is thought that the pollen tubes secrete an enzyme which converts a precursor, tryptophan to auxin.

The presence of large number of seeds in a fruit lowers its commercial value and, therefore, this property of auxins has been employed by horticulturists for developing seedless fruits.

Seedless fruits may be obtained by spraying the flowers with a dilute solution of synthetic auxin. In nature, fruits like bananas, certain varieties of oranges and grapes have achieved the same result.

9. **Eradication of Weeds :**

One of the easiest way to eradicate an unwanted plant is to kill the roots. The roots are extremely sensitive to auxins. Very high concentrations of auxins on overstimulate growth-promoting activities of the cells of the roots. The roots are distorted, the sieve tubes get blocked and the cell divisions are disturbed. The roots ultimately decay and the plant is killed.

Certain synthetic substances, e.g., 2,4-dichlorophenoxyacetic acid (2, 4-D) is very much toxic to dicotyledons or broad-leaved plants, while it is relatively non-toxic to monocotyledons or narrow-leaved plants. The weeds are normally the unwanted dicotyledons, which grow in the fields with cereals (monocots). Thus in a mixed population of such plants the 2,4-D acts as a very useful selective herbicide or weed killer. The fields and the lawns can be thus cleared of the unwanted plant 2,4-D in combination with 2,4,5, trichlorophenoxyacetic acid (2,4,5-T) is more effective. They may be applied to soils (pre-emergence treatment). In the latter case they kill the weeds as soon as seed germination takes place.

There are four main reasons for using auxins as weed-killers.

(a) The selective herbicidal nature of auxins.
(b) Toxic resudies of auxins, unlike the arsenical and oils, disappear from the soil in a short time.
(c) The auxins are economical since they are effective in fairly low concentrations.
(d) The auxins at the concentrations used are not toxic to human beings or animals.

10. **Respiration :**

Auxins has been found to stimulate respiration. The increase in the availability of ADP increases the rate of ATP formation and thus stimulates respiration.

II. THE GIBBERELLINS

Some Japanese farmers noticed that certain diseased rice plants grew abnormally thin and tall. They called it "Bakanae or foolish seedling" disease because it made the young rice plants grow ridiculously tall. Infection by a fungus, *Gibberella fujikuroi* was shown to be responsible for the disease. **Sawada** (1912) hinted that the disease might be caused by something secreted by the fungus. **Kurosawa** (1926) performed experiments to demonstrate that filtrates of the cultures of the fungus produced the characteristic symptoms, when applied to healthy seedlings of rice. In 1938, **Yabuta** and **Sumiki** finally succeeded in isolating a pure crystalline chemical from the fungus and named it 'gibberellin'.

Cross and others (1961) isolated 6 gibberellins from the fungus *Gibberella* and they were termed GA_1,GA_2 ,GA_3 ,GA_4 ,GA_7 , AND GA_9 .The number of gibberellins discovered now stands at more than fifty, out of which 15 have been isolated from *Gibberella fujikuroi* only. They are chemically known as gibberellic acid. They have gibbane ring skeleton.

Unlike the auxins and the cytokinins only one of which predominates in most of the plants, several of the gibberellins are found in the same plant. The gibberellins are widely distributed in nature. They have been found to be present in algae, mosses, ferns, gymosperms and angiosperms. While they are common in higher plants, they are restricted to only certain species of bacteria and fungi. They are concentrated in the regions where the development of the plant is taking place e.g., stem apex, young leaves and seeds, etc.

PHYSIOLOGICAL EFFECTS OF GIBBERELLINS

A variety of responses have been observed in plants by the application of gibberellins. They are discussed below briefly.

1. **Stem Elongation :** The most typical and striking effect of gibberellin is on the elongation of the stem. The internodes increase in length. A lettuce plant, a low head, becomes vine like after it is treated with gibberellins.
2. **Dwarf Plant :** One of the most remarkable effects of gibberellins is in converting a genetically dwarf plant in a plant of normal height. Addition of gibberellin to a cabbage plant converts the dwarf stem into a stem which is 6-8 feet tall. 'Rosette' plant of sugar beet is an extreme case of dwarfism. It has been shown that such a stem can undergo rapid growth or '**bolting**', if it is treated with gibberellin. It is believed that the dwarfism in the mutant varieties of a plant is due to blocking of the capacity for normal gibberellin production.
3. **Promoting Flowering in Long Day Plants :** Gibberellins have been found to promote flowering in a class of plants called long-day plants under unfavourable short day conditions.
4. **Substituting Cold Treatment :** Biennials normally flower only during the second year of growth i.e. only after they have passed through a winter season. Many biennial plants can be induced to complete their whole life cycle in a single year by treatment with gibberellins.
5. **Parththenocarpic Fruits :** Gibberellins have been found to be more effective than auxins in causing parthenocarpic development of fruits in plants like tomatoes, apples and pears. They improve fruit-set in tomatoes. They induce parthenocarpy in pome and stone fruits.
6. **Breaking dormancy :** Gibberellins break dormancy in potato tubers and in buds of trees.

III. CYTOKININS

Miller (1954) was the first to isolate the first crystals of a 'cell division inducing substance' from autoclaved DNA of herring sperms. Since the substance had specific effect on cytokinesis it was named **Kinetin**. Later on **Letham** (1963) coined the word **cytokinins** to include kinetin, zeatin (from maize) and other similar substances. They are derivates of the purine base adenine. They occur naturally in t-RNAs. Coconut milk is a rich source of cytokinins.

PHYSIOLOGICAL ROLES OF CYTOKININS

1. **Cell division :** Permanent cells are capable of dividing only in the presence of cytokinins.
2. **Cell elongation :** Cytokinins have been found to be effective even in causing expansion of cells.
3. **Morphogenesis :** One of the most interesting effects of cytokinins is the phenomenon of organ formation in a variety of tissue cultures.

   It is well known that auxins exert apical dominance on the buds. In one of the most brilliant experiments on tobacco pith-tissue cultures **Skoog** and **Miller** (1957) found that in a balanced medium of 1AA and kinetin the pith grew as an amorphous, undifferentiated **callus**. They found that a relative increase in kinetin level in the medium caused the formation of buds which might grow into shoots and even complete tobacco plants whereas a comparative lowering of the amount of kinetin in the medium caused the pith culture to form roots. Though cytokinins are produced by roots the formation of root itself has been found to be inhibited in the former case probably because of supra-optimal levels of kinetin. Some workers have shown the regeneration of shoots from root segments in the presence of kinetin.

   A host of other morphogenetic response in addition to root and shoot differentiation have been reported e.g. (i) formation of plastids from proplastids, (ii) differentiation of tracheids through activations of lignin biosynthesis, (iii) induction of flowering, and (iv) induction of parthenocarpy.
4. **Concentration of Apical Dominance :** Exogenous application of cytokinin has been found to counteract the usual dominance of the apical bud.
5. **Breaking of Dormancy :** Cytokinins have been demonstrated to be effective in breaking the dormancy of seeds and some other plant organs. They not only break the dormancy but also promote the germination of seeds. The cytokinins substitute the light requirement for breaking the dormancy of seed. Further in combination with red light kinetin reverse the effect of certain naturally occurring inhibitors of seed germination as coumarin and xanthatin.
6. **Delay of senescence :** The **Richmond-Lang** effect : Richmond and Lang (1957) reported the delay of senescence (chlorophyll disappearance and protein degradation) for several days in the detached leaves of *Xanthium* when they were treated with kinetin. This effect of cytokinin in retarding ageing is called the Richmond-Lang effect.

GROWTH INHIBITORS

Abscisic acid (ABA)

ABA was earlier called dormin. It has the following roles :

(1) It regulates the dormancy of buds and seeds.
(2) It causes senescence of leaves.
(3) It inhibits the germination of seeds.
(4) It is knows as anti-gibberellins.
(5) ABA inhibits gibberellin-induced α-amylase formation in barley aleurone.
(6) It causes ageing and abscission of leaves.
(7) ABA has been found to accumulate in high concentration in leaves which are wilting. This increased production of ABA by the leaves is correlated with stomatal closure. It is believed that ABA interferes with uptate or retention of potassium (or sodium) in guard cells.

Mode of Action of Abscisic Acid : ABA is believed to act in the following manner :

(1) It may compete with auxins, gibberellins or cytokinins for a specific enzyme site since it is known to be antagonistic to their effects.
(2) It may inhibit the biosynthesis of other growth hormones or even inactivate them.
(3) ABA may inhibit RNA and protein synthesis.
(4) It may stimulate the production of certain hydrolytic enzymes.

Ethylene

Ethylene which is so well known as a product of combustion and as a common air pollutant is surprisingly a powerful plant hormone. It is a gas, (formula : $CH_2 = CH_2$) and is produced in minute quantities by plant tissues, but is active at extremely low concentrations (well below 1 part in 10 million of air). It is synthesized in the plant from the amino acid methionine. It is not easily soluble in aqueous medium and volatilizes into the intercellular spaces from where it is released in the outer atmosphere.

Ethylene has several effects on the vegetative and reproductive growth of plants. Treatment with auxin stimulates the production of ethylene by plant tissues and, therefore, it is believed that a number of observed effects of auxin are actually due to ethylene. Ethylene also inhibits the transport of auxin in many tissues.

The inhibition of stem elongation (shortening of the internodes) and the accompanied lateral swelling of the cells on application of overdoses of auxin has been now proved to be a response of auxin induced ethylene formation. Similarly, inhibition of root and bud growth by auxin is due to auxin-induced ethylene formation. Flowering in pineapple occurs at a time either by auxin or ethylene treatment. The prevention of auxin transport from the leaves to the petiole by ethylene results in the formation of abscission layer.

The most important effect of ethylene is on fruit ripening when it is produced in large amount which coincides with **respiratory climacteric** i.e. a brief rise to a very high level of respiration. This rise indicates the beginning of senescence and death. Ethylene increases the permeability of the cell because of which the fruit is softened and the entry of oxygen into the fruits is accelerated. The ethylene is also believed to stimulate protein (enzyme) synthesis the result being that in the softened fruit plenty of enzymes easily come in contact with the metabolites. This increases the rate of respiration and climateric is observed. Climacteric can be prevented by eliminating oxygen from the atmosphere to prevent respiration. Fruits like banana etc. during storage in a fridge get spoiled due to production and accumulation of ethylene by ripened fruits. This ethylene stimulates unripened fruits to ripen faster and produce more ethylene. “Thus the ripening process becomes autocatalytic in a stored mass of fruits.” Fruits can be stored long by removing ethylene accumulated within a closed space by flushing the fruit with an inert gas (nitrogen or CO_2). Fruits can be made to ripen before the proper time in a uniform manner by keeping them in an atmosphere of ethylene. Uncontrolled application of ethylene can, however, spoil the fruit.

Ethylene interferes with normal geotropic responses of seedlings probably by interfering with the polar transport of auxin.

The effects of ethylene are as follows :

(1) Induction of respiratory climacteric and ripening in fruits.
(2) Inhibition of elongation growth in stems and roots.
(3) Promotion of femaleness.
(4) Stimulation of germination in seeds of some species.
(5) Promotion of leaf abscission.
(6) Induction of flowering in pineapples.

Maleic Hydrazide (MH) : It prevents storage sprouting in onion, potato and certain root crops. It suppresses suckering in tobacco and retards the growth of grasses along the roadways.

FLOWERING

PHOTOPERIODISM

About eighty years ago, two workers in the US Department of Agriculture, **W.W. Garner** and **H.A. Allard**, found that a tobacco mutant, Maryland Mammoth, flowered at different times at different places (latitudes). After eliminating other factors such as temperature variations, nutrition, and light intensity, they concluded that it was the length of the day which controlled flowering in these plants. They discovered that this particular variety of tobacco flowered in places, where the length of the day was shorter.

Garner and Allard (1920) suggested the term photoperiodism to designate photoperiod to designate the favourable length of day for each plant. They classified the plants into three groups according to their photoperiods.

(a) Short-day plants, (b) Long-day plants, and (c) Day-neutral plants.

Short-day plants flower when the day length is less than, a certain critical length, say twelve hours. In other words the day length must not exceed a critical period of light if they are to flower.

Long-day plants flower when the day length is greater than a certain critical length. In other words the day length must not be less than a certain critical value.

Day-neutral plants are those in which flowering is unaffected by the length of day.

Short-Day Plants :

Most of the plants belong to this category. The salient features of the short-day plants are as follows (Fig.) :

(a) In short-day plants the length of the day is not as important as the length of the night. Such plants require a relatively long period of uninterrupted darkness for flowering. The dark period must be longer than a certain critical length. If the dark period is less than the critical length flowering does not take place, even if the photoperiod is of appropriate length. Minimum effective photoperiods may be very short-less than an hour in some species, but minimum effective dark periods are very much longer.

(b) Flowering is inhibited if a very weak intensity of light is given to the plant for some time during the dark period.

(c) The flowering is also suppressed, if the dark period is interrupted midway by even a single flash of light. The intensity of light needed to inhibit flowering in such a case is quite low. The interruption of the dark period is not very effective, if it is near the beginning or the end of the dark period.

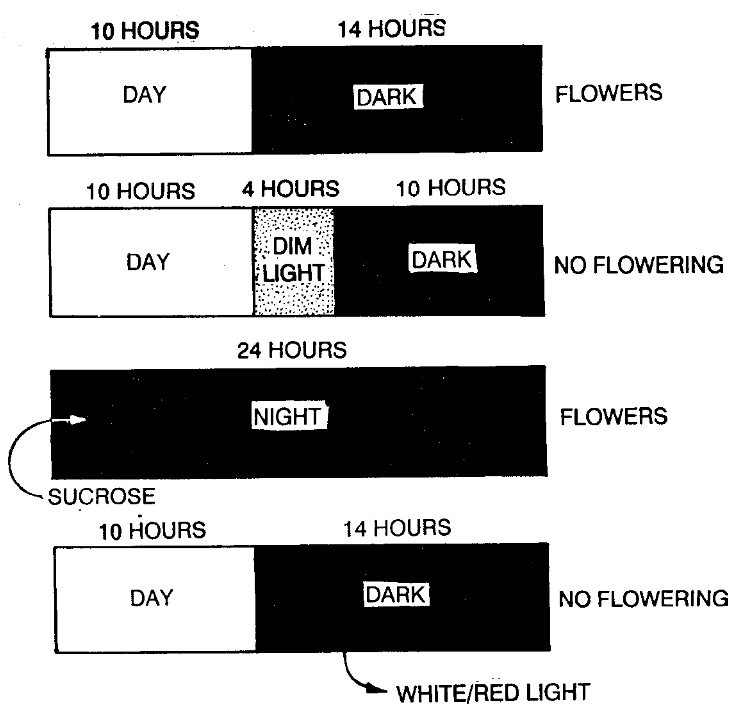

Fig. The effect of light period and darkness on the flowering of SDP.

(d) Short-day plants, unlike the long-day plants, are incapable of flowering under alternating cycles of short dark and short light periods.

(e) Several short-day plants flower in continuous darkness, if they are given sucrose suggesting that light is needed only for the photosynthesis of food material.

All this leads to the conclusion that it is the length of the night and its continuity that are really important in initiating flowering in short-day plants. The short-day plants may, thus, also be called "long night plants'.

Flowering can be induced even under long-day conditions if the dark period is increased by transferring the plant to darkness for sometime after or before the night period. In long-day conditions they can grow well but will never flower.

Long-Day Plants :

They have the following essential features :

(a) Long-day plants require a photoperiod of more than a critical length. The critical photoperiod varies from 4 to over 18 hrs. for such plants. They require either a relatively small period of darkness or no darkness at all. This is supported by the fact that long-day plants usually flower best in continuous light.

(b) In long-day plants, periods of darkness have an inhibitory effect on the flowering of the plants. A long-day plant can be made to flower even under short-day conditions, if a flash of light is given to the plants during the long dark period (Fig.).

(c) Another interesting point regarding the long-day plants is their capability to flower in short photoperiods, provided these were accompanied with still shorter dark periods. A long-day plant, which normally flowers in a day length of 16 hrs. of a normal 24 hrs. cycle of light and darkness, can also flower if it gets 8 hours of light of a 12-hour cycle of light and darkness. Thus the inhibition of flowering in a long-day plant under short days is not because the photoperiods are short but because the dark periods are too long.

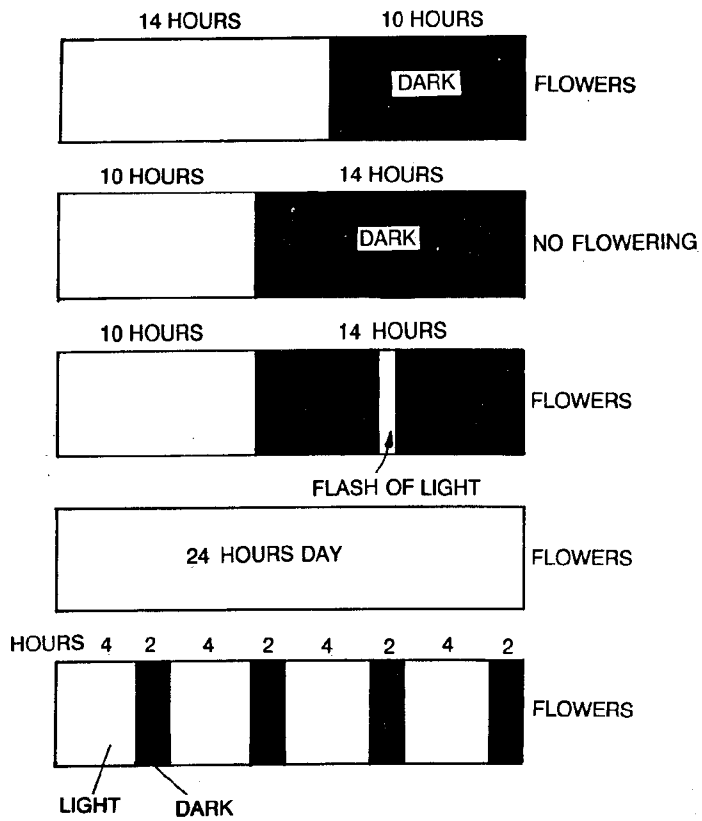

Fig. The effect of photoperiod and darkness on the flowering of LDP.

The long-day plants can justifiably be called 'short night' plants. Fig., shows the response of SDP, LDP to the critical photoperiods.

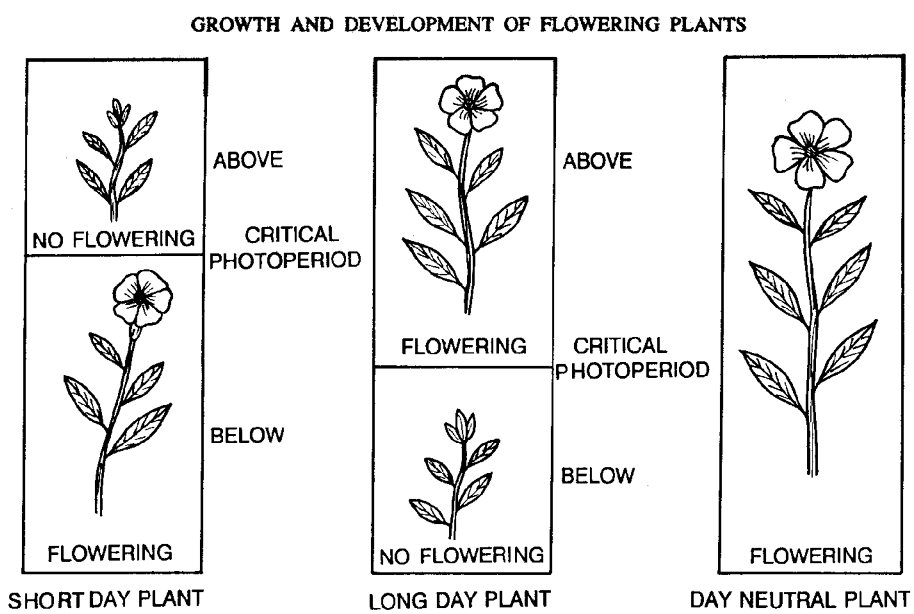

Fig. Response of SDP and LDP to the critical photoperiods.

Day-Neutral Plants :

There are a number of plants which can flower in all possible photoperiods ranging from few hours to 24 hours of uninterrupted light exposure. They are also called photo-neutrals or indeterminate plants. Tomatoes, cocumbers, sunflowers, dandelions and cotton are some of the examples of such plants.

A list of SDP, LDP and Day Neutral Plants is given below :

SHORT-DAY PLANTS

A. Species with an Absolute or Qualitative Short-day Requirement

Amaranthus caudatus (Love-lies bleeding)
Chenopodium album (Pigweed)
Chrysanthemum morifolium
Coffea arabica (Coffee)
Euphorbia pulcherrima (Poinsettia)
Fragaria (Strawberry)
Glycine max (Soybean)
Ipomoea hederacea (Morning glory)
Kalanchoea blossfeldiana
Lemna perpusilla (Duckweed)
Nicotiana tobacum (Tobacco, var. Maryland Mammoth)
Perilla ocymoides
Xanthium strumarium (Cocklebur)

B. Species with Quantitative Short-day Requirement

Cannabis sativa (Hemp)
Cosmos bipinnatus (Cosmos)
Gossypium (Cotton)
Oryza sativa (Rice)
Saccharum officinarum (Sugar cane)
Salvia splendens

LONG-DAY PLANTS

A. Species with an absolute or Qualitative Long-day Requirement

Alopecurus pratensis (Foxtail grass)
Anagallis arvensis (Pimpernel)
Anethum gravealens (Dilli)
Avena sativa (Oat)
Dianthus superbus (Carnation)
Festuca elatior (Fescue grass)
Hyoscyamus niger (Henbane)
Lolium telemuntum (Rye-grass)
Melilotus alba (Sweet clover)
Mentha piperita (Peppermint)
Phleum pratensis (Timothy grass)
Raphanus sativus (Radish)
Rudbeckia bicolor (Coneflower)
Sedum spectabile (Sedum)
Spinacia oleracea (Spinach)
Trifolium spp. (Clover)

B. Species with a Quantitative Long-day Requirement

Antirrhinum majus (Snapdragon)
Beta vulgaris (Garden beet)
Brassica rapa (Turnip)
Hordeum vulgare (Spring barley)
Lactuca sativa (Lettuce)
Oenothera spp. (Evening primrose)
Petunia hybrida (Petunia)
Pisum sativum (Garden pea)
Poa pratensis (Kentucky blue-grass)
Secale cereale (Spring rye)
Triticum aestivum (Spring wheat)

DAY-NEUTRAL PLANTS

There are a number of plants which can flower in all possible photoperiods ranging from few hours to 24 hours of uninterrupted light exposure. They are also called *photoneutrals* or *indeterminate* plants. The examples of such plants are :

Poa annua (Bluegrass)	*Zea mays* (Corn)
Impatiens balsamina (Balsam)	*Phaseolus spp.* (Bean)
Fagopyrum tataricum (Buckwheat)	*Gossypium hirsutum* (Cotton)
Cucumis sativus (Cucumber)	*Hex aquifolium* (Holly)
Helianthus tuberosus (Jerusalem artichoke)	*Solanum tuberosum* (Potato)
Rhododendron (Rhododendron spp.)	*Fragaria chiloensis* (Strawberry)
Nicotiana tabacum (Tobacco)	*Lycoperiscon esculentum* (Tomato)

Perception of light stimulus :

Cajlachjan, working with *Chrysanthemum* and *Perilla*, was the first to demonstrate that the photoperiodic stimulus is perceived by the leaves of a plant.

Group A : Plants were given long days.

Group B : Lower leafy region received short days but the upper defoliated region received long days.

Group C : Lower leafy region received long day but the upper defoliated region received short days.

Group D : Entire plant received short days.

He found that plants of group B and D, in which the leaves received short-day treatment, flowered whereas there was no flowering in plants of group A and C because the leaves received the improper long-day photoperiod.

The photoperiodic stimulus may be localized or systemic. **Garner** and **Allard** (1923, 1925), working with short-day cosmos plants found that if a branch of the plant was exposed to short-days, and another to long-days, flowering took place in the former and was suppressed in the latter. The effect of the photoperiodic stimulus is, therefore, highly localized. In the cocklebur, on the other hand, even if a single leaf is exposed to short-days and the rest of the plant to long days, flowering takes place in the whole plant. The effect in cocklebur is thus systemic. **Hammer** and **Bonner** (1938) also found that both branches of a two-stemmed cocklebur flower even if only one of them is exposed to short days.

Defoliated plants fail to flower even with proper light treatment, whereas proper light stimulus received by even a single leaf is sufficient to induce flowering. It has also been found that mature leaves are very sensitive to the photoperiodic stimulus while very young and old leaves are generally insensitive.

Photoperiodism and Quality of Light :

Green colour of the visible spectrum is normally ineffective in inducing flowering, whereas blue colour induces poor flowering. The wavelengths, 580 nm to 680 nm in the red portion of the spectrum has been found to be most effective as a flower-inducing stimulus in both the short-day and the long-day plants.

PHYTOCHROME

In has already been mentioned that the flowering of a short-day plant can be inhibited if the dark period is broken by a brief flash of light. It has been found that the wave length 660 nm in the orange-red colour is the most effective wavelength for inhibiting the flowering. Far-red radiation, on the other hand, does not break up a long night into two short nights. Besides, far-red radiation of a wavelength of 730 nm has been found to reverse the effect of red light (Borthwick and others, 1952). If a brief flash of red light in the mid-night is followed by a brief flash of far-red radiation flowering will take place. If red and far-red light are given alternately the light used last in the sequence will determine the response of the plant.

This startling discovery led to the search of a pigment, since light energy cannot be effective unless it is absorbed by a pigment. **Butler** and others (1959) finally isolated the pigment in question and called it phytochrome. Phytochrome is universal in distribution in green plants (some algae may be exception).

Phytochrome appears to be a protein with a chromatophore. It is believed that it occurs in two possible forms. The form which absorbed red light (600nm) is designated as P_R and the form which absorbs far-red light (730 nm) is termed P_{FR}.

The red absorbing form of phytochrome is blue-green, and the far-red absorbing form is light green in colour. The chromophoric group which gives two colours to the protein is an open chain tetrapyrrole pigment similar to the phycobilin allophycocyanin. Of the two forms, P_R stimulates flowering while P_{FR} inhibits it. The two forms of the phytochrome are easily interconvertible as shown in Fig. 6.9.

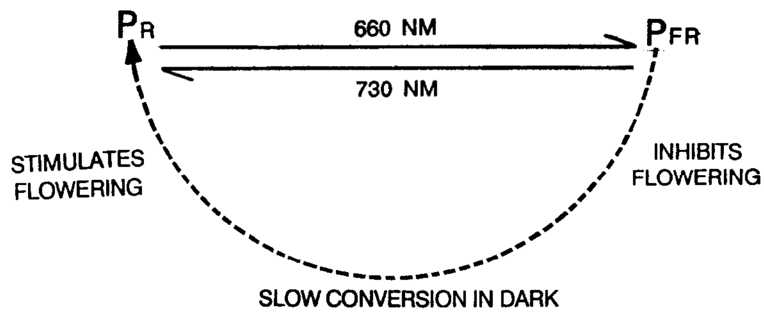

Fig. Diagram showing interconversion of phytochrome in red and far-red light.

In short-day plants, at the end of the light period, the phytochrome is in the far-red light form, P_{FR} due to the wave lengths of sun-light. In the following dark period, P_{FR} is gradually converted into the red absorbing from P_R, which stimulates the synthesis of the flowering substance ('florigen'). When a brief flash of red light is given to the short-day plant in the mid-night P_R is converted back to P_{FR} and flowering is inhibited. If the plants are then exposed to far red radiation, P_{FR} is immediately converted into the P_R form, and flowering takes place.

Phytochrome has been found to control a number of physiological responses of the plants which are shown below :

Algae, bryophytes and pteridophytes	**1.**	Spore germination
	2.	Chloroplast movement
	3.	Protonema growth and differentiation
Gymnosperms	**1.**	Seed germination
	2.	Hypocotyl hook formation
	3.	Internode extension
	4.	Bud dormancy
Angiosperms	**1.**	Seed germination
	2.	Hypocotyl hook formation
	3.	Internode extension
	4.	Root primordia initiation
	5.	Leaflet movement
	6.	Electrical potential
	7.	Membrane permeability
	8.	Phototropic sensitivity
	9.	Geotropic sensitivity
	10.	Anthocyanin synthesis

Flowering Hormone

There is an increasing evidence to suggest that a flowering hormone exists in plants. **Cajlachjan** coined the term florigen for the flowering hormone. Two important evidences regarding the existence of the hormone are given below :

(i) There is a spatial separation of the site of stimulation and the site of the response. The buds do not perceive the stimulus for flowering. The leaves, which perceive the stimulus transmit it to the buds, obviously in the form of a flowering hormone.

(ii) The existence of a flowering hormone is supported by a number of grafting experiments. A short-day plant kept in long-day conditions can be induced to flowers, if a properly photoinduced plant is grafted on to it. It clearly indicates that a diffusible flowering hormone has moved from one plant to the other and has induced the latter to flower.

Lang performed a number of grafting experiments and demonstrated that all grades of grafting are possible-intravarietal, intervarietal, interspecific, and intergeneric. Grafting short-day plants on to long day plants and vice versa are equally successful.

VERNALIZATION

In many plants, the flowering is influenced not only be the correct photoperiod but also by temperature. In annuals the flowering is primarily affected by the photoperiod. The effect of temperature is secondary to light. A biennial plant, on the other hand, grows only vegetatively during the first season and will not initiate flowering until it has been exposed to prolonged periods of low temperature of the winter. A similar phenomenon is to be seen in certain varieties of cereals. In cold countries, there are cereals of two physiological kinds, the winter cereals and the springs cereals. The winter variety is shown in early autumn, i.e., in the months of September or October to make them flower in the following summer. If they are shown in the spring after the winter along with the spring variety, they grow vegetatively but fail to produce ears or flowers. Exposure to low temperature of the winter is evidently essential for the flowering of winter varieties.

It has been shown by several workers that this requirement of low temperature in nature can be satisfied artificially in laboratories in the absence of the winter season, and the plant may be made to flower in summer season. For example, if a biennial seed is germinated and is then exposed to low temperature (0º -5C) for few weeks it will behave as if it has gone through the cold winter after a year of growth. Similar treatment will enable the winter variety of wheat or rye to flower even if they are shown in the spring. This cold (low temperature) treatment to a plant bud or seedling in order to fulfil a specific low temperature requirement for accelerating flowering is called Vernalization or Yarovization. Vernalization is also defined as the “acquisition of the ability to flower by a chilling treatment”. This agricultural practice results in shortening of the interval between sowing and flowering.

Devernalization

Vernalization effect is reversible and the process is termed devernalization. If a vernalized seed or plant is kept at high temperature, the effect of the low temperature treatment is completely removed. High temperature reversal can be counteracted if the duration of the vernalization treatment is increased. Devernalized plants can, however, be again vernalized by low temperature treatment.

Mechanism of Vernalization

The important workers in the field of vernalization have been **Klippart** (1957) and Russian botanists **Gassner** and **Lysenko**. According to Lysenko, growth and development of a plant are two distinct phenomena. Growth is an increase in the size of a plant without any profound qualitative change in the growing parts. During development the plant enters a new phase qualitatively differing from the preceding phase and bringing it nearer to its final phase of life, i.e., fruit bearing. In winter varieties of plants, low temperature is necessary (for tropical plants, high temperature) for a certain phase of development, the **thermophase**, which must be passed before the next phase, the light controlled **photophase**, can begin.

Attempts have been made to explain the mechanism of the temperature effect in terms of a hormone. Grafting experiment with henbane conducted by **Melchers**, has provided a strong evidence for the existence of a new hormone which he called **vernallin**.

PLANT MOVEMENTS AND PLANT RHYTHMS

INTRODUCTION

Movement in plants may or may not be very pronounced. Those lower plant which are aquatic and are provided with cilia have as rapid and efficient locomotion as that of animals of a similar category. In fixed rooted plants, the characteristic mode of nutrition has done away with the necessity of rapid locomotion.

Movements in plants are brought about by definite internal and external stimuli. The movements, which take place spontaneously without the effect of external stimuli are termed spontaneous or **autonomic**. All those movements of plants, which are caused by external stimuli are termed induced or **paratonic**. The paratonic movements are of three types viz., **tactic** movements, **tropic** movements, and **nastic** movements.

CLASSIFICATION OF PLANT MOVEMENTS

Plant movements can be broadly classified into movements of locomotion and movements of curvature. In the former case the plant or the plant structure moves physically from one place to another place. In the latter case the plant is fixed and the movement is in the form of slight bending or curvature of a portion of the plant. The movements of locomotion are limited to some of the aquatic plants or structures while the movements of curvature are largely to be found in rooted terrestrial plants.

The curvature movements are of two types - growth movements and variation movements. In growth movements the curvature is of permanent nature since it is accompanied with the growth of the plant organ. In variation movements the curvature is simply a temporary change in the position of certain plant organs.

In addition to the movements mentioned above certain structures exhibit hygroscopic movements. Such movements are not caused by the physiological activities of the living cells and will not be considered further. The vital plant movements can be classified as under :

AUTONOMIC MOVEMENTS OF LOCOMOTION

Ciliary Movements : Certain algal plants and their zoospores and gametes are provided with cilia. These structures are often seen to move from one place to another place with the help of cilia. Such movements are known as ciliary movements.

Amoeboid Movements : Certain plasmodia of the myxomycetes exhibit amoeboid movements. The naked mass of the protoplasm moves by producing pseudopodia like structures.

Cyclosis : In many plants the protoplasm of the living cells is seen to have streaming movements around the vacuoles. In the leaves of *Hydrilla*, *Vallisneria* and *Elodea* the protoplasm moves in either a clock-wise or anticlockwise- manner. The streaming movement of the protoplasm is seen in the form of the movement of the plastids which are present in it. Such a movement is called rotation. In the staminal hairs of Tradescantia the protoplasm of a cell is separated into different portions on account of the presence of a number of vacuoles. Each portion of the protoplasm has its own independent number of vacuoles. Each portion of the protoplasm has its own independent direction of streaming movement. Some of them move in a clock-wise and others in an anticlock-wise manner. Such a movement is called circulation. Rotation and circulation are collectively know as cyclosis.

PARATONIC MOVEMENTS OF LOCOMOTION
(TACTIC MOVEMENTS)

Tactic movements are movements of locomotion, which are induced by some unidirectional external stimuli. Such movements are also called tactile or taxies. Depending upon the nature of the stimuli viz., light, chemical and heat, the movements are termed phototactic, chemotactic and thermotactic.

Phototactic Movement : Certain ciliated algae and their reproductive structures such as zoospores and gametes are provided with a light-sensitive 'eye' spot. The eye spot is attracted by weak intensity of light and is repelled by intense light. When these algal structures receive weak light from one direction they move towards the source of light. This is an example of positive phototactic movement. A negative phototactic movement takes place when they are exposed to a strong intensity of light. Similar movements are also exhibited by the chloroplasts of the mesophyll cells of leaves.

Chemotactic Movement : In most of the bryophytes and pteridophytes the swimming movement of the antherozoids towards the archegonial tips is in response to the chemical stimulus. The archegonia secrete certain organic substances such as cane sugar, malic acid etc., which attract the antherozoids.

Thermotactic Movement : The ciliated algal structures have been observed to move from a colder to a warmer place. If a glass vessel containing *Chlamydomonas* in cold water is warmed on one side, the algae move to the warm side in response to the heat stimulus. However, if the temperature becomes very high, they move away from that side.

AUTONOMIC GROWTH MOVEMENTS

Nasty Movements : Nasty movements are to be found in leaves, flowers, petals, bud scales, etc. In such structures at some stage in the development growth of one surface is more than the growth of the other surface. If the upper or the inner surface has more growth, the movement is termed epinasty. The opening of the flower and the drooping of a bud are examples of epinasty movement. If the growth is more on the lower surface, the movement is termed hyponasty. The upward bending of a prostrate or a drooping structure, the folding in of a plant part are some of the examples of hyponasty movement. An excellent example of both epinasty and hyponasty is provided by poppy.

Poppy flower-bud assumes a drooping condition due to epinastic growth movement. The subsequent hyponastic growth of the floral axis results in the formation of an upright stalk of the flower (Fig.).

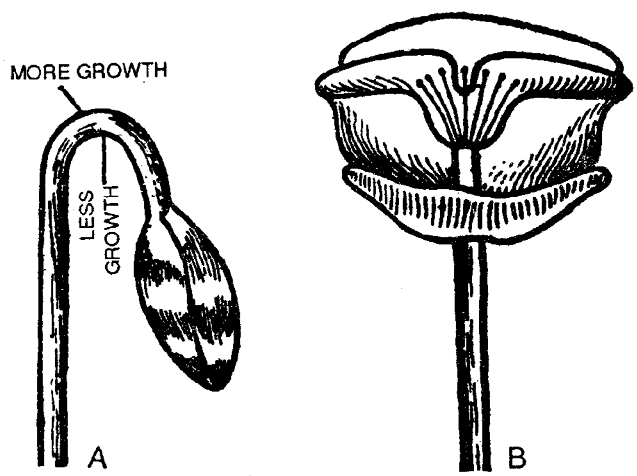

Fig. Poppy flower bud. A. showing epinasty; B. showing vertical stalk due to haponasty.

Nutational Movement : The growth of the shoot tips of certain species takes place in a zigzag manner. This is because of the alternate change in growth rates on opposite sides of the apex. Such movements are very slow and cannot be easily seen. This type of growth movement is known as **nutation**. When the region of maximum growth passes round the growing tip so that it makes a rotational growth around its long axis, the movement is termed **circumnutation**.

PARATONIC GROWTH MOVEMENTS (TROPIC MOVEMENTS)

In many cases growth is induced by certain external stimuli. The stimuli are, however, effective in causing growth movements only when they are unilateral. Such movements are generally called tropic movements and the phenomenon is known as tropism. Depending upon the nature of the external stimuli viz., light, gravity, water, touch, and chemical, the movements are called phototropic, geotropic, hydrotropic, thigmotropic and chemotropic respectively. Some other examples of tropic movements are aerotropic (air), thermotropic (heat), traumatropic (injury), etc.

PHOTOTROPISM (Heliotropism) :

If young plants are exposed to unidirectional light the stem tip grows towards the source of light and the root tip grows away from source of light. The stem thus shows a positively phototropic and the root a negatively phototropic movement.

The curvature in both the cases is obviously due to unequal growth in the illuminated and shaded halves of the tips. In the case of the stem tip the growth is more in the shaded half, while in the root tip growth is more in the illuminated half (Fig.).

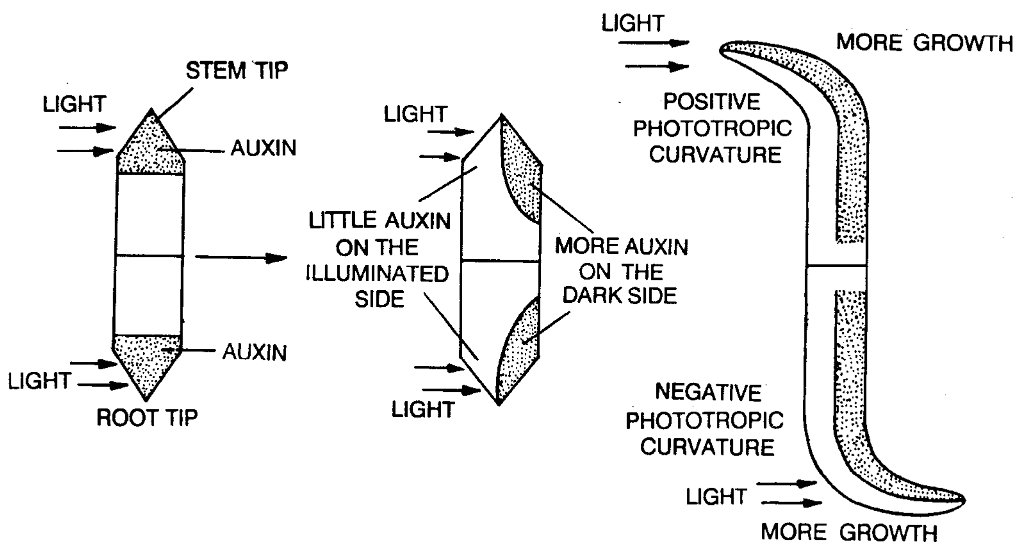

Fig. Phototropic curvature in shoot and root tips.

The unequal amount of growth in the two halves of the stem and the root tips is due to light-induced unequal distribution of the growth hormone, auxin. The amount of auxin is invariably more in the shaded half.

Five theories have been put forward to explain the interaction of light and auxin in the phototropic movement

(a) A light-induced lateral translocation of auxin away from light.

(b) A light-induced inhibition of downward translocation of auxin.

(c) A light-induced inactivation of auxin.

(d) A light-induced inhibition of auxin synthesis at the apex.

(e) A light-induced destruction of auxin.

A light-induced lateral translocation of auxin has been experimentally shown. A light-induced photoinactivation of auxin has been shown by some workers but a large number of other evidences do not suggest such a proposition. The theory of light-induced inhibition of auxin synthesis seems to be very convincing. It suggests that the conversion of auxin precursor into auxin is inhibited on the illuminates side. Went had demonstrated the destruction of auxin in light.

In the tips of both the stem and the root the amount of auxin is more in the shaded half, yet the pattern of growth is different in the two cases. While higher concentration of auxin is favourable for growth in the stem apex, it is unfavourable for growth in the root apex. The optimum amount of auxin for the growth of the stem cells has been found to be 100,000 times more than the optimum for the growth of the root cells. It will be observed that the concentration of auxin at which stem shows maximum growth the growth of root is inhibited and vice-versa. This is why when a plant is illuminated from one side, the high concentration of auxin on the shaded side causes more growth in the stem but less growth in the case of root tips. This results in a positive phototropic curvature of the stem apex and negative phototropic curvature of the root apex. The inhibitory effect of auxin on root elongation is indirect. The auxins are believed to bring about evolution of ethylene in the root tissue, which results in the inhibition of its growth.

GEOTROPISM (Gravitropism)

The stem is negatively geotropic, whereas the root is positively geotropic (Fig.). To study the effect of gravity, the plant is normally kept in a horizontal position. The stem tip would, after some time bend in an upward direction and the root tip would bend in a downward direction. The different plant organs respond to gravity in different ways.

Gravity is believed to increase auxin content on the lower side of a stem or a root apex. A higher concentration of auxin on the lower side of the stem tip stimulates its growth on this side only and, therefore, a negative geotropic curvature takes place. In the case of root tip, high concentration of auxin on the lower side inhibits the growth on this side and, therefore, a positive geotropic curvature takes place.

The negative and the positive responses of the stem and the root tips to gravity are due to increased concentration of auxin on their lower sides. This is supported by the following evidences.

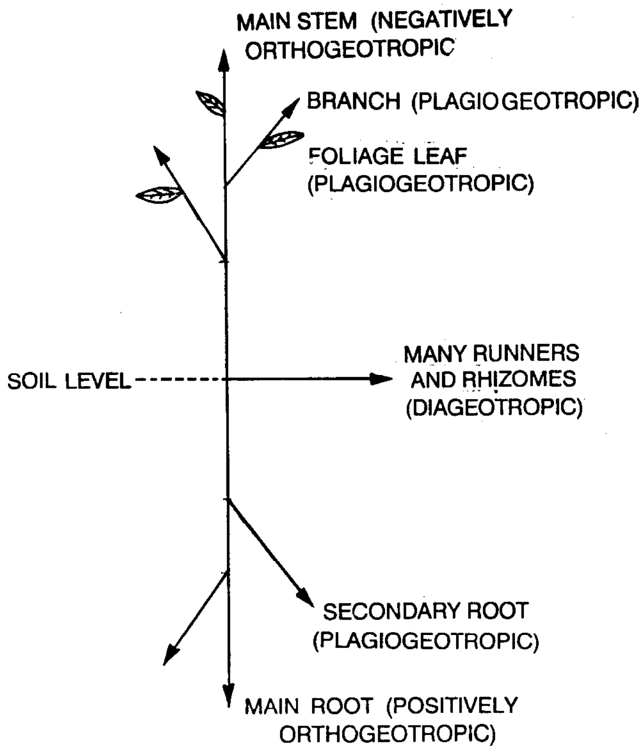

Fig. Responses of the various parts of a plant to the stimulus of gravity.

(a) In a horizontal stem the buds are normally suppressed on the lower surface.
(b) In a horizontal stem kept in contact with the soil adventitious roots are formed.
(c) Agar block containing IAA placed centrally on decapitated roots cause a retradation of growth.
(d) Applications of very low concentrations (0.00001 to 0.001 mgm.) of IAA to decapitated roots result in an acceleration of growth.
(e) If coleoptile tips are placed on decapitated root tips, the growth is retarded.

Geotropism and Statoliths : Many earlier workers believe that the gravitational stimulus causes the displacement of starch grains (statoliths) to the lower surface of the cell. Lately the concept of statoliths has been enlarged to include all sorts of cell inclusions. The statoliths are now believed to modify the trans location pattern of the auxin resulting in its accumulation on the lower surface. It is also believed that the translocation pattern of auxin is altered by formation of electrical potentials (the underside of the stem becoming positive). The chain of reactions in geotropism might be as follows.

Gravity ⟶ displacement of statocysts ⟶ disturbance of cell membrane of lower surface ⟶ altered electric potentials ⟶ modified translocation pattern ⟶ auxin accumulation on lower surface ⟶ negative geotropic curvature.

Clinostat

The effect of gravity can be studied in a detailed manner with the help of an apparatus called clinostat. The clinostat consists of a clockwork which rotates a pot-like container by means of an axial rod (Fig.). If a potted plant is fitted horizontally on the clinostat and is slowly rotated (4 rotations per hour) the effect of gravity is eliminated. This is because all the sides of the plant are equally stimulated by gravity. During rotation, if the clinostat is made to stop for some minutes at a particular place at regular intervals, the shoot may show negative geotropism. This is because a particular side of the stem gets greater gravitational stimulation than the other side.

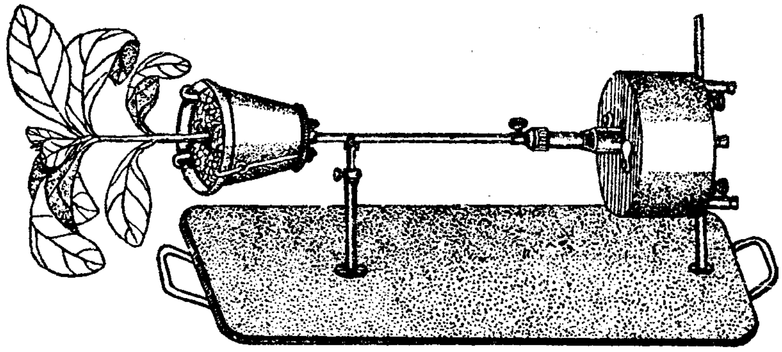

Fig. Clinostat in the horizontal position to eliminate the effect of force of gravity.

The minimum period of exposure to the one-sided stimulus, which produces curvature afterwards, while the plant rotates on the clinostat, is called the **presentation time**. If this time is short, the plant may receive the stimulus but may not give a visible response. The time required to perceive this minimum stimulus is called perception time. If such a condition is repeated several times, stimuli perceived in successive stoppages may accumulate and give visible response. On the other hand, if the clinostat is rotated very slowly, there is no response because one stimulus dies out before the next one is perceived. The time taken for the perceived stimulus to die out is called the **relaxation time**. Normally the visible effect of the stimulus appears after the lapse of sometime. The minimum period taken by plant to produce visible curve is called the **reaction time**.

HYDROTROPISM

In many plants roots have been found to exhibit positive hydrotropic curvature. Some workers have, however, reported the absence of such a response in roots of certain species. Positive hydrotropism can be demonstrated with germinated seedlings, which are allowed to grow on an inclined wire-gauze, covered with moist saw dust. The radicals at first grow in a downward direction due to the effect of gravity (positive geotropism) but after some time the roots bend toward the moist saw dust (positive hydrotroism). This is evidently due to the closeness of the germinating roots to water.

THIGMOTROPISM (Haptotropism)

If actively growing trendril-tips come in contact with solid objects having rough surfaces, they exhibit rapid growth movements. The tendril fails to develop if its tip does not get the touch stimulus. After it gets the contact stimulus, the tendril starts twining around the support. This is because the growth of the tendril is unequal on the two sides. The side in contact with the supporting material has less growth, while the other side has more growth. This results in the coiling of the tendril around the support. The sensitive tip of the tendril transmits the stimulus backwards and the whole of the tendril, therefore, gets spirally coiled.

CHEMOTROPISM

Fungal hypae and pollen tubes exhibit positive tropic movements under the influence of certain chemical substances. The chemicals are normally sugars and other nutrient substances. The fungal hyphae show negative chemotropism in the presence toxic chemicals.

AUTONOMIC VARIATION MOVEMENTS

A very fine example of spontaneous variation in the position of a plant organ is afforded by the Indian Telegraph plant, *Desmodium gyrans*.

The two lateral leaflets on the leaf are always in a state of rotatory movements. The leaflets make a dancing movement, as it were, in different planes and sometimes make an angle of 180º. The movement is normally in an ellipsoidal orbit. One such movement takes about two minutes to complete.

Very little detail is known concerning this type of movement.

PARATONIC VARIATION MOVEMENTS (NASTIC MOVEMENTS)

Many variation movements are brought about by certain external stimuli, viz., light, temperature and touch. Such movements are termed nastic. Nastic movements, unlike the tropic movements, are brought about by stimuli which are **not directional** but **diffuse**. Though nastic movements are largely variation movements, some of them may be accompanied with certain amount of growth.

Nyctinastic : The diurnal variation in the position of flowers and leaves of many plants in day and night is called nyctinastic or 'sleep movements'. If nyctinastic movement is caused by the presence or absence of light, it is called photonastic. If it is caused by the change in the temperature of the surroundings it is termed thermonastic. Photonastic movements are exhibited by flowers and leaves which open in the morning and close at night. Conversely, flowers of certain plants open in the evening and close during the day. Flowers of *Crocus* and tulip exhibit thermonastic movements since they open at high temperature.

Seismonastic : Another important nastic movement is termed seismonastic. It takes place in response to touch (shock) stimulus. Seismonastic movement is best seen in *Mimosa pudica*, the so-called 'sensitive plant'. It is a herbaceous plant with bipinnate compound leaves. A large pulvinus is present at the base of the petiole. Smaller pulvinules are present at the base of the leaflets. If a terminal pinnule is touched, the stimulus is conducted to its base and then to other pinnules. The pinnules droop down in succession with the passage of the stimulus and ultimately the leaflet droops down (Fig.). If the stimulus is strong all the leaflets of a leaf will be affected and the leaf as a whole will bend downward. If the stimulus is strong it is believed to travel at a speed of 20 cm. per second. The vascular bundle passing through the pulvinus divides it roughly into an upper stable and a lower sensitive half. The lower part has also delicate hairs. The cells of both the halves are fully turgid. When the stimulus reaches the pulvinus in the form of a hormone ostomically active ions enter into the cytoplasm of the cells in the lower half of the pulvinus. This lowers the osmotic pressure of these cells. As a result, water is forced out into the intercellular spaces and the turgor of the cells decreases. The flaccid lower half, unable to maintain its upward thrust, causes the drooping down of the pulvinus and hence of the whole leaf. The pulvinus and the pulvinules thus act as hinges. After the excitement period is over, the ions are believed to be released back into the vacuole. This again increases the osmotic pressure of the cells in the lower half of the pulvinus. The cells regain their rurgidity by reabsorbing water and the leaf gradually returns to its normal position.

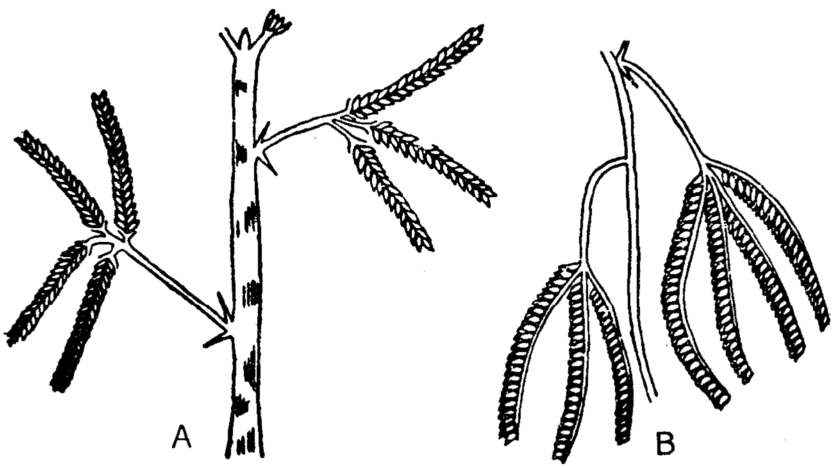

Fig. *Mimosa pudica* showing seismonasty. A. Normal leaf; B. Drooping leaf.

Thigmonastic (Haptonastic) : The tentacles present on the leaves of certain insectivorous plants like *Drosera*, *Dionaea*, etc. exhibit variation movements on the coming in contact with insect. The touch stimulus imparted by the insect is transmitted to the entire leaf and all the tentacles bend upon the insect.

PLANT RHYTHMS

A number of plants are known to exhibit certain features which appear in a rhythmic manner i.e., at regular intervals. Nyctinastic, i.e., the sleeping movements of leaves or flowers are known to be caused by the presence or absence of light (photonastic) or by a change in temperature (thermonastic). Similarly regular fluctuations are observed in the rate of growth, various physiological processes, production of spores, and in size and colour of plants. The time interval for fluctuations could be 24 hours, a week, a month or even a year. It is obvious, therefore, that this type of periodic fluctuation or rhythm in plants is a result of the environmental rhythms. Such periodic activities of plants are termed plant rhythms.

Rhythms in plants are of different types and are classified according to the nature of the stimulus and the length of the period. If the environmental periodicity regulates the plant rhythms, they are termed exogenous and if the rhythms continue to occur even in the absence of fluctuations in the environment, they are called endogenous. According to the length of the period they are termed :

(i) **Circadian Rhythms :** These are endogenous (intrinsic) rhythmic changes recurring in an organism with a periodicity of approximately 24 hours. Examples : Formation of condiospores in *Neurospora crassa*, leaf and petal movements in higher plants, stomatal opening and closing, photosynthesis and respiration etc.

(ii) **Tidal Rhythms :** A marine diatom *Pleurosigma* appears and disappears with the tide.

(iii) **Lunar Rhythms :** A marine brown alga *Dictyota* releases spores and gametes according to the lunar cycle.

(iv) **Annual Rhythms :** Flowering, fruiting, tuber, bulb formation occurs at the same time every year.

(v) **Ultradian Rhythms :** It is of short cycles (minutes to hours). Examples are streaming of protoplasm and coiling of twiners.